A SYSTEMATIC REVISION OF THE
NEOTROPICAL CATFISH FAMILY AGENEIOSIDAE
(TELEOSTEI: OSTARIOPHYSI: SILURIFORMES)

By

STEPHEN JOSEPH WALSH

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The catfish family Ageneiosidae has 12 species that inhabit most major South American rivers. Their taxonomy has always been inadequately understood, despite their widespread distribution and abundance. The aim of this study is to stabilize the nomenclature and to examine species relationships.

Four nominal genera are synonyms of the only two genera here recognized as valid, *Tetranematichthys* and *Ageneiosus*.

Tetranematichthys quadrifilis is widely distributed and is the most primitive member of the family on the basis of features of the barbels and swimbladder.

All other species belong to the type genus of the family, *Ageneiosus*. *A. atronasus*, *A. brevis*, and *A. piperatus* share several primitive characters, and their phylogenetic relationships are unresolved. The poorly known *A. piperatus* occurs in rivers near the Guiana Shield. *A. atronasus* and *A. brevis* occur in the Amazon basin, and each has several distinguishing autapomorphies.

Ageneiosus pardalis is the sister species of a terminal clade of the remaining species, and is the only trans-Andean species of the family; it occurs from southern Panama to northwestern Venezuela. It has a primitively large swimbladder but is otherwise morphologically similar to the terminal lineage of species.

The other species of *Ageneiosus* are a monophyletic lineage that share an encapsulated swimbladder. The most derived species are *A. brevifilis*, *A. marmoratus*, and *A. polystictus*, which have synapomorphies of the pectoral and caudal fins; the first two species are inseparable except on coloration. *A. brevifilis* is broad ranging and is the species most frequently marketed for food. *A. marmoratus* has been poorly studied because of its rarity. *A. polystictus* is confined to the Rio Negro and is also poorly studied.

Relationships among the remaining species are not fully resolved, due to their morphological similarities. However, the species have meristic differences and other features that distinguish them. *A. ucayalensis* is broadly distributed and is the most abundant species in many areas. *A. valenciennesi* is endemic to the Rio Paraná and Rio Paraguay drainages. *A. vittatus* is common in the Orinoco basin and was recently discovered in the upper Amazon basin. An undescribed species exists in the middle and lower Amazon basin.

INTRODUCTION

Members of the catfish family Ageneiosidae are widely distributed throughout major freshwater drainages of the neotropics from Panama southward to Paraguay and Argentina. They are small to moderately sized fishes typically found in open-water habitats, such as lakes and large river channels. Some species comprise a significant element of local fisheries harvests, and are thus familiar to many native South Americans by a variety of vernacular names. In spite of their widespread distribution and popularity as food fishes, the taxonomy and phylogenetic relationships of ageneiosids have remained largely obscure to ichthyologists in this century.

The present study was undertaken to address the following objectives: (1) to compile all pertinent literature of the Ageneiosidae; (2) to elucidate the salient features of morphometry, osteology, and soft anatomy of all known species; (3) to provide a comprehensive systematic revision of the family based on morphological criteria; (4) to test the hypothesis that the nominal genera *Ageneiosus*, *Pseudogeneiosus*, *Tetranematicthys*, and *Tympanopleura* form a monophyletic group; (5) to determine the nomenclatural status of each of these genera and the species included in them; (6) to evaluate the relationships of all included species using phylogenetic methods; (7) to summarize previous studies on higher relationships of ageneiosids to other catfish genera and families; and (8) to compile range maps of all species from museum specimens, and to compare their distributions with those of other neotropical freshwater fishes.

The extremely diverse freshwater fish fauna of South America has received a moderate amount of taxonomic study, beginning in particular with the pioneering work of many notable 19th and early 20th century naturalists and ichthyologists, during an intense period of descriptive ichthyology (Böhlke et al. 1978). However, not until relatively recently have there been detailed studies of selected neotropical fish taxa using more modern and objective systematic methods and theory, particularly quantitative and phylogenetic systematics. Because the task of revising many of these groups is a formidable one, many recent studies have focused on relatively small taxa, well-defined subgroups of larger, more diverse groups, or have tended to neglect detailed species-level taxonomy in favor of attempts to establish a better knowledge of higher-level relationships. There have been relatively few studies of phylogenetic relationships among catfishes, or siluroids, and few recent taxonomic revisions of larger groups. This is particularly true of the neotropical fauna, which constitutes about 59% of the catfishes in the world, as estimated by Nelson (1984). Consequently, although our understanding of neotropical freshwater fish systematics has improved considerably in recent years, the taxonomy of many groups remains in an extremely fragmented state, and the ichthyofauna as a whole is still among the most poorly known worldwide. Emphasizing problems in catfish evolution, Lundberg and Baskin (1969) and Gosline (1975) argued that studies of single structural complexes might reveal a better understanding of phylogenetic relationships, at least among higher groups. However, this assumption is reliable only if one assumes that the comparisons being made are across sufficiently broad taxonomic categories to formulate accurate generalizations, and that the currently accepted taxonomy of groups included under study reflect natural taxa. Furthermore, as Howes (1983) noted, a strong reliance on one or few characters can produce a misleading hypothesis of phylogenetic relationships. Conversely, Böhlke et al. (1978) and the National Research Council (1980) suggested that, in light of

recent and impending perturbations of the neotropical environment, there is an urgent need for faunal and revisionary studies of many taxa in order to permanently document their status and to provide a basis for future research of this rich biological resource. Gosline (1942) emphasized the need for a revision of the Ageneiosidae, as well as a number of other neotropical catfishes.

The opinion expressed by Böhlke et al. (1978) is adopted here; alpha-level taxonomic studies are badly needed to provide a better foundation for more in-depth research of the evolutionary history and ecology of the ichthyofauna. A number of recent studies of neotropical catfishes have resulted in revisions of existing classifications, and, in some cases, the authors proposed significant changes based on hypothesized phylogenetic relationships. However, not all of these studies included critical examinations of all of the taxa in a genus or higher category, and thus were of little help in resolving alpha-level taxonomic problems. Given the diversity of species involved and an overall poor understanding of their systematics and morphology, it is my opinion that attempts to propose higher-level phylogenies for some groups may be premature at present. The possible misrepresentations inherent in such studies are confounded by cases where genera are currently considered monotypic, species are known from very few specimens, and large numbers of species remain undescribed, or even undiscovered.

A revision of the Ageneiosidae is timely, given the previously confused taxonomy of the family, and the drastic recent effects of human alterations of South American river systems. It is anticipated that results of this study will allow biologists to correctly identify ageneiosid species, thus perhaps improving prospects for their management and conservation. In addition, it is hoped that these results will enhance our general understanding of systematic relationships of neotropical catfishes.

Historical Treatment of the Ageneiosidae

Higher Classification of the Family

The family Ageneiosidae, as recognized by previous authors, includes six nominal genera; *Ageneiosus* Lacepède, *Ceratorhynchi* Agassiz, *Davalla* Bleeker, *Pseudogeneiosus* Bleeker, *Tetranematichthys* Bleeker, and *Tympanopleura* Eigenmann. The nomenclatural history of the last five genera, and their taxonomic status as interpreted from prior synonymies and the present study, are reviewed below in separate sections. The more complex history of *Ageneiosus* is addressed in part in the following section, and in greater detail in the synonymies and comments under the species accounts.

The supraspecific classification of the Ageneiosidae has undergone considerable historical change because of poorly resolved systematic problems at the family level. These changes have largely reflected differing classification schemes involving ageneiosids and two other closely related families, the Auchenipteridae and Doradidae. Many of the prior classifications were reviewed by Britski (1972) and Ferraris (1988), but are repeated here chronologically because of their relevance to controversy surrounding the currently hypothesized relationships of the Ageneiosidae to other taxa. Hereafter these three families will be collectively referred to as the neotropical superfamily Doradoidea. Excluded from the present discussion is the African family Mochokidae, which may be phylogenetically close to the neotropical doradoids, and is sometimes lumped together in the superfamily (Chardon 1968; J. G. Lundberg, personal communication).

Among the earliest synoptic classifications that included major groups of siluroids are those of Cuvier and Valenciennes (1840), Bleeker (1862, 1863), Günther (1864), and Eigenmann and Eigenmann (1890). In their classifications,

these authors generally appeared to have grouped together taxa on the basis of presumed evolutionary relationships. However, their classifications were based largely on superficial similarities of external morphology, and thus often involved primitive characters shared among purportedly related groups. Many of the suprageneric categories recognized in early studies, such as the broadly encompassing families Siluroidei of Bleeker (1862) and Siluridae of Günther (1840) and Eigenmann and Eigenmann (1890), were eventually found to be polyphyletic by subsequent authors. Notwithstanding, a relatively close relationship of taxa currently placed in the Ageneiosidae, Auchenipteridae, and Doradidae was advanced by these authors, in the form of subgroups within their various classifications. Although there has been considerable shifting of taxa within these groups, all three have persisted as a larger, cohesive unit in nearly all classifications to the present.

Bleeker (1862) grouped *Ageneiosus*, *Tetranematichthys*, and *Pseudogeneiosus* together (as "phalanx" Ageneiosi) with *Pangasius* and allied genera, as a subgroup ("stirps" Pangasini) of his much larger "subfamily" Bagriformes. They were not, however, listed close to the genera presently placed in the Doradidae or Auchenipteridae, which were given separate rank, near genera currently placed in the Mochokidae.

Günther (1864) lumped the various doradoid taxa together in his group Doradina, within a subfamily (Stenobranchiae) that also included as separate groups some species currently placed in the families Cetopsidae, Mochokidae, and Malapteruridae. The mochokid genus *Synodontis* was placed within Günther's Doradina. His diagnosis of the entire subfamily was based on the anterior position of the rayed dorsal fin, when present, and fusion of the gill membranes to the isthmus, neither character of which is confined to these taxa among catfishes.

The only previous revision of the Ageneiosidae was provided by Eigenmann and Eigenmann (1890), as part of a much broader review of neotropical siluroids. Therein, they recognized the three doradoid groups at subfamilial rank within the broadly defined Siluridae. A dendrogram provided by Eigenmann and Eigenmann aligned the three doradoid subfamilies together (with the Hypophthalmidae as an offshoot of the Ageneiosinae); their tree, however, was based on many characters of overall similarity, as detailed throughout the text, and did not address possible relationships with groups outside of South America. Nevertheless, their review was a substantial contribution in terms of providing a synthesis of previous studies on neotropical catfishes.

Eigenmann (1912) retained the broadly encompassing family Siluridae, in which he placed all of the doradoid genera occurring in the area of coverage (Guyana). Eigenmann and Allen (1942) included in the Pimelodidae five genera considered to be auchenipterids by most other authors; the doradids and ageneiosids were given separate familial rank.

Regan's (1911) classification of siluroids emphasized shared morphological characters, particularly osteology of the cranium. He placed the various genera of doradoids recognized at the time within the family Doradidae, but his division of the genera corresponded to the currently recognized families. Among the principal features by which Regan (1911) united the doradoid genera were the shared presence of posteriorly directed processes of the epioccipitals and the absence of an entopterygoid (= ectopterygoid). Regan's was one of the first siluroid classifications to elevate a number of groups to family status, based on apparently derived structures, although more recent studies have suggested that some of the characters that Regan used may be primitive at the level at which he invoked them.

Miranda-Ribeiro (1911) elevated the doradids and ageneiosids to familial status, but he split the remaining genera into two families, the Auchenipteridae

(*Auchenipterus* and *Epapterus*) and the Trachycorystidae (nine genera). He placed *Tetranematicthys* in the Ageneiosidae. Miranda-Ribeiro's classification was adopted by Ihering (1937), who separated the genera traditionally placed in the Auchenipteridae on the basis of presumed differences in reproduction. However, as noted by Ferraris (1988), this classification did not constitute a natural division, based on more recent information concerning the distribution of reproductive character states.

Gosline (1945) recognized only two families of doradoids, the Ageneiosidae and Doradidae. He placed 16 genera, including *Tetranematicthys*, in the subfamily Auchenipterinae of the Doradidae. Gosline (1945) included only *Ageneiosus* and *Tympanopleura* as valid genera within the Ageneiosidae, and he placed other nominal genera (e.g., *Pseudogeneiosus*) in the synonymy of the type genus. Gosline's inclusion of the auchenipterines in the Doradidae was based on his earlier comments (1942) regarding the presumed intermediacy of *Liosomadoras*, as discussed by Britski (1972), Mees (1974), and Ferraris (1988).

Fowler (1951) gave family rank to all three doradoid groups, although he included *Tetranematicthys* in the Auchenipteridae; he recognized only *Ageneiosus* and *Tympanopleura* within the Ageneiosidae.

Miranda-Ribeiro (1968b) proposed a drastic rearrangement of previous classifications by placing the various ageneiosid and auchenipterid genera into five families. *Ageneiosus* and *Tympanopleura* were placed in the Ageneiosidae, whereas *Tetranematicthys* was placed in the reelevated family Trachycoristidae. Miranda-Ribeiro's (1968b) classification primarily involved a reinterpretation of relationships among the auchenipterids, based on sexually dimorphic characters. However, it is believed that the unavailability of adequate material of sexually dimorphic specimens of some taxa led Miranda-Ribeiro to unite certain genera that are not intimately related (Ferraris 1988).

Chardon (1968) placed ageneiosids, doradids, and auchenipterids together with mochokids as families within his superfamily Doradoidea. His recognition of the superfamily was based on limited similarities of the Weberian apparatus, most notably the presence of an elastic spring mechanism (in modified form in the Ageneiosidae). Chardon (1968) distinguished the doradoid families on the basis of several osteological features that were not regarded by Ferraris (1988) to represent shared, derived characters confined to taxa within each family.

Britski (1972) improved previous concepts of doradoid interrelationships, specifically within the Ageneiosidae and Auchenipteridae, by invoking a more in-depth analysis of a diversity of characters, including sexual dimorphism and osteology. Britski (1972) discussed in detail his interpretation of the distribution of character states, and he provided a provisional phylogenetic tree of the doradoids, exclusive of taxa within the Doradidae. However, his inferences regarding relationships treated primitive and derived characters equally; his tree was apparently heuristic, and did not explicitly denote character states. In spite of these limitations, Britski's study was the first to present detailed analyses of a wide suite of characters across a fairly broad taxonomic range. In the context of his study, Britski (1972) classified the 13 genera of auchenipterids that were available to him into four subfamilies. He recognized only *Ageneiosus* and *Tetranematichthys* within the Ageneiosidae.

Very recently, Royero (1987), Ferraris (1988), and Curran (1989), have offered additional hypotheses of phylogenetic interrelationships within the Doradoidea. Royero (1987) studied the myology and osteology of the dorsal fin and supporting structures in several catfish taxa, including representatives of most of the neotropical families. He recognized the three doradoid groups as distinct families. A cladogram of the "Doradina" given by Royero (1987) included the Ageneiosidae as the most derived group (with *Tetranematichthys* at a basal position within the

family), followed by, in descending hierarchical order, the Auchenipteridae, Doradidae, Mochokidae, and Ariidae.

Both Ferraris and Curran focused on intergeneric relationships within the Auchenipteridae (*sensu lato*), but their conclusions differed considerably. Ferraris (1988) examined a very broad suite of characters among nearly all of the genera of auchenipterids and a number of outgroups, including ageneiosids and doradids. He proposed the most drastic reinterpretation of preexisting classifications, by reelevating one "auchenipterine" group to family status (the Centromochlidae), and placing all of the ageneiosid taxa as a derived group within the Auchenipteridae. Species within Ferraris' (1988) "*Ageneiosus* group" were thought to be more closely related to some auchenipterid genera (the "*Auchenipterus* group"), than were members of the latter related to other auchenipterid taxa. There was no indication by Ferraris (1988) of how his cladograms were generated, or if a search was made for shortest consensus trees, and in some instances it is not clear how certain character states were loaded or how homoplasies were treated. Nevertheless, Ferraris' (1988) study is the most comprehensive review to date of the comparative morphology and relationships between the various genera traditionally included in the Auchenipteridae and Ageneiosidae.

Curran (1989) retained the conventional three-family arrangement of the neotropical doradoids, but he rejected the Ageneiosidae as the closest sister group of the Auchenipteridae, on the basis of five putative synapomorphies that he felt united the Doradidae and Auchenipteridae as sister families. Although Curran analyzed his data set with a popular cladistic computer algorithm, his hypotheses of certain character transformations were not entirely consistent with the opinions of other authors, and one gets the impression that some characters were unduly weighted. Curran (1989) examined very limited ageneiosid material in his analysis,

and he did not include them directly in his cladogram. He tentatively placed *Tetranematichthys* in the Ageneiosidae.

As evident from the preceding review, there is little disagreement among most authors that ageneiosids, auchenipterids, and doradids are closely related. The main differences between previous classifications involve the categorical rank, arrangement, and nomenclatural validity of various taxa, especially genera within the Auchenipteridae. It is neither the intent nor within the scope of this study to present any additional hypotheses of relationships at the family level or above. Nevertheless, some justification of the classification used here is in order. Primarily as a matter of pragmatism, I prefer to retain a three-family classification of neotropical doradoids at the present time, and continue to recognize the family Ageneiosidae. This is done mainly to facilitate ease of communication about characters and the taxa within the derived ageneiosid clade. It should be noted that the most significant changes in classification recently proposed (Ferraris 1988) have yet to be published in a peer-reviewed journal, and thus are not widely known or accepted by researchers unfamiliar with these fishes. Moreover, additional detailed information is critically needed to document the distribution of certain character states and the phylogenetic position of several poorly known auchenipterids. It is conceded, however, that there is a strong possibility that future classifications of the neotropical doradoids may include ageneiosids and auchenipterids under a single categorical rank, perhaps at least with the former representing a subfamily.

Early History of Species Names

The early nomenclatural history of ageneiosids involves a number of names that have been applied to several species, some of which cannot be unequivocally determined from the original descriptions. The genus *Ageneiosus* was established by

Lacepède (1803) for two species, *Silurus inermis* Linnaeus (1766) and *Ageneiosus armatus* Lacepède (1803). The epithet *inermis* is discussed in greater detail below. Ferraris (1988) summarized the confused history of the latter name and several replacement names, and his analysis is, in part, paraphrased here.

Lacepède's (1803) creation of the genus *Ageneiosus* was not accompanied by the designation of a type species, despite acceptance of *A. armatus* as the type species by most subsequent authors. The original description of *armatus* is highly problematic, however, because it included two species in its synonymy; *Silurus militaris*, a synonym of the ariid catfish *Osteogeneiosus militaris* (as noted by Cuvier and Valenciennes in 1840, and Eigenmann and Eigenmann in 1890), and a species misidentified as *Silurus militaris* Linnaeus by Bloch (1794, p. 19, fig. 362). Bloch's *militaris*, therefore, represents a junior primary homonym of *Silurus militaris* Linnaeus (1766). Based on the errors made by Lacepède and Bloch, Cuvier and Valenciennes (1840) applied the name *Ageneiosus militaris* to the species figured by Bloch, an action which Ferraris (1988) regarded as an unwarranted replacement name; hence, the name is a junior objective synonym of *A. armatus* Lacepède. Ferraris (1988) explicitly designated the specimen described and figured by Bloch as a lectotype of *A. armatus*, but he made no attempt to establish an acceptable identification of the taxon involved. As judged from the description and illustration accompanying Bloch's (1794) account, his use of the name *militaris* was applied to the species with the currently accepted name *Ageneiosus brevifilis*.

The first designation of a type species of *Ageneiosus* was that of Bleeker (1862:14), as "*Ageneiosus militaris* Blkr (nec Val.) = *Silurus militaris* Bl[och]."

However, as noted by Ferraris (1988), Bleeker's designation cannot be interpreted as a proposal for a new name, inasmuch as he had previously recognized Valenciennes' (in Cuvier and Valenciennes 1840) attempt to solve the nomenclatural problem, by his statement "*Ageneiosus militaris* CV = ... *Silurus*

militaris Bl[och]" (Bleeker 1858:206). Ferraris (1988) regarded Bleeker's type designation as invalid in accordance with articles 69a and 70c(i) of the International Code of Zoological Nomenclature (ICZN 1985). *Ageneiosus valenciennesi* was proposed by Bleeker (1864) as a replacement name for *A. militaris* Valenciennes (1840). *Ceratorhynchi militaris* Agassiz (in Spix and Agassiz 1829) represents an unwarranted replacement name for Lacepède's *A. armatus*; hence the genus and species names are objective synonyms of those of Lacepède's. As detailed by Ferraris (1988), the first designation of a type species for *Ageneiosus* that conforms with current ICZN policy was that of Eigenmann and Eigenmann (1890). Therein, they cited the type of *Ageneiosus* as "*Ageneiosus armatus* type = *Silurus militaris* Bloch," despite reference to the unavailable name of Bloch. Jordan's (1917:66) designation of *Ageneiosus armatus* Lacepède (= *Silurus militaris* L.[innaeus]) as the type species of the genus postdated that of Eigenmann and Eigenmann (1890), and would necessitate the unacceptable synonymization of *Ageneiosus* within the Ariidae.

Identification of the possible taxa to which the epithet *inermis* was applied is somewhat tenuous. *Silurus inermis* Linnaeus (1766) was repeated by Bloch (1794), and was listed by Cuvier and Valenciennes (1840) and Eigenmann and Eigenmann (1888), but was considered in the first revision of the group (Eigenmann and Eigenmann 1890) to be a "doubtful species." The original description of *Silurus inermis* (Linnaeus 1766:503) is highly suggestive of having been based on the species named *Ageneiosus brevifilis* by most other authors; the specimen(s) that Linnaeus described were from Surinam, an area from which *A. brevifilis* is presently common, and he noted a truncate, weakly bilobed caudal fin, which is a characteristic feature of *A. brevifilis* that is not present in most other members of the family. Moreover, the combined fin ray counts that Linnaeus gave are closest to *A. brevifilis* (pectoral rays = 17, anal rays = 38). Günther (1864) presented the name *Ageneiosus sebae* as

an unwarranted replacement name for Valenciennes' *inermis*, and tentatively placed *Silurus inermis* Bloch in the synonymy of *Ageneiosus dentatus* Kner. However, the illustration in Bloch (1794) appears to have been based on a specimen of *A. brevifilis*. The description and illustration of *A. inermis* provided by Bleeker (1862) and repeated by Valenciennes (in Cuvier and Valenciennes 1840) are somewhat more problematical; the specimen illustrated by Bleeker (1862: fig. 363) does not especially resemble *A. brevifilis*, inasmuch as the fish in his figure has a moderately forked tail and an unusual pigmentation pattern that cannot be clearly assigned to any known species. Because of the difficulty in ascertaining to which species the name *inermis* was based on, and the absence of any specimens that could be considered to represent types, I prefer to treat this name as a *nomen dubium*.

The first revision of the Ageneiosidae included eleven species and their presumed synonyms at the time (Eigenmann and Eigenmann 1890). In fact, as currently recognized, only six species were apparently represented in their synopsis; *A. atronasus*, *A. brevifilis*, *A. brevis*, *A. pardalis*, *A. ucayalensis*, and *A. valenciennesi*. Following the earliest period of new descriptions, summarized in the preceding paragraphs, the greatest number of new species were described between 1900 and 1925, during which time 13 original names were proposed. These descriptions mostly represented the independent work of Franz Steindachner in Austria and Carl Eigenmann in the United States, although several other authors contributed new descriptions. From 1925 to 1950, an additional four putative new species were described. Since 1950, there have been another four species described, all of which represent junior synonyms of previously described taxa (one is currently in press). This general trend is in marked contrast to many neotropical freshwater fishes, for which alpha-level taxonomy has tended to favor an overall increase in the number of species descriptions to the present. I attribute this to the fact that ageneiosids are moderately large in size, and are mostly found in large river channels, where the

greatest collecting activity has been, and thus were not easily overlooked in routine collections by early investigators.

Many descriptions of ageneiosids were not accompanied by explicit designations of type specimens, and in some cases there was no indication of how many specimens provided the basis for a description. A survey of all major institutions that were believed to possibly have specimens on which descriptions may have been based revealed a surprising amount of type material. These types are summarized in Table 1. Whenever possible, an attempt was made to personally examine or obtain detailed information about all of the specimens identified as probable types. In some cases, provisional identification of taxa was possible from original literature sources. For some nominal species, no type material could be located, and it is presumed that specimens on which these names are based were either not saved or subsequently lost.

Table 1.—Current deposition of extant type specimens of nominal species of Ageneiosidae. Museum acronyms as listed in Leviton et al. (1985).

SPECIES	TYPE	MUSEUM NO.	TYPE LOCALITY
<i>Ageneiosus atronasus</i> Eigenmann & Eigenmann 1888	holotype	MCZ 27270	unknown ("South America")
<i>Ageneiosus axillaris</i> Günther 1864	holotype	BMNH 1864-6.2:2	Surinam
<i>Ageneiosus barranquensis</i> Risso & Risso 1964	holotype	MACN III-63	Argentina: Río Negro, Riacho Barranqueros
<i>Ageneiosus brevifilis</i> Valenciennes 1840	holotype	RMNH 2975	Surinam: vicinity of Paramaribo
<i>Ageneiosus brevis</i> Steindachner 1879	syntypes (2)	NMW 47801	Brazil: Coari
<i>Ageneiosus caucanus</i> Steindachner 1879	syntypes (2)	NMW 47811	Venezuela: Río Cauca
<i>Ageneiosus freiei</i> Schultz 1944	holotype	USNM 121260	Venezuela: Río Agua Caliente 2-3 km above Lago Maracaibo
	paratype	USNM 121261	"
	paratype	MCZ 37210	"
<i>Ageneiosus guianensis</i> Eigenmann 1912	paratypes (2)	USNM 121262	Venezuela: Río Negro below mouth of Río Yasa
<i>Ageneiosus madeirensis</i> Fisher 1917	holotype	FMNH 53247	Guyana: Wismar
	holotype	FMNH 58143	Bolivia: San Joaquin
	paratypes (14)	FMNH 58144	"
<i>Ageneiosus marmoratus</i> Eigenmann 1912	holotype	FMNH 53245	Guyana: creek below Potaro Landing
<i>Ageneiosus ogilviei</i> Fowler 1914	holotype	ANSP 39343	Guyana: Rupununi River
<i>Ageneiosus pardalis</i> Lütken 1874	holotype	ZMUC 207	Venezuela
<i>Ageneiosus parnaguensis</i> Steindachner 1910	syntype	NMW 47832	Brazil: Parnagua
	syntype	NMW 47837	"
	syntypes (2)	NMW 47838	"
<i>Ageneius polysictus</i> Steindachner 1915	holotype	NMW 47839	Brazil: mouth of Río Negro
<i>Ageneiosus porphyreus</i> Cope 1867	lectotype	ANSP 8389	Surinam
	paralectotype	ANSP 8388	"

Table 1.--continued.

SPECIES	TYPE	MUSEUM NO.	TYPE LOCALITY
<i>Ageneiosus quadrifilis</i> Kner 1858	holotype	NMW 43343	Brazil: Rio Guaporé
<i>Ageneiosus rondoni</i> Miranda-Ribeiro 1914	syntypes (2)	MNRJ 962	Brazil: Matto Grosso
<i>Ageneiosus therezinae</i> Steindachner 1909	syntypes (2)	NMW 47840	Brazil: Rio Poti (?) at Theresina
	syntype	NMW 47841	" "
<i>Ageneiosus ucayalensis</i> Castelnau 1855	holotype	MNH B.611	Peru: Río Ucayali
<i>Ageneiosus uruguayensis</i> Devincenzi 1933	holotype	CI 317	" "
	paratypes (2)	CI 317	" "
	*	MNH B.690-691	" "
<i>Ageneiosus valenciennesi</i> Bleeker 1864	holotype	NMW 47853	Brazil: Rio Purus
<i>Ageneiosus vittatus</i> Steindachner 1908	holotype	CAS-IU 15790	Peru: Iquitos, Río Marañon
<i>Tympanopleura alta</i> Eigenmann & Myers 1928	paratype	CAS 58259	" "
	holotype	CAS 57940	" "
	paratypes (3)	CAS 57941	" "
<i>Tympanopleura nigricollis</i> Eigenmann & Allen 1942	paratype	CAS 57942	Peru: Río Ucayali near Orellana
	holotype	FMNH 53243	Guyana: Essequibo River at Crab Falls
	paratype	FMNH 53244	" "
	paratype	BMNH 1911.10.31:102	" "
	paratype	MCZ 30189	" "
	paratypes (3)	CAS 58382	" "
<i>Tympanopleura piperata</i> Eigenmann 1912			

* 3 Syntypes of *A. militaris* Valenciennes (in Cuvier and Valenciennes 1840).

METHODS

All morphometric data were taken as straight-line measurements with needle-point dial calipers and recorded to the nearest 0.1 mm, except for lengths exceeding 170 mm, which were made with a strip tape measure to the nearest 1.0 mm. Method of measurements generally followed that of Stewart (1986) and Stewart and Pavlik (1985). Standard length (SL) was recorded as the distance from the tip of the upper lip to the posterior midpoint of the hypural plate. The terms "fin origin" and "fin insertion" are used in the sense of Cailliet et al. (1986), to mean the front and the rear of the fin, respectively, in the case of both paired and unpaired fins. Pre-fin lengths were taken from the tip of the snout to the fin origin. Predorsal length is the distance from the tip of the snout to the base of the first dorsal spinelet. Distances between fins were measured from fin origins in all cases except that from adipose origin to anal insertion. The distance from the tip of the snout to the upper point of the gill cavity was used in morphometric analyses to represent head length (HL). Head depth was taken at a vertical line passing through the midpoint of the orbit. Occipital head depth was taken at the vertical through the supraoccipital-frontal suture. Gape width is the transverse distance between the bony posterior extremities of the premaxillae. Barbel length was measured from the anteriormost point of the maxillary bone to the distal fleshy tip of the barbel, or, in nuptial males, to the posteriormost bony extension of the barbel (frequently corresponding to the base of a recurved odontode). Barbel groove length is the distance from the anteriormost point of the maxillary bone to the fleshy posterior corner of the upper jaw. Fin-base lengths included fleshy membranous

connections to the body. Dorsal and pectoral spine lengths were measured from origin to stiffest distal point or ossified tip, as discernible in whole specimens. Preisthmus length was taken from the tip of the snout to a point midway between the anteroventral position of the opercular openings. Adipose fin height was measured from where the fin erupts anteriorly from the dorsal body surface to the posteriodorsal-most point of the fin. Caudal peduncle length was taken from the anal fin insertion to the midlateral origin of central caudal fin rays. Eye diameter was taken as the horizontal distance between the anterior and posterior margins of the eyeball. Head width is the maximum bony distance between postorbitals. Sample sizes given in tables of body proportions are of the maximum number of specimens included in each analysis; distorted or damaged specimens in some cases precluded certain measurements.

Details of osteology and soft anatomy were studied from dissected or skeletonized specimens and preparations using modifications of the differential staining techniques of Dingerkus and Uhler (1977), Potthoff (1984), and Cailliet et al. (1986); these specimens are designated parenthetically in the Material Examined sections as (skel) or (c/s), respectively. Drawings of skeletal preparations were made with the aid of a camera lucida attached to a stereomicroscope. Nomenclature of osteological elements follows Cailliet et al. (1986), Lundberg (1975), and Lundberg and Baskin (1969) unless otherwise noted. Cartilage is indicated by heavy stippling in the illustrations. Abbreviations used in illustrations are listed in Table 2.

Ray counts of anal and paired fins included all lepidotrichia and often required minor dissection in the case of pectoral fins. Anal ray counts were taken principally from radiographs or counterstained specimens and included, when present, a small anterior flint of bone associated with the anteriormost pterygiophore; in rare cases, anal rays were discernible in whole specimens where

Table 2. – List of abbreviations used in anatomical figures.

B	branchiostegal	MX	maxilla
BB	basibranchial	N	nasal
BLC	basipterygium lateral cartilage	OB	orbitosphenoid
BO	basioccipital	OP	opercle
BPT	basipterygium	OS	os suspensorium
BR	basal radial	PB	pharyngobranchial
CB	ceratobranchial	PCP	postcleithral process
CBP	ceratobranchial tooth patch	PH	parhypural
CH	ceratohyal	PL	palatine
CV	compound vertebra	PMX	premaxilla
D ₁	first dorsal spine	POP	preopercle
D ₂	second dorsal spine	PR	parapophysis
EB	epibranchial	PRO	prootic
EP	epural	PSP	parasphenoid
EPO	epioccipital	PST	posttemporal
EPP	posterior epioccipital process	PTG	pterygiophore
EXO	exoccipital	PTR	pterotic
F	frontal	PTS	pterosphenoid
HM	hyomandibula	PU ₁ +U ₁	compound centrum
HP	hypohyal	PU ₂	preural centra (1-2)
HS	hemal spine	Q	quadrate
HY	hypurals	R	pleural rib
HYB	hypobranchial	1° SC	primary spermatocyte
HYP	hypurapophysis	2° SC	secondary spermatocyte
IH	interhyal	SO	supraoccipital
IO	infraorbitals	SPH	sphenotic
IOP	interopercle	SPO	suprapreopercle
L	lacrimal	ST	spermatid
LE	lateral ethmoid	SZ	spermatozeugmata
LPR	lower principal caudal ray	TR	tripus
LS	longitudinal septum of swimbladder	UH	urohyal
ME	mesethmoid	UPR	upper principal caudal ray
MP	mesopterygoid	V	vertebral centrum
MR	Müllerian ramus	VOM	vomer
MT	metapterygoid		

adipose deposits in the fin did not preclude an accurate count of anterior and posterior principal rays. The posterior anal pterygiophore typically included two (or rarely three) lepidotrichia, counted separately, which often appeared superficially joined at their base, but are distinct elements as revealed by radiography or counterstaining. Vertebral counts were made from radiographs and counterstained specimens, and included one for the fused PU1+U1 centra and six for the Weberian complex. Preanal vertebrae are those with hemal spines anterior to the first proximal anal pterygiophore. Counts of pleural ribs are of pairs as determined from radiographs taken of specimens from the dorsal profile or from alizarin preparations. Counts of branchiostegal rays are very difficult in ageneiosids because the gill membranes are broadly fused to the isthmus and the head is greatly flattened; in this study, determination of branchiostegals, as well as gill raker number, was facilitated by making an acentric incision anterior from the ventral point of the opercular opening and carefully bending the branchiostegals outward. Visibility of the branchiostegals was often enhanced by directing a narrow fiberoptic beam through the flesh. In some cases, questionable counts of branchiostegals were verified by examination of dorsoventral radiographs. Gill raker counts are those of the outer row on the first arch.

