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Feeding mechanics in primitive teleosts and in the halecomorph fish *Amia calva*

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(With 18 figures in the text)

The mechanics of feeding in *Salmo gairdneri* and *Hoplias malabaricus*, two generalized predaceous teleosts, was studied using high-speed movies (200 frames per second). In *Hoplias*, the feeding mechanism is characterized by an extreme anterior swing of the maxilla and rapid depression of the hyoid occurring synchronously with mandibular depression and neurocranial elevation. A similar feeding sequence is observed in *Salmo* although the movements of the head are neither as extreme nor as rapid.

The anterior swing of the maxilla, usually attributed to mandibular depression, increased when the ligamentous connection of the maxilla to the mandible was severed. A mechanical model of the jaw was constructed to elucidate the functional interrelationships of the neurocranium, maxilla and mandible.

Films of the "holostean" *Amia calva* feeding show that the feeding mechanism is of a fundamentally different nature than that of primitive teleost fishes. Extreme anterior swinging of the maxilla occurs synchronously with jaw opening but branchiostegal expansion and hyoid depression only reach a maximum well after the jaws have begun to close. The existence of a highly efficient levator operculi—opercular series—mandible coupling is hypothesized on the basis of the rapid initial jaw opening.

This pattern of feeding movements in *Amia* has necessitated a revision of current theories on the nature and significance of the "holostean" feeding mechanism and sheds new light on the adaptive significance of certain characters in fossil actinopterygians.

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Introduction

Modern teleost fishes, a highly successful group, are represented today by more species than the combined number of all other Recent vertebrates (Myers, 1958). This success is due at least in part to the morphologically complex and highly kinetic teleost jaw which evolved from the generalized predaceous pholidophorid feeding mechanism in the Triassic.

Throughout the course of this evolution, the fundamentally predaceous feeding mechanism seems to have represented the main line of evolutionary advancement, with specialized forms adapted to feeding on specific food items radiating from the generalized predaceous stock. Within the Teleostei, then, a study of the generalized predaceous forms at each level of adaptation can give major insights into the evolutionary significance of morphological innovations in jaw structure.

In particular, a detailed analysis of the feeding mechanisms of generalized fishes at the basal teleostean level can be used as a link between extinct fishes of the holostean grade and morphologically advanced teleostean fishes. Surprisingly, very little data exist on the jaw mechanics of primitive teleosts although a rather large body of data has been accumulated on the advanced teleostean groups (e.g. Alexander, 1967; Eaton, 1935; Liem, 1967, 1970, 1973; Osse, 1969). Those studies that do exist on primitive teleosts (Tchernavin, 1948; 1953, Alexander, 1966, 1969; Vrba, 1968) are based primarily on the manipulation of dead specimens with occasional still photographs to supplement the analysis. No detailed comparison of feeding in basal teleostean fishes has yet been done.

The objectives of this study, then, are (1) to examine the feeding mechanism of two members of basal teleostean superorders: *Hoplias malabaricus* (Ostariophysi) and *Salmo gairdneri* (Protacanthopterygii), (2) to examine the feeding mechanism of the holostean *Amia calva*, (3) to compare the mechanics of feeding in these three fishes with reference to phylogenetic position, morphologic differences, and convergent evolution, and finally (4) to discuss the evolution of the actinopterygian feeding mechanism with particular reference to increased morphological and functional versatility at the holostean level of advancement.

Interrelationships of the ostariophysan fishes (Teleostei)

SARA V. FINK AND WILLIAM L. FINK

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Interrelationships of the ostariophysan fishes (Teleostei)

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The history of ostariophysan classification is summarized and it is noted that traditional concepts of relationships have never been supported by characters found to be unique to the taxa. We present a new hypothesis of relationships among four of the five major ostariophysan lineages: Cypriniformes, Characiformes, Siluroidei, and Gymnotoidei (Otophysi). Cypriniforms are the sister-group of the remaining three (Characiphysi), and characiforms are the sister-group of siluroids plus gymnotoids (Siluriformes). Placement of the Gonorynchiformes as the sister-group of the Otophysi is supported by additional evidence. Each of the five lineages is monophyletic. Analysis was concentrated upon species thought to be the least specialized within each lineage; choices of these species are discussed.

Chanos is determined to be a relatively primitive gonorynchiform morphologically and the sister-group of all other Recent members of the order. *Opsariichthys* and *Zacco* are found to be morphologically primitive cypriniforms. We propose that a monophyletic group comprising the Citharinidae and Distichodontidae forms the sister-group of all other characiforms. Within the two families, *Xenocharax* is the least specialized. We suggest that *Hepsetus,* the erythrinids, and the ctenoluciids are more derived than the distichodontids and citharinids, and may form a monophyletic group within the characiforms. The traditional hypothesis that *Diplomystes* is the primitive sister-group of all Recent siluroids is substantiated. Our evidence suggests that *Sternopygus* is the most primitive gymnotoid morphologically; but rather than being the sister-group of all other gymnotoids, it is the primitive sister-group within a lineage called the Sternopygidae by Mago-Leccia.

Previous explanations of otophysan distribution have been based on notions of relationships which are unsupported by the evidence presented herein. Our own analysis of relationships serves primarily to make clear the extent of sympatry, and therefore the probability of dispersal, among the major ostariophysan lineages. The extent of sympatry, together with the widespread distribution of ostariophysans, suggests that the group is older than previously supposed, and our hypotheses of relationships among the characiforms implies that many of the extent characiform lineages evolved before the separation of Africa and South America. Further understanding of ostariophysan distribution must await phylogenetic analysis within each of the five major lineages so that distributions linked with vicariance patterns and dispersal events can be sorted out.

KEY WORDS:—Ostariophysi – Gonorynchiformes – Cypriniformes – Characiformes – Siluroidei – Gymnotoidei – Siluriformes – phylogenetic systematics.

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INTRODUCTION

The group of teleost fishes traditionally known as the Ostariophysi represents somewhat over 25% of teleost species, and about three-quarters of the world's freshwater fishes. The enormous ecological and evolutionary diversity of the group as well as the restriction of almost all its members to fresh water has made this group a focus of research in evolutionary studies and biogeography.

The major groups of ostariophysans include the minnows and their relatives (suckers, hill-stream fishes, carps, loaches, and some other small groups), the characins (including the popular tetras of the aquarium trade, piranhas, pacus, etc.), the electric eel and its electrogenic relatives (the knifefishes, or gymnotoids) and the catfishes. Since 1970 the gonorynchiforms, previously considered clupeomorph or salmoniform relatives, have been included in the Ostariophysi (Rosen & Greenwood, 1970). Gonorynchiforms are a small group including *Chanos* (the milkfish), the peculiar *Gonorynchus* of tropical seas, and the small freshwater African kneriids and their relatives.

A discussion of ostariophysan diversity would be inappropriate here and the reader is referred to the following for more detail: Greenwood, Rosen, Weitzman & Myers (1966); Fink & Fink (1979); Roberts (1972).

Relationships within the Ostariophysi have long been a problem for ichthyologists and a data-based classification has remained elusive since the definition of the group by Sagemehl (1885:22). Historically, the Ostariophysi has been defined by the presence in all members of a series of modifications of the anteriormost four vertebrae and their associated parts, collectively called the Weberian apparatus (see Weber, 1820). From the time of Regan's (1911a,b) work until Rosen & Greenwood's (1970) classification, the Ostariophysi was limited to those fishes with a Weberian apparatus. Although taxonomic rank of the included groups has changed from author to author, their positions relative to each other have remained the same. Regan (1911a,b) gave the following classification:

Order Ostariophysi
Suborder Cyprinoidea
Division Characiformes (characins)
Division Gymnotiformes (gymnotoids)
Division Cypriniformes
Suborder Siluroidea (catfishes)

Jordan (1923) ranked all these groups as equivalent (Order) but sequenced them in the same order as did Regan.

Greenwood *et al.* (1966) accepted Regan's classification, although they added to the number of families, but they raised all taxa one categorical rank. In addition, Greenwood *et al.* (1966) discussed the gonorynchiform fishes and their significance to ostariophysan history. They concluded that the gonorynchiforms and ostariophysans share a "common stem", probably derived from some ancestral salmoniform (p. 379). These authors placed the Gonorynchiformes in the Protacanthopterygii, sequencing them next to the Ostariophysi. Later Rosen & Greenwood (1970), in a more extensive analysis of the relationships of the two groups, concluded that gonorynchiforms and ostariophysans are sister-groups and in a phylogenetic classification placed the former group within an expanded Ostariophysi, as Series Anotophysi. Fishes with a Weberian apparatus were placed in Series Otophysi. Within the Otophysi, Regan's basic classification was followed, with one exception. Gymnotoids were held, by tradition, to be the sister-group of characins so both groups were listed at equal rank within the Characoidei. Rosen & Greenwood's classification is:

Superorder Ostariophysi
Series Anotophysi
Order Gonorynchiformes
Suborder Chanoidei
Suborder Gonorynchoidei
Series Otophysi
Order Cypriniformes
Suborder Characoidei
Superfamily Characoidea
Superfamily Gymnotoidea
Suborder Cyprinoidei
Order Siluriformes

Gosline (1971) presented a classification which was like that of Regan's (1911a,b), except that characins, minnows, and gymnotoids were each ranked as superfamilies. Gosline tentatively concluded that clupeoids, gonorynchoids, and cypriniforms (=Otophysi, herein) were "basally related lineages, the last two being quite possibly the closer" (p. 122).

Roberts (1973) extensively criticized Rosen & Greenwood's classification, stating that inclusion of gonorynchiforms in the Ostariophysi would make the latter an "unnatural group". He found little conclusive support for Rosen & Greenwood's placement of gonorynchiforms with the ostariophysans. Moreover, Roberts concluded, after an analysis of approximately 22 character complexes, that there is no evidence that characins and minnows are more closely related to each other than either is to catfishes and, therefore, that all should be accorded equal rank. Roberts maintained the sequence of Regan, but with gymnotoids in a higher taxon with characins. Remarkably, after his defense of the taxon

Ostariophysi, he eliminated that name from his classification, which is (abbreviated):

Order Gonorynchiformes
Order Cypriniformes
  Suborder Characoidei
    Superfamily Characoidea
    Superfamily Gymnotoidea
  Suborder Cyprinoidei
  Suborder Siluroidei

The relationship of the gonorynchiforms to other primitive teleosts was left unresolved.

Gosline (1973), while not presenting a formal classification of ostariophysans, did discuss their relationships. Gosline attempted to reconstruct the primitive ostariophysan (=otophysan) morphotype by considering the probable direction of evolution of various aspects of the feeding apparatus, based on functional interpretations. We discuss certain of his interpretations below in our presentation of characters. Gosline concluded that catfishes share a common ancestor with a group consisting of minnows, characins, and gymnotoids (essentially that catfishes are the sister-group of those taxa) and that the common ancestor of the entire assemblage may have been a "small-mouthed, simple-toothed, bottom-feeding fish . . . in general appearance [like] the modern South American genus *Characidium*".

Novacek & Marshall (1976) presented an analysis of ostariophysan biogeography. These authors included a phylogenetic tree of ostariophysans which is essentially isomorphic with Regan's (1911a,b) classification but which is inconsistent with their text, in which characins are considered paraphyletic. We discuss Novacek & Marshall's biogeographic hypothesis below, in the Discussion.

With the exception of the work on ostariophysans by Rosen & Greenwood (1970), classifications of the group have not been explicitly phylogenetic and it is difficult to be certain what their authors intended them to represent. Nevertheless, what we will call the "traditional" hypothesis of relationships can be presented as follows. Characins and gymnotoids are considered to be closely related, with gymnotoids thought to be highly modified characins (Regan, 1922; Weitzman, 1962). Minnows are considered to be more closely related to characins plus gymnotoids than to catfishes. In some cases, in discussion of relationships, characins are considered to be ancestral to minnows and catfishes (e.g. Briggs, 1979).

These traditional ideas have profoundly influenced workers who have been concerned with relationships within the major ostariophysan groups and those who have used ostariophysans as a subject for biogeographic analysis. We present a hypothesis below which radically alters traditional concepts of relationships within the group and which thus demands considerable alteration in concepts of character polarity and biogeographical history.

MATERIALS AND METHODS

Material examined is listed in the Appendix. Cleared and stained fishes were prepared using a modified version of Taylor's (1967) enzyme method. Drawings were sketched with a Zeiss IVb Zoom microscope and camera lucida; details were added using a Leitz Widefield stereomicroscope.

Our methodology is phylogenetic (Hennig, 1966). Presence of a derived character state was determined by outgroup comparisons, sometimes in conjunction with sequences of ontogenetic development. Outgroups considered include the primitive teleostean lineages Osteoglossomorpha, Elopomorpha, Clupeomorpha, and Protacanthopterygii (Patterson & Rosen, 1977; Rosen, 1973). Our estimation of derived character states is based on determination by outgroup comparison that a character uniquely defines a lineage. The character found in outgroups is considered primitive, and any apparently unique feature is considered derived. For example, the more posterior fin-rays of the pectoral fin of catfishes and gymnotoids are offset from the anterior ray while all the fin-rays articulate in an even arc in characins, minnows, gonorynchiforms and in the outgroups Clupeomorpha, Elopomorpha, and Protacanthopterygii. Thus, the presence of offset pectoral fin-rays is considered a character which defines a group consisting of catfishes plus gymnotoids, i.e., it is a synapomorphous character for those taxa. Sequence of ontogenetic development was used in testing some hypothesized character polarities. Juvenile *Hepsetus* examined have an anteriorly bifurcated pelvic girdle while adults have a single anterior process. Outgroup comparison shows that a bifurcated pelvic girdle is found in all developmental stages in cypriniforms, siluroids, and one other characiform lineage. These two lines of evidence lead to the conclusion that a bifurcated pelvic girdle is primitive within the Characiformes.

In the text, when a character is discussed in the context of a group, we mean that it is present in that form in the primitive members of the group, at least. For example, in our discussion of the anteriorly bifurcated pelvic girdle, we note that the character is probably an otophysan one: it is present in most minnows, in primitive characins, and in most catfishes. That it is not present in specialized characins (where the girdle has a single pelvic process), gymnotoids (where the girdle is absent), or some catfishes (where the girdle is trifurcated) does not change the validity of our statement. In view of the enormous morphological diversity of ostariophysans, it is not surprising that many characters present in relatively unmodified form in primitive members are much modified in more specialized members. In such cases, however, the less modified character will be more informative for the purpose of comparison with other lineages.

Because of the enormous size of four of the ostariophysan lineages, it has not been possible to sample all included species. Analysis has been concentrated on those species which appear to be primitive within each lineage, that is, those sharing the fewest specialized characters with other members of that group and thus more of the characters distributed in the outgroups. These comparisons have been supplemented by examination of clearly specialized members of each group to ascertain the character distributions within the lineage. Specific reasons for our choices of taxa examined are given below in Primitive Members of Ostariophysan Lineages.

We follow Greenwood *et al.* (1966) in including "gastromyzonids" within the Homalopteridae.

In the figures, when two sizes of dots are used, small stipple represents bone and large stipple represents cartilage unless noted in the figure caption.

RESULTS

We state our preferred hypotheses of ostariophysan interrelationships at this point rather than at the end of the paper. This is done for ease of communication

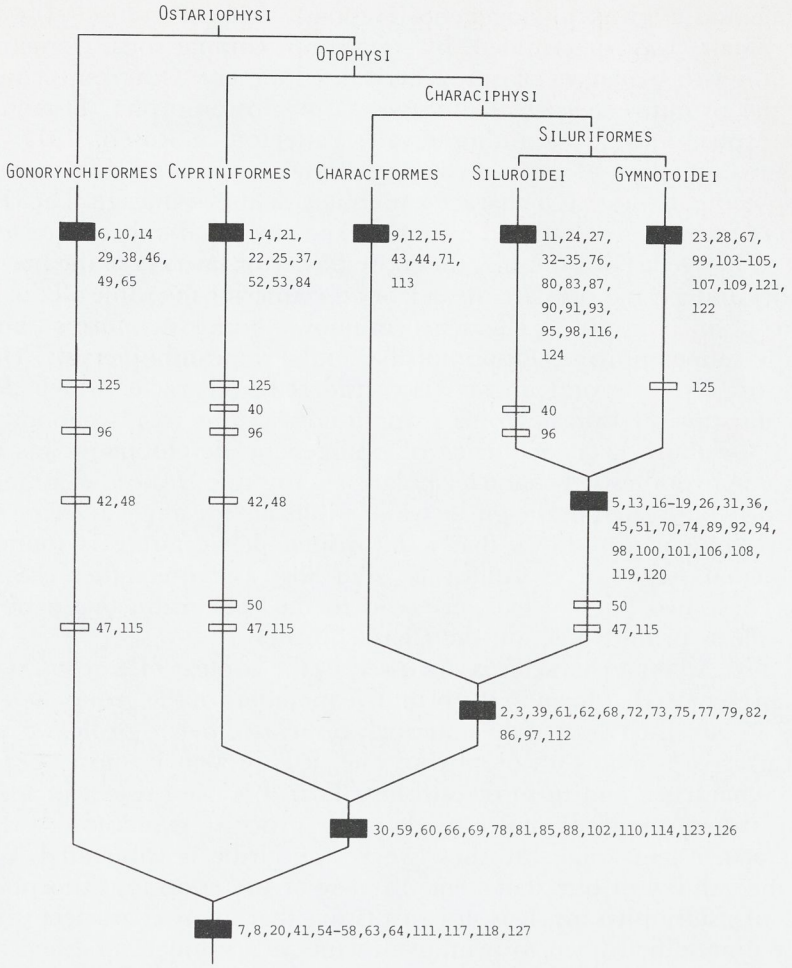

Figure 1. Diagram of the interrelationships of ostariophysan fishes proposed herein. Characters numbered as in Characters section. Characters indicated by solid bars are hypothesized to have evolved only once; characters indicated by open bars are hypothesized to have evolved more than once and to be synapomorphies for each lineage marked by a bar.

throughout the presentation of the characters and in the subsequent discussion. Based on data presented in the following section, we hypothesize that:

(1) each of the five major ostariophysan lineages (gonorynchiforms, cypriniforms, characiforms, siluroids and gymnotoids) is monophyletic

(2) siluroids and gymnotoids form a monophyletic group, here called Siluriformes

(3) the Siluriformes is the sister-group of the Characiformes; together these taxa are called the Characiphysi, emphasizing shared specializations of the otophysic connection

(4) the Characiphysi and the Cypriniformes are sister-groups in a taxon Otophysi

(5) the Gonorynchiformes is the sister-group of the Otophysi.

Our hypothesis is illustrated in Fig. 1 and is represented by the following phylogenetic classification:

Superorder Ostariophysi
  Series Anotophysi
    Order Gonorynchiformes
  Series Otophysi
    Subseries Cypriniphysi **nov.**
      Order Cypriniformes
    Subseries Characiphysi **nov.**
      Order Characiformes
      Order Siluriformes
        Suborder Siluroidei
        Suborder Gymnotoidei

We introduce a category Subseries for two reasons: to facilitate discussion of the monophyletic group comprised of characiforms, siluroids and gymnotoids, and to preserve as much as possible traditional ranking within the groups.

Use of the subseries is, of course, entirely optional and may not be necessary for many discussions concerning ostariophysans. The category and a name are there, however, when such are needed. Those who, like Roberts (1973), object to the "complex" nature of phylogenetic classifications are welcome to use "Characiformes plus Siluriformes" rather than Characiphysi.

The etymology of the subseries names is based on "physi", a Greek word meaning bladder, with the prefix of the lineage which best represents the primitive form of the otophysic connection of the included taxa. While these names do not accurately represent our intention to refer to the Weberian apparatus, they are similar in form to Rosen & Greenwood's (1970) Series names and should be relatively easy to remember.

PRIMITIVE MEMBERS OF OSTARIOPHYSAN LINEAGES

In each of the five major ostariophysan lineages, species which appeared to be morphologically primitive and species which appeared to be morphologically specialized were examined. Species were judged to be morphologically primitive based on the possession of features found in the outgroups, features which appear to have been lost or altered in other members of the lineage. Species which appeared to be morphologically primitive were examined more intensively than those which appeared to have numerous specializations, for two related reasons: to make the search for characters shared by major lineages more efficient, and to prevent mistaking homoplasies shared by derived members of two or more lineages for synapomorphies of those lineages. For example, encapsulation of the anterior chamber of the gasbladder is present in some cypriniforms and in some siluroids but is absent in many members of both lineages and in most members of the outgroups. Examination of morphologically primitive members of each lineage, all of which lack such encapsulation, allows one quickly to omit such features from consideration as possible synapomorphies.

None of the morphologically primitive species examined was found to be

primitive in all features—i.e., each had one or more features peculiar to it. Derived members of the five major lineages were examined to try to insure that such unique features were not mistaken for features general to the lineage.

In gonorynchiforms, characiforms, and siluroids, the available evidence indicates that the morphologically primitive taxa examined intensively are also phylogenetically primitive members of their lineages. Clear evidence regarding major phylogenetic groupings within both cypriniforms and gymnotoids is lacking.

Characters relevant to our hypotheses regarding both morphologically and phylogenetically primitive taxa within each lineage are detailed below.

Gonorynchiformes

Chanos has previously been considered to be a morphologically primitive gonorynchiform (Greenwood & Rosen, 1970). It is more primitive than any other living gonorynchiform in a number of features: (1) presence of a relatively extensive, solid suspensorium with a relatively large metapterygoid and an ectopterygoid which overlaps the palatine anteriorly, (2) autogenous neural arches and paraphophyses anterior to the dorsal fin, (3) presence of the first pharyngobranchial and first basibranchial ossifications, (4) presence of a spine on the anterior neural arch and (5) a complete circumorbital series with an elongate supraorbital and five plate-like infraorbitals. *Gonorynchus* appears more primitive than *Chanos* in having basibranchial and mesopterygoid teeth (although these are modified in form), but *Gonorynchus* has a highly modified ethmoid region and suspensorium. In addition, based on an examination of the gonorynchiforms available to us and on information available in the literature, we suggest that *Gonorynchus* in fact shares several features with the African freshwater forms *Kneria, Parakneria, Cromeria, Grasseichthys* and *Phractolaemus*. These are: reduction of the ectopterygoid and a mobile palatine, fusion of all neural arches and parapophyses to the vertebrae, loss of the spine of the first neural arch, and absence of both the first basibranchial and first pharyngobranchial ossifications (d'Aubenton, 1961; Lenglet, 1974; Ridewood, 1905a, b; Swinnerton, 1903; Thys van den Audenaerde, 1961). *Gonorynchus* and *Kneria* also have specialized scales with numerous, nearly parallel longitudinal striae and circuli which are restricted to the lateral borders of the scale. The scales of *Chanos* are more primitive in form. They are rounder in shape and have numerous circuli over the entire posterior field and only a few striae anteriorly. Unfortunately we have not been able to examine the other scaled gonorynchiforms, *Parakneria* and *Phractolaemus*. On the basis of these features, *Chanos* appears to be the sister-group to all other Recent gonorynchiforms, and has apparently lost basibranchial and mesopterygoid teeth independently from the African forms. *Gonorynchus* appears to be the sister-group to the African freshwater forms, which all have an enlarged foramen magnum bordered in part by the margin of the chondrocranium posterior to the supraoccipital. We provisionally suggest, therefore, that all non-*Chanos* gonorynchiforms be placed in a monophyletic taxon, and that the African freshwater forms be placed in a monophyletic taxon. We do not include this hypothesis in our formal classification, pending a more thorough analysis of all gonorynchiform taxa, fossil and Recent.

Cypriniformes

The cyprinid genera *Opsariichthys* and *Zacco* have previously been proposed to be morphologically primitive cypriniforms (Regan, 1911a; Greenwood *et al.,* 1966). We have chosen to concentrate upon these two genera based on the presence of three features hypothesized to be primitive for cypriniforms: (1) lack of fusion between the second and third vertebrae, (2) presence of an unsubdivided ostariophysan "A1" *adductor mandibulae* muscle, and (3) presence of a metapterygoid-quadrate fenestra similar to that in characiforms. (Gosline (1973) considered the metapterygoid-quadrate fenestra to be specialized; for a discussion of his hypothesis see the Characters section.) While the exact distribution of these features within cypriniforms is as yet unclear, we know of no other taxa which possess all three of these features.

Howes (1980) proposed a phylogeny of the "bariliine" cyprinids in which he suggested that *Opsariichthys* is not as primitive, either morphologically or phylogenetically, as previously supposed. While he did discuss features which appear to link *Opsariichthys* with a subgroup of the "Cyprinidae," Howes relied primarily on comparison with other cyprinids rather than a wider outgroup comparison to propose synapomorphic features. A number of the features used to define both the "bariliine" assemblage and subgroups within that assemblage appear, based on a broader analysis, to be primitive features, including a ventral opening in the posterior myodome (Patterson, 1975a:543), trigeminofacialis foramen entirely within the prootic, metapterygoid with a dorsal posterior process, lateral flange on the hyomandibula, ventral fossa on the frontal adjacent to the sphenotic, and lateral temporal foramen. In addition, some apparently derived features of the "bariliine" assemblage, including a lateral pterosphenoid fossa and epaxial fibers extending from the posttemporal into the subtemporal fossa through a foramen, are present in *Zacco temmincki,* although *Zacco* was excluded by Howes from the "bariliine" group. Finally, all other members of the "bariliine" group are more specialized than *Opsariichthys* in having the second and third vertebral centra fused. Thus, further inquiry into the phylogenetic positions of both *Zacco* and *Opsariichthys* seems worthwhile.

Two features which appear to be primitive for cypriniforms are present in some cypriniforms but not in *Opsariichthys* or *Zacco.* A first pharyngobranchial is present in *Gyrinocheilus* and catostomids (present in the latter as a separate element in juvenile *Catostomus commersoni,* MCZ 56536, 17.5–19.4 mm S.L., and tightly bound to a ventrolateral process of the parasphenoid by about 22 mm S.L.). A posterior cranial fontanelle is present also in catostomids, *Gyrinocheilus* (situated entirely within the supraoccipital), some cobitids and homalopterids (including gastromyzonids), and a few "cyprinids" (Ramaswami, 1952a, b, c, 1953, 1955). Although such a fontanelle is not present in gonorynchiforms, it is present in primitive characiforms, gymnotoids, and siluroids. As in the case of the metapterygoid-quadrate fenestra, such a fontanelle may be an otophysan feature. Loss of the first pharyngobranchial would therefore appear to be a derived feature shared by cyprinids, cobitids, and homalopterids but not by catostomids or *Gyrinocheilus.* Fusion of centra 2 and 3, shared by catostomids, *Gyrinocheilus,* cobitids, and homalopterids with only part of the Cyprinidae, suggests a phylogenetic grouping incongruent with that suggested by loss of the first pharyngobranchial. At least one of these features must therefore have

evolved more than once. This apparent incongruence can only be resolved by future studies on cypriniform phylogeny.

Characiformes

The families Distichodontidae and Citharinidae are a monophyletic lineage (Vari, 1979) hypothesized herein to form the primitive sister-group to all other characiforms. Members of these families possess four features which appear to be primitive for characiforms: (1) neural arch of the fourth vertebra autogenous, (2) a synchondral joint between the third and fourth neural arches, (3) pelvic girdle bifurcated anteriorly, and (4) elongate olfactory tracts. In all other characiforms, the fourth neural arch is fused to the vertebra, the synchondral joint between the third and fourth arches is reduced or absent, and the pelvic girdle is only slightly emarginate or simple anteriorly (young *Hepsetus* have a more deeply bifurcated girdle). Some other characiforms also have elongate olfactory tracts (Vari, 1979). Elongate olfactory tracts are hypothesized to be an otophysan feature based on their presence in cypriniforms and siluroids, although they are absent in gymnotoids as well as some characiforms.

The distichodontid *Xenocharax* was examined most intensively since it is morphologically the most primitive member of the distichodontid-citharinid lineage (Vari, 1979, and see below). *Xenocharax* is also a phylogenetically primitive distichodontid, forming the sister-group to all other distichodontids (Vari, 1979).

Roberts (1969) suggested that the predatory characiforms *Hepsetus, Hoplias,* and *Ctenolucius* were phylogenetically primitive characiforms based on their possession of exclusively unicuspid teeth and relatively shallow tooth-replacement trenches. However, these fishes all possess the derived features of the Weberian apparatus described above and thus their relationships lie with non-distichodontid, non-citharinid characiforms. Moreover, shallow tooth-replacement trenches are present in many other characiforms, including the primitive distichodontid *Xenocharax*. And while possession of simple, conical teeth might be a primitive feature, the teeth in *Hepsetus,* erythrinids and ctenoluciids are large and compressed distally rather than small and conical as is common in gymnotoids, siluroids and in teleosts generally. The tooth form in *Hepsetus,* erythrinids and ctenoluciids would seem therefore to be a synapomorphy rather than a primitive feature. Citharinids and distichodontids all have multicuspid jaw teeth at some point during ontogeny (Vari, 1979:275).

Although the hypotheses of ostariophysan and characiform relationships proposed herein do not alter Vari's (1979) schema of interrelationships among the distichodontids and citharinids, our hypotheses do affect some of Vari's character analysis. Of the fourteen features hypothesized by Vari (1979:324) to be synapomorphies for the distichodontid-citharinid lineage, eight appear to be primitive features for characiforms (bifurcated pelvic bone, lack of (an elongate) premaxillary ascending process, presence of a premaxillary articular fossa, lack of a distinct supraethmoid (=mesethmoid herein) spine, trifurcate articular complex at the anterior margin of the supraethmoid, anterior shift of the olfactory lobe, presence of a suprapreopercle, and lack of an interdigitating symphyseal hinge). One loss feature (lack of lateral supraethmoid wings) appears, based on our analysis, to be actually present (see the discussion of mesethmoid morphology just

below). All but the first of the eight enumerated features are found in a number of other characiforms; the latter two Vari suggested might indicate relationship with other characiforms and the remainder he hypothesized to have evolved separately in other characiforms. If these features are indeed primitive, no hypotheses of convergence in these features are required and hypotheses of relationships with other subgroups of characiforms remain unsubstantiated.

In addition, of the six features hypothesized by Vari to be synapomorphies of the Distichodontidae, at least one appears to be primitive for characiforms on the basis of a revised outgroup comparison (deeply bifurcated pelvic bone). Two more characters may also be primitive for characiforms (attachment of the A_1 portion of the *adductor mandibulae* to the maxilla, present in gonorynchiforms, cypriniforms, and some other characiforms; and posterior process of the lateral ethmoid contacting the anteromedial border of the orbitosphenoid, present in similar although not identical form in some other characiforms, in siluroids, and in the primitive gymnotoid *Sternopygus*). Three of the five autapomorphies suggested to distinguish the most primitive distichodontid *Xenocharax* were not present in the specimens examined for this study (posterodorsal shift in the longitudinal axis of the anterior four vertebrae, reduction in the angle between the axis of the anterior four vertebrae and the axis of the os suspensorium, and reduction in the number of branchiostegal rays to three). All *Xenocharax* specimens examined for this study had four branchiostegal rays. Finally, one feature suggested to be a synapomorphy of the *Nannaethiops-Neolebias* lineage is primitive (presence of ectopterygoid teeth).

Among the features in *Xenocharax* hypothesized to be primitive for characiphysans is the structure of the mesethmoid. Because its morphology is quite different from that presumed to be primitive for characiforms up to this point (Weitzman, 1962), some comments on the mesethmoid in particular seem necessary.

The anterior margin of the mesethmoid in *Xenocharax* has ventrolateral processes which articulate in fossae in the premaxillae. Similar processes, though with differences in proportion, are present in young citharinids, most distichodontids (Vari, 1979), parodontids, hemiodontids, and the "characids" *Characidium* and *Crenuchus* and their close relatives. Ventrolateral processes articulating with the premaxillae are also present in gymnotoids and siluroids (Siluriformes), although the ascending processes of the premaxillae are absent and articular fossae as such cannot therefore be distinguished. Presence of these processes is hypothesized to be a characiphysan feature and their absence to be derived for one or more subgroups of characiforms.

The mesethmoid of *Xenocharax* appears to have some primitive teleostean features, including pointed lateral processes and an anteromedian process. These characteristics are present in many lower teleosts including elopomorphs and clupeomorphs (see, for example, Patterson, 1975a: figs 127–132). Short lateral processes are present in gonorynchiforms and cypriniforms as well as characiforms. In siluroids and gymnotoids (Siluriformes) the lateral processes are absent. The anteromedian process is reduced in gymnotoids and absent in gonorynchiforms and siluroids, indicating that this process in characiforms may be a new feature. However, an anteromedian process is present in some cypriniforms and may be primitive for cypriniforms, although it is not present in *Opsariichthys* or *Zacco*. Moreover, gonorynchiforms and siluriforms each possess unique, highly modified mesethmoid morphology. We suggest that reduction of

the anteromedian process has occurred independently in gonorynchiforms, siluriforms, and some cypriniforms and that the presence of the process in characiforms is conservative, rather than a new feature.

Associated with the morphology of the ethmoid in *Xenocharax* and other distichodontids is a high degree of premaxillary mobility. While this degree of mobility appears to be a specialization of distichodontids, some premaxillary mobility is a feature of many other characiforms and is present in all other ostariophysan lineages, as well as in most other teleosts. The tight syndesmotic joint between the premaxilla and the mesethmoid, previously considered primitive for characiforms, is here hypothesized to be derived for one or more subgroups of the Characiformes.

Siluroidei

Diplomystes species have traditionally been considered morphologically and phylogenetically the most primitive living siluroids. Our survey of catfish anatomy and of the literature (e.g. Bridge & Haddon, 1893; Chardon, 1968; Lundberg & Baskin, 1969) brings us to support that hypothesis. Although *Diplomystes* shares many salient features with other living siluroids, alone among them it shares the following similarities with primitive teleosts: (1) the maxilla is not reduced in size and is primitive in form, being narrow proximally, broad distally, and bearing a large medial process, (2) the maxilla bears teeth along most of its ventral border, and (3) the lagenar otolith is equal in size to or larger than the utricular otolith. In addition, *Diplomystes* alone has a principal caudal fin-ray count of 9/9, which is nearer the 10/9 count of other primitive teleosts than the 8/9 or less found in other siluroids (Lundberg & Baskin, 1969). Maxillary teeth are also apparently present in the North American Eocene catfish *Hypsidoris farsonensis* (Lundberg, 1975a; Lundberg & Case, 1970) but the maxilla in this species is reduced in size and bears teeth along less than a third of its ventral border.

The following primitive features are also present in, though not exclusive to, *Diplomystes:* (1) hypurals 3 and 4 unfused proximally, (2) a full complement of six hypurals, (3) maxillary barbels only, (4) the fifth vertebral centrum not fused or otherwise closely joined to the more anterior vertebrae, and (5) no posterior extension of lamellar bone over the ventral surface of the fifth centrum, either from the fifth centrum or from the more anterior vertebrae (the latter two features are present in the diminutive troglodytic ictalurids *Trogloglanis, Prietella,* and *Satan* [Lundberg, pers. commn], presumably secondarily).

Gymnotoidei

The gymnotoid genus *Sternopygus* appears to be in the sum of its features the most morphologically primitive gymnotoid. *Sternopygus* shares the following primitive features with gonorynchiforms, primitive cypriniforms, and characiforms, most of which are absent in all other gymnotoids: (1) skin of the head not continuous over eye (present also in *Archolaemus,* closely related to *Sternopygus*), (2) posterior chamber of gasbladder large and elongate (*Gymnotus* has a large, specialized posterior chamber as a part of its respiratory system), (3) lateral process (parapophysis) of centrum 2 and pleural rib of centrum 4 not meeting or approaching each other closely, (4) relatively large number (24–26) of precaudal

vertebrae, and (5) presence of posttemporal fossae (shared with the closely related *Rhabdolichops*). In addition, in comparison with other gymnotoids, *Sternopygus* more closely resembles characiforms in having the anterior vertebrae less compressed and the anterior, enlarged supraneural less closely applied to the cranium. *Sternopygus* is also more primitive than any of its proposed closest relatives (Mago-Leccia & Zaret, 1978) in the presence of a mesocoracoid in some species and in having the supracleithrum and posttemporal unfused.

Sternopygus does not appear to be the sister-group to all other gymnotoids, however, but a member of the family Sternopygidae of Mago-Leccia (1978), sharing with other members of the family greatly enlarged infraorbital and cranial sensory canals which are unique among gymnotoids (see Mago-Leccia, 1978: fig. 9). All of the characters used by both Mago-Leccia (1978) and Mago-Leccia & Zaret (1978) to define the family are either primitive teleostean features, primitive for gymnotoids, or absent in *Sternopygus*.

Mago-Leccia & Zaret (1978) considered *Rhabdolichops,* also of the family Sternopygidae, to be the most morphologically primitive gymnotoid based on the presence of an ossified first basibranchial, large gill-rakers on the first gill arch, and presence of posttemporal fossae (see above). While the ossified first basibranchial is shared by *Rhabdolichops* and the non-gymnotoid outgroups, our interpretation of the gill-rakers is that they are specialized. The gill-rakers in *Rhabdolichops* are elongate and narrow in comparison with those in primitive cypriniforms, characiforms and siluroids, and the base of the gill-rakers is broad rather than laterally compressed. Mago-Leccia & Zaret (1978) state that *Rhabdolichops* is a planktivore and that the enlarged gill-rakers are associated with that feeding mode. Planktivory is not characteristic of primitive otophysans but has been independently evolved a number of times in that group (e.g. *Hypophthalmus,* a siluroid; *Clupeacharax,* a characiform). Our own analysis of the characters presented by Mago-Leccia (1978) and Korringa (1970) would place members of the Sternopygidae as follows: *Sternopygus* the sister-group of the others, *Archolaemus* the sister-group of those remaining, and *Rhabdolichops* the sister-group of *Eigenmannia* and *Distocyclus*. If this hypothesis is shown to be preferred by further work, then the gill-raker morphology of *Rhabdolichops* would be more clearly shown to be an autapomorphic feature.

CHARACTERS

The data are listed in a sequence corresponding to a survey of the body of a fish from anterior to posterior, with separate headings for fin spines and miscellaneous features following the caudal characters. For each character, the derived state and the group in which it is found are listed first, followed by the character as found in outgroups.

Characters are delineated and numbered for ease of description and comparison; features which may be associated but are separated for descriptive purposes are noted where appropriate.

Neurocranium

(1) In cypriniforms there is a kinethmoid bone (Figs 2B, 3B). Its ventral margin is attached by oblique ligaments to the anterodorsal margin of the mesethmoid, and

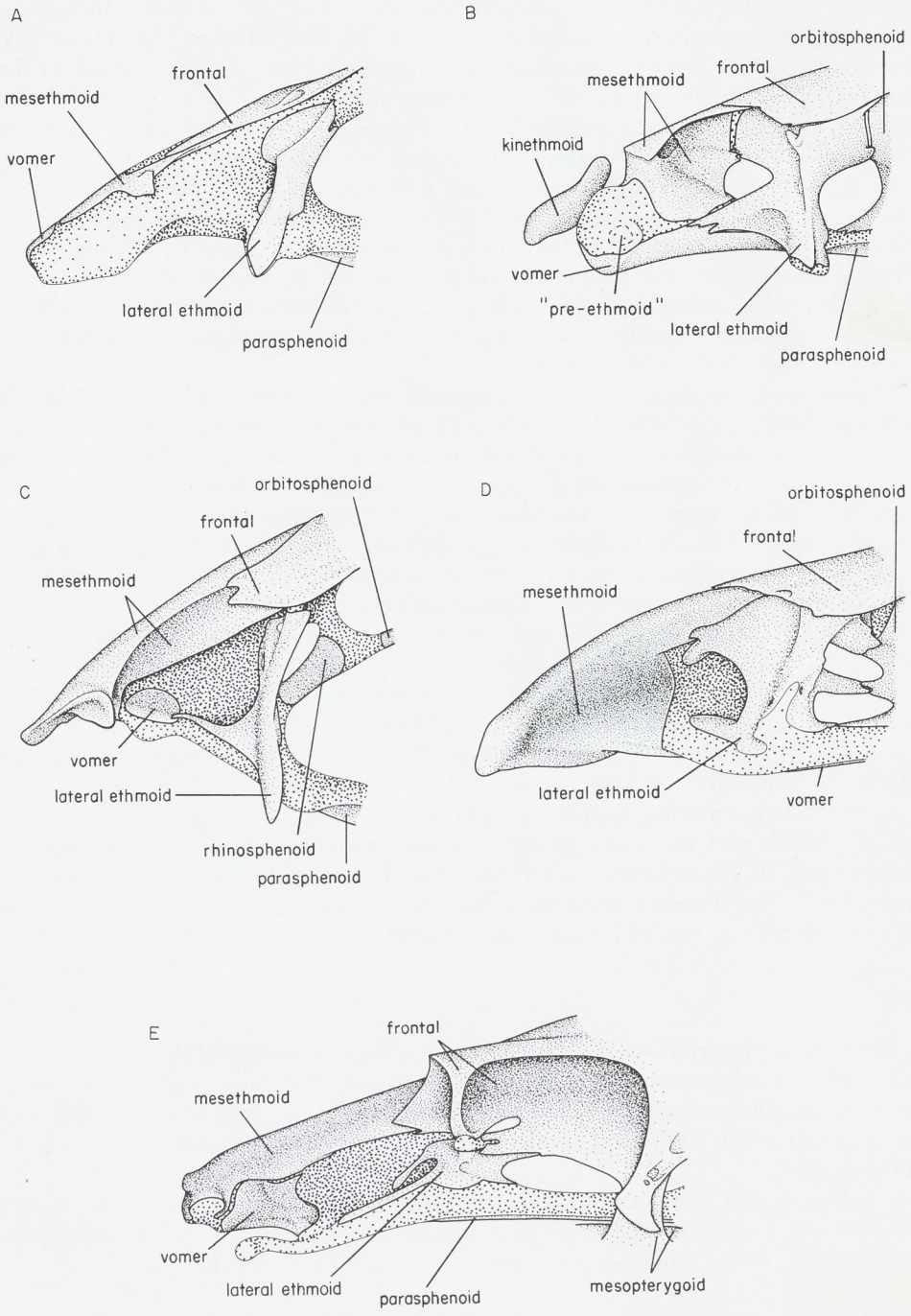

Figure 2. Ethmoid region, left lateral view. A, *Chanos,* USNM 199831. B, *Opsariichthys,* MCZ 32375. C, *Rhoadsia,* MCZ 49955. D, *Diplomystes,* drawn without associated tooth plates, cartilage from alcohol specimen, MCZ 8290. E, *Sternopygus,* CAS(IUM) 12591.

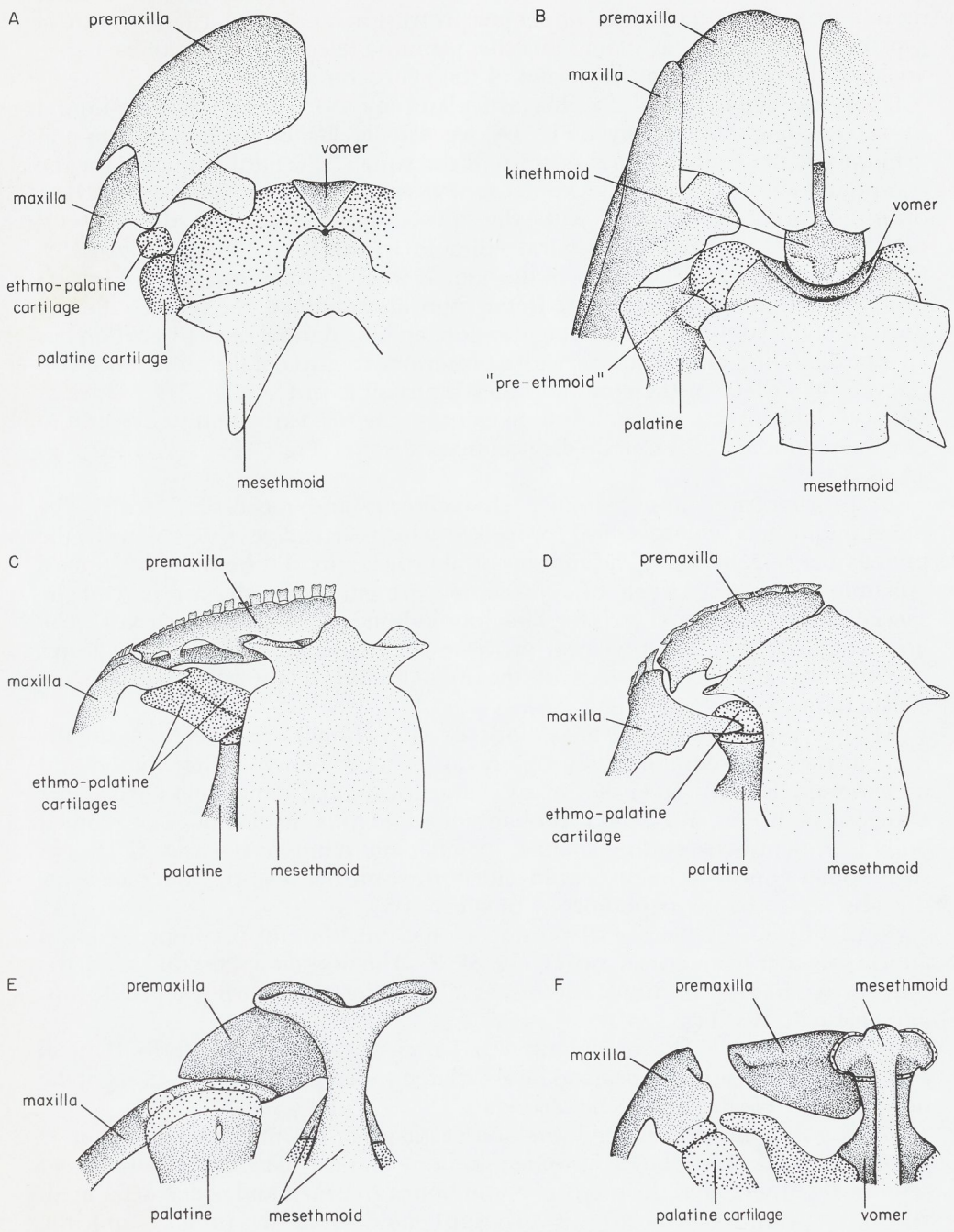

Figure 3. Ethmoid region, dorsal view. A, *Chanos,* USNM 199831. B, *Opsariichthys,* MCZ 32375. C, *Xenocharax,* MCZ 48020. D, *Rhoadsia,* MCZ 49955. E, *Diplomystes,* cartilage from alcohol specimen, MCZ 8290. F, *Sternopygus,* CAS(IUM) 12591.

its dorsal margin is attached to the ascending processes of the premaxillaries. Movement of the dorsal tip of the kinethmoid anteriorly and ventrally during mouth opening is a part of the upper jaw protrusion mechanism characteristic of cypriniforms (Alexander, 1966b). In other primitive teleosts the premaxillaries are attached directly to the anterior end of the neurocranium.

(2) In characiphysans the vomer articulates anteriorly with the mesethmoid (illustrated diagrammatically in Fig. 4A; see also Fig. 2C, E). In characiforms and gymnotoids the endochondral portion of the vomer (=ventral ethmoid; for the compound nature of the teleost vomer see Patterson, 1975a:501) has a vertical or oblique synchondral joint with the mesethmoid (only the dorsolateral perichondral lamella of the ventral ethmoid is visible in the young *Rhoadsia* illustrated in Fig. 2C). The shaft of the vomer, when present, extends posteriorly from the ventral ethmoid portion. In the siluroids examined, the ventral ethmoid portion of the vomer appears not to develop, and the dermal or shaft portion has an interdigitating joint (a suture) with a posterior extension of the mesethmoid on the ventral surface of the ethmoid block (not visible in Fig. 2D). The vomer of gonorynchiforms and cypriniforms, as in most teleosts, extends anteroventral to the mesethmoid (illustrated diagrammatically in Fig. 4B; see also Figs 2A, B, 3A, B).

(3) In characiphysans (primitive characiforms and most siluriforms), the mesethmoid has anteroventral processes which articulate directly with the premaxillae (Fig. 3C,E,F). The anteroventral projections of the ethmoid region of cypriniforms consist largely of vomer and "pre-ethmoid" and are part of the specializations associated with the kinethmoid bone. They thus appear not to be homologous to the anteroventral processes in characiphysans. In most lower teleosts, the anterolateral face of the mesethmoid is a smooth surface for articulation of the maxilla (Fig. 3A).

(4) In cypriniforms a cartilage body or endochondral ossification, usually termed the "pre-ethmoid," is tightly articulated between the vomer and mesethmoid (Fig. 2B). In *Chanos,* many characiforms, and some other teleosts (see Patterson & Rosen, 1977:98) a probably homologous cartilaginous or ossified body is present between the palatine, maxilla, and ethmoid (Fig. 3A, C, D). No such bodies appear to be present in siluriforms; further investigation may show this absence to be a synapomorphy of siluriforms.

(5) In siluriforms the dorsal portion of the mesethmoid is compressed and appears slender from dorsal aspect (Fig. 3E, F). The dorsal mesethmoid surface is fairly broad in most primitive teleosts, as it is in gonorynchiforms, cypriniforms, and characiforms (Fig. 3A-D).

In most siluroids the mesethmoid is flatter and broader dorsally than in *Diplomystes*; this feature appears to be associated with a general broadening of the head and is hypothesized to be secondary.

(6) In gonorynchiforms the bone and cartilage of the interorbital septum is greatly reduced. Both the orbitosphenoid bone and cartilage in the interorbital septum are absent, and the pterosphenoid bones are small and widely separated. In most primitive teleosts, an orbitosphenoid bone is present and the pterosphenoid bones approach each other more closely in the midline.

(7) In ostariophysans a basisphenoid is absent. The basisphenoid is present in most teleosts as a strut between the prootic and pterosphenoid dorsally and the parasphenoid ventrally.

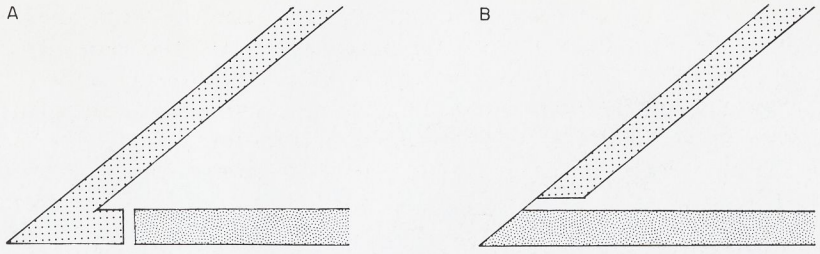

Figure 4. Diagrammatic view of mesethmoid, large stipple, and vomer, small stipple; anterior to left. A, Characiphysan condition. B, Usual teleostean condition.

In siluroids, a horizontal lamina extends from the parasphenoid dorsal to the cartilage of the trabeculum communis and in some siluroids the parasphenoid also has laminae which contact the pterosphenoid; Kindred (1919) and others have misinterpreted these laminae as a fragment of basisphenoid fused to the parasphenoid.

(8) In ostariophysans the sacculi and lagenae are situated more posteriorly and nearer the midline than in other primitive teleosts (Rosen & Greenwood, 1970).

(9) In characiforms there is a foramen in the prootic (the auditory foramen of Weitzman, 1962:fig. 4). It is usually an ovoid opening on the ventral face of the prootic through which the utricular otolith is visible. Although Roberts (1973) listed an auditory foramen as present in some (unspecified) cypriniforms, it is not present in specimens we examined. The foramen in characiforms differs in topography from the auditory fenestra of Recent clupeomorphs, which is situated between the exoccipital, prootic, and basioccipital and opens into the region of the saccular otolith rather than the utricular. A prootic foramen is not present in other primitive teleosts or non-characiform ostariophysans.

(10) In gonorynchiforms the parietals are reduced in size, being little more than canal-bearing bones; the frontals extend further posteriorly than in the primitive condition (Fig. 5A). In most otophysans and other primitive teleosts, the parietals cover a large portion of the back of the skull and meet or closely approach each other in the midline (Fig. 5B, C).

(11) In siluroids parietals are not present as separate ossifications (Fig. 5D); they appear to be present but fuse to the supraoccipital during ontogeny (Bamford, 1948). Presence of separate parietals is primitive for teleosts.

(12) In characiforms there is a dorsomedial opening into the posttemporal fossa (Fig. 5C). In primitive teleosts and in other ostariophysans, no dorsomedial opening is present (Fig. 5A, B, D, E). This feature appears to be secondarily absent in citharinids and gasteropelecids.

(13) In siluriforms the intercalar is absent (Fig. 5D, E). In other ostariophysans and in primitive Recent teleosts, the intercalar is present as a bone applied to the surface of the endochondral cranium in the region where the pterotic, epioccipital, and exoccipitals meet (Fig. 5A-C).

(14) In gonorynchiforms the exoccipitals (*Chanos* and *Gonorynchus*) or exoccipitals and supraoccipital (kneriids and probably *Phractolaemus*) have a prominent posterodorsal cartilaginous margin, shown in dotted outline in Fig. 6 of *Chanos*. In other ostariophysans and primitive teleosts, the posterior margin of the exoccipitals and supraoccipital forms the smooth, slightly sloping posterior margin of the cranium.

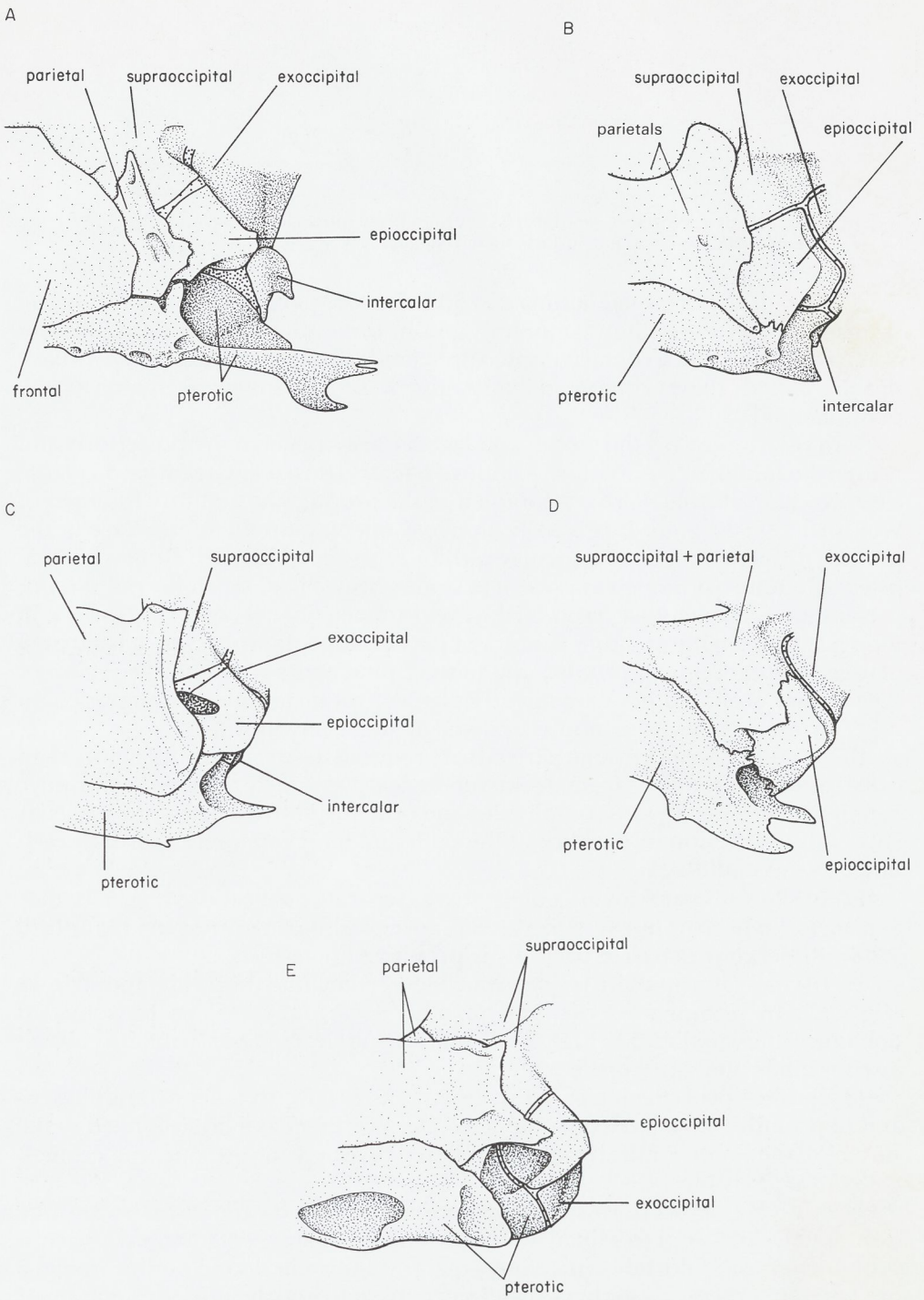

Figure 5. Cranium, posterolateral region, dorsal view. A, *Chanos,* USNM 199831. B, *Opsariichthys,* CAS (SU) 32568. C, *Hepsetus,* MCZ 48104. D, *Diplomystes,* MCZ 8290. E, *Sternopygus,* USNM 218830.

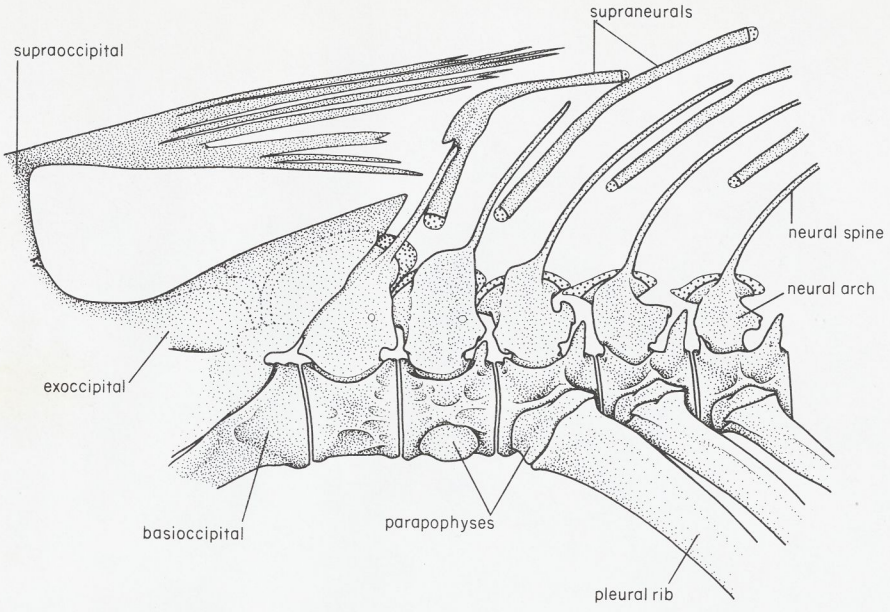

Figure 6. Anterior vertebral region, left lateral view, *Chanos,* USNM 199831. Dotted outlines indicate borders of bone and cartilage medial to exoccipital flange.

(15) In characiforms the lagenar capsule is large, globular, and projects well lateral to the cranial condyle. In most primitive teleosts, the lagenar capsule is evident only as a slightly protruding bulla.

Orbital region

(16) In siluriforms the eye is reduced in size relative to the surrounding circumorbital bone series (eye indicated by solid circle in Fig. 7D, E). In most other primitive teleosts, including gonorynchiforms, most cypriniforms, and characiforms, the eyes closely approach the inside border of the circumorbitals (Fig. 7A-C).

(17) In siluriforms sclerotic bones are absent. Sclerotic bones are present in other ostariophysans and in most primitive teleosts.

(18) In siluriforms the infraorbital series consists largely (gymnotoids) or entirely (siluroids) of the canal-bearing portions of the bones (Fig. 7D, E). In primitive gonorynchiforms, cypriniforms and characiforms and in other primitive teleosts, the infraorbitals also have bony plates which cover part or all of the adductor musculature of the cheek (Fig. 7 A-C).

Some plate-like development is present, apparently secondarily, in some advanced siluroids (e.g. callichthyids, loricariids).

(19) In siluriforms a supraorbital bone is absent (Fig. 7D, E). A supraorbital bone is present in primitive gonorynchiforms, cypriniforms and characiforms (Fig. 7 A-C) and in other primitive teleosts.

Suspensorium

(20) In ostariophysans the dermal portion of the palatine (dermopalatine) is absent (Figs 8–12). In primitive teleosts such as *Elops* and *Denticeps,* the palatine

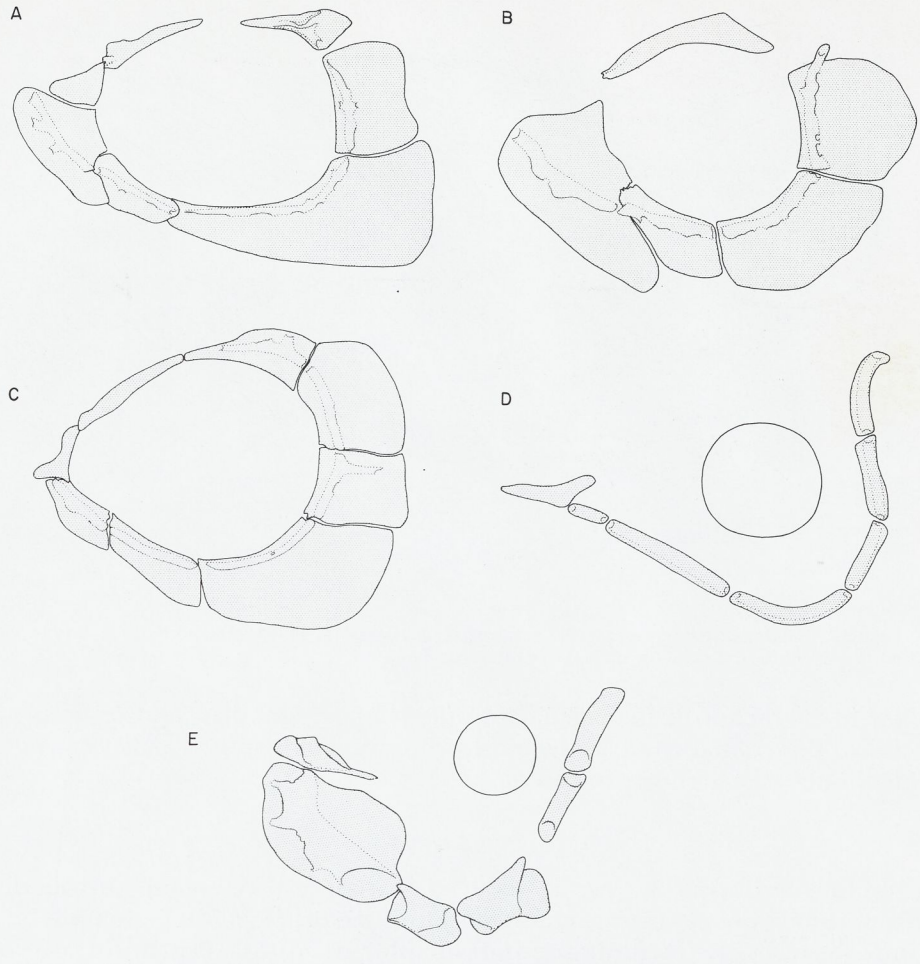

Figure 7. Orbital bones, left lateral view. A, *Chanos,* USNM 199831. B, *Opsariichthys,* right side drawn and reversed, MCZ 32375. C, *Brycon,* MCZ 48668. D, *Diplomystes,* from alcohol specimen, MCZ 8290. E, *Sternopygus,* USNM 128830.

consists of a chondral portion (autopalatine) and a dermal portion (dermopalatine) which are fused together.

The tooth plates in the region of the palatine in the characiforms *Hoplias* and *Hepsetus* are not attached to the palatine and are in fact part of an anteriorly elongate ectopterygoid in *Hoplerythrinus*. We therefore agree with Weitzman (1964) that these are accessory ectopterygoid tooth plates. (Roberts (1969) stated that the tooth plate in *Hepsetus* was autogenous in all specimens that he examined, 19–200 mm S.L.; it is clearly fused to the premaxilla in our 73.4 mm S.L. example, MCZ 48104.)

The teeth often present on the palate of siluroids (not associated with the autopalatine but often associated with the vomer) are also borne on autogenous tooth plates. Presence of these tooth plates appears to be a neomorphic feature.

(21) In cypriniforms the anterior portion of the palatine has a dorsomedial process which abuts against the mesethmoid (Figs 3B, 9). Such a process is not

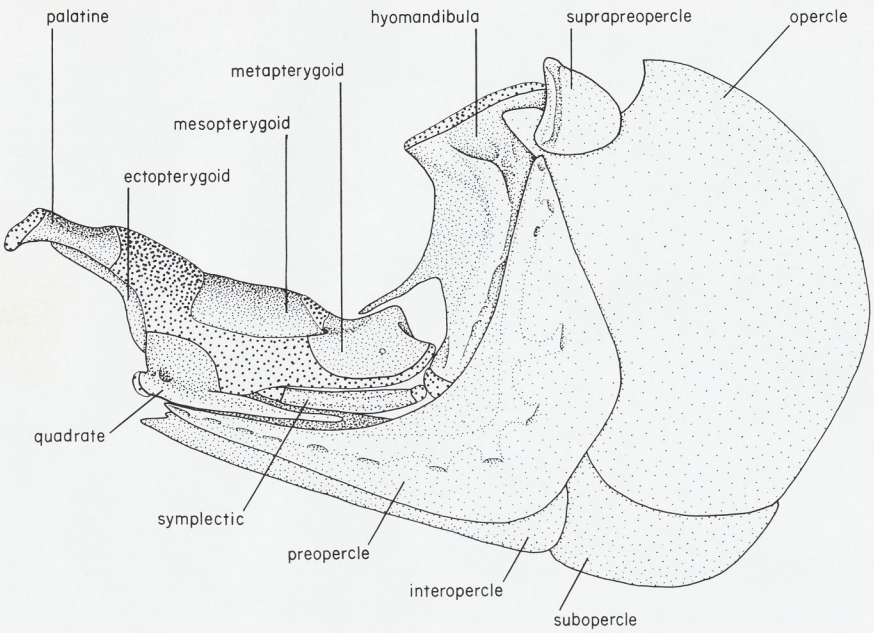

Figure 8. Suspensorium and opercular series, left lateral view, *Chanos,* USNM 199831.

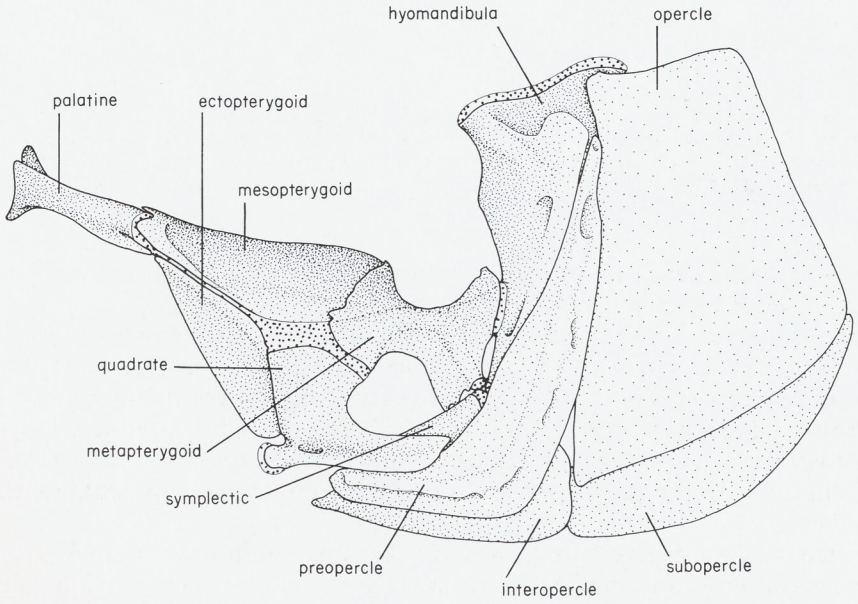

Figure 9. Suspensorium and opercular series, left lateral view, *Opsariichthys,* MCZ 32375.

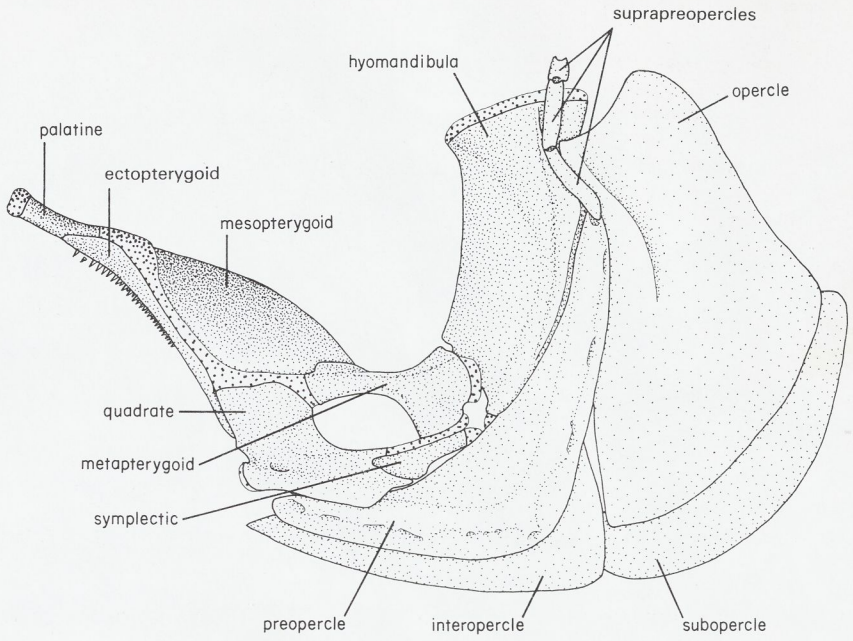

Figure 10. Suspensorium and opercular series, left lateral view, *Xenocharax,* MCZ 48020.

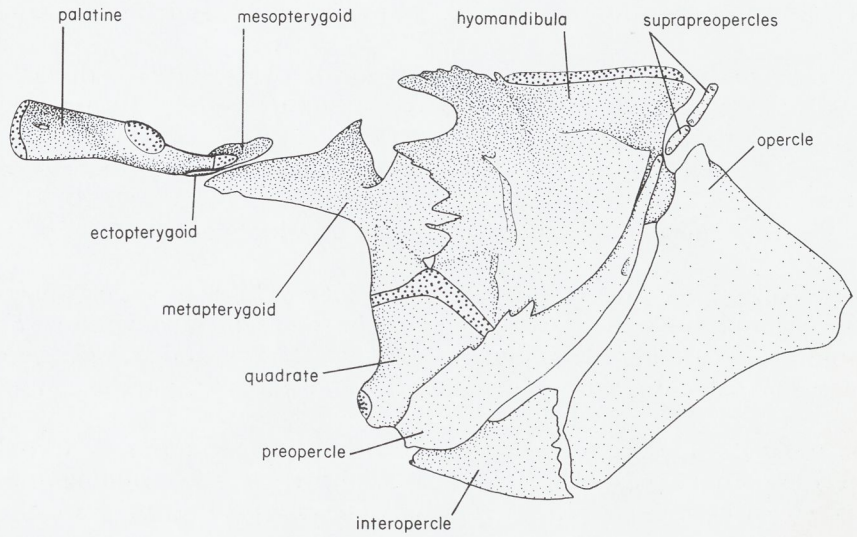

Figure 11. Suspensorium and opercular series, left lateral view, *Diplomystes,* right side drawn and reversed, from alcohol and alizarin specimens, MCZ 8290.

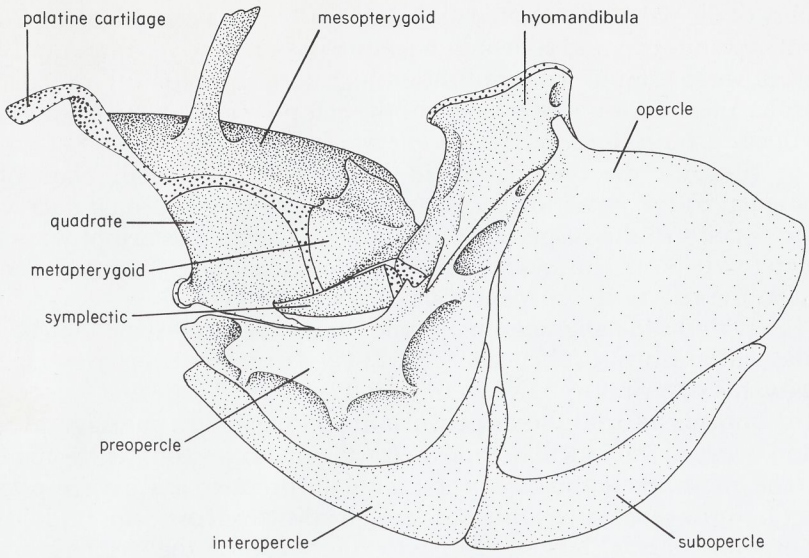

Figure 12. Suspensorium and opercular series, left lateral view, *Sternopygus,* CAS(IUM) 12591.

present in other ostariophysans (Figs 3A, C-F, 8, 10–12) or in other primitive teleosts.

(22) In cypriniforms the palatine articulates posteriorly in a concave facet on the mesopterygoid (Fig. 9). No special articulation is present in other ostariophysans (Figs 8, 10–12) or in other primitive teleosts.

(23) In gymnotoids the palatine ossification is absent and the palatine cartilage has a flexure which permits mobility of the palatine cartilage (Fig. 12). A palatine ossification is present in other ostariophysans (Figs 8–11) and in other primitive teleosts.

(24) In siluroids the palatine extends posterior to its articulation with the lateral ethmoid and the posterior articular cartilage of the palatine is not continuous with the cartilage of the quadrate or metapterygoid (Fig. 11). A separate anterior division of the *adductor arcus palatini* (termed *abductor tentaculi*) attaches to this posterior extension of the palatine and presumably abducts the maxillary barbel. None of these modifications is present in other ostariophysans or other primitive teleosts.

(25) In cypriniforms the ectopterygoid does not overlap the palatine anteriorly, permitting mobility of the palatine relative to the rest of the suspensorium (Fig. 9). In primitive teleosts, including *Megalops, Etrumeus, Chanos,* and characiforms, the ectopterygoid extends anteriorly over the ventral surface of the autopalatine (Figs 8, 10).

(26) In siluriforms the ectopterygoid is greatly reduced posteriorly (siluroids) or absent (gymnotoids) (Figs 11, 12). In most primitive teleosts, including primitive gonorynchiforms and characiforms, the ectopterygoid is present as an elongate bone along the anteroventral border of the suspensorium, overlapping the autopalatine anteriorly and the quadrate posteroventrally (Figs 8, 10). (*Contra* Gosline 1973:768, the ectopterygoid is not mobile in *Brycon* or in most other characiforms but is similar to that bone in *Chanos* and *Elops.*)

Mobility of the palatine was cited by Roberts (1973) as a possible shared derived feature of cypriniforms and siluroids (a feature present also in gymnotoids). Such mobility, however, results from non-homologous morphological specializations, in particular the anterior abbreviation of the ectopterygoid in cyprinoids and the great reduction posteriorly of the ectopterygoid in siluroids.

(27) In siluroids the mesopterygoid is reduced to a small plate of bone posteromedial to the posterior tip of the palatine and is not in contact with the posterior portion of the suspensorium (Fig. 11). In other ostariophysans and in most primitive teleosts, the mesopterygoid is a relatively large plate of bone firmly attached to the rest of the suspensorium (Figs 8–10, 12).

(28) In gymnotoids the mesopterygoid has a vertical strut which usually articulates with the orbitosphenoid (Figs 2E, 12). No such strut is present in other ostariophysans or primitive teleosts (Figs 8–11).

(29) In gonorynchiforms the suspensorium is elongate in a parasagittal plane in the region between the articular condyle for the quadrate and the hyomandibula (Fig. 8). The interopercle and the lower limb of the preopercle are correspondingly elongate. In most other ostariophysans and primitive teleosts, this middle region of the suspensorium is shorter relative to the height of the suspensorium and opercular series (Figs 9–12).

(30) In otophysans the endochondral portion of the metapterygoid is an axe-shaped bone, either double-headed (most cypriniforms and characiforms), or single-headed, with the posterior half of the bone absent (siluriforms, see character 31). The posterior border of the metapterygoid (siluriforms) or homologous ventral border (all other otophysans) is bony rather than cartilaginous (Figs 9–12). In *Chanos* (Fig. 8) and in most primitive teleosts, the metapterygoid is an approximately rectangular bone with a continuous cartilaginous border along the hyomandibula, symplectic and quadrate.

A metapterygoid-quadrate fenestra is present in primitive otophysans including a number of cypriniforms (e.g., cobitids, some homalopterids (Ramaswami, 1952b, c; 1953), and the cyprinids *Zacco* and *Opsariichthys,* Fig. 8), and most characiforms. Gosline (1973:769) argued that a metapterygoid-quadrate fenestra was independently acquired in cypriniforms and characiforms, citing its presence in some advanced clupeomorphs (e.g., *Brevoortia*). We consider the fenestra to be an otophysan character for several reasons: (1) the fenestra is found in members of groups which are phylogenetically primitive otophysans (cypriniforms and characiforms), (2) the fenestra is present in cypriniform and characiform species which appear to be morphologically conservative, but is not found in primitive members of any outgroups, and (3) in many of the cypriniforms in which the fenestra is absent, the endochondral portion of the metapterygoid still has a double-headed axe-shape although a thin bony plate extends ventrally and abuts against the symplectic. Therefore, a hypothesis of independent loss of the foramen in derived cypriniforms and characiforms seems simpler to us than one of independent acquisition of the fenestra in primitive members of both lineages.

(31) In siluriforms the endochondral portion of the metapterygoid is triangular and appears to be equivalent to the anterior half of the metapterygoid in primitive otophysans (compare Figs 12 and 9). The posterior border of the metapterygoid abutting against the hyomandibula is bony, rather than cartilaginous as in most other ostariophysans and primitive teleosts.

As part of the modifications of the suspensorium in siluroids, the triangular endochondral portion of the metapterygoid projects dorsally rather than posteriorly from the quadrate (shown in dotted outline in Fig. 11; see character 32).

(32) In siluroids the metapterygoid is situated anterodorsal to the quadrate and forms part of the ventral border of the suspensorium (Fig. 11). In other ostariophysans and primitive teleosts, the metapterygoid is posterodorsal to the quadrate (Figs 8–10, 12).

Only a small triangular area of the metapterygoid adjacent to the quadrate is endochondrally ossified; the rest of the metapterygoid consists of a posterodorsal laminar outgrowth which has a suture with a flange of the hyomandibula, and an anterodorsal flange, extensive in *Diplomystes,* which approaches the mesopterygoid and palatine.

(33) In siluroids the symplectic and the associated ventral process of the quadrate are absent (Fig. 11). Both these elements are present in other ostariophysans and primitive teleosts (Figs 8–10, 12).

(34) In siluroids the preopercle and interopercle are shortened considerably on an antero-posterior axis, so that there is no horizontal limb on the preopercle and the interopercle is a short triangular bone (Fig. 11). These bones are longer in other ostariophysans and primitive teleosts (Figs 8–10, 12).

(35) In siluroids the subopercle is absent (Fig. 11). The subopercle is present in other ostariophysans and primitive teleosts (Figs 8–10, 12).

(36) In siluriforms the opercle is approximately triangular in shape rather than approximately rectangular as in other ostariophysans and primitive teleosts (compare Figs 11 and 12 with Figs 9 and 10).

Jaws

(37) In cypriniforms the premaxilla extends furthest dorsally adjacent to the midline (Fig. 3B). In gonorynchiforms, characiforms, and most other primitive teleosts, the premaxilla extends furthest dorsally at a point more lateral to the midline (Fig. 3A, C, D).

(38) In gonorynchiforms the premaxilla is a very thin, flat bone. In most other primitive teleosts, the premaxilla is thicker and more robust.

(39) In characiphysans, the maxilla is positioned posterolateral to the lateral processes of the mesethmoid and does not articulate directly with the mesethmoid (Fig. 3 C-F). In gonorynchiforms, cypriniforms, and most other primitive telosts, the maxilla articulates directly against the anterolateral face of the ethmoid (Fig. 3A, B).

(40) Many cypriniforms and all siluroids have maxillary barbels. In cypriniforms the barbel is at the rictus of the mouth and may or may not be closely associated with the tip of the maxilla. In siluroids, the barbel extends from the distal part of the maxilla, and the skin of the maxilla and the barbel are separated from the skin of the cheek by a deep cleft. Other ostariophysans and primitive teleosts lack a maxillary barbel.

The barbels of cypriniforms and siluroids appear to have evolved independently (see Fig. 1 and Discussion).

(41) In ostariophysans supramaxillary bones are absent as separate ossifications. Such bones are present in most other primitive teleosts. A few

characiforms have a small, separate bony element which appears to be a reduced posterior supramaxillary bone (*Chilodus,* MCZ 46051; *Chilodus, Tylobranchus,* and *Chalceus macrolepidotus,* R. P. Vari, pers. commn). Another *Chalceus* specimen (MCZ 21142) has a small process on the maxilla which may represent a fused posterior supramaxilla. We would suggest that if absence of a separate posterior supramaxilla in ostariophysans is due to suppression of a developmental pathway, presence of a small, separate element may be due to re-expression of that pathway. Alternatively, if absence of the posterior supramaxillary is due to fusion, presence of a separate element may be paedomorphic.

(42) Gonorynchiforms and cypriniforms, unlike most primitive teleosts, lack teeth in the jaws. This feature appears to have evolved independently in these two lineages (see Fig. 1 and Discussion).

(43) In characiforms replacement teeth for the outer row dentary teeth and some premaxillary teeth form in trenches or crypts in the bone. In other primitive teleosts, replacement teeth form in the epithelium.

(44) Most characiforms have multicuspid jaw teeth. Other primitive teleosts have conical jaw teeth. *Contra* Roberts (1969), we hypothesize multicuspid teeth to be primitive for characiforms, and the presence of unicuspid teeth in such predators as *Hepsetus* and *Salminus* to be derived within the characiforms (see discussion of characiforms in Primitive Members of Ostariophysan Lineages).

(45) In siluriforms, a ligament extends between the maxilla adjacent to its articulation with the palatine and the dorsal tip of the anguloarticular at the coronoid process of the lower jaw. In characiforms and many other primitive teleosts the ligament (termed the ligamentum primordium) attaches posteriorly to the anguloarticular near its articular facet with the quadrate.

In gonorynchiforms, cypriniforms and apteronotids, this ligament attaches to part of the *adductor mandibulae* muscle rather than to the lower jaw; similar modification of the ligament in some siluroids appears to be a specialization associated with the presence of an *adductor tentaculi* muscle (Gosline, 1975a:9).

Gill arches

(46) Gonorynchiforms have "epibranchial organs", bilateral pouches in the branchial chamber located posterior to the fourth epibranchials (Greenwood *et al.,* 1966). In most other ostariophysans and lower teleosts, such pouches are not present.

Similar pouches occur in other teleosts (e.g., some clupeomorphs, characiforms, and cypriniforms) but are hypothesized to have been independently acquired in those groups (Nelson, 1967; Bertmar *et al.,* 1969).

(47) In gonorynchiforms, cypriniforms, and siluriforms, teeth are absent from the second and third pharyngobranchials and the basihyal. Such teeth are present in some characiforms and in other primitive teleosts. This reduction is hypothesized to be independent in the three lineages (see Fig. 1 and Discussion). Additional but varying reduction of pharyngeal dentition is present in each of these lineages; see characters 48–51.

(48) In gonorynchiforms and cypriniforms, the two posterior pharyngobranchial toothplates present in most primitive teleosts are absent. This loss is hypothesized to be independent in the two lineages (see Fig. 1 and Discussion).

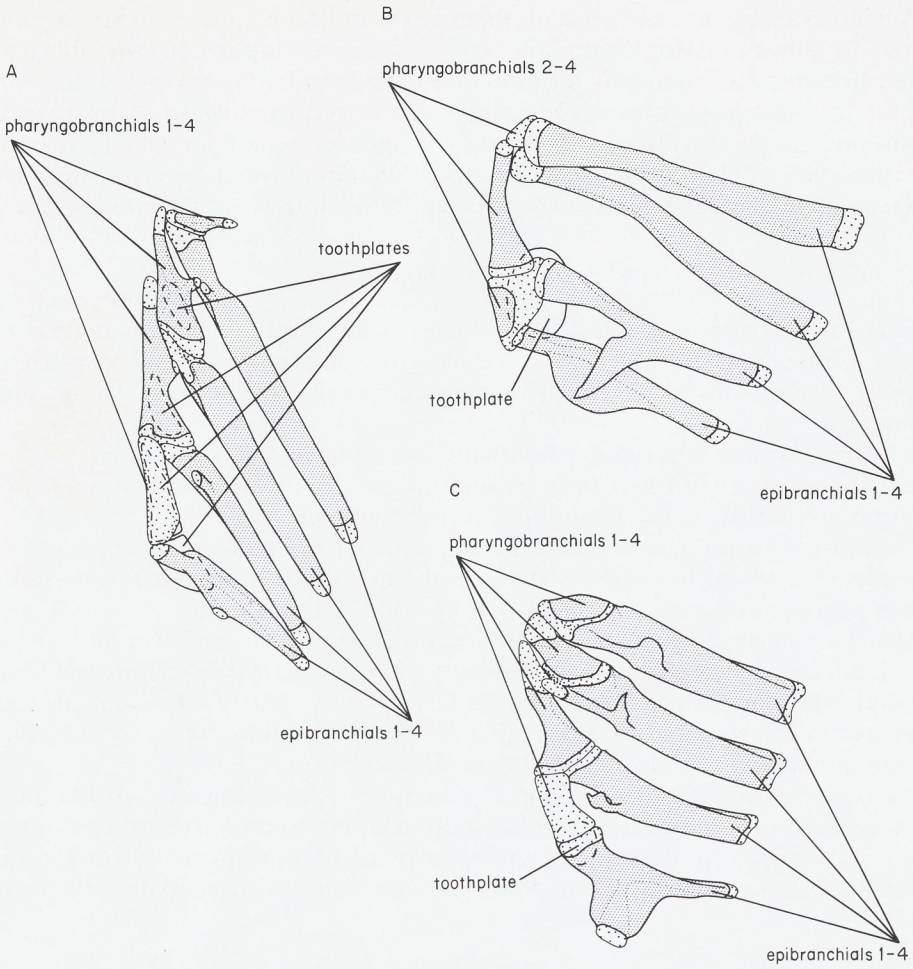

Figure 13. Bones of upper gill arches, right side, dorsal view. Toothplates or patches on ventral surface indicated by dashed lines. A, *Hepsetus,* MCZ 48104. B, *Parauchenoglanis,* MCZ 50747. C, *Eigenmannia,* MCZ uncat.

(49) In gonorynchiforms, no teeth are present on the fifth ceratobranchial. Such teeth are present in other ostariophysans and primitive teleosts.

(50) In cypriniforms and siluriforms the toothplate associated with basibranchials 1–3 is absent. This toothplate is present in primitive characiforms and other primitive teleosts. This loss is hypothesized to be independent (see Fig. 1 and Discussion).

(51) In siluriforms only one pharyngobranchial toothplate is present; whether this is the toothplate of the fourth pharyngobranchial, or the posterior toothplate, or a fusion of the two is unclear (Fig. 13B, C). Four pharyngobranchial toothplates are present in primitive characiforms and other primitive teleosts (Fig. 13A).

(52) In cypriniforms the fifth ceratobranchial is enlarged, extending much further dorsally than the other ceratobranchials. In other ostariophysans and primitive teleosts the fifth ceratobranchial extends no further dorsally than the other ceratobranchials.

(53) In cypriniforms the teeth on the fifth ceratobranchial are ankylosed to the bone. In other ostariophysans and most primitive elopocephalans, the teeth, when present, are bound to the bone by collagenous fibers.

Fink (1981) has shown that fully ankylosed teeth are primitive for actinopterygians and that teeth bound to the jaws by collagenous fibres are a specialization of elopocephalans. The ankylosed dentition of cypriniforms is thus regarded as secondarily derived and synapomorphous within the Ostariophysi.

Gasbladder

(54) In ostariophysans the gasbladder is divided into a smaller anterior and larger posterior chamber, with the ductus pneumaticus near the constriction (Rosen & Greenwood, 1970). The gasbladder of most teleosts has a single chamber.

The gasbladder is absent, presumably secondarily, in *Gonorynchus,* and the posterior chamber of the bladder is reduced or absent in a number of lineages, including cobitids, many gymnotoids, and many siluroids.

(55) In ostariophysans the anterior chamber of the gasbladder is partially or completely covered by a silvery peritoneal tunic. Such a tunic is not present in other primitive teleosts (Rosen & Greenwood, 1970).

(56) In ostariophysans the peritoneal tunic of the anterior chamber of the gasbladder is attached to the anteriormost two pleural ribs (the tripus and fourth pleural rib of otophysans) (Rosen & Greenwood, 1970). In other primitive teleosts, the gasbladder is suspended in the peritoneal cavity by the dorsal mesentery and is not closely bound to the ribs.

(57) In ostariophysans, the dorsal mesentery suspending the gasbladder is heavily thickened anterodorsally near its attachment to the vertebral column and has many transverse fibers ("dorsal adventitia" of Alexander, 1962). In other primitive teleosts the dorsal mesentery is thin and undifferentiated anteriorly.

Anterior vertebrae

(58) In ostariophysans the supraneural anterior to the neural arch of the anteriormost vertebra is absent (Figs 6, 14–18). In other primitive teleosts this supraneural is present.

(59) In otophysans the supraneural anterior to the neural arch of the second vertebra is absent (Figs 14–18). In *Chanos* and other primitive teleosts, this supraneural is present (Fig. 6).

(60) In otophysans the anterior two (cypriniforms) or one (characiphysans) supraneurals are expanded ventrally to form a synchondral joint with the neural arches of the third and fourth vertebrae (Figs 14–18). These appear to represent the supraneurals anterodorsal to the neural arches of the third and fourth, or just the fourth, centra. In other primitive teleosts the supraneurals do not form a synchondral joint with the neural arches (Fig. 6).

(61) In characiphysans the supraneural anterodorsal to the neural arch of the third centrum is absent (Figs 15–18). It is present in cypriniforms (Fig. 14) and in most primitive teleosts (e.g. Fig. 6).

(62) In characiphysans the single modified supraneural is tilted anteriorly and articulates with the posterior margin of the cranium (Figs 15–18). This is a shift in

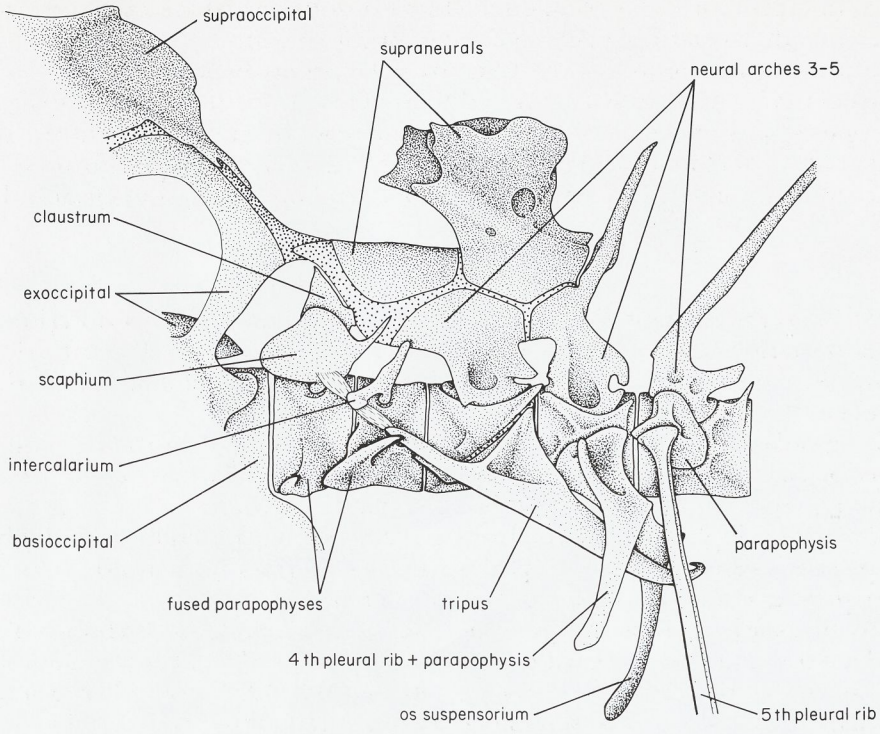

Figure 14. Anterior vertebral region, left lateral view, *Opsariichthys,* MCZ 32375.

position of the supraneural relative to its position in cypriniforms (Fig. 14) and other primitive teleosts (Fig. 6) and is associated with a foreshortening of the anterior vertebrae in characiphysans (see character 79 below).

(63) In ostariophysans the dorsomedial portions of the anterior neural arches are expanded and abut against each other and the posterior margin of the exoccipital, forming a roof over the neural canal. In other primitive teleosts, the neural arches are smaller and do not meet each other or the exoccipital.

In gonorynchiforms, the dorsomedial portions of the first four neural arches are large but relatively unmodified in form (Fig. 6). In otophysans, although the anterior two neural arch elements are highly modified, the dorsomedial portion of the anterior neural arch (the claustrum, or the cartilage in that region) still abuts against the posterior margin of the exoccipital, and a solid roof is still present over the neural canal anteriorly (Figs 14–18). The dorsomedial portion of the second neural arch is not developed as part of the intercalarium; like the claustrum, it forms part of the cartilage block roofing the neural canal anteriorly (Watson, 1939:455).

Rosen & Greenwood (1970) and others have used the term "supradorsal" for the dorsal part of the neural arch. However, supradorsal properly refers to a separate median cartilage dorsal to the neural arch (basidorsal) element in elasmobranchiomorphs and has been only tentatively applied to the paired cartilages in many actinopterygians (Goodrich, 1958:34). Since these paired cartilages appear not to be separate elements but simply cartilage of the arches

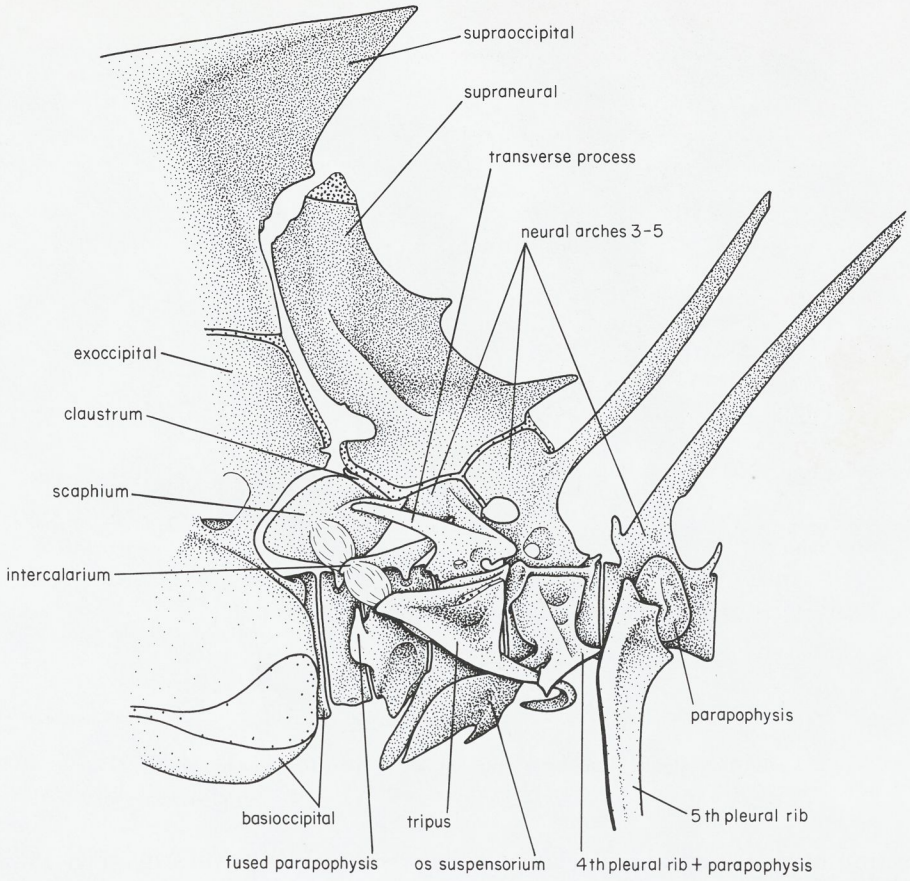

Figure 15. Anterior vertebral region, left lateral view, *Xenocharax,* MCZ 48020.

along their midline synchondral joint, the term supradorsal seems inappropriate.

(64) In ostariophysans the unattached neural arch anterior to the arch of the first vertebral centrum is absent. Such an arch is present in *Polypterus, Amia,* and in many primitive teleosts (e.g. *Elops, Dorosoma, Harengula, Anchoa, Esox, Diplophos*).

(65) In gonorynchiforms, the anterior neural arch is especially enlarged and has an extensive, tight joint with the exoccipital (*Chanos,* Fig. 6 and *Gonorynchus*) or with the exoccipital and supraoccipital (kneriids and *Phractolaemus*). In other ostariophysans, the articulation between the exoccipital and the dorsal margin of the anterior neural arch (the cartilage just dorsal to the claustrum) is small (Figs 14–18).

We note that only *Chanos* has the prominent triangular flange extending lateral to the endochondral portion of the exoccipital and covering part of the first neural arch, and that the position of the first neural arch in *Chanos* in a recess formed by this flange is not homologous with the position of the scaphium in a recess formed by the endochondral portion of the exoccipital in otophysans. Presence of a recess for the first neural arch does not, therefore, support

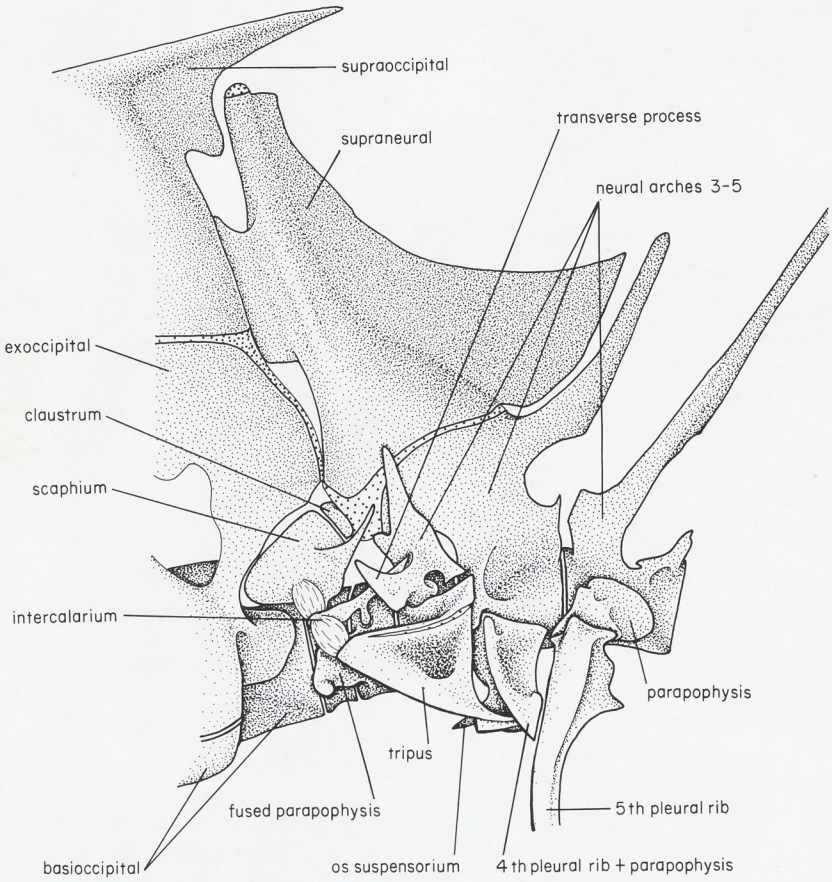

Figure 16. Anterior vertebral region, left lateral view, *Bryconamericus,* MCZ 48665.

gonorynchiform-otophysan relationship as suggested by Rosen & Greenwood (1970).

(66) In otophysans the first neural arch is modified to form the scaphium and claustrum, the claustrum being formed by the dissociated dorsomedial portion of the first neural arch (Rosen & Greenwood, 1970) (Figs 14–18). The claustrum is secondarily absent in gymnotoids; see character 67, below. The scaphium has a characteristic rounded outline anteriorly and a small process which articulates with the first centrum. The claustrum is variable in shape. These features are part of the Weberian apparatus, unique to otophysans.

(67) In gymnotoids, the claustrum is absent as a separate ossified element (Fig. 18) although it may be present as part of the cartilage mass roofing the neural canal. In most otophysans the claustrum is present as an ossification on the anteroventral border of the chondral block that roofs the neural canal anteriorly.

(68) In characiphysans the scaphium extends well anterior to the border of centrum 1 (Figs 15–18). In primitive cypriniforms such as *Opsariichthys,* the scaphium sits more directly dorsal to the centrum (Fig. 14), as is the case in primitive non-otophysan teleosts (Fig. 6).

(69) In otophysans the second neural arch is modified to form the inter-

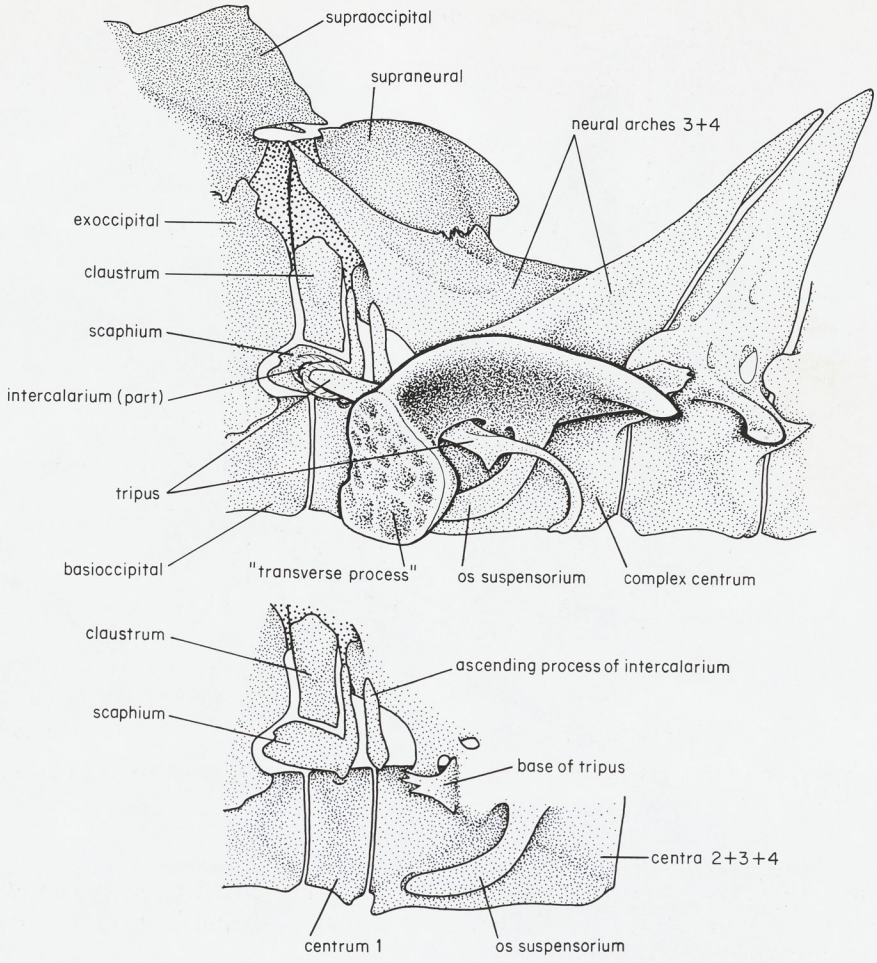

Figure 17. Anterior vertebral region, left lateral view, *Diplomystes,* right side drawn and reversed, cartilage from alcohol specimen, MCZ 8290. Insert with 4th pleural rib, tripus, interossicular ligaments, and interossicular portion of intercalarium removed.

calarium (Figs 14–18). Primitively, the intercalarium consists of an ascending process, a horizontal process (which serves as an attachment for the interossicular ligaments connecting scaphium, intercalarium, and tripus) and a small, peg-like articular process which articulates with the second centrum. In characiforms the ascending process sits medial to the transverse process of the third neural arch (Figs 15, 16). The intercalarium is part of the Weberian apparatus and unique to otophysans.