Tissues selected for study with a scanning electron microscope (SEM) were prepared by dehydration through a graded ethanol series, dried in a critical point dryer using liquid carbon dioxide as the transition medium, then mounted on observation stubs and sputter coated with palladium-silver prior to examination on a Hitachi S-570 SEM using an accelerating voltage of approximately 65 Kv. Tissues used for light microscopy were dehydrated and cleared through an ethanol-xylene series, infiltrated and embedded in paraffin, then sectioned on a rotary microtome and mounted on slides using conventional histological techniques (Humasson 1979). Sectioned tissues were stained with Harris hematoxylin/eosin Y or a modified

Biebrich Scarlet-Orange G protocol prior to examination and photography with an Olympus BH-2 compound microscope.

Distribution maps are based solely on museum specimens examined and a few reliable literature records, and are intended only to be general guides of species ranges. The base drainage map was redrawn from a pre-1940 edition released from the University of Michigan Museum of Zoology, and thus does not accurately reflect more recent changes in hydrological flow patterns resulting from natural causes or hydroelectric reservoirs. In many cases, single dots represent more than one collection at the same or a nearby locality. In some cases, locality data were vague or may have actually represented the nearest settlement or a fish market; cases of suspected inaccurate or imprecise locality information were not plotted on the maps.

The material examined section under each species account is arranged in the following sequence: country, state or major province when known, museum catalog number, number of specimens of each sex (when known) and standard length in mm in parentheses, locality, date, and collector(s). Institutional acronyms are from Leviton et al. (1985). Locations of specimens from the Thayer expedition (Harvard University) to Brazil were extracted from Dick (1977) and an unpublished manuscript by Horacio Higuchi. Material collected by the MZUSP Expedição Permanente da Amazônia are listed as having been collected by EPA. Uncatalogued specimens collected by Goulding (1988), currently deposited at MZUSP, are cited parenthetically by his field numbers prefixed by "MG" in the Material Examined sections. Locality data accompanying specimens (now at FMNH) collected by J. D. Haseman were supplemented with information from Eigenmann (1911). Material formerly in the collections of Stanford University and Indiana University, now at the CAS, are listed as CAS-SU and CAS-IU, respectively.

Synonymies include original descriptions as well as the body of literature containing additional information on the morphology, distribution, and ecology of ageneiosids; lists of references are not purported to be exhaustive, but it is believed that all major accounts dealing with the taxonomy of ageneiosids are included. Additional references can be found in Fowler (1951).

Inferences of evolutionary relationships were made using the phylogenetic methods of Hennig (1966), as elaborated and espoused by Wiley (1981) and numerous recent studies. Determinations of polarity trends among character states were made by outgroup comparisons of a variety of taxa from personal observations and a survey of available literature on siluroids. Characters of uncertain polarity were treated as unordered in phylogenetic analyses. The Diplomystidae (*Diplomystes* and *Olavaichthys*) is generally regarded as the most primitive family of catfishes (Regan 1911, Fink and Fink 1981, Roberts 1973, and Arratia 1987) and was considered to be the basal group for character analyses. The Doradidae and Auchenipteridae were considered as sister groups of the Ageneiosidae, based on the studies of Regan (1911), Eigenmann (1925), Chardon (1968), Britski (1972), Ferraris (1988), and Curran (1989). Within the Auchenipteridae (*sensu lato*), genera in the "*Auchenipterus* group" (= *Auchenipterus*, *Entomocorus*, and *Epapterus*) and *Trachelyopterus* were considered to represent the closest sister taxa of the Ageneiosidae following Ferraris (1988) (see section on phylogenetic systematics for a more detailed discussion). Phylogenetic analyses were performed using the computer programs PAUP ("Phylogenetic Analysis Using Parsimony", version 2.4, by David Swofford), and MacClade (version 2.1, by Wayne and David Maddison).

GENERIC NOMENCLATURE

Status of *Pseudogeneiosus* and *Davalla*

The genus *Pseudogeneiosus* was first proposed by Bleeker (1862, 1863) to distinguish *A. brevifilis* Valenciennes on the basis of its fleshy maxillary barbel, edentulate dorsal fin spine, and reduced, encapsulated swimbladder. In his original type designation, Bleeker (1862) only briefly listed these characters, along with counts of branchiostegal rays and fin rays, and did not present his rationale for recognizing a new genus. However, he subsequently gave a detailed morphological description of *brevifilis*, and indicated his reasons for considering the distinctive characters of the species as sufficient to warrant placement in a separate genus (Bleeker 1864). Apparently, he based his description of *Pseudogeneiosus* in part on the inconclusive statements of Valenciennes (in Cuvier and Valenciennes 1840) and Kner (1858a) regarding sexual dimorphism (for a more detailed discussion see section on reproductive biology). In essence, Bleeker diagnosed *Pseudogeneiosus* almost solely on the alleged absence of toothed maxillary barbels.

A few authors have adopted the use of *Pseudogeneiosus* at the generic level (e.g., Pozzi 1945, Achenbach and Bonetto 1957), but most others continued to place *brevifilis* in *Ageneiosus* (e.g., Günther 1864, Eigenmann and Eigenmann 1890, Eigenmann 1912, Gosline 1945, Stigchel 1947, and Fowler 1951). Even fewer authors considered *Pseudogeneiosus* as a subgenus (Berg 1897, Eigenmann 1909, Eigenmann and Allen 1942).

Based on the original diagnosis of *Pseudogeneiosus*, I elect not to recognize this genus as valid for the following reasons. Bleeker (1864) clearly indicated that he regarded the absence of toothed maxillary barbels as sufficient evidence to consider *brevifilis* as distinct from *A. militaris* Valenciennes (= *A. valenciennesi* Bleeker) and *Silurus militaris* Bloch. Like most other authors, Bleeker had inadequate material of nuptial males, and thus he erroneously assumed that specimens of *brevifilis* never exhibited the secondary sexual characteristics present in other species. However, as observed in the present study and by other authors, males of *brevifilis* at the peak of their reproductive cycle have well developed nuptial structures similar to those of all other *Ageneiosus*, i.e., ossified maxillary barbels with recurved odontodes, an elongate serrated dorsal fin spine, and a gonopodium formed by modified anal fin rays. In this context, *Pseudogeneiosus* represents an unnatural, paraphyletic taxon and therefore is regarded herein as a junior subjective synonym of *Ageneiosus*. Moreover, Bleeker seemed to repetitively propose replacement generic names based on previously described species (Boeseman 1972), an action which, if arbitrary, cannot be construed as sufficient grounds for recognition of new taxa. Bleeker's designation of *Pseudogeneiosus* is somewhat enigmatic, considering the fact that he was familiar with the illustration of a nuptial male *brevifilis* by Bloch (1794: fig. 362), which clearly illustrated the external sexually dimorphic features of the dorsal fin and maxillary barbels. Apparently, Bleeker failed to recognize other diagnostic features of *brevifilis* and assumed that nuptial structures were characteristic of *A. militaris* Valenciennes, with which he synonymized *A. ucayalensis* Castelnau. According to Boeseman (1972), neither Bleeker (1864) nor Stigchel (1947) were cognizant of the fact that the larger of two specimens (RMNH 2975) of *Pseudogeneiosus brevifilis* that they recorded probably represented the holotype of *A. brevifilis* Valenciennes. Both authors may have been

mislead by an error in the type locality, given as Cayenne (French Guiana), but which is presumably from an area near Paramaribo, Surinam (Boeseman 1972).

Schomburgk (1841) presented a colorful description of a fish that he called "Dawalla of the Arawaaks", for which he gave the name *Hypothalmus dawalla*. Bleeker (1858) subsequently replaced the name with *Davalla schomburgkii*, the specific epithet of which apparently was intended to avoid tautonymy of his proposed new genus (Boeseman 1972). The name *Davalla* was thought by Boeseman (1972) to represent a misspelling of the original species name, although it is more probable that Bleeker simply repeated the alternate spelling that accompanied Schomburgk's original figure (Schomburgk 1841: fig. 9). Schomburgk's generic designation was subsequently emended to *Hypophthalmus* by most authors, beginning with Bleeker (1858), an action that obviously represented a correction of Schomburgk's misspelling of the type genus of the family Hypophthalmidae. Eigenmann and Eigenmann (1888, 1890) recombined the name as *Ageneiosus dawalla*, and later authors placed *Davalla* in the synonymy of *Ageneiosus*. Based on the original account and figure, there is no question that *Hypothalmus dawalla* Schomburgk represents a junior synonym of *Ageneiosus brevifilis* Valenciennes. As discussed by Boeseman (1972), Bleeker apparently proposed *Davalla schomburgkii* without examining the two specimens collected by Dieperink in Surinam, which was the material that Valenciennes had earlier based his description of *A. brevifilis* on.

Status of *Tetranematicthys*

The genus *Tetranematicthys* was proposed as a replacement name by Bleeker (1858) to emphasize the distinctiveness of *Ageneiosus quadrifilis* Kner (1858a). The main diagnostic feature of this monotypic form, as originally

perceived, is the presence of a single pair of mental barbels in adults, which are absent in all other ageneiosids. Following its original description, the taxonomic placement of *A. quadrifilis* has been discordant among most authors. This has been partly due to fluctuating classification schemes, inadequate hypotheses of relationships among genera of the Doradidae, Auchenipteridae and Ageneiosidae, and a lack of detailed information about the morphology of *Tetranematichtys*. There is little doubt that the presence of chin barbels provided the main rationale for periodic placement of the genus outside the Ageneiosidae.

Regan (1911) classified *Tetranematichtys* with most other currently recognized genera of auchenipterids (in his family Doradidae), based on the shared presence of a large, unencapsulated swimbladder. Eigenmann and Eigenmann (1890) placed the genus within their subfamily Auchenipterinae (family Siluridae), also apparently on the basis of swimbladder morphology. Günther (1864) also recognized *Tetranematichtys* as a distinct genus, but classified it between *Ageneiosus* and a number of auchenipterid genera within his group Doradina, which also included a number of doradids and mochokids. Miranda-Ribeiro (1911) placed the genus within the Ageneiosidae. Gosline (1945) listed the genus within the subfamily Auchenipterinae of the Doradidae. Fowler (1951) included *Tetranematichtys* in his family Auchenipteridae. Based on reproductive structures, Miranda-Ribeiro (1968b, posthumously) proposed a novel classification scheme in which he placed the genera traditionally recognized in the Ageneiosidae and Auchenipteridae into five families, with *Tetranematichtys*, *Trachycoristes* (= *Trachycorystes*) and *Auchenipterichthys* together in the family Trachycoristidae; however, in another paper (1968c) he synonymized *Tetranematichtys* with *Trachycoristes*. Most other studies have generally grouped *Tetranematichtys* together with various auchenipterid genera.

Among recent studies, Britski (1972) was the first to firmly indicate a close relationship between *Tetranematichtys* and *Ageneiosus*. Britski based his conclusion on several similarities in morphology, most notably osteological features of the cranium, but he did not explicitly present his hypothesis of relationships within a strict phylogenetic context. To that end, Ferraris (1988) placed *Tetranematichtys* and *Ageneiosus* in a monophyletic clade, based on shared, derived characters of the the skull and pectoral fin, although he classified both as a subgroup of the Auchenipteridae. Curran (1989) excluded *Tetranematichtys* from a cladistic analysis of the Auchenipteridae, and suggested the genus was related to ageneiosids based on a combination of two putative synapomorphies involving the barbels and additional characters thought to be absent in the auchenipterids.

The historical confusion in the placement of the genus *Tetranematichtys* as outlined above reflects largely the discrepant classification schemes presented for doradoid catfishes in general. Based on the work of Britski (1972), Ferraris (1988), and the present study, it is clear that *Tetranematichtys* should be classified together with the remaining ageneiosids. Ferraris (1988) examined more genera and a larger number of characters than any previous study, in a phylogenetic context, and concluded that *Tetranematichtys* and *Ageneiosus* were sister taxa that formed a monophyletic group within the Auchenipteridae and should not be accorded family status. He made no recommendation regarding their subfamilial classification beyond placement within the tribe Auchenipterini, together with five additional genera. For reasons detailed elsewhere in the present study, I choose to continue recognizing the family Ageneiosidae, and regard the treatment of *Tetranematichtys* as a primary nomenclatural question.

The presence of a single pair of mental barbels in *Tetranematichtys* has in the past provided the main basis for recognition of this taxon at the generic level. *Ageneiosus* and allied nominal genera (*Pseudogeneiosus* and *Tympanopleura*) have

traditionally been diagnosed as lacking all barbels except the maxillary pair. All auchenipterids (*sensu lato*) have two pairs of chin barbels, with the exception of *Gelanoglanis stroudi* (Böhlke 1980), which, like *Tetranematichtys*, has only a single pair. However, these two taxa are apparently not closely related; *Gelanoglanis* was placed in a clade with five other genera in the reelevated family Centromochlidae by Ferraris (1988).

The loss of chin barbels in *Ageneiosus* is thought to be a derived reduction from a primitive state, in which there is at least one pair in all other catfishes except diplomystids and a few unrelated taxa that have independently lost the chin barbels. Ferraris (1988) interpreted the presence of a single pair of mental barbels as an autapomorphy for *Tetranematichtys*, and assumed that it was independently derived only in *Gelanoglanis* among other neotropical catfishes. However, there is ontogenetic evidence that postlarval *Ageneiosus* have a mental barbels that are resorbed during early development (see morphological comparisons for a more detailed discussion). Therefore, it is more parsimonious to conclude that retention of mandibular barbels in adults of *Tetranematichtys* represents a plesiomorphic condition within the ageneiosid clade, although their unique morphology may be an independent derivation. Moreover, *Tetranematichtys* exhibits additional primitive characters among ageneiosids, including a large swimbladder, untoothed maxillary barbels in nuptial males, and a postcleithral process. Thus, the genus is diagnosed primarily on the basis of primitive character states.

From the standpoint of nomenclatural stability, nevertheless, it seems desirable to retain the generic status of *Tetranematichtys*. In spite of its probable basal position among ageneiosids, *T. quadrifilis* is a highly distinctive species with no obvious close relative among the remaining ageneiosids. Although the relationship of this species to other neotropical siluroids has until recently been questionable,

nearly all previous references gave it generic rank. Thus, I prefer to recognize *Tetranematichthys* as a currently monotypic genus within the Ageneiosidae.

Status of *Tympanopleura*

The ageneiosid genus *Tympanopleura* was described by Eigenmann (1912) for a new species, *T. piperata*, from the Essequibo River at Crab Falls, British Guiana (now Guyana). The distinctive features of this new genus as detailed in the original description were as follows:

Air-bladder projecting into the abdominal cavity, naked laterally, the skin over it forming a large pseudo-tympanum....This is evidently a young fish. To what extent the large, protruding air-bladder and the large pseudo-tympanum are characters of immaturity I am unable to say. The short snout very probably is due to the age of the specimen.
(Eigenmann 1912:203)

Etymology of the generic name (from Latin *tympanum*, meaning drum, and New Latin *pleur*, meaning side) was clearly based on the single putative diagnostic character involving the large swimbladder. The new species was described from three male and five female specimens ranging in size from 57 to 64 mm (presumably TL). Although the description of *T. piperata* was brief, this taxon agrees in all respects with other ageneiosids, i.e., in having a single pair of barbels and with fin rays similar to other species of the family. My examination of the extant type specimens of *T. piperata* do not entirely confirm Eigenmann's observations suggesting immaturity, and there are additional problems with the types. Unfortunately, one of the types designated by Eigenmann was not located in the present study, and the holotype (FMNH 53243) and one paratype (FMNH 53244) are in very poor condition. The specimens on which the description was based were apparently sexually mature, insofar as the males have incipient gonopodia and long,

ossified maxillary barbels, despite additional comments suggesting their immaturity (Eigenmann and Myers, in Myers 1928:85). I have found only one other specimens in the material examined during this study that can be reliably placed within this taxon. The status of this species remains enigmatic, as discussed below and in the species account in greater detail.

A second species of the genus, *T. alta*, was described by Eigenmann and Myers (in Myers 1928) from the Rio Marañon, Peru. The very short description of *T. alta* provided no additional characters useful in distinguishing the genus. In fact, the description of *T. alta* made only cursory comments about a "tympanal shade", and the authors even suggested that *T. alta* may not be different from *T. piperata*; they distinguished *T. alta* qualitatively on the basis of a deeper body, larger head, longer fins, and different coloration. Eigenmann and Myers designated a single type specimen, IU 15790 (now at CAS; length given as 135 mm in the original description and as 132 mm in Eigenmann and Allen 1942); the length given for this specimen was presumably TL, insofar as my examination revealed it to be a 109 mm SL female. In addition, another female specimen was designated as a paratype in Eigenmann and Allen (1942), IU 15977 (now CAS 58259, length given as 128 mm in Eigenmann and Allen 1942, measured at 105 mm SL in the present study).

The genus was accorded slightly greater attention by Eigenmann and Allen (1942), who described (following Eigenmann's death in 1927) another new species from Peru, *T. nigricollis*, and provided additional comments and an illustration of *T. alta*. Again, the only distinctive feature of *Tympanopleura* presented by these authors involved the large swimbladder producing a "pseudo-tympanum" visible in the lateral musculature. Eigenmann and Allen (1942) also examined the swimbladder itself, and noted that it was large in the two species of *Tympanopleura* examined, with two caecae in *T. nigricollis* but without caecae in *T. alta*. These authors also suggested that *T. nigricollis* was related to *Ageneiosus polystictus*

Steindachner and *A. rondoni* Miranda-Ribeiro, and that the latter two species could be allocated to *Tympanopleura*, but they did not present their rationale for this conclusion.

No other species of *Tympanopleura* have been described and most studies subsequent to the original descriptions accepted the genus as valid (e.g., Fowler 1945, 1951, Gosline 1945, Ortega and Vari 1986). However, Britski (1972) chose not to recognize *Tympanopleura*, based on interspecific and ontogenetic variation of the swimbladder in several species, although his conclusions were never published. Based on examination of limited material of *T. nigricollis*, Ferraris (1988) hypothesized that the three species described in *Tympanopleura* do not share derived characters defining a more restricted clade of *Ageneiosus*, and hence do not constitute a natural group that warrants separate generic status. For the reasons detailed below, I regard the nominal genus *Tympanopleura* as an unnatural taxon and consider the name to be a junior subjective synonym of *Ageneiosus*.

As noted by Britski (1972), there are significant interspecific differences in the degree of swimbladder encapsulation among ageneiosids, as well as ontogenetic variation in those species with encapsulated swimbladders in adults. I found no complete developmental series of any species within the material examined during this study, and, in fact, there are relatively few juvenile specimens available in museum collections. Nonetheless, my observations corroborate those of Britski (1972). Juveniles of all species for which material was available have comparatively large swimbladders, as revealed through radiographs and in counterstained specimens. In some species (e.g., *T. quadrifilis*, *A. atronasus*, *A. piperatus*, *A. brevis*), the swimbladder remains large and unencapsulated throughout life. In other species (e.g., *A. brevifilis*, *A. ucayalensis*, *A. pardalis*, *A. valenciennesi*), there is a gradual reduction and ossification of the swimbladder during growth, typically culminating in maximal reduction at sizes greater than about 100 mm SL in most species. For

instance, in the smallest specimen of *A. brevifilis* examined (MZUSP 9384, 77 mm SL), the swimbladder is large (6.5 mm long) and has pliable anterior chambers, but in adults the swimbladder is greatly reduced and encapsulated by a superficial ossification of the compound vertebral centrum (see Fig. 8 in anatomical description). Ferraris (1988) noted that swimbladder encapsulation in *A. marmoratus* occurred at a slightly larger size (170 mm SL) than in *A. ucayalensis* and *A. guianensis* (= *A. ucayalensis*) (120 mm and 92 mm SL, respectively). Variation of swimbladder morphology among species is discussed in greater detail in a separate section.

In its original context, the genus *Tympanopleura* was diagnosed on the basis of having a large, unencapsulated swimbladder, evident externally as a window or "tympanum" in the lateral epaxial musculature immediately posterior to the operculum and just below the dorsal fin and above the pectoral fin. This feature is not unique to *Tympanopleura* and, in fact, is found in most if not all catfishes lacking unencapsulated swimbladders. As Alexander remarked,

in some Cyprini...muscle is absent from a patch of body wall lateral to the anterior end of the swimbladder...This condition seems to be universal in Siluri. The muscle-free areas of skin are bounded anteriorly by the post-temporals and cleithra, and dorsally by the expanded parapophyses when these reach to the skin. Bridge & Haddon (1894) call them the 'lateral cutaneous areas'. The swimbladder lies very close below them. A little loose fatty connective tissue lies between swimbladder and dermis at the edges of this area.
(Alexander 1964a:425)

In his study of functional morphology in catfishes, Alexander further stated,

In catfish, muscle is absent from a patch of body wall (the lateral cutaneous area) on each side lateral to the anterior end of the swimbladder. These areas serve to reduce the impedance of the body wall to changes of swimbladder volume, and so increase the sensitivity of the Weberian apparatus.
(Alexander 1965:109)

Other authors (e.g., Chardon 1968, Roberts 1973) also remarked on the occurrence of this state in various siluroids.

The primitive condition of the swimbladder in siluroids is believed to be one in which it consists of a large organ, free from the vertebral parapophyses, lacking posterior chambers, and with the ductus pneumaticus emerging from the anterior transverse chamber (Bridge and Haddon 1894; Alexander 1964; Howes 1983). There is considerable variation involving the development of caecae and ossified encapsulation of the siluriform swimbladder, and, in all probability, many of these involve homoplasies (see morphological comparisons). Moreover, there are incongruencies in swimbladder encapsulation involving taxa that also possess an elastic spring apparatus, or ESA (Howes 1983). Based on features of the swimbladder and Weberian apparatus, Howes (1983:fig. 22) placed ageneiosids within a clade that included astroblepids and loricariids, despite his comments about differences in the nature of encapsulation between ageneiosids and the latter two taxa, and his suggestion that encapsulation has occurred independently in at least two lineages. Apparently, Howes (1983) failed to observe the ESA in his specimen(s) of *Ageneiosus*, which led to his exclusion of the family from the clade with other families having an ESA, which is where most authors have placed the Ageneiosidae.

In addition to the characteristics of the siluriform swimbladder as outlined above, the genus *Tympanopleura* is paraphyletic, since other taxa with unencapsulated swimbladders were described extragenerically (i.e., *T. quadrifilis*, *A. atronasus*, *A. brevis*, *A. madeirensis*). In a cladistic context, *Tympanopleura* was diagnosed on the basis of a shared plesiomorphic character state, and, hence, does not warrant generic status as a natural monophyletic group. Consequently, the three species originally described in the genus *Tympanopleura* are herein allocated to the genus *Ageneiosus* (*T. piperata* [= *A. piperatus*], *T. nigricollis* [= *A. atronasus*], *T. alta* [= *A. brevis*]).

ANATOMICAL DESCRIPTION AND COMPARISONS

There have been a moderate number of comparative reviews dealing exclusively with single-character complexes of siluriform morphology. These include those of the pectoral girdle (Tilak 1963, Gosline 1977), the pelvic girdle (Shelden 1937), the caudal fin (Lundberg and Baskin 1969), the Weberian apparatus and associated structures of the swimbladder (Bridge and Haddon 1894, Alexander 1964, Chardon 1968), the posterior cranial and superior pectoral osteology (Lundberg 1975), functional morphology of the jaw (Gosline 1975), and myology and osteology of the dorsal fin (Royero 1987). Many recent evolutionary studies of neotropical catfishes have dealt with a diversity of morphological characters among closely related taxa, and included fairly broad taxonomic comparisons with outgroups (e.g., Baskin 1973, Howes 1983, Lundberg and McDade 1986, Stewart 1986, Vari and Ortega 1986, Arratia 1987, Schaeffer 1987, Stewart and Pavlik 1985, and Ferraris 1988). There have been relatively few comprehensive reviews of a broad suite of characters among a wide variety of taxa, the most commonly cited of which are those of Regan (1911) and Alexander (1965). Some studies of higher ostariophysan relationships have provided useful morphological data of a limited number of catfish groups (e.g., Greenwood et al. 1966, Roberts 1973, Fink and Fink 1981).

The above sources, along with many studies more restricted in scope, provide a basis on which neotropical catfish systematists have been able to infer assumptions regarding character polarities and homoplasies, and to make other morphological comparisons among the diverse taxa involved. However, detailed anatomical

studies are lacking for many species, and, within nearly all families, there is still a tremendous dearth of information on inter- and infraspecific variation, ontogenetic changes, and genetic and ecological plasticity. Consequently, there are few uniformly accepted concepts of relationships among species, genera, and even families, despite the fact that many of the groups form distinctive, putatively monophyletic clades. Fortunately, there has been a recent surge of systematic interest in neotropical siluroids, and valuable comparative data are becoming more readily available. Nevertheless, large voids remain in our understanding of relationships and the distribution of character states, resulting in considerable confusion and, occasionally, conflicting information of anatomical terminology or taxonomic nomenclature.

In the following summary, the general features of ageneiosid morphology are presented. Wherever possible, inferences regarding the hypothesized polarity or transformation of a structure is advanced on the basis of evidence provided from literature sources, or direct observations from outgroup taxa. In addition to a discussion of the morphological features associated with sexual dimorphism, a detailed review of the available literature on the reproductive biology is provided.

Physiognomy

Ageneiosids have a rather unusual general body appearance that is atypical of most extant siluroids. They are characterized by flattened heads with laterally directed eyes (Fig. 1), an extremely laterally compressed body, their reduced barbels, and relatively short adipose and dorsal fins. Alexander (1965) remarked that:

the Siluridae and Schilbeidae differ markedly in shape from typical catfish...Though the head is depressed and the mouth wide, the trunk is strongly compressed. The anal fin is very long, and the body cavity is accordingly short. The adipose fin is very small or absent, and the dorsal fin tends to be small. The similarities between these families

are probably convergent (Regan 1911). *Ageneiosus* and *Helogenes* are rather similar and may resemble the Siluridae and Schilbeidae in their habits.
(Alexander 1965:122)

With his description, Alexander proposed that the compressed shape of silurids (*Cryptopterus*) and schilbeids (*Schilbe*, *Eutropiella*) was related to their pelagic swimming habits. To the above list Howes (1983) added *Hypophthalmus*, *Ompok* (a schilbeid), and the families Pangasiidae and Auchenipteridae (i.e., *Auchenipterus*). Alexander (1966) further included descriptions of the hydrodynamics of a generalized pelagic schilbeid. His suggestion was that free-swimming catfishes tend to exhibit this morphology, in contrast to the more common depressed body shape characteristic of most sedentary, benthic catfishes.

Howes (1983) compared the body shape of *Ageneiosus* to that of *Hypophthalmus*, and also commented on the ramified lateral line, the reduced swimbladder, the high fat content, and other characters shared between the two taxa. With regard to *Hypophthalmus*, Howes (1983:5) was hesitant to classify this genus as pelagic, but he did conclude that the "schilbeid morphotype" described by Alexander was probably independently derived within several lineages, and that within each group it represents a derived feature with concomitant modifications of the swimbladder and acousticolateralis system. Moreover, *Hypophthalmus* exhibits morphological features unlike most other catfishes, and its body shape may in part be related to its planktivorous feeding habits (Howes 1983).

Although the above comparisons characterize the generalized body shape of a pelagic siluroid, there is unquestionably strong convergence in body shape between several unrelated taxa. As suggested by the above authors, this condition may be correlated with the semipelagic habits of the various genera. Although ageneiosids are generally confined to large river channels and may migrate great distances (Smith 1979), little is known of their behavior. In captivity they have been

Fig. 1.— Ventral profile of the head. (A) *Ageneiosus brevifilis* (MCNG 11334); (B) *A. ucayalensis* (ANSP 128224); (C) *A. valenciennesi* (MZUSP 21634); (D) *A. pardalis* (USNM 270815); (E) *A. vittatus* (UF 80895); (F) *A. brevis* (MZUSP 7871); (G) *A. atronasmus* (UF uncat.); (H) *Tetranematichthys quadrifilis* (ANSP 135821). Scale: A, C = 20 mm; B, D, G, H = 10 mm; F = 5 mm.

A

B

C

D

E

F

G

H

observed to rest on debris or on the bottom at negative buoyancy (L. Nico and L. Finley, personal communication), except when foraging for prey. Under natural conditions, however, they have been observed to actively swim in the upper layers of the water column and forage at the surface (L. Nico, personal communication).

The compressed body of ageneiosids is superficially similar to that of many of the taxa discussed above, but the combination of a compressed trunk and the extremely flattened head with ventrolaterally displaced eyes is unique among catfishes. In some auchenipterids and in *Hypophthalmus*, the body is compressed and the eyes are ventrolaterally positioned, but none of the species in these groups have the head depressed to the extreme degree that *Ageneiosus* does. I believe that the uniquely combined depression of the head and compression of the body is a derived condition characteristic only of the family Ageneiosidae. Lundberg (1982) suggested that a greater depth of the shape of the head and anterior part of the body are correlated, at least in ictalurids, and probably is a shared primitive condition within catfishes in general. *Tetranematichthys* has a relatively deep body and more dome-shaped head, superficially resembling some auchenipterids (e.g., *Trachelyopterus* spp.) in general body shape. However, aspects of the neurocranium and a number of other internal features of *Tetranematichthys* are clearly more like *Ageneiosus* than in the auchenipterid species that it resembles. Among auchenipterids and ageneiosids, there is a large clade of species that is defined by a relatively long anal fin and a laminar epioccipital, assigned to the subfamily Auchenipterinae by Ferraris (1988). Within this group, there appears to have been a trend toward greater elongation and compression of the body, and some degree of flattening of the head; *Ageneiosus* and *Tetranematichthys* appear to be further derived from the condition present in all other taxa of this lineage. The differences in head shape are correlated with osteological differences of the neurocranium, discussed in greater detail below.

The maximum body size of ageneiosids varies widely among species, and is of some diagnostic value in their taxonomy. The smallest species, *A. piperatus*, reaches sexual maturity at less than 50 mm SL. At the other extreme, *A. brevifilis* commonly exceeds 400 mm SL, and there are unconfirmed reports that *A. pardalis* may reach lengths exceeding 1.5 meters. Most achenipterids and doradids are relatively small fishes, although there are some extremely large doradids. Lundberg (1982) speculated that small body size, less than about 100 mm SL, is probably a derived feature among catfishes in general, but he noted that considerable parallel evolution has probably occurred. An extreme condition is found in numerous miniaturized neotropical taxa (Weitzman and Vari 1988; Schaeffer et al. 1989), many of which have independently acquired small size. Presumably among doradoids in general, a relatively moderate body size is the ancestral condition, and the evolution of small body size may represent a derived condition, such as found in some achenipterid genera (e.g., *Centromochlus*, *Gelanoglanis*). If this assumption is correct, then, on the basis of body size alone, *A. piperatus*, *A. atronasus*, and *A. brevis* are derived relative to other species of the family Ageneiosidae. However, it seems reasonable to me that an opposite argument can be made, and that large body size may in fact represent a derived state in certain lineages. Among neotropical siluroids, some pimelodids and doradids get extremely large, although most of the species of these two families are relatively small to medium-sized. If the ancestral condition was of a moderate body size within any given lineage, it is logical to assume that either smaller or larger body size could represent derived states in terminal taxa. Within the Ageneiosidae, most species are between 100 and about 200 mm SL, but several species reach much larger sizes. Since all of the small species of *Ageneiosus* also have the plesiomorphically large, unencapsulated swimbladder, it seems most parsimonious to assume that evolution of larger body size is the derived state within the family. Nevertheless, *A. piperatus*, the most diminutive species of the family, has

a number of apparently paedomorphic characters (i.e., lower meristic counts), and its small body size may be represent a derived state.

Body Coloration

Ageneiosids exhibit a wide variety of pigmentation patterns, ranging from species with relatively unspectacular countershading and no prominent spotting or banding to species with very distinctive mottling or spotting. The coloration pattern is of considerable use in identifying most species, but general descriptions must be interpreted with caution due to pronounced intraspecific variation.

Prior to this study, it was apparently generally assumed by most authors that species of ageneiosids, like many other fishes, have characteristic pigmentation patterns that varied little among individuals, either temporally or spatially, within the same or between different populations. Many of the early species descriptions emphasized differences in pigmentation from what was published in the literature or apparent in relatively few specimens available for comparisons; in several cases the alleged differences between nominal species were quite subtle. During the initial phases of the present work, I noted extensive variation in pigmentation of several species, and suspected prior to examining types that some names were synonyms on this basis alone; in fact, this is the case, as revealed through examination of a fair amount of material of most species, collected from different areas and varying in the quality of preservation.

The most extreme case of color variability was observed in *A. vittatus* collected from flooded caños in the middle Orinoco basin. The normal pigmentation of fish from this area is relatively light, with one or two incomplete lateral stripes and two large caudal spots, as seen in the specimen on the lower right

Fig. 2.—Chromatic polymorphism in *Ageneiosus vittatus*. Both specimens collected together from Caño Maporal, state of Apure, Venezuela, 19 May 1985. Individual at lower right preserved immediately after capture; individual at upper left maintained alive in an aquarium for several days prior to fixation. Photograph by Leo G. Nico.

of Fig. 2. Another fish, collected with this individual and exhibiting virtually the same pigmentation, was kept alive in an aquarium for several days, during which time it became darkly mottled over the entire head and body (upper left of Fig. 2). Additional specimens of this species that were taken from relatively clear natural waters, or maintained in aquaria, had a similar mottled pattern (cf. photographs in Köpke 1986 and Burgess 1989).

I believe that the tremendous variation in coloration exhibited by *A. vittatus* and several other species is primarily attributable to variation in the hydrological composition of the water from which specimens are collected. Those taken from relatively turbid waters, corresponding to the whitewater classification of various authors, are much lighter in coloration than specimens from clearer rivers. Some species that are found in different water types exhibit color variation between populations; for example, specimens of *A. ucayalensis* in the Rio Negro, Río Essequibo, and other nutrient-poor, clearwater rivers draining the Guiana shield are overall much darker than conspecifics from whitewater rivers in other parts of the species' range (in fact, *A. guianensis* was separated from the nominate form almost solely on the difference in color). It is worth noting that *A. polystictus*, a species confined to the Rio Negro, is one of the darkest and most distinctively colored. In addition to environmentally induced color changes, it may be possible that individuals undergo behaviorally mediated changes. Some auchenipterids are also capable of similar dramatic color changes (D. C. Taphorn, personal communication), but, to the best of my knowledge, nothing has previously been published documenting this phenomenon.