(70) In siluriforms the articular process of the intercalarium, present in primitive cypriniforms and in characiforms, is absent, and the intercalarium does not articulate with the centrum (Figs 17, 18). In gymnotoids and in many, but not all, siluroids, the ascending process has also been lost, apparently independently in the two lineages, so that the intercalarium consists only of a nodule of bone in the interossicular ligaments. Some more primitive siluroids, such as *Mystus* ("*Macrones*", Bridge & Haddon, 1893:83) and *Diplomystes,* retain an ascending

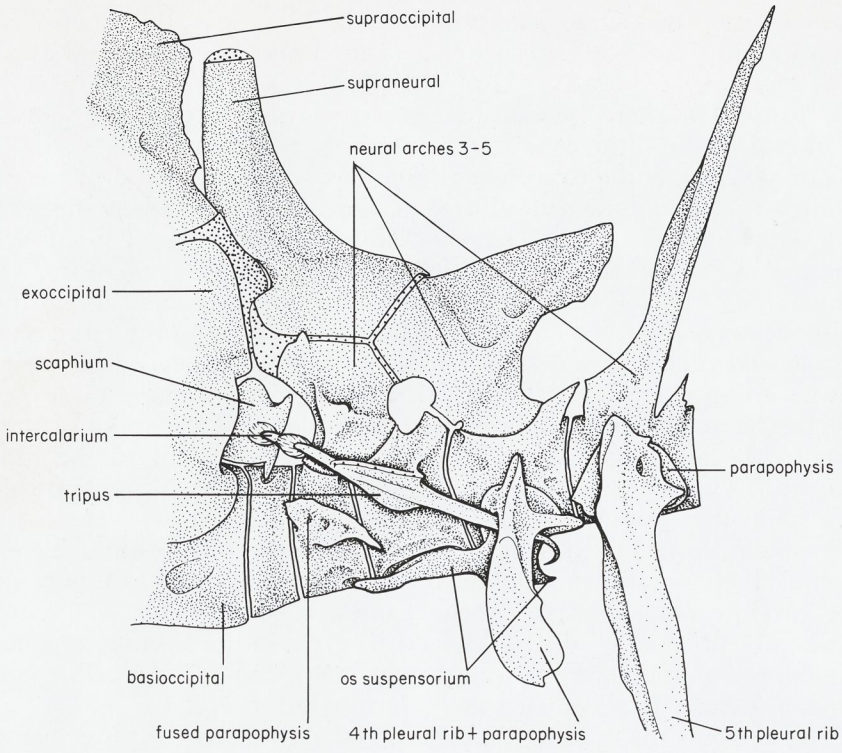

Figure 18. Anterior vertebral region, left lateral view, *Sternopygus,* right side drawn and reversed, CAS(IUM) 12591.

process. *Diplomystes* appears unique (and not representative of the condition primitive for siluroids) in that the ascending process is separate from the nodule in the interossicular ligaments (Fig. 17).

Statements that some siluroids have an articular process on the intercalarium (such as those of Alexander, 1964:425, and Chardon, 1968:26, 28) are errors apparently due to misinterpretation of the "horizontal process" of Bridge & Haddon (1893) as an articular process.

(71) In characiforms the third neural arch has an elongate anterodorsal process, usually termed the transverse process of the third neural arch, which projects lateral to the ascending process of the intercalarium (Figs 15, 16). In other otophysans a shallow ventrolateral shelf (cypriniforms, Fig. 14) or lateral shelf (gymnotoids, Fig. 18) may be present; this feature is indistinguishable, if present, in the fused elements of the siluroid apparatus. Other primitive teleosts may have a small prezygapophysis in this position.

(72) In characiphysans the anterior margin of the third neural arch approaches the posterior border of the neurocranium much more closely than in cypriniforms or other primitive teleosts (compare Figs 15–18 with Figs 14 and 6). This feature is associated with the foreshortening of the anterior three vertebrae in characiphysans.

(73) In characiphysans the dorsal part of the third neural arch has a distinct, short anterior margin which is vertical in orientation (Figs 17, 18; small or absent

in characiforms, Figs 15, 16). In cypriniforms and in *Chanos,* this anterior margin (less distinct in *Chanos*) is fairly elongate and closer to a horizontal alignment (Figs 6, 14).

This feature in characiphysans is associated with loss of the supraneural anterodorsal to the third neural arch (character 61, above).

(74) In siluriforms the third neural arch has an anteroventral process which articulates with (gymnotoids) or is fused to (siluroids) a dorsal prominence on the second centrum (Figs 17, 18). That this feature is present in the fused vertebral complex of adult siluroids is indicated by an examination of young *Ictalurus* specimens (MCZ 54389) in which the individual components can still be distinguished. At 12.1 mm S.L., a partly cartilaginous dorsal prominence is present on the second centrum, and at 14.8 mm S.L. this prominence is entirely bony and fused to an anterior extension of the third neural arch.

(75) In characiphysans, the presumed homologue of the spine of the third neural arch extends anterodorsally from the arch, lateral to the modified supraneural (Figs 15–18), rather than posterodorsally as in gonorynchiforms (Fig. 6) and other primitive teleosts.

The spine is short, but present, in gymnotoids examined. Although absent in adult citharinids and distichodontids, the spine is present, also as a short process, in the juvenile *Distichodus* specimen examined (MCZ 48110; 16.7 mm S.L.). Because this process is absent altogether even in the young cypriniforms examined, we cannot be certain whether the anterior tilt is a characiphysan or an otophysan feature. It is depicted as characiphysan in Fig. 1.

(76) In siluroids the third and fourth neural arches are fused together and to the complex centrum (Fig. 17). Such fusion is not present in vertebrae anterior to the dorsal fin in most primitive teleosts and is not present in *Chanos,* most cypriniforms, primitive characiforms, or most gymnotoids (Figs 6, 14, 15, 18).

Fusion of the fourth arch to the centrum is present in a subgroup of characiforms (non-distichodontid and non-citharinid characiforms, Fig. 16) and fusion of the third and fourth arches to their respective centra in a subgroup of cypriniforms (including cobitids and homalopterids). Non-chanid gonorynchiforms, *Denticeps,* and engraulids show fusion of all arches to centra. In none of these groups, however, do the third and fourth arches also fuse together, and fusion of arches to centra is therefore hypothesized to be independent in siluroids and within each of the major lineages where it is found (see also character 80, below).

(77) In characiphysans, the fifth neural arch is fused to its centrum (Figs 15–18). Such fusion is not present in vertebrae anterior to the dorsal fin in most primitive teleosts, and is not present in *Chanos* or most cypriniforms (Figs 6, 14). Such fusion appears to have been independently acquired in *Denticeps,* in engraulids, in non-chanid gonorynchiforms, and in a group including cobitids and homalopterids.

(78) In otophysans the first four centra all show some foreshortening relative to the more posterior centra (Figs 14–18). In gonorynchiforms and in other primitive teleosts, the anterior one or two vertebrae are only slightly foreshortened relative to those following (Fig. 6).

(79) In characiphysans the anteriormost three vertebrae are foreshortened in comparison with primitive cypriniforms and other primitive teleosts, with the anterior centrum being especially foreshortened, the second centrum less so, and the third slightly less again (Figs 14–18).

In siluroids, the second, third, and fourth centra are fused into a single "complex centrum" (see character 80, below) but the foreshortening is still evident in the length of the anterior vertebral elements and the relative size of the component vertebrae can be seen in juvenile *Ictalurus* specimens (MCZ 54389).

Many cypriniforms show foreshortening of the anterior vertebrae greater than in such primitive forms as *Zacco* and *Opsariichthys,* but in most of these, including forms with centra 2 and 3 fused, centrum 2 is foreshortened more than centrum 1. A few cypriniforms, such as homalopterids and some catostomids (e.g., *Carpiodes*) also have centrum 1 very reduced.

(80) Siluroids have centra 2–4 fused into a "complex centrum" (Fig. 17). Such fusion is not present in other characiphysans. Many cypriniforms show fusion of centra 2 and 3, associated with enlargement of centrum 3 dorsally and ventrally around a reduced centrum 2. However, the absence of this feature in a number of cypriniforms and the difference in shape of the fused vertebral elements indicates that such fusion evolved independently in cypriniforms and siluroids.

(81) In otophysans, the anteriormost two parapophyses, when present, are fused to the centra (Figs 14–16, 18). In most primitive teleosts, including *Chanos* (Fig. 6), the parapophyses of the centra anterior to the dorsal fin are present as autogenous elements. (The parapophysis of the first centrum is present irregularly in *Chanos*; it is present on the right but not the left side of the specimen illustrated.) The occurrence of fused parapophyses in osteoglossomorphs, *Denticeps,* engraulids, and non-chanid gonorynchiforms is interpreted here as independently derived in those fishes.

(82) In characiphysans no parapophysis, fused or autogenous, is present on the anterior centrum (Figs 15–18). A parapophysis is present on the anterior centrum in most primitive teleosts.

Since the anterior parapophysis is present in many primitive teleosts, in gonorynchiforms (albeit irregularly in *Chanos*), and in cypriniforms, Rosen & Greenwood (1970) were incorrect in pointing to the absence of a parapophysis in the specimen of *Chanos* they illustrated and in the characiform *Brycon* as indicative of shared common ancestry in gonorynchiforms and otophysans.

(83) In siluroids the parapophysis of the second centrum is absent (Fig. 17). In other otophysans, the parapophysis is present as a lateral process fused to the centrum (Figs 14–16, 18).

(84) In cypriniforms, the lateral process of the second centrum is elongate, projecting well into the somatic musculature (Fig. 14). In other otophysans the lateral process, when present, is short.

(85) In otophysans, the rib and parapophysis of the third centrum are anteriorly elongate proximally, the rib is truncate distally, and a thin, curved posterior process (termed the transformator process) is attached to the gasbladder. The resulting ossification is unique to otophysans and is termed the tripus.

The primitive members of all otophysan lineages except gymnotoids show at least partial fusion of the parapophysis and rib portions of the tripus as adults; presumably such fusion is primitive for otophysans.

(86) In characiphysans, the parapophysis portion of the tripus is attached to the centrum by a thin, flexible bony lamella which projects posterodorsally from the centrum (Figs 15–18), a feature previously noted by Alexander (1964:425). The attachment of the lamella to the centrum is restricted to the posterodorsal quadrant of the lateral face of the centrum. In cypriniforms, *Chanos,* and most

other primitive teleosts, the parapophysis of the third centrum is autogenous (see character 81) and has a more extensive attachment site on the lateral or ventrolateral face of the centrum (Figs 14, 6).

(87) In siluroids the transformator processes of the tripus are separated posteriorly by the width of the complex centrum (Fig. 17). In cypriniforms, characiforms, and gymnotoids, the transformator processes approach the midline posteriorly. Although no outgroup comparison is possible for this feature, we hypothesize the latter state to be the primitive condition for otophysans based on the most parsimonious cladogram of other features.

(88) In otophysans the pleural rib of the fourth centrum is shortened, and the rib and parapophysis are fused to each other and have a median process, the os suspensorium, which is attached both to the anteriorly thickened dorsal mesentery suspending the gasbladder and to the gasbladder itself (Figs 14–18). In most otophysans the os suspensorium of each side of a fish meets its fellow in the midline (except in siluroids, see character 93, below). In other primitive teleosts, the pleural rib is elongate, the rib and parapophysis are separate elements, and no median process is present (Fig. 6).

(89) In siluriforms the "transverse process" of the fourth centrum has an ovoid, anterolateral face which approaches the suspensorium of the pectoral girdle (Figs 17, 18). Although in siluroids this element has been termed simply the parapophysis or transverse process of centrum 4, similarities in morphology to the fused parapophysis and pleural rib of other otophysans indicate that the rib portion may still be present. In other otophysans and primitive teleosts, the anterior face is not ovoid and does not approach the suspensorium of the pectoral girdle.

(90) In siluroids, the "transverse process" of the fourth centrum is expanded broadly in a horizontal plane and the ovoid anterior face articulates with the suspensorium of the pectoral girdle (Figs 17, 19C).

(91) In siluroids, the "transverse process" of the fourth centrum is fused to the complex centrum (as are the third and fourth neural arches, see character 76, above). Fusion of the parapophysis of the fourth centrum to that centrum is not present in the primitive members of other otophysan lineages and does not occur in most other primitive teleosts (see character 81).

(92) In siluriforms the os suspensorium has an elongate anterior horizontal process which is closely applied to the ventrolateral surface of vertebral centra 2–4 in gymnotoids and of the complex centrum in siluroids (Figs 17, 18). This process is not found in other otophysans or primitive teleosts.

(93) In siluroids the os suspensoria lack the posteromedial processes but consist of only the anterior horizontal processes described as character 92 (Fig. 17). The posteromedial processes are present in all other otophysan lineages.

(94) In siluriforms all pleural rib elements, particularly the fourth pleural rib and tripus, project from the centra at an angle close to the horizontal; only the edge of the tripus is evident from lateral view (Figs 17, 18). In cypriniforms, characiforms, and other primitive teleosts the pleural rib elements project ventrolaterally from the centra (Figs 14–16, 6).

Pectoral girdle

(95) In siluroids the suspensorium of the pectoral girdle consists of a single ossified element which comprises the supracleithrum, the ossified Baudelot's

ligament, and perhaps also the posttemporal (Fig. 19C). This structure articulates with an ovoid facet on the anteriorly expanded pleural rib of centrum 4 and provides a sling for the cleithrum. There is never fusion of these three elements in other otophysans; fusion of the posttemporal and supracleithrum occurs in some gymnotoids and characiforms but not in the primitive members of those groups.

Ossification of part of Baudelot's ligament is present in the primitive gymnotoid *Sternopygus* (Fig. 19D) and in some other gymnotoids and may, therefore, be a siluriform feature. If so, such ossification has been lost a number of times within the gymnotoids.

The homology of the pectoral girdle suspensorium has historically been a subject of debate; most recently Lundberg (1975b) has argued that the posttemporal is not part of the large ossified element but is represented by a plate-like element, often identified as the extrascapular, tightly bound to the posterodorsal margin of the neurocranium in many siluroids. Based on a hypothesis of homology between a posterolateral branch of the temporal sensory canal in the extrascapular of some characiforms and a similar branch in the pterotic of siluroids, Lundberg suggested that the extrascapular canal of characiforms was incorporated into the pterotic of siluroids and that the remainder of the extrascapular was absent in siluroids. We concur with the alternative hypothesis, that the plate-like bone represents the extrascapular rather than the posttemporal, not only because the bone lacks the elongate dorsal limb of the posttemporal of other teleosts, but because the extrascapular in gymnotoids is immovably articulated to the cranium. Such immobility, not present in most other teleosts, would therefore seem to be a siluriform feature. Moreover, the small branches and pores in sensory canals are not invariant in other ostariophysans; we therefore see no reason why the small branch in the pterotic of siluroids should not be a new feature. The canal of the supratemporal cross-commissure, a major feature which would permit a more definitive identification of the plate-like bone as the extrascapular, is absent in siluroids; however Bamford (1948) considered two free lateral line organs located in a groove on this bone (his "tabular") in the ariid *Galeichthys* to be the remnant of the supratemporal cross-commissure. Presence of such a feature in other catfishes, especially more primitive ones, would corroborate the identification of the plate-like bone as the extrascapular.

Lundberg also suggested that because ontogenetic fusion between the posttemporal and supracleithrum had not been observed, only one of these bones must be present. We would suggest that observations on more complete ontogenetic series than have heretofore been examined might reveal such fusion. In a specimen of *Ictalurus* 21.1 mm S.L. (MCZ 54389), the suspensorium, though thinly ossified, is like that of the adult in form. Bamford (1948) described the suspensorium of *Galeichthys* as developing from only one ossification, but he did not examine any stages between 8 mm T.L., when apparently no dermal ossifications were present, and 14 mm T.L., when the suspensorium was nearly adult in form (Bamford mistook the ossified Baudelot's ligament for the lower limb of the posttemporal, a feature which is absent in all siluriforms). Furthermore, the presence of only one ossification centre might indicate phylogenetic fusion as easily as phylogenetic loss. In many siluroids, the suspensorium has an elongate dorsal ramus similar in form to the dorsal ramus of the posttemporal in other teleosts. If the posttemporal was lost rather than

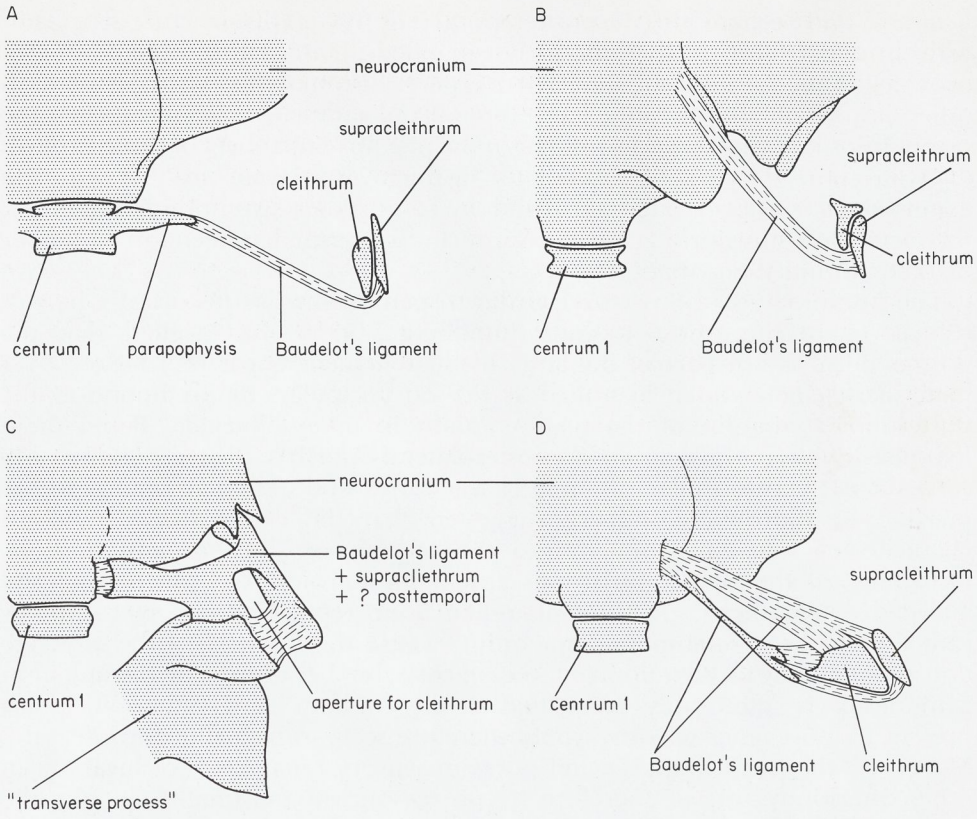

Figure 19. Baudelot's ligament and surrounding bones, ventral view. A, *Opsariichthys,* supracleithrum and cleithrum shown in cross-section, basioccipital process removed, CAS(SU) 32568. B, *Bryconamericus,* supracleithrum and cleithrum shown in cross-section, MCZ 48665. C, *Diplomystes,* cleithrum not shown, MCZ 8290. D, *Sternopygus,* supracleithrum and cleithrum shown in cross-section, CAS(IUM) 12591.

fused, the supracleithrum must have expanded dorsally and acquired a dorsal ramus similar in form to that of the lost posttemporal. The possibility of loss of the posttemporal and subsequent expansion of the supracleithrum is lent some support by the fact that *Diplomystes* has a short dorsal ramus. However, until it is clear that a short dorsal ramus is present in other fairly primitive siluroids and is therefore not an autapomorphy of *Diplomystes,* we will prefer the more conservative hypothesis.

(96) In gonorynchiforms, cypriniforms, and siluroids the number of postcleithra is reduced to one (cypriniforms) or none (gonorynchiforms and siluroids). Three are present in some characiforms, gymnotoids and many other primitive teleosts. We hypothesize reduction of postcleithra to be independent in gonorynchiforms, cypriniforms, and siluroids, and also in some characiforms and gymnotoids (see Fig. 1 and Discussion).

(97) In characiphysans Baudelot's ligament attaches to the skull in the region of the cranial condyle or the lagenar capsule (Fig. 19B-D). In primitive cypriniforms and most primitive teleosts, Baudelot's ligament attaches to the parapophysis of the anteriormost centrum (Fig. 19A).

A few cypriniforms also have Baudelot's ligament attaching to the skull, including *Cyprinus,* some catostomids (e.g. *Catostomus, Erimyzon*), and homalopterids. In most of these (all specimens examined except *Gastromyzon borneensis*), the lateral process of centrum 1 is also absent.

(98) In siluriforms, Baudelot's ligament is well developed, thick, and bifurcate distally (Fig. 19C, D). In other otophysans and most primitive teleosts, the ligament is less heavy and single distally, extending posterior to the cleithrum to attach to the supracleithrum (Fig. 19A, B).

In the primitive gymnotoid *Sternopygus* (Fig. 19D), Baudelot's ligament has a thick, single attachment to the neurocranium; more distally the ligament separates into two parts, the posterior ossified and the anterior fibrous. In siluroids (Fig. 19C), Baudelot's ligament is ossified and the anterior ramus is co-ossified with the supracleithrum-posttemporal (see character 95); the posterior ramus is ossified where it abuts against the anterior process of the fourth pleural rib and fibrous where it passes posterior to the cleithrum to attach to the supracleithrum.

(99) In gymnotoids both the anterior and posterior parts of Baudelot's ligament attach to the cleithrum (Fig. 19D). Attachment to the supracleithrum, present in the primitive gymnotoid *Sternopygus,* is absent in many more specialized gymnotoids. In most other otophysans and other primitive teleosts, Baudelot's ligament attaches solely to the supracleithrum (Fig. 19A, B).

In homalopterids Baudelot's ligament attaches solely to the cleithrum.

Pectoral fins

(100) In siluriforms the more posterior fin-rays are offset posteriorly from the anterior ray (Fig. 20B, C). In cypriniforms, characiforms and most other primitive teleosts, the fin-rays articulate in an even arc (Fig. 20A).

(101) In siluriforms the flanges for muscle attachment proximally on the ventral ray halves are about equal in size to those on the dorsal ray halves. In cypriniforms, characiforms, and most other primitive teleosts, the flanges on the ventral ray halves are much larger than those on the dorsal ray halves.

Pelvic girdle and fins

(102) In most otophysans, the pelvic girdle is bifurcated anteriorly (Fig. 21B-E). In gonorynchiforms, as in most primitive teleosts, the pelvic girdle has a single anterior ramus (Fig. 21A).

Although the pelvic girdle has a single anterior ramus in many characiforms, it is bifurcated in young *Hepsetus* (Fig. 21D) and more deeply bifurcated in the characiforms considered by us, on other evidence, to form the sister-group of all other characiforms, the citharinids and distichodontids (Fig. 21C). (See character 103 for gymnotoids.)

(103) In gymnotoids, the pelvic girdle and fin are absent. Both are present in most other teleosts.

Dorsal and anal fins and fin supports

(104) In gymnotoids the dorsal fin is absent. It is present in most other teleosts.

(105) In gymnotoids, the anal fin is elongate, extending along nearly the entire ventral margin of the body, from the region of the pectoral-fin origin anteriorly

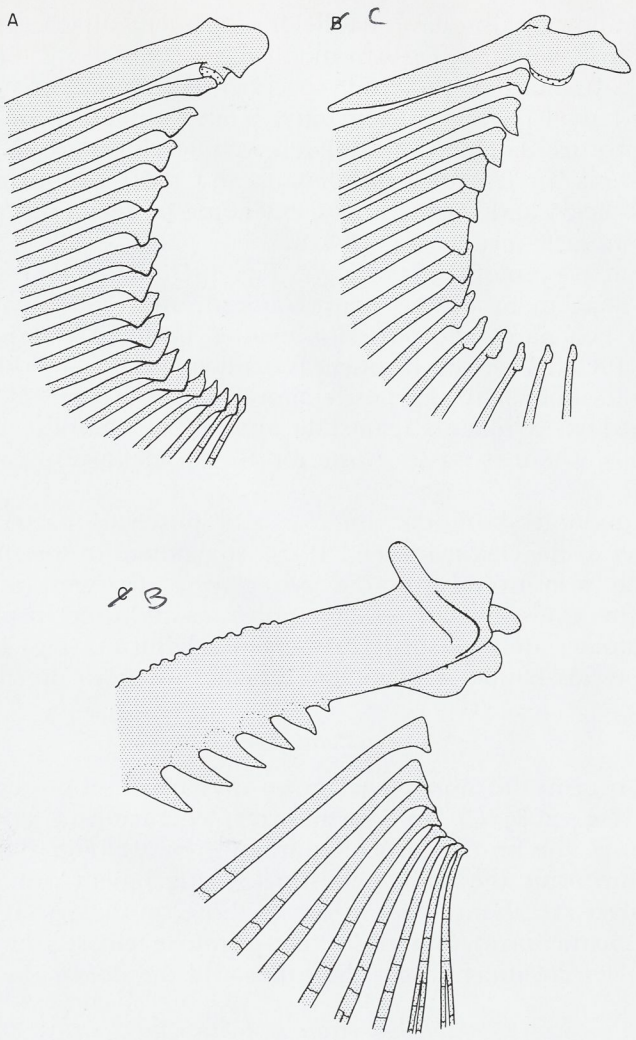

Figure 20. Pectoral fin rays, left side, dorsal view. A, *Xenocharax,* MCZ 48020. B, *Parauchenoglanis,* MCZ 50747. C, *Rhabdolichops,* MCZ 54336.

to the caudal fin or caudal filament posteriorly. The anal fin extends along less than half of the ventral margin of the body in most other teleosts.

(106) In siluriforms the middle radial ossification is absent along the entire length of both the dorsal and anal fin pterygiophores (Fig. 22B, C). In primitive characiforms, cypriniforms, and most other primitive teleosts, distal, middle, and proximal radials are present over most of the length of both fins (Fig. 22A). Within ostariophysan subgroups, absence of the middle radial is not uncommon. Among gonorynchiforms, *Chanos* has three ossified elements, *Kneria* and *Grasseichthys,* two. Among characiforms, *Hoplias, Ctenolucius, Parodon, Saccodon,* citharinids and many distichodontids have two ossified elements (*Xenocharax* has three).

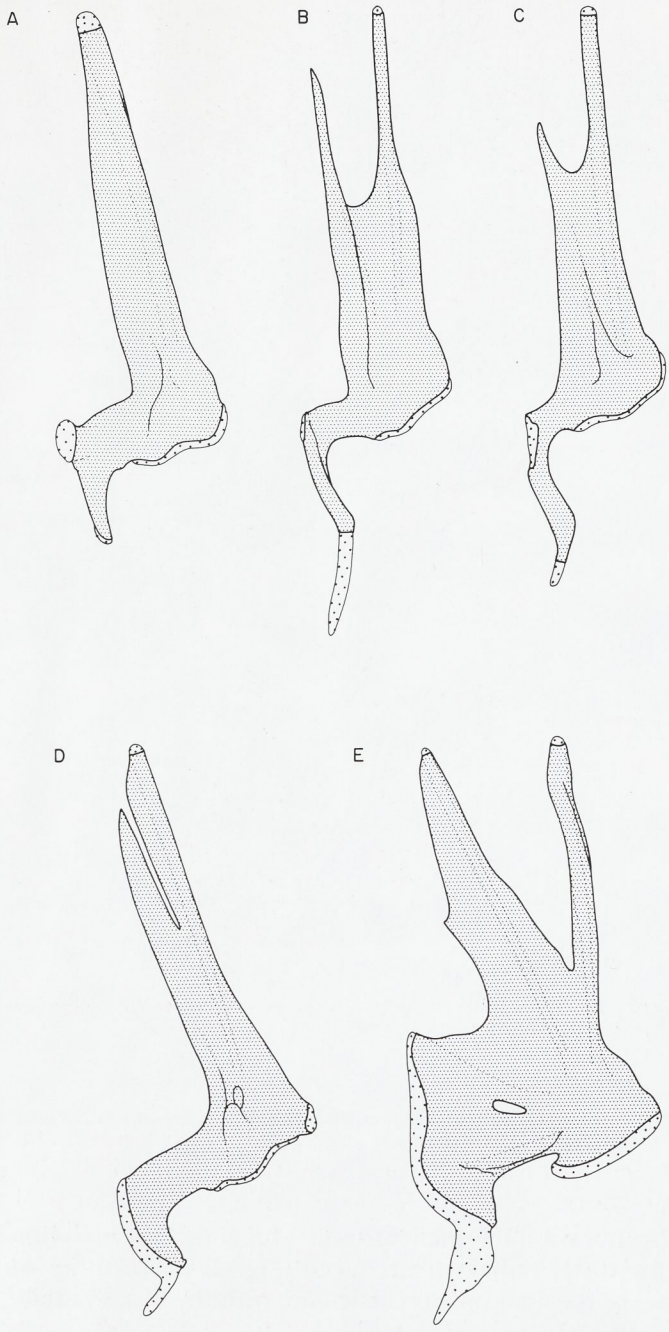

Figure 21. Left pelvic girdle, ventral view. A, *Chanos,* USNM 199831. B, *Notemigonus,* MCZ 52751. C, *Xenocharax,* MCZ 48020. D, *Hepsetus,* MCZ 48104. E, *Diplomystes,* MCZ 8290.

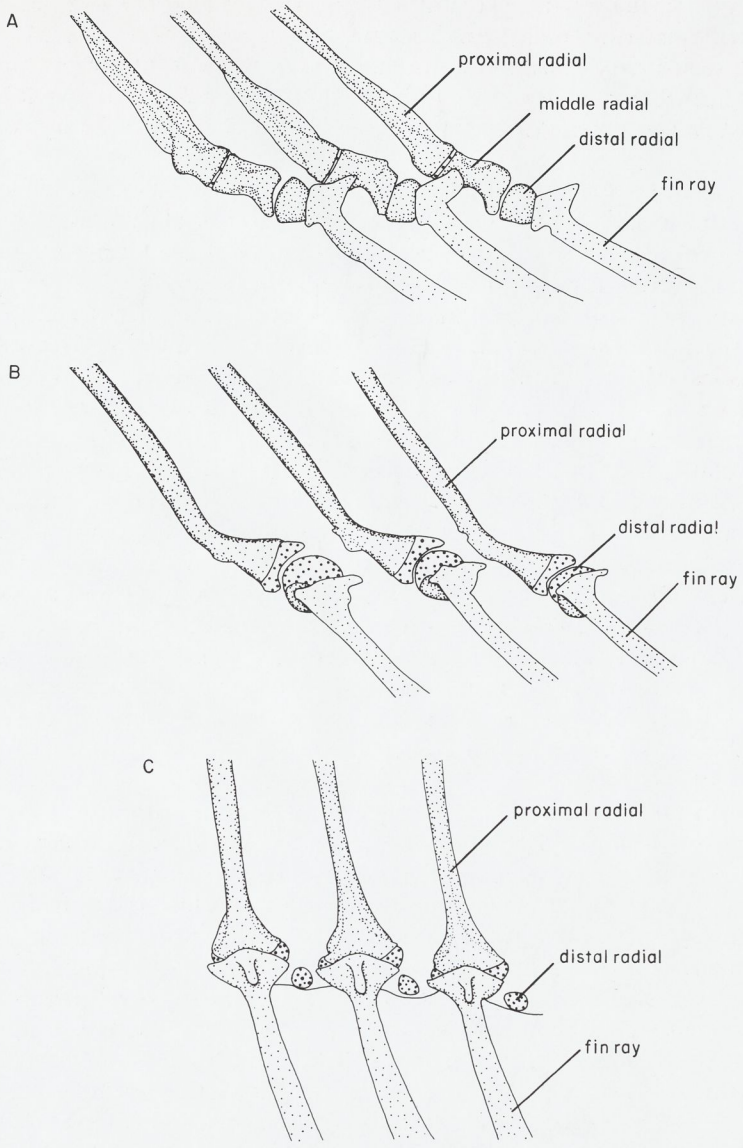

Figure 22. Anal fin pterygiophores and fin rays, left lateral view. A, *Chalceus,* MCZ 21142. B, *Diplomystes,* MCZ 8290. C, *Sternopygus,* MCZ 45193.

(107) In gymnotoids, the anal fin-rays articulate directly with the proximal radials and the distal radials are reduced (Fig. 22C). In other otophysans and primitive teleosts, the anal fin-rays articulate with the distal radials (Fig. 22A, B).

Caudal fin and fin supports

(108) In siluriforms with a caudal fin, the principal caudal fin-ray count is 9/9 or less (9 principal rays in the upper lobe, 9 principal rays in the lower). In

primitive gonorynchiforms, cypriniforms, almost all characiforms, and primitive members of most lower teleostean lineages, the principal ray count is 10/9.

Among siluroids, *Diplomystes* alone has a count of 9/9, all others having fewer fin-rays (Lundberg & Baskin, 1969). Of the gymnotoids available to us, *Sternarchorhamphus macrostomus* has a count of 9/9, with others having fewer fin-rays.

(109) In gymnotoids the caudal support skeleton is consolidated into a single element and the caudal fin is greatly reduced in size or absent (Fig. 23E). Among adult gymnotoids, only apteronotids have a caudal fin, although juveniles of other gymnotoids may also possess a fin (Kirschbaum & Denizot, 1975; Kirschbaum, pers. commn). In most adult gymnotoids other than apteronotids the caudal support skeleton consists of a slender bony rod extending from the last recognizable centrum; this rod appears to consist largely of an endochondral ossification induced by the opisthural cartilage (Meunier & Kirschbaum, 1978).

(110) In otophysans, the caudal support skeleton has a compound terminal centrum consisting, in at least the primitive cypriniforms, characiforms, and siluriforms, of the first preural centrum (PU1), the two ural centra (U1 and U2), and the anterior pair of uroneurals (for gymnotoids see character 109). In primitive members of other lower teleostean lineages, including the clupeomorph *Denticeps* and a fossil chanid *Tharrhias* from the Santana Formation of Brazil (Patterson, 1975b), the three centra and uroneurals are all separate elements. Consolidation of the caudal centra and uroneurals therefore appears to have occurred independently not only in some clupeomorphs and advanced teleosts, but at least three times in ostariophysans: in chanids, in other gonorynchiforms, and in otophysans.

In some otophysans, the U2 centrum fuses to the base of hypural 3 rather than to the compound centrum. This fusion has been found in most siluroids (Lundberg & Baskin, 1969) and is present also in some catostomids (e.g., *Catostomus*). In other catostomids, hypural 3 and, presumably, U2 are both fused to the compound centrum (e.g., *Carpiodes, Erimyzon*); this type of fusion occurs in only a few, apparently advanced, siluroids (Lundberg & Baskin, 1969). We hypothesize fusion of U2 to hypural 3 rather than to the compound centrum to be derived for some subgroups of otophysans, rather than primitive for the group as suggested by Lundberg & Baskin (1969). U2 is adjacent to but not fused to hypural 3 in young *Brycon* specimens (MCZ 49964, 12.8–13.4 mm S.L.) which have hypurals 1 and 2 and the parhypural fused to the PU 1+U1 centrum (character 112). Young *Notemigonus crysoleucas* specimens (MCZ 52751, 14.4–14.5 mm S.L.) also have U2 adjacent to but not fused to hypural 3, and U2 is fused to the compound centrum in all but one specimen of *Notemigonus* 14.8 mm S.L. and larger. The U2 centrum is fused to the compound centrum also in a young *Distichodus notospilus* (MCZ 48110, 16.7 mm S.L.). In addition, although our observations of *Ictalurus* corroborate those of Lundberg & Baskin regarding fusion of U2 and hypurals 3 and 4, hypurals 3 and 4 are completely separate in *Diplomystes papillosus* (and in members of the Trichomycteridae, Lundberg & Baskin, 1969), and no evidence of a U2 centrum is present at the base of hypural 3 in *Diplomystes papillosus*. The decision on whether fusion of U2 to hypural 3 is a general feature of siluroids must therefore await examination of young *Diplomystes* specimens.

(111) In ostariophysans, all haemal spines anterior to that of the second

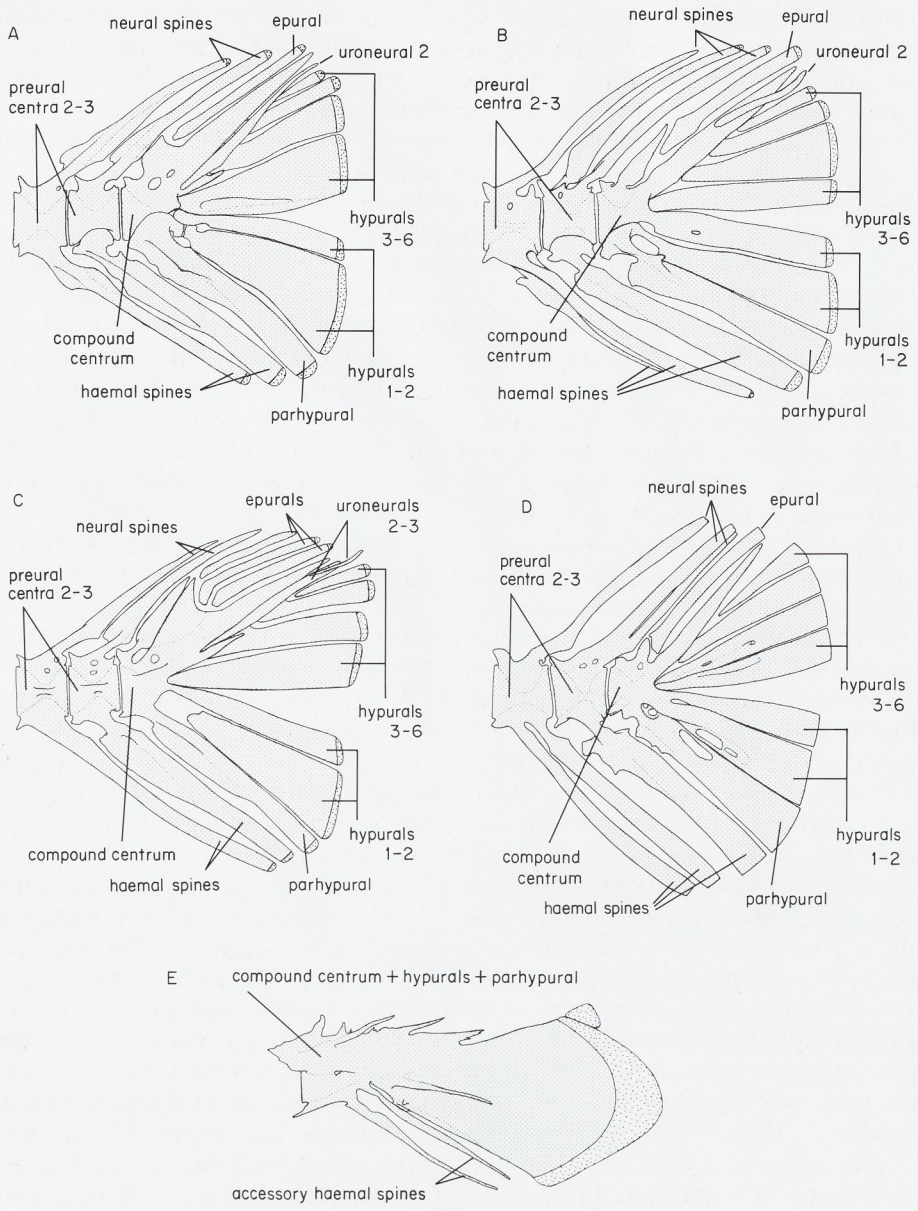

Figure 23. Caudal skeleton, left lateral view. A, *Chanos,* USNM 199831. B, *Opsariichthys,* MCZ 32375. C, *Prochilodus,* MCZ 20169. D, *Diplomystes,* cartilage absent, MCZ 8290. E, *Sternarchorhamphus,* MCZ 50983.

preural centrum (PU2) are fused to the centra from a young juvenile stage (e.g., specimens of *Notemigonus* 14.4 mm S.L., MCZ 53751, and *Catostomus* 17.5 mm S.L. MCZ 56537) (Fig. 23A-D). In the primitive members of most other primitive teleostean lineages, including *Scleropages, Elops, Esox,* and *Diplophos,* four or more haemal spines are autogenous in much larger juveniles (*c.* 60–80 mm S.L.). An adult *Esox* specimen has five autogenous haemal spines, and an adult *Salmo* two (dry skeletal material).

Clupeomorphs have all haemal spines fused to the centra, suggesting relationship between the Clupeomorpha and the Ostariophysi. However, clupeomorphs lack the adipose fin and breeding tubercles which link ostariophysans with other members of the Euteleostei (Patterson & Rosen, 1977).

(112) In characiphysans, the haemal spine of PU1, the parhypural, and hypural 1 are fused to the compound centrum at some stage in development. In siluroids, these elements are clearly present and fused to the centra (Fig. 23D). In gymnotoids, the parhypural and hypural 1 are not distinguishable, but all haemal spines and all hypural elements present are fused to the centra (Fig. 23E). Fusion of hypural 1 to the compound centrum is present in young characiforms examined (*Poecilocharax* sp., USNM 222028, 16.4 mm S.L.; *Brycon* sp., MCZ 49964, 12.8, 13.4 mm S.L.). In a young *Distichodus* (MCZ 48110, 16.7 mm S.L.), a small hiatus is present between the proximal part of hypural 1, which extends as a process from the compound centrum, and the main body of hypural 1 (fused in distichodontids to hypural 2); hypural 2 is fused to the compound centrum although it is separated by a hiatus in adult *Distichodus*. For adult characiform condition, see character 113.

(113) In adult characiforms, hypural 1 is separated from the compound centrum by a hiatus (Fig. 23C). Such a hiatus is not present in most other primitive teleosts.

A hiatus appears to have been independently acquired in some gonorynchiforms (Rosen & Greenwood, 1970) and in clupeoids.

(114) In otophysans hypural 2 is fused to the compound centrum (Fig. 23B-D). Although hypural 2 is not distinguishable in gymnotoids, all hypural elements present are fused to the compound centrum (Fig. 23E). In primitive members of the Osteoglossomorpha, Elopomorpha, Clupeomorpha (*Denticeps*), Ostariophysi (*Chanos,* the Eocene gonorynchid *Notogoneus, Kneria*), and Protacanthopterygii, hypural 2 is a separate element.

Separation of hypural 2 from the compound centrum, presumably secondary, is present in a few groups of characiforms; in all of these but one species (*Hepsetus odoe*), the hypural is separated from the centrum by a space like that separating hypural 1 from the centrum in characiforms (character 113).

(115) Gonorynchiforms, cypriniforms, and siluriforms have two or fewer epurals (Fig. 23A, B, D, E). Primitive characiforms and many other primitive teleosts have three epurals, the primitive number for Recent teleosts.

Two well developed epurals are present in the fossil chanid *Tharrhias* (Patterson, 1975b: fig. 7), in *Parakneria* (Rosen & Greenwood, 1970), and in our example of *Kneria wittei*. One is present in other gonorynchiforms, cypriniforms, and siluroids. Gymnotoids have none. Many characiforms also have a reduced epural number. It is possible that the characiforms with three epurals are atavistic in this respect, but multiple loss of features is such a well documented feature of teleostean history that we see no reason to prefer a hypothesis of atavism in some characiforms over one of repeated independent reduction of epural number.

Fin spines

(116) Siluroids have dorsal and pectoral fin spines which consist of very robust, serrated fin-rays in which both the ray segments and ray halves are fused together. These spines can be locked into an erect position due to modifications

in some supraneurals and dorsal fin pterygiophores and modifications in the pectoral girdle (Alexander, 1966a). This series of modifications is present in no other ostariophysans.

Some cypriniforms also have dorsal fin spines with serrae, although in all specimens examined for this study the segments do not fuse completely and the fin-ray halves do not fuse. Since dorsal spines appear to be restricted to one or more subgroups of cypriniforms, such spines lend no support to a hypothesis of relationship between cypriniforms and siluroids.

In some catfishes the dorsal fin spine is absent (e.g. some silurids and schilbeids) and in a few both the dorsal fin and pectoral fin spines are absent (most trichomycterids). Such absence of spines appears to be secondary.

Miscellaneous

(117) Ostariophysans have a unique alarm substance present in the epidermis which when released into the water by damage to the skin will cause a stereotyped fright reaction in other ostariophysans. Although the reaction is strongest in conspecifics, it is not restricted to conspecifics. Some ostariophysans have apparently lost the fright reaction, and a few have also lost the fright substance. Gymnotoids lack both the reaction and the substance (summary and references in Pfeiffer, 1977).

(118) Ostariophysans have nuptial tubercles with a well developed keratinous cap (Wiley & Collette, 1970). Although other euteleosts have nuptial tubercles, the keratinous layer is restricted to a thin cuticle (Wiley & Collette, 1970).

In ostariophysans tubercles are known in some gonorynchiforms, many cypriniforms, and a few characiforms. Keratinous tubercles are known in some siluroids also, but do not appear to be associated with breeding behaviour (Wiley & Collette, 1970). Gymnotoids have no tubercles.

(119) Siluriforms are electroreceptive. The literature on electroreception in gymnotoids is extensive (e.g. Bennett, 1970, 1971a, b). Szabo (1974) summarized the research on siluroid electroreception, listing species in 11 genera and seven families in which electroreceptors have been found. Most teleosts lack electroreceptive capabilities, but they are present, independently evolved, in mormyrids (Osteoglossomorpha).

(120) In siluriforms, the anterior lateral line nerve has a recurrent branch which innervates the electroreceptors of the trunk; a posterior lateral line nerve innervates the trunk neuromasts (Szabo, 1974: fig. 23). In cypriniforms and other primitive teleosts, the body trunk is innervated by only the posterior lateral line nerve. This character was suggested to us by G. Northcutt. Pending his examination of characiforms, we consider this to be a siluriform character, a hypothesis based in part on the presence of electroreceptors in siluriforms.

(121) Gymnotoids are electrogenic. Most other ostariophysans and most other teleosts are not electrogenic. Electrogenesis has been acquired independently in the siluroid *Malapterurus* and, among primitive teleosts, in mormyrids (Osteoglossomorpha). For a review of electrogenesis, see Bennett (1970, 1971a, b).

(122) In gymnotoids, the anus is located well anterior on the body, ventral or anterior to the pectoral-fin origin. In most other primitive teleosts, the anus is located posterior to the midlength of the body, between the pelvic and anal fins.

In some specialized siluroids, the anus is anterior to the midlength of the body, but still lies posterior to the pectoral-fin origin.

(123) In most otophysans (cypriniforms, siluroids, some characiforms including citharinids and distichodontids), the olfactory tracts are elongate and the olfactory lobes are located near the nasal rosette. In most primitive teleosts, the olfactory tracts are short and the olfactory lobes are adjacent to the telencephalon (Bardach & Villars, 1974; Vari, 1979).

In most characiforms and in gymnotoids, the olfactory tracts are short and the lobes are adjacent to the telencephalon. This appears to be a secondary condition.

(124) In siluroids scales are absent except for bony tubes of the lateral line. Almost all other primitive teleosts have scales.

The dermal bony plates present in doradids, loricariids, and callichthyids do not resemble true scales and appear to be a derived rather than primitive feature among siluroids.

(125) In gonorynchiforms, cypriniforms, and gymnotoids, there is no adipose fin. An adipose fin is present in most primitive euteleosteans, including most characiforms and siluroids, and has been considered a feature defining that group (Rosen, 1973). It is hypothesized here that loss of an adipose fin has occurred independently in each of the three lineages. Gymnotoids have lost the pelvic fins and rayed dorsal fin also (and in some species, the caudal fin). Some characiforms have also lost the adipose fin (e.g., erythrinids; some *Nannostomus* species, variably absent in *N. trifasciatus* and *N. eques* [Weitzman & Cobb, 1975]; *Grundulus*; and *Nematobrycon*).

(126) In otophysans, there is a posteromedial extension of the perilymph system of the ear, termed the sinus impar, which communicates to the ear vibrations transmitted from the gasbladder by the modified skeletal structures of the anterior vertebrae. The cavum sinus impar is a single opening ventral to the foramen magnum; the sinus impar is separated from the spinal cord by a shelf of bone formed by the exoccipitals (see Fig. 14). In other primitive teleosts which have an otophysic connection, e.g. clupeomorphs, some osteoglossomorphs, and some elopomorphs (Greenwood, 1970, 1973), the connection is paired and lateral to the region of the anterior vertebrae and foramen magnum, and is clearly not homologous with that of otophysans.

(127) In ostariophysans the *adductor mandibulae* muscle has a superficial ventral division, termed A_1 by most authors (Takahasi, 1925; Howes, 1976; Vari, 1979; Winterbottom, 1974), but not homologous with the A_1 of higher euteleosts (Lauder, in prep.). In most lower teleosts, including osteoglossomorphs, primitive elopomorphs, clupeomorphs, and protacanthopterygians, the *adductor mandibulae* muscle is undivided.

Notacanthids also have a superficial ventral division (Greenwood, 1977); we hypothesize this feature to have evolved independently in notacanthids and ostariophysans.

In primitive ostariophysans, the ventral division attaches directly to the maxilla (gonorynchiforms, cypriniforms, and primitive characiforms including most distichodontids) or to the ligamentum primordium (some characiforms). In gymnotoids the ventral division attaches only to the lower jaw and in siluroids it is absent. The conditions in some characiforms and in siluriforms are hypothesized to be secondary reductions from a primitive attachment to the maxilla.

DISCUSSION

Our finding that cypriniforms are the sister-group of characiforms, siluroids and gymnotoids is contrary to widely held opinion. Yet an examination of the basis for the traditional hypothesis, i.e., that characiforms are the primitive otophysans and that cypriniforms are the close relatives of the characiforms plus gymnotoids, shows that it was never supported by critically examined characters but rather was a matter of consensus. For example, the widely cited notion that characiforms are the most generalized of ostariophysans and thus the "basal" group appeared early in the literature but has received little analysis (e.g., Boulenger, 1910:574; Regan, 1911a:14; Weitzman, 1962:4; Roberts, 1973:389). Although Regan (1911a) did not discuss the interrelationships of cypriniforms, characiforms, and gymnotoids, he placed them together in his "Suborder Cyprinoidea". As noted by Roberts (1973), the characters Regan used to establish that inclusive taxon are characters found in many primitive teleosts and are therefore plesiomorphous. Greenwood *et al.* (1966) added to Regan's (1911a) list of characters, but those added are either found in gonorynchiforms and/or other primitive teleosts or are restricted to one of the included ostariophysan subgroups. Thus, there have been no characters shown to be exclusive to cypriniforms, characiforms and gymnotoids. Roberts (1973) was unable to find convincing evidence to establish whether cypriniforms are more closely related to characiforms or siluroids and thus was the first author in this century to challenge the traditional concepts.

The presumed relationship of gymnotoids and characiforms has never been supported by any presentation of characters. Reinhardt (1852, 1854) was apparently the first author to note that gymnotoids were more similar to characiforms in the shape of the gasbladder than to other "Physostomi" (the comparison was with the "Apodes"). This was expanded by Boulenger (1910), citing Reinhardt, to "[Gymnotoids] are strongly modified, degraded characinids. . .". Regan (1911a) made no statements about gymnotoid-characiform relationships, but did note that they "closely resemble" each other in cranial and vertebral morphology. Later, Regan (1922) stated that gymnotoids were related to characiforms but were "very aberrant." Weitzman (1962) stated that the gymnotoids were almost certainly derived from characiforms but offered no evidence. Greenwood *et al.* (1966) repeated the hypothesis that gymnotoids were derived from characiform ancestors. Rosen & Greenwood (1970) placed the gymnotoids and characiforms as sister-groups, stating in a footnote (p. 23) that ". . . it is generally accepted that the characoids and gymnotoids had a common ancestry. . .". Roberts (1973) noted that the "restricted geographical distribution" of gymnotoids suggests an origin later than that of other ostariophysans but added that their presumed relationship to characiforms was an untested assumption. In short, the grouping of gymnotoids and characiforms has never been supported by data but has passed from one generation of ichthyologists to another as a tradition.

It should be clear that the traditional ostariophysan classification was based on a pre-Hennigian notion of character usage which did not discriminate between the usefulness of primitive similarities and special features for delineating shared common ancestry. Thus characiforms, cypriniforms and gymnotoids were placed together on the basis of such features as the presence of scales and conservative Weberian apparatus morphology relative to catfishes. In addition, undue

emphasis on so-called "morphological gaps" caused many to confound morphological distinctiveness with phylogenetic remoteness. Catfishes were placed apart from the other lineages for this reason. The apparent inconsistency in the placement of the distinctive gymnotoids close to characiforms probably resulted from a consideration of geographic factors.

Another factor hindering analysis of relationships has been the search for "linking taxa." This search has often become a search for ancestors, a preoccupation which Patterson (1977) has shown to have had a significant dampening effect on paleontological research. An example of this is Roberts's (1973) contention that no "characoids exhibit structures suggesting an origin of the protractile jaws and pharyngeal structures of cyprinoids." Roberts is not alone in this consideration of ancestry and it is present, sometimes explicitly, usually implicitly, in much of the literature bearing on ostariophysan relationships. Those who seek "ancestral" types or "linking" taxa in considerations of phylogeny apparently forget that during the course of evolution, members of lineages often gain specializations (such as the protrusible mouth of cypriniforms) while retaining attributes of other members of the group (much of the Weberian apparatus of cypriniforms). This pattern is well known in many groups of organisms as mosaic evolution. What is important to remember is that the specializations obtained never rule out sister-group relationships, although they do indeed rule out ancestor-descendent relationships. The mouth characters mentioned by Roberts are unique to cypriniforms; similarly the "complex vertebra" of catfishes and anal-fin/pterygiophore morphology of gymnotoids are unique to those taxa. These attributes must have appeared at or after the origins of these lineages and, as unique specializations, they are simply uninformative about the interrelationships of the groups.

In spite of the congruence of the clear majority of the characters, as shown in Fig. 1, there are eight features that apparently are in conflict with our hypothesis of relationships. Of these eight, seven are reductive or loss characters, including lack of jaw teeth (character 42), lack of teeth on the second and third pharyngobranchials and the basihyal (character 47), lack of the two posterior pharyngobranchial toothplates (character 48), lack of a toothplate associated with basibranchials 1–3 (character 50), a single or no postcleithrum (character 96), 2 or fewer epurals (character 115), and lack of an adipose fin (character 125). Four of these losses (42, 47, 48, 50) are apparently associated with specialized feeding modes. The other three are present in many teleost groups. We interpret all of these features to be specializations which have evolved independently in the various lineages as indicated in Fig. 1.

The presence of barbels in many cypriniforms and in siluroids (character 40) is the only incongruent character which involves the evolution of a new morphological structure. The maxillary barbel in siluroids and the posterior maxillary barbel in cypriniforms are the only barbels at issue here since they are the only barbels common to primitive members of both groups. All the other barbels (submental, narial, anterior maxillary, etc.), found in various combinations in advanced siluroids and cypriniforms, have presumably been independently derived within the two major lineages, and perhaps several times in some cases. For example, Howes (1980) found that in the "bariliine" cypriniforms some species have anterior and posterior maxillary barbels, some have only posterior maxillary barbels, and some have no barbels. Other cypriniforms show

similar barbel distributions, and intraspecific variability is not uncommon. Thus evolution of barbels within the Cypriniformes has probably been a frequent occurrence. In addition, as we have noted in the Characters section, there are differences in the structure of the cypriniform and siluroid barbels, particularly in the relation of the barbel to the maxilla and the skin covering the cheeks. In siluroids, including *Diplomystes,* the maxillary barbel extends from the distal tip of the maxilla and is separated from the skin of the cheek by a deep cleft which extends well proximal to the distal end of the maxilla. In cypriniforms examined, the barbel is located at the rictus and may not be closely associated with the distal tip of the maxilla.

The apparent evolutionary lability of barbels in cypriniforms, combined with the overwhelming number of characters that mitigate against a hypothesis of relationship between cypriniforms and siluriforms, added to the fact that barbels are lacking in characiforms and gymnotoids, force us to conclude that barbels have been independently evolved in cypriniforms and siluroids.

There are several characters which, as interpreted by other authors, apparently conflict with our hypothesis of relationships. These include fin spines in siluroids and some cypriniforms (discussed by Roberts, 1973), mobile palatine in cypriniforms and siluroids (Roberts, 1973) and also in characiforms (Gosline, 1971), and fused vertebral centra (Roberts, 1973). These characters have been shown to be either non-homologous, appropriate as indicators of relationship within the major lineages, or inaccurate observations. For more detailed discussion, see the presentation of characters, above.

Ostariophysan biogeography

The past history of ostariophysan distributions has been the subject of lively discussion for many years, primarily because these fishes are nearly restricted to fresh water. Thus, their history is supposed to be closely linked to patterns of earth history. As early as 1909, Eigenmann discussed the possible past connection of Africa and South America based on the presence of characiforms on both those continents. The most recent summaries of ostariophysan biogeography are those of Gosline (1975a, b), Patterson (1975b), Novacek & Marshall (1976) and Briggs (1979); combined these authors provide fairly complete coverage of the various hypotheses proposed in the past to account for ostariophysan distributions. A brief summary of the most commonly presented hypotheses is worth repetition here since our new phylogeny may stimulate competing hypotheses. Eigenmann's (1909) early attempt to reconcile characin distributions with von Ihering's Archiplata/Archhelenis landbridge theories was followed by Regan's (1922) strikingly modern analysis of otophysan distributions with a continental drift model. These theories were followed by more dispersalist-oriented theories, summarized in great detail for otophysans by Darlington (1957). That author envisioned an origin of characiforms in tropical Asia, followed by active dispersal to Africa on the one hand, and South America via the Bering landbridge and North America on the other. In Asia, characiforms were supposed to have given rise successively to siluroids and cypriniforms, which then followed the characiform dispersal routes; cypriniforms were seen to have replaced characiforms in Asia through competition. This view has recently been reiterated, in essence, by Briggs (1979).

With acceptance of plate tectonic theory there have been attempts to relate continental movements with the origins and distribution of ostariophysan groups (summarized by Novacek & Marshall, 1976). In these constructions, otophysans are seen to originate in the southern continents (either Gondwanaland, Africa, or South America) from a "proto-characoid" or characiform ancestor, with dispersal of siluroids and cypriniforms into the northern continents via Africa.

We think it unnecessary to discuss these previous hypotheses in detail, since all were based on phylogenetic hypotheses which we reject. All authors accepted the traditional concept of relationships, and all assumed that characiforms, of whatever rank proposed, were paraphyletic. All but Patterson (1975b) neglected the Pangean occurrence of gonorynchiforms. The plate tectonic models virtually ignored the existence of the northern continents and the history of the groups after the fragmentation of Gondwanaland. With our new phylogeny, adherents of dispersalist models are faced with choosing between two of their most basic assumptions: (1) that the phylogenetically primitive members of a group are displaced from the centre of origin by more "dominant" forms, and (2) that the tropical Orient has been the dominant evolutionary center for many organisms, with dispersal from that area to other parts of the globe. If phylogenetically primitive taxa are displaced to peripheral regions, then the presence of cypriniforms in Asia would suggest an ostariophysan "center of origin" in South America. If, on the other hand, one wishes to regard Asia as the center of origin, the corollary of "primitive taxa to the periphery" must be invalid.

The primary implication of our own phylogenetic hypothesis is that the biogeographic history of the group has been long and complex. All sister taxa among the major ostariophysan lineages are broadly sympatric, and the siluroids are sympatric with each of the other four lineages. Regardless of one's preferred theoretical model, substantial dispersal, over a substantial period of time, is required to explain such extensive sympatry. The nearly universal continental distribution of ostariophysans, coupled with data from the fossil record (Patterson, 1975b), also suggest that the group is very old. Fitch's (1975) report of upper Cretaceous ariid siluroid otoliths supports this inference since, based on our phylogeny, siluroids cannot be as old as characiforms or cypriniforms. It may very well be that the details of the earliest distributions have been obscured by the long history of subsequent distribution/geological events. Current geological hypotheses on the breakup of Gondwanaland and the formation of the present-day continents suggest that the process was much more complex than previously supposed (Tarling, 1980). It is now becoming evident that the tropics, rather than being the great stable areas they were once thought to be, have been affected by both geological and climatic factors we are only beginning to understand. The work on Pleistocene refugia in South America (see Simpson & Haffer, 1978) is one view to account for some aspects of tropical diversity, but older phenomena are required to explain diversity at most clade levels. It remains to be seen whether phylogenetic groupings within the five major ostariophysan lineages can be correlated with geological events in such a way as to sort out vicariant patterns and dispersal events in ostariophysan history.

Our phylogeny of relationships within the characiforms does have implications regarding their evolution before the Gondwanaland fracture. While the hypothesis that the African Citharinidae plus Distichodontidae is the sister-group of all other characiforms seems to suggest a drift-induced vicariance event, our

suggestions that the African *Hepsetus* is in the lineage including the South American *Ctenolucius* and *Hoplias* and that the phylogenetically rather advanced African "characids" may be the sister group of some subset of the South American "characids" implies that a good bit of characiform evolution took place before the Gondwana separation. Indeed, if some of our hypotheses are correct, most of the major characiform lineages had originated before the Africa-South America split. Our evidence on this latter point will be presented elsewhere.

We predict that the most fruitful avenue of ostariophysan research will be comparison of the phylogenetic histories of the subgroups of cypriniforms and siluroids in Asia, subgroups of characiforms in South America and subgroups of all three taxa in Africa. We stand at the beginning of such studies since there are extremely few sound phylogenetic analyses of the ostariophysan subgroups (e.g. Vari, 1979). Such work could be of great significance in unraveling the complex history of much of the surface of the earth.

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APPENDIX

Material examined

Material examined is listed below. Number of specimens signifies number examined, not number in lot. Species listed alphabetically within each higher taxon. BMNH: British Museum (Natural History), London, England; CAS: California Academy of Sciences, San Francisco, California; CAS (SU): Stanford University collection, now at CAS; CAS(IUM): Indiana University Museum, now at CAS; MCZ: Museum of Comparative Zoology, Cambridge, Massachusetts; UMMP: University of Michigan Museum of Paleontology, Ann Arbor, Michigan; USNM: National Museum of Natural History, Washington, D.C. Unless otherwise noted, the specimens are undissected, in alcohol. Abbreviation for cleared and stained material is cl & st.

Brachiopterygii			
Polypterus senegalus Cuvier	MCZ 48572	1 ex.	cl & st
Halecomorphi			
Amia calva Linnaeus	MCZ 8970	1 ex.	cl & st
Teleostei			
Osteoglossomorpha			
Hiodon alosoides (Rafinesque)	MCZ 54926	1 ex.	cl & st
Osteoglossum bicirrhosum Vandelli	MCZ 54927	1 ex.	cl & st
Scleropages formosus (Müller & Schlegel)	MCZ 54924	1 ex.	cl & st
Elopomorpha			
Albula sp.	MCZ uncat.	1 ex.	skeletal
Elops saurus Linnaeus	USNM 128290	2 ex.	cl & st
Megalops atlantica Valenciennes	USNM 199836	1 ex.	cl & st
Megalops cyprinoides (Broussonet)	USNM 199836	2 ex.	cl & st
Megalops sp.	MCZ uncat.	1 ex.	skeletal
Clupeomorpha			
Alosa pseudoharengus (Wilson)	MCZ 52771	1 ex.	cl & st
Anchoa compressa (Girard)	CAS 19658	5 ex.	cl & st
Brevoortia tyrannus (Latrobe)	CAS(IUM) 4991	4 ex.	cl & st
Brevoortia tyrannus	MCZ 52351	1 ex.	dissected
Denticeps clupeoides Clausen	USNM 195992	1 ex.	cl & st
Denticeps clupeoides	BMNH uncat.	1 ex.	cl & st
Etrumeus teres (DeKay)	USNM 188950	2 ex.	cl & st
Harengula pensacolae Goode & Bean	USNM 221203	5 ex.	cl & st
Euteleostei			
Ostariophysi			
Gonorynchiformes			
Chanos chanos (Forskal)	USNM 199830	2 ex.	cl & st
Chanos chanos	MCZ 56538	1 ex.	dissected
Chanos chanos	USNM 199831	3 ex.	cl & st
†*Charitosomus lineolatus* (Pictet & Humbert)	MCZ 8139	1 ex.	fossil
Gonorynchus greyi (Richardson)	MCZ 8441	2 ex.	
Grasseichthys gabonensis Géry	BMNH 1966.10. 20:1–10	1 ex.	cl & st
Kneria katangae Poll	BMNH 1976.10. 20:116–137	2 ex.	1 cl & st
Kneria wittei Poll	BMNH 1976.10. 20:142–160	2 ex.	1 cl & st
†*Notogoneus osculus* Cope	MCZ 5350	1 ex.	fossil

Cypriniformes			
Barbus barbus (Linnaeus)	MCZ 25519	2 ex.	
Barbus setivimensis Cuvier & Valenciennes	MCZ 32711	3 ex.	
Barbus versluysii Holly	MCZ 35476	1 ex.	
Carpiodes carpio (Rafinesque)	MCZ 49609	1 ex.	cl & st
Carpiodes sp.	MCZ uncat.	1 ex.	skeletal
Catostomus commersoni (Lacépède)	MCZ 52777	2 ex.	cl & st
Catostomus commersoni	MCZ 56537	3 ex.	cl & st
Catostomus commersoni	MCZ 56536	5 ex.	cl & st
Catostomus sp.	MCZ uncat.	3 ex.	skeletal
Cobitis aurata (Filippi)	MCZ 40968	2 ex.	cl & st
Cyprinus carpio Linnaeus	MCZ uncat.	2 ex.	cl & st
Erimyzon oblongus (Mitchill)	MCZ 52752	1 ex.	cl & st
Gastromyzon borneensis Günther	MCZ 34823	2 ex.	cl & st
Gyrinocheilus sp.	MCZ uncat.	3 ex.	cl & st
Homaloptera sp.	MCZ 47282	1 ex.	cl & st
Ictiobus niger (Rafinesque)	MCZ uncat.	2 ex.	skeletal
Myxocyprinus asiaticus (Bleeker)	MCZ 916	1 ex.	
Nemacheilus spilotus Fowler	MCZ 35552	1 ex.	cl & st
Notemigonus crysoleucas (Mitchill)	MCZ 52751	8 ex.	cl & st
Opsariichthys uncirostris (Temminck & Schlegel)	CAS(SU) 32568	2 ex.	cl & st
Opsariichthys uncirostris	MCZ 32375	2 ex.	cl & st
Zacco temminckii (Schlegel)	CAS(SU) 7349	1 ex.	cl & st
Characiformes			
Abramites sp.	MCZ 49957	2 ex.	cl & st
Alestes macrolepidotus (Cuvier & Valenciennes)	MCZ 48578	2 ex.	cl & st
Anodus melanopogon Cope	MCZ 49950	1 ex.	cl & st
Apareiodon sp.	MCZ 49949	4 ex.	cl & st
Astyanax mexicanus (Filippi)	MCZ 52104	1 ex.	cl & st
Brycon dentex Günther	MCZ 48668	2 ex.	cl & st
Brycon sp.	MCZ 49964	4 ex.	cl & st
Bryconamericus brevirostris (Günther)	MCZ 48665	2 ex.	cl & st
Chalceus macrolepidotus Cuvier	MCZ 21142	1 ex.	cl & st
Characidium sp.	MCZ 49961	4 ex.	cl & st
Chilodus punctatus Müller & Troschel	MCZ 46051	2 ex.	cl & st
Citharinus gibbosus Boulenger	MCZ 50443	3 ex.	1 cl & st
Creagrutus sp.	MCZ 49953	1 ex.	cl & st
Crenuchus spilurus Günther	USNM 225688	2 ex.	cl & st
Ctenolucius sp.	MCZ uncat.	1 ex.	cl & st
Curimata macrops Eigenmann & Eigenmann	MCZ 46801	3 ex.	cl & st
Distichodus notospilus Günther	MCZ 48110	1 ex.	cl & st
Distichodus sp.	MCZ 5820	1 ex.	skeletal
Grundulus bogotensis (Humboldt)	CAS(IUM) 12844	1 ex.	cl & st
Gymnocorymbus sp.	MCZ 49962	4 ex.	cl & st
Hemiodis quadrimaculatus Pellegrin	MCZ 29926	1 ex.	cl & st
Hemiodus semitaeniatus Kner	MCZ 49072	2 ex.	cl & st
Hemiodus sp.	MCZ 52668	1 ex.	dissected
Hepsetus odoe (Bloch)	MCZ 31285	1 ex.	dissected
Hepsetus odoe	MCZ 48104	1 ex.	cl & st
Hoplerythrinus unitaeniatus (Spix)	MCZ 46012	1 ex.	cl & st
Hoplias malabaricus (Bloch)	MCZ 51522	1 ex.	cl & st
Lebiasina bimaculata Valenciennes	MCZ 49951	3 ex.	cl & st
Leporinus despaxi Puyo	MCZ 56552	1 ex.	cl & st
Mesoborus sp.	MCZ 50961	1 ex.	skeletal
Paradistichodus dimidiatus Pellegrin	MCZ 48583	2 ex.	cl & st
Paradon caliensis Boulenger	MCZ 47682	1 ex.	cl & st
Phagoborus ornatus (Boulenger)	MCZ 48290	1 ex.	cl & st
Phenacogrammus altus (Boulenger)	MCZ 48239	3 ex.	cl & st
Poecilocharax sp.	USNM 222028	7 ex.	cl & st
Prochilodus vimboides Kner	MCZ 20169	2 ex.	cl & st
Rhoadsia altipinna Fowler	MCZ 49955	3 ex.	cl & st
Saccodon wagneri Kner & Steindachner	MCZ 48745	3 ex.	dissected
Saccodon wagneri	MCZ 48745A	1 ex.	dissected
Saccodon wagneri	MCZ 49956	3 ex.	cl & st
Schizodon fasciatus Agassiz	MCZ 46796	1 ex.	cl & st
Xenocharax spilurus Günther	MCZ 48020	4 ex.	2 cl & st

Siluriformes			
Siluroidei			
Astroblepus sp.	MCZ 31512	2 ex.	cl & st
Astroblepus sp.	MCZ 48755	2 ex.	cl & st
Atopochilus guentheri Schilthuis	MCZ 50538	1 ex.	cl & st
Auchenoglanis ballayi (Sauvage)	MCZ 50746	2 ex.	cl & st
Bunocephalus sp.	MCZ 46133	1 ex.	cl & st
Chiloglanis carnosus Roberts & Stewart	MCZ 50541	3 ex.	cl & st
Clarias sp.	MCZ uncat.	1 ex.	skeletal
Diplomystes chilensis (Gmelin)	MCZ 54388	1 ex.	
Diplomystes papillosus (Valenciennes)	MCZ 36195	1 ex.	
Diplomystes papillosus	MCZ 8290	3 ex.	cl & st
		1 ex.	dissected
†*Hypsidoris farsonensis* Lundberg & Case	UMMP V 57142	1 ex.	fossil
Ictalurus nebulosus (Le Sueur)	MCZ 54248	2 ex.	dissected
Ictalurus sp.	MCZ 54389	3 ex.	cl & st
Ictalurus sp.	MCZ uncat.	1 ex.	cl & st
Parauchenoglanis guttatus (Lönnberg)	MCZ 50747	1 ex.	cl & st
Vandellia sp.	MCZ uncat.	3 ex.	cl & st
Gymnotoidei			
Adontosternarchus sp.	MCZ 46877	1 ex.	dissected
Apteronotus albifrons (Linnaeus)	MCZ 45204	1 ex.	dissected
Apteronotus albifrons	MCZ 52013	1 ex.	cl & st
Eigenmannia sp.	MCZ 52611	1 ex.	dissected
Eigenmannia sp.	MCZ uncat.	1 ex.	cl & st
Gymnotus carapo Linnaeus	MCZ 45189	2 ex.	dissected
		1 ex.	cl & st
Rhabdolichops troscheli (Kaup)	MCZ 54336	1 ex.	cl & st
Sternarchorhamphus macrostomus (Günther)	MCZ 50983	1 ex.	cl & st
Sternarchorhamphus mulleri (Steindachner)	MCZ 9400	1 ex.	cl & st
Sternopygus macrurus (Bloch & Schneider)	CAS(IUM) 12591	2 ex.	cl & st
Sternopygus macrurus	MCZ 45193	1 ex.	dissected
		1 ex.	cl & st
Sternopygus sp.	USNM 218830	1 ex.	dissected & cl & st
Protacanthopterygii			
Brachymystax lenok (Pallas)	USNM 105110	1 ex.	cl & st
Coregonus sp.	MCZ uncat.	1 ex.	skeletal
Dallia pectoralis Bean	USNM 111643	1 ex.	cl & st
Esox niger Le Sueur	MCZ 54929	1 ex.	cl & st
Esox sp.	MCZ uncat.	1 ex.	skeletal
Galaxias delfini Filippi	MCZ 46279	16 ex.	cl & st
Salmo gairdneri Richardson	CAS(SU) 49265	3 ex.	cl & st
Salmo sp.	MCZ uncat.	1 ex.	skeletal
Umbra limi (Kirtland)	MCZ 54024	2 ex.	cl & st
Neoteleostei			
Stomiatiformes			
Diplophos taenia Günther	MCZ 52535	1 ex.	cl & st

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Do assemblages of *Coregonus* (Teleostei: Salmoniformes) in the Central Alpine region of Europe represent species flocks?

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Abstract

To examine models of evolution for *Coregonus* from the Central Alpine region of Europe, 20 populations from nine lakes were assessed for variation at six microsatellite DNA loci. Patterns of variation were tested against three evolutionary models: phenotypic plasticity, multiple invasions of lakes by divergent forms, and within-lake radiation of species flocks. All sympatric and all but one allopatric pairs of populations were significantly divergent in allele frequencies. Pairwise *F*-statistics indicated reduced gene flow among phenotypically divergent sympatric populations. These results reject the hypothesis that within-lake morphological and ecological diversity reflects phenotypic plasticity within a single gene pool. Genetic similarity was higher among forms within lakes than between populations of the same form in different lakes. Among-lake divergence was primarily a product of allele size differences. Mantel tests contrasting patterns of genetic divergence against patterns predicted from the multiple invasions and species flocks models indicated that the latter is the best explanation of the observed genetic variation. Thus, reproductively isolated species diverged within lakes, with similar patterns repeatedly emerging among lakes. While this study argues for a particular mode of evolution in Central Alpine *Coregonus*, the taxonomy of these forms remains unresolved.

Keywords: Central Alps, *Coregonus*, Mantel test, microsatellite DNA, population genetics, species flocks

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Introduction

Diversity is a fundamental aspect of biology (Wilson 1988), yet its quantification depends upon a firm taxonomic basis (May 1990). A common method for accomplishing this is enumeration of clades with independent evolutionary histories (Mayden & Wood 1995). However, the shallow evolutionary histories of recently evolved groups are often difficult to resolve because of methodological limitations.

Freshwater fishes of the northern hemisphere provide examples of recently evolved clades. They often display a number of divergent forms with uncertain taxonomic status that coexist in sympatry (Smith & Skúlason 1996). Many fulfil criteria for recognition as biological species (Mayr 1963). This tendency towards extensive, taxonomically unrecognized diversity is perhaps greatest in salmoniforms (Behnke 1972). Virtually every family (as defined by Sanford 1990) has evolved 'sibling taxa': Salmonidae (Sandlund *et al*. 1992; Hindar & Jonsson 1993; Taylor *et al*. 1997), Osmeridae (Taylor & Bentzen 1993a; Bernatchez 1997) and Coregonidae (Bernatchez & Dodson 1990; Pigeon *et al*. 1997). Sympatric forms within lakes are often referred to as 'ecotypes' or 'morphs', in spite of reproductive isolation. The occurrence of morphologically different forms within lakes has been replicated among lakes, particularly within the Coregonidae, where the existence of multiple forms within and among lakes is especially common. Thus, the questions become not only 'Have these forms arisen in sympatry?' but also, 'How did they arise multiple times?' Local assemblages of coregonids have been referred to as single, but plastic species (Steinmann 1951), as products of multiple invasions by

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divergent forms (Bernatchez & Dodson 1990; Bernatchez *et al*. 1996), and as 'species flocks' (Smith & Todd 1984). Here, the term 'species flock' is used to accommodate the rapid evolution of Central Alpine *Coregonus*, and to define an aggregate in a single lake where forms are more closely related to one another than to phenotypically similar forms in other lakes. The latter would hence represent parallel (but separate) divergence.

In this study, coregonids in Central Alpine lakes of Europe are used in an assessment of the various models of evolution in this group. Most lakes in this relatively small region contain at least two coregonid forms, whereas several contain three or more (Steinmann 1950a; Kirchhofer 1996; Kottelat 1997), and one may have up to six coregonid forms (M. R. Douglas, unpublished). Sympatric forms differ in a variety of life-history and ecological traits (Steinmann 1950a; Kottelat 1997), which are often correlated with striking size differences (Douglas 1998). During the year, populations may intermix within the water column, but they segregate spatially and/or temporally at spawning time (Steinmann 1950a,b; Kirchhofer & Tschumi 1986). This indicates an affinity by individuals to a specific, reproductively isolated group.

Fish communities within Central Alpine lakes have been studied extensively from an ecological and fisheries perspective, but rarely from a systematic or evolutionary stance (Kottelat 1997). Understanding the evolutionary history of resident *Coregonus* forms would provide insights into mechanisms and processes responsible for their variability. Namely, it is crucial to determine whether similarity among forms represents plasticity, homology or homoplasy. Conservation and management of diversity within *Coregonus* hinges upon understanding the evolutionary history of individual populations.

Microsatellite DNA loci were used to determine relatedness and test hypotheses of origin for 20 *Coregonus* populations distributed within and among nine lakes in the Central Alpine region of Europe. Microsatellite loci offer several advantages over other types of molecular markers in that they are abundant, highly variable and can be assayed from minute quantities of DNA (Ashley & Dow 1994). In salmonids, microsatellite loci are particularly appropriate for studying divergence over a microgeographical scale (Angers & Bernatchez 1998) and for detecting levels of genetic differentiation when other markers fail to do so (Brunner *et al*. 1998).

Patterns of genetic divergence were tested against three alternative evolutionary scenarios (Fig. 1): phenotypic plasticity in a single species (model I), multiple invasion of lakes by divergent species (model II) and occurrence of species flocks (model III). Model I predicts that morphologically or ecologically divergent forms of *Coregonus* reflect plasticity within a single gene pool (i.e. ecophenotypes). Phenotypic plasticity has been the favoured hypothesis to explain diversity among *Coregonus* forms from the Central Alpine region (Steinmann 1950a,b; 1951).

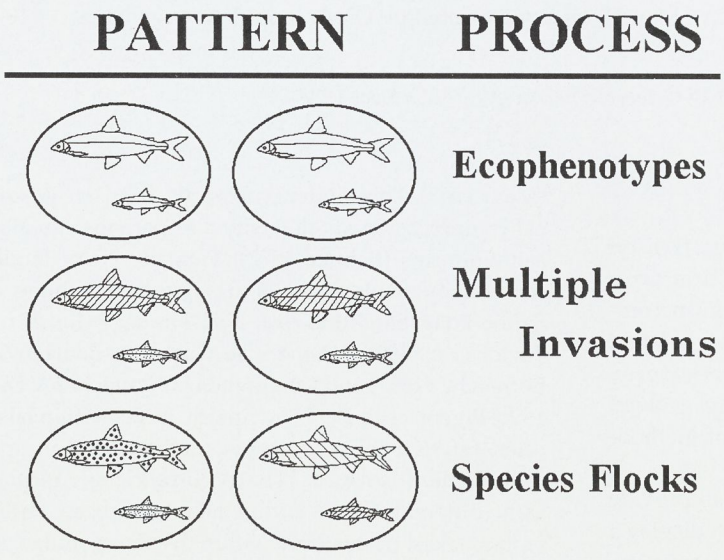

Fig. 1 Schematic depiction of three alternative evolutionary scenarios to explain diversity in Central Alpine *Coregonus* populations. 'Pattern' depicts the array of phenotypes found within lakes. 'Process' refers to the evolutionary mechanism that produced the pattern. Three hypotheses are listed beneath Pattern. 'Ecophenotypes' suggest forms are different with regard to morphology and ecology, but are genetically identical. They are the result of extrinsic factors acting upon a plastic phenotype. The 'multiple-invasion' hypothesis suggests that phenotypically equivalent forms are genetically most similar among lakes, while divergent forms are genetically most different. This pattern is produced by repeated invasions of lakes by lineages already differentiated. The 'species flock' hypothesis argues that forms within a lake are more closely related to one another genetically than are forms among lakes. Here, the pattern is produced by invasion of a lake by a single ancestral lineage that undergoes within-lake radiation.

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HYDRODYNAMICS OF PREY CAPTURE BY TELEOST FISHES

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SUMMARY

The dominant mode of prey capture in teleost fishes is inertial suction: rapid expansion of the mouth cavity creates a negative (suction) pressure relative to the surrounding water. This pressure differential results in a flow of water into the mouth cavity carrying in the prey. Previous models of the suction feeding process have predicted the pattern and magnitude of pressure change in the mouth cavity based on kinematic profiles of jaw bone movement and the application of the Bernoulli equation and the Hagen-Poiseuille relation. These models predict similar pressure magnitudes and waveforms in both the buccal and opercular cavities, and rely on the assumption of a unidirectional steady flow. In vivo simultaneous measurement of buccal and opercular cavity pressures during feeding in sunfishes shows that (1) opercular cavity pressures average one-fifth buccal pressures (which may reach -650 cm H_2O), (2) the opercular and buccal cavities are functionally separate with distinct pressure waveforms, (3) a flow reversal (opercular to buccal flow) probably occurs during mouth opening, and (4) the kinetic energy of the water and inertial effects must be considered in hydrodynamic models of suction feeding.

INTRODUCTION

Despite the dramatic advances in our understanding of the hydrodynamics of fish locomotion in the last decade (Lighthill, 1969; Webb, 1975; Weihs, 1972, 1973), very

little work has been done on the hydrodynamics of fish prey capture. This may in part be due to experimental difficulties involved in studying feeding behavior. Water-tunnel respirometers allow the study of locomotion under controlled circumstances in a fixed location. The process of locomotion is cyclical and allows repeated measurements over an experimental trial. Investigators of fish locomotion have also greatly benefited from the input of hydrodynamic engineers and theoretical physicists who have applied a large body of relevant experimental and theoretical work to problems of fish locomotion. In contrast, prey capture by teleost fishes occurs extremely rapidly (often within 50 ms), is not cyclical, and the fish cannot be excessively restrained or subjected to experimental trauma without eliminating the feeding response.

The difficulties of studying the hydrodynamics of feeding in fishes have been ably summarized by Holeton and Jones (1975: 547) (in the context of respiration). " The analysis of the breathing mechanics of fish is difficult because it involves the measurement of an unsteady flow of a dense fluid through a non-uniform system which is ill-defined. The compliance of the respiratory tract is variable, both spatially and temporally, and certain resistive elements (such as the gill filaments) are mobile, both actively and passively, throughout a breathing cycle." These difficulties are all compounded during feeding by the extremely short duration of the prey capture event.

In spite of these formidable problems, a number of investigators have modeled the process of prey capture using simple hydrodynamic equations and the kinematics of jaw bone movement to predict the pattern of pressure change in the mouth cavity. In this paper I will review these models and examine the few experimental studies with actual pressure measurements from the mouth cavity during feeding. I will then present new experimental data on the suction feeding mechanism in sunfishes and propose a new model of fluid flow and pressure change in the teleost mouth cavity.

II. ANATOMICAL BASIS OF THE SUCTION FEEDING MECHANISM

Prey capture in most teleost fishes occurs by inertial suction feeding. Mouth cavity volume is rapidly expanded by the contraction of certain jaw muscles (see Lauder and Liem,

1980; Liem, 1978), and this expansion results in the creation of a negative pressure (relative to the surrounding water) in the mouth cavity. This pressure differential creates a flow of water into the mouth from the region directly in front of the head and draws the prey in. The jaws are then closed trapping the prey in the mouth cavity while the water flows out over the gills.

The mouth cavity may be divided into an anterior buccal cavity and two posterolateral opercular cavities (Fig. 1B), separated from the buccal cavity by the gill curtain. The gills are supported on four gill arches and form a resistance to fluid flow within the mouth cavity. Changes in volume of the buccal and opercular cavities for the most part do not occur independently: anatomically they are coupled. Expansion of the buccal cavity may occur by elevation of the neurocranium, opening of the front jaws, depression of the hyoid apparatus, and lateral expansion of the suspensory apparatus (Fig. 1; also see Lauder and Liem, 1980; Liem, 1970, for a more detailed account of anatomical couplings). These movements may also effect opercular cavity expansion. However, some bone movements (such as opercular adduction) (Fig. 1) do predominantly affect only one cavity. In general, the dorsal, ventral, and lateral walls of the mouth cavity all rapidly expand to create a low pressure center during the attack at a prey item.

The role of the gills as a resistant element separating the buccal and opercular cavities was first recognized by Woskoboinikoff and Balabai(1937) and van Dam (1938), and the concept of gill resistance to water flow has received considerable attention in recent studies of fish respiration (Ballintijn, 1972; Hughes and Morgan, 1973; Hughes and Shelton, 1958; Jones and Schwarzfeld, 1974; Pasztor and Kleerekoper, 1962; Shelton, 1970). The resistance of the gills to flow is not equal in both directions: flow directed anteroposteriorly (i.e., from the buccal to opercular cavity) encounters less resistance than reverse flow from the opercular cavity into the buccal cavity due to the orientation of the gill filaments (Fig. 1). While several attempts have been made to measure gill resistance to anteroposterior flow (e.g., Brown and Muir, 1970; Davis and Randall, 1973; Hughes and Umezawa, 1968; Jones and Schwarzfeld, 1974), no data exist on the values of gill resistance to reverse flow. It is well established, however, that gill configuration (and thus resistance) may be actively modified by intrinsic gill

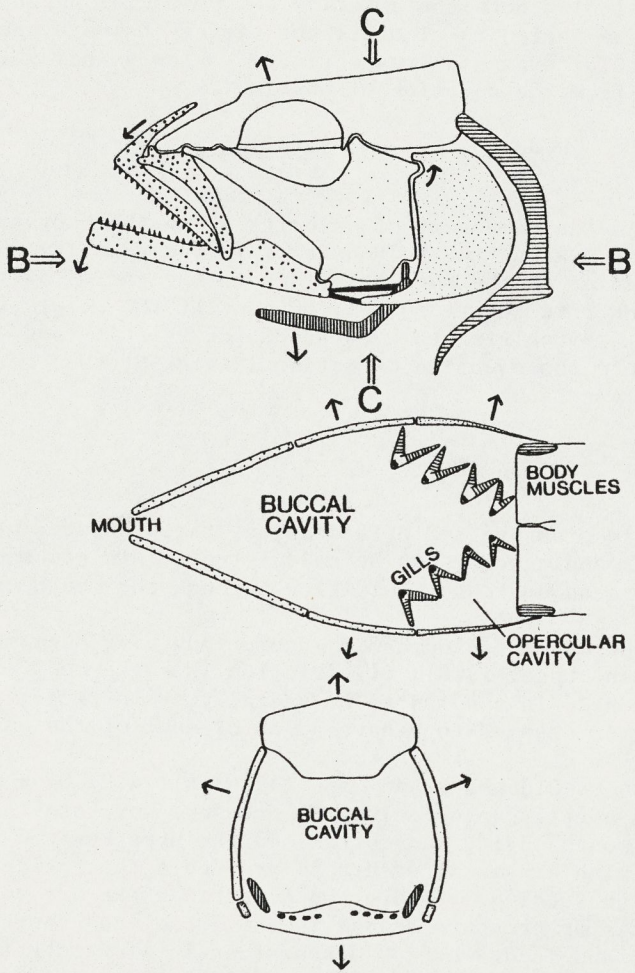


Fig. 1. Diagrammatic view of the head of an advanced teleost fish with protrusible jaws. B and C represent sections of the head at the level indicated in A. Arrows indicate major bony movements during prey capture. Key: white = neurocranium; vertical lines = hyoid apparatus; horizontal lines = pectoral girdle; dense stipple = opercular apparatus; fine stipple = suspensorium; large stipple = jaw apparatus.

arch musculature (Pasztor and Kleerekoper, 1962). Other resistance to flow occurs at the mouth opening and at the opercular and branchiostegal valves where water exits through a narrow slit of high resistance. Osse (1969: 371) and Alexander (1967) have suggested that gill resistance is very low during feeding.

III. RESPIRATORY HYDRODYNAMICS

Research on respiratory hydrodynamics has provided the conceptual basis for current models of fluid flow during feeding. The early work of Hughes (1960), Hughes and Shelton (1958), and Saunders (1961) established that water flow through the teleost mouth cavity is unidirectional and is regulated by two "pumps." An opercular suction pump draws water through the gill resistance by lateral expansion of the operculum which creates a pressure differential from the buccal to the opercular cavities. Shortly after opercular expansion has reached its peak, the buccal pressure pump is initiated by jaw closure and suspensorial adduction (Ballintijn and Hughes, 1965). This creates a positive buccal pressure (of 1-2 cm H_2O) which drives water through the gills and into the opercular cavity where it exits to the outside. Throughout this process buccal pressure is nearly always positive with respect to opercular pressure.

The key points established by studies of respiratory hydrodynamics are (1) that the gill cover functions as a fundamental element of the "opercular suction pump," drawing water over the gills, (2) that pressures in the opercular cavity are negative with respect to buccal cavity pressures, (3) that this pressure differential must exist if water is to flow unidirectionally through the mouth cavity (Saunders, 1961).

Holeton and Jones (1975) provided the first velocity measurements of flow during respiration and noted that water velocity varied within the buccal cavity. Velocities of up to 38 cm/sec were recorded during normoxic respiration.

IV. PREVIOUS MODELS OF SUCTION FEEDING IN FISHES

A. Pressure Waveforms and Magnitudes: Predictions

Osse (1969) first attempted to predict the magnitude of mouth cavity pressures in fishes using simple hydrodynamic

relationships between velocity and pressure. The equation

$$\frac{P_1}{\rho g} + \frac{\frac{1}{2}V^2}{g} = \frac{P_o}{\rho g}$$

(where P_1 is the pressure near the mouth within the mouth cavity, P_o the pressure of the surrounding water, V the velocity of water entering the mouth, ρ the density of the liquid, and g the acceleration due to gravity) was applied to the fish head with V=200 cm/sec, and a buccal pressure of -20 cm H_2O was calculated. Velocity of water flow was calculated from the estimated change in buccal volume, the estimated rate of volume change, and the mean cross-sectional area of the mouth during mouth opening. This approach was indicated as a first approximation to problems of fluid flow in the mouth cavity and involved a number of assumptions. The most important of these is the assumption of steady flow in the Bernoulli equation, a condition that is certainly not met during feeding. Lauder (1979) also assumed steady flow conditions during his consideration of the effect of mouth geometry on flow rate. Osse (1969: 371) concluded that expansion of both the buccal and opercular cavities contributes to suction feeding: "The suction force due to enlargement of the opercular cavity is directly applied to the water entering the buccal cavity, thus increasing the quantity of water and the velocity of the current."

More recently, Pietsch (1978) has applied the Bernoulli equation and the Hagen-Poiseuille relation to the tubular mouth of Stylephorus to calculate the buccal cavity pressure and flow velocity during feeding. Assumptions of the Hagen-Poiseuille relation, none of which apply to fishes, include (1) a small pipe diameter, (2) steady flow, (3) absence of particles (i.e., prey) in the flow, and (4) that the relationship is not valid near the pipe entrance (see Prandtl, 1949; Streeter and Wylie, 1979). The predicted buccal pressure was -53 cm H_2O with a flow velocity of 325 cm/sec.

Muller and Osse (1978) and Osse and Muller (in press) have developed an elegant hydrodynamic model to predict the pattern of pressure and velocity change with time during feeding. The fish head is modeled as a radially symmetrical cone that expands to reduce the pressure inside. The timing

of expansion of both the anterior and posterior bases of the cone can be varied to simulate the timing of mouth opening and opercular expansion respectively. Flow velocity is obtained from the equation of continuity

$$\frac{\partial u}{\partial x} + \frac{1}{r} \cdot \frac{\partial (vr)}{\partial r} = 0$$

where u is the component of velocity along the body axis, x the distance along the body axis, v is the velocity component perpendicular to the body axis (along the radius of the cone), and r is the radius of the cone at the point of interest. By solving this equation for velocity and substituting into the equation of motion (Navier-Stokes, for frictionless flow),

$$\frac{\partial u}{\partial t} + u \frac{\partial u}{\partial x} = \frac{-1}{\rho} \cdot \frac{\partial p}{\partial x}$$

where p is pressure and ρ is density, the pressures generated by the expanding cone can be calculated. This procedure does not assume steady fluid flow through the mouth cavity.

Three major hydrodynamic assumptions have been made (Muller and Osse, 1978): (1) friction is neglected, (2) the fish head is assumed to be radially symmetrical, and (3) the prey is assumed to behave as an element of the water.

Elshoud-Oldenhave and Osse (1976: 411-412) have made the most specific predictions of pressure waveform in the teleost mouth cavity and correlated the hypothesized pressure changes with kinematic events to produce a theoretical model of suction feeding. Figure two summarizes the present hypothesis of pressure change in the buccal and opercular cavities and is drawn from discussions in Alexander (1969, 1970), Elshoud-Oldenhave and Osse (1976), Lauder (1979), Nyberg (1971), and Liem (1978).

A preparatory phase occurs first as the fish approaches the prey (Fig. 2:P). The volumes of both the buccal and opercular cavities are reduced and the pressure goes positive relative to the surrounding water. The mouth cavity then begins to expand (Fig. 2:mce) while the front jaws remain closed, and this results in a pressure decrease in both cavities. The mouth then opens (Fig. 2: mo), pressures reach their peak negative value, and compression of the

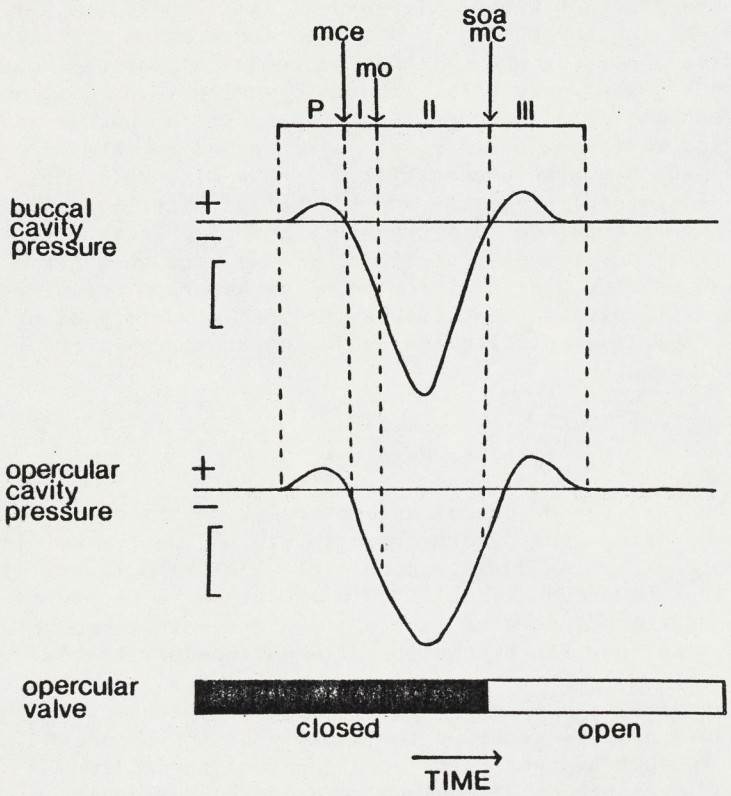


Fig. 2. Current model of buccal and opercular cavity pressure change with time during suction feeding. Phases P, I, II, and III are defined after Elshoud-Oldenhave and Osse (1976), as are the kinematic correlates of pressure change: mce, mouth cavity expansion; mo, mouth opening; soa, suspensorial and opercular adduction; mc, mouth closing. Note the close similarity in both waveform and magnitude (see arbitrary scale bar on left) between buccal and opercular cavity pressures.

mouth cavity occurs. Finally, as the buccal pressure reaches zero, suspensorial and opercular adduction commences and the mouth closes (Fig. 2: soa, mc), resulting in a positive pressure as water is forced out the opercular slit.

The key elements of this model are (1) the close similarity between buccal and opercular pressure waveforms and magnitudes, (2) the role of opercular abduction in the generation of a negative opercular cavity pressure, (3) pressure decrease before the mouth begins to open, and (4) unidirectional flow through the mouth cavity. O'Brien (1979:579) has also emphasized the importance of opercular expansion in contributing to the unidirectional flow of fluid through the mouth.

B. Experimental Data

Alexander (1969, 1970) provided the first direct measurements of pressures in the teleost mouth cavity. He used a pressure transducer attached to a nylon tube which was fixed in the aquarium. A small piece of food was attached to the tube and the fishes were trained to suck off the food by placing their mouths around the tube. Pressures were measured during the feeding act.

A survey of nine different species showed that the maximum negative pressure varied from -80 cm H_2O to -400 cm H_2O in the buccal cavity. Pressure waveforms typically showed a sharp negative pressure drop shortly after the mouth opened and a slight positive pressure pulse of +1 to 9 cm H_2O as " water which has been sucked in with the food is ... driven out through the opercular openings" (Alexander, 1969). These pressure traces agree well with the pattern of buccal pressure change hypothesized from kinematic analyses (Fig. 2), although data on the occurrence of a preparatory phase were not available since the fish had to open its mouth before pressures could be recorded. Casinos (1977) using similar equipment recorded pressures of -150 cm H_2O in cod (Gadus).

Osse (1976) presented preliminary pressure measurements from the buccal and opercular cavities of Amia calva and reported pressures as low as -170 cm H_2O and -95 cm H_2O respectively. Most recently, Liem (1978) measured buccal pressure profiles in two cichlid fishes and found a preparatory pressure pulse corresponding to phase P in Fig. 2.

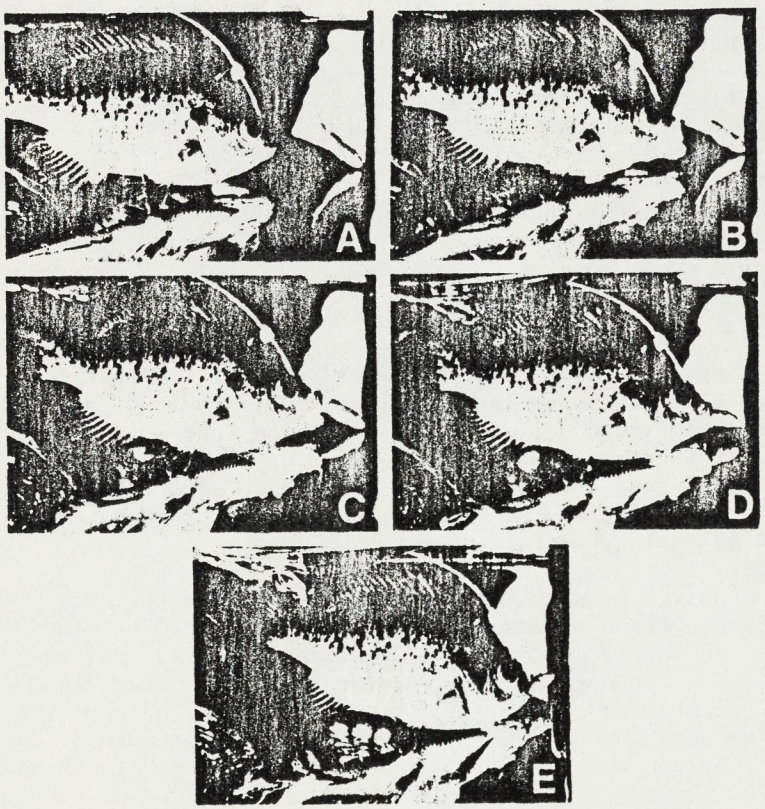


Fig. 3. Representative frames from a high-speed film (200 frames per second) of the bluegill (Lepomis macrochirus) capturing a goldfish. Note the plastic cannula leading into the buccal cavity and the attachment of the cannula to the clamp. Also note abduction of the gill filaments as seen in the ventral view of frame E. Frames A, B, C, D, and E correspond to frames 1, 4, 6, 8, and 15 from the film.

V. EXPERIMENTAL ANALYSIS OF FEEDING IN SUNFISHES

A. Materials and Methods

The suction feeding mechanism in the bluegill sunfish Lepomis macrochirus (Family Centrarchidae) was studied by

the simultaneous recording of buccal and opercular cavity pressures together with a high-speed film (200 frames per second) of jaw movements. A detailed description of the recording apparatus and calibration technique may be found in Lauder (1980). Briefly, plastic cannulae (o.d. 1.52 mm, i.d. 0.86 mm) were chronically implanted in the buccal and opercular cavities (see Fig. 3) and attached to Statham P23 Gb pressure transducers filled with a mixture of 53% boiled (degassed) glycerine and 47% boiled distilled water. This mixture resulted in a transducer damping factor of 0.65 and a frequency response of 75 Hz. Films were then taken of the fish feeding over a mirror to allow accurate measurement of kinematic events. The fishes were fed a variety of prey types, from live goldfish (Carassius auratus) to earthworms and mealworms.

B. Results

The patterns of buccal and opercular cavity pressure recorded during feeding are shown in Fig. 4 and typical jaw movements occurring during capture of a goldfish in Fig. 3. There is tremendous variability in the pressure waveform between different feeding events and these variations correlate with specific kinematic patterns (Lauder, 1980).

Buccal pressures very rarely exhibit a preparatory phase. A pressure drop is recorded immediately after the mouth begins to open and peak gape occurs before the maximum negative pressure. The maximum recorded buccal cavity pressure was -650 cm H_2O. Pressure magnitudes correlate with prey type (goldfish elicit the greatest negative pressures, mealworms the least), and pressure varies inversely with the degree of satiation (Lauder, 1980). The most common buccal pressure waveform contains an initial large negative peak followed by a smaller positive pressure pulse and then by a final negative phase (see Fig. 4A: 1, 5, 7, 9). Occasionally the positive pulse or the second negative is absent (Fig. 4: 2, 10).

Opercular pressure waveforms exhibit an initial sharp positive phase which is followed by a negative pressure peak that may reach a maximum of about -130 cm H_2O (Fig. 4B). A positive pulse may follow the negative (Fig. 4B: 1, 2, 4, 5, 7) or it may be absent (Fig. 4B: 3, 8, 9). Feeding on stationary prey produced opercular pressures in the -10 to -40

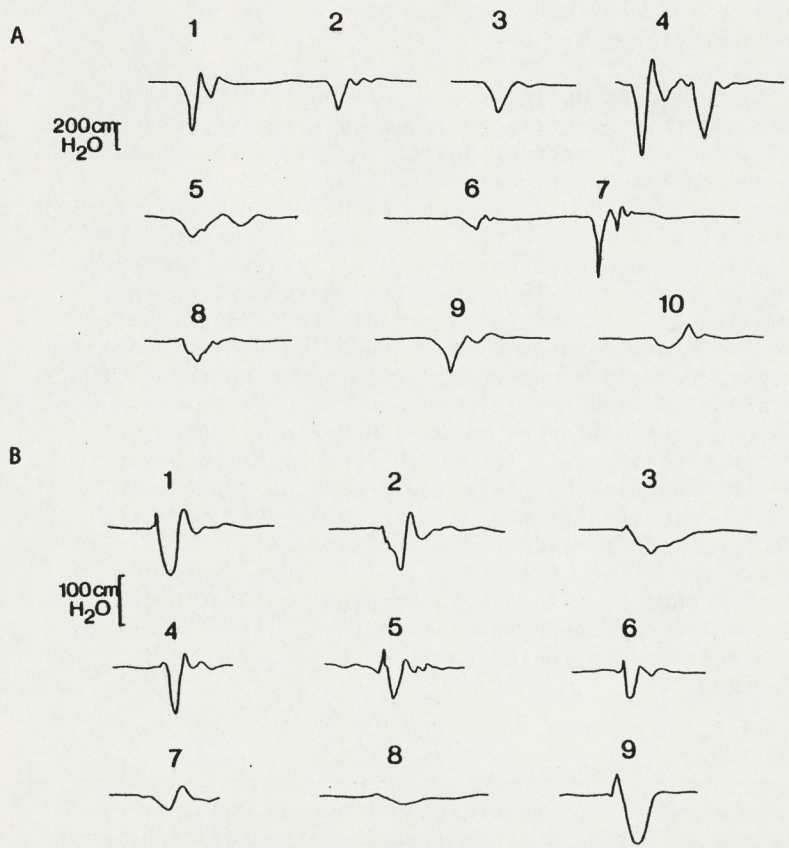


Fig. 4. Representative traces of pressure change in the buccal cavity (A) and the opercular cavity (B) in bluegill (Lepomis macrochirus) during feeding. Note the differing scales and the variation in pressure waveform and magnitude. See text for discussion.

cm H_2O range and tended to flatten out the pressure profile (Fig. 4B: 3, 8).