In spite of the extensive intra- and interspecific variation in coloration, certain pigmentation patterns are characteristic of individual species and serve as important identifying features. In the species accounts, general descriptions of coloration are based on the typical condition found in preserved material. While

exceptions can be found, I believe that most species can be identified from the pigmentation pattern, in combination with other obvious external features and additional criteria (e.g., shape of the tail, geographic location, etc.).

Phylogenetic relationships of fishes can be notoriously difficult to evaluate on the basis of pigmentation, due to difficulties in coding color patterns and determining polarities, transformation sequences, and homoplasies. For these reasons, I have avoided using pigmentation to infer possible relationships among ageneiosids. Certain patterns may represent shared derived conditions, such as strong mottling and the presence of one or two large crescentic spots in the tail (most intense in *A. vittatus*, present to a lesser degree in *A. pardalis*, *A. ucayalensis*, and *A. valenciennesi*). However, in the absence of clearly defined patterns in outgroups, one is unable to determine whether in fact such patterns are derived or not. In many cases, generalized pigmentation patterns are common in other neotropical fishes, thus indicating convergence that has probably resulted from selection based on ecological factors. For instance, many doradids, some auchenipterids, and a number of unrelated catfishes and characins have prominent spots or stripes in the caudal fin; such disruptive coloration, perhaps functioning to confuse predators, has undoubtedly evolved independently in many unrelated lineages of fishes.

Neurocranium

Few previous studies have presented detailed accounts or illustrations of the ageneiosid cranium. Regan (1911) briefly characterized the skull of all doradoids (as his family Doradidae), many of the salient features of which are found in ageneiosids. His distinction of the doradoid neurocranium included the following: palatine rod-like; pterygoid absent; mesopterygoid connecting the metapterygoid

with the lateral ethmoid; nuchal shield present; epiotics prominent, with posterior processes and sutured to both nuchal plates; posttemporal absent; supracleithrum with the upper limb sutured to the pterotic and epiotic, and with the lower limb sutured to the basioccipital and exoccipital. In addition, he discussed features of the anterior axial skeleton that are intimately associated with the dorsal fin and rear of the skull. Although Regan's (1911) characterization of the doradoid skull included important details useful in distinguishing the included taxa from other families, his analysis was much too superficial to adequately diagnose the ageneiosid cranium. Structures of doradoid neurocrania were described, subsequently, in studies of doradids (Eigenmann 1925) and auchenipterids and ageneiosids (Britski 1972, Ferraris 1988). In addition, a number of other sources included cursory observations on aspects of a limited number of doradoid taxa.

Both Britski (1972) and Ferraris (1988) presented detailed morphological descriptions of the ageneiosid skull, but both authors examined relatively few species, and, in some cases, their identifications of the species are questionable due to the previously confused taxonomy of the family. In both studies, the ageneiosid neurocranium was compared with that of several auchenipterid taxa, and generalized characterizations were made at the genus level. The above two studies have provided the greatest amount of information about the ageneiosid neurocranium to date. The only other studies that presented any significant information about the ageneiosid skull were those of Chardon (1968), Howes (1983), and Royero (1987); in each of these cases, limited comparisons were made between ageneiosids and other catfishes. The only previous illustrations of ageneiosid neurocrania were those of *A. ucayalensis* (Chardon 1968), *A. atronasus* (Britski 1972), *A. vittatus* (Royero 1987), and *A. brevifilis* (Ferraris 1988).

The neurocranium of ageneiosids is elongate and considerably depressed, with a relatively broad "T" formed anteriorly by the mesethmoid, and an hourglass-

shaped occipital-nuchal region posteriorly (Figs. 3-6). The general shape in dorsal profile varies little among species. Many of the elements are extremely porous, especially in small species and juveniles of larger species. The surface texture of the bones is weakly rugose or ridged. The cancellous nature of cranial bones was considered by Stewart (1986) to be a derived condition, and it has apparently evolved independently in some pimelodids, *Hypophthalmus*, and ageneiosids. Cranial bones are relatively nonporous in the auchenipterid genera that I have examined, and most doradoids have extremely solid cranial bones; thus, I consider the poor ossification of skull bones in ageneiosids to be uniquely derived among doradoids. Ageneiosids also have porous bones in other parts of the body, especially the basipterygia and the caudal skeleton. Cancellous bones and a high body-fat content in ageneiosids and *Hypophthalmus* may be involved in maintaining neutral or positive buoyancy (Howes 1983).

The nasal bones are thin, tubular, and bifurcated at their midline. The forked nasal was thought by Ferraris (1988) to be a synapomorphy of ageneiosids. In all other catfishes, the nasal is penetrated by three foramina for the supraorbital sensory canal (Lundberg 1982). The main portion of the canal passes through the anterior and posterior foramina, but a second branch passes through an anterolateral foramen to the second supraorbital pore. In ageneiosids, the proximal portion of the lateral canal is ossified by cancellous bone.

The mesethmoid bears broad lateral cornua, as in the majority of catfishes (Lundberg 1982). The front margin has a relatively shallow median cleft (Figs. 3-6). Anteroventrally, the mesethmoid supports the premaxillae, which are broadly expanded mesially, and gently to strongly curved laterally, depending on the species. The premaxillae are heavily toothed over their entire ventral surface with relatively short, sharp, recurved teeth (further described under oromandibular region).

Fig. 3.—Dorsal view of neurocranium of *Tetranemataichthys quadrifilis* (MCNG 6334). Scale = 10 mm.

Fig. 4.—Dorsal view of neurocranium of *Ageneiosus brevis* (FMNH 58144). Scale = 5 mm.

Fig. 5.—Dorsal view of neurocranium of *Ageneiosus vittatus* (UF uncat.). Scale = 5 mm.

Fig. 6.—Dorsal view of neurocranium of *Ageneiosus atronasmus* (UF uncat.). Scale = 5 mm.

Fig. 7.—Ventral view of neurocranium of *Ageneiosus atronatus* (UF uncat.). Scale = 5 mm.

Fig. 8. – Ventral view of anterior region of vertebral column and posterior portion of neurocranium in *Ageneiosus brevifilis* (UMMZ 207464). Scale = 10 mm.

The paired lateral ethmoids are large and highly porous (Figs. 3-7). Anteroventrally they form large cartilaginous blocks encircling the nasal capsule. Dorsally the lateral ethmoids are broadly expanded and suture medially with the mesethmoid and frontals. The antorbital process is generally ossified except for a cartilaginous facet for the palatine. The mesopterygoid articulates with a shallow groove on the posteroventral margin of the lateral ethmoid. A dorsomedial ridge of the lateral ethmoid contacts the frontal anteriorly and forms a small portion of the bony orbit.

The frontals suture deeply to the mesethmoid and lateral ethmoids anteriorly (Figs. 3-6). The frontals are strongly constricted at their middle and expanded posteriorly. There is a large cranial fontanelle, corresponding to the anterior fontanelle of many other catfishes, beginning at the posterior end of the mesethmoid and extending to about the narrowest constricted area of the frontals. The frontals are sutured at their midline posteromedially, and the fontanelle is continued as a shallow groove above the suture. There is no posterior fontanelle. Posterolaterally the frontals contact the sphenotics, and posteromedially they suture deeply to the supraoccipital. Ventrally the frontals contact the orbitosphenoids, parasphenoids, and pterosphenoids.

The supraoccipital is large and broadly rounded, and usually ornamented with weak ridges or rugosities. Anterolaterally the supraoccipital meets the sphenotics. Most of the lateral margins of the supraoccipital suture with the paired pterotics, which are relatively large and roughly quadrangular in dorsal profile. The epioccipitals extend dorsally and contact the supraoccipital to form the posterolateral margin of the neurocranium. The posterior margin of the supraoccipital sutures with the broad anterior margin of the nuchal shield, formed by the dermal component of the first dorsal-fin pterygiophore (discussed under the dorsal fin morphology).

The sphenotics are relatively small, anvil-shaped bones forming the upper posterolateral margin of the bony orbit. The infraorbital canal exits the sphenotic at its anteriormost point and extends through an unossified portion for a short distance before entering the last infraorbital.

The dorsal profile of the neurocranium in all auchenipterids is considerably different from that of ageneiosids, and varies widely among genera and species. In auchenipterids, the sphenotics and frontals, and, to a lesser extent, the pterotics and lateral ethmoids, are large elements forming a broad cranial vault. The sphenotics are especially large and form a significant medial portion of the bony orbit. In some groups (*Auchenipterus* and *Epapterus*) the sphenotics do not contact the supraoccipital. A complete review of the auchenipterid neurocranium is beyond the scope of this work, but it should be noted that there are a number of derived features that serve to unite various auchenipterid genera (Britski 1972, Ferraris 1988). The general structure of the ageneiosid neurocranium is relatively primitive in comparison to the skull morphology of both doradids and auchenipterids.

Excluding the broadly flared ethmoid bones, the ageneiosid skull in ventral profile is broadly rounded posteriorly and sharply tapered anteriorly (Fig. 7). The parasphenoid is long and thin, contacting the vomer anteriorly and deeply suturing with the basioccipital posteriorly. The vomer is broadly rounded anteriorly. Ferraris (1988) felt that the nonangular shape of the vomer is a synapomorphy of ageneiosids. Apparently this is a derived condition, inasmuch as the anterior end of the vomer changes from a triangular shape to a more rounded shape during ontogeny (personal observation of juvenile specimens).

The orbitosphenoid sutures anteriorly with the lateral ethmoid and extends posteriorly for a short distance along the parasphenoid. The lateral ridge of the orbitosphenoid, which is moderately large in most other catfishes, is relatively small in ageneiosids.

The prootics of ageneiosids are large elements that suture broadly with the basioccipital, pterotics, and epioccipitals. They form a relatively large area of the floor of the neurocranium, similar to a derived condition found in loricariids (Schaeffer 1987). I have not made a detailed study of the foramina associated with the auditory region.

Homology of bones associated with the upper portion of the siluriform pectoral girdle and the posterolateral region of the neurocranium has been extensively discussed in the literature (e.g., Lundberg 1975, Fink and Fink 1981, Schaeffer 1987). Much of the debate involves terminology of two elements: the supracleithrum and the posttemporal. In most catfishes, there is fusion of certain elements in this region of the skull, with the result that authors have not uniformly applied the same names to homologous bones. A detailed review of the problem is beyond the scope of this study. Lundberg (1975) stated that a posttemporal was probably absent in all ageneiosids. However, other authors have considered the bone at the posterolateral corner of the neurocranium to be a posttemporal (e.g., Britski 1972, Ferraris 1988). In the absence of ontogenetic series to demonstrate derivation or the extent of fusion of elements in this region, I follow Britski (1972) and Ferraris (1988) in calling this bone a posttemporal. In all ageneiosids, the posttemporal is a large, triangular bone extending posterolaterally at the rear margin of the neurocranium (Figs. 3-7). Anterodorsally it sutures with the epioccipital and supraoccipital.

In doradoids the epioccipitals are prominent bones that contribute to a significant portion of the posterolateral dorsum of the neurocranium. This is one of the characters that Regan (1911) used to unite all doradoids, and is generally considered to be the most important synapomorphy uniting these taxa (Chardon 1968, Britski 1972, Ferraris 1988, Curran 1989). In ageneiosids, the dorsal portion of the epioccipital is similar to that found in auchenipterids and doradids, where it

forms part of the posterior portion of the neurocranium. Dorsally the epioccipital forms a small plate that is sutured posterolaterally with the posttemporal, anterolaterally with the sphenotic, and medially with the supraoccipital (Figs. 3-6). In most auchenipterids and all ageneiosids, the epioccipital has prominent posteriorly directed spines or processes. In several taxa, the posterior extensions of the epioccipital contact the complex centrum of the Weberian apparatus. In auchenipterids, the length of the epioccipital spine(s) and degree of fusion with the vertebral centra varies among genera and has been used to unite some taxa (Ferraris 1988, Curran 1989). In ageneiosids, the epioccipital process is considerably more extensive than in most auchenipterids, and may represent the most derived configuration. In ageneiosids, the posterior process of the epioccipital is fused medially with broadly expanded parapophyses of the fifth and six vertebra; the entire structure forms a broad, laminar shelf extending from the posterior margin of the neurocranium to the center of the complex centrum (Figs. 3-8, 24). Near the posterior medial end of the epioccipital, where it contacts the parapophyses of the fifth and sixth vertebrae, there is a large foramen; a medial ramus of the vagus nerve (vagus lateralis of Howes 1983) passes across the Müllerian ramus dorsolaterally, then passes through the foramen and extends laterally along the vertebral column (Fig. 17).

I add the following anecdotal comments on sensory reception in ageneiosids. Assuming that olfactory acuity may be diminished as a consequence of the reduced barbels, one is left to speculate that perhaps ageneiosids have compensated for sensory reception in other ways. Little is known of their ecology, and virtually nothing is known about their physiology. At least some species are active both diurnally and nocturnally. The eyes and optic centers of the brain are moderately well developed, thus vision is probably fairly acute. The lateral line is also well developed, and the acousticolateralis canals on the head are moderately developed,

as in most other catfishes. However, perhaps one of the most important sensory aspects of these fishes may be electroreception; a survey of many catfishes has revealed that ageneiosids have among the most highly developed acoustic tubercles in the central sensory areas of the brain, which have been implicated in very low threshold electroreception (R. J. Miller, unpublished data, personal correspondence).

Infraorbital and Laterosensory Canals

Primitively among ostariophysans, the ossicles surrounding the infraorbital branch of the latero-sensory canal system, commonly called infraorbitals or the infraorbital series, are relatively large bony plates covering portions of the cheek adductor musculature (Fink and Fink 1981). In catfishes, the infraorbitals are reduced to the canal-bearing portions of the bones, although plate-like elements have been secondarily derived in loricariids and callichthyids (Fink and Fink 1981, Schaeffer 1987), and, to a lesser extent, in doradids (Eigenmann 1925). There is extensive variation in the number of infraorbitals among catfishes in general, and the homologies of individual elements has never been thoroughly established. The primitive number of infraorbitals in siluroids is thought to be five (Lundberg 1982), including the anteriormost ossicle, which is uniformly termed the lacrimal. This represents a reduction of two from the presumed primitive teleost number of seven (Nelson 1969), due to loss or fusion of the antorbital with the lacrimal and the dermosphenotic with the chondral portion of the sphenotic.

There is extensive variation in the shape and number of the infraorbital bones among doradoids (Ferraris 1988). The primitive number, as in other catfishes, is believed to be five. Ferraris (1988) concluded that doradids and ageneiosids share a derived condition of having lost an additional element, which he

considered to have occurred independently in the two lineages. However, my observations do not confirm those of Ferraris, inasmuch as the presumably derived condition of four infraorbitals is not uniformly present in all ageneiosids; in fact, several species have five infraorbitals, and their shape and position varies somewhat. In all species the lacrimal is relatively large, with two long anterior processes, a short posteromedial process, and a long posteroventral process (Figs. 3-6, 9). Variation among species occurs in the remaining three or four elements, and, in the absence of developmental series, their homologies cannot be unequivocally determined. The last infraorbital is relatively long and remote from the sphenotic, and I assume that it is homologous among all species (Figs. 3-6, 11). This leaves the observed variation attributable to infraorbitals 2-3 (numbered antero-posteriorly). In *A. pardalis*, *A. n. sp.*, and *Tetranematicthys* there are five infraorbitals, with the third being the smallest of the series, which, in *A. n. sp.* and *Tetranematicthys*, is reduced to a very short cylinder that is just slightly longer than its diameter. I have also observed five infraorbitals in specimens of *A. atronasus*, *A. brevis*, and *A. vittatus*; in these three species, the fourth element is the smallest, and the third and fifth surround the main posterior and ventral curve of the sensory canal. The absence of a small posterior canal ossification, anteroventral to the sphenotic, was considered by Ferraris (1988) to be synapomorphic for ageneiosids, although this condition is homoplasious in outgroups, being found in doradids, *Asterophysus*, and *Trachelyopterichthys* (Britski 1972, Ferraris 1988). In some species, including at least *A. brevifilis*, *A. brevis*, *A. vittatus*, *A. ucayalensis*, and *A. n. sp.*, the second infraorbital is flared at its posterior end, apparently where an anterior branch of the sensory canal passes into the dentary. Ferraris (1988) considered this to be a synapomorphy of *Ageneiosus*, but I have not observed it in either *A. atronasus* or *A. pardalis*. Apart from obvious interspecific variation, I suspect that there may also be significant

intraspecific variation in the number and size of infraorbitals 2-4 in ageneiosids, based on examination of a limited amount of material.

Among the genera of auchenipterids, there is extreme variation in the number, shape, and relative positioning of the infraorbital bones, which Ferraris (1988) used extensively in phylogenetic comparisons. While I agree that several of his observations probably represent unique, derived characters, it appears that the extreme degree of variation may in some cases be of limited value for determining relationships; at least, this is the case among species of ageneiosids. Until more data become available on variation, ontogeny of the ossification sequence, and probable homologies of the various infraorbital elements, I defer using them in a phylogenetic analysis of ageneiosid species.

There is some variation among ageneiosids in the latero-sensory canals of the head, but I have not made an extensive survey of this variability. In most species, there appear to be relatively few pores passing to the surface, but the pores are small and difficult to observe in whole, preserved specimens. *Ageneiosus brevifilis* and *A. marmoratus* have a number of star-like clusters of short canals on the dorsal surface of the head, especially on the snout and near the eyes, and a row of similar pores on the chin overlying the dentaries. Similar clusters were occasionally observed in other species, but never appeared as prominent or numerous as in *A. brevifilis*.

The lateral-line canal exits from the upper half of the posterior margin of the posttemporal bone and extends along the upper half of the trunk to the caudal fin. The lateral line is sinusoidal along its entire length, and gives off several short, irregular rami that are directed posterodorsally and posteroventrally, passing to the surface and ending in small pores. At the base of the caudal fin, the lateral line bifurcates, and sends a branched ramus onto each lobe of the fin. The dendritic structure of the lateral line is derived, and is apparently shared by all auchenipterids

(Ferraris 1988). At least some auchenipterids have a more extensively branched lateral line, consisting of dorsal and ventral rows of neuromasts over most of the trunk musculature, but this presumably further-derived condition is absent in ageneiosids and closely related auchenipterids (Ferraris 1988). *Hypophthalmus*, some pimelodids, and various Old World catfishes have similar ramified lateral lines, indicating that this character state has evolved independently several times.

Splanchnocranium

Oromandibular Region

The jaws of ageneiosids are large and heavily toothed. The premaxillae are typically expanded at the midline and tapered near the rictus, and bear numerous sharp, retrorse, setiform teeth. In *A. atronasus*, *A. brevis*, *A. piperatus*, and *T. quadrifilis*, however, the premaxillary tooth patch is relatively thin and the teeth are notably weaker and fewer than in larger species. In *A. ucayalensis*, and, to a lesser extent in the other large species, the premaxillae are moderately to extremely recurved, and bear proportionally more teeth on their ventral surface, especially at the midline. The dentary of ageneiosids is relatively broad, club-shaped and produced anteriorly, with heavy dentition similar to the premaxilla. Expansion of the anterior dentary margin was considered by Ferraris (1988) to be a synapomorphy of the ageneiosid clade. The anguloarticular is relatively elongate and triangular, with a greatly expanded coronoid process. There is an extensive block of cartilage between the dentary and anguloarticular, with an ascending process extending above the lower margin of the premaxillae when the mouth is closed. The relatively large oral gape and expanded tooth-bearing surfaces in

ageneiosids is probably correlated with their feeding habits; most species for which there are data feed predominately on whole fishes and decapods.

The siluroid palatine is fairly variable in structure and orientation, relating to the mechanism of adduction of the maxillary barbel, and is of considerable systematic value (Gosline 1975). In ageneiosids, the palatine typically is a rod-shaped bone with cartilaginous plates at each end, articulating in a sliding mechanism with the maxillary anteriorly and the lateral ethmoid medially. This condition occurs in females and immature males, and is similar to that found in a number of other catfishes (Alexander 1965, Gosline 1975). In nuptial male ageneiosids, however, the palatine is considerably modified, with an enlarged anterior facet and a slightly expanded medial cartilage. This modification of the palatine is also present in nuptial males of certain auchenipterids, including *Auchenipterus*, *Entomocorus*, *Epapterus*, and at least some species of *Trachelyopterus*. Ferraris (1988) regarded the modified palatine as a synapomorphy of a restricted clade within his subfamily Auchenipterinae; the absence of a modified palatine in *Trachelyichthys* and some species of *Trachelyopterus* were thought by Ferraris (1988) to be secondary losses from the presumably derived modification. Functionally, the expansion of the palatine is apparently correlated with the sexually dimorphic hyperossification of the maxillary barbel in nuptial males. In taxa with this apomorphy, the barbels of breeding males are abducted in a lateral to anterodorsal plane and have a tactile function during courtship and spawning. A hypothesized close relationship between the taxa sharing this character state is corroborated by additional characters associated with sexual dimorphism (Ferraris 1988). However, I tentatively question the distribution of this character state as proposed by Ferraris (1988), inasmuch as published data are unavailable for breeding males of most species, including some members of his non-monophyletic "group 1" species of

Trachelyopterus. Future studies may reveal that dimorphism of the palatine is more widespread than currently known.

The maxilla is typically a teardrop-shaped bone with an expanded base (Fig. 9). As in other catfishes, it supports the maxillary barbel, and articulates as a hinge joint with the anterior facet of the palatine. Posterolaterally, the maxilla extends as a short cartilaginous core into the maxillary barbel. In nuptial males, the maxilla becomes hyperossified, extends into the barbel for its entire length, and develops sharp, recurved odontodes on the dorsal surface, as discussed below in greater detail.

Suspensorium

The ageneiosid suspensorium is characterized by its relatively large surface area, comprised of obliquely angled, laminar ossifications on the anterodorsal margins of the metapterygoid, quadrate, hyomandibular, and an additional pterygoid bone. The quadrate, in particular, has a dorsomedial lamina that extends between the metapterygoid and hyomandibular and sutures broadly to each bone (Fig. 10). Anterodorsally, it sutures along most of its margin with the metapterygoid. The metapterygoid is laminar and roughly quadrangular, articulating synchondrally with the quadrate near its posteroventral corner. Ferraris (1988) considered this arrangement of suspensorial elements to be uniquely derived in ageneiosids; the primitive condition in doradoids, as in most catfishes (Alexander 1965), is one in which the hyomandibular and metapterygoid contact each other dorsal to the quadrate. Dorsally the hyomandibula articulates synchondrally and by a short anterodorsal process with the sphenotic. Posterior to the sphenotic articulation there is a short, broad process contacting a shallow groove in the pterotic. Ventromedially, the hyomandibula sutures along most of its margin with

Fig. 9. – Left oromandibular region of *Ageneiosus ucayalensis*, anterolateral view. (USNM 265691). Scale = 2 mm.

Fig. 10.—Left suspensorium, lateral view. (A) *Ageneiosus atronasus* (UF uncat). (B) *Ageneiosus pardalis* (FMNH 26358). Scale of both = 3 mm.

the laminar process of the quadrate, the only synchondral articulation being a short cartilaginous bar at its posteroventral corner. The suprapreopercle is a small, rod-like element, investing a short portion of the preopercular latero-sensory canal anteroventral to its exit from the pterotic. The preopercle is a moderately large blade, smooth on all margins, and sutured anteroventrally with the quadrate. The preopercular latero-sensory canal gives off a posterior branch and a ventral branch before exiting at the anteroventral corner, below and behind the condyle articulation with the anguloarticular of the lower jaw.

There is one additional element of the suspensorium in ageneiosids that deserves some comment. The bone in question is situated anterior to the metapterygoid and posteromedially to the palatine. In the literature on siluriforms there is considerable confusion associated with the terminology and homologies of the anterior suspensorial bones, or the pterygoid complex, as discussed in greater detail by Gosline (1975), Howes (1983) and Schaeffer (1987). An exhaustive review of the problem is beyond the scope and intent of this work. Fink and Fink (1981) stated that in catfishes the ectopterygoid is greatly reduced and that the mesopterygoid is also reduced and not in contact with the rest of the suspensorium posteriorly. In several groups of siluriforms the ectopterygoid has been lost altogether, and the endopterygoid is variably reduced or absent (Lundberg 1982, Schaeffer 1987). Regan (1911) diagnosed the neotropical doradoids as lacking a pterygoid, but having a mesopterygoid that connects the metapterygoid with the lateral ethmoid. Following Regan, Chardon (1968) included the absence of a pterygoid in his definition of the various families, but he termed the bone an entopterygoid. Ferraris (1988) called the lost element an ectopterygoid, and homologized it with the element of the same name in other teleosts (after Fink and Fink 1981). Loss of the ectopterygoid, then, is a character shared by all doradoids, but it has been independently lost in a number of other families. The question

remains of what to call the element that has not been lost. Ferraris (1988) did not discuss this bone, but in his illustrations of various suspensoria he indicated that the entopterygoid was omitted. This may be the currently accepted name for the bone in question, at least in other teleosts (Cailliet et al. 1986), but there is little uniformity in terminology. Nevertheless, I prefer to consider the above element a mesopterygoid, equivalent to the same bone of Gosline (1975) and Fink and Fink (1981).

The mesopterygoid in ageneiosids is a moderately large bone, superficially contacting the vomer anteromedially, passing medial to the palatine, and abutting near or loosely suturing with the anterior margin of the metapterygoid. Its shape varies from broadly triangular to quadrangular. In most species the mesopterygoid does not extend very far posterodorsally, but in *A. pardalis* it is relatively long, and in *A. n. sp.* it extends over the entire dorsal margin of the metapterygoid and contacts the anterodorsal corner of the quadrate.

The shape and orientation of the combined elements of the suspensorium vary somewhat among species, and appears to be correlated with the degree of flattening of the head. In *A. atronasus*, *A. brevis*, and *Tetranematichtys*, the suspensoria are not extremely elongated, and are oriented at moderately oblique angles in a ventro-dorsal plane. In other species with more flattened heads, the suspensoria are elongated, and are angled obliquely in a much more latero-medial plane.

Opercular Series

The opercle and interopercle of ageneiosids have a relatively primitive shape. Both bones are very cancellous. The opercle is moderately large and broadly triangular (Fig. 11). The interopercle is slightly flared posteriorly, as in

Fig. 11.— Ventrolateral view of left opercular series of *Ageneiosus ucayalensis* (USNM 265691). Dashed line indicates margin of eye. Dorsomedial lamina of hyomandibula not shown. Scale = 2 mm.

ictalurids and a variety of other catfishes (Lundberg 1982). Little variation in the appearance of the opercular bones was observed among species.

Hyoid and Branchial Arches

Ferraris (1988) found that ageneiosids have a number of uniquely derived features of the hyoid arch and branchial series. The hyoid arch consists of the unpaired urohyal and paired hypohyal, ceratohyal, interhyal, epihyal, and branchiostegal bones. The urohyal is broadly rounded anteriorly, with a long, laminar projection posteriorly (Fig. 12). Anteromedially, the urohyal has a vertical extension that projects between the hypohyals, which Ferraris (1988) regarded as a synapomorphy of ageneiosids. Anteriorly, the ceratohyal is sutured to the ventral ossification of the hypohyal along its ventromedial surface. This was also regarded by Ferraris (1988) as a synapomorphy of ageneiosids, in comparison to the condition of other doradoids, in which the two bones are separated by a large bar of cartilage along their lateral surfaces. Posteriorly, the ceratohyal articulates both suturally and synchondrally with the interhyal. The interhyals is a relatively long, rectangular bone, slightly tapered at the posterior corner. The epihyal is a small osseous nodule at the medial face of the hyomandibula, near its anteroventral suture with the preopercle.

The ceratohyal supports up to six or seven branchiostegals, with the remaining ones supported by the interhyals. The number of branchiostegals in ageneiosids ranges from seven to twelve, and is of some use in distinguishing species. However, there is a fair amount of intraspecific variation. Most species have between eight and ten branchiostegals. *Ageneiosus brevifilis* and *A. marmoratus* have modal counts of eleven branchiostegals, followed by *A. polystictus*, *A. ucayalensis*, and *A. valenciennesi*, all with modal counts of ten branchiostegals.

Fig. 12. - Hyoid and branchial arches. (A) *Ageneiosus atronatus* (UF uncat.), dorsal view, scale = 2 mm; (B) *A. brevis* (MCZ 50742), ventral view, scale = 5 mm. Fifth ceratobranchial not shown in A.

The lowest branchiostegal count (seven) is found in *A. piperatus*. *Tetranematicthys* has ten to twelve branchiostegals, but too few specimens were examined to accurately determine a modal count for this species. Among catfishes in general, high branchiostegal counts are considered derived (Gosline 1973, Lundberg 1982). However, most catfishes have between nine and eleven (Howes 1983), which is a range that is entirely within the intraspecific variation that I have observed in some species of ageneiosids. In some catfishes, an increase in the number of branchiostegal rays is correlated with a depressed head and the length of the free opercular sleeve (Gosline 1973). In ageneiosids, however, the opercular flaps are fused to the isthmus well behind the center of the throat, thus contradicting any correlation with the length of the free sleeve. An increase in the number of branchiostegals has undoubtedly evolved independently in many lineages of catfishes. Nevertheless, within any ingroup an increase in the number of branchiostegals may be used to infer phylogenetic relationships (Lundberg 1982). Thus, I consider this character state to be synapomorphic in those species of ageneiosids with relatively high branchiostegal counts.

The ossification pattern of the gill arches in ageneiosids is similar to that of ictalurids and many other catfishes (Lundberg 1982). Only the second and third basibranchials are ossified. The first two hypobranchials are ossified and obliquely concave on their anterior margins, and have the medial cartilaginous flanges situated anterior to the lateral edges of the bones (Fig. 12). Ferraris (1988) found that this structure and arrangement of the first two hypobranchials was unique to ageneiosids. All five ceratobranchials are ossified, and the fifth pair are expanded to support large pharyngeal tooth plates, each bearing a large number of moderately strong teeth. The ceratobranchials bear the majority of the gill rakers on each arch. All five epibranchials are ossified and bear gill rakers in two rows. There is a pair of large oval pharyngeal tooth plates supported by the infrapharyngobranchials and

posterior tips of the third and fourth epibranchials. The infrapharyngobranchials of the third and fourth arch are ossified; that of the third is relatively elongate and club-shaped, while that of the fourth is broad and squarish. The anteromedial tip of the first epibranchial is broadly flared and overlaps the medial tip of the second; Ferraris (1988) considered this to be synapomorphic of ageneiosids.

Ageneiosids have numerous, relatively large gill rakers on the medial and lateral margins of the ceratobranchials and epibranchials (Fig. 13). In most species the rakers are compressed and have a crenulated medial margin, but in *A. brevifilis*, *A. marmoratus*, and *A. polystictus* the rakers are conical and relatively short. Britski (1972) surveyed the gill rakers in several auchenipterid and doradid taxa, and found considerable variation in their structure and number. Depending on the taxon, the rakers on the first arch may be in any combination of one or two rows, and relatively long, short, or even absent. Based on Britski's comparisons, and from what is known in other catfishes, the primitive condition for length is one in which the rakers are relatively short; lengthening of the rakers is presumably derived, but has probably occurred independently in a number of taxa. Similarly, arrangement of the rakers into two rows is presumably primitive, since this is the condition in diplomystids and ictalurids (Arratia 1987, Lundberg 1982), and, I assume, many other catfishes. Based on what is available in the literature, I have the impression that the shape, number, and arrangement of gill rakers has been relatively neglected in catfish systematics; from what I have observed in ageneiosids, it seems that this character has considerable systematic value, at least in the alpha-level taxonomy.

Apart from differences in gill-raker shape, the number of gill rakers varies widely among ageneiosid species. In addition, there is considerable intraspecific variation in gill-raker number. I was unable to find any geographic component to this variation. However, there appeared to be some correlation with size (larger specimens with more gill rakers), although I did not test this hypothesis statistically;

Fig. 13. – Lateral view of left first gill arch. (A) *Ageneiosus ucayalensis* (USNM 265717; right arch, reversed); (B) *A. valenciennesi* (MZUSP 21634); (C) *A. n. sp.* (MG 27149); (D) *A. polystictus* (MG 27304). Scale: A = 1.0 mm; B, D = 2.5 mm; C = 5 mm.

perhaps, gill rakers increase in number during growth, at least until a certain body size is reached. Regardless of the intraspecific variation, the ranges and/or mean number of gill rakers was sufficient to separate several species, as detailed in the species accounts. Among catfishes in general, high gill-raker counts are probably derived (Lundberg 1982); thus, I hypothesize that a high gill-raker count is a synapomorphy among some species of ageneiosids.

Barbels

The barbels of catfishes are prominent sensory and tactile structures that, although not unique to these fishes, characterize the order because of their conspicuous appearance in most species. All catfishes have at least one pair of maxillary barbels, which are reduced or vestigial in ageneiosids and a few other taxa, including some species of the eastern hemisphere genera *Cryptopterus* and *Pangasianodon* (Günther 1864; Alexander 1964, 1965; Roberts 1973 [who erroneously stated that they were absent in some female ageneiosids]). The majority of catfishes have additional barbels that are variable in number and structure and associated with the mandibular skin or with the external nares. Diplomystids have only a pair of maxillary barbels. In many taxa, some or all of the barbels are elaborately developed and may have fleshy branches or diverticuli, such as in the Loricariidae, Doradidae, and Mochokidae. Siluroid barbels differ from those of other teleosts, including the related cyprinoids, by their histologically distinctive ultrastructure, consisting of an elastin core (Alexander 1965; Roberts 1973; Ghiot and Bouchez 1980; Dimmick 1988), and, in the case of the maxillary pair, myological and osteological adaptations that allow for independent adduction and motility of the barbels for increased tactile and gustatory functions (Alexander 1965; Gosline 1975). In the context of their study, Fink and Fink (1981) concluded

that the barbels of Siluriformes and Cypriniformes were independently derived, and, citing the lability of barbel development and placement among members of their subseries Cypriniphyi, probably had evolved several times within the Cypriniformes. Excluding the maxillary pair, there is considerable variation among catfishes in the structure, topography, and taxonomic distribution of the remaining barbels, which may suggest that they too were derived independently in certain lineages. Moreover, there is considerable variation in the ontogenetic development of barbels, leading Fuiman (1984:137) to suggest that "heterochrony in barbels may be an important consideration for classification within siluroids." Nevertheless, given the universal distribution and unique, complex morphology of the siluroid maxillary barbel and associated structures (Gosline 1975), there is no compelling evidence to refute a hypothesis that this organ is homologous among all extant siluroid taxa, and perhaps represents a synapomorphy of equal weight as the degree of fusion of the Weberian complex in defining the monophyly of siluroids.

The enigmatic nature of the barbels in the Ageneiosidae is reflected in the family name, from the Greek *ageneios*, meaning beardless. Excluding *Tetranematichthys*, most previous diagnoses of the family emphasized reduction of the maxillary barbels and the absence of any on the chin. Toothed maxillary barbels were occasionally mentioned in original descriptions, but, with very few exceptions (e.g., Kner 1858a, Eigenmann and Bean 1907), sexual dimorphism of the barbels was apparently not known or understood by most authors. Thus, in all prior classifications, the absence of barbels except for the maxillary pair has been used to separate ageneiosids from other families of catfishes (notwithstanding confusion surrounding the placement of *Tetranematichthys*, reviewed separately in a section on its taxonomic status). No studies have suggested that chin barbels are present, during any stage of development, in individuals of any species of *Ageneiosus*.

Chin barbels

One of the most surprising and significant findings of this study was the discovery that juveniles of several species of *Ageneiosus* have barbels on the chin. Unfortunately, adequate developmental series of juveniles were unavailable in the collections examined to thoroughly elucidate ontogenetic changes in the barbels. Nevertheless, it appears that some, and perhaps all species begin life with at least a single pair of chin barbels, which are subsequently resorbed during growth. There is little consistency in the literature associated with terminology of the chin barbels. As used here, the term mandibular refers to the anterior pair of barbels, situated nearest the lower lip, and the term mental is applied to the posterolateral pair, nearest the posterior edge of the dentaries; a similar distinction in terminology was made by Schaeffer et al. (1989), although the position, and, possibly, the ontogenetic derivation of the barbels in the taxa they studied (*Scoloplax* spp.) is considerably different than in ageneiosids. Initially I only observed the mental pair of barbels, but examination of additional specimens revealed two pairs of chin barbels. In one postlarval *Ageneiosus* sp. (MCNG 7595; 20.4 mm SL), there is a pair of relatively long, fleshy mental barbels, medial to the dentaries and at a plane about equal with the front margin of the eyes, and a pair of shorter mandibular barbels, near the edge of the lower lip (Fig. 14a). A somewhat larger specimen (43.8 mm SL) from the same collection lacks the mandibular pair, and the mental barbels are considerably shorter relative to the length of the head (Fig. 14a). There apparently is considerable heterochrony involved in the resorption of both pairs of chin barbels among species. One relatively large specimen (80 mm SL) of *A. pardalis* has both pairs of barbels (Fig. 14b), whereas none of six specimens of *A. ucayalensis* (several lots; 44-73 mm SL) show traces of either pair. In two specimens of *A. vittatus* (MCNG 1477; 39.9 and 43.3 mm SL) the mental barbels are reduced to minute

Fig. 14. – Chin barbels in juvenile *Ageneiosus*. (A) *Ageneiosus* sp. cf. *A. ucayalensis* (MCNG 7595), scale = 2.5 mm; (B) *A. pardalis* (NRM-SOK 1989044.5855), scale = 10 mm.

stubs. One juvenile of *A. marmoratus* (AMNH 56068; 44.8 mm SL) has a single pair of relatively long mental barbels. A series of three *A. brevis* (MZUSP 27818; 51.2-69.0 mm SL) all have mental barbels, but they are progressively shorter with increasing body size. Likewise, eight specimens (56-105 mm SL) of *A. atronasus* from several lots all have a single pair of mental barbels. There are no chin barbels evident in a nuptial male of the diminutive species *A. piperatus* (ANSP 137688; 40 mm SL), and one can only speculate that, if chin barbels develop in this species, they must appear at a very early stage. At the other extreme, some large adults of *A. brevifilis* have very small epidermal indentations or pores that correspond in position to the mental barbels present in other species, and occasionally there are traces of similar pores corresponding to the mental pair, despite the absence of any distinct chin barbels in one 77-mm juvenile. In all of the specimens examined, the chin barbels appear to be derived from the superficial integument, and there is no evidence from counterstained specimens that there are cartilaginous supporting structures, as in *Hypophthalmus* and several genera of pimelodids (Howes 1983), *Auchenipterus* (Ferraris 1988), and a number of other catfishes. More complete series of juveniles of all species are needed in order to determine the developmental sequence and taxonomic implications of chin barbels in *Ageneiosus*.

The ontogenetic loss of chin barbels in *Ageneiosus* is herein considered to represent a derived state relative to most other catfishes. This condition is analogous to the situation in some species of the Asian family Pangasiidae, in which the mental and/or nasal barbels become progressively reduced and eventually disappear during growth (Karamchandani and Motwani 1956, Fumihito 1989). These observations underscore the suggestion by Fuiman (1984) that the timing of barbel development is important in siluroid systematics, but it must be emphasized that at present there is little evidence to corroborate a hypothesis that pairs of chin barbels are uniformly homologous among families of catfishes. Arratia (1987)

briefly discussed problems of determining homologies of the barbels, and recommended that future studies include data about supporting tissues.

Tetranematicichthys differs from all other ageneiosids in having a single pair of chin barbels in adults. These barbels have a peculiar frilled tip (Fig. 15), and roughly correspond in position to the mental pair of *Ageneiosus*. No small juveniles of *Tetranematicichthys* were available, so it remains unknown if more than one pair of chin barbels is present during early ontogeny in this species. Presumably, the retention of mental barbels in adults, albeit reduced in size, and the absence of the mandibular pair, represents a more primitive state than that found in *Ageneiosus*. Among other neotropical catfishes, only the auchenipterid *Gelanoglanis* has a single pair of chin barbels, but Ferraris (1988) regarded the presumed loss of one pair of barbels in *Tetranematicichthys* and *Gelanoglanis* to have occurred independently. The papillate tip of the chin barbel in *Tetranematicichthys* has not been observed, to the best of my knowledge, in any other auchenipterid, and is presumably an apomorphy of this taxon. Its function remains unknown, although SEM photomicrographs indicate that it is covered with tastebud-like projections. Many doradids have superficially similar frilled barbels, but they are generally much larger and lack the filamentous stalk as in *Tetranematicichthys*; their branched structure is herein considered to have been independently derived.

Maxillary barbels

Unlike other doradoid catfishes, ageneiosids have inconspicuous, diminutive maxillary barbels that are normally concealed within deep clefts above the corners of the upper lip. This is the condition in females and nonbreeding males, and is the reason why they have occasionally been overlooked by some investigators.

Reduction in size of the maxillary barbels is regarded as a derived state of the

Fig. 15. — Papillate tip of left mental barbel of *Tetranematoichthys quadrifilis* (ANSP 135821; male, 135 mm SL).

Fig. 16. – Dorsal view of right maxillary barbel of nuptial male.
 (A) *Tetranematicichthys quadrifilis* (MCNG 3018); (B) *Ageneiosus ucayalensis* (MHNG 2394.36); (C) *A. vittatus* (MCNG 5862).
 Scale: A = 5 mm; B-C = 2 mm.

ageneiosids; Ferraris (1988) separated *Ageneiosus* from *Tetranematichtys* (and all other doradoids) on this basis, but all of the females of *Tetranematichtys* that I have examined have very short barbels (it is unknown whether males undergo seasonal elongation of the barbel, as in *Ageneiosus*). Breeding males of *Ageneiosus* develop antrorse, tooth-like outgrowths on the dorsal surface of the maxillary bone, which extend along the entire length of the core of the barbel (Fig. 16b-c). The development of hooked barbels is apparently seasonal, as evidenced from large males with normal, filiform barbels during nonbreeding periods, and direct observations from captive specimens (Köpke 1986; Ferraris 1988; L. Finley, personal communication). Males of *Tetranematichtys* differ from *Ageneiosus* in having a much more elongate, weakly tuberculate maxillary barbel (Fig. 16a), similar to that found in several achenipterid genera. Ferraris (1988) invoked the hyperossified barbel as a synapomorphy uniting the "*Ageneiosus* group" with the "*Achenipterus* group" and *Trachelyopterus* (see phylogenetic relationships). While I agree that sexual dimorphism of the maxillary barbels (and other nuptial structures) represents a shared, derived character among these taxa, I would argue that a paucity of information on sexual dimorphism available for several achenipterid genera does not at present allow for an unequivocal generalization regarding the distribution of this character state. Suffice it to say, there is no evidence that any other genera develop sharply hooked barbels; thus, the extreme condition in *Ageneiosus* is regarded as uniquely derived (Ferraris 1988). I interpret the edentulate, elongate maxillary barbels of *Tetranematichtys* and various genera of achenipterids to represent a more primitive state relative to the condition in *Ageneiosus*.

Weberian Apparatus and Axial Skeleton

The ageneiosid Weberian apparatus involves the six anteriormost vertebrae, the rear of the neurocranium, and the supporting elements of the rayed dorsal fin. The most distinctive aspect of the complex is the presence of an elastic spring mechanism, discussed below in greater detail.

The tripus of doradoids and some other catfishes (e.g., the Mochokidae) is modified from the typical siluriform condition in having a recurved transformator process that penetrates the peritoneal tunica of the swimbladder (Chardon 1968). This is the condition in ageneiosids with large, free swimbladders, but in species with encapsulated swimbladders (discussed below), the transformator process of the tripus has an expanded, disc-like posterior lamina that contacts the swimbladder anterodorsally (Fig. 8). The correlation between an enlarged transformator process and an encapsulated swimbladder suggests that there has been some functional compensation for auditory reception. The os suspensoria of ageneiosids are small, ovoid elements attached ligamentously to the tripus and complex centrum (Fig. 7), as in other doradoids (Chardon 1968, Ferraris 1988). I have not examined in detail the structure and orientation of the remaining Weberian ossicles.

Anteriorly the complex centrum is strongly sutured to the exoccipitals, which is characteristic of all other doradoids (Royero 1987, Ferraris 1988). In addition, the neural arches of the fifth and sixth vertebra are expanded into laminar ossifications that suturally unite with the first and second dorsal-fin pterygiophores, forming a rigid plate between the complex centrum and the dorsal fin (Figs. 17, 24). Laterally, the parapophyses of the fifth and sixth vertebrae extend horizontally and suture with each other and the posterior process of the epioccipital, forming a broad laminar plate above the swimbladder (Figs. 3-6, 24). The extent of fusion of the vertebral parapophyses with the epioccipital process is much more extensive than a

similar arrangement found in some auchenipterids. Curran (1989) proposed a transformation series to account for the variably developed posterior epioccipital process in auchenipterids; he hypothesized that a longer process, and/or one that contacts the parapophyses of the complex centra is a more derived character state than one in which the epioccipital process is short or does not contact the parapophyses. However, Curran (1989) did not include ageneiosids in his analysis. In a similar fashion, Ferraris (1988) considered various shapes of the epioccipital process to represent derived states in some auchenipterids.

At least some auchenipterids have seven vertebral centra fused to form the complex centrum. This was one character that Britski (1972) and Royero (1987) used to separate ageneiosids and auchenipterids, although Ferraris (1988) did not mention it in his analysis. Britski (1972) qualified his use of this character by stating that he did not know if fusion of seven vertebrae was uniform among all auchenipterids. Nevertheless, all of the auchenipterids used as outgroups for my analysis of ageneiosid relationships have seven fused vertebrae, presumably representing a derived state relative to that in all of the ingroup taxa. A maximum of seven fused centra has also been observed in some ariids (Howes 1983).

Doradoids, together with ariids, mochokids, malapterurids, and some pangasiids, have a unique modification of the Weberian complex generally referred to as an elastic spring apparatus (ESA) by most authors (e.g., Bridge and Haddon 1894, Regan 1911, Tavalga 1962, Alexander 1965, Chardon 1968, Howes 1983). In most catfishes, the parapophysis of the fourth vertebra is usually a transverse laminar sheet of bone that overlies the swimbladder and contacts the posttemporal-supracleithral complex. In taxa with an ESA, however, the parapophysis of the fourth vertebra is free from the posttemporal and has a distally enlarged plate that impinges laterally or anterolaterally on the wall of the swimbladder. The plate or disc-like expansion of the fourth parapophysis is often called the Müllerian ramus,

named after its discoverer, Johannes Müller (the history of studies of the ESA were summarized by Tavalga 1962). There are ligaments extending between the anterior face of the expanded plate and the posterior occipital region, which, when contracted, cause oscillations in the volume of the swimbladder. The ESA is involved in sound production and has been well studied in ariids (Tavalga 1962), but relatively unstudied in the remaining taxa. The presence of an ESA has been used widely as a defining character for the neotropical doradoids, and some authors have used it at a wider level of universality to suggest interfamilial relationships (Chardon 1968, Curran 1989).

Taxa with an ESA usually have large swimbladders. Because several ageneiosids have encapsulated swimbladders, some investigators have erroneously assumed that an ESA was absent in ageneiosids (Tavalga 1962, Howes 1983). However, all ageneiosids do have an ESA, although its structure varies between those species with large swimbladders and those with encapsulated swimbladders. In all species with large, unencapsulated swimbladders, the Müllerian ramus is a relatively large, discoidal plate closely apposed anterodorsally to the swimbladder peritoneal tunica (Figs. 17, 18a-c). In species with an encapsulated swimbladder, however, the Müllerian ramus is relatively reduced in size (Fig. 18d), although it maintains a ligamentous connection with the posteroventral margin of the nuchal shield (Royero 1987). In those species with enclosed swimbladders, there is a large foramen in the anterodorsal wall of the capsule where the Müllerian ramus contacts the soft tissue of the swimbladder.

Including six for the anterior elements that are fused to form the Weberian complex, and one for the fused preural centra, counts of total vertebrae in ageneiosids range from 39 to 58, with most species tending toward the upper end of this range. Howes (1983:36) noted that few comparative data exist for vertebral counts in siluroids, although he indicated a "mean siluroid count" of about 40-45;

Fig. 17. – Lateral view of longitudinal swimbladder septum and anterior region of vertebral column in *Ageneiosus* sp. cf. *A. brevis* (MCZ 50742). Scale = 1 mm.

Fig. 18. — Distal tip of anterior ramus of fourth vertebral parapophysis (= Müllerian ramus). Anterior to left. (A) *Tetranematicichthys quadrifilis* (MCNG 6334); (B) *Ageneiosus brevis* (MZUSP 34417); (C) *A. atronasus* (UF uncat.); (D) *A. ucayalensis* (MCZ 7608). Scale: A-C = 1.0 mm; D = 0.5 mm.

ageneiosids were included with taxa of four additional families considered to have relatively high counts (presumably of post-Weberian elements; Howes' conclusion based on this count was questioned by Stewart 1986). Species of *Diplomystes* have on the order of 40-43 total vertebrae (Arratia 1987). Stewart (1986) considered relatively high total vertebral counts of 49-61 in one clade of pimelodids to represent a derived condition. Similarly, Howes (1983) stated that an increase in the number of vertebrae represents a derived state, but it presumably has occurred independently in many catfish lineages, and therefore is of limited usefulness for determining probable relationships. While data such as these provide much needed information, counts given by various authors are not always directly comparable; variation in the number of fused centra, and failure of some authors to clearly indicate which elements are included, has led to discrepancies in the literature. Few authors have been as meticulous as Lundberg (1982), Stewart (1986) or Roberts (1989a) in explaining how counts are presented. In spite of these limitations, I follow Stewart (1986) in treating the presumably derived state of an increase in vertebrae to be of some use for inferring relationships within a relatively close group of species.

Although ageneiosids have relatively high numbers of vertebrae in comparison to many other siluroids, they are not significantly different from many species of achenipterids. Britski's (1972) vertebral counts, presumably of post-Weberian centra, ranged from 38 to 51 for various achenipterid genera; not unexpectedly, he found a correlation between body length and vertebral number. Relatively elongate forms, such as *Ageneiosus* spp., *Auchenipterus*, and *Trachelyopterichthys* have the highest counts. From the limited data available for other doradoid taxa, it appears that the derived condition of an increase in the number of vertebrae has been obtained independently in several clades, considering a lack of corroborative evidence linking these taxa. Among species of *Ageneiosus*, I

consider an increase in number of vertebrae as derived, the most extreme condition therefore being shared by *A. brevifilis*, *A. marmoratus*, *A. polystictus*, and the large-bodied, fork-tailed species, all of which have a mean number of total vertebrae exceeding 49. Among doradoids in general, an increase in vertebrae may represent a shared character at a higher level of universality, but, until more complete data are available, I defer making any comparisons outside of *Ageneiosus*.

The ribs of ageneiosids, like other catfishes, are pleural. The first rib articulates with the transverse process of the sixth vertebra. The basal end of the rib is curved and hooks around the tip of the transverse process in a manner that is unique to doradoids (Ferraris 1988). The number of paired ribs in most species of ageneiosids varies by two or three, but the modal value is useful in separating some species. The number of ribs parallels the number of branchiostegals among species, with the fewest in small species and the most in *A. brevifilis* and *A. marmoratus*. Few comparative data are available for outgroups, although a survey by Britski (1972) indicated that most auchenipterid genera have between six and thirteen pairs. An increase in the number of ribs is probably derived, at least within ageneiosids, and may be correlated with expansion of the coelomic cavity associated with increased body length.

Swimbladder

The ageneiosid swimbladder has been the subject of considerable attention, stemming from the fact that most species, when originally described, were known or thought to have a very reduced swimbladder that was encased in a bony capsule associated with the complex centrum (the encapsulation process is discussed below). The original description of *Tetranematicichthys* (as *Ageneiosus quadrifilis*; Kner 1858a) was accompanied by an illustration of that species' swimbladder, which is large,

globular, and bipartite; the unusual appearance of its swimbladder, relative to other ageneiosids known at the time, may have contributed to the early confusion over the correct taxonomic affinities of the genus. The traditional concept of an encased swimbladder in the family was modified when Eigenmann (1912) described a new genus, *Tympanopleura*, the diagnostic feature of which was a large, unencapsulated swimbladder. The taxonomic status of *Tetranematichthys* and *Tympanopleura* is addressed in separate sections, and it is only relevant to note here that both genera have continually been recognized by most authors until relatively recently.

As briefly discussed elsewhere (status of *Tympanopleura*), there are extensive interspecific differences in swimbladder morphology, as well as changes that occur during development. Britski (1972) was the first to present evidence that there is a reduction in swimbladder size during ontogeny in at least some species of ageneiosids; his evidence was based on a small series of *A. valenciennesi* and juveniles of an unidentified species. Ferraris (1988) briefly discussed encapsulation, as observed in only a few specimens of three species, and he concluded that *A. nigricollis* (= *A. atronasus* ?) retained a large swimbladder throughout life. My observations of many specimens confirms Britski's, and to some extent Ferraris' conclusions, although good developmental series are unavailable for most species. In ageneiosids, as well as in many other catfishes, the relative size of the swimbladder can be approximated in juveniles by study of the epaxial musculature, below the region where the epioccipital plates contact the lateral body wall, and above the postcleithral process, if present. Generally, there is a relatively large, opaque or slightly translucent area (corresponding to the "lateral cutaneous area" of Alexander 1964) in juvenile specimens with a large swimbladder. This muscle-free window, or "tympanum", generally becomes progressively obliterated during growth in those species with encapsulated bladders. In species with a free swimbladder as adults, the "tympanum" may remain large and visible at all sizes (e.g., *A. brevis* and

A. piperatus), although this is not the case in *A. pardalis*, and in adults of *A. atronasus* and *Tetranematichtys* the "tympanum" is relatively small and obscured by heavy pigmentation of the overlying skin.

The surface of an encapsulated swimbladder, and in some cases the longitudinal septum, is easily observed in radiographs, thus providing a direct method of measuring its size without necessitating dissection of the specimen. In species with an encapsulated swimbladder, the swimbladder is proportionally large at relatively small body sizes (< 50 mm SL), but there is strong negative allometry with increasing SL (Fig. 19). Encapsulation proceeds by ventrolateral laminar ossifications of the complex centra, which progressively encircle the swimbladder on the sides and anteriorly, as discussed in greater detail below. In *A. ucayalensis*, the swimbladder is fully encapsulated at a relatively small size, and the negative allometry is due entirely to somatic growth. In other species (e.g., *A. vittatus*), allometry is due to a combination of an increase in SL and an overall slower rate of encapsulation. The posterior caecae may or may not become thinly ossified, depending on the species and size of the specimen. Ferraris (1988) reported that a single 85-mm SL specimen of *A. marmoratus* had a relatively large, unossified swimbladder, and that encapsulation in this species began to occur around 170 mm SL. However, I observed a much smaller specimen of *A. marmoratus* (FMNH 96585; 83 mm SL) with an almost fully encapsulated swimbladder (I have not verified the identification of Ferraris' specimens).

The swimbladder itself, or the encapsulated capsule, varies widely in structure among species, and is of considerable taxonomic use (Figs. 20-21). Primitively, the siluroid swimbladder consists of a relatively large, flexible sac corresponding to the anterior chamber of other ostariophysans, and with a characteristic arrangement of internal transverse and longitudinal septae and surrounding epithelial layers (Alexander 1964, 1965). In some ageneiosids, and a

Fig. 19. – Allometry of encapsulated swimbladder length in six species of *Ageneiosus*. Cluster indicated by solid arrow includes five specimens of *A. n. sp.* and one each of *A. marmoratus* and *A. vittatus*.

Fig. 20.—Unencapsulated swimbladders of auchenipterid and ageneiosid species. Ventral view, anterior toward top. (A) *Trachehyopterus galeatus* (UF 37033); (B) *Entomocorus gameroi* (UF uncat.); (C) *Tetranematichthys quadrifilis* (MCNG 6334); (D) *Ageneiosus atronasmus* (UF 44926); (E) *A. brevis* (MZUSP 7862); (F) *A. pardalis* (FMNH 23648). Scale: A, C-E = 5 mm; B = 2 mm; F = 20 mm.

C

F

B

E

A

D

Fig. 21.—Swimbladder capsules of ageneiosid species. Ventral view, anterior toward top. (A) *Ageneiosus vittatus* (USNM 297400); (B) *A. n. sp.* (MG 27153); (C) *A. valenciennesi* (MZUSP 91634); (D) *A. ucayalensis* (ANSP 152850); (E) *A. polystictus* (MG 27304). Scale: A-B, D-E = 2 mm; C = 5 mm.

A

B

C

D

E

number of other catfishes, there are accessory caecae or diverticuli, which I consider to be derived in those taxa with them. Many species of doradids have very elaborate accessory chambers (Eigenmann 1925), but their condition is herein considered to be independently apomorphic from that in ageneiosids.

Tetranematicthys quadrifilis has a very unusual swimbladder, consisting of a very large, oval, semi-turgid anterior chamber, and an equally large, fleshy posterior caecum (Fig. 20c); presumably, the swimbladder is hydrostatically functional, and it may also be involved in sound production (as evidenced by the large ESA, discussed below).

Four species of *Ageneiosus* have large, unencapsulated swimbladders as adults: *atronasus*, *brevis*, *pardalis*, and *piperatus*. The first two have posterior caecae, which are short and broad in *A. atronasus*, but somewhat more variable in *A. brevis*, some specimens of which have considerably shorter caecae than illustrated in Fig. 20e. Limited material of *A. piperatus* prevented a detailed study of the swimbladder in this species; however, it apparently has a very large, spherical swimbladder, without posterior caecae, as observed in one paratype (CAS 58382; 47 mm SL). Perhaps the most atypical species is *A. pardalis*, which has a relatively large, turgid, unencapsulated swimbladder without any posterior caecae, a condition that defies the general trend of a negative correlation between swimbladder size and maximum body size observed in other species.

The remaining species all have encapsulated swimbladders as adults (Fig. 21). The capsule is similar in shape among all of these, although slightly variable; the caecae in *A. vittatus* are slightly longer and more divergent than in the other species.

I consider encapsulation of the swimbladder in some ageneiosids to be a shared, derived character. Encapsulation is well known in a variety of other taxa (Alexander 1964, Howes 1983), many of which are benthic and often rheophilic,

thus requiring negative buoyancy. Encapsulation of the swimbladder in ageneiosids and *Hypophthalmus* is difficult to account for, given their semipelagic swimming habits (Howes 1983); possibly, they maintain positive buoyancy by a high lipid content in the body, but the selective factors responsible for reduction of the swimbladder remain unknown. Encapsulation has undoubtedly occurred independently in many lineages, as evidenced by the widespread occurrence among unrelated taxa (Alexander 1964, Howes 1983, Stewart 1986). Nevertheless, among doradoids, I know of no other species that have encapsulated swimbladders; thus, this character is uniquely derived within a restricted clade of the Ageneiosidae. This is supported by morphological differences in the encapsulation process; in other catfishes, the capsules are generally formed from a combination of elements that usually include portions of the posttemporal and/or transverse processes of the complex centra (Alexander 1964; Howes 1983). In ageneiosids, the transverse process of the fourth vertebra is modified for the ESA, and the parapophyses of the fifth and sixth centra are fused to the posterior process of the epioccipital; the capsule of the swimbladder is derived from the ventral surface of the complex centra and, possibly, *in situ* ossification of the peritoneal tunica (*sensu* Rosen and Greenwood 1970). Howes (1983) placed ageneiosids on the same branch with loricarioids in a hypothesized cladogram of several families, based on the shared condition of an encapsulated swimbladder, despite his discussion of the differences between these taxa. The situation involving swimbladder encapsulation in ageneiosids is analogous to that described by Stewart (1986), in which an intrafamilial clade of pimelodids (the so-called *Callophysus* group) has an unusual, partially encapsulated swimbladder, but modified much differently than in any other catfishes.

The development of posterior swimbladder caecae in some species may also represent a derived state. Among sister taxa, neither *Trachelyopterus* or

Entomocorus have posterior caecae (Fig. 20a,b), a presumably primitive condition shared with *A. pardalis* and *A. piperatus*. The extremely large, single sac in *Tetranematichthys* is unlike the shorter, paired caecae found in the remaining species of *Ageneiosus*, and possibly represents a separately derived state.

Ageneiosids with encapsulated swimbladders have concomitant modifications of the transverse processes of the fourth vertebra, involved in formation of the ESA, as detailed below in a discussion of the Weberian apparatus. In these taxa, there is a moderately large anterolateral foramen in each side of the swimbladder capsule, where the Müllerian rami contact the membranous tunica of the swimbladder.

Dorsal Fin

The ageneiosid dorsal fin consists of one small spinelet, one large defensive spine, and six branched rays and their associated proximal supporting structures. The entire fin is relatively small and situated anteriorly, above the pectoral-fin origin and immediately behind the supraoccipital.

The first lepidotrichium, which normally forms part of the locking mechanism in siluroids (Alexander 1965), consists in ageneiosids of a bifurcated bone with strongly recurved ventral limbs (Fig. 22), similar to that found in other doradoids (Royero 1987, Ferraris 1988). The curved shape of the first dorsal spine also resembles that of some eastern hemisphere catfishes (members of the Mochokidae and Sisoridae), but the phylogenetic significance of this similarity, if any, is not known (Ferraris 1988).

The second lepidotrichium typically forms a relatively elongate, stiffened spine; in females and non-nuptial males, this element generally consists of a thin spine with a single row of moderately weak, retrorse teeth along the proximal two

Fig. 22. – First dorsal-fin spinelet of *Ageneiosus brevifilis* (UMMZ 207464).
Anterior to left. Above: left lateral view. Below: ventral view.
Scale = 5 mm.

thirds or more of the posterior margin and weak crenulations along the basal anterior margin. In nuptial males the dorsal spine is modified into an elaborate mating structure, consisting of a long, sinuous spine with sharp, antrorse odontodes along the anterior margin and a completely edentulate posterior margin (Fig. 23). Several genera of auchenipterids are known to have similar dimorphism of the dorsal-fin spine, although no information is available for many other species, due to a lack of enough preserved museum material, and, possibly, to seasonality of dimorphism. Ferraris (1988) considered dimorphism of the dorsal-fin spine to be a synapomorphy of the family Auchenipteridae (in which he included ageneiosids), despite an absence of data for many species. He further suggested that one group of species in *Trachelyopterus* may have secondarily lost the dimorphic spine. Given a putatively important role of the dimorphic spine of males during mating, it seems to me that a secondary loss of this character is counter-intuitive. Rather, I suspect that either the above clade of species is primitive with respect to this character, or, more likely, that dimorphic males of the included species have simply not been observed. In any case, sexual dimorphism of the dorsal-fin spine is unique to ageneiosids and at least some auchenipterids, and, in combination with the large number of other corroborative characters, supports a hypothesis that the included taxa are monophyletic.

Morphology of the dorsal spine is of limited use in distinguishing ageneiosid taxa. Nuptial males of all species of *Ageneiosus* have numerous sharp, antrorse odontodes along most or all of the anterior margin of the dorsal spine, and an edentulate posterior margin. In at least some species, these odontodes are distributed in a basal cluster of laterally directed serrae, followed by a hiatus of no serrae, and the distal half or more of the spine with antrorse serrae arranged in an alternating anterolateral, sinistral-dextral fashion (Fig. 23). There may be some species-specific differences in the arrangement of these odontodes; for instance, all

Fig. 23. – Dimorphic dorsal-fin spine of nuptial male *Ageneiosus*. Left lateral view: (A) *A. brevifilis* (MG 27298); (B) *A. atronasus* (FMNH 93488). Dorsal view: (C) *A. ucayalensis* (MHNG 2394.36); (D) *A. vittatus* (MCNG 5862). Scale: A-C = 10 mm; D = 5 mm.

A

B

C

D

peak nuptial males of *A. brevifilis* that were examined had the odontodes arranged in the above fashion, whereas in *A. atronasus* and *A. n. sp.*, the serrae are distributed along the entire anterior margin of the spine. However, limited material of nuptial males, and incomplete information about the development and hypertrophy of the dimorphic spine, precludes a thorough taxonomic comparison among species at present.

In all species, the distal tip of the defensive dorsal-fin spine beyond the posterior ossified portion is continued as a short, segmented, membranous ray. In *A. brevifilis* and *A. marmoratus*, the entire spine is segmented, flexible, and unserrated in all but breeding males. A somewhat intermediate condition between these two species and all other species is found in *A. polystictus*, in which approximately the distal one-third of the spine is relatively feeble. Reduced ossification of the dorsal-fin spine of these species is a derived condition, relative to all other ageneiosids and the majority of other catfishes. This condition has occurred independently in several unrelated catfish groups, including some clariids and pimelodids.

In *A. brevis*, the spine is relatively short and stout, with prominent lateral ridges and rugosities, especially near the base. In addition, the posterior odontodes are somewhat stronger than in other species, and are often bifurcated or split into two rows proximally. The relatively strong spine of *A. brevis* is presumably somewhat more primitive than that of other species. The odontodes along the rear margin of the spine in most other species are somewhat longer and lanceolate-shaped, although in *Tetranematichtys* the serrae are relatively weak.

In ageneiosids, the basal support of the dorsal fin is intimately associated with the rear of the neurocranium and the front of the vertebral column, as is the case in other doradoids. There is considerable confusion of terminology associated with these basal elements, however, which deserves further comment.

The proximal elements supporting the teleost dorsal fin have been variously termed radials and/or pterygiophores. Primitively in teleosts, there are three elements supporting each ray of the median fins: a relatively long, tapered internal element, usually interdigitating with neural spines of the vertebrae (and, thus, sometimes called the interneural); a short, medial element; and a small, often cartilaginous, distal element, that articulates directly with the lepidotrichium. The positional description of these elements is what is important, whether they are called radials or pterygiophores.

Among spiny-rayed fishes, in general, the middle element is often fused to the proximal bone. In catfishes, the middle elements of both the dorsal and anal-fin rays are absent as separate ossifications (Fink and Fink 1981), but they typically remain evident as cartilaginous blocks. Furthermore, the distal elements are usually reduced to round cartilaginous nodules located between the bases of the soft fin rays. Weitzman (1962) made the distinction that a pterygiophore is composed of radials, which may or may not become fused. Sometimes, when the proximal and medial elements are fused, they are collectively called a basal. In spite of the distinction between pterygiophores and radials that is occasionally made, some authors have used the terms interchangeably. I follow Lundberg (1982) and Schaeffer (1987) in loosely applying the term "pterygiophore" to the combined proximal and medial elements, and the term "radial" or "distal radial" when referring to the distal cartilaginous element.

In most catfishes, the pterygiophores associated with the first two fin-ray elements are exceptionally modified to form part of the spine-locking mechanism, as described in detail by Alexander (1965) and Royero (1987). In many catfishes, the expanded anterior pterygiophores, and sometimes more posterior ones, loosely contact or even suture with the neural spines of the vertebral column. In ageneiosids, both the first and second pterygiophores are expanded as laminar

plates, sutured together along their entire vertical lengths, and ventrally they are sutured to laminar expansions of the neural spines of the fourth and fifth vertebrae (Figs. 17, 24). Anterodorsally, the laminar plate suturally contacts the nuchal shield, and posteriorly forms a medial plate for the dorsal-fin spine articulation.

In doradoids and many other catfishes there are prominent dermal components sutured posterodorsally to the rear of the skull, which are herein collectively termed the nuchal shield, or, individually, nuchal plates. In many catfishes the supraoccipital has an expanded posterior process or spine, surrounded partially by the nuchal plates. In doradoids a supraoccipital spine is absent, however, but contact between the rear of the skull and the dorsal fin is made via a broad, well developed nuchal shield.

Currently there is no uniform agreement on the homology of the bones forming the nuchal shield, and the problem is confounded by the terminology used by different authors. In his text, Ferraris (1988) equated the three elements typically forming the doradoid nuchal shield with a dermal component of expanded basal radials of the first three dorsal-fin rays, but, in his illustrations and list of abbreviations, he called the elements of the nuchal shield pterygiophores (Ferraris 1988; cf. p. 44 and figs. 14-19). His description of these bones is problematic, however, by his statement that "in the *Ageneiosus* group, the first pterygiophore is either absent or lacks a dermal component, and, therefore, lies entirely ventral to the expanded second element" (Ferraris 1988:44). The anterolateral process of the laminar plate described in the preceding paragraph was considered to be a first proximal radial by Britski (1972) and a first basal radial by Royero (1987). I concur with the last two authors regarding the identification of that bone, but I call it the first pterygiophore, in order to be consistent with the terminology I have adopted above. Both Britski (1972) and Royero (1987) referred to the three dorsal elements forming the nuchal shield as nuchal plates (one through three by Britski; anterior, medial, and posterior by Royero).

Fig. 24. – Lateral view of dorsal-fin supporting elements and anterior region of vertebral column in *Tetranemachthys quadrifilis* (MCNG 6634).
Scale = 5 mm.