The temporal relationship between the buccal and opercular pressures is shown in Fig. 5A. Buccal cavity pressure begins to decrease immediately after the mouth

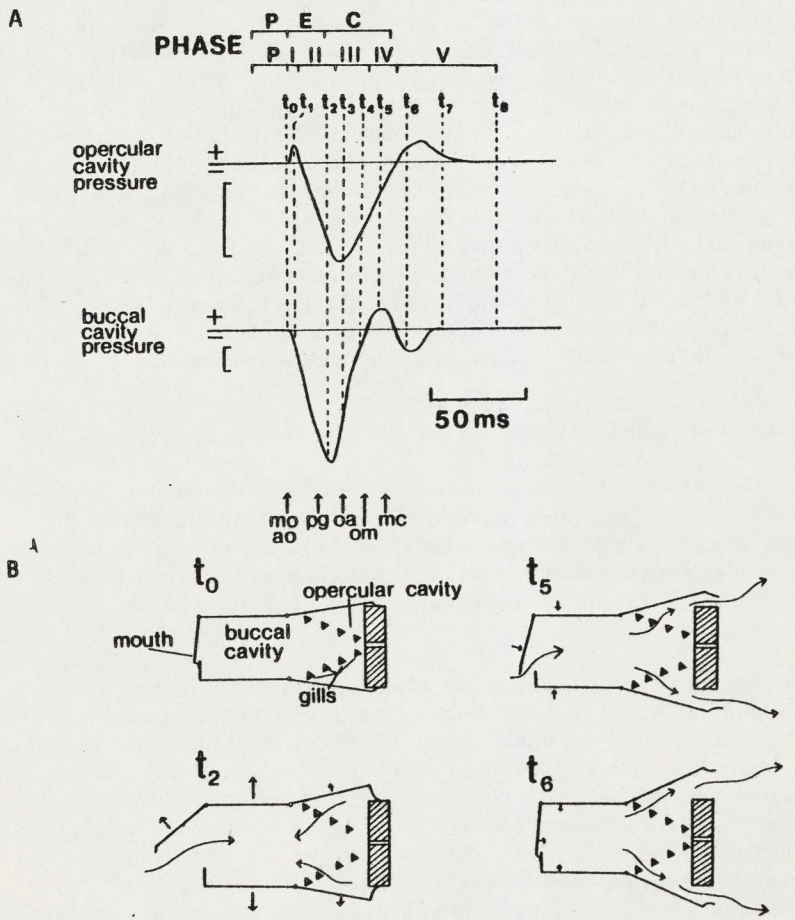
starts to open (Fig. 5A: t_0 to t_1). During this same time interval, the operculum is adducted and opercular cavity pressure actually rises. Buccal pressure reaches its peak (usually 5 times the peak opercular pressure) 5 to 10 ms prior to the opercular pressure peak although the two peaks are occasionally temporally coincident. Buccal pressure then starts to rise and passes through zero while the opercular cavity pressure is still negative. The positive phase of the buccal waveform (Fig. 5: phase IV) occurs while the opercular cavity pressure is negative. In phase V, opercular pressure goes positive as the second negative buccal pressure pulse occurs. Opercular abduction is initiated at the peak in opercular cavity pressure (Fig. 5: oa); throughout the first third of the feeding sequence the operculum exhibits no lateral movement (see ventral view in Fig. 3B). Considerable opercular abduction occurs before the opercular and branchiostegal valves open (Figs. 3B; 5:om). Mouth closure, usually against partially protruded premaxillae, occurs before opercular pressure passes zero and at or near the peak of the positive buccal pressure pulse (Fig. 5:mc). The operculum often remains abducted after the mouth has closed and the pressures have returned to their ambient values (Fig. 5: t_7, t_8). At this point the gill filaments from adjacent arches are clearly seen to be abducted (Fig. 3E: ventral view) and gill resistance is presumably low.

C. New Model of Fluid Flow in the Mouth Cavity

A comparison of simultaneously recorded buccal and opercular cavity pressure waveforms and magnitudes (Fig. 5A) strongly suggests the hypothesis that flow is not unidirectional in the mouth cavity. Figure 5B illustrates the hypothesized flow pattern at representative stages of the feeding cycle.

During phase I, the period when opercular cavity pressure is positive (Fig. 5A), buccal cavity pressures may reach -150 cm H_2O. Between $t_1$and t_2 (Fig. 5A) the ratio of buccal to opercular cavity pressure is about 8. This large pressure differential and the lack of opercular abduction indicate a reverse flow from the opercular to buccal cavity between t_0 and t_2 (Fig. 5). After the end of phase II, opercular abduction occurs and the direction of flow is hypothesized to be from the buccal into the opercular cavity. This change is due both to opercular cavity volume increase

and the momentum of water entering the mouth. The branchiostegal membrane opens at t_4 and this allows flow between the opercular cavity and the exterior. If opercular abduction were delayed beyond t_3, then the anteroposterior flow pattern would likely not be established by t_4, and opening of the branchiostegal valve (by the hyohyoideus inferioris muscle) should actually result in water flow into the opercular cavity from the outside. This anterior flow would be temporary because by t_5 (Fig. 5B) the anteroposterior flow is well established as buccal pressure becomes positive with respect to that of the opercular cavity. At this point,



resistance of the opercular slit is high because of its small cross-sectional area.

The mouth closes during the buccal positive pulse (phase IV) and this event is followed by a rapid pressure decrease in the early part of phase V. This second buccal negative pressure is hypothesized to be due to the water hammer effect. Rapid closing of the mouth acts like the closing of a valve in a pipeline during flow. On the upstream side of the valve the pressure rapidly increases and a high pressure wave is propagated upstream. On the downstream side, the pressure is rapidly reduced (a cavity forms and the fluid returns with the same velocity) and a low pressure wave travels downstream. This tends to reduce the velocity of fluid flow and to contract the pipe downstream of the valve. The analagous situation during feeding is depicted in Fig. 5B: t_6). The mouth rapidly closes, water tends to continue flowing posteriorly causing a pressure reduction just inside the mouth (early phase V). Positive pressures are often recorded as water flows anteriorly after the pressure reduction (Fig. 4A: 1, 7, 9, 10). This phenomenon is analagous to events causing the dichrotic notch in the mammalian cardiac pressure waveform. Finally, by t_8 both the buccal and opercular cavities have returned to ambient pressure.

Fig. 5. A, simultaneous recordings of buccal and opercular cavity pressures during a typical strike at a goldfish. Scale bar equals 100 cm H_2O. P, E, and C refer to the preparatory, expansive, and compressive phases of the strike as conventionally defined (see Liem, 1978). Phases below are those proposed in this paper. Note the dissimilarity of pressure waveforms and magnitudes in the two cavities: e.g., the lack of a preparatory phase and the two negative phases in the buccal waveform. B, proposed pattern of fluid flow through the mouth cavity during feeding. t_0, t_2, t_5, and t_6 correspond to the times in A. Small arrows indicate movements of the mouth cavity. Note the hypothesized reverse flow between t_1 and t_2. Kinematic events are: mo, mouth opening; ao, opercular adduction; pg, peak gape; oa, opercular abduction; om, branchiostegal valve opens; mc, mouth closure.

VI. DISCUSSION

The assumptions and predictions of previous models of pressure change and fluid flow in the teleost mouth cavity during feeding are not supported by the experimental analysis of suction feeding in sunfishes presented here; no previous simultaneous buccal and opercular cavity pressure measurements exist. Current conceptions of the hydrodynamics of teleost feeding have been framed by the large body of data on respiratory mechanics and hydrodynamics. Thus, flow is assumed to be unidirectional, inertial effects have been generally neglected (but see Holeton and Jones, 1975; Muller and Osse, 1978), and the process of creating suction during feeding is viewed as a modification of the respiratory two-pump system. In particular, the operculum is suggested to be of key importance in creating negative mouth cavity pressures (Alexander, 1967; Muller and Osse, 1978; Nyberg, 1971; O'Brien, 1979; Osse, 1969), in a manner analagous to the opercular suction pump during respiration. Additional elements of current concepts of feeding hydrodynamics are the close similarity between buccal and opercular cavity pressure waveforms and magnitudes, the correlated view that the buccal and opercular cavities are a functional unit, and the assumption that gill resistance is low during feeding.

None of these assumptions appear to be true. Buccal cavity pressures in sunfishes consistently average five times the opercular pressures (Fig. 5). In addition, pressure waveforms from the two cavities differ significantly and do not agree with expected patterns (Fig. 2). Flow reversal also appears to occur while the mouth is opening.

Inertial effects play a fundamental role in the hydrodynamics of feeding. The process of creating suction is best viewed as being composed of a powerful buccal suction pump that draws water into the buccal cavity from both the area in front of the mouth and from the opercular cavity. The operculum functions only as a passive element at this stage, preventing water influx from the outside. Flow from in front of the mouth is much greater than from the opercular cavity because the mouth opening is much less resistant to flow than the gill curtain. The inertia of the water drawn in through the mouth is primarily responsible for the transition to the anteroposterior flow pattern and the exit of water out over the gills to the exterior. Opercular abduction appears to contribute relatively little

to the direction of fluid flow, the magnitude of opercular cavity negative pressure, or flow velocity.

The asymmetry of gill resistance plays a key role in this model. In the early stages of feeding, the drop in opercular cavity pressure is due both to the buccal cavity pressure reduction and perhaps also to expansion of opercular cavity volume as a result of anatomical couplings between the two cavities, not to opercular abduction. Opercular cavity pressures do not equal those in the buccal cavity because of gill resistance, and the filaments of adjacent arches may be adducted. As the inertia of water sucked in through the mouth results in flow into the opercular cavity, the gill filaments are abducted and resistance becomes low.

Based on the synchronously recorded buccal and opercular cavity pressures and the hydrodynamic considerations outlined above, a number of kinematic correlates of pressure waveform attributes may be predicted (Table I). The correspondence between the occurrence of different kinematic patterns and variations in pressure waveform will be considered in detail elsewhere (Lauder, 1980), but variations during phases IV and V (Figs. 4, 5A) may be correlated with the timing of opercular abduction and mouth closing.

The large negative pressures recorded in the mouth cavity (up to -650 cm H_2O) invite considerations of the structural demands imposed on the teleost head. Lauder and Lanyon (1979) have considered the morphology of the sunfish operculum to be primarily a response to deformation induced by negative opercular cavity pressures. Two prominent orthogonal bony struts on the operculum were hypothesized to resist bending and twisting moments imposed by the pressure reduction. This view of the role of the operculum is consistent with the model of suction feeding presented here: the gill cover acts primarily as a passive element preventing fluid influx from the exterior.

A number of clearly defined areas may now be outlined for future work. Of particular interest is a characterization of the velocity field, both anterior to the mouth in the vicinity of the prey, and within the buccal and opercular cavities. Opercular cavity flow velocity determinations would provide a test of the reverse flow hypothesis. The pressure -- velocity relationship during feeding is also of importance. Because of the prominence of inertial effects

TABLE I

Predicted Kinematic Correlates of Pressure Waveform Attributes

	Pressure Waveform Characteristic (See Fig. 5A)	Predicted Kinematic Correlate
BUCCAL PRESSURE	Phase P: Positive	Hyoid protraction; suspensorial adduction.
	Phase I, II: Negative	Mouth opening; suspensorial abduction; hyoid depression.
	Phase III: Negative → 0	Mouth closing; start of hyoid and suspensorial adduction.
	Phase IV: Positive	Delay in opercular abduction relative to mouth closing; hyoid, suspensorial adduction.
	Phase V: Negative	Rapid closing of jaws relative to mouth cavity expansion.
OPERCULAR PRESSURE	Phase P: Positive	Opercular adduction; suspensorial adduction; hyoid protraction.
	Phase I: Positive	Opercular adduction.
	Phase II: Negative	Mouth opening; suspensorial abduction; hyoid depression.
	Phase III: Negative	Opercular abduction; mouth closing.
	Phase IV: Negative → 0	Opercular abduction; mouth closing; hyoid and suspensorial adduction.
	Phase V: Positive	Hyoid and suspensorial adduction.

and changing gill resistance during the strike, calculation of flow velocity from measured pressures is unlikely to yield satisfactory results. Finally, correlation of attributes of the suction feeding mechanism (such as volume flow rate, pressure, velocity) with morphological features, feeding efficiency, and prey type in a number of closely related taxa, may provide insights into the evolutionary mechanisms governing changes of shape and function in teleost fishes.

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Elassoma alabamae, a New Species of Pygmy Sunfish Endemic to the Tennessee River Drainage of Alabama (Teleostei: Elassomatidae)

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ABSTRACT: Richard L. Mayden. 1993. *Elassoma alabamae*, a New Species of Pygmy Sunfish Endemic to the Tennessee River Drainage of Alabama (Teleostei: Elassomatidae). Bulletin Alabama Museum of Natural History Number 16, 14 pages, 6 tables, 3 figures. The spring pygmy sunfish, *Elassoma alabamae*, is described and distinguished from other members of the genus, bringing the total number of described species in the family Elassomatidae to six. *Elassoma alabamae* is distinguished from congeners by meristic, mensural, and coloration characteristics. Most notable among these include the lack of humeral spots and dorsal head scales, the occurrence of three dorsal fin spines, clear or white windows in the dorsal and anal fins, usually 6 or 7 broad, dark bars, and usually 5 or 6 narrow, iridescent interbars along the flanks of both sexes. This species has been recorded from only three springs and associated habitats in the Tennessee River Drainage of north Alabama. Today a native population survives in only one spring complex; a planned repopulation of one other spring complex previously inhabited by the species represents a potential secondary stronghold for the species. Potential threats from cropdusting practices, vegetation control, the byproducts of livestock, and agricultural practices threaten this rare and geographically restricted pygmy sunfish.

Introduction

The endemic North American fish family Elassomatidae is presently known to include five described and two undescribed species. All of these species are diminutive in size and, with the exception of *Elassoma zonatum*, rarely exceed 30 millimeters in standard length. About one half of the members of this family have restricted geographic distributions, occupying only portions of one or two river systems to only one or two springs, while others such as *Elassoma zonatum* and *E. evergladei* are more widespread in distribution. The banded pygmy sunfish, *E. zonatum*, occurs throughout drainages of the Coastal Plain from eastern Texas to North Carolina and north on the Mississippi Embayment to southern Illinois. All *Elassoma* are generally associated with spring- and swamp-like habitats.

Over a half century ago, on 5 November 1937, Tennessee Valley Authority biologist L. F. Miller sampled Cave Spring, Lauderdale County, Alabama and captured, among other fishes, a new species of pygmy sunfish. The fishes collected by Miller were sent to the University of Michigan Museum of Zoology and some specimens were identified by Dr. Carl L. Hubbs and Mr. Milton B. Trautman as an undescribed species of *Elassoma*. Since that time this species has been known only by its informally adopted common name, the "spring pygmy sunfish." This species has been recorded historically from only three small, isolated spring locations in northern Alabama, all three of which occur above the Fall Line. Unfortunately, two of three populations have since been extirpated.

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This paper presents a taxonomic description of the spring pygmy sunfish. The new species is endemic to Alabama and is the most geographically restricted member of the family. Today, this rare species has its native distribution restricted to only one spring complex and associated habitats, and is in imminent danger of extinction.

Methods

Institutional symbolic codes used below follow Leviton and Gibbs (1988). Methods used for making body measurements and scale counts follow those outlined in Hubbs and Lagler (1974) and Rohde and Arndt (1987). Body measurements of *Elassoma alabamae* and *E. zonatum* were taken with electronic needle-point calipers using a dissection microscope; meristic data follow traditionally used variables for the family. Comparative meristic and morphometric data for *E. boehlkei* and *E. okatie* were derived from Rohde and Arndt (1987) and museum specimens; data for *E. evergladei*, *E. okefenokee*, and *E. zonatum* were derived from museum specimens.

Statistical analysis of mensural and meristic data for *E. alabamae* and *E. zonatum* included SAS univariate and multivariate analyses. Students' T test was used to test for sexual dimorphism and differences between *E. zonatum* and *E. alabamae*. Sheared principal components analysis (Rohlf and Bookstein, 1990) was used with head, body, and fin measurements to summarize mensural differences; standard principal component analysis was used to summarize meristic variation. A correlation matrix was used in the principal component analysis of meristic data; a covariance matrix was used in analysis of $\log_{10}$ transformed measurement data. Sexes were analyzed separately in the analysis of mensural data because of observed sexual dimorphism in some characters.

Details of body and fin coloration of *E. zonatum* and *E. alabamae* were taken from live specimens and color transparencies of live and freshly-preserved specimens; a detailed description of *E. zonatum* is presented in Walsh and Burr (1984). Comparative coloration data of other species were derived from personal observations of live specimens, color transparencies, and color descriptions provided in Rohde and Arndt (1987).

Elassoma alabamae, new species
Spring Pygmy Sunfish
Figure 1A and 1B

Holotype.—University of Alabama Ichthyological Collection, UAIC 10275.01, adult male, 17.4 mm SL, Tennessee River Drainage, Alabama, Limestone County, Moss Spring and effluent run into Beaverdam Creek, 1.4 mi N of Greenbriar (T4S, R3W, Sec. 16), 2 March 1992, R. L. Mayden, B. R. Kuhajda, H. T. Boschung, T. S. Jandebeur, and J. R. Tomelleri.

Allotype.—UAIC 10275.05, adult female, 17.4 mm SL, same locality and collection information as holotype.

Paratypes.—UAIC 10275.06, 50 specimens (13.7–18.8 mm SL), same locality and collection data as holotype. UAIC 4129.04, 36 specimens (11-15), Alabama, Limestone County, Moss Spring, Beaverdam Creek, vicinity of Greenbriar (T4S, R3W, Sec. 16), 31 July 1973, J. C. Hall, M. F. Mettee, and E. C. Beckham. UAIC 4606.01, 5 specimens (17–23), Alabama, Limestone County, Pryor Spring, 9 mi S of Athens (T4S, R4W, Sec. 22), 25 April 1941, C. M. Tarzwell (formerly UMMZ 133263). UAIC 4923.11, 13 alcoholic and 3 cleared and stained specimens (11–15), same locality data as holotype, 5 August 1974, M. F. Mettee, R. D. Suttkus, and G. Clemmer. UAIC 10146.05, 4 specimens (21.4–24.5), same locality data as holotype, 25 April 1989, R. L. Mayden, H. T. Boschung, J. D. Williams, N. M. Burkhead, M. T. Ferguson. UAIC 10454.01, 8 specimens (18.8–19.7), Alabama, Limestone County, unnamed spring run, tributary to Beaverdam Creek (T4S, R3W, Sec. 15), 19 April 1983, M. F. Mettee. INHS 28324, 10 specimens (15–20), same collection and locality data as UAIC 10275.06. SIUC 20341, 10 specimens (17–20.5), same collection and locality data as UAIC 10275.06. TU 165003, 10 specimens (15–20), same collection and locality data as UAIC 10275.06. UF 93287, 10 specimens (15–20), same collection and locality data as UAIC 10275.06. UMMZ 132689, 1 specimen (22), Alabama, Lauderdale County, Cave Spring near Smithsonia (T3S, R13W, Sec. 15; TVA Map 35 SW, preimpoundment), 5 November 1937, L. F. Miller (original TVA number 37–638). UMMZ 132690, 5 specimens (20–23), same collection and locality data as UMMZ 132689. UMMZ 133263, 50 specimens (16.0–26.0), same collection and locality data as UAIC 4606.01, received from Tennessee Valley Authority. UMMZ 200793, 2 specimens (20–21.5), Alabama, Limestone County, Pryor Spring Branch, (T4S, R4W, Sec. 28; Wheeler Reservoir, TVA Map 68 NW, preimpoundment), 25 April 1941, C. M. Tarzwell. USNM 218407, 14 alcoholic and 3 cleared and stained specimens (17.6–19.3), Alabama, Limestone County, Moss Spring, swampy area above and below beaver dam on Beaverdam Creek (T4S, R3W, Sec. 15, SW 1/4), 23 February 1975, T. S. Jandebeur and J. D. Williams. USNM 243805, 20 specimens (16.1–20.3), Alabama, Limestone County, Beaverdam Creek and Moss Springs, 1.5 mi NE of Greenbriar, 7 March 1975, R. D. Suttkus, G. H. Clemmer, W. C. Starnes. UT 90.92, 5 specimens (19–21), Alabama, Limestone County, Moss Spring at extreme headwaters, ca. 5 mi W Madison (T4S, R3W, Sec. 10), 17 February 1973, D. A. Etnier, R. A. Stiles, R. L. Henson, F. V. Oakberg, G. R. Boronow, and J. Winfield.

Nontype materials.—AUM 23966, 13 specimens (19.1–23.0 mm SL), same locality data as holotype, M. F. Mettee, 19 April 1983. UAIC 8799.02, 1 alcoholic and 5 cleared

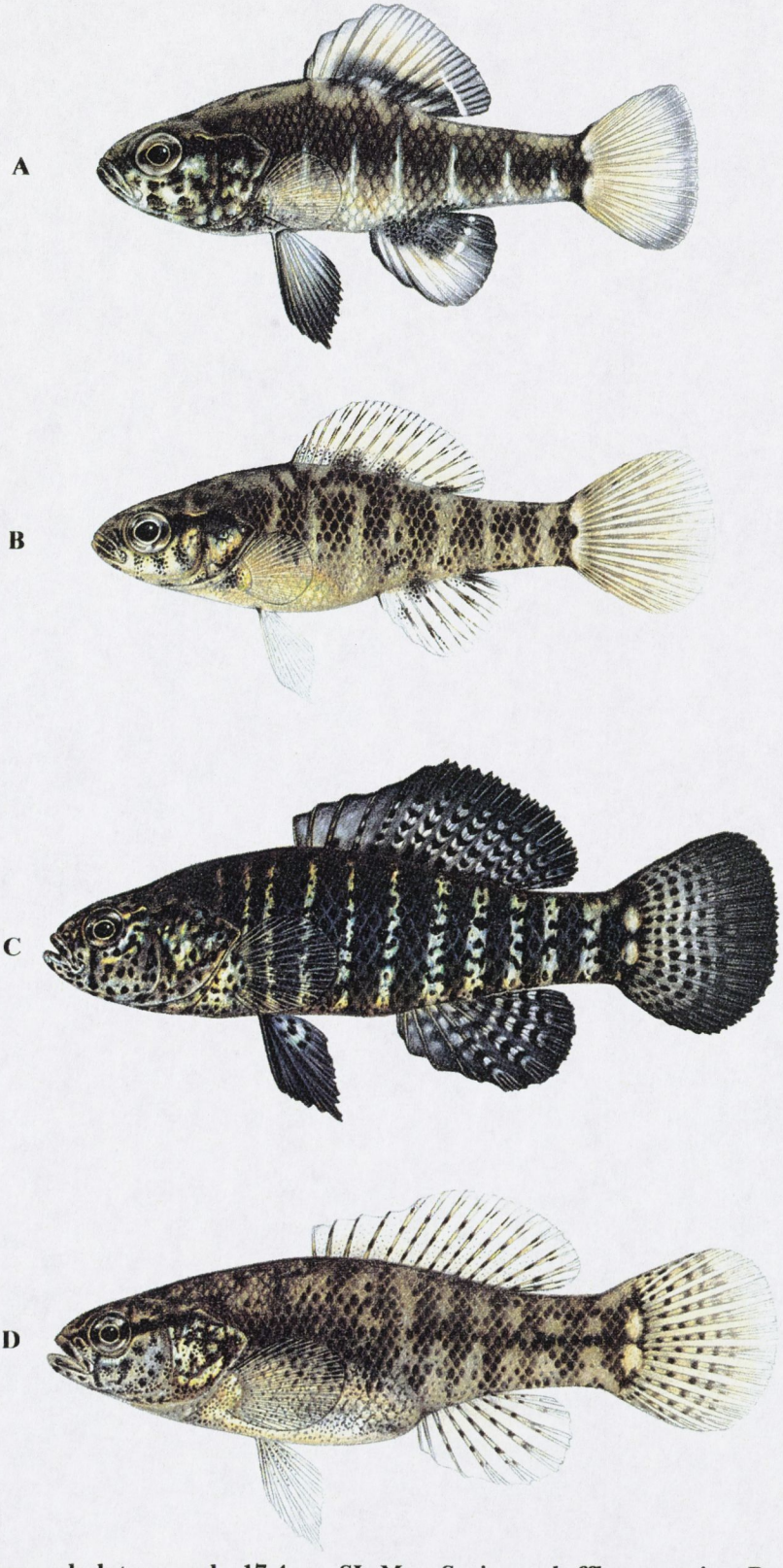

Figure 1. A. *Elassoma alabamae*, holotype, male, 17.4 mm SL, Moss Spring and effluent run into Beaverdam Creek, 1.4 mi N of Greenbriar (T4S, R3W, Sec. 15), Limestone County, Alabama, 2 March 1992 (UAIC 10275.01). B. *Elassoma alabamae*, allotype, female, 17.4 mm SL, (UAIC 10275.05) same locality and collection information as holotype. C. *Elassoma zonatum*, male, 29.2 mm SL, Five Runs Creek at Alabama Hwy 55, 5.5 mi S of Andalusia, Covington County, Alabama, 4 March 1992, (UAIC 10280.01). D. *Elassoma zonatum*, female, 28.8 mm SL, same collection and locality data as male.

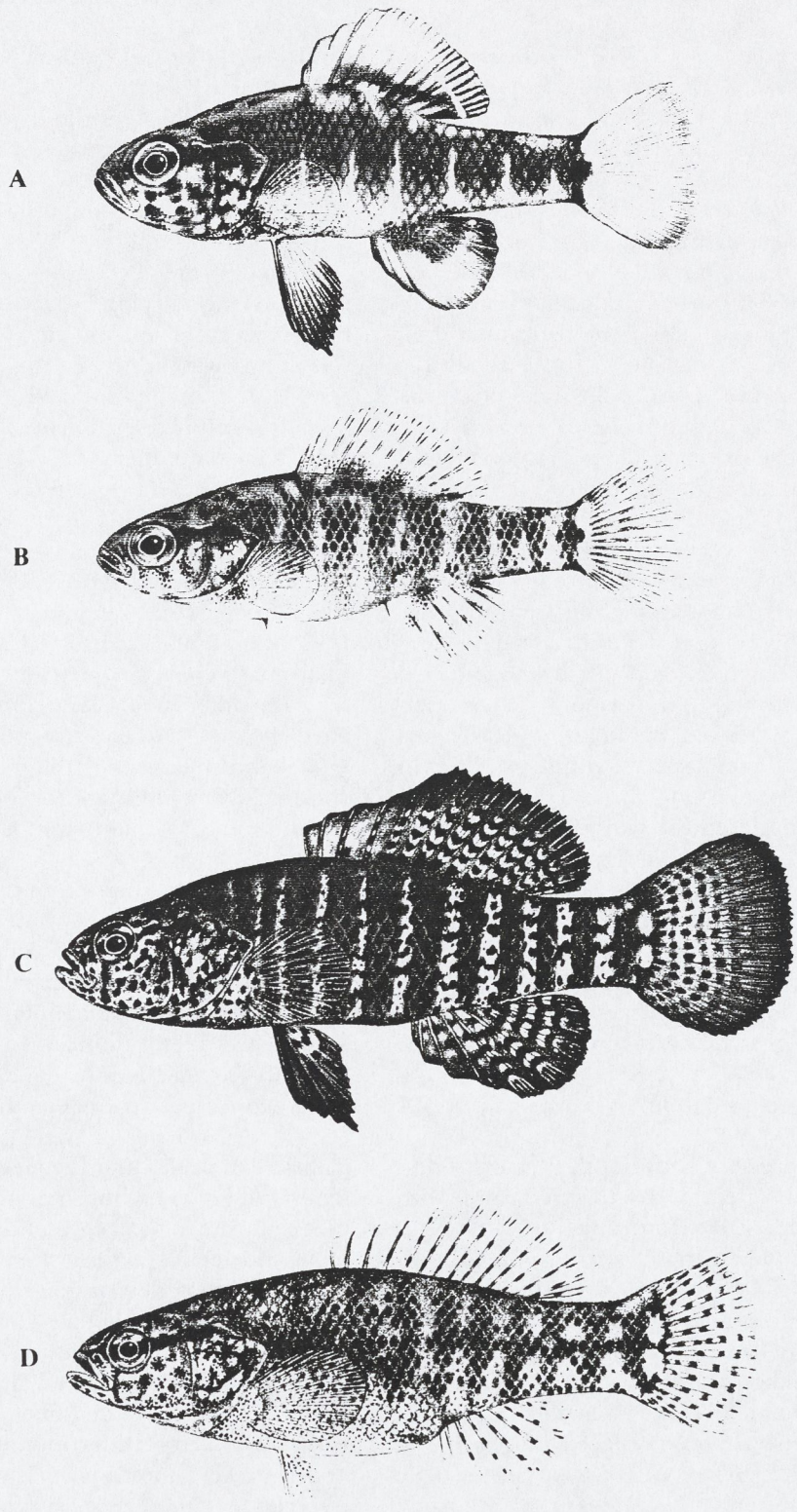

Figure 1. A. *Elassoma alabamae*, holotype, male, 17.4 mm SL, Moss Spring and effluent run into Beaverdam Creek, 1.4 mi N of Greenbriar (T4S, R3W, Sec. 15), Limestone County, Alabama, 2 March 1992 (UAIC 10275.01). B. *Elassoma alabamae*, allotype, female, 17.4 mm SL, (UAIC 10275.05) same locality and collection information as holotype. C. *Elassoma zonatum*, male, 29.2 mm SL, Five Runs Creek at Alabama Hwy 55, 5.5 mi S of Andalusia, Covington County, Alabama, 4 March 1992, (UAIC 10280.01). D. *Elassoma zonatum*, female, 28.8 mm SL, same collection and locality data as male.

and stained specimens (15–17), Moss Spring Run in Beaverdam Swamp, ca. 1.8 mi NNE of Greenbriar (T4S, R3W, Sec. 15), 17 September 1977, B. H. Bauer, J. E. Böhlke, E. B. Böhlke, D. A. Etnier, J. L. Harris, W. C. Starnes, and L. B. Starnes. UT 90.260, 5 specimens (15–17), same collection and locality data as UAIC 8799.02.

Diagnosis.—*Elassoma alabamae* is the smallest member of Elassomatidae, attaining an average adult body size of about 17.4 mm SL (N=122); maximum adult body size observed was a 25 mm SL female. This species is distinguished from all other Elassomatidae on the basis of meristic, mensural, and coloration characters. Dorsal spines II–IV, usually III; lateral scale rows 27–32, usually 28 or 29; transverse scale rows usually 11 or 12; caudal peduncle scale rows 15–20, usually 16–18; broad, black or dark olive bars along flanks 5–8, usually 6 or 7, separated by 4–8, usually 5 or 6 narrow iridescent blue-green or cream-colored interbars; broad, dark bars with discrete edges in males, edges less discrete in females; broad bars wider than those of other species of *Elassoma*; narrow interbars less numerous than in other *Elassoma*; dorsal fin of breeding males with basal dark band containing two large depigmented ocelli; dorsal and anal fins of males with clear to white narrow windows in posteriormost membranes, accentuated by adjacent darkly pigmented rays and membranes; females without windows in dorsal and anal fins; base of caudal fin with two indistinct, cream to white ocelli bordered anteriorly by dark brown to olive bar, not bounded posteriorly by bar; scales absent on the dorsum of head; dark scapular or shoulder blotches absent; gular region and lips pigmented.

Description.—Variation in head, body, and fin measurements for males and females are presented in Table 1. Variation in number of scale rows, fin rays and spines, lateral bars, and gill rakers are presented in Tables 2–4. General head and body physiognomy is shown in Figure 1A and B.

Body laterally compressed; body depth greatest at dorsal fin origin. Head laterally compressed and with rounded anterior profile. Dorsal and anal fins with spines and rays and with rounded distal profile. Caudal fin with rounded distal profile. Pelvic fin with spine and rays; median rays longest and presenting pointed fin margin.

Small species of *Elassoma*, mean adult body length 17.6 mm SL (N=44) in males and 18.8 mm SL (N=26) in females. Largest specimen 25 mm SL female.

Bars along flanks generally evenly spaced, numbering 5–8, usually 6 or 7 ($\bar{x}$=6.2, SD=0.66). Bars broad, in male average 1.7 mm in width (range 1.2–2.5, SD=0.38), averaging 13.1 times wider than iridescent interbar width (range 4.2–22.0, SD=5.35) (interbar width range 0.06–0.43, $\bar{x}$=0.16, SD=0.09). In females, average dark bar width 1.9 mm (range 1.0–2.8 , SD=0.54), averaging 9.5 times wider than lighter interbar width (range 4.7–16.0, SD=3.18) (interbar width range 0.10–0.48, $\bar{x}$=0.24, SD=0.10).

Lateral scales 27–32, usually 28 or 29, not pored. Transverse scale rows 10–13, usually 11 or 12. Scales around caudal peduncle 15–20, usually 16–18. Total vertebrae 28 (5 specimens) or 29 (3) ($\bar{x}$=28.4, SD=0.48). Scales cover trunk; top of head without scales. Nape, opercle, and breast with embedded scales. Cheek and preopercle without scales.

Dorsal fin spines II–IV, usually III; dorsal fin rays 8–13, usually 10 or 11. Anal fin spines I–III, usually III; anal fin rays 5–8, usually 6 or 7. Pectoral fin rays 14–19, usually 16 or 17. Pelvic fin long and pointed, generally extending beyond anal fin origin in males, but not females ($P<0.0001$); pelvic spines I; pelvic fin rays 5 (63 specimens) or 6 (7) ($\bar{x}$=5.1, SD=0.30). Branched caudal fin rays 10–13, usually 12.

Gill rakers on lower arch usually small, generally as long as wide. Rakers number 2–5, usually 3. Branchiostegal rays 4 (6 specimens), 5 (69), or 6 (3) ($\bar{x}$=5.0, SD=0.36). Sensory pores on head common and conspicuous. Supraorbital-postemporal canal usually uninterrupted, pores 7 (18); canal interrupted, pores 8 (2). Prenasal canal pores 2 (20). Preopercular canal uninterrupted, pores 3 (1) or 4 (19). Mandibular and suborbital canals absent. External neuromasts common on head; single row along each mandible (mandibular line, sensu Branson and Moore, 1962), on cheek below eye to and along prenasal canal (infraorbital line), between naris and orbit (nasal line), across preopercle (postmaxillary line), and on dorsum of head above eye, around snout (median supraorbital line), and around occiput.

Palatine and vomer without teeth. Premaxilla and mandible with elongate and villiform teeth; teeth in two or three rows anteromedially and one row laterally. Teeth slightly recurved near symphysis and generally erect laterally. Infrapharyngeals two and not fused, covered with elongate and erect teeth similar to larger teeth on jaws. Ceratobranchials 5 with enlarged surface covered with large, elongate, and erect teeth.

Coloration. Males and females are sexually dichromatic; males are generally more brightly colored than females, especially during spring months. Coloration of breeding male and female is illustrated in Figure 1A and B. The following color descriptions are based on live breeding males, live breeding females, live juveniles and non-breeding adults, and preserved specimens.

Males. Breeding males (Fig. 1A) brilliantly colored. Body of freshly captured male may be very dark to black except for narrow iridescent blue-green bars along flanks and iridescent mottling on cheeks, preopercles, central opercles, preopercles, and subopercles. Body coloration of these males becoming more subdued with handling. Dorsum olive green to light brown and, in some males, crossed by five to six narrow, dark saddles from flank coloration; first saddle forming near origin of dorsal fin and last saddle forming along caudal peduncle. Predorsal region may be mottled with patches of dark olive over light

Table 1. Proportional measurements of adult males and females of *Elassoma alabamae* and *Elassoma zonatum*. Proportions expressed as thousands of standard length except for the last three measurements which are proportions of head length. Significant differences between sexes are indicated by asterisks (P<0.05).

Elassoma alabamae	Males (N=21; includes holotype)				Females (N=20)		
	Holotype	Range	$\bar{x}$	SD	Range	$\bar{x}$	SD
Standard Length*	17.4	16.1–20.4	18.1	1.3	14.2–24.5	20.4	2.5
Head Length*	339	311–361	338	12.4	286–359	323	17.9
Head Depth*	167	115–192	175	15.9	142–190	162	11.7
Body Depth	305	271–356	301	19.5	276–353	302	20.2
Preanal Length*	552	528–574	552	15.4	528–630	583	25.4
Predorsal Length*	443	417–474	445	14.5	436–502	462	17.7
Prepelvic Length	362	347–405	374	16.2	339–393	367	15.0
Caudal Peduncle Length	276	254–328	287	20.1	248–307	280	15.4
Caudal Peduncle Depth*	138	106–147	129	10.6	99–141	114	9.7
Dorsal Fin Length*	397	364–448	405	23.9	332–393	357	17.4
Anal Fin Length*	253	225–320	280	25.2	189–275	227	18.6
Pectoral Fin Length*	144	106–148	133	12.0	74–122	105	11.9
Pelvic Fin Length*	241	181–260	223	21.1	145–197	169	15.3
Snout Length	75	54–90	73	9.3	62–84	73	5.6
Eye Diameter*	80	80–102	89	5.4	69–92	81	5.6
Upper Jaw Length*	75	67–91	78	6.3	63–79	71	5.2
Bar Width	75	71–132	95	17.6	68–123	96	18.4
Interbar Width	3	3–22	9	4.8	5–21	11	4.3
Snout Length	220	161–268	218	28.6	189–257	226	18.1
Eye Diameter*	237	233–296	264	16.4	227–281	251	12.8
Upper Jaw Length	220	196–273	231	21.6	176–257	220	20.1

Elassoma zonatum	Males (N=10)			Females (N=10)		
	Range	$\bar{x}$	SD	Range	$\bar{x}$	SD
Standard Length*	22.4–32.1	28.1	3.1	22.8–28.8	25.5	1.9
Head Length	327–366	352	13.5	329–349	342	5.9
Head Depth*	158–188	173	10.4	154–167	160	4.0
Body Depth	277–315	297	12.5	285–341	310	15.4
Preanal Length*	601–627	612	8.9	635–667	654	9.9
Predorsal Length	418–469	448	17.8	414–475	456	18.4
Prepelvic Length	346–392	374	15.6	339–408	383	20.7
Caudal Peduncle Length*	229–309	257	22.1	202–257	231	19.1
Caudal Peduncle Depth*	145–169	155	8.5	124–156	136	9.8
Dorsal Fin Length*	487–546	522	19.1	447–502	469	22.7
Anal Fin Length*	308–341	324	9.7	247–278	264	11.3
Pectoral Fin Length*	184–212	197	7.6	158–184	169	8.6
Pelvic Fin Length*	227–283	250	15.9	198–240	215	15.1
Snout Length	73–92	83	6.4	73–85	78	4.0
Eye Diameter	65–84	77	6.0	69–88	79	5.8
Upper Jaw Length	67–100	87	10.1	70–85	80	4.5
Bar Width*	31–51	40	7.1	35–77	56	12.9
Interbar Width	17–30	23	4.8	14–28	20	4.4
Snout Length	207–255	234	16.2	211–253	227	13.0
Eye Diameter	194–234	218	12.5	202–253	230	18.3
Upper Jaw Length	183–286	246	30.4	200–253	233	14.5

Table 2. Variation in lateral scale rows, transverse scale rows, and caudal peduncle scale rows in *Elassoma alabamae* (N=70) and select samples of *Elassoma zonatum* (N=76) from Alabama. Holotype is indicated with asterisk.

	Lateral Scale Rows														
	27	28	29	30	31	32	33	34	35	36	37	38	39	$\bar{x}$	SD
Elassoma alabamae	8	23	21*	10	7	1								28.9	1.20
Elassoma zonatum					2	7	11	15	17	14	6	3	1	34.6	1.73

	Transverse Scale Rows							
	10	11	12	13	14	15	$\bar{x}$	SD
Elassoma alabamae	5	29	31*	5			11.5	0.73
Elassoma zonatum			11	35	29	1	13.6	0.72

	Caudal Peduncle Scale Rows														
	15	16	17	18	19	20	21	22	23	24	25	26	27	$\bar{x}$	SD
Elassoma alabamae	4	10	29*	12	8	7								17.4	1.31
Elassoma zonatum						1	10	15	28	16	5		1	22.9	1.24

olive background. Lateral coloration above midline darker olive brown; edges of scales highlighted with melanophores. Dark shoulder blotches absent. Below midline flanks lighter olive to tan; some scales outlined with melanophores or iridescence along margins. Scales along flanks and above belly, posterior to pectoral fin insertion and anterior anal fin with peach to light orange iridescence. Flanks with five to seven broad, dark brown to olive bars separated by five to seven narrow iridescent blue-green interbars; iridescent interbars extending from just above midline to belly and lower caudal peduncle where expanded slightly; first bar just posterior to pectoral fin insertion, last bar anterior to hypural plate. Belly and ventral caudal peduncle light tan to cream with some some scales margined with iridescence.

Dorsum of head olive green to brown; mottled in some individuals. Postorbital and preorbital stripes well developed and continuous through eye; postorbital stripe extending along dorsal margin of opercle. Preorbital stripe extending anteriorly across both lips and continued inside mouth along mandibles. Lips dusky between preorbital bars; laterally, lips immaculate or lightly pigmented with melanophores. Snout between preorbital stripes brown to dark olive. Pupil black and surrounded by yellow ring; remainder of eye brown to tan. Cheek, preopercular region, ventral opercle, and subopercle brilliantly colored with iridescent blue, green, and yellow spots. Spots separated by three to four bars radiating from anteroventral and posteroventral margins of orbit; bars broken and composed of clusters of grouped melanophores. Subopercle, preopercle, and interopercle with large iridescent blue to green spots against dark olive to brown background coloration. Gular region and branchiostegals with scattered melanophores, most intense on adult males. Prepectoral region heavily pigmented with melanophores and with iridescent blue-green cast. Breast and interpelvic regions cream colored and heavily pigmented with melanophores.

Dorsal fin with distinctive banding pattern. Fin with broad dusky distal band, forming narrow margin in spinous membranes and broad margin in membranes of rays; band occupying up to one half of last membrane. Basal portions of interspinal membranes cream; basal portions of interradial membranes with broad dusky band. Basal band beginning at first ray and continuing to last ray. Band with two large basally clear to white ocelli contained within band. Central portions of spines, rays, and interspinal and interradial membranes cream to light yellow-orange. Posteriorly, dusky distal and basal bands separated by distinct clear to white narrow stripe creating distinctive "window." Spines and rays of dorsal fin lined with melanophores and darkest distally, except in clear spots of basal band and posterior window; first spine and distal tips of posterior spines black. Caudal fin with broad dusky distal band; band continuous along distal edges of all branches of caudal rays. Base of caudal fin with two poorly defined cream or white basicaudal ocelli, separated by posterior extension of lateral band; ocelli bounded anteriorly by dark bar extending onto procurrent rays but not bordered posteriorly by dark bar. Medially, caudal fin membranes and rays yellow to cream. All rays lined by melanophores. Anal fin with leading spine and membrane black; dark dusky band extending along distal edge of fin. Band narrow anteriorly,

expanded at first anal ray, and extending to posterior-most ray and membrane as broad dusky band. Base of fin from third spine to last ray darkly pigmented; band shallow anteriorly and broad posteriorly. Distal and basal bands separated posteriorly by narrow white to clear stripe, creating distinctive "window." Pelvic fins dusky with broad dark distal margin; dark pigment best developed at distal edges of central rays. Pectoral fin clear; rays lined with melanophores.

Females. Breeding females (Fig. 1B) generally drab in coloration; body not as brightly colored as males. Dorsum light brown. Nape may appear mottled with large, dark olive blotches over tan to light brown background coloration. Flanks with five to eight broad dark olive to dark brown bars; bars may extend dorsally and connect with blotches on nape or cross dorsum as narrow saddles; saddles forming from dorsal fin origin to procurrent rays of caudal fin, creating a regular saddled pattern. Margins of broad bars along flank generally irregularly formed; bars separated by four to eight narrow iridescent to tan interbars. Narrow interbars extending ventrally to belly and ventral caudal peduncle; interbars more iridescent anteriorly. Belly and lower flanks iridescent yellow-green to orange; belly cream to white. Lower caudal peduncle dark brown to olive brown.

Dorsum of head olive to light brown with some mottling posteriorly. Midline of snout olive to light brown. Postorbital and preorbital stripes dark olive brown and well developed; postorbital stripe extending posteriorly across dorsum of operculum and terminating at opercular margin. Preorbital stripe extending anteriorly across both lips and present inside mandible. Lips, between preorbital stripes, dusky; lateral to preorbital stripe, lips white or lightly pigmented with melanophores. Cheek region with three to four darkly colored bars radiating anteroventrally to posteroventrally from eye; bars formed from dusky concentrations of melanophores. Areas between bars with light cast of iridescent green yellow. Dorsal one half of opercle below postorbital stripe brightly iridescent yellow-green or green-orange. Center of operculum and suboperculum bright iridescent yellow-green and orange. Branchiostegals, gular region, and breast cream colored to white and lightly pigmented with melanophores. Prepectoral region iridescent yellow-orange over background of cream to light tan.

Dorsal fin with broad basal dusky band; band with three large centrally and posteriorly located dark spots; spots occur in same locations as where basal band of males connects with dorsum of body. Medially, dorsal fin yellow to cream. Distally, dorsal fin clear to dusky. Dorsal fin spines and rays lined with melanophores, creating three to four dusky bands; distal dusky band formed from melanophores along rays and spines. First dorsal spine darkly pigmented. Posteriorly located depigmented or white window of males absent. Caudal fin as in males except that dusky distal band lighter and bar on caudal peduncle not as intense. Anal fin coloration similar to dorsal fin; base with two dark spots, one located centrally and one posteriorly. First anal spine black. Centrally, anal fin cream to yellow; membranes clear; rays outlined by melanophores, creating light dusky edge. Posteriorly located depigmented or white window of males absent. Pelvic and pectoral fins immaculate except for few melanophores along edges of rays.

Juveniles and non-breeding adults. Juveniles and non-breeding females as in live breeding females except that irides-

Table 3. Variation in dorsal fin spines and rays, anal fin spines and rays, pectoral rays, and caudal rays in *Elassoma alabamae* (N=70) and select samples of *Elassoma zonatum* (N=76) from Alabama. Holotype is indicated with asterisk.

	Dorsal Fin Spines						Dorsal Fin Rays							
	2	3	4	5	$\bar{x}$	SD	8	9	10	11	12	13	$\bar{x}$	SD
Elassoma alabamae	11	57*	2		2.9	0.41	1	4	27*	31	6	1	10.6	0.84
Elassoma zonatum		2	41	33	4.4	0.54	2	16	34	22	1	1	10.1	0.88

	Anal Fin Spines						Anal Fin Rays						
	1	2	3	4	$\bar{x}$	SD	4	5	6	7	8	$\bar{x}$	SD
Elassoma alabamae	1	7	62*		2.9	37		5	28*	36	1	6.5	0.65
Elassoma zonatum			74	2	3.0	0.16	2	43	26	5		5.4	0.66

	Pectoral Fin Rays								Caudal Fin Rays							
	14	15	16	17	18	19	$\bar{x}$	SD	10	11	12	13	14	$\bar{x}$	SD
Elassoma alabamae	2	11	21	25*	7	1	16.5	1.02	1	12	46*	11		12.0	0.62
Elassoma zonatum	7	22	36	10	1		15.7	0.87	1	13	29	30	3	12.3	0.84

Table 4. Variation in number of dark lateral bars, iridescent interbars, and gill rakers in *Elassoma alabamae* (N=70) and select samples of *Elassoma zonatum* (N=76) from Alabama. Holotype is indicated with asterisk.

	Number Dark Bars									
	5	6	7	8	9	10	11	12	$\bar{x}$	SD
Elassoma alabamae	6	42*	20	2					6.2	0.66
Elassoma zonatum				14	27	21	13	1	9.5	1.03

	Number Light Interbars									
	4	5	6	7	8	9	10	11	$\bar{x}$	SD
Elassoma alabamae	1	24	35*	8	2				5.8	0.77
Elassoma zonatum				12	23	20	16	5	8.7	1.16

	Number Gill Rakers									
	2	3	4	5	6	7	8	$\bar{x}$	SD
Elassoma alabamae	8	41*	14	7				3.3	0.80
Elassoma zonatum		5	10	28	18	11	4	5.4	1.24

cence subdued or lacking from face, opercle, and narrow bars. Body coloration of juveniles generally with greater contrast between cream background coloration and darker bars or mottling along flanks and dorsum. Some juveniles or non-breeding females may have some iridescence on operculum and along narrow bars.

Coloration of non-breeding males as in breeding males except coloration more subdued. Broad bars with distinct edges and separated by narrow interbars. Depigmented areas at base of dorsal fin; posterior clear to white window present. Mottling on face with reduced iridescence. Pelvic fins as in breeding males except that distal band not as intense. Caudal fin as in breeding males except that yellow central coloration and distal dark margin not as intense.

Alcohol preserved males. Iridescent coloration of males lost soon after fixation. Flanks and dorsum of body straw colored with narrow dark brown saddles crossing dorsum posterior to nape. Nape occasionally mottled tan and dark brown. Broad bars along flank dark brown; narrow interbars cream. Margins of bars with discrete edges. Venter cream colored with some melanophores along scale margins of lower caudal peduncle. Breast, gular region, and branchiostegals cream colored with some melanophores; melanophores more heavily concentrated anteriorly along branchiostegal rays, gular region, and tip of snout.

Dorsum of head brown to tan. Preorbital and postorbital stripes black to dark brown. Cheek region, preopercle, subopercle, and opercle with cream colored background with mottling of black to dark brown; cream colored background coloration formerly iridescent in breeding males. Postorbital stripe creates dark brown dorsal margin on operculum.

Dorsal fin medially and distally dusky from dense concentration of melanophores. Base of fin darker, with dark dusky band and two depigmented spots. Posteriorly, narrow white to clear stripe or "window" extending perpendicular to rays and separating basal and distal dusky bands. Caudal fin dusky from melanophores along margins of rays and on membranes. Vertical basicaudal band and cream-colored basicaudal spots distinct. Anal fin with broad dusky basal band. Distally, anal fin dusky with heavy concentration of melanophores on rays and membranes. Distal and basal bands separated posteriorly by white to clear stripe or "window." Pelvic fins dusky, especially along broad distal margin. Pectoral fins clear, except for melanophores along membranes.

Alcohol preserved females. Iridescence of head and body lost immediately following fixation. Dorsum and flanks tan to cream colored; mottling of nape and dorsal saddles dark brown, if present. Broad bars brown and separated by narrow and light cream bars. Edges of bars irregular as in live females. Belly and lower flanks cream to tan.

Dorsum of head brown. Preorbital and postorbital stripes dark brown. Dorsum of opercle dark brown to black from postorbital stripe. Remainder of opercle, cheeks, interopercle, and subopercle mottled dark brown over cream background coloration; mottling formed from three to four poorly developed bars radiating anteroventrally to posteroventrally from eye. Cream background coloration of opercle, subopercle, and cheek formerly lightly iridescent. Gular region and branchiostegals cream colored with light speckling of melanophores.

Coloration of fins as in live females except that medial yellow coloration of dorsal, caudal, and anal fins lost. Melanophores along rays form basal dusky band and dark spots in dorsal and anal fins. Caudal rays distinctly outlined with melanophores.