Alexander (1965) equated the first two nuchal plates of catfishes with a fused supraneural and dermal ossifications of the first proximal radial, and he considered the second nuchal plate(s) to be formed from the second proximal radial. At present, there are few data available to account for the osteological derivation of the nuchal plates, but most authors have considered them to be dermal ossifications associated with the anterior pterygiophores. Thus, although homology of the plates among taxa has not been thoroughly established, many investigators have treated them as though they are homologous. Based on the available literature, and in the absence of comparative embryological material, one is left with little choice but to treat the nuchal plates of doradoids as homologous, and to assume that they are derived from dermal ossifications of the first three dorsal-fin pterygiophores.

The detailed discussion of dorsal fin-ray supports and the nuchal shield presented above is relevant to ageneiosids in the following important respect. Most doradoids have two large, unpaired nuchal plates, and a pair of smaller posterior plates. In ageneiosids (and *Centromochlus* among auchenipterids; Ferraris 1988), however, the plate corresponding in position to the anterior one of other doradoids is absent. The absence of the first nuchal plate was considered by Britski (1972), Royero (1987), and Ferraris (1988) to be one of the characters separating ageneiosids from all remaining doradoids. Both Royero (1987) and Ferraris (1988) felt that the element that normally forms the anteriormost nuchal shield of doradids and auchenipterids was fused to the posteroventral margin of the supraoccipital, but neither author gave ontogenetic evidence to support this idea.

Thus, the ageneiosid nuchal shield consists of two plates, presumably derived from the second and third dorsal-fin pterygiophores. The anterior nuchal plate is very large and roughly triangular, being sutured along its entire anterodorsal margin to the supraoccipital (Figs. 3-6), and posteroventrally sutured with the epioccipital. The posterior nuchal plates consist of two small laminar bones that are suturally

united to the bifid horns of the apex of the anterior plate, situated on either side of the dorsal-fin spine (Figs. 3-6).

Since most doradoids have three prominent nuchal plates (counting the posterior pair as one), Royero (1987) and Ferraris (1988) regarded the absence of the anterior plate in *Ageneiosus* to be a derived state. Presumably, loss of the plate in *Centromochlus* (Ferraris 1988) is convergent with the condition in *Ageneiosus*, in the absence of any corroborative evidence to support a close relationship between these taxa.

The remaining pterygiophores of the ageneiosid dorsal fin are much smaller than the first two, similar in shape, and do not contact the vertebral column. Each bears a cartilaginous bar corresponding to the medial radial, and a distal cartilaginous radial lying between the bifid halves of the branched lepidotrichia (Figs. 17, 24).

Pectoral Girdle

The siluriform pectoral skeleton has been investigated in a number of phyletic studies of ostariophysan relationships and functional morphology (Regan 1911, Tilak 1963, Alexander 1965, Lundberg 1975, and Gosline 1977). In his benchmark revision, Regan (1911) noted the highly characteristic pectoral girdle of catfishes, and stated that the mesocoracoid arch was absent in the Ariidae, Bunocephalidae (= Aspredinidae), and the Doradidae (including the auchenipterids and ageneiosids). Absence of the mesocoracoid was repeated by Ferraris (1988) as a uniform condition among doradoids. However, *Diplomystes* lacks a well-developed mesocoracoid (Alexander 1965, Arratia 1987), suggesting that its presence in some catfishes represents a derived state.

The ageneiosid pectoral girdle is relatively generalized in comparison with most other catfishes. The long vertical limb of the cleithrum is bifurcated dorsally,

where it articulates with a notch in the posttemporal (Fig. 25). The relatively long horizontal limb extends obliquely forward and is broadly sutured with its antimere at the midline. The cleithrum is broadly fused to the coracoid along the entire anteroventral margin. The coracoids broadly suture at the midline anterior to the cleithral suture.

There is no postcleithral process (PCP) in most ageneiosids, although a short one is always present in *Tetranematichthys*, and it is usually present in *A. brevis*. All other doradoids have a PCP. The primitive condition for catfishes is the presence of a moderately developed, unornamented PCP (Lundberg 1982), so that loss or reduction of this structure is derived in ageneiosids (Ferraris 1988). There has been considerable divergence among siluriforms in the morphology of the PCP, indicating parallel evolution (Lundberg 1982). Several other lineages of neotropical catfishes have independently lost the process (Stewart 1986). At the other extreme, nearly all doradids have a very strong, heavily ornamented PCP, which probably represents a separately derived state. Stewart (1986) stated that there is a positive correlation between the relative size of the PCP and strength of the pectoral-fin spine and locking mechanism in pimelodids. This argument can be applied to ageneiosids, in which the pectoral-fin spine is relatively weak in comparison to many other catfishes. The two species in which the PCP is present have relatively robust fin spines within the family.

The ageneiosid first pectoral lepidotrichium is a relatively thin, moderately serrated defensive spine in most species (Fig. 26). In *A. brevifilis* and *A. marmoratus* the first pectoral ray is segmented, weakly serrated, flexible, and tapers to a thin membranous tip (Fig. 26a). A somewhat intermediate condition between these two species and other ageneiosids is found in *A. polystictus*, in which the spine is stiff and unsegmented proximally, but flexible and branched distally. A strong and heavily ossified spine is primitive for catfishes; thus, the reduced strength of the spine is derived in the above species. The spines of *A. atronasus*, *A. brevis*, and

Fig. 25.—Medial view of right pectoral girdle of *Ageneiosus brevifilis* (UMMZ 207464). Scale = 10 mm.

Fig. 26. – Dorsal view of right pectoral-fin spine. (A) *Ageneiosus brevifilis* (UMMZ 207464; left ray, reversed); (B) *A. n. sp.* (MG 27152); (C) *A. pardalis* (USNM 270813); (D) *A. valenciennesi* (MHNG 2394.36); (E) *A. atronasus* (UF uncat.); (F) *Tetranematichtys quadrifilis* (USNM 269994). Scale: A = 10 mm; B-F = 5 mm.

Tetranematicthys are somewhat more robust and strongly serrated than in the large, fork-tailed species. The outgroup taxa generally have a much stronger spine than is found in ageneiosids; nearly all doradids and several auchenipterids have very strong spines that are serrated on both margins. Several genera of auchenipterids (e.g., *Auchenipterus*, *Epapterus*) do not have serrae on the anterior face of the spine, a condition that is shared with ageneiosids, but one that Ferraris (1988) suggested has occurred independently in at least three lineages.

In ageneiosids there are three ossified radials supporting from 7 to 17 branched pectoral-fin rays. The third radial is expanded posteriorly and supports several fin rays (Fig. 25). Ferraris (1988) suggested that the expanded third radial was a synapomorphy of the ageneiosid clade. The number of rays varies by three or four within every species, but modal fin-ray counts can be used to separate some species. The fewest rays are found in *A. atronasus*, *A. brevis*, *A. piperatus*, and *Tetranematicthys*, all with modal counts under 12. The large fork-tailed species have modal counts of 12 to 13. The greatest number of fin rays is found in *A. polystictus*, *A. brevifilis*, and *A. marmoratus*, all with modal counts of 14 to 15. The number of pectoral-fin rays among outgroup taxa varies widely (Britski 1972); thus, fin-ray number is of limited use in assessing phylogenetic relationships between genera. Nevertheless, an increase in the number of fin rays possibly represents a derived state within the Ageneiosidae, since most auchenipterids have fewer fin rays and lack the expanded third radial.

Pelvic Girdle

The ageneiosid pelvic skeleton is a remarkably conservative structure, varying relatively little in morphology among species, and thus is of no systematic value in determining relationships within the family. By virtue of its constancy in form, however, it is of some use as a diagnostic character of the family.

The basipterygia of *Ageneiosus* are relatively flat, typically consisting of very porous bone (especially in juveniles), and have a pair of bifurcated prongs anteriorly and a pair of flattened, cartilaginous processes posteriorly (Fig. 27). Typically, each basipterygium also has an anterolateral extension of cartilage, termed the lateral process of the basipterygium (Shelden 1937). The lateral process was thought by Ferraris (1988) to be present in all other doradoids, subject to some variation, and is also found in at least one unrelated family, the Plotosidae; functional variation in the myology and osteology associated with the lateral process was discussed in greater detail by Shelden (1937). *Tetranematicthys* differs from other species, however, in that the lateral processes are absent or reduced to small cartilaginous plates (Fig. 27c). The pelvic girdle of *Tetranematicthys* also differs from other ageneiosids in having relatively short anterior processes and in being more solidly ossified. The basipterygium of *A. brevifilis* is somewhat broader than in other species, and is also less porous (Fig. 27a). I did not examine skeletal material of large specimens of most other medium-sized species, but I speculate that there is greater ossification with increased size. Ferraris (1988) found that the pelvic girdle of *Auchenipterus* has a derived condition among doradoids, characterized by a dorsal convexity of the basipterygia, and with the anterior processes directed obliquely ventrally. Among the ageneiosids examined, some slight variation in curvature of the basipterygia was noted (e.g., slightly more concave in *A. atronasus*), but no species exhibited the extreme condition found in *Auchenipterus*; not enough material was examined to determine if there are species-specific differences. Likewise, some species appeared to have more elongate and flattened posterior cartilages, but there were no obvious trends in the shape among species. At present, there is not enough comparative ontogenetic or interspecific information available for doradoids to use the pelvic girdle in phylogenetic comparisons below the generic level.

Fig. 27.—Ventral view of basipterygia, anterior toward top. (A) *Ageneiosus brevifilis* (UMMZ 207464); (B) *A. n. sp.* (MG 27153); (C) *Tetranemataichthys quadrifilis* (MCNG 6334). Scale: A = 10 mm; B = 2 mm; C = 4 mm.

The ageneiosid basipterygium invariably supports seven lepidotrichia, the first of which is unbranched and thicker than the remaining elements. The primitive condition for siluriforms is thought to be one in which there is a small bony splint and six functional rays (one unbranched and five branched, designated $i + 5$), which Ferraris (1988) suggested might be a synapomorphy of all siluriforms, since other otophysans generally have more branched rays; his implication was that fewer rays in siluroids was derived relative to other otophysans. However, Ferraris subsequently concluded that the primitive count for doradoids was $i + 5$ (*Trachelyopterus*, *Centromochlus*, and allied taxa), and that a high fin-ray count in several genera was a derived state that had occurred independently. Considering all catfishes, therefore, the primitive condition is a low number of fin rays (thus not a synapomorphy), and the derived condition of an increase in fin rays has almost certainly occurred independently in many unrelated lineages. Relative to all other doradoids, the structure of the pelvic girdle and the fin-ray count of ageneiosids is relatively primitive.

The innermost ray of the ageneiosid pelvic fin has a membranous connection with the skin on the belly for a substantial portion of the length of its inner branch, up to half in some specimens examined. Ferraris (1988) found the same condition in some species of *Epapterus*, but he erroneously considered it to be apomorphic of that genus only; this character may in fact represent an additional synapomorphy between ageneiosids and *Epapterus*. Like most other genera of auchenipterids, however, *Epapterus* has a variable and substantially greater number of pelvic rays than ageneiosids (e.g., 14 to 16 in *E. blohmi*; Vari et al. 1984), representing a more derived state.

Anal Fin

Ageneiosids have a relatively long anal fin. The number of lepidotrichia varies considerably within every species, although the range and mean number of rays differs significantly between some species (Table 3). *Ageneiosus atronasus* has the shortest anal fin (23-30 rays), and *A. ucayalensis* has the longest (41-50 rays). The ranges of rays in the remaining species overlap widely; thus, anal-fin ray counts must be used in combination with other morphological characteristics to separate these species.

Lundberg (1982) concluded from a survey of the literature that the most common anal fin-ray counts among catfishes fall in a range between 16 and 20, and this range is presumably primitive. Elongation of the fin, therefore, is a derived condition, albeit unquestionably acquired independently in a moderate number of unrelated taxa. Britski (1972) gave a range of anal-fin rays for ageneiosids, several auchenipterid genera, and doradids. From those data, Ferraris (1988) concluded that elongation of the anal fin was a synapomorphy of his Auchenipterinae, although homoplasious within the Doradoidea. However, he considered elongation of the anal fin, "with at least 16 rays and usually more than 20" (Ferraris 1988:51) to be the derived condition. If the range presented by Lundberg (1982) is indeed primitive, then taxa with less than 20 rays cannot be considered derived. Among doradoids, this includes members of the Doradidae, Centromochlidae (*sensu* Ferraris 1988), *Pseudauchenipterus*, *Trachelyopterus*, *Asterophysus*, and *Entomocorus*, if the counts given by Britski (1972) are accurate. Given the variability and wide range of anal-fin rays among auchenipterids and ageneiosids, this character seems to be of limited use for determining intergeneric relationships. Taxa with relatively few rays are probably primitive for this character, but it appears that a parallel increase in the number of anal-fin rays may have occurred in several lineages. Even so, an increase

in rays probably represents a synapomorphy among species within any given ingroup, including *Ageneiosus*.

Ferraris (1988) found that the last four or five basal radials of the anal fin in *Auchenipterus* have enlarged lamina on their ventral processes. Other doradoids lack such laminar structures, although *Ageneiosus* has weak lamina, representing a somewhat intermediate condition between *Auchenipterus* and other doradoids, including *Tetranematichthys* (Fig. 28). This character state supports Ferraris' (1988) hypothesis suggesting a close relationship between ageneiosids and *Auchenipterus*.

The first pterygiophore typically has one or two very short splints of bone and one large lepidotrichium. Likewise, the last pterygiophore of the fin typically supports two branched lepidotrichia, but may support from one to three. In this study, all elements, regardless of size, were counted from radiographs or skeletal preparations. Often the very small splints of bone associated with the anterior and posteriormost pterygiophores cannot be observed externally, and their inclusion in anal fin-ray counts is undesirable. In ageneiosids and auchenipterids with long anal fins, future studies should include counts of anal-fin pterygiophores in order to allow for uniform comparisons.

Ageneiosids, as well as all auchenipterids for which there are available data, have unique sexual dimorphism involving a portion or all of the anal fin. The most unusual morphology is found in the Centromochlidae (*sensu* Ferraris 1988), but a review of the details of anal-fin structure in that group and other auchenipterids is beyond the scope of this study. Ferraris (1988) used the structure of the anal fin extensively in his phylogenetic analysis, particularly involving the Centromochlidae. Unfortunately, however, there is no information available for many other auchenipterid taxa. Previous literature was reviewed by Vari et al. (1984) and Ferraris (1988).

The nature of sexual dimorphism of the anal fin in ageneiosids involves only the anteriormost portion of the fin, including the third through about the seventh or

Fig. 28.—Lateral view of left side of posterior pterygiophores and lepidotrichia of anal fin. (A) *Auchenipterus nuchalis* (UF 44927); (B) *Ageneiosus* n. sp. (MG 27153); (C) *Tetranematoichthys quadrifilis* (MCNG 6334). Scale in all = 2 mm.

Fig. 29. – Lateral view of left side of anterior pterygiophores and lepidotrichia of gonopodium in nuptial male *Ageneiosus* n. sp. (MG 27153). Scale = 5 mm.

eighth lepidotrichia. In prereproductive males, the lepidotrichia become thicker and elongated, and are closely apposed (Fig. 29). There is negligible to slight thickening of the corresponding pterygiophores, but the normally cartilaginous distal radials become large, ossified nodules. The urogenital pore migrates from its usual position at the base of the fin to the distal tip of the coalesced rays, the entire structure therefore being transformed into an intromittent organ, or gonopodium. Among ageneiosid species there is little variation in osteology of the gonopodium. Development of the gonopodium is subject to seasonality, as discussed below in greater detail.

Caudal Skeleton

Early descriptions of ageneiosids generally mentioned few details about the caudal fin; comments about the tail were usually limited to descriptions of the general shape or coloration of the fin. Some authors gave ray counts, presumably of branched lepidotrichia. From these accounts, no generalizations could be made about osteology of the ageneiosid caudal skeleton.

Lundberg and Baskin (1969) examined caudal skeleton morphology in a variety of catfishes, but included *A. pardalis* (AMNH 11395) as their only representative ageneiosid. While providing valuable data for interfamilial comparisons, Lundberg and Baskin's (1969) study failed to adequately characterize the hypural morphology of ageneiosids. Three major features of the siluroid caudal skeleton were examined by these authors; the degree of fusion of the hypural elements, evolutionary development of the hypurapophysis, and the number of principal rays. Data on the first two characters were presented that compared a large number of taxa, and the authors provided evidence of possible relationships and general phyletic trends based on these characters. With regard to the number of rays, Lundberg and Baskin (1969) admitted that many studies, including theirs,

consider the principal rays to comprise one plus the number of branched rays in each lobe. However, ontogenetic variation in the branching of caudal rays, first recognized in *Noturus* by Taylor (1969), and discussed in greater detail by Lundberg and Baskin (1969) for other groups, prompted the latter authors to propose that the number of lepidotrichia impinging on the primary hypural plates or muscle insertions might provide more reliable comparative data among taxa. Arratia (1987, partially based on earlier studies) found that procurrent rays became progressively segmented during ontogeny in *Nematogenys*, and she suggested that comparisons of segmented, unbranched caudal rays in young and adults could provide valuable information for inferring phylogenetic relationships among siluroids. Despite suggestions of the above authors, most recent studies have included caudal fin-ray counts based on branched rays in adults.

The ageneiosid caudal skeleton has the parhypural fused with the lower plate, formed by the coalesced first and second hypurals (Fig. 30). The hemal spine of the second preural typically has a laminar anterior keel along its proximal two-thirds. The upper hypural plate consists of fused third and fourth hypurals. The fifth hypural is separate from the remaining elements, but is closely adjoined to the upper hypural plate, formed by fused third and fourth hypurals. The thin, rod-like uroneural closely abuts the dorsoanterior margin of the fifth hypural. A second ural centrum is not evident in adults. There is a single epural. The uppermost principal ray articulates basally with the top edge of the fifth hypural. In forked-tailed species, the lowermost principal ray crosses the bottom edge of the fused first hypural and articulates basally with the hemal spine of the second preural; in emarginate-tailed species, the lower principal ray subtends the first hypural and impinges directly on the second preural hemal spine.

In immature specimens, the plates formed by the fused first plus second and third plus fourth hypurals often have an ovoid, incompletely ossified, partially cartilaginous area near the center. In larger specimens these areas are replaced by

Fig. 30.—Lateral view of left side of caudal skeleton. (A) *Ageneiosus brevifilis* (UMMZ 207464); (B) *A. ucayalensis* (USNM 265691); (C) *A. vittatus* (UF uncat.). Scale: A = 10 mm; B-C = 2 mm.

extremely porous ossifications. These weakly ossified areas may have a hemopoietic function, but their cytology has not been studied. The porous nature of the caudal skeleton, in combination with cancellous neurocranial bones, is unique to ageneiosids among doradoids.

The above fusion pattern corresponds to the PH+1+2;3+4;5 designation of Lundberg and Baskin (1969). They found that *A. pardalis* shares the same hypural fusion pattern as all auchenipterids studied (eight species in five genera), *Doras*, two species of mochokids, and several pimelodids. Phylogenetic comparisons based on hypural fusion patterns are confounded by ontogenetic changes, intraspecific variation, and homoplasies among the taxa studied by Lundberg and Baskin (1969). Despite these problems, any given fusion pattern is often characteristic of taxa at the species, genus, or even family level. This is the case in ageneiosids, all species of which have an identical fusion pattern (and this pattern may be indicative of relationships at a higher level of universality).

In very large individuals there are laminar ossifications between the uroneural and fifth hypural, and on the anterior vertical edges of the last few hemal spines; this condition reaches an extreme in *A. brevifilis*, large specimens of which have the entire caudal skeleton heavily ossified, with lamina between the hypural elements and the last four or five hemal spines (Fig. 30a). Increased laminar ossifications are partially correlated with large body size, as well as number of fin rays. Ferraris (1988) observed thickened hemal spines of preural vertebrae in several genera of auchenipterids, all of which have emarginate or truncate caudal fins. The presence of expanded posterior hemal spines is correlated with an emarginate or truncate caudal fin, and is related to support of the lower principal fin rays. In taxa with a tail of this shape, there are ten principal rays in the lower lobe of the fin, compared to nine rays in fork-tailed species. A combination of one additional lower principal ray and an oblique shape has led to an anterior shift in

procurrent rays, and increased osteological support contributed by the distal tips of the last few preural hemal spines.

All ageneiosids except *A. brevifilis*, *A. marmoratus*, *A. polystictus*, and *Tetranematicthys* have a forked tail with sharply pointed, symmetrical lobes. *Ageneiosus polystictus* has the same principal fin-ray count (8 + 9) as the sharply pointed, fork-tailed species, but the fin lobes of this species are broadly rounded, the fin thus appearing moderately emarginate. A forked tail is primitive for catfishes in general (Lundberg and Baskin 1969), so the exceptions listed above are derived with respect to tail morphology. However, an emarginate or truncate tail has evolved independently in many catfishes, so this character state must be interpreted with caution. This is especially true of ageneiosids and auchenipterids. Ferraris (1988) listed several genera of auchenipterids with truncate caudal fins, and he identified, correctly, the homoplasious nature of its occurrence. Among ageneiosids, I consider the presence of a truncate caudal fin to have been independently derived in *Tetranematicthys* and *A. brevifilis*. However, I interpret it as a synapomorphy of *A. brevifilis* and *A. marmoratus*, if in fact these two taxa are distinct from one another (see comments under species account of *A. marmoratus*).

Lundberg and Baskin (1969) classified ageneiosids as having a type "B" hypurapophysis, in which the two hypurapophyses fuse to form a horizontal shelf that extends onto the first hypural. To the contrary, most of the specimens that I have examined have the type "C" condition, in which the hypurapophysial shelf extends onto the second hypural. In some species (e.g., *A. ucayalensis*), the degree to which the hypurapophysial shelf extends posteriorly increases during growth, so that in small specimens it appears to end before the second hypural plate, but in larger specimens it extends toward the distal margin of the second hypural. I have not examined the material of *A. pardalis* on which Lundberg and Baskin (1969) based their conclusion, but it is probable that they had an aberrant or juvenile specimen with an incompletely developed hypurapophysial shelf. The type "C"

condition is widespread among many unrelated catfish lineages (Lundberg and Baskin 1969); thus, its occurrence in ageneiosids is convergent.

Coloration of the caudal fin is of considerable use in identifying species of *Ageneiosus*, in spite of extensive intraspecific variation in body and fin coloration. Typically, the distal margin of the tail is black in *A. brevifilis* and the large bodied, fork-tailed species (*A. pardalis*, *A. ucayalensis*, *A. valenciennesi*, and *A. vittatus*). That is generally the extent of pigmentation in *A. brevifilis*, but in the other species there is usually a crescentic spot at the base of the upper lobe, and, occasionally, a similar spot at the base of the lower lobe. In *A. vittatus*, both spots are always prominent, and serve to identify this species. A separate apomorphic state is found in *A. atronasus*, in which the tail has a distinctive stripe in each lobe.

Sexual Dimorphism and Reproductive Biology

Undoubtedly the most unusual and least understood aspect of ageneiosid morphology and ecology concerns their unique reproduction. Together with the Auchenipteridae, these catfishes exhibit, during their reproductive periods, pronounced sexual dimorphism of the head, barbels, and dorsal and anal fins. The seasonal development of nuptial structures in males is correlated with a unique mechanism of internal fertilization in the various taxa involved, discussed below in greater detail. A few early authors made cursory remarks about sexual dimorphism, but it is clear from the literature that many investigators failed to recognize or understand the significance of these dimorphic characters. Consequently, some descriptions were based on diagnoses involving differences in the characters listed above, and thus resulted in species names that are synonyms of previously described taxa. Such descriptions probably resulted from inadequate series of sexually dimorphic specimens available to the various authors. In the following discussion, a brief review of references to sexual dimorphism is presented first, followed by

analysis of the morphological and functional aspects of the characters themselves, and concludes with comments on the systematic significance of dimorphic characters. A proportionally large amount of attention to the reproductive biology is given here, resulting from a combination of the systematic implications and the inherently interesting aspect of this feature of ageneiosids and auchenipterids.

Kner (1858a) dealt briefly with the taxonomic problems associated with sexual dimorphism in his account of *A. brevifilis*, and he illustrated or described aspects of the reproductive system in *A. valenciennesi* and a variety of other neotropical catfishes. However, Kner's discussion of the reproductive anatomy in *Ageneiosus* is highly problematic. In his account of *A. brevifilis*, he cited comments by Valenciennes (Cuvier and Valenciennes 1840:239) and unpublished notes of Natterer, which suggested that *A. inermis* Lacepède and *A. brevifilis* Valenciennes possibly represented females of *A. militaris* Bloch. Kner dispensed with this idea, by arguing that the opinions of Valenciennes and Natterer about sexual dimorphism were based on conjecture of local fishermen; he refuted the notion of possible sexual dimorphism by stating that his specimens did not differ externally, despite the fact that he had specimens of both sexes. It is not likely that Kner (1858a) misidentified the sexes, inasmuch as he illustrated and discussed gross dimorphism of the gonads in a number of catfish species, including a brief description at the end of his account of *A. brevifilis*. Based on his conclusions and description of the gonads, it seems likely that Kner (1858a) had only nonreproductive individuals available to him, and thus he erroneously assumed that sexual dimorphism does not occur in *A. brevifilis*. The fact that Kner failed to appreciate seasonality of reproductive dimorphism is further evident from his account of *A. militaris* Valenciennes (= *A. valenciennesi* Bleeker, although he wrongly synonymized this species with *Silurus militaris* Bloch). In that account, Kner described in detail the external nuptial structures in males, but he equated the sexual dimorphism of males with a taxonomic difference. The most enigmatic part of Kner's (1858a) treatment

of ageneiosids is his description and illustration of the gonads in *A. militaris* (= *A. valenciennesi*). In that account, he described the internal anatomy as consisting of an encapsulated swimbladder, the kidney, a long duct leading to the urinary bladder, and an unpaired medial organ filled internally with granular material, which Kner called the ovary. His identification of the kidney and urinary bladder appears to have been correct, based on the accompanying illustration (Kner 1858a; plate 9, fig. 27b). However, identification of the organ that he called an ovary is uncertain. The structure appears as a single, large sac, and resembles an ovary. The fact that Kner (1858a) referred to it as unpaired is especially puzzling, since the ovaries of ageneiosids are paired except near their posterior end. Furthermore, Kner (1858a) described the ovaries and the testes in *A. brevifilis* as unpaired, so he was familiar with the normal, nonreproductive appearance of both gonads. Moreover, his description of *A. militaris* is apparently based entirely on nuptial males, which, had Kner examined them internally, would have been found to have enormously swollen, lobulated testes. I believe that one of the following two possibilities is the most likely explanation to account for the discrepancies in Kner's (1858a) descriptions. First, the illustration of the reproductive system may have been based on a female, and the structure identified by Kner was indeed an ovary, with perhaps the other ovary being missing. This possibility conflicts with Kner's belief that the name *A. militaris* applied only to those specimens with the external dimorphic structures of nuptial males. The second possibility is that Kner may have mistaken the posterior segment of the testes as an ovary. In nuptial males, the posterior segment is unpaired, medial, and becomes swollen, thus superficially resembling an ovary. However, the anterior lobes of the testes also become greatly swollen, and it seems unlikely that Kner would have overlooked these. Kner apparently based his description of the reproductive system on a single specimen that had been preserved for some time in the Kaiserliche Museum. One is left to speculate that, perhaps, if that specimen was a nuptial male, the anterior lobes of the testes had been damaged

or removed prior to Kner's study of it. In spite of the problems with Kner's ageneiosid accounts, his study was a significant contribution, inasmuch as it was the first to provide detailed gross descriptions of the gonads.

Bleeker (1864) also recognized taxonomic problems associated with sexual dimorphism in ageneiosids, but, like Kner, he failed to interpret correctly the nature of these differences. Based on a large nuptial male that he considered to belong to the same species as figured by Bloch (1794: pl. 362, i.e., *Silurus militaris*), Bleeker (1864:82) suggested that *A. militaris* Valenciennes differed in details of the dorsal spine and maxillary barbels, and represented a separate species, for which he proposed the name *A. valenciennesi*. Subsequently, Bleeker (1864:83) stated that the development of hooks on the barbels and spines was apparently a character present only in male *Ageneiosus*, and he suggested that Castelnau (1855) based his description of *A. ucayalensis* on females of *A. militaris* (from his text it is unclear whether Bleeker was referring to *A. militaris* Valenciennes or *S. militaris* Bloch). By apparently adopting the conclusion of Kner, Bleeker (1864) proposed as new the genus *Pseudogeneiosus* for the putative "form" lacking ossified, serrated barbels (see section on status of *Pseudogeneiosus*).

Eigenmann and Bean (1907) also recognized sexual differences in *Ageneiosus*. They concluded that the name *A. valenciennesi* Bleeker was based on male specimens that represented conspecifics of females of *A. ucayalensis* Castelnau. It is unclear whether they based their conclusion in part on the paper by Bleeker (1864), but judging from their synonymy it appears that Eigenmann and Bean (1907) failed to understand a taxonomic distinction of the taxa involved. They clearly indicated salient dimorphic characters of *A. ucayalensis*, but in their synonymy they included names that I place in the synonymies of two different allopatric species. Like previous authors, Eigenmann and Bean (1907) noted sexual differences in the maxillary barbels and dorsal spine, but they also commented on

dimorphism between the sexes involving the dorsal profile of the head, size of the eye, and pigmentation of the caudal fin.

The above references are the principal studies that addressed, to any significant extent, sexually dimorphic characters in species of ageneiosids. In addition to the above sources, a few other early studies included remarks about sexual dimorphism in various auchenipterids, as summarized by Vari et al. (1984) and Ferraris (1988).

The first paper that explicitly implicated the functional significance of sexually dimorphic characters in a doradoid catfish was that of Ihering (1937). Therein, he described the gross morphology, gametogenesis, and internal fertilization of the auchenipterid *Trachycorystes striatulus* (= *Trachelyopterus striatulus*, possibly synonymous with *T. galeatus* according to Ferraris 1988). Ihering gave a relatively detailed account of the gross anatomy of the gonad of both sexes, and described the general appearance of the gametes in ripe individuals. He did not observe courtship or copulation behavior, but Ihering provided evidence of internal fertilization in this species on the basis of the unique anal fin and testes morphology in males, and direct observation of spermatozoa suspended in a gelatinous plug within the oviducts of gravid females. Females apparently retain sperm within their reproductive tracts for at least four months, and fertilization was believed to occur at the time of oviposition. Ihering briefly summarized previous classification schemes of various auchenipterids, and, based on observations of a "pseudopenis" in some and speculation of its occurrence in others, divided the family into two subfamilies on the presumed presence or absence of "oviducal" (internal) fertilization in the group; he further suggested that no less than 30 species (in his subfamily Trachycoristinae) probably had internal fertilization.

Ihering's (1937) study went largely unnoticed until the work of Miranda-Ribeiro (1968a, 1968b), who provided additional illustrations of external, sexually dimorphic characters in several species. Miranda-Ribeiro presented no additional

information about behavior or the actual mechanism of internal fertilization in these fishes. Rather, he summarized in detail the prior classifications of various authors, and provided a novel arrangement of twelve genera of ageneiosids and auchenipterids into five families, two of which were new (Centromochlidae and Asterophysidae). The main contribution of Miranda-Ribeiro's (1968b) work was his recognition of the fact that sexual dimorphism represents a character that suggests a relationship between auchenipterids and ageneiosids. He further indicated that the classification proposed by Ihering (1937) was impractical, since it necessitated confirmation of a mode of reproduction (i.e., internal versus external fertilization) to accurately determine taxonomic placement.

Britski (1972) gave additional information about sexual dimorphism in various auchenipterid and ageneiosid genera. He examined the gross morphology of external characters and the testes of many taxa, and speculated on the functional significance of sexually dimorphic structures. Britski found what he considered to be taxonomic differences in these characters, and included them in a hypothesis of relationships of the auchenipterid and ageneiosid genera. He designated taxa as having "incomplete" or "complete" sexual dimorphism, based on whether only a partial or entire complement of dimorphism was observed involving the dorsal and anal fins and barbels. Britski's was the first study to include extensive comparisons of sexually dimorphic characters, in combination with many other morphological features, in a broad attempt to elucidate relationships among auchenipterids and ageneiosids. Nevertheless, a relatively limited amount of large series and/or seasonally collected material of some species was examined, at least in terms of providing unequivocal data on the presence or absence and detailed nature of sexual dimorphism in nuptial males.

In addition to the aforementioned studies, more recent descriptions of species in three auchenipterid genera (*Entomocorus*, *Epapterus*, and *Trachelyopterichthys*) were accompanied by morphological information and limited

taxonomic comparisons of sexually dimorphic characters (Mago-Leccia 1983, Vari et al. 1984, Ferraris and Fernandez 1987).

Ferraris (1988) discussed extensively the distribution of sexually dimorphic structures, and their implication in the systematics of doradoids. His study is the most comprehensive to date, in terms of providing information for a large number of species, and he considered the available information in a phylogenetic study of relationships among the included taxa. Detailed information was presented on the external appearance and the osteology of the barbels and dorsal and anal fins among a variety of taxa. A most unusual modification of the anal fin in *Centromochlus* and allied genera led Ferraris to re-elevate that clade to separate family status. While recognizing the tremendously informative value of sexually dimorphic structures in evaluating relationships of these catfishes, Ferraris recognized the limitations of inferring relationships based on the current state of knowledge. His implication was that mature males of many taxa are needed before phylogenetic relationships can be further resolved.

Nearly all of the information about sexual dimorphism provided in the above references is limited to gross morphological descriptions, including some osteological features, especially of the anal fin. Very little has been published concerning the soft anatomy or functional morphology of dimorphic structures, or the reproductive behavior and ecology of these fishes. Aside from Ihering's (1937) observations, the only other published studies in which the activity of live animals was observed, in both cases made by amateur aquarists, were those of Burgess (1982) on *Trachycorystes insignis* (= *Trachelyopterus galeatus*, fide Ferraris 1988), and Köpke (1986) on *Ageneiosus vittatus*. Both recorded and photographed copulatory behavior, thus apparently confirming all previous speculation of internal fertilization in these fishes. Burgess reported that females of *T. galeatus* laid fertilized eggs 2-4 weeks after spawning, but Köpke did not observe oviposition in *A. vittatus*. In addition to these observations, Ferraris (1988) and Curran (1989) made cursory

remarks that they or associates had observed spawning in *Ageneiosus* sp. and *Auchenipterichthys*, respectively, but neither author gave details about the behavioral events following spawning.