Sexual Dimorphism.—The most conspicuous difference between males and females is coloration. The head, body, and dorsal and anal fins of males are more brilliantly colored than those of females throughout most of the year. The broad, dark bars along the flanks of males generally have well defined vertical edges; in females the edges of bars are more irregularly formed, often making it difficult to discern distinct bars.

Males and females differ significantly ($P<0.05$) in standard length; males are generally smaller than females (Table 1). The sexes also differ significantly in head, body, and fin proportions (Table 1). Males possess longer dorsal, anal, pectoral, and pelvic fins, longer and deeper heads, deeper caudal peduncles, larger eyes, and longer upper jaws, relative to standard length. Pelvic fins of most males extend posterior to origin of anal fin. Females have both the dorsal and anal fins placed more posterior on the

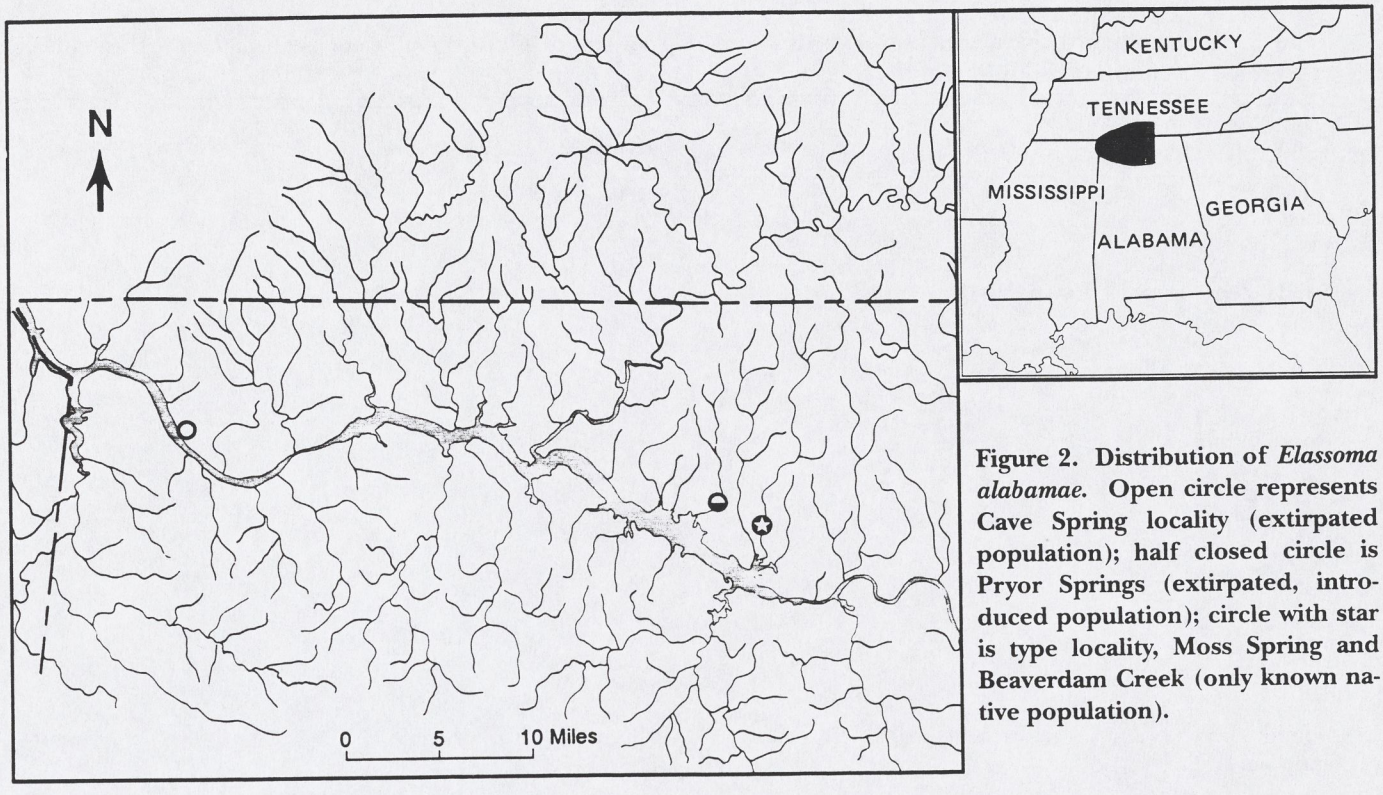

Figure 2. Distribution of *Elassoma alabamae*. Open circle represents Cave Spring locality (extirpated population); half closed circle is Pryor Springs (extirpated, introduced population); circle with star is type locality, Moss Spring and Beaverdam Creek (only known native population).

body, relative to standard length, than do males. When upper jaw length, snout length, and eye diameter were considered relative to head length only eye diameter differed significantly between the sexes; males possess larger eyes (Table 1). Bar width did not differ significantly for males and females; however, relative bar width did differ significantly. Broad, dark bars are wider relative to interbar space in males than in females ($P<0.01$). No significant differences between sexes were noted for meristic variables or number of bars or interbars along flanks.

ETYMOLOGY.—The species epithet *alabamae* refers to this rare species being endemic to the State of Alabama. The common name, spring pygmy sunfish, refers to the macrohabitat typically occupied by this species.

DISTRIBUTION.—The spring pygmy sunfish is known only from the Tennessee River Drainage in northern Alabama, and is the only known species in the genus *Elassoma* to have its entire geographic distribution above the Fall Line (Fig. 2). *Elassoma alabamae* was first collected by Tennessee Valley Authority biologist L. F. Miller on 5 November 1937 from Cave Spring near Smithsonia (T3S, R13W, Sec. 14), Lauderdale County, Alabama (Fig. 2; open circle), prior to impoundment of the adjacent Tennessee River. About four years later, on 25 April 1941, a collection by C. M. Tarzwell (TVA) from Pryor Springs System provided an additional record of the species (Fig. 2; half open circle). Both of these collections were forwarded to and identified as a distinct species by the late Dr. Carl L. Hubbs, then at the University of Michigan Museum of Zoology, and Mr. Milton B. Trautman, Ohio State University.

Natural populations of *Elassoma alabamae* from the Cave Spring and Pryor Springs areas have been extirpated. The Cave Spring locality, and habitat for the spring pygmy sunfish, was inundated by the formation of Pickwick Lake three months after the new pygmy sunfishes were found (dam closure on 8 February 1938; reservoir filled to elevation of 124.4 meters by 18 February 1938). Subsequent collection efforts and general surveys of this and surrounding areas for potential habitat have resulted in no additional specimens nor any potential habitat (Jandebeur, 1979, 1982). Native pygmy sunfishes were likely extirpated from the Pryor Springs system in the 1940's when (1) the indigenous vegetation in the springs was replaced by the parrots feather (*Myriophyllum brasiliense*) and (2) the waters were treated on 28 May 1945 with the herbicide 2, 4, D to control existing vegetation (Jandebeur, 1979). Subsequent to these disturbances the Pryor Springs system has also been channelized and subjected to agricultural pollutants.

Between 1941 and 1973 the spring pygmy sunfish was thought to be extinct. However, in January 1973 Dr. David A. Etnier (University of Tennessee, Knoxville) and students discovered *E. alabamae* along the margins of a spring-fed lake formed below Beaverdam Spring (T4S, R3W, Sec. 10) in Limestone County, Alabama (Fig. 2; circled star). Subsequent to this discovery, *E. alabamae* was also found in

Table 5. Morphological characters useful in distinguishing species of *Elassoma*. For each characteristic the state shown represents the common condition for the species.

Characteristic	*E. alabamae*	*E. zonatum*	*E. evergladei*	*E. okefenokee*	*E. boehlkei*	*E. okatie*
Lateral Scale Rows	28-30	33–36	23–32	31–34	26–28	25–29
Caudal Peduncle Scale Rows	16–18	21–24	20–24	19–20	19–20	18–20
Transverse Scale Rows	11–12	13–14	11–13	11–12	11–12	10–12
Dorsal Spines	3	4–5	4	4	4	4–5
Dorsal Rays	10–11	9–11	8–10	10–13	9–11	9–11
Anal Rays	6–7	5–6	4–6	6–8	5–7	5–7
Pectoral Rays	16–17	15–16	13–15	14–17	14–15	14–16
Windows on Dorsal and Anal Fins	present	absent	absent	absent	absent	absent
Shoulder Spots[1]	none	1–3	none	none	none	non
Vertical Bars[2]	broad; 6–7	narrow; 8–11	indistinct[3]	indistinct[3]	narrow; 12–14	narrow; 9–12
Head scales	no	no	yes	no	no	no
Pigmentation on Center of Lips	dusky	dusky	dusky	light	dusky	dusky
Postocular Stripe	present	present	absent	absent	absent	absent
Subocular Bar	poorly developed	well developed	absent	absent	well developed	well developed
Basicaudal Ocelli	not clearly bordered posteriorly	bordered posteriorly	bordered posteriorly	bordered posteriorly	bordered posteriorly	bordered posteriorly

1. May not be obvious in live specimens; more obvious in preserved specimens and generally formed as dorsal portion of dark bars.
2. In breeding males dark bars may be obliterated by very dark overall breeding coloration or bars may be separated by only narrow iridescent interbars; dark bars more obvious in preserved specimens.
3. Bars indistinct anteriorly on adults; body coloration appears mottled, dark, or dusky, depending upon breeding condition and sex. Bars best developed posteriorly on caudal peduncle, especially on males; number of bars may vary from 1–5, generally less than 3. Flanks of juveniles distinctly mottled anteriorly and barred posteriorly. Dark bars on *E. evergladei* wider than interbar spaces; width of bars on *E. okefenokee* about equal to width of interbar space.

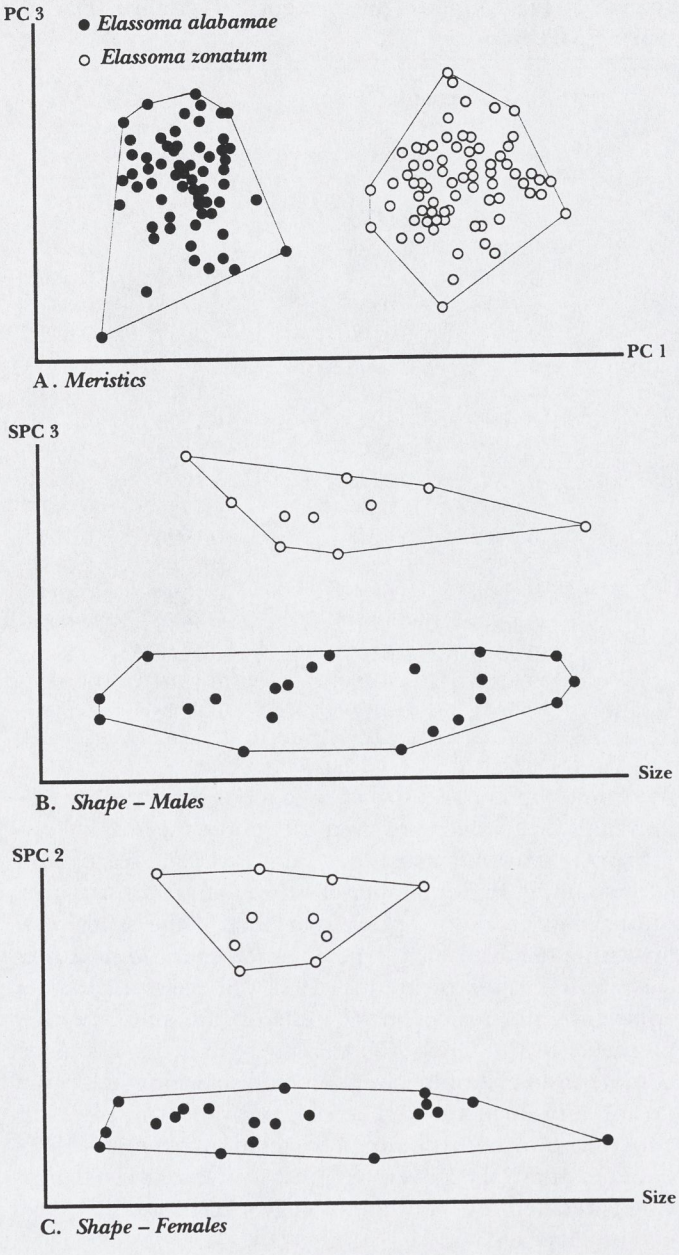

Figure 3. Principal component (PC) analysis of variation in fourteen meristic and eighteen mensural variables for *Elassoma alabamae* and *Elassoma zonatum*. Variable loadings are presented in Table 6. SPC = Sheared principal component.

Moss Spring (T4S, R3W, Sec. 16) and Lowe's Ditch and run, both draining into the lake within Beaverdam swamp (T. S. Jandebeur, pers. comm., 8 December 1992). Significant collecting efforts in other potential spring and swamp locations in north Alabama have failed to reveal any additional populations of this species outside of Beaverdam Spring and swamp complex (inclusive of Moss Spring and Lowe's Ditch) (Jandebeur, 1979, 1982). Within the Beaverdam Spring and swamp system *E. alabamae* has been collected from a number of locations, appears to be seasonal in its habitat selection, and is generally common within Moss Spring (Jandebeur, 1979; Darr and Hooper, 1991; pers. obs.). No specimens of *E. alabamae* have been found in Beaverdam Spring proper or in the Beaverdam Creek and swamp below the confluence with Moore Branch (T. S. Jandebeur, pers. comm., 8 December 1992).

As a conservation measure, on 17 February 1984, 36 adult specimens (11 males, 25 gravid females) of *E. alabamae* from Moss Spring (T4S, R3W, Sec. 16) were successfully introduced into its former range. These specimens were placed in "an unnamed spring tributary (T4S, R4W, S21) to Pryor Branch, which is located approximately 300 yards west of U. S. hwy 31" . . . "also called Lower Pryor Spring" (Mettee and Pulliam, 1986:14) or spring number 2 of the Pryor Springs system (Mettee et al., 1986). In the following year, 120 additional specimens (37 males and 83 females) were transferred to Pryor Spring #2 upon determination of successful stocking effort in this spring in the previous year. In January 1987, 58 males and 59 females were moved from Moss Spring to the original Pryor Spring where the species had been extirpated. The status of this latter introduction was reported as unknown by Pierson (1990), but was considered successful by T. S. Jandebeur (pers. comm., 8 December 1992). Jandebeur (pers. comm.) surveyed the Pryor Spring System as recent as 19 and 28 September 1992. On both occassions *E. alabamae* was determined to be common and occupying, in addition to the springs, flooded and impounded (beaver dam on Pryor Branch) regions west of Hwy 31S, between Pryor Spring and Pryor Spring #2, in areas formerly not inhabitated by this species. Today, extant populations of *E. alabamae* are restricted to the Beaverdam Creek watershed and Pryor Spring system where they live in close association with nearby wetlands and swamps.

HABITAT.—In 1937 L. F. Miller described Cave Spring as having clear water and abundant and thickly matted vegetation along the shoreline. The substrate was a fine sand and mud. The shoreline was lined with blue-grasses and weeds and was marshy in some areas. Depth of capture was from 15 cm to 1 m, in waters that were up to 1.4 m deep. This characterization of the Cave Spring ecosystem accurately describes the Moss Spring area where *E. alabamae* is commonly found today.

In the Moss Spring and Beaverdam Creek/Swamp area *Elassoma alabamae* is most commonly found above the substrate in association with rooted, submergent vegetation (generally *Ceratophyllum, Myriophyllum, Utricularia,* and *Elodea*). The water is clear and the substrate consists largely of fine sand, clay, mud, and/or limestone. The shoreline is generally lined with sparse to abundant hardwood trees, some shrubs, and grasses (sometimes as a marsh-like wetland). Apparently, the species is very mobile and uses the different spring and swamp macrohabitats at different times of the year (Jandebeur, 1979; Darr and Hooper, 1991).

Table 6. Principal component (PC) loadings for fourteen meristic variables (Fig. 3A) and eighteen mensural variables (Fig. 3B and C) in *Elassoma alabamae* and *Elassoma zonatum*. SPC=Sheared principal component.

Meristics		Measurements				
			Males		Females	
Variable	PC1	Variable	Size	SPC3	Size	SPC2
Dorsal fin spines	0.8604	Standard length	-0.1316	0.0692	-0.1706	0.0411
Dorsal fin rays	-0.2506	Preanal length	-0.1286	0.1284	-0.2167	0.0777
Anal fin spines	0.3163	Predorsal length	-0.1150	0.1084	-0.1561	0.0463
Anal fin rays	-0.6560	Prepelvic length	-0.1439	0.0439	-0.1745	0.0676
Pectoral fin rays	-0.3333	Body depth	-0.1667	0.0400	-0.2034	0.0324
Pelvic fin rays	-0.5057	Caudal peduncle length	-0.1709	-0.0058	-0.1744	-0.0880
Caudal fin rays	0.2233	Caudal peduncle depth	-0.2184	0.1013	-0.1310	0.1982
Lateral scales	0.8897	Head length	-0.1095	0.1242	-0.1208	0.1136
Transverse scales	0.8101	Head depth	-0.1257	0.0705	-0.1052	0.0862
Caudal peduncle scales	0.9170	Eye diameter	-0.1352	-0.0275	-0.1240	0.0451
Broad vertical bars	0.9353	Snout length	-0.2705	-0.0678	-0.1736	0.0917
Interbars	0.9030	Upper jaw length	-0.2412	-0.0238	-0.1920	0.1080
Branchiostegals	-0.0613	Dorsal fin length	-0.1878	0.1361	-0.1545	0.2290
Gill rakers	0.7276	Anal fin length	-0.2290	0.0725	-0.1123	0.1891
		Pectoral fin length	-0.1280	0.3261	-0.1245	0.3956
		Pelvic fin length	-0.2014	0.0392	-0.1119	0.2502
		Dark bar width	-0.2107	-0.8125	-0.4310	-0.5964
		Interbar width	-0.6791	0.0169	-0.6496	-0.0034

Other fish species found in association with the spring pygmy sunfish in Cave, Pryor, and Moss springs include *Amia calva, Clinostomus funduloides, Cyprinella whipplei, Hemitremia flammea, Luxilus chrysocephalus, Notemigonus crysoleucas, Pimephales vigilax, Semotilus atromaculatus, Erimyzon sucetta, Minytrema melanops, Ameiurus natalis, Esox americanus, Esox niger, Gambusia affinis, Chaenobryttus gulosus, Lepomis cyanellus, L. macrochirus, L. microlophus, L miniatus, Micropterus dolomieu, Etheostoma duryi, E. nigripinne,* and *E. tuscumbia.*

Life History.—No one study has focused on all aspects of the life history of *Elassoma alabamae.* General habitat has been described Ramsey et al. (1972), Mettee (1974), Ramsey (1976), Jandebeur (1979, 1982), Mettee and Ramsey (1986), and Darr and Hooper (1991). Jandebeur (1979, 1982) reported that critical habitat for the species existed in heavily vegetated areas within Moss Spring and its discharge into Beaverdam Creek, Lowe's Ditch, and the Beaverdam Creek and swamp system. Reproductive biology and development was studied by Mettee (1974). Most spawning occurs in March and April (Darr and Hooper, 1991; pers. obs.). Females can produce up to 65 eggs per spawning (Mettee and Ramsey, 1986). Based on results from Mettee (1974), Mettee and Ramsey (1986)and Darr and Hooper (1991), the spring pygmy sunfish is thought to be an annual species; adults spawn at one year of age and die within a few days to months after spawning. Population demography data presented by Darr and Hooper (1991) support this hypothesis; however, population estimates were not provided in this study. These authors recorded number and size of specimens captured, condition of the specimens, sex, maturity, and parasites. Following spring spawning activities adults die in late spring and early summer. By September, the population consists only of offspring from the spring spawning of the same year. Spawning behavior of *E. alabamae* and other *Elassoma* species was described by Mettee (1974). Species of *Elassoma* apparently do not construct nests on the substrate like members of the family Centrarchidae and possess more complex and elaborate courtship and spawning behaviors (Walsh and Burr, 1984). The eggs of pygmy sunfishes are generally attached to aquatic vegetation (usually *Ceratophyllum*) above the substrate. Walsh and Burr (1984) provide a detailed review of the biology of *Elassoma.*

Conservation status.—The extremely small geographic distribution and short life span of *E. alabamae* affords this species a largely precarious future. *Elassoma alabamae* is known to be sensitive to habitat alterations and an unsuccessful spawning season could easily result in its extinction. Two populations have already been lost through impoundment and poor land-use practices. Today, the stronghold for the species is surrounded by pasture lands, secondary growth, and agriculture. Many acres of farm and pasture lands, some of which are dusted aerially with pesticides and herbicides, surround the spring and serve as a significant portion of its watershed. Unless safe land-use practices are monitored and enforced in the Pryor Springs Complex and the Moss Spring and Beaverdam Creek watershed, one careless mistake might result in the loss of the only known native population of this species.

In the Pryor Springs Complex, where *E. alabamae* has been introduced from Moss Spring, the species appears to be reproducing with some success and has even spread its range to occupy new flooded and impounded areas formed by beaver dams on Pryor Springs Branch (T. S. Jandebeur, pers. comm., 8 December 1992). In the Moss Spring system *E. alabamae* is common. Darr and Hooper (1991) monitored this population to determine mortality and recruitment estimates. Their monitoring study indicated that *E. alabamae* was the most common fish species in the spring complex, the preferred habitat of the species included margins of the spring in submerged and surface vegetation, and that most reproduction occurred in March.

Given the restricted distribution of *E. alabamae* and its generally fragile life history, this species has been considered endangered by Ramsey et al. (1972), Ramsey and Mettee (1986), and Pierson (1990). An informal and renewable agreement has existed between landowners at Moss Spring and Beaverdam Swamp, U. S. Fish and Wildlife Service, and Alabama Department of Conservation and Natural Resources to continue to preserve the habitat quality for the spring pygmy sunfish. However, given the close proximity of both extant populations to local highways, livestock, and active agricultural practices, and their potential exposure to harmful levels of pesticides and herbicides, it would be advisable that this extremely rare species receive State and Federal protection as an endangered species and have populations monitored regularly. Furthermore, a more complete study of the biology and phylogenetic relationships of this species may provide a better understanding of the factors limiting the geographic range of this species. Likewise, a more thorough understanding of the genetic variation in *E. alabamae* is warranted before any additional transfers to new locations is conducted.

COMPARISONS.—Diagnosable characters for species of *Elassoma* are presented in Table 5. *Elassoma alabamae* differs from all other species of *Elassoma* in having only three dorsal fin spines, six or seven broad and dark bars along flanks separated by narrow and lightly colored interbars, 16–18 caudal peduncle scale rows, a single narrow, white to clear window in the dorsal and anal fins of males, and cream to white basicaudal ocelli bounded anteriorly, but not posteriorly, by a dark bar. Other species of *Elassoma* generally possess 4–5 dorsal fin spines, greater than 7 dark bars along flanks, narrower dark bars along flanks, more narrow and lightly colored interbars, 18–24 caudal peduncle scale rows, no white windows in dorsal and anal fins, and basicaudal ocelli bounded anteriorly and posteriorly by dark bars. *Elassoma alabamae* may be further separated from *E. zonatum*, geographically the closest congeneric, on the basis of coloration (Fig. 1, Table 5), meristic features (Fig. 3A, Tables 2–6), and body shape (Fig. 3B and C, Tables 1 and 6).

Elassoma alabamae differs significantly from *E. zonatum* with respect to all meristic variables ($P<0.0001$) (Tables 2–4), except for number of branchiostegal rays. Variation in all meristic variables for both species and both sexes is summarized in the principal component analysis of these variables (Fig. 3A, Table 6). The first principal component provides the best separation of *E. alabamae* and *E. zonatum*; variables loading heavily on this axis include number of bars and interbars along flanks, dorsal fin spines, anal fin rays, caudal peduncle scale rows, transverse scale rows, lateral scale rows, and gill rakers (Fig. 3A, Table 6). The second and third principal components provided no separation using meristic variables. Variability of mensural features for males and females of both species is summarized in sheared principal component analysis of these characters (Fig. 3B and C, Table 6). Males differ primarily in width of dark bars, head length, preanal and predorsal lengths, caudal peduncle depth, and length of the dorsal and pectoral fins; *Elassoma alabamae* possesses wider bars, a shorter head and preanal and predorsal length, a narrower caudal peduncle, and shorter dorsal and pectoral fins relative to *E. zonatum* (Fig. 3B, Tables 1 and 6). Females differ primarily in width of dark bars, head length, caudal peduncle depth, and length of fins; *E. alabamae* possesses wider bars, a shorter head, a narrower caudal peduncle, and shorter fins relative to *E. zonatum* (Fig. 3C, Tables 1 and 6).

Comparative Materials

The following specimens were employed in various aspects of comparisons with *Elassoma alabamae*. *Elassoma boehlkei*: ANSP 158482 (25 specimens), NCSM 12832 (61), NCSM 12833 (61). *Elassoma okatie*: ANSP 150053 (67), 158484 (71), NCSM 12834 (6), NCSM 12835 (3). *Elassoma okefenokee*: UAIC 8777.04 (28), UAIC 8833.03 (40), UAIC 8932.05 (15). *Elassoma evergladei*: UAIC 1226.08 (5), UAIC 1556.05 (28), UAIC 1559.08 (13), UAIC 4690.05 (3), UAIC 5277.04 (2). *Elassoma zonatum*: UAIC 44.03 (1), UAIC 1834.02 (42), UAIC 2027.01 (6), UAIC 2806.24 (11), UAIC 2854.01 (2), UAIC 3601.10 (1), UAIC 4210.05 (1), UAIC 4211.07 (2), UAIC 4212.13 (2), UAIC 4676.06 (2), UAIC 8334.09 (5), UAIC 8335.03 (3), UAIC 8403.02 (4), UAIC 9597.04 (3), UAIC 9640.08 (1), UAIC 10280.01 (28).

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Systematics of the *Etheostoma jordani* Species Group (Teleostei: Percidae), With Descriptions of Three New Species

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ABSTRACT: Wood, Robert M., and Richard L. Mayden. 1993. Systematics of the *Etheostoma jordani* species group (Teleostei: Percidae), with descriptions of three new species. Bulletin Alabama Museum of Natural History, Number 16:31–46, 5 tables, 6 figures. Members of the *Etheostoma jordani* species group are endemic to and distributed throughout the Mobile Basin, largely above the Fall Line. Variation in 22 standard and truss measurements, 18 meristic characters, and coloration was examined throughout the range of this species group. Analysis of these characters supports the recognition of four distinct and allopatrically distributed species. The four species are endemic to the: 1) Black Warrior River System; 2) the Cahaba, Coosa, and lower Tallapoosa river systems; 3) the Etowah River System; and 4) the upper Tallapoosa River System. State and Federal protection is recommended for each of the three species from the Black Warrior, upper Etowah, and upper Tallapoosa rivers.

Introduction

Rivers of the Mobile Basin contain one of the most distinctive ichthyofaunas in North America, characterized by at least 40 endemic species (Swift et al., 1986; Burr and Mayden, 1992). Faunal diversification within this basin has followed from a long history of drainage exchange and isolation of gene pools, combined with a limited impact of the detrimental processes associated with Pleistocene glaciation (Swift et al., 1986; Wiley and Mayden, 1985; Mayden, 1988).

The greenbreast darter, *Etheostoma jordani* Gilbert, endemic to the Mobile Basin primarily above the Fall Line, has long been considered a single species (Zorach, 1969). Evaluation of variation in morphology and color in the greenbreast darter from throughout its range has revealed that in reality four distinct species are represented. The focus of this paper is to describe variation within this group of darters, redescribe *Etheostoma jordani* Gilbert, and present formal taxonomic descriptions of the three new species.

Methods

Variation within the *Etheostoma jordani* species group was explored using standard meristic and morphometric characters following Hubbs and Lagler (1974) and truss variables sensu Humphries et al. (1981) except as follows. Transverse scale rows were counted from the anal fin origin to the first dorsal fin. A total of 18 meristic variables were examined including: lateral line scale rows, transverse scale rows above and below lateral line, caudal peduncle scale rows above and below lateral line, dorsal fin spines, dorsal fin rays, anal fin spines, anal fin rays, pelvic fin rays, pectoral fin rays, caudal fin rays, branchiostegal rays, and breast, opercle, cheek, and nape squamation. Caudal fin rays include principal rays plus two. Body measurements were generated using electronic calipers (nearest 0.01 mm) and were input directly into a computer data base. All body lengths reported are standard lengths. A total of 22 standard and truss measurements were examined (Fig. 1). Standard measurements included standard length (SL:D1–15), head length (HL:D1–8), head depth

Bull. Alabama Mus. Nat. Hist. 16:31–46

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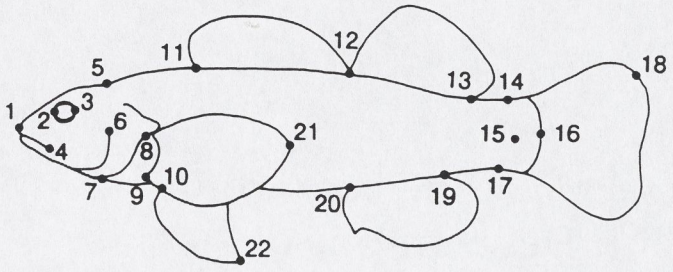

Figure 1. Numbered points indicate landmarks from which corresponding measurements below were taken. When a number is duplicated in a measurement this indicates that the second landmark was in the same position as the first on the opposite side of the fishes body from that shown.

Landmarks

D1	**Anterior-most tip of snout**
D2/D3	**Greatest bony distance of orbit**
D4	**Posterior-most point of closed mouth**
D5	**Occiput**
D6	**Dorsal-most point of preopercular margin**
D7	**Breast posterior to isthmus**
D8	**Posterior-most margin of opercle below opercular spine**
D9	**Insertion of pectoral fin**
D10	**Insertion of pelvic fin**
D11	**Origin of spinous dorsal fin**
D12	**Origin of soft dorsal fin**
D13	**Insertion of posterior-most ray of soft dorsal fin**
D14/D17	**Least depth of caudal peduncle along line through hypural plate**
D16	**Insertion of medial caudal ray**
D18	**Tip of longest caudal ray**
D19	**Insertion of posterior-most anal fin ray**
D20	**Insertion of first anal fin spine**
D21	**Tip of longest pectoral ray**
D22	**Tip of longest pelvic ray**

(HD:D5–7), head width (HW:D6–6), snout length (SN:D1–2), predorsal length (PL:D1–11), eye diameter (ED:D2–3; 2 and 3 being at greatest bony distance), gape width (GW:D4–4), pectoral fin length (PT:D9–21), pelvic fin length (PV:D10–22), spinous dorsal fin base length (DIL:D11–12), soft dorsal fin base length (DIIL:D12–13), anal fin base length (AL:D20–19), caudal fin length (CL:D16–18), caudal peduncle width (CW:D15–15), and caudal peduncle depth (CD:D14–17); truss measurements included spinous dorsal origin to pelvic fin origin (D11–10), spinous dorsal origin to anal fin origin (D11–20), spinous dorsal insertion to anal fin origin (D12–20), soft dorsal fin origin to anal fin insertion (D12–19), soft dorsal fin origin to pelvic fin origin (D12–10), anal fin origin to soft dorsal insertion (D20–13).

Characters derived from coloration included head, body, and fin pigmentation patterns. Details of coloration patterns were obtained from live specimens and color transparencies of live and recently preserved specimens. Consistency of these traits was verified by the examination of live and freshly preserved breeding and non-breeding adult specimens throughout the Mobile Basin over a four year period.

Statistical analysis of morphometric variables included Student's t-test ($P<0.05$) for comparisons of males and females for sexual dimorphism within each species and sheared principal component analysis for differences among species (SAS code for running sheared PCA provided by D. L. Swofford). Because males and females were divergent for some body measurements, sexes were evaluated separately for principal component analysis of morphometric variables. Principal component analysis of meristic variables employed a correlation matrix; analysis of morphometric variables employed a covariance matrix.

Etheostoma jordani species group

Diagnosis.—Members of subgenus *Nothonotus* as diagnosed by Zorach (1972) and Page (1981). Distinguished from other members of *Nothonotus* by lack of dark horizontal lines between scale rows, presence of a partially scaled nape [only found elsewhere in *E.* (*Nothonotus*) *bellum*], presence of dark mottling on side of body forming 3 to 11 weak vertical bars, presence of broad subdistal red band in caudal fin of males. Distributed widely throughout the Mobile Basin, primarily above the Fall Line.

Etheostoma jordani Gilbert
Greenbreast Darter
Figures 2 and 3A

Lectotype.—USNM 125110, adult male, 48 mm, Choccoloco Creek at Oxford, Coosa River System, Calhoun County, Alabama, 23 May 1889, P. H. Kirsch, W. M. Andrews, and E. O. Jones. Designated by Collette and Knapp (1967).

Diagnosis.—A member of the *Etheostoma jordani* species group of the subgenus *Nothonotus*. Distinguished from other members of the species group by presence of red spots without dark halos on side of body, olivaceous lips, blue-turquoise anal fin, and exposed scales on opercles.

Description.—Morphometric measurements and some diagnostic meristic variables are reported in Tables 1 and 2. General head and body shape and pigmentation are shown in Figures 2 and 3a.

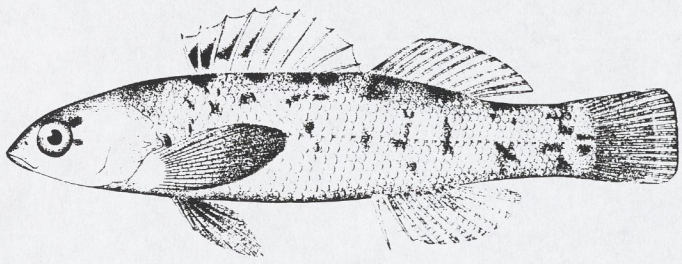

Figure 2. Original illustration of *Etheostoma jordani* (Gilbert, 1891).

Dorsal spines 9(5 specimens), 10(129), 11(86), 12(5); $\bar{x}$=10.4, SD = 0.58. Soft dorsal rays 10(2), 11(29), 12(169), 13(25); $\bar{x}$ = 11.9, SD = 0.52. Anal fin rays 6(4), 7(81), 8(134), 9(6); $\bar{x}$ = 7.6, SD = 0.57. Pectoral fin rays 12(51), 13(168), 14(6); $\bar{x}$=12.8, SD=0.46. Caudal fin rays 16(6), 17(215), 18(4); $\bar{x}$=16.1, SD=0.21. Scale rows above lateral line 6(70), 7(144), 8(11); $\bar{x}$=6.7, SD=0.54. Scale rows below lateral line 6(2), 7(160), 8(63); $\bar{x}$=7.3, SD=0.47. Scale rows above lateral line at caudal peduncle 7(38), 8(118), 9(67), 10(2); $\bar{x}$=8.2, SD=0.69. Scale rows below lateral line at caudal peduncle 8(6), 9(140), 10(74) 11(5); $\bar{x}$=9.4, SD=0.57. Branchiostegal rays 5(2), 6(222), 7(1); $\bar{x}$=6.0, SD=0.12. Nape squamation 0% (6), 10% (11), 20% (6), 30% (41), 40% (13), 50% (111), 60% (10), 80% (21), 90% (4), 100% (2); $\bar{x}$=0.5, SD=0.19. Cheek without scales, opercle with scales, breast generally without scales (217) occasionally 1–4 embedded scales (8).

Male genital papilla is a broad based, shortened conical structure. Female genital papilla is a thick elongate conical structure.

Preoperculomandibular canal pores 10(10). Infraorbital canal pores 6(1), 7(2), 8(7); $\bar{x}$=7.6, SD=0.66. Lateral canal pores 4(10). Supratemporal canal pores 2(5), 3(5); $\bar{x}$=2.5, SD=0.50. Supraorbital canal pores 3(2), 4(8); $\bar{x}$=3.8, SD=0.40. Coronal pore 1(10).

Males were found to possess significantly greater head depth, gape width, caudal peduncle depth and caudal peduncle width than females, while females possessed a significantly larger eye diameter than males ($P<0.05$, Table 1). No other significant differences were found in either morphometric or meristic traits.

Coloration.—Males and females are dichromatic; males being more brightly colored than females throughout the year, dichromatism reaching its peak during the spring. Coloration of a male in breeding condition is depicted in Figure 3A.

Breeding males. Body olivaceous with concentrations of melanophores forming pattern of 3–11 weakly defined vertical bars along flanks. Flanks with red spots, lacking dark halos typical of other *Nothonotus*; spots equally distributed above and below lateral line, more concentrated from distal tip of pectoral fin posteriorly. Dorsum with 8–9 distinct olivaceous to brown quadrate blotches, most prominent blotch lying across anterior portion of nape. Head olivaceous dorsally, slightly turquoise on ventral surface. Lips olivaceous. Sub-orbital bar weak, extending from eye toward ventral-most portion of cheek. Post-orbital bar distinct, extending from eye to one-half distance across dorsal margin of opercle. Breast and branchiostegal rays and membranes turquoise. Caudal peduncle at caudal fin insertion with four brown to black spots; two at midline may coalesce to form a single spot, one at dorsal-most and one at ventral-most portions of caudal peduncle.

Spinous dorsal fin with thin clear to white margin followed proximally by intense red band (1.0–2.0 mm in width); red band most prominent anteriorly, becoming thinner posteriorly. Basal four-fifths of spinous dorsal fin olivaceous with black elliptical blotches in membranes between first 3–7 spines; anterior two blotches most intense. Soft dorsal fin with narrow turquoise to black margin followed proximally by thin clear to yellow band, followed proximally by red band (2.0–4.0 mm). Basal one-half of soft dorsal fin olivaceous. Distal one-half of caudal fin with turquoise band (1.0–2.0 mm) at fin margin followed proximally by broad red band (3.0–5.0 mm). Proximal one-half of caudal fin with yellow to clear membranes and black rays. Pelvic fins white at margin, followed proximally by broad turquoise band becoming black toward insertion. Pectoral fins clear; occasional orange chromatophores near insertion. Distal one-half of anal fin turquoise; basally, fin olivaceous to black.

Breeding females. Body brown and mottled with 3–11 weakly defined vertical bars along flanks, more pronounced along and below lateral line. Sub-orbital bar prominent, extending from eye to ventral-most portion of cheek; post-orbital bar distinct, extending from eye to one-half width of opercle. Breast and branchiostegals may have faint turquoise cast. Four distinct spots at caudal fin insertion as in males.

Spinous dorsal fin, olivaceous to black basally; distally, fin with thin red marginal band. Soft dorsal fin mottled basally; thin black band at margin. Caudal fin mottled, yellow to orange in color, with black marginal band. Anal fin with prominent black wash on basal one-half to two-thirds of fin, becoming clear at margin. Pelvic fins clear to faintly mottled on rays and membranes. Pectoral fins clear, occasionally with some yellow to orange pigment on membranes near insertion of fin rays.

Coloration of preserved males.—Body tan to olivaceous. Along flanks, melanophores forming pattern of 3–11 weakly defined vertical bars; melanophores more prominent just below lateral line generally coalescing to form distinct spot. Body scales with concentration of melanophores at margins forming a black marginal band on each

Table 1. Proportional measurements of the *Etheostoma jordani* species group. * Indicates significant differences between the sexes at P < 0.05 level.

Etheostoma jordani

	Males (N=102)			Females (N=90)		
	Range	$\bar{x}$	SD	Range	$\bar{x}$	SD
SL (mm)	33.690–52.360	43.036	4.012	31.390–54.370	38.205	4.328
HL	9.360–15.310	12.470	1.150	8.880–15.430	11.157	1.306
HL/SL	0.268–0.312	0.290	0.010	0.254–0.330	0.291	0.014
HD/HL*	0.521–0.774	0.610	0.042	0.514–0.764	0.597	0.045
HW/HL	0.386–0.591	0.468	0.040	0.383–0.574	0.462	0.041
SN/HL	0.196–0.282	0.239	0.017	0.199–0.282	0.234	0.017
GW/HL*	0.171–0.299	0.224	0.027	0.146–0.271	0.208	0.025
EY/HL*	0.173–0.245	0.210	0.015	0.165–0.258	0.221	0.016
PL/SL	0.340–0.392	0.360	0.010	0.333–0.402	0.362	0.012
PT/SL	0.191–0.281	0.242	0.017	0.184–0.285	0.241	0.018
PV/SL	0.175–0.236	0.207	0.013	0.168–0.236	0.206	0.014
CL/SL*	0.124–0.210	0.168	0.019	0.134–0.212	0.172	0.018
CD/SL	0.105–0.142	0.121	0.007	0.097–0.134	0.114	0.007
CW/SL*	0.025–0.046	0.034	0.004	0.025–0.043	0.033	0.004

Etheostoma douglasi

	Males (N=31; includes holotype)			Females (N=30)		
	Range	$\bar{x}$	SD	Range	$\bar{x}$	SD
SL (mm)	32.290–63.270	46.271	8.401	31.780–54.570	39.923	6.084
HL	10.330–18.110	13.681	2.168	9.800–16.330	12.056	1.518
HL/SL	0.265–0.323	0.297	0.012	0.274–0.333	0.303	0.013
HD/HL	0.496–0.732	0.610	0.050	0.520–0.645	0.589	0.035
HW/HL	0.392–0.623	0.490	0.043	0.410–1.009	0.488	0.103
SN/HL	0.214–0.276	0.234	0.015	0.208–0.272	0.236	0.016
GW/HL*	0.191–0.301	0.229	0.022	0.179–0.255	0.215	0.019
EY/HL*	0.180–0.239	0.214	0.014	0.183–0.263	0.225	0.022
PL/SL*	0.331–0.387	0.367	0.015	0.351–0.406	0.380	0.013
PT/SL	0.183–0.285	0.244	0.022	0.222–0.288	0.251	0.018
PV/SL	0.172–0.236	0.214	0.015	0.187–0.237	0.214	0.013
CL/SL	0.151–0.205	0.182	0.015	0.135–0.226	0.186	0.019
CD/SL*	0.116–0.145	0.128	0.008	0.106–0.133	0.123	0.007
CW/SL	0.027–0.042	0.034	0.004	0.026–0.038	0.033	0.003

Table 1. continued

Etheostoma chuckwachatte

	Males (N=15; includes holotype)			Females (N=15)		
	Range	$\bar{x}$	SD	Range	$\bar{x}$	SD
SL (mm)	35.520–44.250	39.484	2.821	33.500–41.980	37.781	2.751
HL	10.590–12.950	11.589	0.690	9.630–12.790	11.038	0.946
HL/SL	0.276–0.311	0.294	0.009	0.269–0.315	0.292	0.012
HD/HL	0.546–0.640	0.594	0.025	0.534–0.640	0.586	0.033
HW/HL	0.439–0.520	0.480	0.023	0.407–0.532	0.478	0.033
SN/HL	0.214–0.255	0.231	0.011	0.221–0.272	0.234	0.013
GW/HL	0.203–0.275	0.235	0.019	0.196–0.268	0.227	0.021
EY/HL*	0.206–0.244	0.224	0.011	0.211–0.284	0.236	0.019
PL/SL	0.350–0.386	0.372	0.010	0.351–0.397	0.370	0.012
PT/SL	0.213–0.275	0.236	0.019	0.222–0.268	0.243	0.014
PV/SL	0.195–0.226	0.208	0.010	0.186–0.233	0.207	0.012
CL/SL*	0.127–0.160	0.146	0.010	0.135–0.181	0.154	0.012
CD/SL	0.105–0.135	0.118	0.008	0.103–0.123	0.113	0.006
CW/SL	0.026–0.042	0.034	0.005	0.028–0.038	0.032	0.003

Etheostoma etowahae

	Males (N=7; includes holotype)			Females (N=16)		
	Range	$\bar{x}$	SD	Range	$\bar{x}$	SD
SL (mm)	43.350–47.240	44.664	1.266	30.130–46.370	39.964	5.070
HL	12.080–13.860	12.871	0.567	8.680–13.590	11.486	1.388
HL/SL	0.271–0.300	0.288	0.009	0.273–0.305	0.288	0.009
HD/HL	0.559–0.653	0.591	0.029	0.522–0.642	0.578	0.040
HW/HL	0.402–0.492	0.442	0.031	0.408–0.501	0.448	0.030
SN/HL*	0.234–0.290	0.268	0.025	0.217–0.262	0.239	0.016
GW/HL	0.188–0.232	0.211	0.014	0.168–0.241	0.199	0.022
EY/HL	0.200–0.227	0.214	0.011	0.183–0.236	0.218	0.014
PL/SL	0.347–0.381	0.360	0.012	0.335–0.385	0.357	0.013
PT/SL	0.237–0.282	0.250	0.015	0.197–0.257	0.236	0.017
PV/SL	0.194–0.234	0.210	0.016	0.175–0.251	0.203	0.017
CL/SL	0.140–0.174	0.164	0.012	0.146–0.193	0.171	0.015
CD/SL	0.107–0.124	0.113	0.006	0.098–0.120	0.108	0.007
CW/SL	0.027–0.038	0.033	0.004	0.025–0.036	0.032	0.003

Table 2. Variation in some meristic characters in the *Etheostoma jordani* species group.

Lateral Scale Rows

	42	43	44	45	46	47	48	49	50	51	52	53	54	55	N	$\bar{x}$	SD
Etheostoma jordani																	
Coosa River				8	4	8	19	30	21	32	21	12	3	6	164	50.2	2.3
Cahaba River				3	1	3	7	4	10	1		1			30	48.6	1.8
Lower Tallapoosa River			1	1	4	5	5	3	7	3	1				30	48.3	2.0
Etheostoma douglasi			1	4	5	3	6	6	13	9	5	5	2	1	60	49.5	2.5
Etheostoma etowahae	2	2	5	11	4	7	7	2	1	1					35	45.5	1.8
Etheostoma chuckwachatte			1	1	8	8	9	10	9	4	2				52	48.3	1.8

Transverse Scale Rows

	11	12	13	14	15	16	17	N	$\bar{x}$	SD
Etheostoma jordani										
Coosa River				38	77	40	9	164	15.1	0.82
Cahaba River				19	7	3	1	30	14.5	0.81
Lower Tallapoosa River				12	8	10		30	14.9	0.86
Etheostoma douglasi			2	26	16	13	3	60	14.8	0.98
Etheostoma etowahae	5	7	16	6	1			35	12.7	1.01
Etheostoma chuckwachatte			3	22	16	11		52	14.6	0.87

Caudal Peduncle Scale Rows

	15	16	17	18	19	20	21	22	23	24	N	$\bar{x}$	SD
Etheostoma jordani													
Coosa River			5	31	62	30	33	1	2		164	19.4	1.18
Cahaba River				1	14	7	8				30	19.7	0.90
Lower Tallapoosa River			1	1	12	10	5	1			30	19.6	1.02
Etheostoma douglasi				5	15	7	18	11	3	1	60	20.4	1.46
Etheostoma etowahae	1	7	16	8	3						35	17.1	0.94
Etheostoma chuckwachatte			8	7	26	7	3	1			52	18.8	1.13

Percent Squamation on Opercle

	0.0	0.05	0.10	0.20	0.25	0.30	0.40	0.50	0.60	0.75	0.80	1.00	N	$\bar{x}$	SD
Etheostoma jordani															
Coosa River			1	1	14	2	6	111	2	25		2	164	0.5	0.14
Cahaba River						5	1	19	3	2			30	0.5	0.11
Lower Tallapoosa River					5			25					30	0.4	0.09
Etheostoma douglasi	60												60	0.0	0.00
Etheostoma etowahae	2	1	1	9	5	8	7	2					35	0.3	0.12
Etheostoma chuckwachatte				2	1	4	13	29			3		52	0.4	0.12

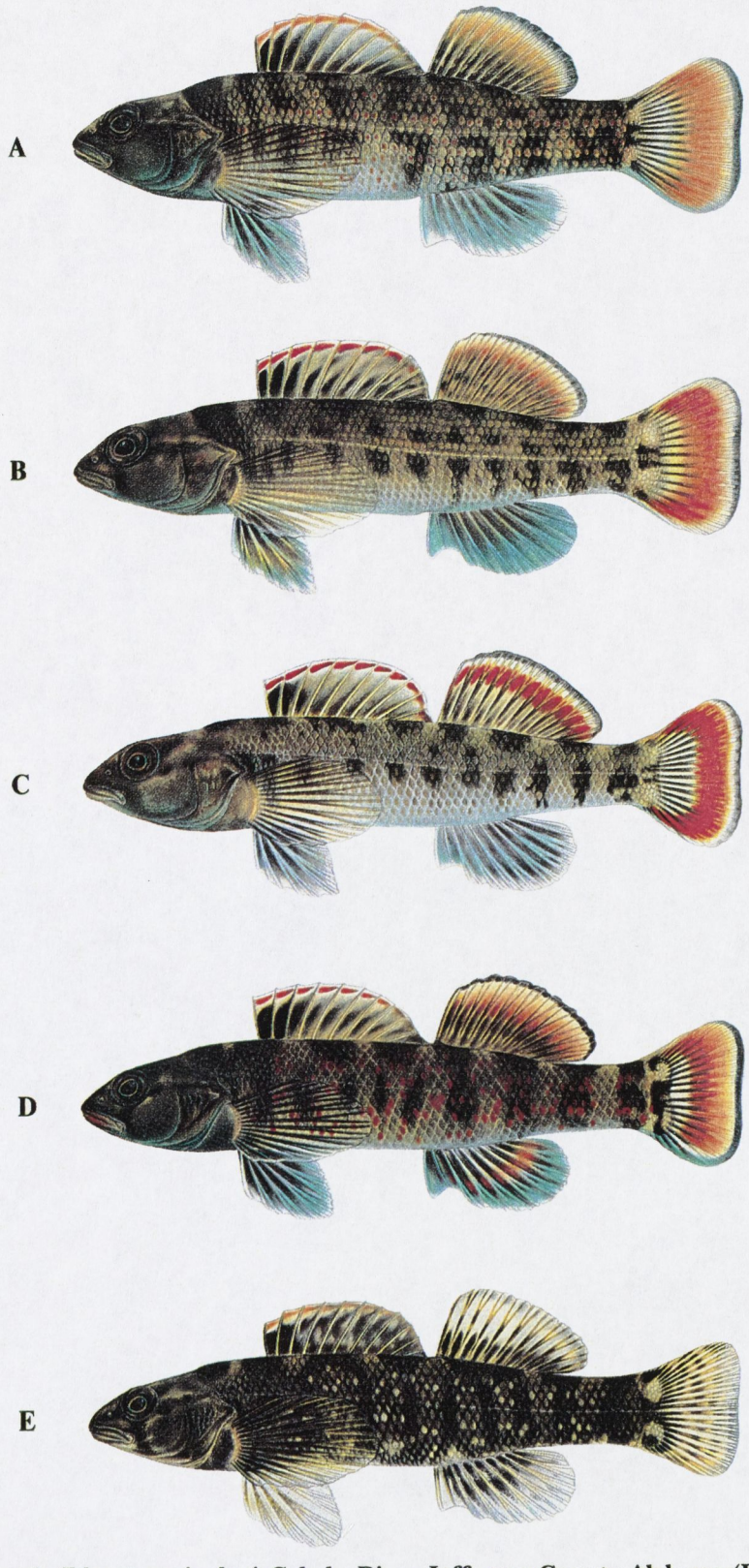

Figure 3. A. Breeding male *Etheostoma jordani*, Cahaba River, Jefferson County, Alabama (UAIC 10286.01). B. Breeding male *Etheostoma douglasi*, West Fork Sipsey River, Winston County, Alabama (UAIC 10273.01). C. Breeding male *Etheostoma etowahae*, Amicalola Creek, Dawson County, Georgia (UAIC 10471.01). D. Breeding male *Etheostoma chuckwachatte*, Hillabee Creek, Tallapoosa County, Alabama (UAIC 10284.01). E. Female *Etheostoma chuckwachatte* (same collection data as male).

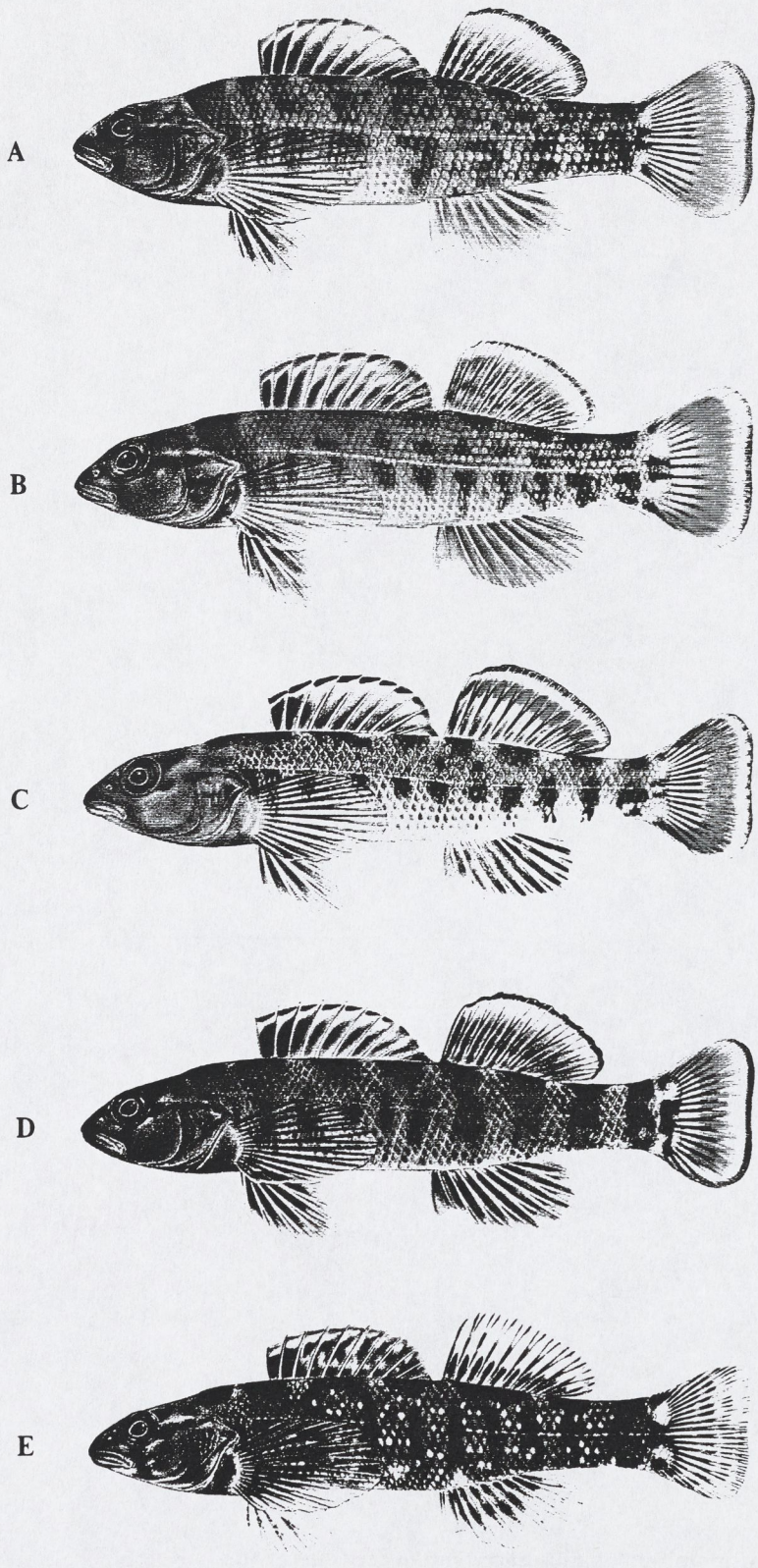

Figure 3. A. Breeding male *Etheostoma jordani*, Cahaba River, Jefferson County, Alabama (UAIC 10286.01). B. Breeding male *Etheostoma douglasi*, West Fork Sipsey River, Winston County, Alabama (UAIC 10273.01). C. Breeding male *Etheostoma etowahae*, Amicalola Creek, Dawson County, Georgia (UAIC 10471.01). D. Breeding male *Etheostoma chuckwachatte*, Hillabee Creek, Tallapoosa County, Alabama (UAIC 10284.01). E. Female *Etheostoma chuckwachatte* (same collection data as male).

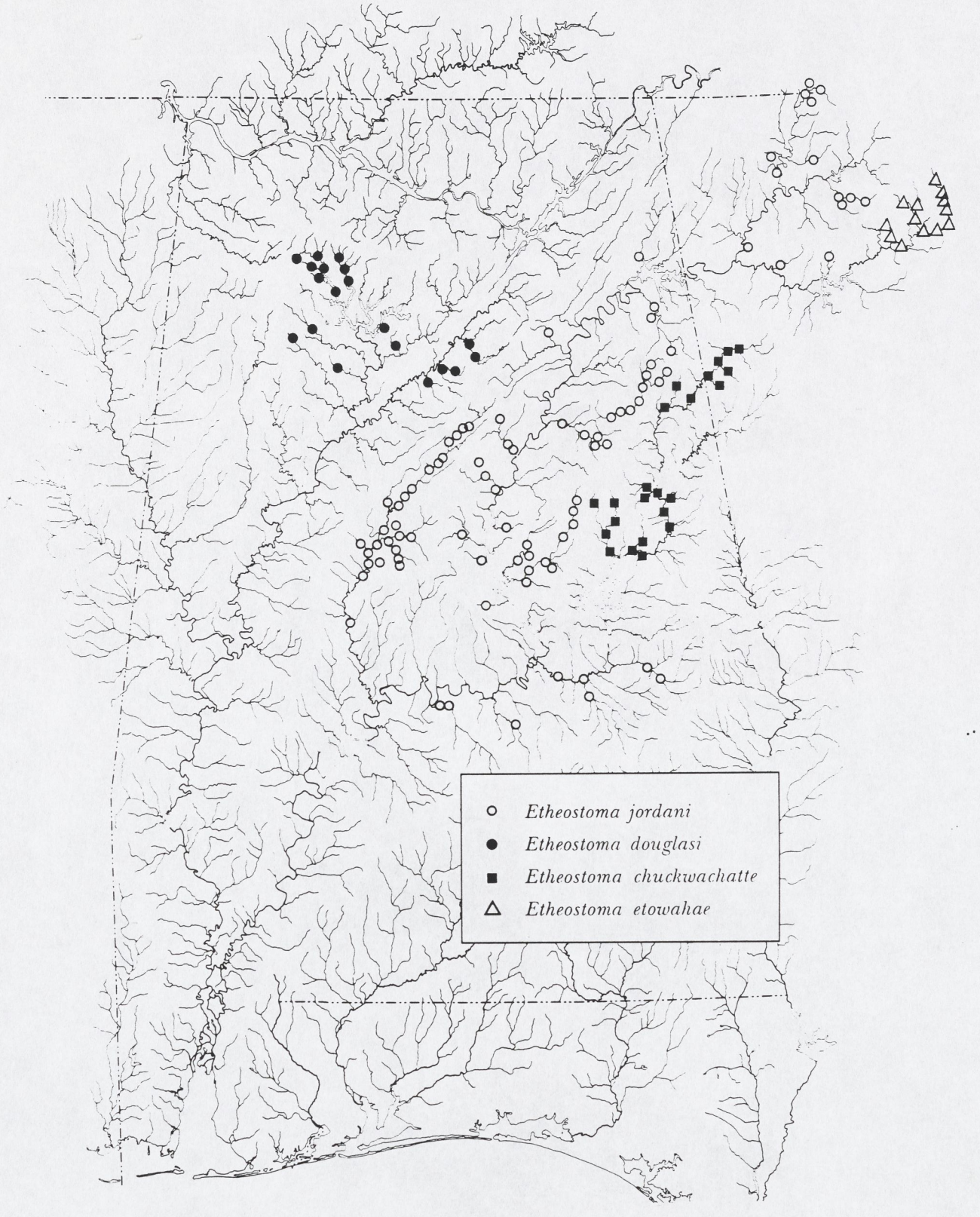

Figure 4. Map of known localities of members of *Etheostoma jordani* species group.

scale. Dorsum crossed by 8 quadrate blotches, generally not extending ventrally more than 4 scale rows; first immediately posterior to the occiput, second at insertion of spinous dorsal fin, third near middle of spinous dorsal fin base, fourth at termination of spinous dorsal fin, fifth at insertion of soft dorsal fin, sixth near end of soft dorsal fin base, seventh posterior to end of soft dorsal fin base and underlying rays of soft dorsal fin, eighth at caudal peduncle. Head olivaceous dorsally; cheek olivaceous. Sub-orbital bar distinct; extending from eye toward ventralmost margin of cheek. Postorbital bar dusky; pre-orbital bar present but may be obscured by overall head pigmentation in darker individuals. Black humeral spot present.

Spinous dorsal fin olivaceous basally, with thin white marginal band; basally membranes between first three spines with black elliptical spots. Soft dorsal fin olivaceous basally, followed distally by narrow white band and narrow olivaceous band at fin margin. Caudal rays olivaceous in basal three-fourths of fin; membranes white; distally, fin with narrow white band followed by narrow olivaceous margin. Four distinct black spots present at insertion of caudal fin; two spots immediately posterior to hypural plate at midline, one at insertion of dorsal procurrent caudal rays, one at insertion of ventral procurrent caudal rays. Anal fin membranes dusky basally; color fades toward margin of fin. Anal fin rays overlain by melanophores; generally bordered by membrane void of any pigment. Distal margin of anal fin with melanophores coalescing to form band; band best developed posteriorly, fading anteriorly. Pelvic fins dusky basally and medially; melanophores fade at margin giving appearance of white marginal band. Pectoral fin rays overlain with melanophores; membranes white.

Coloration of preserved females.—Body tan to olivaceous as in males except with much more speckled appearance. Head as above; cheek tan but with slight concentration of uniformly scattered melanophores. Sub-orbital and post-orbital bars as in males, pre-orbital bar more distinct than in male. Dorsum of head, lips, cheeks, branchiostegals, breast, and belly heavily speckled with profusion of discrete melanophores. Black humeral spot present. Spinous dorsal fin heavily pigmented with discrete melanophores, giving overall speckled appearance; melanophores may coalesce near margin giving appearance of a dusky submarginal band. Soft dorsal fin olivaceous basally, followed distally by alternating patterns of unpigmented and pigmented zones, giving rise to a speckled appearance; melanophores on rays and membranes. Margin of soft dorsal fin with thin olivaceous band. Caudal fin membranes unpigmented; rays overlain by alternating areas with and without melanophores, creating speckled appearance. Margin of caudal fin with dusky brown band, bordered proximally by area more or less void of pigment, forming white band. Anal fin heavily speckled basally, fading toward margin where clear. Pectoral and pelvic fins as in males except more speckled in appearance.

Distribution.—*Etheostoma jordani* is distributed throughout the Coosa River System, including the Conasauga and Coosawattee rivers, the Cahaba River System, and the Tallapoosa River System below the Fall Line. Known populations of *E. jordani* are depicted in Figure 4.

Ecology.—Adults of *Etheostoma jordani* typically inhabit riffles with a moderate to strong current (Zorach, 1969; Orr, 1989) over gravel or cobble substrate. Orr (1989) reported that larvae of dipterans, ephemeropterans, and trichopterans accounted for the majority of the diet in *E. jordani* from Opintlocco Creek (Tallapoosa River System; Macon County, Alabama). Orr and Ramsey (1990) reported details of reproductive ecology for *E. jordani* from Opintlocco Creek. Based on mean gonadosomatic indices they found that the peak reproductive activity for *E. jordani* in 1986 occurred in the third week of April, females with ripe ova were found from 22 April through 3 June at water temperatures of 18.0–29.4 C (Orr and Ramsey, 1990). The smallest mature female of *E. jordani* captured during their investigation was 23.0 mm SL. In addition, they report that *E. jordani* spawns by burying its eggs in sand at a site selected by the female. O'Neil (1980) reported that females of *E. jordani* in Barbaree Creek (Coosa River System; Clay County, Alabama) were at a reproductive peak in mid to late May 1977 based on monthly gonadosomatic indices.

Etymology.—The species epithet *jordani* is used in honor of David Starr Jordan. The common name greenbreast darter refers to the blue-green coloration on the breast and underside of head.

Etheostoma douglasi Wood & Mayden, new species
Tuskaloosa Darter
Figure 3B

Holotype.—UAIC 10345.02, adult male, 51.2 mm, West Fork Sipsey River at Lawrence Co. Rd. 6, Sipsey River Recreational Site, T9S, R8W, Sec. 8, Winston County, Alabama, 14 March 1991, R. M. Wood, S. R. Layman, and A. M. Simons.

Paratopotypes.—NLU 66886 (5 specimens; 33.0–45.3 mm SL), UAIC 10345.01 (22; 26.9–48.5), USNM 31992.6 (5; 30.0–35.9), collected with the holotype. INHS 28458 (3; 33.4 to 45.3), SIUC 20338 (3; 32.5–40.8), UAIC 10273.01 (8; 21.6–36.9), UF 92303 (3; 29.7–36.2), UGAMNH 2432 (3; 30.6–37.0), UT 91.4171 (3; 31.8–35.5), 2 March 1992, R. L. Mayden and B. R. Kuhajda.

Paratypes.—UAIC 3851.08 (14 specimens; 23–50 mm SL), Sipsey River, 4.0 km W of Grayson and 16.1 km NNE of Double Springs, T9S, R8W, Sec. 10, Winston County, Alabama, 29 October 1971, D. Dycus and D. Johnson; UAIC 3852.09 (18; 31–52), Sipsey River 2.8 km W of Hwy 242 and

6.4 km SW of Double Springs, T9S, R8W, Sec. 22, Winston County, Alabama, 3 November 1971, D. Dycus and D. Johnson; UAIC 3854.07 (4; 41–53), Sipsey River at low pressure bridge, 6.4 km E of Alabama Hwy 195 and 8.9 km NNE of Double Springs, T9S, R8W, Sec. 33, Winston County, Alabama, 8 November 1971, D. Dycus, W.M. Howell, and M. Hopiak; UAIC 3858.06 (10; 30–44), Sipsey River, 8.1 km W of Alabama Hwy 33 and 2.8 km NW of Sipsey River recreation area, T9S, R8/9W, Sec. 6/1, Winston County, Alabama, 17 November 1971, D. Dycus and M. Hopiak; UAIC 3868.06 (8; 37–54), Borden Creek on Bunyan Hill Rd., 4.8 km W of Alabama Hwy 33, T8S, R8W, Sec. 32, Lawrence County, Alabama, 22 August 1970, W. M. Howell, M. Hopiak, and J. Manasco; UAIC 4111.06 (4; 24–45), Sipsey River at low pressure bridge, 6.4 km E of Alabama Hwy 195 and 8.9 km NNE of Double Springs, T9S, R8W, Sec. 33, Winston County, Alabama, 15 October 1971, D. Dycus and M. Hopiak.

Diagnosis.—A member of the *E. jordani* species group, distinguished from other members by the combination of no red spots along flanks, no scales on the opercles, and no trace of red pigmentation on the lips or in the anal fin.

Description.—Morphometric measurements and some significant meristic variables are reported in Tables 1 and 2. General head and body shape and pigmentation are shown in Figure 3b.

Dorsal spines 10(41), 11(19); $\bar{x}$=10.3, SD=0.47. Soft dorsal rays 11(15), 12(40), 13(5); $\bar{x}$ =11.8, SD=0.56. Anal fin rays 7(23), 8(34); $\bar{x}$=7.7, SD=0.57. Pectoral fin rays 12(7), 13(52), 14(1); $\bar{x}$=12.9, SD=0.35. Caudal fin rays 15(1), 16(6), 17(53); $\bar{x}$=16.9, SD=0.39. Scale rows above lateral line 5(1), 6(32), 7(27); $\bar{x}$=6.4, SD=0.53. Scale rows below lateral line 6(2), 7(37), 8(18), 9(3); $\bar{x}$=7.4, SD=0.64. Scale rows above lateral line at caudal peduncle 7(7), 8(20), 9(29), 10(3), 11(1); $\bar{x}$=8.5, SD=0.83. Scale rows below lateral line at caudal peduncle 9(20), 10(24), 11(15), 12(1); $\bar{x}$=10.0, SD=0.81. Branchiostegal rays 6(59), 7(1); $\bar{x}$=6.0, SD=0.13. Nape squamation 20% (1), 30% (5), 40% (15), 50% (30), 60% (1), 80% (6), 90% (2); $\bar{x}$=0.5, SD=0.14. Breast generally without scales (58) occasionally 1–2 embedded scales (2). Cheek and opercle without scales.

Preoperculomandibular canal pores 9(2), 10(7), 11(1); $\bar{x}$=9.9, SD=0.54. Infraorbital canal pores 8(9), 9(1); $\bar{x}$=8.1, SD=0.30. Lateral canal pores 4(10). Supratemporal canal pores 2(10). Supraorbital canal pores 4(10). Coronal pore 1(10).

Males were found to possess a significantly greater gape width than females, while females possessed greater eye diameter, predorsal length, and caudal peduncle depth than males ($P<0.05$, Table 1). No other significant differences were found in either morphometric or meristic traits.

Coloration.—Males and females are dichromatic; males being more brightly colored than females throughout year, dichromatism reaching its peak during the spring. Males possess same coloration as in *E. jordani* with the exception that red spots along flanks are lacking. Coloration of a male in breeding condition is depicted in Figure 3b. Coloration of females same as in *E. jordani*.

Distribution.—*Etheostoma douglasi* is known from the upper Black Warrior River System in Alabama. Known populations of *E. douglasi* are depicted in Figure 4.

Ecology.—Adults of *E. douglasi* typically inhabit riffles in streams of moderate to strong current over gravel or cobble substrate. O'Neil (1980) reported females of *E. douglasi* in Gurley Creek (Black Warrior River System; Jefferson County, Alabama) with differentiating ova scattered throughout the ovary on 1 April 1966 and in Blackburn Fork (Black Warrior River System; Blount County, Alabama), females with fully differentiated ova scattered throughout the ovary and in oviducts on 24 May 1977.

Etymology.—Named for Dr. Neil H. Douglas, Director and Curator, Northeast Louisiana University Museum of Zoology, in recognition of his contributions to our understanding of the freshwater fish fauna of Louisiana and his dedication to teaching. The common name, Tuskaloosa darter, is in reference to the Mississippian chieftan met by Hernando de Soto and to the Choctaw Indian name for Black Warrior, the river system to which this species is endemic.

Etheostoma etowahae Wood & Mayden, new species
Etowah Darter
Figure 3C

Holotype.—UAIC 9169.14, adult male, 54.7 mm, Etowah River at Georgia Hwy 52, 13.7 km NNE of Dawsonville, Lumpkin County, Georgia, 5 April 1989, R. M. Wood, R. L. Mayden, B. R. Kuhajda, R. H. Matson, and M. T. Ferguson.

Paratopotypes.—INHS 28460 (2 specimens; 45.6–46.6 mm SL), NLU 66888 (2; 44.3–50.6), SIUC 20340 (2; 46.5–48.4), UAIC 9169.11 (6; 34.6–43.0), USNM 319924 (2; 44.5–50.7), collected with the holotype. UAIC 2912.03 (4; 40.9–43.2), 20 April 1968, J. D. Williams, E. Crowder, and H. Harima. UAIC 9811.08 (1; 44.7), 1 June 1990, R. L. Mayden, R. M. Wood, and R. H. Matson.

Paratypes.—UAIC 6219.04 (1 specimen; 45.5 mm SL), Etowah River at Co. Rd. 75, 3.2 km N of Georgia Hwy 52, Lumpkin County, Georgia, 31 May 1980, R. T. Bryant and J. A. Walton; UAIC 9822.10 (3; 38.2–54.4), Amicalola

Creek at Co. Rd. 25 and 26, Dawson County, Georgia, 1 June 1990, R. M. Wood, R. L. Mayden, and R. H. Matson; UMMZ 157952 (5; 41.9–46.7), Etowah River, 6.4 km SW of Dahlonega on US Hwy 19, Lumpkin County, Georgia, 25 August 1939, R. M. Bailey and M. K. Bailey; UF 84777 (8; 38.4–53.2), Amicalola Creek at Co. Rd. 25, 14.4 km NNW of Dawsonville, Dawson County, Georgia, 2 May 1990, N. M. Burkhead, C. R. Gilbert, J. D. Williams, S. J. Walsh, and B. J. Freeman.

Diagnosis.—A member of the *E. jordani* species group distinguished from other members of the group by the absence of red spots on flanks, lack of red pigment on lips, lack of a red band in anal fin, and presence of scales on opercle. Additionally, *E. etowahae* differs from remaining three members of the *E. jordani* species group in having a mean of 12.7 tranverse scale rows (versus a minimum mean of 14.5); 45.5 lateral line scales (minimum mean of 48.3); and a mean of 17.1 caudal peduncle scale rows (minimum mean of 18.8) (Table 2).

Description.—Morphometric measurements and some significant meristic variables are reported in Tables 1 and 2. General head and body shape and pigmentation are shown in Figure 3c.

Dorsal spines 10(18), 11(15), 12(2); $\bar{x}$=10.5, SD=0.61. Soft dorsal rays 11(1), 12(33), 13(1); $\bar{x}$=12.0, SD=0.24. Anal fin rays 7(9), 8(26); $\bar{x}$ =7.7, SD=0.44. Pectoral fin rays 12(3), 13(28), 14(4); $\bar{x}$=13.0, SD=0.45. Caudal fin rays 16(3), 17(29), 18(3); $\bar{x}$=17.0, SD=0.42. Scale rows above lateral line 5(11), 6(23), 7(1); $\bar{x}$=5.7, SD=0.52. Scale rows below lateral line 5(7), 6(20), 7(8); $\bar{x}$=6.0, SD=0.66. Scale rows above lateral line at caudal peduncle 6(3), 7(28), 8(4); $\bar{x}$=7.0, SD=0.45. Scale rows below lateral line at caudal peduncle 7(6), 8(19), 9(10); $\bar{x}$=8.1, SD=0.67. Branchiostegal rays 6(35). Nape squamation 10% (5), 20% (5), 30% (8), 40% (9), 50% (8); $\bar{x}$=0.3, SD=0.14. Cheek and breast naked, opercles scaled.

Preoperculomandibular canal pores 9(2), 10(7); $\bar{x}$= 9.9, SD=0.54. Infraorbital canal pores 8(8), 9(1); $\bar{x}$=8.1, SD=0.30. Lateral canal pores 4(9). Supratemporal canal pores 2(9). Supraorbital canal pores 4(9). Coronal pore 1(9).

Males of *E. etowahae* possessed a significantly greater snout length than females ($P<0.05$, Table 1). No other significant differences were found in either morphometric or meristic traits.

Coloration.—Males and females are dichromatic; males being more brightly colored than females throughout year, dichromatism reaching its peak during the spring. Coloration of males same as in *Etheostoma jordani* with the exception that there are no red spots along flanks. Coloration of a male in breeding condition is depicted in Figure 3C. Coloration of females same as in *E. jordani*.

Distribution.—*Etheostoma etowahae* is restricted to the Etowah River System of Georgia above Lake Allatoona. Known localities of *E. etowahae* are depicted in Figure 4.

Ecology.—Adults of *E. etowahae* typically inhabit riffles in streams of moderate to strong current over gravel or cobble substrate. Nothing has been reported on the diet or reproductive habits of this species.

Etymology.—The species epithet *etowahae* is an adjective referring to the Etowah River to which the new species is endemic. The common name, Etowah darter, also refers to the Etowah River.

Etheostoma chuckwachatte Mayden & Wood, new species
Lipstick Darter
Figures 3D and 3E

Holotype.—UAIC 9815.07, adult male, 45.5 mm, Hillabee Creek at Alabama Hwy 22, 11.7 km NE of Alexander City, T23N, R22E, Sec. 16, Tallapoosa County, Alabama, R. M. Wood, R. L. Mayden, B. R. Kuhajda, and S. R. Layman, 3 Feb. 1990.

Paratopotypes.—INHS 28459 (2 specimens; 37.5–39.7 mm SL), NLU 66887 (2; 34.5–41.7), SIUC 20339 (2; 37.4–38.8), USNM 319925 (2; 37.3–40.0), UAIC 9815.02 (7; 29.2–34.9), UF 92304 (2; 37.3–37.5), UGAMNH 2431 (2; 35.6–44.5), UT 91.4172 (2; 35.1–37.3), collected with the holotype. UAIC 6418.09 (26; 22.8–39.7), 16 November 1980, D. L. Nieland and R. A. Kasperzak; UAIC 10284.01 (5; 36.2–39.2), 6 March 1992, B. R. Kuhajda, R. L. Mayden, H. T. Boschung, and J. R. Tomelleri.

Diagnosis.—A member of the *E. jordani* species group distinguished from other members of the group by the presence of red lips, bright red spots along flanks, a broad red band in the anal fin of adult males, and scales on opercles.

Description.—Morphometric measurements and some meristic variables are reported in Tables 1 and 2. General head and body shape and pigmentation are shown in Figures 3d and 3e.

Dorsal spines 9(1), 10(19), 11(30), 12(2); $\bar{x}$=10.6, SD=0.50. Soft dorsal rays 10(2), 11(32), 12(17), 13(0), 14(1); $\bar{x}$ =11.4, SD=0.65. Anal fin rays 7(30), 8(22); $\bar{x}$ =7.4, SD=0.50. Pectoral fin rays 12(3), 13(45), 14(4); $\bar{x}$=13.0, SD=0.37. Caudal fin rays 17(52). Scale rows above lateral line 6(28), 7(24); $\bar{x}$=6.5, SD=0.50. Scale rows below lateral line 6(3), 7(35), 8(14); $\bar{x}$=7.2, SD=0.54. Scale rows above lateral line at caudal peduncle 7(12), 8(30), 9(10); $\bar{x}$=8.0, SD=0.66. Scale rows below lateral line at caudal peduncle

8(9), 9(38), 10(4), 11(1); $\bar{x}$=8.9, SD=0.57. Branchiostegal rays 6(52). Nape squamation 0% (4), 10% (5), 20% (4), 30% (7), 40% (5), 50% (18), 60% (3), 70% (4), 80% (1), 100% (1); $\bar{x}$=0.4, SD=0.22. Cheek and breast naked. Opercles scaled.

Preoperculomandibular canal pores 10(12). Infraorbital canal pores 7(1), 8(9), 9(2); $\bar{x}$=8.1, SD=0.49. Lateral canal pores 3(1), 4(11); $\bar{x}$=3.9, SD=0.28. Supratemporal canal pores 2(11), 3(1); $\bar{x}$=2.1, SD=0.28. Supraorbital canal pores 4(12). Coronal pore 1(12).

Males of *E. chuckwachatte* were found to have a significantly greater caudal fin length than females, while females possessed a larger eye diameter than males ($P<0.05$, Table 1). No other significant differences were found in either morphometric or meristic traits.

Coloration.—Males and females are dichromatic; males being more brightly colored than females throughout year, dichromatism reaching its peak during the spring. Coloration of males same as in *E. jordani* with the exception that males of *E. chuckwachatte* have bright red lips and a broad red band through the anal fin. Coloration of females same as in *E. jordani*. Coloration of a male and female in breeding condition are depicted in Figures 3D and 3E.

Distribution.—*Etheostoma chuckwachatte* is known from throughout the Tallapoosa River System above the Fall Line in Alabama and Georgia. Known localities of *E. chuckwachatte* are depicted in Figure 4.

Ecology.—Adults typically inhabit riffles with a moderate to strong current (Zorach, 1969; Orr, 1989) over gravel and/or cobble substrate. Orr (1989) reported that larvae of dipterans, ephemeropterans, and plecopterans accounted for the majority of the diet in *E. chuckwachatte* from Hillabee Creek (Tallapoosa County, Alabama). Orr and Ramsey (1990) presented details of the reproductive ecology of *E. chuckwachatte* from Hillabee Creek. Based on mean gonadosomatic index, peak reproductive activity occurred in the first week of May. Females with ripe ova were found from 7 April through 30 June at water temperatures of 20.0-25.6 C. The smallest mature female captured during this investigation was 29.0 mm SL (Orr and Ramsey, 1990). While *E. chuckwachatte* has not been observed spawning, it is assumed to be an egg burier.

Etymology.—*Etheostoma chuckwachatte* ('shŭck wə 'shä tē) is named from the anglicized version of the Creek Indian words for mouth, chuckwe; and red, chattee; and refers to the bright red lips on the mouths of breeding males of this species. The common name, lipstick darter, is also in reference to the bright red lips on breeding males.

Comparisons.—Species of the *Etheostoma jordani* group are easily distinguished from one another on the basis of squamation, meristic characters, general head and body shape, and pigmentation patterns (Table 3). *Etheostoma douglasi* is distinguished from other members of the species group, and all other members of *Nothonotus* except *E. acuticeps*, with its lack of exposed scales on the opercle (Table 2). While meristic characters among the species are similar, *E. etowahae* has fewer lateral line scales, fewer scale rows above and below lateral line at the caudal peduncle, and fewer transverse scale rows than the remaining three species in the group (Table 2). This pattern of interspecific variation is further summarized by principal component analysis of meristic variables for both males and females (Fig. 5; Table 4). *Etheostoma etowahae* is almost completely separated from the remaining three species along PCI. Meristic variables loading most heavily along PCI include scale rows above and below lateral line, caudal peduncle scale rows, and lateral line scale rows (Table 4).

General patterns of variation of head and body shape

Table 3. Characters useful in distinguishing species of the *Etheostoma jordani* species complex.

Characteristic	*E. jordani*	*E. douglasi*	*E. etowahae*	*E. chuckwachatte*
Transverse scale rows	14–16	14–16	11–14	14–16
Caudal peduncle scale rows	18–21	19–22	16–18	17–20
Red spots on side of body	present	absent	absent	present
Red stripe in anal fin	absent	absent	absent	present
Red pigment on lips	absent	absent	absent	present
Scales on opercle	present	absent	present	present

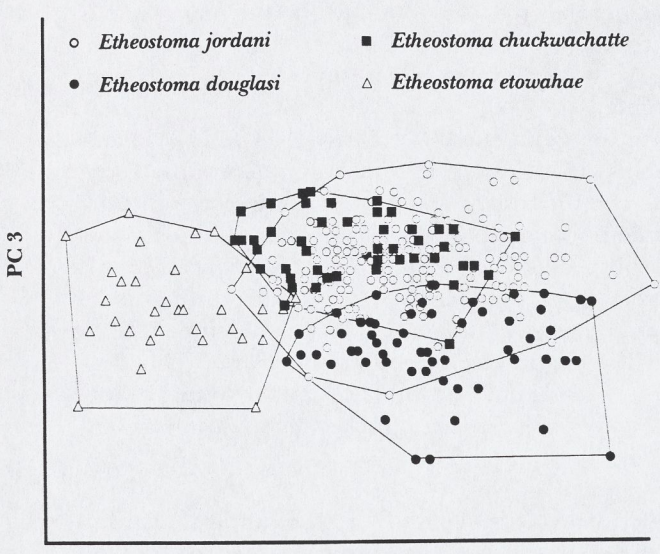

Figure 5. Principal component analysis of meristic variables for males and females of the *Etheostoma jordani* species group.

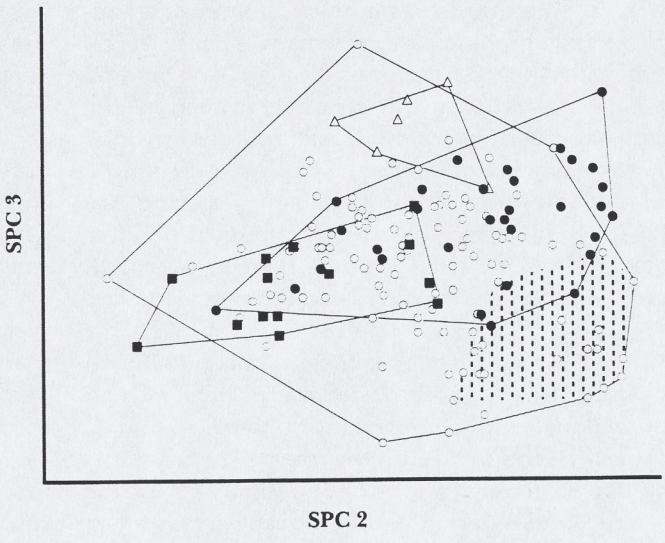

Figure 6. Principal component analysis of sheared morphometric variables for males of the *Etheostoma jordani* species complex. Shaded area represents the population of *E. jordani* below the Fall Line in the Tallapoosa River system.

differentiation are best summarized in sheared principal component analysis (Fig. 6; Table 5). While variation of mensural characters within *E. jordani* broadly overlap the remaining three species, *E. etowahae* is completely separated from *E. chuckwachatte* and almost entirely separated from *E. douglasi* in shape features summarized primarily by sheared PCIII. Along sheared PCII, *E. chuckwachatte* is completely separable from those populations of *E. jordani* in closest geographic proximity, namely populations in the Tallapoosa River below the Fall Line (the latter population highlighted by shading). Mensural variables loading heavily along sheared PCII include caudal fin length, pectoral and pelvic fin lengths, and head length; along sheared PCIII head length, snout length, pectoral fin length, and anal fin base length loaded most heavily. Generally *E. etowahae* has a shorter head, snout, and pectoral fins, and a longer anal fin base than the other three species in the group. *Etheostoma chuckwachatte* generally has a longer head, and shorter pectoral, pelvic, and caudal fins relative to populations of *E. jordani* in closest geographic proximity (Fig. 6; Table 5).

Table 4. Variance loadings for the principal components in the analysis of meristic variables for males and females of species of the *Etheostoma jordani* species group.

Variable	PC I
Lateral Line Scales (L.L.)	0.53173
Scale Rows Above L.L.	0.74112
Scale Rows Below L.L.	0.79677
Scale Rows Above L.L. at Peduncle	0.77490
Scale Rows Below L.L. at Peduncle	0.78444
Dorsal Fin Spines	-0.13191
Dorsal Fin Rays	0.05877
Anal Fin Rays	-0.01361
Pectoral Fin Rays	-0.04835
Caudal Rays	-0.06424
Percent Breast Squamation	0.13814
Percent Opercle Squamation	0.03977
Percent Nape Squamation	0.36931

Several pigmentation characters also serve to distinguish the four species in the group. Males of *Etheostoma jordani* and *E. chuckwachatte* are distinguished from those of *E. etowahae* and *E. douglasi* by the presence of red spots on the side of the body. Males of *E. chuckwachatte* are distinguished from all other members of *Nothonotus*, except *E. rufilineatum*, by the presence of red lips; they are further distinguished from all other members of the *E. jordani* group by this character and the presence of a broad red band through a typically blue—turquoise anal fin.

COMPARATIVE BIOGEOGRAPHY.—Within the Mobile Basin a number of other species possess geographic patterns of disjunction and endemism consistent with those exhibited by members of the *Etheostoma jordani* species group. The genus *Cyprinella* contains sister taxa that are congruent in distribution with *E. jordani* and *E. chuckwachatte*. *Cyprinella gibbsi* is restricted to the Tallapoosa River largely above Lake Martin (compare to *E. chuckwachatte*) while its sister species *C. trichroistia* is found in the Cahaba and Coosa River systems with a few reported populations in the Alabama River (compare to *E. jordani*) and upper Black War-

rior River *(E. douglasi)*. Within the topminnow genus *Fundulus* a biogeographic pattern emerges that is largely consistent with the distributions of *E. jordani* and *E. chuckwachatte*. *Fundulus bifax* is nearly restricted to the Tallapoosa River System (one population known from a tributary to the lower Coosa River), while *F. stellifer* is more wide ranging and found in the Cahaba, Coosa, and Alabama River systems as well as the Chattahoochee River System. While this pattern is not identical to that of *Etheostoma jordani* and *E. chuckwachatte*, the similarities are striking.

Within the genus *Etheostoma*, there are a number of species within the snubnose darter clade which exhibit distributional patterns consistent with those of the *E. jordani* species group. Within the range of *Etheostoma douglasi* there is currently at least one endemic species, the undescribed Warrior darter. Within the range of *E. jordani* and *E. etowahae*, *E. coosae* and *E. brevirostrum* are restricted to the Coosa River System (Suttkus and Etnier, 1991). The distribution of the Tallapoosa darter *E. tallapoosae* is almost identical with that of *E. chuckwachatte*, while the undescribed Cherokee darter is found within the same regions of the Etowah River System as *E. etowahae* although the two species are not known to be syntopic (N. M. Burkhead, pers. comm.).

Within the genus *Cottus*, Robins (1954) and Williams and Robins (1970) recognized that members of the *Cottus carolinae* complex from the Mobile Basin were distinct from other populations of *C. carolinae* and belonged to two distinct subspecies. One of these, *Cottus carolinae zopherus* is restricted to the Coosa River System and is distinct from forms in the upper Tallapoosa River, the upper Black Warrior River, and the upper Etowah River. This geographic pattern is once again quite similar to that exhibited by *Etheostoma jordani*, *E. chuckwachatte*, *E. douglasi*, and *E. etowahae*.

Table 5. Variance loadings for the principal components in the analysis of morphometric variables for males of species of the *Etheostoma jordani* species group.

Variable	Sheared PC II	Sheared PC III
SL	-0.07502	-0.16617
HL	-0.23828	-0.26374
HD	0.00162	0.07227
HW	-0.00034	0.14862
SN	-0.21025	-0.48111
PL	-0.13408	-0.22175
ED	-0.18404	-0.22324
PT	0.35903	-0.27995
PV	0.22997	-0.17345
DIL	-0.10372	-0.04041
DIIL	-0.13887	0.11064
AL	0.03278	0.52794
CL	0.78391	-0.13876
CD	-0.02959	0.01532
D10—11	0.01639	0.11432
D11—20	-0.08775	-0.09025
D12—20	-0.01702	0.11432
D12—19	-0.04800	0.18956
D10—12	-0.04383	-0.00001
D13—20	-0.01299	0.23299

Conservation Status.—Based on the known distributional status of the four species contained within the *Etheostoma jordani* species group, three of the species are in need of special status by state and federal agencies. We recommend minimally according the status of threatened to *E. douglasi* and *E. chuckwachatte; E. etowahae* merits endangered species status. The wider distribution of *E. jordani* and its relative abundance in some streams in which it occurs prevent us from recommending protection until a thorough status survey has been conducted.

To date, a thorough status survey has only been conducted on one of these species, *E. etowahae* (Burkhead, 1992). In this study Burkhead recommended that *E. etowahae* be listed as Federally endangered due to its extremely restricted range and continuing habitat degradation. We fully agree with these conclusions and support his recommendation for endangered species status. Similar studies must be conducted on the remaining three members of the complex. *Etheostoma chuckwachatte* and *E. douglasi* have fragmented and restricted geographic distributions (Fig. 4) in watersheds that are also suffering from general habitat degradation and have recently been targeted for impoundments and/or proposals aimed at water removal for urban usage. In either case, habitats necessary for the continued existence of either species will be eliminated or severely jeopardized. While *E. jordani* is more widespread geographically than other members of the group, its range is fragmented (Fig. 4). Habitat degradation in any area inhabited by species in this group could result in permanant loss of a population or series of populations and their gene pools. Unfortunately, this has apparently already occurred at the type locality for *E. jordani*. Recent efforts to locate *E. jordani* near Oxford, Alabama and vicinity failed. In fact, no fishes were collected from the heavily polluted Choccoloco Creek near Oxford.

Because of the general predilection in this species group and other *Nothonotus* for high-gradient, clear

streams with silt-free gravel and cobble substrate, these species will be sensitive to both indirect and direct habitat degradation. These traits, combined with the general distribution of these fishes in the upper Mobile Basin, make them valuable indicator species of the general quality of many aquatic ecosystems in the basin. Their fragmented ranges, together with impending threats to aquatic and nearby terrestrial ecosystems warrant concern for their continued existence.

Acknowledgments

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Material examined not designated as types.

Etheostoma jordani. Etowah River: Bartow County, Georgia: UF 80098 (3), INHS 75088 (3), RMW-91-50 (4), Stamp Cr. at GA Hwy 269, 6.4 km SE of White; UAIC 9814.06 (1) Two Run Cr., S of Kingston off new US Hwy 411. Paulding County, Georgia: UF 80125 (25), UAIC 10103.11 (2), Raccoon Cr. at Braswell Mountain Road, 6.0 km NE of Braswell. Conasauga River: Bradley County, Tennessee: UAIC 3901 (42) Conasauga R. on TN Hwy 74, 1.6 km downstream from TN-GA state line; UAIC 5663.07 (11) Conasauga R. at TN Hwy 74. Polk County, Tennessee: UAIC 6768.05 (11) Ball Play Cr., 1.8 km NE of Conasauga; USNM 231368 (57) Minnewauga Cr. off of US Hwy 411. Murray County, Georgia: UAIC 6240.13 (25) Conasauga R. at Co. Rd. 173. Coosawattee River: Pickens County, Georgia: CU 53247 (13), CU 63900 (5) Talking Rock Cr. on GA Hwy 5, 18.4 km SSW of Ellijay; TU 40727 (16) Talking Rock Cr. on GA Hwy 5, 21.8 km S of Ellijay. Murray County, Georgia: CU 24938 (7) Unnamed tributary of Coosawattee R., 8.2 km S of Chatsworth on US Hwy 411. Oostanaula River. Whitfield County, Georgia: USNM 162367 (6) Tributary of Oostanaula R., 9.8 km S of Dalton on US Hwy 41; USNM 168011 (1) Triburary of Oostanaula R., 9.3 km S of Dalton on US Hwy 41. Murray County, Georgia: USNM 168037 (14) Tributary of Oostanaula R., 8.3 km SSE of Chatsworth on US Hwy 411. Coosa River. Clay County, Alabama: UAIC 5565.08 (11), UAIC 5814.09 (18), UAIC 5816.12 (22), Cheaha Creek; UAIC 5550.15 (10), UAIC 5566.12 (16), Threemile Creek; UAIC 8532.12 (3) 11.5 km WNW of Millerville at AL Hwy 7. Cleburne County, Alabama: UAIC 6626.09 (14), Shoal Creek at Forest Service Rt. 509, Choccoloco Wildlife Management Area; AU 385 (21) Hatchet Cr., 8.0 km N of Goodwater on AL Hwy 7. Coosa County, Alabama: UAIC 2174 (2) Tributary to Swamp Cr., 2.7 km ENE of Rockford; UAIC 8470.16 (3) Weogufka Ck., 1.3 km NW of Moriah; UAIC 8529.10 (10) Peckerwood Cr., 5.3 km NNE of Marble Valley; AU 1092 (7) Hatchett Creek, 8.3 km N of Goodwater on AL Hwy 7; AU 16780 (13) Weogufka Cr., 9.1 km SSE of Weogufka; AU 18581 (8) Hatchet Cr., 6.1 km N of Rockford on AL Hwy 231; AU 20083 (7) Peckerwood Cr., 3.4 km SSE of Talladega Springs; AU 20916 (14) Hatchett Creek, 6.6 km N of Rockford. Talapoosa River: Macon County, Alabama: UT 91.1911 (33), AU 5472 (10) Line Creek, 7.5 km WSW of Shorter on US Hwy 85; AU 6562 (22), AU 12159 (3), AU 21960 (9), Uphapee Ck., 5.6 km N of Tuskegee at US Hwy 85. Cahaba River: Bibb County, Alabama: UAIC 5576.09 (9), UAIC 5581.16 (16), UAIC 5604.25 (17), Little Cahaba River at Bulldog Bend; UAIC 5585.13 (30) Schultz Creek at AL Hwy 219, 6.4 km N of Centreville; UAIC 8339.15 (11) Cahaba River at AL Hwy 27 bridge. Shelby County, Alabama: UAIC 5593.05 (5) Cahaba River at AL Hwy 251.

Etheostoma douglasi. Sipsey River: Winston County, Alabama: UAIC 4329.15 (92) Sipsey River at Sipsey Fork Rec. Area; UAIC 6265.12 (49) Hubbard Creek at Sipsey River Rec. Area, AL Hwy 60 in Bankhead Natl. Forest. Jefferson County, Alabama: UAIC 1906 (31), UAIC 3305 (16), UAIC 3342 (19), Gurley Creek on AL HWY 79, 0.4 km S of Blount-Jefferson Co. line.

Etheostoma etowahae. Etowah River: Dawson County, Georgia: UF 15789 (2) Etowah R. 1.1 km NW of Landrum on GA Hwy 136; UT 91.1902 (4) Etowah R. at GA Hwy 53, 6.4 km SE of Dawsonville.

Etheostoma chuckwachatte. Tallapoosa River: Randolph County, Alabama: UAIC 8487.11 (7) Crooked Cr., 7.4 km NW of Malone; UAIC 8488.10 (6), UAIC 8489.14 (8)

Cornhouse Cr., 4.2 km NE of Malone. Tallapoosa County, Alabama: 8486.20 (20) Eumuckfaw Cr., 5.3 km SSE of New Site; UAIC 8476.15 (48) Tallapoosa R., 10.7 km SSW of Daviston.

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Etheostoma chermocki, a New Species of Darter (Teleostei: Percidae) from the Black Warrior River Drainage of Alabama

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ABSTRACT: Boschung, Herbert T., Richard L. Mayden, and Joseph R. Tomelleri. 1992. *Etheostoma chermocki*, a new species of darter (Teleostei: Percidae) from the Black Warrior River Drainage of Alabama. Bulletin Alabama Museum of Natural History, Number 13:11–20, 3 tables, 3 figures. A new species of snubnose darter, *Etheostoma chermocki*, is described. The new species, vermilion darter, is endemic to a relatively small portion of Turkey Creek, a tributary to Locust Fork of the Black Warrior River drainage in Alabama. *Etheostoma chermocki* differs from other snubnose darters on the basis of fin and body color patterns in males and females. The species is compared with populations of the undescribed Warrior river snubnose darters for coloration, meristic variables, and head and body measurements. Both sexes differ from Warrior river darters in coloration; only males can be separated completely on the basis of body shape. *Etheostoma chermocki* varies in color with the seasons, the males being most colorful in early March and the females in late July. *Etheostoma chermocki* is morphologically most similar to species of the *E. duryi* group of snubnose darters. With its limited range and deteriorating habitat, the species requires immediate conservation measures.

Introduction

The subgenus *Ulocentra* sensu Bouchard (1977) and Bailey and Etnier (1988), or *Nanostoma* sensu Page (1981), commonly known as snubnose darters, contains 12 and 14 described species, respectively. Page (1981) includes *Etheostoma zonale* (recognized by Etnier and Starnes (1986) as two species, *E. zonale* and *E. lynceum*), as a "snubnose darter," thereby relegating *Ulocentra* to the synonymy of *Nanostoma*. Based on morphological and allozyme character variation, Robert M. Wood (pers. comm.) concluded that the snubnose species belong in the subgenus *Etheostoma*. Subgeneric placement of these fishes remains controversial and it is not for us to argue the cases here. The *E. zonale* complex is widely distributed throughout much of the Mississippi Basin (Tsai and Raney, 1974); however, most other snubnose darters, described and undescribed, are limited to southerly drainages of the

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Ohio Basin and Mobile Basin, except for an undescribed species in Coastal Plain drainages of Alabama and the Florida panhandle. Many snubnose darters have limited geographical distribution and are more often endemic to a single drainage or system (e.g., *E. etnieri*, *E. coosae*, *E. barrenense*, *E. rafinesquei*, *E. baileyi*, and *E. tallapoosae*).

Several new species of snubnose darters have been described in the past decade (Page and Burr, 1982; Bailey and Etnier, 1988; Etnier and Bailey, 1989; Suttkus and Etnier, 1991), and several more, some of which have been known for decades, await formal taxonomic description. Recently, another undescribed snubnose darter has captured our attention. The species, described herein, is endemic to Turkey Creek, Jefferson County, Alabama. Turkey Creek is a tributary of Locust Fork of the Black Warrior River drainage in the Mobile Basin. The new species, the vermilion darter, has a limited geographic distribution and is replaced in nearby streams throughout the Black Warrior drainage by more common undescribed snubnose darters that we call collectively "Warrior snubnose darters."

Methods

Counts and measurements were made following most recent descriptions of snubnose darters (Bailey and Etnier, 1988; Etnier and Bailey, 1989; and Suttkus and Etnier, 1991).

The new species is compared morphometrically and meristically with four other populations of Warrior River drainage snubnose darters: (1) Gurley Creek, tributary to Locust Fork, (2) Mill and Murphy creek, tributaries to Mulberry Fork, (3) Sipsey Fork proper and a tributary, Borden Creek, and (4) Fivemile Creek, tributary to Valley Creek. Observations of breeding and non-breeding coloration of males and females were taken from live specimens, color transparencies, and color prints. Color comparisons of the vermilion darter were made with the geographically proximate Gurley Creek population within the Locust Fork.

Statistical analysis of meristic and morphometric variables included bivariate and multivariate methods. Student's T test was employed for determining significant differences in sexual dimorphism within samples of the vermilion darter and other Warrior snubnose darter populations. Multivariate comparison of the five populations involved principal component analyses. Meristic and morphometric variables were evaluated separately. For meristic characters a standard PCA was used on a correlation matrix. Sheared PCA on a covariance matrix was used for $\log_{10}$ transformed morphometric variables (Mayden, 1988).

Institutional symbolic codes follow Leviton and Gibbs (1988). The following abbreviations are used: SL (standard length), HL (head length), BD (body depth), SNL (snout length), SDL (spinous dorsal length), LDS (longest dorsal spine), SDL (soft dorsal length), LDL (longest dorsal ray), CPL (caudal peduncle length), CPD (caudal peduncle depth), AFL (anal fin length), ASL (first anal spine length), LAR (longest anal ray), CFL (caudal fin length), PCFL (pectoral fin length), PVFL (pelvic fin length), and TPW (transpelvic width).

All specimens of the new species that were available to us for study are designated types.

Etheostoma chermocki, new species
Vermilion Darter
Figure 1A and B.

Etheostoma (*Ulocentra*) sp.—Caldwell, 1965 and Barclay and Howell, 1973 (in part; not distinguished from other Warrior snubnose darters).

Etheostoma sp. B.—Mettee et al., 1989 (in part; not distinguished from other Warrior snubnose darters).

Etheostoma species/"Black Warrior Snubnose Darter".—Kuehne and Barbour, 1983 (species account referred in part to *E. chermocki*; photograph (plate 12, page 98) labeled "Black Warrior snubnose darter" is *E. chermocki*).

Etheostoma (Ulocentra) sp. ("Black Warrior snubnose darter").—Gilbert and Walsh, 1991 (account for deposition of photographic materials from Kuehne and Barbour, 1983).

HOLOTYPE.—UAIC 10288.02, adult male, 52.5 mm standard length. Collected in Turkey Creek, tributary to Locust Fork of the Black Warrior River drainage in Jefferson County, Alabama, T 15 S, R 1 W, Sec. 29, NW 1/4 of SW 1/4., on Tapawingo Drive, about one mile north of Pinson and east off Hwy 75. Elevation 600 feet. Collected 9 March 1992 by B. R. Kuhajda, J. R. Tomelleri, R. L. Mayden, and H. T. Boschung.

ALLOTYPE.—UAIC 10288.03, 43.5 mm standard length, collected with the holotype.

PARATOPOTYPES.—UAIC 10288.04 (2 males, 4 females), collected with the holotype. UAIC 10441.01 (3 males, 2 females, one each of which were cleared and stained), 2 April 1992, R. L. Mayden and H. T. Boschung.

PARATYPES.—TURKEY CREEK AT HWY 79 BRIDGE (T15S, R1W, Sec 30, SW 1/4: CU 42112 (4 males, 6 females), 22 April 1962, Leslie W. Knapp and Robert V. Miller; UAIC 1400.04 (7 males, 3 females), 2 August 1964, R. Dale Caldwell and W. Mike Howell; UF 44006 (2 males, 6 females), 10 April 1972, Robert A. Kuehne; UAIC 10444.01 (1 female), 31 July 1992. TAPAWINGO SPRING AND SPRING RUN, TRIBUTARY TO TURKEY CREEK (near type locality): UAIC 1402.02 (3 males, 3 females), 2 August 1964, R. Dale Caldwell and W. Mike Howell; UAIC 3245.02 (1 female), 24 October 1966, W. Mike Howell. TRIBUTARY TO TURKEY CREEK BETWEEN HWYS 75 AND 79, T15S, R1W, Sec.30, SW 1/4: UAIC 1905.09 (1 male), 1

April 1966, James D. Williams and W. Mike Howell. TURKEY CREEK AT DUG HOLLOW ROAD, T15S, R1W, Sec.29, SE 1/4.: UAIC 10442.01 (1 male, 2 females), 31 July 1992. TURKEY CREEK UPSTREAM FROM GOODWIN ROAD, T15S, R1W, Sec. 33, NW 1/4: UAIC 10443.01 (1 male), 31 July 1992. DRY CREEK, TRIBUTARY TO TURKEY CREEK, T15S, R1W, Sec. 20, SE 1/4: UAIC 10445.01 (4 males, 3 females), 31 July 1992; SIUC 20116 (1 male, 1 female); UMMZ 220470 (1 male, 1 female); USNM 319766 (1 male, 1 female); UT 91.4159 (1 male, 1 female). TURKEY CREEK AT THE "NARROWS," T15S, R2W, Sec. 25, NE 1/4, off old Crosston-Pinson Road: UAIC 10446.01 (3 males, 12 females), 31 July 1992. All 31 July 1992 collections were made by B. R. Kuhajda, C. G. Haynes, P. E. Boschung, Jr., R. L. Mayden, and H. T. Boschung.