Unfortunately, as evident from a paucity of detailed information available in the above studies, our knowledge of the reproductive biology of these fishes is extremely limited. At present, gross morphological descriptions of sexually dimorphic structures are the only available criteria for systematic comparisons. In spite of the lack of information about these structures in many taxa, however, they appear to have considerable potential for future analysis. In addition, studies of the ecology and behavior of these fishes will undoubtedly have implications in future taxonomic studies.

External Sexual Dimorphism of the Ageneiosidae

External dimorphism in ageneiosids involves seasonal modifications in males of the maxillary barbels, the nuchal region, the dorsal fin, the anal fin, and possibly pigmentary differences. The morphological details of these differences are presented in the anatomical descriptions given above, and are only briefly reviewed here.

During the height of the breeding period, the maxillary barbels of males become stiffened and elongated, relative to their size during immaturity or reproductive inactivity. Enlargement of the maxillary barbel is due to hyperossification of the maxilla, which extends from its normal basal position above the upper lip, as a single, long bony projection into the core of the barbel (Fig. 16). The surface of the barbel retains its epidermal integrity, confluent with the skin on the surface of the upper lip. In breeding male *Ageneiosus*, the barbels develop a variable number of irregular, sharp, recurved odontodes along the dorsomedial and dorsolateral margin (Fig. 16). In *Tetranematichthys* and a number of auchenipterids,

the barbels are much longer and lack any sharp recurved odontodes, although they may be rugose or weakly tuberculate on their dorsal margin.

The dorsal fin of nuptial males is curved and much longer than in females or nonbreeding males, and is armed along its anterior margin with numerous sharp odontodes (Fig. 23). The anterior part of the base of the fin is swollen, and the spine can be thrust and locked in position above the head. The nuchal region in nuptial males is also enlarged, and has a much more acute angle behind the supraoccipital than is present in females or nonbreeding males. The swollen appearance of the nape is apparently due to osteological changes (Ferraris 1988), as well as an increase in the mass of the musculature encircling the base of the dorsal fin (personal observation).

The anal fin is modified into an intromittent organ, formed from thickened and elongated anterior rays, and displacement of the gonopore to the distal tip of the swollen rays (Figs. 29, 31). The interradi al membranes and the inclin ator and erector muscles surrounding the gonopodium are enlarged.

The sexual dimorphism exhibited by ageneiosids is paralleled by dimorphism in a number of auchenipterids. There are significant morphological differences among the various genera for which there are available data (Ferraris 1988). Nevertheless, from the nature of these differences and the observations and photographs published in Burgess (1982) and Köpke (1986), it appears that males use the barbels and dorsal fin spine to court and manipulate females, accompanied by spawning or copulation, in which the gonopodium is either closely apposed or inserted into the gonopore of the female.

Gonad Anatomy of the Ageneiosidae

There has been no previous study of the soft anatomy of the reproductive system in any of the sexually dimorphic doradoids. Ihering (1937) examined the

Fig. 31. – Sexual dimorphism of the anal fin and external genitalia of *Tetranematichthys quadrifilis* (ANSP 135821). Above: female, 164 mm SL. Below: nuptial male, 130 mm SL. Gonopore indicated by solid arrow. Scale = 10 mm.

Fig. 32.—Cytological detail of the gonad of reproductive ageneiosids. Left: testis of nuptial male *Ageneiosus ucayalensis* (MHNG 2394.36; 218 mm SL), showing spermatogonia and other spermatogenic stages (see Table 2 for abbreviations). Right: post-copulatory female *A. atronatus* (MZUSP uncat.; 112 mm SL), with spermatogonia (dark mass at center right) lodged between thecae of vitellogenic oocytes. Magnification = 400 X.

gross morphology of the gonads, and removed and studied sperm from the genital tracts of female *Trachycorystes insignis* (= *Trachelyopterus galeatus*). Other than his study, and general descriptions of the gonads, eggs, and developing embryos provided by Burgess (1982) and Köpke (1986), there has been no information published about the gonads and gametes.

I have examined, using scanning electron microscopy and histological preparations, the gonads of several species of ageneiosids and a few nonreproductive achenipterids, and provide the following descriptions. This is the result of an ancillary study of gametogenesis in ageneiosids and achenipterids, and does not purvey any systematic information at present. However, there is hope that future studies of these fishes will include descriptions of the soft anatomy of their reproductive systems, since there are likely to be some significant taxonomic differences.

In gross appearance, the testes of ageneiosids are paired, lobulated organs, similar in general appearance to the testes of many other catfishes (Roberts 1989b). Like ictalurids and several other families, the testes consist of at least two distinctive regions: anterior, lobulated portions, in which spermatogenesis occurs in cysts of synchronously developing germ cells, and a single posterior putatively secretory portion (Sneed and Clemens 1963). The testes are invested by a mesenteric connection to the dorsal coelomic peritoneum and lie immediately ventral to the kidneys. The unpaired section of the testes extends posteriorly as the urogenital duct, where it exits near the base of the anal fin, or, in nuptial males, at the terminus of the gonopodium.

Cytological composition of the spermatogenic portion of the ageneiosid testis is unlike that of any other catfishes that I have examined (mostly ictalurids). Cysts containing germ cells in synchronous stages of development are similar to those of other non-atherinomorph teleosts (Grier 1981). The main difference is in the arrangement of the spermatozoa, which are oriented parallel to each other and form

tightly bound clusters (Fig. 32). These bundles of spermatozoa are similar to the spermatozeugmata or spermatophores described in a number of internally fertilizing teleosts (reviewed by Grier 1981). The distinction between spermatophores and spermatozeugmata requires study of encapsulating secretory products and the association of sperm with Sertoli cells; I have not examined the sperm morphology in sufficient detail to resolve the exact nature of the sperm bundles (to adequately do so requires transmission electron microscopy). However, I have observed the outwardly projecting sperm heads that are characteristic of spermatozeugmata (Grier 1981), and thus I tentatively identify ageneiosid sperm bundles as this type. Each spermatozoan has a round nucleus, a short midpiece, and a very long flagellum. Grier et al. (1990) briefly discussed previous generalizations that the midpiece and/or sperm nucleus of viviparous teleosts are elongated. However, Grier and his associates (1981, 1990) found that elongation of the midpiece is not always present in viviparous species (for the purpose of comparing sperm morphology I do not distinguish between ovoviviparity and viviparity [Wourms 1981]). Ageneiosids provide an additional exception to the generalization that internal fertilization in teleosts is coupled with an elongation of the anterior region of the spermatozoan.

I have been unable to adequately study the structure of the posterior region of the ageneiosid testis. In ictalurids, the cells of the posterior region are predominately columnar in appearance (Sneed and Clemens 1963), and they are known to be involved in steroid secretion (Rosenblum et al. 1987). Spermatogenesis does not occur in this region. The caudal testicular region of ageneiosids is superficially similar to that of ictalurids. In breeding males, the entire posterior region becomes greatly enlarged, forming a cylindrical tube. In one histological preparation, the lumen was extensive and filled with spermatozoa suspended in an amorphous substance. Possibly, the enlarged posterior region of the testes secretes a mucoid plug, as suggested by Ihering (1937). It may also be

involved in endocrine functions, but further studies are needed to confirm such a hypothesis. Rosenblum et al. (1987) reported that germ cells were never present in the caudal testicular region of *Ictalurus nebulosus*, in contrast to the condition I have observed in ageneiosids. Roberts (1989b) has suggested that there is a dire need for more studies to elucidate variation of testes morphology among groups of catfishes; this is especially true for the caudal testicular region.

The ovaries of ageneiosids are smooth-walled, elongate sacs suspended from the dorsal ceiling of the body cavity, just ventral to the kidneys. They are fused at their posterior end. In immature fish the ovaries are small and do not reach the anterior end of the kidney. Posteriorly, the urogenital duct is membranously joined by the urinary duct before exiting the body anterior to the anal-fin origin. The gonopore is deeply invaginated. There is no putative sperm storage structure associated with the female reproductive tract.

In gravid females the ovaries are greatly swollen and fill a large portion of the coelom. They extend anterior to the kidneys and the posterior apex of the stomach. Internally, the germ cells line an expanded lumen. In gross appearance, oocytes of many size classes are visible, including small white ones, and very large, vitellogenic eggs. In some specimens examined, ovulation had occurred prior to fixation, and the vitellogenic oocytes loosely filled the ovarian lumen.

Histologically, the ovaries of immature females resemble those of other catfishes, with randomly distributed oogonia and primary oocytes in a continuum of size classes. The ovaries of gravid females consist of small, nonrecrudescent oocytes, and many large, vitellogenic and yolk vesicle oocytes (terminology after Wallace and Selman 1981). The extremely large, yolk-laden follicles are difficult to infiltrate and section with paraffin-based histological techniques, but the procedures used in this study did allow for some crude preparations. In gravid females, spermatzeugmata were observed in the interstices between vitellogenic follicles (Fig. 32). In terms of their shape, the spermatzeugmata appeared unchanged from

their structure while in the testis, suggesting that they may be bound by an encapsulating layer.

Based on cytology of the gonads, I speculate that fertilization in ageneiosids occurs near the time of ovulation. The spermatozeugmata are probably retained in the ovary for an extended period, since oviposition may not occur for several weeks after insemination (Burgess 1982, Köpke 1986). Studies of the gonad morphology and reproductive behavior are needed to confirm this speculation.

Evolutionary Significance of Internal Fertilization in the Ageneiosidae

Possible selective factors that have led to the evolution of sexual dimorphism and internal fertilization in ageneiosids and auchenipterids remain unknown, in the absence of meaningful ecological data. A fair amount of attention has been given to a general correlation between migratory patterns of tropical fishes and seasonal rainfall patterns (e.g., Lowe-McConnell 1987, Smith 1981, Goulding 1980). Roberts (1989b) speculated that many tropical freshwater fishes may in fact have prolonged reproduction, and he suggested that generalizations about reproductive life-history patterns may have to be considerably modified and revised as more ecological data are obtained. Roberts specifically stated that discussions of reproductive seasonality in tropical freshwater fishes should be avoided, since in many cases there is no clear correlation with seasonal ecological or climatological phenomena; he speculated that other factors, such as food or mate availability, may be the proximate factors responsible for the evolution of unique reproductive patterns in tropical fishes. With respect to auchenipterids, Roberts (1989b) further remarked that internal fertilization could allow for temporal and spatial separation of mating and spawning, potentially leading to a more prolonged reproductive period. He stated that internal fertilization may be more widespread in catfishes than is presently known.

Britski (1972) and Ferraris (1988) implied that dimorphism of the anal fin and the barbels is characteristic of maturity, at least in some auchenipterid taxa. In ageneiosids there is a definite seasonal, albeit prolonged, elaboration of sexually dimorphic structures, as discussed by Britski (1972). During latent reproductive periods, mature males have unmodified barbels and dorsal and anal fins, and resemble females and immature males. I suspect that this is also true of at least some auchenipterids. In the species of ageneiosids that I have examined, males are in prenuptial or nuptial condition for a relatively extended period, ranging approximately four to six months, and roughly corresponding to the middle or end of low rainfall periods. Notwithstanding the objections of Roberts (1989b) in applying a concept of seasonality to the reproduction of tropical fishes, it appears to me, from the available evidence, that male ageneiosids are reproductively inactive during a significant and predictable time of the year. Nevertheless, the ability of females to retain sperm in their reproductive tracts for an extended period after insemination supports Robert's (1989b) hypothesis that there may be temporal separation of mating and oviposition. Perhaps, females ovulate and oviposit fertilized eggs when ecological conditions (e.g., food availability, reduced abundance of predators, etc.) favor maximal survival of propagules, but, until ecological studies are done, such predictions remain strictly conjectural.

Britski (1972) and Ferraris (1988) considered sexual dimorphism to be one of the *prima facie* characters supporting a hypothesis that auchenipterids and ageneiosids share a common ancestry. I agree fully with this conclusion. There is currently no evidence to support speculation by Roberts (1989b) that internal fertilization may be widespread among catfishes. In fact, of the over 2000 species of catfishes worldwide, internal fertilization has only been demonstrated in the ageneiosids and auchenipterids. Furthermore, the sexual dimorphism exhibited by these taxa is unparalleled among siluriforms (many others have additional forms of sexual dimorphism, but in no case is there development of a gonopodium or similar

tubular sperm conduit associated with the anal fin). Among all ostariophysans, which comprise about 72% of the world's freshwater fishes, internal fertilization has only been demonstrated in one other group, the so-called glandulocaudine characins (Weitzman and Fink 1985), despite the independent evolution of internal fertilization in many other teleost lineages (Gross and Shine 1981). Thus, there is no evidence to suggest that this phenomenon arose independently in auchenipterids and ageneiosids.

The reproductive biology of ageneiosids and auchenipterids has been grossly neglected in the past. Given the unique morphology of these fishes and their unusual reproductive biology, future studies will be extremely valuable in providing information about their systematics, and about the evolution of reproductive life-history patterns in neotropical fishes.

PHYLOGENETIC RELATIONSHIPS

The purpose of the present study is to resolve the taxonomy of the species that have hitherto been classified in the family Ageneiosidae, and to propose a provisional cladistic hypothesis of relationships among these species. At the onset of this study, it became apparent that there are significant taxonomic problems at the generic and familial levels involving ageneiosids and several other larger groups of catfishes, and that these problems could not be ignored if a revision of the Ageneiosidae were to be adequately accomplished. I have not personally attempted to analyze any of the more significant higher-level problems that exist, nor have I examined a large number of species in outgroups or sister taxa. Rather, I have relied on published data that are available, many of which are anecdotal or limited in scope to relatively few taxa. Additionally, I have relied on some other more extensive unpublished sources for anatomical and systematic information. Fortunately, there has been a very recent surge of interest in catfish systematics, as evidenced by an increase in the number of published papers, but we are only beginning to unravel the myriad of systematic complexity of this remarkable order. Attention to the neotropical doradoids has been relatively limited in the past, but the following people have recently completed graduate degrees based on systematic studies of various subgroups: Carl J. Ferraris (AMNH; auchenipterid relationships); Daniel J. Curran (UCLA; auchenipterid relationships); Horacio Higuchi (MCZ; doradid subgroups); and, Roberto Royero (MBUCV); dorsal fin of siluroids). In addition to these individuals, I must mention Heraldo Britski (MZUSP), whose unpublished doctoral dissertation was a result of the first comprehensive study of

the neotropical doradoids (Britski 1972). I have not examined Higuchi's dissertation, but the remaining studies have been used extensively in my character analysis and inferences about higher systematic relationships. Statements of relationships outside of the Ageneiosidae are based principally on these and other studies, and I make no attempt to provide additional hypotheses of interfamilial relationships. However, in the following discussion, I do provided some of my objections or disagreements to certain conclusions of the above authors, based on conflicting information or personal observations.

Suprafamilial Relationships of Doradoid Catfishes

As summarized in the introduction, there has been a long history of studies that have suggested a taxonomic relationship between the Doradidae, Auchenipteridae, and Ageneiosidae. Early classifications were largely typological, and often excluded related taxa from this assemblage, or included members of other unrelated families. Regan (1911) studied the osteology of a diversity of siluroids, and was the first to propose relationships based at least in part on putatively derived structures. His interpretation of primitive versus derived characters was questionable in certain cases, however, and some of his family designations were more inclusive than presently recognized. Regan placed all neotropical doradoids known at the time into one family, the Doradidae, but he arranged the various genera in a taxonomic key roughly corresponding to the presently delimited families. In spite of the shortcomings of Regan's monograph, his study was a template on which most subsequent classifications of siluroids were based.

As diagnosed by Regan (1911), neotropical doradoids share a number of characters that, in combination, separate them from nearly all other catfishes. The most important characters cited by Regan as defining for the doradoids were the

strong development of the epiotics (= epioccipitals) at the rear of the skull, with expanded posterior processes; the presence of an elastic spring apparatus; absence of nasal barbels; absence of a mesocoracoid; fusion of seven or eight vertebrae in the complex centrum; and, associated modifications of the vertebral parapophyses and swimbladder (after Bridge and Haddon 1894). These characters, especially the first, have been repeated by nearly all subsequent authors when diagnosing the doradoid families.

Subsequent to Regan's classification, a number of authors, beginning with Chardon (1968), proposed relationships between several families based principally on the shared possession of an elastic spring apparatus (ESA; see anatomical description of the Weberian apparatus and axial skeleton). Chardon (1968) lumped the African family Mochokidae with the Doradidae, Auchenipteridae, and Ageneiosidae, into a large superfamily, the Doradoidea [sic]. As discussed in the introduction, and as has been used throughout this text, I follow Ferraris (1988) in restricting the superfamily name Doradoidea to include only the neotropical families.

Howes (1983: fig. 22) included the families Ariidae, Auchenipteridae, Doradidae, Mochokidae, Malapteruridae, and Pangasiidae into a single clade, based on the shared ESA and a relatively large, free swimbladder; he included ageneiosids in a lineage with loricariids and astroblepids, based on the shared presence of an encapsulated swimbladder. Howes' (1983) placement of the ageneiosids with the loricarioids is certainly the most extreme sister-group relationship that has ever been proposed for ageneiosids, although it is not clear that he was seriously suggesting such a relationship. In some other respects, Howes' (1983) cladogram is incongruent with certain widely accepted phylogenies; for example, he included the callichthyids in a separate lineage apart from the remaining loricarioids (see Baskin [1972] and Schaeffer [1987] for corroborative hypotheses of loricarioid

relationships). However, Howes based his cladogram on the degree of vertebral fusion, structure of the swimbladder, and the ESA, based primarily on data obtained from Chardon (1968), to demonstrate how misleading a phylogenetic hypothesis can be if based on relatively few weighted characters. In the case of each putatively derived character state, Howes (1983) was able to provide evidence that conflicted with some of the relationships suggested by his cladogram. In the case of taxa with an ESA, Howes noted that no other groups except the neotropical doradoids (although he erroneously excluded ageneiosids) had epioccipitals contacting the vertebral parapophyses. Howes (1983) repeated the suggestion made by Alexander (1964) that the ESA may have been independently derived in several lineages. Moreover, Howes presented evidence to support the idea that increased vertebral fusion and swimbladder encapsulation has occurred independently in two or more lineages. In spite of his detailed arguments, Howes (1983) was unable to provide any significant hypotheses of relationships outside of the Hypophthalmidae and Pimelodidae.

Convergence of an ESA suggested by Alexander (1964) and Howes (1983) was apparently not seriously considered by Royero (1987) and Curran (1989), both of whom invoked the presence of an ESA as a synapomorphy of some or all of the families listed at the beginning of the previous paragraph. Ferraris (1988) was more cautious in interpreting the taxonomic distribution of an ESA; he used it only to define doradids, auchenipterids, and ageneiosids, but he did not rule out the possibility that it may be synapomorphic at a higher level of generality.

As evident from the brief summary presented above, there has been undue emphasis on the ESA in uniting families of catfishes. The morphological diagnosis of the neotropical doradoids made by Regan (1911) still stands as the first definitive study to support a hypothesis that a lineage including the Doradidae, Auchenipteridae, and Ageneiosidae is monophyletic. In addition to the ESA, the

combination of other characters listed by Regan (1911) is unique to these three families (although, individually, several of the characters are plesiomorphic and/or homoplasious with respect to all other catfishes). Britski (1972) and Ferraris (1988) presented additional shared, derived characters that support monophyly of the neotropical doradoids.

Royero (1987) found four characters of the dorsal fin that further supports the idea that mochokids may be related to the neotropical doradoids. Ferraris (1988) also found some characters shared among these taxa, but he deferred suggesting a close phylogenetic relationship pending more detailed anatomical comparisons. I agree with the reservations expressed by Ferraris; the state of knowledge about possible relationships of all of the families listed above, excluding the neotropical doradoids, is insufficient at present to conclusively identify a sister group of the neotropical doradoids.

Relationships of neotropical doradoid families have been much less contested than relationships among the other families listed above. Most species of the Doradidae are highly distinctive and not easily mistaken for any other family. Numerous similarities between ageneiosids and auchenipterids have been used to suggest a relationship between them, especially their shared sexual dimorphism (see introduction and anatomical descriptions for additional details). The historically long distinction between ageneiosids and auchenipterids was challenged by Ferraris (1988), who felt that differences between these two families overshadowed similarities between the ageneiosids and a restricted clade within the Auchenipteridae, and he found that some auchenipterid genera are more distantly related to each other than one group is to ageneiosids, as discussed below.

Curran (1989) asserted that doradids and auchenipterids are sister taxa on the basis of five putative synapomorphies. He placed great weight on these shared character states in rejecting any consideration of ageneiosids as the closest relatives

of auchenipterids. The conclusions of Curran (1989) are highly problematic. Four of the characters that he used to unite auchenipterids with doradids are also present in ageneiosids: epioccipital bones contributing to the roof of the skull; ligamentous attachments of the ESA to the anterior wall of the swimbladder; presence of a postcleithral process (secondarily lost in most ageneiosids, but present in *Tetranematichtys* and *A. brevis*); and unique arrangement of the dorsal fin. The other synapomorphy cited by Curran was the presence of three nuchal plates; this condition is shared only by doradids and auchenipterids, but it may be primitive for doradoids, with ageneiosids having reduced the number of plates secondarily (see anatomical discussion of dorsal fin, and Royero [1987]). Curran's discussion of the last alleged synapomorphy, reduced neural spines and dorsal-fin proximal radials (= pterygiophores), is especially perplexing; he partly defined doradids and auchenipterids by this character, but he further split the character into two states that define separate lineages within the Auchenipteridae, one clade of which has expanded neural spines. In addition to the above problems, two of the three characters used by Curran (1989) to define monophyly of the Auchenipteridae are also shared with ageneiosids; a posterior process of the epioccipital, and a gonopodium, which he further divided into five character states. There are additional problems with some of the characters in Curran's (1989) analysis, lending me to question the credulity of his hypothesis of phylogenetic relationships among the auchenipterid genera.

Despite conflicts among conclusions of the above authors (e.g., Howes 1983 and Curran 1989), there is overwhelming evidence that the Auchenipteridae (*sensu lato*) and the Ageneiosidae are sister taxa, and that, together, they form a sister group to the Doradidae. Relationships above the family level remain completely unresolved, as is the case with many other groups of catfishes. The most significant

nomenclatural problem at present involves the infrafamilial classification of auchenipterids and ageneiosids.

Infrafamilial Relationships of the Auchenipteridae and Ageneiosidae

Relationships among genera of the Auchenipteridae are still rather poorly known, although three studies have attempted to define lineages within the family (Britski 1972, Ferraris 1988, Curran 1989). An exhaustive survey of the results of these studies is irrelevant to my objective of resolving the taxonomy and elucidating relationships among ageneiosids. Nevertheless, some comments are necessary because of their implications to my phylogenetic comparisons among ageneiosid species and family-group nomenclature adopted herein.

Britski (1972) surveyed the morphology of a number of auchenipterids and ageneiosids, and presented a provisional dendrogram of relationships among them. He recognized four subfamilies of the Auchenipteridae (for 13 genera), and placed the Ageneiosidae as a separate lineage on his tree. He included *Tetranematichtys* with *Ageneiosus*. Britski's (1972) grouping of genera was based, in part, on symplesiomorphies among taxa, as explicitly noted by Ferraris (1988). Some of the currently accepted genera of auchenipterids were either unavailable to Britski or undescribed at the time of his study. Nevertheless, Britski (1972) recognized phyletic affinities between some of the same genera that Ferraris (1988) lumped together.

Ferraris' (1988) cladistic analysis of the Auchenipteridae and Ageneiosidae is the most rigorous study to date of interrelationships among these taxa. He provided detailed comparisons of character states, and explicitly stated his interpretation of their role in providing evidence of the shared evolutionary histories of various taxa. Many of Ferraris' (1988) conclusions about polarities of anatomical characters have

been incorporated into the present study, for the purpose of evaluating relationships among species of ageneiosids. There are significant problems with Ferraris' analysis, but these mostly involve relationships among auchenipterid genera. One of the most drastic implications of Ferraris' study was his conclusion that the long-standing nomenclature of the family-group names must be changed:

The family Auchenipteridae, as most generally delimited, is not a monophyletic group. Species of the Ageneiosidae are more closely related to *Auchenipterus* than are many species that have traditionally been put in the Auchenipteridae. If we accept the constraint that a classification must be based on monophyletic groups and that named taxa include all members of a lineage, the Auchenipteridae must either include *Ageneiosus* and its relatives, or the auchenipterids must be split into a number of different families. The approach adopted here partakes of both of these solutions. Ferraris (1988:141)

Ferraris proposed a reclassification in which he lumped *Ageneiosus* and *Tetranematchthys* with several other genera as a subfamily of the Auchenipteridae, and he re-elevated *Centromochlus* and allied genera to family status (Table 4).

The greatest problem with Ferraris' classification involves contradictions between his morphological analysis and his cladograms, and extensive homoplasy. For example, in recognizing the Centromochlidae as a monophyletic group, he cites numerous unique morphological characters throughout the text, but he includes only three putative synapomorphies of this group in his cladogram of the doradoid families (Ferraris 1988; fig. 41), two of which cross-reference to *Auchenipterus*, *Epapterus*, and *Entomocorus* in the text (pp. 52 and 54); displacement of the gonopore to the distal tip of the anal fin, and laminar ossifications of the last few anal-fin pterygiophores. Many of the characters that Ferraris considered to be synapomorphies of the family Centromochlidae involve the anal fin; in males of these taxa (*Centromochlus*, *Glanidium*, *Gelanoglanis*, and *Tatia*), the anal fin is markedly different from that found in any of the other auchenipterid genera, having

Table 4. – Classification of the neotropical doradoids, exclusive of the Doradidae, proposed by Ferraris (1988).

Centromochlidae

Centromochlus

Genus A

Glanidium

Tatia

Genus B

Gelanoglanis

Auchenipteridae

incertae sedis

Pseudotatia

Tocantinsia

Asterophysus

Trachycorystinae

Trachycorystes

Liosomadoras

Trachelyoterichthys

Auchenipterinae

incertae sedis

Auchenipterichthys

Pseudauchenipterus

Auchenipterini

Trachelyichthys

Trachelyopterus

Ageneiosus

Tetranematicthys

Auchenipterus

Epapterus

Entomocorus

a greater number of reduced, reoriented fin rays and supporting elements. Ferraris (1988) went so far as to speculate that internal fertilization does not occur in centromochlids, and he used this argument to partially rationalize family status for the group. I question the assumption that centromochlids lack internal fertilization, in the absence of direct evidence to support the idea. Spermatozeugmata are present in the testes of *Centromochlus* (personal observation), which is highly suggestive of internal fertilization. Moreover, the unusual anal fin may be an extremely derived structure, which would argue in favor of a more advanced type of gonopodium than is present in other taxa. Regardless of my opinion about the probable mode of fertilization in these species, however, I have little doubt that the taxa included in Ferraris' Centromochlidae are monophyletic. Consideration of the family-group nomenclature rests on the phylogenetic relationships among the remaining genera, and this is where there are the greatest incongruencies in Ferraris' analysis.

The cladogram of ageneiosids and the remaining achenipterid genera presented by Ferraris has four unresolved polychotomies (Fig. 33). I have not included the character states supporting Ferraris' hypothesized phylogeny; to do so, and to discuss their distribution, would be very exhaustive. The following comments are provided only for their relevance in assessing a probable sister group of *Ageneiosus* and *Tetranematicthys*, and their bearing on the family-group nomenclature.

Many of the characters that Ferraris (1988) included on his cladogram as synapomorphies of putatively monophyletic lineages were considered to be homoplasious, both within the ingroup and among other doradoids (centromochlids and doradids). Some of the convergences or reversals were discussed by Ferraris, but several were not explained. Given this, and the number of unresolved nodes, there are probably several equally parsimonious trees to the one presented by

Fig. 33. — Cladogram of hypothesized phylogenetic relationships among genera of neotropical doradoids, exclusive of the Doradidae and Centromochlidae, presented by Ferraris (1988).

Ferraris (1988). However, at no place in his text did Ferraris discuss how he arrived at the topology of the cladogram presented in Fig. 33; thus, one is left to assume that he used manual argumentation to produce his tree(s), and that he had some rational justification for choosing the topology he did. In any case, alternate arrangements of branches would primarily involve genera outside of the lineage that includes the ageneiosid clade.

I find the number of unresolved polychotomies in Ferraris' (1988) analysis especially disturbing, at least in terms of his proposal to rearrange the prevailing family-group nomenclature. The problem of homoplasy is confounded by a simple lack of informative data for several taxa. Ferraris used many sexually dimorphic characters to unite genera, especially within the centromochlid clade, and those in his tribe Auchenipterini (Table 4). However, reproductively mature or nuptial males of several genera were unavailable to him, and, from his list of material examined, it is apparent that he did not examine many nominal species of several genera. He splits *Trachelyopterus* into three species assemblages, one of which does not share any derived characters with the other two subgroups; what is especially disconcerting about treatment of this genus, however, is his assertion that the other two subgroups are sister taxa by a shared loss of sexual dimorphism (Ferraris 1988:117). I find that this is a precarious assumption, since Ferraris did not provide any evidence to support such a hypothesis. The use of reductive characters to define groups, in my opinion, rests on strong evidence that there has been paedomorphosis or character reversal. This has not been unequivocally established with respect to sexually dimorphic structures in *Trachelyopterus*. Thus, I choose to disregard Ferraris' cluster of species into subgroups within *Trachelyopterus*, pending additional data to support possible monophyletic lineages within the genus. Polychotomies in Ferraris' cladogram more basal to the node defining for his Auchenipterini will not

be addressed here; suffice it to say, he presents a large number of characters that suggest most of these other genera are not intimately related to this tribe.

Ferraris (1988) placed ageneiosids in an unresolved trichotomy with *Trachelyopterus* and what he called the "*Auchenipterus* group", which includes *Auchenipterus*, *Entomocorus*, and *Epapterus* (Table 4, Fig. 33). As delimited by Ferraris (1988), the only other genus of the tribe is *Trachelyichthys*; he presented very little information about the morphology of this genus, and only remarked that it possesses characters of the Auchenipteridae and Auchenipterini. Inclusion of *Trachelyichthys* in the tribe Auchenipterini is somewhat enigmatic, however, inasmuch as Ferraris (1988:109-110) excluded the genus from his diagnosis of the tribe, which was defined on the basis of the following derived characters: enlarged basisphenoid process of parasphenoid that forms both optic foramen and anterior and ventral walls of trigeminofacialis complex fissure; anteriorly expanded palatine in nuptial males; distal ossification of elastin core of maxillary barbel; papillose dorsal surface of ossified barbel of nuptial males; hyperossification of dorsal-fin spine, with the development of basally and distally clustered serrae on the anterior margin of the spine; and the ability of males to hyperextend the dorsal-fin spine anterodorsally. Since I have not studied the morphology of *Trachelyichthys*, I cannot comment on its inclusion by Ferraris with the remaining genera of his Auchenipterini. The only four apomorphies of *Trachelyichthys* that Ferraris included on his cladogram were homoplasious with other doradoids (three involved modifications of the caudal skeleton associated with a truncate fin).

The three clades that form an unresolved trichotomy within Ferraris' (1988) Auchenipterini seem to be relatively well-defined groups. Ferraris presented a strong argument for monophyly of the "*Ageneiosus* group", discussed below and extensively throughout the anatomical descriptions in this study. Problems of relationships within *Trachelyopterus* are alluded to above, but in general the taxa in

this genus are distinctive and apparently monophyletic. A relationship between *Epapterus* and *Auchenipterus* was recognized earlier by Britski (1972), and Ferraris provided additional characters to support this. Inclusion of *Entomocorus* within the above clade, however, is problematical, as indicated by Ferraris himself.

Reproductive males of *Entomocorus* have a peculiar modification of the pelvic fins (Mago-Leccia 1984), and the anal fin is not modified as in other members of the tribe (i.e., there is no displacement of the gonopore onto the distal tips of the fin rays). Furthermore, the epioccipital process is not bifurcated and does not contact the expanded parapophyses of the complex centrum, and there is no laminar basisphenoid process of the parasphenoid. Ferraris (1988) argued that reduction or absence of the above characters represents secondary losses from the derived state in other auchenipterins. He tentatively suggested that internal fertilization might be absent in *Entomocorus*, or that insemination could involve the modified pelvic fin rays; however, as with the situation in centromochlids (discussed above), statements about mechanisms of fertilization in these fishes is entirely speculative at present. Thus, even within the Auchenipterini, possible homoplasies have confounded inferences about relationships among the genera.

Results of Curran's (1989) cladistic analysis of auchenipterid relationships conflicts in several ways with those presented by Ferraris (1988); however, these will not be discussed in detail here. Curran's cladogram is presented in Fig. 34. Since Curran did not consider ageneiosids to be a sister group to any of the auchenipterid genera, his statements about the family-group names are biased by previous classifications. Some of the characters that Curran used to define monophyly of the auchenipterids are actually found in ageneiosids (reviewed above). In any case, his omission of ageneiosids from the analysis does not affect consideration of the characters or taxa he used. What is worth noting about Curran's cladogram, however, is the relative position of the taxa placed in Ferraris' Auchenipterini.

Fig. 34.—Cladogram of hypothesized phylogenetic relationships of the Auchenipteridae presented by Curran (1989).

Curran included all of the genera of that tribe, except *Entomocorus*, near the top of his tree; taxa above this node also included *Trachelyopterichthys* and *Trachelyichthys*. *Pseudepapterus* is synonymous with *Epapterus* according to Ferraris (1988:140). The clade of genera above this node (at the point where *Parauchenipterus* branches off in Fig. 34) were defined on the basis of having the epioccipital process contacting the fifth vertebral parapophysis. This character-state is the same one used by Ferraris to define the Auchenipterini. Curran united *Trachelyopterichthys* with *Epapterus* on the basis of three characters that are of questionable utility: length of dorsal fin; length of pelvic fin; and shape of postcleithral process. His use of *Parauchenipterus* includes taxa under Ferraris' *Trachelyopterus* (the confusing nomenclature involving *Trachycorystes*, *Parauchenipterus*, and *Trachelyopterus* was discussed extensively by Ferraris). If one disregards the topological placement of *Tatia* in Curran's cladogram, all of the taxa above his node below the point where the *Entomocorus*-*Pseudauchenipterus* clade branch off are those that make up Ferraris' Auchenipterini. The characters that contribute to branching among major lineages above this node primarily involve size of the gonopodium, size and degree of fusion of the epioccipital process, and size of the adipose fin. The last character is relatively labile, and of limited systematic value in some cases (reviewed by Vari and Ortega 1986, and Ferraris 1988). The epioccipital process is of some use in uniting auchenipterid taxa, but Curran's polarization of this structure into a transformation series of six character states is somewhat arbitrary (although he discusses this on p. 415). There are many unresolved questions about the nature of the gonopodial structure in several of these taxa, as discussed elsewhere. Thus, with the exception that some taxa are included in the same lineage (primarily on the basis of labile characters or some of limited systematic value), Curran's analysis clustered the same species that Ferraris found to be related (his Auchenipterini).

The extent of the problems discussed above are detailed here to illustrate the point that phylogenetic relationships among auchenipterids are still not well understood. There is good evidence that species within several groups are monophyletic, but the relationships among the genera are not clearly resolved. While I feel that Ferraris (1988) contributed more information about systematics of auchenipterids and ageneiosids than all previous authors, I hesitate to adopt his cladogram as dogma, and prefer to retain the present, widely-accepted designation of family-group names (Nelson 1984) until more data become available. The present situation is one in which there is unequivocal evidence that all of the currently recognized auchenipterid and ageneiosid genera form a monophyletic group, but some relationships among them are uncertain, due to unavailable morphological and reproductive information. While I concur with Ferraris (1988; quoted above) that the ultimate goal of classification is to accurately reflect evolutionary history, I feel that it is necessary to have strongly corroborated hypotheses of relationships before an accurate classification scheme can be constructed. Eventually, perhaps, all of the genera currently placed in the Auchenipteridae (*sensu lato*) and Ageneiosidae will be classified together in one higher category, but I am confident that the lineage including *Ageneiosus* and *Tetranematichthys* will continue to be recognized as a monophyletic unit.

Based on the studies by Britski (1972), Ferraris (1988), and Curran (1989), it appears that ageneiosids share closest affinities with some or all of the taxa included in the genera *Trachelyopterus*, *Auchenipterus*, *Epapterus*, and perhaps *Entomocorus*. A better resolution of the relationships among all of these taxa requires additional research, including, most importantly, anatomical study of the reproductive anatomy of males.

Species Relationships of the Ageneiosidae

Relationships within the family Ageneiosidae were evaluated by analyzing 35 morphological characters listed in Table 5. The data on the morphological features with two to four character states were analyzed initially using the MULPARS algorithm of PAUP, which searches for equally parsimonious trees by branch-swapping routines (global branch swapping was used). The number of trees estimated by MULPARS was verified by using the branch and bound algorithm, which is guaranteed of finding the most parsimonious tree(s). A hypothetical ancestor polarized as plesiomorphic for all characters was included. In addition, data were included for single species belonging to three of the four outgroup genera hypothesized by Ferraris (1988) to be the sister taxon of ageneiosids; *Trachelyopterus galeatus*, *Entomocorus gameroi*, and *Auchenipterus nuchalis* (members of Ferraris' Auchenipterini). *Ageneiosus marmoratus* and *A. brevifilis* were coded as the same OTU for the cladistic analysis. The data matrix used for numerical analysis is presented in Table 6. Characters with more than two character states (i.e., meristic counts) were designated as unordered.

Initially I included relative body size and the presence or absence of swimbladder caecae in the analysis; the polarity and significance of both of these characters are of questionable value in evaluating relationships among ageneiosids, and added considerable homoplasy to the analysis, so they were deleted from the matrix. Input of the remaining data matrix into PAUP resulted in six equally parsimonious trees of 54 steps with a consistency index (CI) of 0.722. The relatively low CI indicates that approximately 28% of the character-state changes required by the alternate tree topologies of the data set represent character reversal or convergence (homoplasy). Examination of the six trees revealed that they differed in topology as a result of an unresolved polychotomy involving species at a basal

Table 5. – Characters used to analyze relationships among species of Ageneiosidae. The plesiomorphic state is followed by the apomorphic state(s). Character numbers correspond to those in Table 6.

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1. Hyomandibula sutured to metapterygoid (0); hyomandibula not separated from metapterygoid by dorsomedial laminar ossification of quadrate (1).
 2. Nasal bone not bifurcated (0); nasal bone bifurcated, lateral canal ossified basally (1).
 3. Vomer with anterolateral processes (0); vomer broadly rounded anteriorly, without angular projections (1).
 4. Dermal component of first dorsal-fin pterygiophore forming prominent nuchal plate sutured to supraoccipital (0); no nuchal plate formed from first dorsal-fin pterygiophore (1).
 5. Postcleithral process moderately to strongly developed (0); postcleithral process absent (1).
 6. Third basal radial of pectoral fin not expanded (0); third pectoral-fin basal radial expanded and supporting many fin rays (1).
 7. Anteromedial tips of first two hypobranchials approximately straight and perpendicular to axis of branchial basket (0); anteromedial tips of first two hypobranchials concave and obliquely angled anteromedially (1).
 8. Second epibranchial not enlarged (0); medial tip of second epibranchial expanded and covering first epibranchial dorsally (1).
 9. Urohyal without dorsomedial process between hypohyals (0); process of urohyal projecting dorsomedially between hypohyals (1).
 10. Anterior ossification of ceratohyal separated from ventral ossification by bar of cartilage (0); anterior ossification of ceratohyal sutured to ventral ossification along ventromedial margin (1).
 11. Ventral surface of palatine smooth (0); ossified splint on ventral margin of palatine (1).
 12. Two pairs of chin barbels not oriented transversely near lower lip (0); two pairs of chin barbels arranged transversely near lower lip (1).
 13. Lacrimal free or loosely associated with mesethmoid and lateral ethmoid, and without ventral ossified process (0); lacrimal sutured to lateral ethmoid and mesethmoid, and with a spinous ossification extending ventrally from canal-bearing portion of bone (1).
 14. Ventral surface of basipterygium flat or nearly so (0); basipterygium convex dorsally (1).
 15. Palatine not expanded in either sex (0); palatine of nuptial males expanded anteriorly (1).
 16. Maxillary barbel without ossified central core (0); maxillary barbel with ossified central core (1).
 17. Pterosphenoid forming part of anterior margin of trigeminofacialis foramen (0); pterosphenoid excluded from contact with anterior margin of trigeminofacialis foramen (1).
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Table 5. – continued.

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18. Dorsal-fin spine not sexually dimorphic (0); reproductive males with dorsal-fin spine elongated and with antrorse serrae (1).
 19. Posterior epioccipital process not a broad plate formed by expanded medial fork (0); medial fork of posterior epioccipital process expanded, broadly contacting vertebral parapophysis and forming laminar shelf (1).
 20. One pair of mandibular barbels in adults (0); mandibular barbels absent in adults (1).
 21. One pair of mental barbels in adults (0); mental barbels absent in adults.
 22. Maxillary barbel of nuptial males smooth or weakly tuberculate (0); maxillary barbels of nuptial males with sharp odontodes on dorsal surface (1).
 23. Müllerian ramus enlarged (0); Müllerian ramus reduced in size (1).
 24. Swimbladder large and free (0); swimbladder encapsulated by ossification of complex centrum (1).
 25. Caudal fin with 8 + 9 principal rays (0); caudal fin with 8 + 10 principal rays (1).
 26. Caudal fin deeply forked (0); caudal fin moderately emarginate or obliquely truncate (1).
 27. Fewer than 20 gill rakers on outside row of first arch (0); greater than 20 gill rakers on outside row of first arch (1).
 28. Fewer than 50 total vertebrae (0); greater than 50 total vertebrae (1).
 29. Less than 30 anal-fin rays (0); 30-40 anal-fin rays (1); greater than 40 anal-fin rays (2).
 30. Mean number of pectoral-fin rays less than 11 (0); mean number of pectoral-fin rays 11-12 (1); mean number of pectoral-fin rays greater than 12 (2).
 31. Modally 7 or fewer ribs (0); modal number of ribs = 8 (1); modally 9 or more ribs (2).
 32. 6 vertebral centra fused to complex centrum (0); 7 vertebral centra fused to complex centrum (1).
 33. First pectoral-fin lepidotrichium ossified, unsegmented, forming moderate to strong spine (0); first pectoral-fin lepidotrichium weakly ossified, segmented, not forming stiff spine (1).
 34. Pectoral-fin spine with serrae on anterior margin (0); serrae absent from anterior margin of pectoral-fin spine (1).
 35. Modally fewer than 8 branchiostegals (0); modally 8-9 branchiostegals (1); modally greater than 9 branchiostegals (2).
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Fig. 35. – Consensus tree of ageneiosid relationships generated from analysis of characters presented in Tables 5-6.

node for *Ageneiosus*. The six trees were input into Swofford's CONTREE program, which constructs a strict consensus tree of all of the equally parsimonious trees. The resulting tree topology is presented in Fig. 35.

An analysis of the character-state distributions among the six equally parsimonious trees indicates that most of the homoplasy involves meristic data. In the following detailed analysis of characters themselves, parenthetical references are to character numbers listed in Table 5 and the character suites or nodes designated by letters on Fig. 35.

Ferraris (1988) determined that the Ageneiosidae is monophyletic (Node A on Fig. 35) on the basis of the following partial suite of characters: hyomandibula separated from metapterygoid by a dorsomedial laminar ossification of the quadrate (1); nasal bones bifurcated, with anterolateral canal ossified at base (2); vomer broadly rounded, without anterolateral angular projections (3); nuchal plate formed from dermal element of first dorsal-fin pterygiophore absent or fused to posteroventral margin of supraoccipital (4); third basal radial of pectoral fin expanded, supporting many fin rays (6); tips of first and second hypobranchials concave and obliquely angled anteromedially (7); medial tip of first epibranchial enlarged and dorsally covering medial tip of second epibranchial (8); urohyal with a laminar ossification extending dorsomedially between anterior tips of hypohyals (9); and, anterior ceratohyal sutured to ventral hypohyal along ventromedial surface (10). I have little to add to Ferraris' (1988) list of synapomorphies of the Ageneiosidae, but note the following. All ageneiosids lack a mandibular pair of barbels, and, with the exception of *Tetranematichthys*, lose the mental barbels early in their ontogeny. The presence of only a single pair of barbels on the chin is found only in the auchenipterid genus *Gelanoglanis*, among all other neotropical catfishes, and is considered to be convergent with the condition in ageneiosids (Ferraris 1988) in the absence of corroborative evidence to unite these taxa. Ferraris (1988)

considered the reduction of infraorbital bones to four to be derived within the ageneiosid clade; however, as discussed in the text, this character is variable and not diagnostic of the family. In addition to the above character states, ageneiosids have extremely cancellous bones of the head and fin skeletons, which represents a derived condition not found in any of the outgroups that I have examined.

Within the family, monophyly of *Ageneiosus* (node B on Fig. 35) is supported by two unequivocal characters: absence of mental barbels in adults (21), and dorsal margin of the maxillary barbel of nuptial males with enlarged, tooth-like odontodes formed by outgrowths of the maxillae (22). Eleven valid species are recognized in this clade (Fig. 35).

Tetranematichthys has all of the character states synapomorphic for the family, but adults of this genus have a diminutive pair of mental barbels, and males have elongate, untoothed maxillary barbels; both of these characters are plesiomorphic for the family (although reduction in size of the mental barbels can be considered derived relative to auchenipterids). Thus, *Tetranematichthys quadrifilis* is the sister species of *Ageneiosus*.

Three distinctive clades exist within *Ageneiosus*, but relationships among several of the species remain unresolved. The most derived species are *A. brevifilis* and *A. marmoratus* (node J on Fig. 35). Both species share the uniquely derived truncate caudal fin, with 8 + 10 principal fin rays (25), and the first pectoral-fin lepidotrichium not forming a stiffened, serrated spine. These two species are identical in nearly all respects except coloration, and their present specific status is tenuous (see comments under species accounts). *Tetranematichthys* and several auchenipterids, including *Trachelyopterus*, have a truncate caudal fin, with the derived condition of an additional lower principal ray. The shared presence of this derived character state is considered to be the result of parallel evolution (Ferraris 1988). The sister species of *A. brevifilis* and *A. marmoratus* is *A. polystictus*, which

has an incompletely ossified first pectoral-fin spine (33) and an emarginate caudal fin (26), representing an intermediate condition between the plesiomorphic states found in most species of *Ageneiosus* and the *A. brevifilis*-*A. marmoratus* clade (node I).

A broadly inclusive lineage of species shares the uniquely derived encapsulated swimbladder (24), with a correlated reduction of the Müllerian ramus of the fourth vertebra (23). This clade (node E) includes *A. ucayalensis*, *A. valenciennesi*, *A. vittatus*, *A. n. sp.*, and the lineage defined in the preceding paragraph. All of these species also have modally greater than 9 branchiostegals (35, state 2). Within the above clade relationships are inferred on the basis of the following meristic characters. The taxa above node H in Fig. 35 all have modally greater than 20 gill rakers (27), but the shape of the rakers themselves is different in *A. brevifilis* and *A. marmoratus* than in *A. ucayalensis* and *A. polystictus*; the rakers are short and conical in the former two species, but long and medially scalloped in the latter two. A similarly high gill-raker count was apparently derived independently in *A. brevis* and in *Auchenipterus nuchalis*, both species of which have extremely long, thin gill rakers. A clade of species that includes *A. valenciennesi* and those above node H all share the derived state of a mean number of total vertebrae exceeding 50 (28); the next most inclusive clade includes this one and *A. n. sp.* (node F), the species of which all have a mean pectoral-fin ray count of 13 or more (30, state 2). *Ageneiosus vittatus* is the sister species to the clade represented by node F.

Ageneiosus pardalis is phenetically similar to the species of the broadly inclusive clade outlined above, excluding those above node I. However, *A. pardalis* has a large, unencapsulated swimbladder. *Ageneiosus pardalis* is united with the above lineage (node D) on the basis of a mean number of pectoral-fin rays of 11-12 (30, state 1), and having a modal rib count of 8 (31, state 1). *Ageneiosus pardalis* is

very similar in terms of physiognomy, coloration, and meristic counts to the fork-tailed species with encapsulated swimbladders, and therefore is considered to be the sister species to the lineage defined by an encapsulated swimbladder.

Some of the extensive homoplasy of the character state data is reflected in node C of the consensus tree, which includes an unresolved trichotomy involving *A. atronasus*, *A. brevis*, and *A. piperatus*. All three species are diminutive and share the plesiomorphically large, unencapsulated swimbladder. *Ageneiosus brevis* is the only species of the genus that has a moderately developed postcleithral process (5, state 0), which is a primitive state shared with *Tetranematichthys* and all other doradoid catfishes. Ferraris (1988) reported that he observed a postcleithral process in a juvenile specimen of *A. marmoratus* (= *A. vittatus* ?), but that it was absent in a larger specimen. Presence of the postcleithral process is variable in *A. brevis*, and some populations have individuals with and without the structure. On the basis of the postcleithral process alone, *A. brevis* could be considered more primitive than either *A. atronasus* or *A. piperatus*, but the latter taxa do not share any obvious synapomorphies. In contrast, *A. atronasus* and *A. brevis* appear to be sister species by virtue of sharing the presumably derived pair of posterior swimbladder caecae (not included in the numerical analysis). Paired swimbladder caecae are believed to be absent in both *A. piperatus* and *A. pardalis*, but are present in all other species of the genus, including those with encapsulated swimbladders. This character-state distribution is difficult to account for. *Ageneiosus pardalis* shares a number of features with a more inclusive clade (discussed above) than with *A. piperatus*; in fact, these two species are phenetically very different, representing almost the full extreme of morphological differences in the family (*A. piperatus* is the most diminutive species and has a number of reductive character states, whereas *A. pardalis* is very large and has derived meristic states). Two explanations are possible to account for the swimbladder caecae; the first is that paired caecae may have

evolved independently in *A. atronatus* and *A. brevis* on one hand, and all of the species in the clade above node E. The second possibility is that paired caecae was the ancestral condition of all species of *Ageneiosus*, and that a secondary reversal occurred separately in *A. piperatus* and *A. pardalis*. Both possibilities are equally likely, but there are no corroborative data to support either one. Interpretation of the evolution of swimbladder caecae is further complicated by the condition in *Tetranematichtys*, in which there is a single, extremely large posterior caecum. Species in the outgroups examined lack any caecae, so the absence of any is considered to be the plesiomorphic state for all ageneiosids. Thus, the phylogenetic reconstruction provided by an analysis of other characters is uninformative to an understanding of the evolution of swimbladder caecae. This situation can only be redressed by examination of additional characters, including a broader comparison with auchenipterid genera, to determine if convergence has occurred in swimbladder structure. Moreover, homoplasy of meristic characters requires that future studies include more in-depth analysis of additional characters, structural or otherwise, to test the hypothesized phylogenetic reconstruction presented here.

DISTRIBUTION AND ZOOGEOGRAPHY

Considered in its entirety, the family Ageneiosidae is widely distributed throughout lowland waters of South America and the Isthmus of Panama. Ecological data are unavailable for nearly all species to adequately characterize their habitat requirements and behavior. All species of *Ageneiosus* appear to be ecologically confined to main river channels, oxbow lakes, lagoons, backwater sloughs, and other open-water habitats associated with the large rivers of South America. *Tetranematicthys* is apparently found in smaller lowland tributaries and forested creeks (H. A. Britski, personal communication), a fact that may account in part for this species' dark pigmentation pattern. The apparently generalized habitat requirements and vagility of most species has probably contributed significantly to their widespread ranges.

There are scant substantive biogeographical studies of neotropical fishes, due mainly to a poor state of knowledge about faunal composition of most drainages, evolutionary relationships of the fishes, and inadequate geological and paleontological data. The earliest serious attempts to explain distribution patterns were made by Carl H. Eigenmann, who surveyed expansive areas of the continent. He published numerous faunal lists (e.g., Eigenmann 1912, 1920a, 1920b, 1920c, 1920d, 1921), and attempted to correlate the observed distribution patterns of the ichthyofauna with historical geological events known at the time. Virtually all of the significant studies that addressed geographical diversification were summarized by Weitzman and Weitzman (1982). In the last ten or fifteen years, a limited number of phylogenetic studies have included comments about past climatological and

geological events and their implications to the evolutionary history of the taxonomic groups; the most informative studies have been of various characiform fishes (e.g., Vari 1988, 1989a, 1989b, 1989c). Relationships in most groups of neotropical catfishes are unresolved, and no major phylogenetic studies have included discussions of historical biogeography. Since hypotheses about the role of vicariance in speciation require well-resolved phylogenies, there are presently few catfish groups that are available for zoogeographical analysis.

Based on extensive studies of curimatid characiforms, Vari (1988) recognized ten major regions of endemism in South America. The most thoroughly studied region is at the northern reaches of the Andes, where the fauna has been most intensively studied cladistically, and where there are several subregions of endemism. The remaining regions correspond largely to physiographically distinct areas of the continent, associated with major river systems. The largest area encompasses the Amazon itself. Other regions include the following: Orinoco basin; coastal rivers to the northeast of the Guiana Shield; the Rio São Francisco basin; separate coastal areas to the north and south of the Rio São Francisco; and, the Paraná-Paraguay system, which is separable into upstream and downstream divisions. Ageneiosids occupy all of these regions except the Rio São Francisco drainage and the coastal drainages to the south.

The widespread distribution of most species of ageneiosids, and their relatively poorly resolved relationships, precludes a thorough evaluation of their zoogeography. There are, however, several noteworthy considerations.

Ageneiosus pardalis is the only ageneiosid occurring west of the easternmost Andean cordillera. It is found in the Lake Maracaibo basin, and occurs westward in the major drainages of northwestern Colombia and southern Panama. This distribution parallels that of a number of other species (Vari 1988). Schultz (1944) considered the Maracaibo population to be specifically distinct from the more

western populations, but I have not found morphological evidence to support this idea (see comments under species account of *A. pardalis*). Vari (1988) noted variation between the Lake Maracaibo populations of *Cyphocharax magdalena* and *Roestes alatus* and conspecific populations to the west of the Lake Maracaibo basin, and attributed the differences to reduced gene flow (due to partial isolation resulting from the intervening central cordillera of the Andes between the Río Magdalena basin and the Lake Maracaibo basin). Nevertheless, the presumed nonconspecificity of populations of several other taxa between these two areas has not been critically studied.

The distribution of *A. pardalis* is phylogenetically informative, although somewhat problematic. The faunal region that it occupies has been discussed extensively, and is the best known of the continent (the western region of Vari 1988). There is considerable endemism in the Río Magdalena, and various degrees of faunal distinction among the other river drainages to the west and south (Vari 1988, 1989c). Prior to the uplift of the Andes, the circum-Magdalena region was in contact with the Orinoco-Amazon basin. Following vulcanism in the region, there were widespread local extinctions, accounting for the present-day lower faunal diversity of the Magdalena basin, in comparison to the Orinoco and Amazon basins (Lundberg et al. 1986). The separation of the Magdalena fauna from the Orinoco and Amazon basins subsequently allowed for allopatric speciation to occur. In spite of the speciation in this region, however, Lundberg and his colleagues (1986, 1988) found evidence of remarkable evolutionary stasis in two species, based on Miocene fossils of the characid *Colossoma macropomum* and the pimelodid *Phractocephalus hemiliopterus* from the coastal areas of the northwest Andes. Both of the above extant species are presently widely distributed throughout the Amazon and Orinoco basins, but neither species occurs today in the Río Magdalena. Lundberg used the fossil evidence and the current distributions of these fishes to demonstrate that

there has been virtually no morphological divergence in these two species for at least the last 6-15 million years.

Vari (1989a) found that there was significant speciation among curimatids prior to the uplift of the Andes. The evidence for this was an area cladogram based on a well-corroborated phylogeny, in which the Río Magdalena basin fell at a relatively high node on his tree, thus suggesting that more basal clades had differentiated prior to the Miocene. In this study, unfortunately, the closest sister relationship of *A. pardalis* was not determined; thus, the significance of its trans-Andean distribution is obscure. Phenetically, this species is most similar to the fork-tailed species with encapsulated swimbladders, which includes species distributed throughout the entire extent of the range of the family. This would suggest that speciation of taxa involving the ancestor of the latter clade occurred prior to the uplift of the Andes.

Ageneiosus valenciennesi is found only in the lower reaches of the Rio Paraná-Rio Paraguay system, which is a region of high ichthyofaunal endemism (Vari 1988). The only congeners that also occur in this system are *A. brevifilis* and *A. ucayalensis*, which are very broadly distributed throughout the continent. The relationship of *A. valenciennesi* with the large fork-tailed species of the Amazon is not surprising, considering that there are a number of characiforms that occur in both basins (Vari 1988), suggesting a more extensive historical connection between the Amazon and Paraguay basins than is commonly cited. Nevertheless, isolation of the Paraguay apparently allowed for allopatric speciation of *A. valenciennesi*. If *A. ucayalensis* and *A. valenciennesi* are sister species, their present distributions is indicative that *A. ucayalensis* redispersed into the Rio Paraná basin following speciation.

The distribution of *A. piperatus*, as currently known, is restricted to the area around the Guiana Shield, in the Rio Essequibo and in the Rio Branco. This region

is also known to harbor a large number of endemic fishes. The relative plesiomorphy of *A. piperatus* suggests that it may have speciated in the area of the Guiana Shield as a result of vicariance associated with formation of the shield.

Ageneiosus polystictus is confined to the Rio Negro. This huge drainage is ecologically and ichthyofaunally distinct, and has a number of other endemic fishes (Goulding et al. 1988). Because the systematics of its fauna has not been vigorously studied, there are currently no zoogeographical hypotheses concerning observed distribution patterns of fishes in the Rio Negro. Presumably, some of the endemism is related to the formation of the Guiana Shield, but there are probably many ecological factors involved in some of the diversification of fishes in this region.

The remaining species of ageneiosids have relatively widespread distributions. There are no species in the Orinoco basin that are not also found in the Amazon basin. On the other hand, three species are found only in the Amazon basin; *A. brevis*, *A. atronasus*, and *A. n. sp.* *Ageneiosus atronasus* and *A. brevis* seem to be limited primarily to the upper half of the Amazon basin (as is *A. vittatus*, although it also occurs in the Orinoco), whereas *A. n. sp.* appears to be limited to the Rio Negro, lower Amazon, and Rio Amapá. Movement of some species (*A. ucayalensis*, *A. brevifilis*, possibly *A. vittatus*) between the Orinoco and Amazon basins almost certainly occurs via the Rio Casiquiare connection.

Vari (1989a) found that only two species of *Curimata* do not have distributions overlapping to some degree those of other species of the genus; many are largely sympatric. The situation involving the distributions of most ageneiosid species is very similar to that in *Curimata*, and, since both groups are principally large river fishes, some parallels are probably the result of similar historical events that led to speciation. Vari (1989a) suggested that the pattern he found in *Curimata* was best explained by allopatric speciation followed by dispersal and secondary sympatry. Presumably, isolation of clades within hydrographic systems occurred

during major rearrangement of flow patterns associated with Andean orogeny, contributing to allopatric speciation. Following the formation of the Andes, reorganization of the river drainages would have allowed for dispersal and the present sympatric distributions. Some of the endemism observed today (e.g., the Guianas, lower and upper Amazon) may be the result of hydrographic stability following geological vicariant events, thereby reducing potential for dispersal between drainage basins.

At present, little else can be said about the biogeography of ageneiosids, due to their incompletely resolved phylogenetic relationships and the lack of detailed ecological and distributional information.

SPECIES ACCOUNTS

Artificial Key to the Species of Ageneiosidae

- 1a. Caudal fin obliquely truncate or weakly emarginate, with rounded lobes and 8 + 10 principal rays2.
- 1b. Caudal fin moderately to deeply forked or strongly emarginate, usually with pointed lobes and 8 + 9 principal rays4.
- 2a (1a). Adults of both sexes with a single pair of filiform mental barbels, each bearing a small tuft distally. Swimbladder large, ovoid, not encapsulated by bone, and with a large fleshy caecum posteriorly. Nuptial males with an elongate, rod-like, ossified maxillary barbel (extending beyond posterior margin of eye), lacking sharp, recurved odontodes. Coloration on body deep brown, variably mottled with irregularly arranged black spots or blotches on sides.
.....*Tetranematicthys quadrifilis*.
- 2b. Mental barbels absent in adults of both sexes. Swimbladder variable, but never with a single, large posterior caecum. Maxillary barbels of nuptial males ossified, relatively short (not extending beyond posterior margin of eye), and with several recurved, tooth-like odontodes on dorsal margin. Coloration variable, often with spots or blotches, but rarely or never dark brown over most of sides.....3.

3a (2b). Head and body heavily marbled, pigment consisting of prominent, large, dark black blotches and spots. Coloration on body not uniformly countershaded. Paired fins nearly uniform black or with broken stripes over interradi al membranes. Caudal fin with a large triangular black patch encircling a lightly pigmented central spot. Blotches on sides extending onto anal fin*Ageneiosus marmoratus*.

3b. Head and body not heavily marbled. Coloration on body countershaded, the upper half typically slate gray, diminishing in intensity below midline. Paired fins often striped or mottled, but never uniformly black. Caudal fin without large dark black blotches, with a narrow black band on distal margin. Anal fin pale; pigment, if any, confined to dark black marginal band ..*Ageneiosus brevifilis*.

4a (1b). Caudal fin weakly forked to strongly emarginate, with broadly rounded lobes. Most of tail darkly colored, but tips of lobes unpigmented, appearing white or yellow. Color on body and fins dark purplish to black, with numerous small, irregularly shaped black spots on sides and top of head and body. Size large, adults commonly exceeding 250 mm SL. Swimbladder small, encapsulated by bone. Distribution limited to the Rio Negro drainage.....*Ageneiosus polystictus*.

4b. Caudal fin strongly forked, with sharply pointed lobes. Tail coloration variable, often pigmented and slightly mottled, but never appearing uniformly dark throughout and with tips of lobes immaculate. Color on body variable, with or without spots, but rarely appearing dark black. Adult size small or large. Swimbladder encapsulated or not encapsulated5.

- 5a (4b). Size large, adults commonly exceeding 200 mm SL. Swimbladder generally small (< 10% SL in longitudinal length), encapsulated in a pyriform or heart-shaped bony ossification of the complex centrum (except in *A. pardalis*). Pigmentation often consisting of one or more distinct stripes along body, and/or prominent, irregular blotches on top of the head and along the entire length of the back.....6.
- 5b. Size small, adults rarely exceeding 200 mm SL. Swimbladder very large and not encapsulated by bone, with a slightly turgid anterior chamber, and usually with two fleshy caecae on posterior margin. Pigmentation either plain or with diffuse spotting, but never with large, irregular blotches on top of head and back.....10.
- 6a (5a). Anal fin rays 41-50. Head very spatulate, snout moderately pointed in dorsoventral profile. Mouth strongly inferior. Countershaded pigmentation, ranging from a narrow, thin brown or gray stripe along dorsum, to uniform brown shading over most of sides; never strongly mottled or heavily spotted. Total gill rakers on outside row of first arch 18-25, long, strongly crenulate on medial margin*Ageneiosus ucayalensis*.
- 6b. Anal fin rays rarely greater than 40. Head shape variable, ranging from broadly rounded to slightly pointed in profile. Mouth weakly to moderately inferior. Pigmentation variable, but body and head usually prominently mottled, speckled, or striped. Total gill rakers on outside row of first arch less than 18, moderately long, crenulated on medial margin.....7.
- 7a (6b). Total vertebrae behind complex centrum, including the preural centrum, 38-42. Distribution in the Orinoco and/or Amazon river basins8.

7b. Total vertebrae behind complex centrum 42-45. Absent from Orinoco and Amazon river basins; distribution in the Rio Paraná-Paraguay basin, or in the trans-Andean drainages of northwestern Venezuela, Colombia, and southern Panama.....9.

8a (7a). Pigmentation on body consisting of a very distinct, sharply delineated, midlateral brown stripe extending entire length of side, bordered above and below by unpigmented stripes of nearly equal width. Body very compressed behind head. Free vertebrae behind complex centrum and anterior to first anal pterygiophore 9-12. Pairs of pleural ribs 7-8, modally 7. Pectoral rays 12-15, modally 13. Recorded only from the Amazon river and its tributaries, and the Rio Amapá. *Ageneiosus* n. sp.

8b. Pigmentation highly variable, but always with traces of a thin, black or brown midlateral stripe over anterior portion of lateral line, a similar stripe extending obliquely downward from the top of the operculum to above the pelvic fin, a mottled pair of stripes just lateral to the midline of the back, and a large black spot in the middle of each caudal-fin lobe. Free vertebrae behind complex centrum and anterior to first anal pterygiophore 11-14. Pairs of pleural ribs 8-10, modally 9. Pectoral rays 11-13, modally 12. Present in the Orinoco and upper Amazon basins..... *Ageneiosus vittatus*.

9a (7b). Found only in trans-Andean rivers of northwestern Venezuela (in the Maracaibo basin), Colombia (including the Magdalena, Cauca, Atrato, and San Juan rivers), and southern Panama (Río Tuira and smaller drainages). Pigmentation heavily mottled on head and dorsum, often extending over most of

the sides of the body. Swimbladder large, not encased in bony capsule.

Branchiostegal rays 8-9, modally 9*Ageneiosus pardalis*.

9b. Found only in the Rio Paraná-Paraguay and Rio Uruguay basins of southern Brazil, Paraguay, Uruguay, and Argentina. Pigmentation typically mottled on head and top of back, but rarely on sides of body below lateral line.

Swimbladder small, encapsulated by bone. Branchiostegal rays 9-11, modally 10 *Ageneiosus valenciennesi*.

10a (5b). Maximum adult body size greater than 50 mm SL. Pigmentation variable, but generally either with some evidence of discrete black or brown spots or blotches on the head, chin, and/or sides of the body. Swimbladder with two posterior caecae. Branchiostegal rays 7-10, modally 8 or 9 11.

10b. Maximum adult body size less than 50 mm SL. Pigmentation consisting of numerous small, diffuse brown specks on top of head and sides of body. A dark brown, hourglass-shaped band of pigment at base of caudal fin. Swimbladder without posterior caecae. Branchiostegal rays 7-8, modally 7. Presently known only from specimens collected in clearwater rivers draining the Guiana Shield*Ageneiosus piperatus*.

11a (10a). Body typically with many small, discrete brown or black spots distributed on top of the head, along the back, and on the sides (some specimens, however, are nearly immaculate or have only a light brown cast on the dorsum). Occipital region of head angled sharply upward to dorsal fin origin. Postcleithral process usually present, but very small or absent in some specimens. Anal-fin length variable but relatively long, with 29-42 rays. Preanal vertebrae 13-16. Paired

ribs 5-6. Gill rakers relatively long and numerous, totalling 21-32 on outside row of first gill arch.....*Ageneiosus brevis*.

11b. Prominent large black patches of pigment on top of the snout, the lips, the chin, on the sides above the anal fin, and with a stripe in each lobe of the caudal fin. Top of head relatively flat and smoothly angled upward to dorsal fin origin. Postcleithral process never present. Anal fin short, with 23-30 rays. Preanal vertebrae 17-19. Paired ribs 7-8. Total gill rakers on outside row of first arch 14-23*Ageneiosus atronasus*.

Family Ageneiosidae

Diagnosis

Distributed in the neotropics south of the isthmus of Panama. Members of the Ageneiosidae have internal fertilization and exhibit unique sexual dimorphism of the maxillary barbels, dorsal fin spine, and anal fin, a condition that is shared among other siluriforms only with at least some taxa currently classified in the family Auchenipteridae (*sensu lato*). Further distinguished from all other catfishes by the following unique combination of characters: body strongly compressed and head greatly flattened, with ventrolaterally positioned eyes; maxillary barbels short in females and immature males, concealed within rictal grooves above upper lip; maxilla of nuptial males extending into maxillary barbel as an osseous core, with sharp, recurved hooks on dorsal margin in all species except *Tetranematichtys quadrifilis*; chin barbels absent or reduced to a single pair in adults; dermal component of basal radial of first dorsal fin element not expanded into a broad plate on posterodorsal aspect of neurocranium; anterior margin of basal radial of second dorsal fin element sutured to posteroventral margin of supraoccipital;

epioccipital with a posterior laminar extension, broadly sutured with expanded parapophyses of fifth and sixth vertebrae; hyomandibula separated from metapterygoid by broad lamina of quadrate; vomer without anterolateral processes; urohyal with anterodorsal spur extending between paired hypohyals; nasal bifurcated, with anterolateral ossified branch; first two hypobranchials concave and oriented anteriorly along medial margin; first epibranchial enlarged dorsomedially and overlapping second epibranchial; first infraorbital posterior to lacrimal flared anteriorly.