The entire range of *E. chermocki* is located on a single 7.5 minute series topographic map, the Pinson Quadrangle.

DIAGNOSIS.—*Etheostoma chermocki* is a member of the subgenus *Ulocentra/Nanostoma* as diagnosed by Bailey and Etnier (1988), and Page (1981) and Page and Burr (1991), respectively. It is distinguished from other members of the subgenus by coloration of the spinous and soft dorsal fins, caudal, anal, and pectoral fins, and lateral aspects of body. The spinous dorsal fin of breeding male *E. chermocki* has a cherry-red ocellus in first membrane and broad brick-red subdistal band in the remaining membranes. The soft dorsal fin has a dusky basal band, a broad brick-red medial band, and a dusky distal band. The caudal fin has two red-orange basicaudal spots separated by a clear membrane. The anal and pelvic fins are turquoise and black; pectoral fins are lemon yellow. The vermilion-colored venter extends dorsally and is adjacent to lateral band; lateral band composed of an olive-colored lateral stripe and blotches and a broad, wavy brick-red band. Lateral blotches and brick-red coloration are separated from the ventral vermilion coloration by straw-colored halos. Scales of the venter in males have narrow line of melanophores along distal edge, producing a single crescent on each scale.

DESCRIPTION.—*E. chermocki*, a relatively large snubnose darter, reaches 60.2 mm SL (UF 44006; Kuehne and Barbour, 1983). Sexual dichromatism conspicuous (Fig. 1A and B). Meristically no significant differences in sexes; however, morphometrically sexes differ significantly ($p = <0.5$) in 12 of 16 traits (Table 1). Males with longer head, greater body depth, greater snout length, longer spinous dorsal fin base, longer dorsal fin spines and soft dorsal fin rays, greater caudal peduncle depth, longer anal fin base, longer anal spine, longer anal fin rays, longer caudal fin length, and wider trans-pelvic base. Colors of both sexes differ markedly from spring to summer.

Frequency distributions of fin-ray and scale counts are provided in Tables 2 and 3, respectively. Lateral line complete and virtually straight from upper margin of gill opening to base of caudal fin. Lateral scale rows 44 to 52, usually 46 to 48. Transverse scale rows 11 to 14, usually 13. Caudal peduncle scale 16 to 19, usually 17. Scales absent from breast and nape but present on cheeks and opercle.

Frenum hidden in a shallow premaxillary groove; premaxillae slightly protractile. Gill membranes broadly joined; branchiostegal rays 5. Gill rakers 5 to 7 on both limbs (including rudiments), knobby, longest hardly more than twice its greatest diameter. Teeth of upper jaw conical, closely set, recurved, in four indistinct rows anteriorly, becoming two rows posteriorly. Lower jaw teeth similar, in three rows anteriorly and becoming a single row posteriorly. Vomer bone supports 2 or 3 small canine-like teeth. Infraorbital canal pores 5 (2 specimens), 6 (3), 7 (4), and 8 (6); preoperculomandibular pores 8 (4), 9 (11); lateral canal pores 5 (15); supratemporal canal complete (13) or interrupted (2), pores 0 (1), 1 (2), 3 (10), or 4 (2); supraorbital canal pores 3 (2) or 4 (13); and coronal pore single (15).

Coloration. Males and females are sexually dichromatic; males are more brightly colored than females throughout year, especially during spring. Coloration of breeding male and non-breeding female is illustrated in Figure 1A and B. The following color descriptions of males and females are based upon early March specimens.

Males. Dorsum of head and body of breeding males light olive to straw colored. Post-, sub-, and preorbital stripes dark olive. Upper margin of opercle dark olive. Ventral portion of opercles, subopercles, preopercles, cheeks, branchiostegals, and gular region with cream base color and/or with light lemon-green tint; breast, gular region, snout, and lips with light turquoise tint. Prepectoral region light orange and lemon green.

Dorsum of body crossed by eight dark olive saddles, beginning at nuchal region where darkest and separated from cranium by narrow cream-colored bar, to first procurrent ray of caudal fin. Dorsal saddles separated from one another by straw background coloration; saddles extend ventrolaterally three or four scale rows and interdigitate with dorsal extensions of wavy brick-red coloration along flank. Coloration along flanks complex; composed of large brick-red spots and dark olive-green blotches above and below lateral line. Above lateral line, lateral band consists of cream-colored line tracing lateral line and brick-red spots in wavy and regular pattern. Red coloration beginning at postemporal region and ending at base of caudal rays in basicaudal spot. Anterior to soft dorsal fin red blotches may be bisected by narrow, cream-colored line tracing lateral-line scale row, providing general appearance of two separate lateral bands; posterior to soft dorsal fin origin cream-colored line absent. Flank, belly, and ventro-lateral caudal peduncle scales below lateral band dark vermilion; coloration may extend dorsal to and connect with dark olive lateral stripe and/or brick-red blotches from dorsal portion of band; vermilion coloration separated from olive blotches by narrow halo of straw

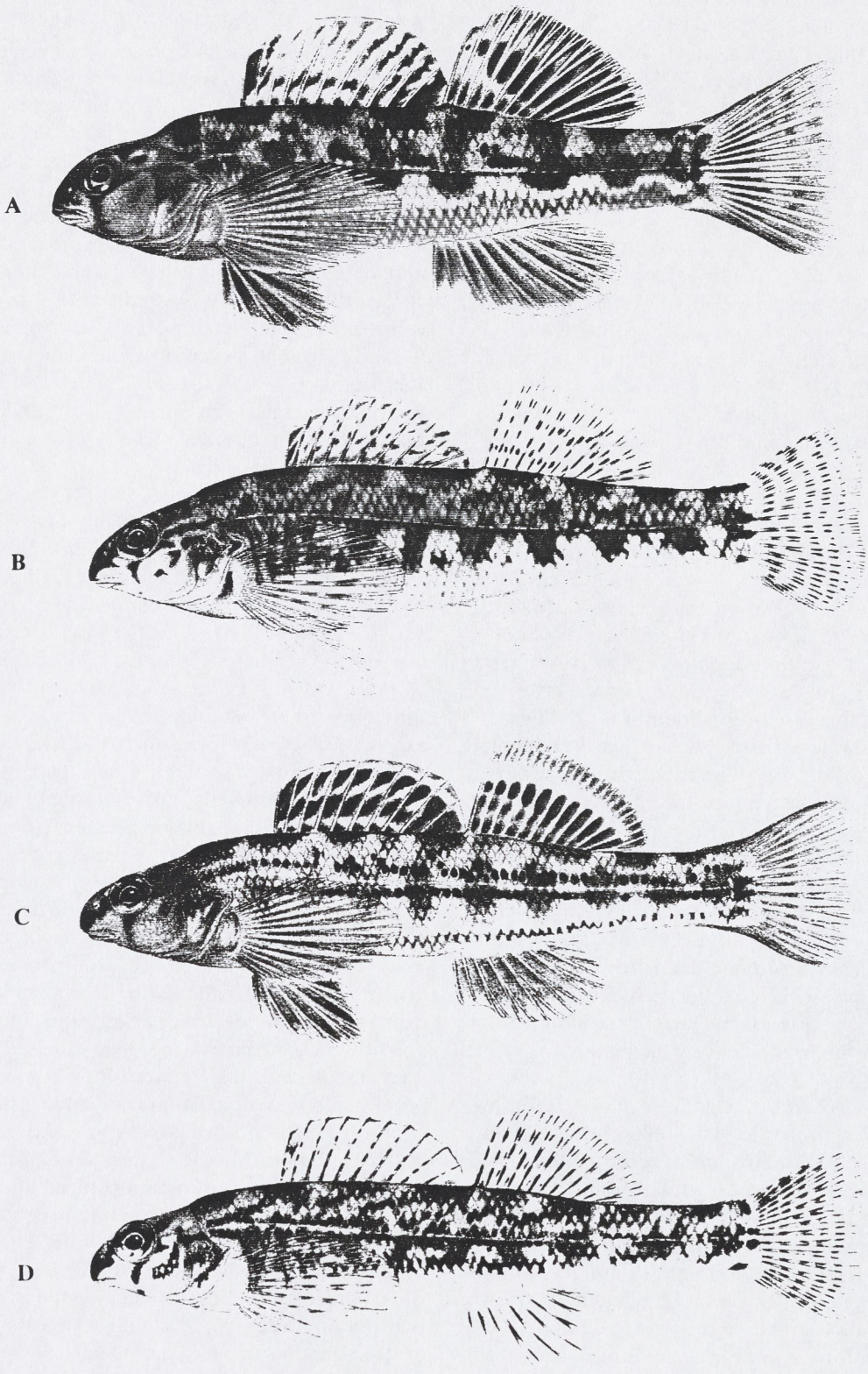

Figure 1. A. *Etheostoma chermocki*, holotype, male, 52.5 mm SL, UAIC 10288.02, Turkey Creek, 9 March 1992. B. *Etheostoma chermocki*, paratype, female, 45 mm SL, UAIC 10445.01, Dry Creek, tributary to Turkey Creek, 31 July 1992. C. *Etheostoma* sp., male, 42 mm SL, UAIC 10455.01, Gurley Creek, 2 April 1992. D. *Etheostoma* sp., female, 45 mm SL, UAIC 10447.01, Gurley Creek, 31 July 1992.

Figure 1. A. *Etheostoma chermocki*, holotype, male, 52.5 mm SL, UAIC 10288.02, Turkey Creek, 9 March 1992. B. *Etheostoma chermocki*, paratype, female, 45 mm SL, UAIC 10445.01, Dry Creek, tributary to Turkey Creek, 31 July 1992. C. *Etheostoma* sp., male, 42 mm SL, UAIC 10455.01, Gurley Creek, 2 April 1992. D. *Etheostoma* sp., female, 45 mm SL, UAIC 10447.01, Gurley Creek, 31 July 1992.

Table 1. Morphometric data of male and female *Etheostoma chermocki* and four populations of Warrior snubnose darters. Measurements are expressed in thousands of the standard length. * Indicates significant differences between the sexes at p = < 0.05 level.

E. chermocki

	Males (N=19)			Females (N=19)		
	Range	$\bar{x}$	SD	Range	$\bar{x}$	SD
SL	36–55	48		40–51	45	
HL *	233–251	240	4.9	221–251	236	7.6
BD *	200–244	223	11.4	195–236	206	9.3
SNL *	53–70	61	4.6	53–64	59	3.5
SDL *	261–312	294	12.5	236–306	273	16.9
LDS *	132–166	145	10.0	105–138	116	7.6
SDL	161–197	183	9.1	163–191	178	7.4
LDL *	154–183	168	8.8	137–172	149	8.8
CPL	265–302	280	9.3	263–304	282	10.6
CPD *	106–124	112	4.6	99–122	105	6.1
AFL *	120–154	138	9.6	112–146	123	9.0
ASL *	64–107	92	10.6	64–92	78	6.3
LAR *	138–167	154	7.3	111–162	135	15.5
CFL *	183–229	208	12.4	174–218	196	13.1
PCFL	243–291	264	13.9	238–288	258	13.4
PVFL	192–233	214	11.6	195–242	210	11.9
TPW *	74–91	82	5.1	69–86	75	4.0

Gurley Creek, Locust Fork population

	Males (N=10)			Females (N=10)		
	Range	$\bar{x}$	SD	Range	$\bar{x}$	SD
SL	41–51	44		36–41	38	
HL	217–228	223	4.2	219–232	224	4.2
BD	188–211	202	7.5	189–213	199	8.0
SNL	55–67	62	3.0	60–68	63	2.6
SDL *	268–301	285	8.6	252–291	274	10.8
LDS *	120–134	127	4.4	110–122	116	3.8
SDL	180–202	188	7.9	171–203	184	11.9
LDL *	140–160	151	6.4	136–149	142	4.8
CPL *	271–313	298	13.1	269–338	300	17.6
CPD	97–108	103	3.5	93–112	98	5.6
AFL	114–136	125	7.6	103–131	120	9.5
ASL	71–92	84	7.6	65–88	80	6.8
LAR	124–153	136	9.0	118–146	130	9.6
CFL	172–207	192	11.3	182–205	194	7.8
PCFL	239–265	247	7.5	223–251	240	7.5
PVFL	191–217	203	8.6	189–216	205	9.0
TPW *	73–81	77	2.7	67–76	72	3.4

Mulberry Fork population

	Males (N=10)			Females (N=10)		
	Range	$\bar{x}$	SD	Range	$\bar{x}$	SD
SL	37–47	42		36–46	39	
HL	230–245	239	4.9	222–244	236	6.9
BD	190–214	203	8.0	179–226	206	15.0
SNL	56–70	64	3.9	59–67	62	2.5
SDL *	277–305	295	8.0	279–299	287	5.6
LDS *	118–145	132	8.4	97–148	116	13.8
SDL	173–194	182	7.3	178–195	185	5.7
LDL *	150–171	160	6.0	145–165	154	6.0
CPL	294–320	307	9.1	276–323	300	13.2
CPD	104–112	108	2.3	103–110	106	2.9
AFL	121–140	129	6.0	120–133	127	4.9
ASL *	81–103	91	7.2	78–96	85	5.6
LAR *	129–156	146	8.9	117–156	137	10.2
CFL	190–224	207	8.8	192–219	207	8.8
PCFL	245–274	262	8.1	247–279	260	10.0
PVFL	195–220	211	8.6	200–227	215	8.2
TPW	71–81	75	3.0	73–80	76	2.2

Sipsey Fork population

	Males (N=10)			Females (N=10)		
	Range	$\bar{x}$	SD	Range	$\bar{x}$	SD
SL	36–44	37		36–42	38	
HL	223–239	232	4.9	228–243	236	5.2
BD	166–205	181	10.6	169–189	179	6.8
SNL	55–67	60	3.4	54–65	60	3.3
SDL	250–300	279	13.3	270–294	279	6.6
LDS *	120–138	130	6.4	107–119	116	3.2
SDL	164–189	178	8.0	168–195	178	7.8
LDL	133–152	141	6.8	135–158	144	6.2
CPL	289–307	299	6.5	281–308	295	8.9
CPD	97–107	103	3.9	97–105	101	2.9
AFL *	122–140	131	7.6	113–135	123	7.9
ASL	83–95	90	4.1	78–95	87	5.8
LAR	125–153	139	8.7	122–149	132	9.2
CFL	182–217	202	11.0	189–220	207	8.9
PCFL	242–272	255	10.4	243–276	257	10.4
PVFL	202–223	214	6.8	205–230	216	7.8
TPW	69–78	73	3.6	71–79	75	2.5

Valley Creek population

	Males (N=10)			Females (N=10)		
	Range	$\bar{x}$	SD	Range	$\bar{x}$	SD
SL	30–49	43		38–46	42	
HL	213–246	230	9.5	203–237	227	10.7
BD	173–200	188	8.7	153–190	178	12.4
SNL	52–64	59	4.2	47–62	57	4.2
SDL	261–297	278	10.9	231–283	265	16.8
LDS *	114–137	124	7.1	90–118	110	8.6
SDL *	167–221	190	15.6	153–180	172	9.8
LDL *	126–152	142	8.8	114–138	131	7.9
CPL	276–319	302	11.1	271–302	293	10.8
CPD *	91–106	100	4.4	82–97	93	4.7
AFL *	118–144	133	7.2	103–123	116	6.8
ASL	76–98	89	6.7	70–92	80	7.4
LAR	117–149	131	10.8	99–132	124	10.3
CFL *	185–222	199	9.7	180–205	189	7.8
PCFL	213–263	242	13.7	204–254	235	15.9
PVFL	198–212	205	4.4	168–208	195	13.6
TPW	64–76	70	3.9	61–74	69	4.0

Table 2. Frequency distribution of rays and spines in fins of *E. chermocki* and four populations of warrior darters.

	Dorsal spines					
	9	10	11	12	$\bar{x}$	SD
E. chermocki (N=74)		22	49	3	10.7	0.52
Warrior darters						
Locust Fork (N=77)	1	51	22	3	10.4	0.58
Mulberry Fork (N=80)	6	58	16		10.1	0.51
Sipsey Fork (N=63)	4	48	11		10.1	0.48
Valley Creek (N=78)		40	38		10.5	0.50

	Dorsal rays					
	10	11	12	13	$\bar{x}$	SD
E. chermocki (N=74)	8	58	8		11.0	0.47
Warrior darters						
Locust Fork (N=77)	4	62	10	1	11.1	0.48
Mulberry Fork (N=80)	4	53	23		11.2	0.53
Sipsey Fork (N=63)		50	13		11.2	0.41
Valley Creek (N=78)	1	62	15		11.2	0.42

	Anal rays					
	6	7	8	9	$\bar{x}$	SD
E. chermocki (N=74)		53	21		7.3	0.45
Warrior darters						
Locust Fork (N=77)	19	56	2		6.8	0.48
Mulberry Fork (N=80)	6	67	7		7.0	0.40
Sipsey Fork (N=63)	5	47	11		7.1	0.50
Valley Creek (N=78)	6	57	14	1	7.1	0.54

	Left pectoral rays					
	12	13	14	15	$\bar{x}$	SD
E. chermocki (N=74)		29	43	2	13.6	0.54
Warrior darters						
Locust Fork (N=77)		28	49		13.6	0.48
Mulberry Fork (N=80)		8	68	4	14.0	0.38
Sipsey Fork (N=63)	1	46	16		13.2	0.46
Valley Creek (N=78)	2	36	40		13.5	0.55

	Principal caudal rays						
	14	15	16	17	18	$\bar{x}$	SD
E. chermocki (N=74)	1	6	33	34		16.4	0.69
Warrior darters							
Locust Fork (N=77)		4	31	42		16.5	0.60
Mulberry Fork (N=80)		1	17	61	1	16.8	0.48
Sipsey Fork (N=63)		3	18	42		16.6	0.58
Valley Creek (N=78)	1	3	22	52	16.6	0.63	

background coloration, especially posterior to soft dorsal fin origin. Vermilion coloration extending posteriorly to hypural plate and base of ventral caudal rays, terminating in a basicaudal spot. Ventro-lateral and belly scales distinctly outlined along distal edges with narrow line of melanophores, creating a crescent pattern on each scale.

Spinous dorsal fin with four separate bands of coloration plus narrow clear distal and narrow black basal bands. First membrane of spinous dorsal fin with large, cherry-red ocellus subdistally, bordered ventrally by broad black band and dorsally by clear membrane; base of membrane with cream-orange band. Broad brick-red band below distal clear band of spinous dorsal fin extends from second membrane to end of fin; band expands from covering one half of the second membrane to all of membranes posterior to ninth spine. Anteriorly, red band may appear as broken and mixed with small slivers of clear membrane; posteriorly, red band is solid and darkest. Between second and ninth spines, broad brick-red band bordered ventrally by narrow cream band, narrow black band, and broad subbasal cream-orange band, respectively. Soft dorsal fin of breeding males with narrow black basal band, broad brick-red medial band, broad and dusky subdistal band, and narrow clear distal band. Black basal band deepest anteriorly and like broad subdistal black band, formed from dense concentrations of melanophores on membranes. Caudal fin membranes cream yellow centrally; dorsal- and ventral-most rays and procurrent rays turquoise. Proximal half of caudal rays dusky; distally rays with alternating subtle light and dark bands. Base of caudal fin with two distinct basicaudal spots formed as extensions of lateral bands; spots separated by clear membranes; dorsal spot brick red, ventral spot vermilion. Anal and pelvic fins turquoise with all interradial membranes dark dusky; some males with red in last two interradial membranes of anal fin. Interradial membranes of pelvic fins of some males entirely dark dusky; spines, rays, and distal edge of fin opaque. Pectoral fins lemon yellow to lime green. Spines and rays of all fins lightly pigmented with melanophores.

Females. Without bright coloration. Dorsum of body and head dark olive and cream colored, as in males. Lateral band less distinctly colored; brick red coloration above lateral line distributed as in males, but restricted to only a few red pigmented scales. Lateral band below lateral line similar to males except that blotches are more intense and contrast strongly with cream background coloration. A few small, dark olive clusters of melanophores may interdigitate between blotches. Anal, pelvic, and pectoral fins immaculate; no melanophores on rays or membranes. Dorsal fins with 2 or 3 dusky bands formed from melanophores along rays and membranes. Anal and pelvic fins, flanks below lateral blotches, and venter, from gular area to caudal fin, immaculate.

Table 3. Frequency distribution of scales counts in *E. chermocki* and four populations of warrior darters.

	Lateral line scale rows															
	42	43	44	45	46	47	48	49	50	51	52	53	54	55	$\bar{x}$	SD
E. chermocki (N=74)			8	5	12	16	12	8	8	2	3				47.4	2.08
Warrior darters																
Locust Fork (N=77)				8	7	10	17	15	9	6		4		1	48.4	2.15
Mulberry Fork (N=80)	1	1	1	7	7	18	10	7	16	8	1	1	2		48.2	2.36
Sipsey Fork (N=63)				3	8	13	12	10	6	7	2	2			48.4	1.98
Valley Creek (N=78)				2	7	8	11	19	16	10	4		1		49.0	1.82

	Transverse scale rows						Caudal peduncle scale rows					
	11	12	13	14	$\bar{x}$	SD	16	17	18	19	$\bar{x}$	SD
E. chermocki (N=74)		11	49	14	13.0	0.58	10	40	17	7	17.3	0.82
Warrior darters												
Locust Fork (N=77)		5	63	9	13.0	0.43	3	41	22	11	17.5	0.79
Mulberry Fork (N=80)	1	9	57	13	13.0	0.57		12	40	28	18.2	0.68
Sipsey Fork (N=63)	1	6	42	14	13.1	0.62	2	36	16	9	17.5	0.78
Valley Creek (N=78)		6	61	11	13.1	0.46		19	27	32	18.2	0.80

Seasonal color changes. Both males and females of *E. chermocki* vary in color with the seasons. While July females have attained brighter colors, males have become less colorful. The completely chromatic venter of spring males is reduced to a ventro-lateral vermilion band, one on each side but not converging at the mid-ventral line. The melanophores that formed crescents on the ventro-lateral and belly scales disappear. The red band of the spinous dorsal has weakened, but leaving the intense cherry-red ocellus in the first interradial membrane. Interradial membranes 3 through 6 are essentially without red pigment, but the last four membranes keep much of their red color. The color of the soft dorsal is virtually unchanged. The pelvic and anal fins are immaculate; the pectorals are very pale peach color with some melanophores on the upper rays. Melanophores on the caudal fin form four vertical bars.

Females, which are rather drab in early spring when the males are at the height of their coloration, become more colorful by late summer. Bright red-orange ocelli are in the first and last three spinous dorsal membranes, the latter more orange. The proximal third of the pectoral fin is peach color and the remainder of the fin is lemon yellow. Scattered brick-red colored spots form an indistinct narrow band above the pale lateral line. The spaces between the lateral blotches are pale lemon color; the lower flanks are streaked with pale orange chromatophores; and the belly is white. The pelvic and caudal rays are light lemon yellow. Melanophores on the caudal fin form 5 vertical stripes.

COMPARISONS.—*Etheostoma chermocki* is easily distinguished from the geographically proximate Warrior snubnose darters by fin and body coloration (Fig. 1C and D), as well as by male morphometrics (Fig. 2). In the Warrior snubnose darters the olive-colored median lateral band is narrow and separate from both the narrow brick-red band dorsally and the ventrolateral orange coloration. The median olive-colored lateral band terminates posterior to the hypural plate in a rectangular basicaudal spot more or less continuous with the posterior-most lateral blotch. The 7 or 8 olive-colored lateral blotches are larger, rectangular in shape, and extend 2 or 3 scale rows above and below the narrow lateral band. The red band above the lateral line is generally straight, not arched around lateral blotches as in *E. chermocki* and is rarely connected to dorsal saddles. It is generally formed by a single row of red-colored scales and is always separate from the narrow lateral band for most of its length by cream background coloration. Together, the dorsally located red band and the medially located olive band present a double lined pattern along the flanks. Below the lateral band the orange coloration is confined to 1 or 2 scale rows ventrolaterally and is separated from the olive lateral band above. The belly and ventral caudal peduncle are cream colored, not orange.

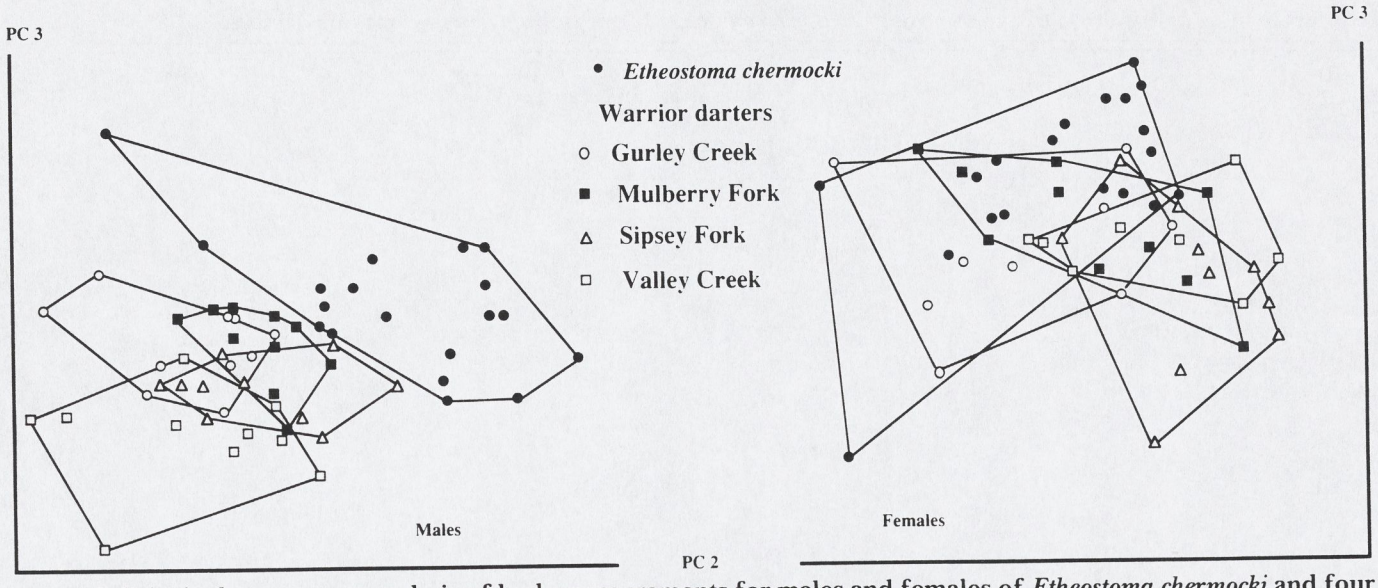

Figure 2. Principal component analysis of body measurements for males and females of *Etheostoma chermocki* and four populations of undescribed Warrior snubnose darters.

The spinous dorsal fin of *E. chermocki* is similar to that of the Warrior snubnose darters in having a cream-orange band above a black basal band. However, the red band of the latter is narrower, the red ocellus in the first membrane is smaller, and the narrow distal band is turquoise. The soft dorsal fin differs from that of *E. chermocki* in having a narrower medial brick-red band bordered dorsally by a narrow yellow band and a turquoise distal band. The caudal fin is turquoise with two cream-colored ocelli basally, separated by a median, rectangular olive blotch as an extension of the lateral stripe.

Females of *E. chermocki* differ from female Warrior snubnose darters in lateral coloration and pigmentation of fins. The latter possess melanophores in the anal fin and have dense concentrations of melanophores below the lateral band and between the lateral blotches, presenting a solid or nearly solid band below the medial lateral band.

Male and female *E. chermocki* are compared morphometrically with four different populations of Warrior snubnose darter (Table 1; Fig. 2). The sheared principal component analysis reveals considerable overlap in all populations of female Warrior snubnose darters and female *E. chermocki*; however, morphometrically male *E. chermocki* are completely separable from males of four populations of Warrior snubnose darters. Head, body, and anal fin measurements contribute significantly to the separation of *E. chermocki* from Warrior snubnose darters in PC analysis. *Etheostoma chermocki* males consistently possess a shorter snout, deeper body, taller spinous dorsal fin, shorter soft dorsal fin base, shorter caudal peduncle, and shorter anal spines and rays. *Etheostoma chermocki* was not found to differ significantly from any populations of Warrior snubnose darters for meristic characters (Tables 2 and 3).

Etheostoma chermocki is distinguished from some members of the subgenus *Ulocentra/Nanostoma* (*E. barrenense*, *E. duryi*, *E. etnieri*, *E. rafinesquei*, and *E. simoterum*) with its possession of the cream-colored stripe tracing the lateral line anteriorly, making it appear distinct from the red or orange lateral stripe anteriorly. *Etheostoma chermocki* is distinguished from *E. tallapoosae*, *E.* sp. (Coastal Plain darter), and *E.* sp. (Yazoo Darter) in its possession of the red ocellus in the first membrane on the spinous dorsal fin. *Etheostoma chermocki* differs from *E. brevirostrum*, *E. coosae*, *E. tallapoosae*, *E. zonistium*, and Warrior snubnose darters in lacking a turquoise-blue distal band on the spinous dorsal fin. Finally, *E. chermocki* differs from *E. pyrrhogaster* and *E. zonistium* in lacking a broad red basal band on the anal fin.

Bailey and Etnier (1988) recognize two species groups of snubnose darters based on the presence or absence of a premaxillary frenum and vomerine teeth: the *E. duryi* group (*brevirostrum*, *duryi*, *coosae*, *etnieri*, *flavum*, *pyrrhogaster*, *tallapoosae*, *zonistium*, and other unnamed species) lack a distinct premaxillary frenum (i.e., the premaxilla is free from the snout and a needle can be passed under the free flap of snout tissue) and in having vomerine teeth; whereas, the *E. simoterum* species group (*s. simoterum*, *s. atripinne*, *baileyi*, *barrenense*, and *rafinesque*) has a narrow frenum that allows only minimal protraction of the premaxillae and lacks vomerine teeth. *Etheostoma brevirostrum* often has vomerine teeth and either lacks a frenum or has a poorly developed one, therefore it is assigned to the *duryi* group. *Etheostoma chermocki* is most similar to the *E. duryi* group of snubnose darters.

ETYMOLOGY.—The species epithet *chermocki* is a patronym honoring Ralph L. Chermock (1918–1977) who founded the University of Alabama Ichthyological Collection. The

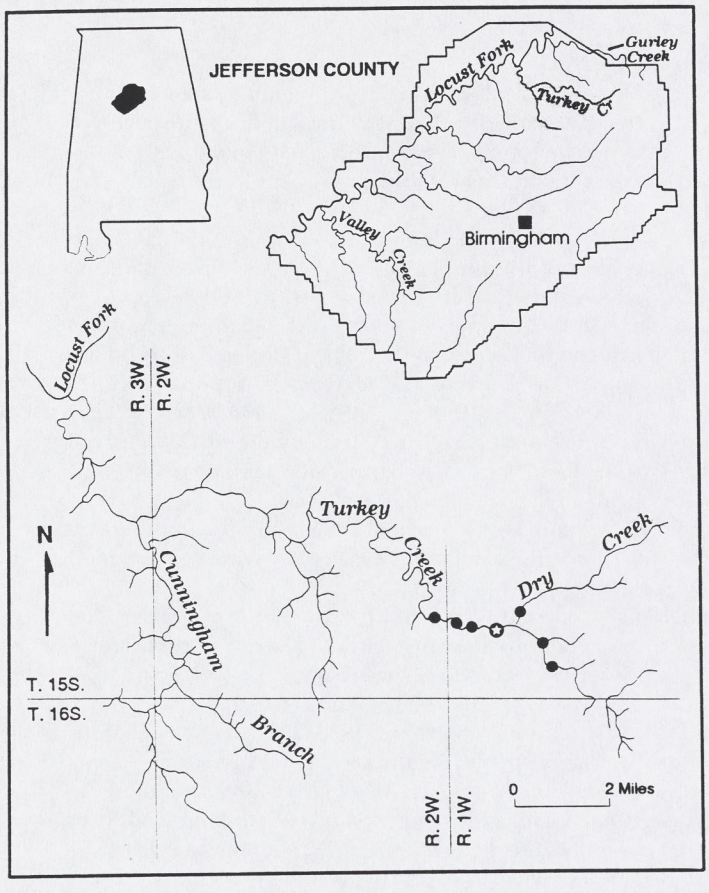

Figure 3. Distribution of *Etheostoma chermocki* within Locust Fork of Black Warrior River of the Mobile Basin. ✪ Type locality; ● Collection sites.

common name, vermilion darter, calls attention to the vermilion-colored ventro-lateral flanks and belly of breeding males. The color vermilion can refer to a broad spectrum of reds or red-oranges. Our use of vermilion refers to a red-orange coloration.

Distribution and Habitat.—*Etheostoma chermocki* is known only from the headwaters of Turkey Creek, a tributary to Locust Fork, Black Warrior River in Jefferson County, Alabama, at the sites cited above (Fig. 3). The habitat of *E. chermocki* is small to medium-sized (3–20 meters wide), gravel-bottom streams with pools of moderate current alternating with riffles of moderately swift current. The riffles are of coarse gravel and cobble, and small rubble, whereas the bottoms of the pools are rock (sometimes bedrock), sand and silt. The most favorable habitat seems to be the swifter chutes where some vegetation abounds, such as watercress (*Nasturtium officinale*) or pondweed (*Potomogeton foliosus*).

Species collected with *E. chermocki* throughout its range are: *Campostoma anomalum, Cyprinella callistia, Luxilus chrysocephalus, Notropis stilbius, Semotilus atromaculatus, Hypentelium etowanum, Moxostoma duquesnei, Gambusia affinis, Cottus carolinae, Lepomis cyanellus, Lepomis macrochirus, Micropterus coosae, Micropterus salmoides, Etheostoma whipplei,* and *Percina nigrofasciata.*

Conservation Status.—Inasmuch as this darter has a very limited range (Fig. 3), consisting of no more than about three miles of stream, which is in urban and suburban areas, its conservation status should be considered ENDANGERED. Undoubtedly the darter was formerly more widespread; however, parts of Turkey Creek are so degraded by domestic pollution, especially from silt issuing from construction projects, that the vermilion darter only occurs sporadically. Specimens were collected in good numbers in the 1960s and 70s at the Hwy 79 bridge site. At the same site, on 31 July 1992, 10 man-hours of collecting yielded one specimen. It is indeed unfortunate that we did not realize the uniqueness of the Turkey Creek darter 20 or 30 years ago. Measures could have been taken to name and describe this rare species and therefore afford it the protection of an endangered species. We think that the population is sufficiently small that immediate attention should be given to its protection.

Acknowledgement

The collections acquired by many students and colleagues over the past 30 years made this study possible. We are pleased to list their names in the section on type materials and in the following section on comparative materials. Carter Gilbert (Florida State Museum) and Julian Humphries (Cornell University) loaned specimens of the new species, and Lawrence M. Page (Illinois Natural History Survey) loaned specimens from Mulberry Fork. Joseph R. Tomelleri prepared the color figures (Fig. 1). Bernard R. Kuhajda ran the principal components analysis and gave freely of his time in collecting fresh specimens. Robert Wood ran the bivariate analysis. Andrew Simons prepared cleared and stained specimens. W. Mike Howell read the original manuscript and shared his knowledge and insights regarding the distribution and systematics of Mobile Basin snubnose darters. We thank two peer reviewer's for helpful suggestions that improved the paper. This research was supported by NSF (BSR9007513) and the Tanglewood Fund.

Comparative Materials

Locust Fork. GURLEY CREEK AT HWY 79, Jefferson County, T14S, R1W, Sec.30, NW 1/4, about 0.2 mi from Jefferson-Blount county line: UAIC 1879 (1 female), 8 February 1966, J. D. Williams and J. G. Armstrong; UAIC 1906.14 (2 males, 2 females), 1 April 1966, R. D. Caldwell, W. M. Howell, and J. D. Williams; UAIC 3305.17 (1 female), 17 March 1969, L. A. Barclay and W. M. Howell; UAIC 10447.01 (2 males, 2 females), 31 July 1992, B. R. Kuhajda, C. G. Haynes, P. E. Boschung, Jr., R. L. Mayden, and H. T. Boschung. GURLEY CREEK AT HWY 75, 0.4 mi north Jefferson-

Blount county line in Blount County, T14S, R1W, Sec. 34, SW 1/4: UAIC 6258.07 (4 females), 22 September 1980, D. L. Nieland, H. T. Boschung, R. A. Kasprzak, and K. Newkirk; UAIC 6364.06 (12 males, 15 females), 6 March 1981, D. L. Nieland; UAIC 6425.01 (9 males, 36 females), 13 April 1981, D. L. Nieland; UAIC 6428.01 (2 males, 4 females), 19 April 1981, D. L. Nieland; UAIC 7164.01 (2 males, 2 females), 10 March 1984, D. L. Nieland, R. E. Smith, Jr., and D. R. Woods; UAIC 9843.01 (1 male), 9 February 1990, R. L. Mayden, B. R. Kuhajda, S. R. Layman, A. M. Simons, and R. M. Wood.

Mulberry Fork. MILL CREEK, Blount County, T13S, R2W, Sec. 4, SW 1/4, SW 1/4: UAIC 3804.07 (9 males, 8 females), 13 February 1970, C. R. Duckett, W. M. Howell, and L. A. Barclay. MILL CREEK, Blount County, T13S, R3W, Sec. 12, SE 1/4, NW 1/4: UAIC 3806.06 (2 males, 8 females), 20 February 1970, C. R. Duckett and L. A. Barclay; UAIC 5347.05 (1 male, 6 females), 27 May 1977, D. A. Black. MILL CREEK, Blount County, T13S, R3W, Sec. 2, SE 1/4: UAIC 5346.04 (1 male, 2 females), 27 May 1977, D. A. Black. MURPHY CREEK, Blount County, T13S, R3W, SEC. 12, SW 1/4: INHS 76157 (7 males, 13 females), 19 April 1977, L. M. Page, M. C. Retzer, R. L. Mayden, D. L. Swofford; INHS 87637 (9 males, 11 females), 6 April 1982, B. M. Burr and L. M. Page; UAIC 10267.01, 2 April 1992, R. L. Mayden and H. T. Boschung.

Sipsey Fork. BORDEN CREEK, TRIBUTARY TO SIPSEY FORK, Lawrence County on Bunyard Road, T8S, R8W, Sec. 32, NE 1/4, (Bee Branch Quad.): UAIC 1696.14 (1 male, 4 females), 12 July 1978, B. R. Wall, P. E. O'Neil, and W. B. Brown; UAIC 3868.08 (4 males, 6 females), 22 August 1970, W. M. Howell, Mike Hopiak, and Jim Manasco; UAIC 3886.06 (1 male, 3 females), 31 August 1970, W. M. Howell, Mike Hopiak, and Don Dycus; UAIC 6264.09 (2 males, 17 females), 11 October 1980, D. L. Nieland; UAIC 6427.02 (2 males, 3 females), 19 April 1981, D. L. Nieland. BORDEN CREEK, Lawrence County, T8S, R8W, Sec. 28, NE 1/4: UAIC 4963.12 (2 males, 2 females), 19 August 1974, Monte Seehorn, H. T. Boschung, and T. S. Jandebeur. SIPSEY FORK PROPER, Winston County, T9S, R8W, Sec. 22, NW 1/4: UAIC 3852.12 (3 males, 4 females), 3 November 1971, Don Dycus and David Johnson; UAIC 3855.10 (4 males), 8 November 1971, Don Dycus, W. M. Howell, and Mike Hopiak. CANEY CREEK, Winston County, T9S, R8W, Sec. 20, NW 1/4: UAIC 3859.08 (1 male, 5 females), 17 November 1971, Don Dycus and Mike Hopiak.

Valley Creek. FIVEMILE CREEK NEAR BESSEMER, Jefferson County, T19S, R5W, Sec. 36, NW 1/4, NW 1/4: UAIC 1934.10 (6 males, 22 females), 11 April 1966, R. D. Caldwell and W. M. Howell; UAIC 2011.02 (1 female), 20 April 1966, R. D. Caldwell and W. M. Howell. UAIC 2504.08 (1 male, 3 females), 19 March 1966, J. D. Williams and J. G. Armstrong; UAIC 3041.15 (8 males, 3 females), 15 August 1968, H. Harima and T. S. Jandebeur; UAIC 6481.01 (1 male, 1 female), 8 October, 1976, D. A. Black; UAIC 10448.01 (1 male, 1 female), 6 August 1992, W. M. Howell, B. R. Kuhajda, and H. T. Boschung. FIVEMILE CREEK, Jefferson County, T19S, R5W, Sec. 24, SW 1/4: UAIC 10449.01 (2 males, 5 females), 6 August 1992, W. M. Howell, B. R. Kuhajda, and H. T. Boschung. FIVEMILE CREEK, Jefferson County, T19S, R5W, Sec. 14, SE 1/4: UAIC 10450.01 (8 males, 15 females), 6 August 1992, B. R. Kuhajda, W. M. Howell, and H. T. Boschung.

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Comments on the proposed conservation of the specific name of *Cliola* (*Hybopsis*) *topeka* Gilbert, 1884 (currently *Notropis topeka*) (Osteichthyes, Cypriniformes)
(Case 2808; see BZN **49**: 268–270; **50**: 144, 287–289)

(1) Richard L. Mayden
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I read with great interest the reply (BZN **50**: 289) by Drs Frank B. Cross & Joseph T. Collins to my previous comment co-authored with Dr Carter R. Gilbert (BZN **50**: 287–288). I consider that it is both inaccurate and inappropriate with regard to the nomenclatural change we (Mayden & Gilbert, 1989) proposed for *Notropis topeka* to *N. tristis*.

Cross & Collins criticize the Girard (1856) description of *Notropis tristis* as being inaccurate and poor. They regard this description as such because it 'has not enabled assignment of the name to any known taxon without reference to the type material'. This is neither a fair assessment of Girard's research nor the information provided in the description. They state that 'There are several species to which Girard's description might apply ...'. This is also incorrect. There are few species that are found in the region where Girard conducted his research that are consistent with the description. The description is much better than that for many species that we accept today as valid and have no extant types.

Cross & Collins use the argument of *Notropis tristis* being considered for listing by the U.S. Fish and Wildlife Service as a 'Category One' species in need of further study and protection. This is also a very weak argument and one without substance. The nomenclatural change from *Notropis topeka* to *N. tristis* has already been accepted by the Fish and Wildlife Service. The list of candidate species for federal protection lists the species as *N. tristis*, not *N. topeka*!

I believe that the arguments provided by Cross & Collins in their application and in their subsequent comment are without scientific merit and reflect a personal bias towards a local name for the species. While it may be nice to accommodate personal preferences on such issues it is clear that the rules of zoological nomenclature were established to eliminate such foolishness.

(2) Reeve M. Bailey
Division of Fishes, Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109, U.S.A.

The date for Girard's name *Moniana tristis* is given as 1857 in the application by Drs F.B. Cross & J.T. Collins. Since about 23 genera and 133 new species were described in Girard's work accurate dating is important. Although 1857 is often used, 1856 is more common and is correct.

Girard's paper was published in the *Proceedings of the Academy of Natural Sciences of Philadelphia*, vol. 8, pp. 165–213 in 1857 and was recorded (1913) with this date in the 'Index to the scientific contents of the Journal and Proceedings of the Academy ... 1812-1912'. However, an entry (p. 1) in the 'Correspondence-1857'

section of the *Proceedings*, vol. 9 (1858) certifies receipt of '*Proceedings*, vol. viii, No. 5' (Girard's paper) by the Trustees of the New York State Library on or before 27 December 1856. Thus, Girard's paper was issued sometime between the date of acceptance, 30 September (*Proceedings*, vol. 8, p. 163) and 27 December 1856. It was the practice of the Academy to publish and distribute parts of the *Proceedings* when printed, with the title page of the volume showing the date when the volume was to be assembled (1857 for vol. 8 of 1856). The situation is further complicated since Girard's paper, with slightly changed title (the words 'of America' are lacking) and different pagination (pp. 1–54), was issued as an offprint in September 1856. The (1913) 'Index ... 1812-1912' (p. vii) noted 'The issue to authors of separate copies of papers from the *Proceedings* antedates the publication of the numbers of which they form a part, the record being printed on the covers of the separata but not otherwise preserved'. The type bed in the volume and the separate were the same; the separate had a terminal four pages of a list of species and an index (pp. 51–54).

I have been aware of the application to conserve the specific name of *Notropis topeka* (Gilbert, 1884) since its inception. In fact, I intended to request the conservation of this name myself until I learned that Drs Cross and Collins were doing so. I therefore support with enthusiasm the proposed conservation of the name for the familiar cyprinid fish of north-central United States.

Identification of the two located syntypes of *Moniana tristis* Girard, 1856 with two well-marked species, *Lythrurus* (or *Notropis*) *umbratilis* Girard, 1856 and *Notropis topeka* (see Mayden, 1987, Mayden & Gilbert, 1989 and paras. 3 and 4 of the application) emphasizes the inadequacy of Girard's original description, which C.R. Gilbert (1978, p. 84), following others, ranked as not definitely identifiable. It is difficult to rationalize the observation by Mayden & Gilbert (BZN **50**: 287, para. 4; see above also) that Girard's description 'was good according to the standards at the time'.

As Cross & Collins have shown, the consistent and unquestioned use of *Notropis topeka* during this century has served scientific communication well. In their opposition to the application, Mayden & Gilbert defend their (unnecessary) selection of a lectotype for *Moniana tristis* that dictates replacement of *topeka*. They do not address the issue of conservation of the latter name but defend nomenclatural priority with spirit. In so doing they overlook evidence that the Commission is not blind to the fundamental importance of stability (see Article 23b of the Code). Recommendation 24A comments on the action of first reviser (which could have been exercised in this case; see paras. 3 and 4 of the application): 'An author should choose the name, homonym, spelling, or nomenclatural act that will best serve stability and universality of nomenclature'. Mayden & Gilbert (1989) disregarded this exhortation and then (BZN **50**: 288, para. 7) challenged the 'scientific integrity' of a choice that could have avoided a name change.

I have discussed Cross & Collins's application, the previous comments and this statement with four local ichthyological colleagues, William L. Fink, William A. Gosline, Robert Rush Miller and Gerald R. Smith. They agree with me that the three actions proposed in para. 6 of the application will contribute substantially to nomenclatural stability, and we strongly endorse them. Approval from these colleagues indicates that support is not only regional (Kansas), as suggested by Kuhajda (BZN **50**: 289) and Mayden (above).

OPINION 1821

Cliola (*Hybopsis*) *topeka* Gilbert, 1884 (currently *Notropis topeka*; Osteichthyes, Cypriniformes): specific name conserved

Keywords. Nomenclature; taxonomy; Osteichthyes; Cypriniformes; freshwater fish; *Notropis topeka*; North America.

Ruling

(1) Under the plenary powers the specific name *tristis* Girard, 1856, as published in the binomen *Moniana tristis*, is hereby suppressed for the purposes of the Principle of Priority but not for those of the Principle of Homonymy.

(2) The name *topeka* Gilbert, 1884, as published in the binomen *Cliola* (*Hybopsis*) *topeka*, is hereby placed on the Official List of Specific Names in Zoology.

(3) The name *tristis* Girard, 1856, as published in the binomen *Moniana tristis* and as defined by the lectotype (specimen no. MNHN 427 in the Muséum National d'Histoire Naturelle, Paris) designated by Mayden & Gilbert (1989), suppressed in (1) above, is hereby placed on the Official Index of Rejected and Invalid Specific Names in Zoology.

History of Case 2808

An application for the conservation of the specific name of *Cliola* (*Hybopsis*) *topeka* Gilbert, 1884 was received from Drs Frank B. Cross and Joseph T. Collins (*Museum of Natural History, The University of Kansas, Lawrence, Kansas, U.S.A.*) on 11 January 1991. After correspondence the case was published in BZN **49**: 268–270 (December 1992). Notice of the case was sent to appropriate journals.

A comment in support from Prof Hobart M. Smith (*University of Colorado, Colorado, U.S.A.*) was published in BZN **50**: 144 (June 1993). Opposing comments from Prof Richard L. Mayden (*University of Alabama, Tuscaloosa, Alabama, U.S.A.*) & Dr Carter R. Gilbert (*Florida Museum of Natural History, University of Florida, Gainesville, Florida, U.S.A.*), and from Dr Bernard Kuhajda (*University of Alabama, Tuscaloosa, Alabama, U.S.A.*), were published in BZN **50**: 287–289 (December 1993). A reply by the authors of the application was published at the same time (BZN **50**: 289). A further comment from Prof Mayden was published in BZN **51**: 262 (September 1994). A comment from Dr Reeve M. Bailey (*Museum of Zoology, University of Michigan, Ann Arbor, Michigan, U.S.A.*), published in BZN **51**: 262–263, supported the application and also pointed out that Girard's paper, in which the name *Moniana tristis* appeared, was first published in 1856 (and not 1857 as cited in the application).

Decision of the Commission

On 1 March 1995 the members of the Commission were invited to vote on the proposals published in BZN **49**: 269. At the close of the voting period on 1 June 1995 the votes were as follows:

Affirmative votes — 17: Bock, Cocks, Corliss, Hahn, Heppell, Holthuis, Kraus, Mahnert, Martins de Souza, Minelli, Nielsen, Nye, Ride, Savage, Schuster, Starobogatov, Štys

Negative votes — 6: Bouchet, Dupuis, Kabata, Lehtinen, Macpherson and Thompson.

No votes were received from Cogger, Halvorsen, Trjapitzin and Uéno.

Bayer was on leave of absence.

Voting for, Bock commented: 'It is essential for all zoologists to realize that the only goal of zoological nomenclature is to facilitate communication between all workers interested in the biology of animals. Nothing is gained and much is lost every time an established name is replaced by an unused senior synonym regardless of why the senior synonym had become unused. Hence I urge all zoologists to apply to the Commission every time they discover such an unused senior synonym rather than to introduce this name into the zoological literature. Every effort should be made to conserve well-established names and to suppress unused senior synonyms'. Cocks commented: 'This is clearly a case of the 'rules' versus 'established usage'. I was swayed in the end by Dr Bailey's support'. Voting against, Dupuis commented: 'Owing to some taxonomic uncertainties and doubts concerning the syntypes and lectotypes of the two nominal species in question, I vote against. This is not a vote in favour of the inscription of *tristis* Girard, 1856 on the Official List, which would be premature'. Thompson commented: 'The arguments of Mayden & C.R. Gilbert should be heeded. The application requests that a junior name be conserved on the basis of 'usage'. 'Usage' is difficult to define; it is not merely the number of authors and titles. Adoption of the senior name *tristis* Girard in a Peterson field guide undoubtedly accounts for more than all the scientific papers cited by Cross & Collins. When there are reasonable arguments on both sides the final arbiter is priority, not usage'.

Original references

The following are the original references to the names placed on an Official List and an Official Index by the ruling given in the present Opinion:

tristis, *Moniana*, Girard, 1856, *Researches upon the cyprinoid fishes inhabiting the fresh waters of the United States, west of the Mississippi Valley, from specimens in the museum of the Smithsonian Institution*, p. 37. (First issued as a separate in September 1856; published in the *Proceedings of Natural Sciences of Philadelphia*, **8**: 201 in 1857).

topeka, *Cliola* (*Hybopsis*), Gilbert, 1884, *Bulletin of the Washburn College Laboratory of Natural History*, **1**(1): 13.

The following is the reference for the designation of the lectotype of *Moniana tristis* Girard, 1856:

Mayden, R.L. & Gilbert, C.R. 1989. *Copeia*, **1989**(4): 1087.