Genus *Tetranematichtys* Bleeker

Generic Synonymy

Ageneiosus Kner 1858a (type species: *Ageneiosus quadrifilis* by original description).

Tetranematichtys Bleeker 1858 (replacement name; type species: *Ageneiosus quadrifilis*, by original designation and monotypy).

Diagnosis

The genus *Tetranematichtys* differs from all other members of the Ageneiosidae by the retention of a single pair of mental barbels in adults. Further distinguished from confamilials by a combination of the greater body depth; very elongate, edentulate maxillary barbels in nuptial males; a fatty middorsal keel between the dorsal fins; swimbladder large and with a single, fleshy, posterior caecum; caudal fin truncate, with 8 + 10 principal rays, and relatively few (8-11) lower procurrent rays; presence of a short postcleithral process, shared only with *A. brevis*; and the unusually dark, cryptic coloration. Apart from these differences,

Tetranematicthys can be distinguished from all other catfishes by a combination of the features presented in the family diagnosis and the description of *Ageneiosus*.

Tetranematicthys quadrifilis (Kner)
Figs. 1, 3, 15, 16, 18, 20, 24, 26-28, 31, 36-37
Table 7

Ageneiosus quadrifilis Kner 1858a:442-443, fig. 29 (original description [type locality: Rio Guaporé, Brazil]).

Tetranematicthys quadrifilis: Bleeker 1858:357 (replacement name for *Ageneiosus quadrifilis* Kner); 1862:14 (diagnosis; designation of type species); 1863:108 (after 1862 account). Günther 1864:192-193 (generic diagnosis; description). Eigenmann and Eigenmann 1888:151 (citation); 1891:35 (citation). Gosline 1945:15 (citation). Miranda-Ribeiro 1911:399-400 (in key; description). Miranda-Ribeiro 1962:4 (museum records). Miranda-Ribeiro 1968a:2 (reference); 1968b:1, 3, 6-8, 11 (sexual dimorphism; figure of male; comparison with auchenipterids; placed in family Trachycoristidae); 1968c: 3-5 (genus name misspelled as *Tatranematicthys*; sexual dimorphism; generic synonymization with *Trachycorystes*). Britski 1972:24, 31, 33, 38, 46, 102-103 in part; synonymy; description; morphology; relationships). Böhlke 1980:151 (barbels). Sands 1984:15, 23 (mentioned in account of *Gelanoglanis*; specific epithet misspelled *quadrifilis*). Ferraris 1988:3-4, 21, 29, 30, 37, 56, 58, 71, 120-121, 151, figs. 5, 45 (morphology; diagnosis and phylogenetic relationships). Burgess 1989:285-286 (in key; illustration after Fowler 1951; taxonomic remarks and brief description; citation). Curran 1989:412, 414, 418 (phylogenetic relationships).

Diagnosis

As given above for the genus. Only one species of *Tetranematicthys* is presently known.

Description

Maximum size to 190 mm SL in the material examined. Head blunt, body moderately robust, compressed, and very deep in comparison to species of *Ageneiosus*. Principal morphometric characters are summarized in Table 7. The number of specimens is indicated parenthetically following meristic counts in the following description; values for the holotype are indicated with an asterisk.

Head short (24-28% SL in length), broad (20-23 % SL in width), and relatively deep (66-76% at occiput). Dorsal profile acutely sloping upward to dorsal fin origin, very concave above occiput in larger specimens, the supraoccipital and nuchal shield forming a prominent convex hump in mature males. Snout short (47-53% SL), very broadly rounded in dorsoventral profile. Gape broad, gently recurved (Figs. 1, 3). Lips thick and fleshy. Premaxillary tooth patch narrow, with numerous minute, villiform teeth. Dentary teeth similar to those on premaxillary, symphysis of dentaries with an upturned knob. Maxillary barbels of females and immature males filiform, extending to or beyond rictus. Maxillary groove continued beyond corner of mouth as furrow beneath eye, reaching to interopercle as shallow groove in mature males. Maxillary barbels of nuptial males very long and sinuous, ossified most of length and covered by thin, pigmented epidermis, with a series of transverse ridges or weak tuberculations on the dorsal surface (Fig. 16a); barbels lying within shallow postriatal groove when retracted, held vertical to the main body axis when adducted. Skin on top of head thick, generally not exposing superficial texture of the neurocranial bones, except on the nuchal plate. Fontanelle relatively short, terminating posteriorly at a point about even with a plane passing through the middle of the orbit; internal opening of fontanelle considerably smaller than at surface of frontals, evident as an opaque, elliptical area near the posterior part of the surface groove. Eyes fairly deeply recessed, covered by thick opaque skin.

Anterior nares directed forward, just medial to bases of maxillaries, completely surrounded by short tubular valves. Posterior nares remote from anterior pair, lateral to but not bordering edges of frontals, each surrounded anteriorly and laterally by a continuous thin flap which overlaps at back. Prominent neuromast pores on head and chin arranged as follows: three between and medial to each pair of nares, two proximal to each other and behind anterior nare, the third near the lateral margin of the frontal, slightly in front of the posterior nare; one pore above the middle of the orbit; one pore immediately behind the eye; a pair on the inner margins of the posterior portion of the fontanelle; one on each side of the supraoccipital; one just behind the sphenotic; a series of 10-11 on each side of the chin, extending from the symphysis of the lower jaw, along the surface of the dentary, to a point above and behind the orbit. Gill membranes narrowly fused to isthmus. Branchiostegals 10-12, moderately recessed beneath relatively thick skin.

Dorsal fin relatively short in females and non-breeding males. Dorsal fin spine stout, with a series of relatively short, retrorse serrae on outer two thirds or more of posterior margin. Back with a very thick, rounded, fatty keel, gently rising above dorsal contour of the body, beginning about where longest adpressed dorsal rays reach, and extending to and continuous with top margin of adipose fin. Base of adipose fin obliquely angled downward, the fin forming a short, posteriorly directed flap. Caudal fin truncate or only slightly emarginate, obliquely slanted forward from tip of upper to tip of lower lobe, due to the asymmetrical number of procurrent elements; 8 + 10 principal rays, 18-23 (modally 20) lower procurrent, and 8-11 (modally 9) upper procurrent rays. Base of anal fin gently sloping upward from front to back; fin relatively long, total rays numbering 38 (1), 39 (1), 40 (2), 41* (3), 42 (6), 43 (4), 44 (1), or 48 (1). Two or three fewer anal pterygiophores than anal rays, ranging from 36 to 44, modally 40. Pectoral fin short, barely reaching to or slightly beyond pelvic origin in small specimens, falling considerably short of pelvic

origin in larger specimens. Pectoral-fin spine relatively short, pungent (Fig. 26f); anterior margin rugose, posterior margin with from about 13 to 25 sharp, retrorse serrae, which increase in number with larger body size (the count given here is for specimens ranging from 80 to 164 mm SL). Soft pectoral rays 9 (2), 10* (15), or 11 (3), the innermost lepidotrichia very short.

Color in Alcohol

Entire head and body overall tan to chocolate brown, darkest dorsally, with a variable degree of mottling (Fig. 36). Top of head and dorsum very dark brown to black, slightly mottled. A dark brown or black stripe just in front of eye, extending posteriorly as a prominent broad stripe slanting slightly obliquely downward from rear margin of orbit to edge of opercular flap at or just above pectoral origin. Top half of opercular flap generally somewhat lighter than rest of head. Chin, throat, and belly dark brown. Dorsum and sides of body irregularly mottled with dark brown or black blotches or spots, and always with a large triangular black spot just behind upper end of gill opening and a thin black line along most or all of entire length of lateral line. Background color on body consists of relatively large, discrete chromatophores that often have a reticulated or honeycomb-like appearance at high magnification; the spots and blotches are formed from dense accumulations of pigment.

All fins are relatively dark brown. The dorsal, adipose, and paired fins are rather uniformly pigmented throughout, except for a thin white stripe along entire distal margin of the dorsal and paired fins (slightly broader near the base of the posterior dorsal rays). The caudal and anal fins often have some degree of mottling similar to that on the body. Tail occasionally with one or two faint vertical light bars or bands towards the base, and generally with a thin unpigmented stripe on the

distal margin, slightly wider at tip of upper lobe. Anal fin with several large brown or black spots near the base, and with a dark black marginal band.

Distribution

Tetranematicthys quadrifilis is widely distributed throughout both the Orinoco and Amazon basins (Fig. 37). The widely disjunct records and the relatively small amount of material deposited in museums probably reflects difficulty in collecting this species, rather than natural rarity.

Etymology

The generic name from the Greek *tetra*, four, and *nematos*, thread; the specific epithet from the Latin *quadrus*, fourfold, and *filum*, thread. Both names of the binomen emphasize the presence of four barbels in adults of this species.

Ecology

Nothing published. In terms of its preferred habitat, *Tetranematicthys* may be more similar to most auchenipterids than to other ageneiosids; cursory observations by H. A. Britski (personal communication) are that *T. quadrifilis* is found in relatively slow-moving backwater areas or small streams, such as in gallery forests, in contrast to species of *Ageneiosus*, all of which are most commonly collected in the main channels, lakes, or oxbows of large rivers.

Comments

See section on nomenclatural status of the genus *Tetranematichthys* for a detailed discussion of the taxonomic history of this species.

Material Examined

Type Material. – Holotype: NMW 43343 (female, 76.5), Rio Guaporé, Brazil.

Brazil. – Para: CAS 6424 (male, 109), Rio Amazonas, Santarem market, December 1924. MZUSP 9354-9355 (male, 130; female, 155), Igarape, Pacui, km 97 on road between Belem and Brasilia, 15 August-20 October 1959. MZUSP uncat. (male, 66.4), Igarape, bank of Rio Tapajos, near Boim, 27 October 1970, EPA. MZUSP uncat. (female, 125), Igarape do Limão, bay on Rio Tocantins, 9 September 1970, EPA. Amazonas: MZUSP 30590 (female, 141), Rio Negro, M. Goulding. MZUSP 30591 (male, 122), Rio Negro, Rio Arirara, near mouth, 8 October 1979, M. Goulding. Mato Grosso: MZUSP 37517 (2 males, 115-116; 4 females, 119-142), Rio Guaporé, Vila Bela da Santissima Trindade, 28-30 September 1984, J. C. Garavello.

Venezuela. – Bolivar: ANSP 135821 (8 males, 76-136; 4 females, 78-164), Caño Morichal Zamorai between Rio Tiquire on Maripa-Cuidad Bolivar highway, approximately 7°28' N, 64°54' W, 3 February 1977, J. E. Böhlke et al. MCNG 6697 (male, 139), Caño Caripito at El Palomo, 6°34' N, 66°51' W, 30 March 1982, D. C. Taphorn et al. Amazonas: MCNG 3018 (male, 129), Río Manapiare, between Yutaje and El Salto, 16 March 1981, S. Reid and C. G. Lilyestrom. MCNG 6334 (male, 163; female, c/s), procedentes del Acuario de Valencia, November 1981. USNM 269994 (male, 146), Caño Chola where crossed by road from San Carlos de Rio Negro to Solano, 5 December 1984, R. P. Vari et al. USNM 269995 (female,

121), Caño Urami just upstream of Santa Lucia, 1°17'N, 66°51'W, 6 December 1984, R. P. Vari et al. USNM 270008 (female, 190), Caño Loro where crossed by road from San Carlos de Rio Negro to Solano, 1°59'N, 66°58'W, 7 December 1984, A. Machado and D. Ibarra.

Colombia. - Meta: ANSP 128688 (male, 110), Caño el Viento-Finca el Viento S of Mata Azul, approximately 4°8-9' N, 72°39' W, 18 March 1973, J. E. Böhlke et al. ANSP 134591 (female, 146), "Rancho el Viento", stream about 33.5 km NE of Puerto López, approximately 4°8-9' N, 72°39' W, 31 May 1969, J. E. Böhlke et al.

Locality Unknown: USNM 179477 (male, 138), aquarium specimen.

Table 7. – Proportional measurements of *Tetranematichtys quadrifilis*. Measurements 2-21 are expressed as thousandths of standard length (SL); measurements 22-34 are expressed as thousandths of head length (HL).

	HOLOTYPE (NMW 43343)	NON-TYPES (N = 12)	
		Range	Mean
1. Standard length (SL, mm)	79	93-164	----
2. Preadipose length	835	823-892	846
3. Preanal length	554	542-604	571
4. Predorsal length	289	288-321	307
5. Prepelvic length	443	422-477	443
6. Prepectoral length	304	262-305	280
7. Pectoral origin to dorsal origin	202	215-235	223
8. Pelvic origin to dorsal origin	278	260-315	282
9. Pelvic origin to adipose origin	476	459-514	488
10. Dorsal origin to adipose origin	481	531-589	558
11. Adipose origin to anal insertion	139	143-168	155
12. Body depth at dorsal origin	215	217-261	237
13. Caudal peduncle depth	99	90-119	107
14. Caudal peduncle length	76	81-92	85
15. Body width at pectoral origin	239	208-247	223
16. Body width at pelvic origin	----	105-123	113
17. Dorsal spine length	----	137-377	*
18. Pectoral spine length	148	141-206	156
19. Pelvic fin length	177	152-180	169
20. Anal-fin base length	405	366-405	389
21. Head length (HL)	291	245-284	266
22. Head depth at occiput	652	656-758	702
23. Head width at postorbitals	----	735-885	821
24. Dorsal interopercular width	----	496-550	522
25. Anterior internarial distance	326	358-409	389
26. Anterior-posterior narial distance	----	177-217	198
27. Preisthmus length	522	621-708	667
28. Isthmus width	----	84-128	112
29. Snout length	426	469-529	504
30. Gape width	570	607-708	653
31. Upper jaw length	457	404-491	449
32. Lower jaw length	348	376-447	409
33. Eye diameter	196	146-204	173
34. Barbel length	143	208-770	**

*Mean length of dorsal fin spine in nuptial males = 342 (N = 4); females and non-nuptial males = 163 (N = 8).

**Mean barbel length in nuptial males = 724 (N = 4); females = 255 (N = 7).

Fig. 36.—Composite illustration of nuptial male *Tetranematichthys quadrijilis*. Outline redrawn from Miranda-Ribeiro 1968b (pl. 6), MNRJ 3580, about 150 mm SL; coloration based on several preserved specimens.

Fig. 37. – Geographic distribution of *Tetranematicthys quadrifilis*.

Genus *Ageneiosus* LacepèdeGeneric Synonymy

Ageneiosus Lacepède 1803 (type species: *Silurus armatus* Lacepède, by subsequent designation of Eigenmann and Eigenmann 1890).

Ceratorhynchi Agassiz 1829 (type species: *C. militaris* Agassiz in Spix and Agassiz 1829 [= *A. armatus* Lacepède], by monotypy; genus name emended to *Ceratorhynchus* by most authors).

Hypothalmus Schomburgk 1841 (type species: *Hypothalmus dawalla* Schomburgk [= *A. brevifilis* Valenciennes], by monotypy).

Davalla Bleeker 1858 (type species: *Hypophthalmus davalla* Schomburgk [error in spelling of *Hypothalmus dawalla*], by monotypy).

Pseudogeneiosus Bleeker 1862 (type species: *Ageneiosus brevifilis* Valenciennes in Cuvier and Valenciennes 1840, by original designation).

Ageniosus Günther 1864 (incorrect subsequent spelling).

Tympanopleura Eigenmann 1912 (type species: *T. piperata* Eigenmann, by original designation).

Ageneisus Steindachner 1915 (incorrect subsequent spelling).

Diagnosis

As given in the family diagnosis, exclusive of the character states that are unique to *Tetranematichthys*.

Description

Small-to-medium sized, sexually dimorphic, semipelagic catfishes with the following unique combination of characters.

Body naked, without dermal plates or scutes, moderately elongate and strongly compressed from behind pectoral fin to base of tail. Body depth greatest at dorsal fin origin, gradually tapered to middle of caudal peduncle. Body width greatest at origin of pectoral spines, least at middle of caudal peduncle. Lateral line on body consisting of a midlateral central canal, with numerous short rami, directed posterodorsally and posteroventrally, and bifurcated at the base of the caudal fin, with a long, branched ramus extending onto each lobe of the fin.

Head large, broad, and strongly depressed. Eyes moderately large, ventrolaterally placed, slightly recessed in orbits and visible in ventral profile. Optic nerve displaced laterally and obliquely across the upper surface of the adductor mandibulae musculature. Orbital rim entire, covered with thick integument that is confluent with skin on head. Eye frequently invested by adipose tissue, especially along anterior and posterior margins. Skin on head relatively thin, smooth, covered with minute tastebuds. Snout moderately long, mouth weakly to strongly inferior. Gape moderately to very broad, usually exposing a portion of the premaxillary teeth. Lips generally thin. Nares widely separated, each surrounded with a very low fleshy fold. A deep groove above the upper lip at each corner of the mouth, beginning just behind the maxilla, extending slightly beyond edge of premaxillary, and curving around and beneath the corner of dentary for a short distance anteriorly. Maxillary barbels of females and nonbreeding males short, filiform, lying concealed within aforementioned rictal grooves. Maxillary barbel of nuptial males extending to corner of eye or beyond, with a bony core formed from an ossified extension of the maxilla, and with several sharp, anterodorsally curved protuberances on upper margin. Barbels on chin present only in small juveniles, consisting of a single pair positioned posterolaterally, about even with the front margin of the eye in most species, and another pair situated anteromedially, near the apex of the dentary; barbels completely resorbed or reduced to very minute stubs in adults, and with no

apparent cartilaginous or fibrous core. Gill membranes broadly joined to isthmus at a plane even with or behind the orbits. Branchiostegal rays displaced onto throat in a fan-like fashion, covered by thick skin.

Neurocranium very flattened, with relatively thin bones that often are highly vacuous except in very large individuals. Frontals constricted along lateral margins, forming medial border of orbit. Sphenotic relatively small, with a short anterolateral projection at posterior position of infraorbital canal. Palatine broad, plate-like. Nasals forked, each with an anterolateral accessory branch. Cranial fontanelle relatively large on upper surface, converging to a smaller posteroventral opening above brain. Supraoccipital relatively flat and broad, weakly rugose; strongly concave in nuptial males, posterior end strongly inflected upward at base of dorsal fin. Accessory bone formed from modified second dorsal fin basal absent from surface of nuchal shield.

Six anteriormost vertebrae fused to form Weberian complex. Anterior parapophysis of fourth vertebra elongate, with triangular or oval plate-like tip (= Müllerian ramus), closely impinging on anterolateral face of swimbladder in species with an unencapsulated swimbladder. Müllerian ramus of species with encapsulated swimbladders relatively small. Anterior supracarinalis muscles originating on ventral surface of supraoccipital and inserting on anterodorsal aspect of Müllerian ramus, thereby forming an elastic spring mechanism (ESA). Swimbladder oval to pyriform-shaped, with posterior caecae in most species, and either large and relatively turgid, or enclosed by bony capsules formed from superficial ossification of the complex centrum. First pleural rib articulating with parapophysis of sixth vertebra; four to eleven additional pairs of ribs posteriorly. Total vertebrae, including six for the Weberian complex and one for the fused preural centra, ranging from 38-58.

Dorsal fin small, anteriorly situated to just behind neurocranium and above Weberian complex, first basal inserted above fourth vertebral centrum. First dorsal fin lepidotrichium forming a small, "V"-shaped locking spine. Second dorsal fin lepidotrichium of females and nonbreeding males typically forming a relatively weak, posteriorly serrated spine, except in *A. brevifilis*, *A. marmoratus*, and *A. polystictus*, in which the element forms an unbranched, segmented ray. Dorsal fin spine of nuptial males elongated and hyperossified, smooth on posterior margin, with numerous antrorse serrae along anterior margin. Dermal component of basal radial of second dorsal fin ray completely fused to supraoccipital. Adipose fin relatively small, constricted at base.

Caudal fin deeply forked, emarginate, or obliquely truncate; upper lobe with 8 principal rays, lower lobe with 9-10 principal rays, and a variable but relatively large number of procurrent rays in each lobe. Lower hypural plate consisting of fused parhypural and lower two hypurals; upper hypural plate formed by fused third and fourth hypurals; fifth hypural free or only weakly co-ossified with upper hypural plate. One epural present, closely abutting posterior margin of neural spine of last free vertebra. Primary and secondary hypurapophyses fused to form a shallow horizontal keel that extends midway or beyond the upper margin of the second hypural.

Anal fin relatively long, with between 25 and 45 lepidotrichia; first anal pterygiophore generally with one or two very small, deeply embedded splints anteriorly and a longer ray posteriorly. Last anal pterygiophore with a laminar posterior extension, usually supporting two or three branched rays. Anal fin of nuptial males with third through seventh lepidotrichia elongated, thickened, and coalesced, forming an intromittent organ; interradsial membranes over thickened rays swollen; gonopore displaced on distal tip of modified anal rays.

Pelvic fins abdominal, horizontally oriented. Pelvic basipterygia relatively flat or weakly concave ventrally, with a broad cartilaginous plate medially, cartilaginous spurs anterolaterally, and flat, pointed processes posteriorly. Pelvic fin with one anterior, unbranched ray and six multifurcated rays; last ray joined by interradial membrane to belly integument basally for about one-third of its length. Shape of pelvic fin broadly triangular.

Pectoral fin base horizontal, originating at posteroventral curve of opercular flap. First pectoral lepidotrichium normally thickened and unsegmented, forming weak to moderate spine with relatively weak serrae on posterior margin and no serrae on anterior margin; in some species, however, the first element is not formed into a stiffened spine, although it remains unbranched. Rest of fin with 5-15 branched rays, progressively shorter medially. Mesocoracoid absent. Third pectoral radial expanded distally and supporting several rays. Cleithra broadly sutured at midline. Superior cleithral process forked dorsally, deeply articulating with posttemporal. Posterior cleithral (= humeral) process absent, or, if present, forming very short, weakly rugose spine.

Pigmentation on head and body variable, but frequently consisting of irregular mottling or spotting. Pigmentation on fins also variable, ranging from virtually immaculate to weakly or strongly mottled or striped; pigment on tail often in the form of crescent-shaped or oblong spots or stripes.

Ageneiosus brevis Steindachner

Figs. 1, 4, 17, 18, 20, 38-39

Tables 8-9

Ageneiosus brevis Steindachner 1879:16-17 (original description [type locality: Amazon river at Coari, Brazil]). Eigenmann and Eigenmann 1888:149 (citation); 1890:300-302 (in key; partial synonymy; description); 1891:35 (citation). Miranda-Ribeiro 1911:403-404 (in key; description). Gosline 1945:24 (citation). Fowler 1951:452 (partial synonymy; distribution). Britski 1972:99, 106 (citation). Ferraris 1988:124 (citation). Burgess 1989:286 (citation).

Ageneiosus rondoni Miranda-Ribeiro 1914:12-13 (original description [type locality: Rio Negro, Manaus, Brazil]). Miranda-Ribeiro 1962:4 (holotype listed). Gosline 1945:25 (citation). Fowler 1951:453, fig. 480 (partial synonymy; distribution; figure possibly based on *A. atronasus*). Santos 1954:123-124, fig. 64 (reference). Britski 1972:100, 109-110 (swimbladder unencapsulated; citation). Ferraris 1988:126 (citation). Burgess 1989:286 (citation).

Ageneiosus madeirensis Fisher 1917:426-427, pl. 42 (original description [type locality: Río Machupo, San Joaquin, Bolivia]; comparisons with *A. ucayalensis* and *A. valenciennesi*). Henn 1928:74 (holotype listed). Gosline 1945:24 (citation). Fowler 1951:452-453, fig. 479 (partial synonymy; distribution). Britski 1972:100, 108 (citation). Ibarra and Stewart 1987:6, 86 (type specimens listed). Ferraris 1988:126 (citation). Burgess 1989:285-286 (citation; illustration after Fisher 1917 [erroneously attributed to Eigenmann]).

Tympanopleura alta Eigenmann and Myers, in Myers 1928:85 (original description [type locality: Río Marañon, Peru]). Eigenmann and Allen 1942:139-140, plate 6, fig. 4 (types listed; description). Fowler 1945:67 (citation). Gosline 1945:26 (citation). Fowler 1951:456, fig. 483 (partial synonymy; distribution). Britski 1972:105 (placed in *Ageneiosus*). Ortega and Vari 1986:14 (citation; common name). Burgess 1989:285-286 (citation; illustration after Fowler 1951).

Ageneiosus altus: Britski 1972:100,105 (new combination; citation).

Ageneiosus alta: Ferraris 1988:126 (citation).

Diagnosis

A distinctive ageneiosid characterized by the combination of a small adult body size; strongly arched occiput; short and broad snout; moderately stout pectoral-fin spine; large swimbladder; and a short postcleithral process (shared only with *Tetranematichthys*). Some individuals in life have pronounced spots on the head, dorsum, and upper sides of the body in a configuration unlike any other species, with the exception of *A. polystictus*. *Ageneiosus brevis*, however, is not likely to be confused with *A. polystictus*, due to many external differences, including maximum body size and shape of the tail. A combination of the small size and the large, unencapsulated swimbladder separates *A. brevis* from all congeners except *A. atronasus* and *A. piperatus*. Distinguished from *A. atronasus* by a much longer anal fin (29-42 rays versus 23-30); fewer preanal vertebrae (modally 14 versus 17); fewer pleural ribs (5-6 versus 7-8); longer and more total gill rakers on outside row of first arch (21-32 versus 14-18); and usually an unmistakable difference in pigmentation. *Ageneiosus brevis* is distinguished from *A. piperatus* by its larger adult body size; greater number of pectoral fin rays (modally 11 versus 9); fewer preanal vertebrae (modally 14 versus 16); greater number of branchiostegals (modally 9 versus 7); presence of posterior swimbladder caecae; and differences in pigmentation.

Description

A small ageneiosid, most specimens not exceeding 125 mm SL; the largest specimen examined measured 160 mm SL. The principal meristic and proportional measurements are summarized in Tables 8-9.

Head relatively short (26-32% SL) and broad (19-23% SL). Dorsal contour of head smoothly sloping upward to eye, acutely angled from rear margin of fontanelle to dorsal origin; strongly concave in breeding males. Snout broadly

rounded or squared off in dorsoventral profile. Gape small and gently curved near rictus. Mouth weakly inferior, upper jaw extending slightly beyond lower, by a distance equal to or slightly less than premaxillary tooth band. Teeth on premaxillae short, setiform, in relatively narrow bands tapering gradually to corners of mouth. Dentary tooth patches similar to those on premaxillae, slightly curved upward at symphysis. Anterior nares at edge of upper lip, just lateral to mesethmoid cornua, directed forward. Posterior nares remote from anterior pair, encircled by short, posteriorly directed flap of skin. Surface groove of fontanelle moderately long (20-40% HL), the inside opening considerably shorter. Eyes moderately small (15-21% HL) and sublateral. Gill membranes broadly connected to isthmus. Branchiostegal rays 7-10, modally 9. First epibranchial with 7-10 long, crenulate gill rakers in outer row; first ceratobranchial with 13-23 rakers; total number of gill rakers on outside row of first arch 21-32. One or two pairs of very short chin barbels in small specimens, reduced to tiny vestiges or completely absent in individuals greater than about 50 mm SL. Maxillary barbel short and filiform, concealed in rictal groove in females and nonbreeding males; maxillary barbels of nuptial male long, reaching to or beyond front of eye, with about 7-14 sharp, antrorse odontodes on dorsal margin.

Body moderately broad at pectoral-fin base, markedly compressed posteriorly to caudal peduncle. Body depth relatively great at dorsal fin origin (18-24% SL). Dorsal contour from dorsal fin to tail nearly straight to weakly convex. Ventral profile from snout to anal-fin origin gently curved.

Dorsal fin in all but nonbreeding males relatively short. Dorsal-fin spine moderately robust and short (14-21% SL), weakly serrated along most of posterior margin. Dorsal spine of nuptial males elongated and strongly serrated along entire anterior margin, with from about 20 to 65 sharp, antrorse odontodes. Adipose small and flap-like, free portion of posterior margin large. Caudal fin deeply forked, with

8 + 9 principal rays, and about 17-25 ($\bar{X}$ = 21) upper and 13-18 ($\bar{X}$ = 16) lower procurent rays. Number of anal-fin rays extremely variable, ranging from 29-42 ($\bar{X}$ = 35). Anal pterygiophores equally variable, ranging from 27-38. Anterior 3-6 or 7 anal rays thickened and lengthened to form slightly recurved gonopodium in nuptial males. Pectoral-fin spine short (16-23 %SL) and relatively robust in comparison to congeners; dorsal and ventral margins of shaft with 2-3 prominent longitudinal grooves and ridges, granular near base; posterior margin of spine with about 12-30 fairly long, sharp, retrorse serrae, in a single row distally, broken into 2 or 3 rows near base. Soft pectoral rays 9-12, modally 11.

Total vertebrae 38-43, modally 40. Preanal vertebrae 13-16, modally 14. Swimbladder of adults very large, peritoneal tunica moderately turgid and thickened where internal septae contact interior walls, with two long, tubular posterior caecae (Fig. 20e). Müllerian ramus expanded into discoidal plate (Fig. 18b), impinging on large anterolateral opening of swimbladder.

Color in Alcohol

Many specimens show little trace of pigmentation, presumably due to an overall light coloration at the time of initial fixation, but also possibly the result of bleaching during long-term storage in preservative. Many specimens, however, have pronounced spots on the head, dorsum, and sides of the body, which is thought to be the typical coloration pattern of the species (Fig. 38). As in other species, there is probably some variation in intensity of pigmentation depending on water clarity. The background color of the entire body consists of an off-white or yellowish tinge. The top of the head, dorsum, and sides above the lateral line are typically peppered with large, discrete brown or black spots consisting of minute, densely aggregated chromatophores, as illustrated by Fisher (1917) in the original description of *A.*

madeirensis; some specimens exhibit an overall darker background coloration, but still have a strongly spotted pigmentation pattern on the sides and body. Heavily pigmented specimens have a crescentic band of melanophores on the anterior half of the chin between the dentaries. Paired fins are generally unpigmented except for scattered brown flecks on top of the pectoral spine and/or the first interradial membrane. Dorsal, adipose, and anal fins are usually unpigmented, but occasionally there are diffuse brown specks at the base and along the distal margin of the anal and the anterior margin of the dorsal.

Distribution

This species is confined to the Amazon River basin, primarily from the headwater drainages in Peru and Bolivia and the upper half of the Amazon (Rio Solimões) proper (Fig. 39). The scattered localities from which specimens are available presumably reflects a lack of intense collecting efforts rather than locally disjunct populations.

Ecology

Nothing published. This species, like *A. atronasus*, matures at a very small size; nuptial males were identified at sizes of about 55-60 mm SL.

Etymology

From the Latin *brevis*, meaning short, in reference to the blunt snout of this species.

Comments

Ageneiosus brevis was described by Steindachner from four specimens ranging in length from 4 to 4.5 inches. Only two specimens (NMW 47801) from the original type series were found in the present study. The larger of these (NMW 47801:1, 104 mm SL) is herein designated the lectotype, and the other specimen (NMW 47801:2, 95 mm SL) becomes the paralectotype. Both were collected from Coary (= Coari), Brazil, by Hyavary.

Two syntypes of *A. rondoni* were examined (MNRJ 962); the larger of these (160 mm SL) is designated the lectotype, and the smaller specimen (134 mm SL) the paralectotype.

In the original description of *A. madeirensis*, Fisher (1917) designated 13 paratypes; the parotypic series (FMNH 58144) presently has 14 specimens, however, and I assume that either Fisher miscounted his specimens or there was a typesetting error.

The type specimens of *T. alta* were listed as from the Rio Maraon, Iquitos, Peru; the city of Iquitos, however, is not on the Rio Maraon proper, and the precise area from which these specimens were collected cannot be ascertained.

Specimens of *Ageneiosus brevis* examined in this study were relatively variable in the number of anal-fin rays, gill rakers, and vertebrae, and also in the presence of a postcleithral process, general body shape, and in coloration. At present, I consider this variation to be intraspecific, since in some cases individuals from the same collection exhibited extremes of polymorphism. No clearly defined geographic differences could be found in these characters in the material examined. With regard to the presence of a postcleithral process (PCP), I consider *A. brevis* to be intermediate between *Tetranematichthys*, in which the PCP is invariably present, and all other species of *Ageneiosus*, in which it is consistently absent. Relative to

other doradoids, the PCP of both *Tetranematicthys* and *A. brevis* is very weak, which I assume is a derived condition relative to outgroups, but primitive with respect to other species of *Ageneiosus*. This reduction or loss of the PCP is analogous to the absence of an adipose fin in some catfishes, such as in *Helogenes*, in which both character states were observed to be present among individuals in the same population (Vari and Ortega 1986).

Material Examined

Type Material. – NMW 47801 (2, 95-104, syntypes of *A. brevis* [see designations above]), Coary (= Coari), Brazil.

Bolivia. – Beni: AMNH 56069 (1, 63.2), Río Mamore, Puerto Siles, 4 December 1965, S. Anderson. FMNH 58143 (holotype of *A. madeirensis*; probable male, 102), San Joaquin, 6 September 1909, J. D. Haseman. FMNH 58144 (14 paratypes of *A. madeirensis*; 32.8-108.3 [1 c/s]), San Joaquin, 6 September 1909, J. D. Haseman. MZUSP 27805 (2 males, 119.6-124.0; 3 females, 79.5-110.8), Laguna San Jose, Trinidad, September 1983, Conv. Pisc. ORSTOM-UTB. MZUSP 27818 (3, 51.2-69.0), canal San Gregório, Trinidad, September 1983, Conv. Pisc. ORSTOM-UTB.

Brazil. – Amazonas: MCZ 7733 (1, 74.8), Coary (Thayer expedition), L. Agassiz. MCZ 36190 (1, 93.5), Coary (Thayer expedition). MNRJ 962 (syntypes of *A. rondoni*, 2 females, 134.4-160.4), Rio Negro at Manaus, 1908, A. Miranda-Ribeiro. MZUSP 6998 (male, 59.0), Rio Madeira, 25 km below Nova de Olinda, 27 November 1967, EPA. MZUSP uncat. (3 males, 63.2-66.0; 1 female, 65.4), mouth of Rio Ituxi, 22 December 1974, P. E. Vanzolini. MZUSP uncat. (1, 58.1), mouth of Rio Pacia, 23 December 1974, P. E. Vanzolini. MZUSP uncat. (3, 47.5-49.8), Rio Purus, Cassiã, 3 January 1975, P. E. Vanzolini. MZUSP uncat. (1, 65.1), Rio Purus,

Santa Luzia, 11 January 1975, P. E. Vanzolini. MZUSP uncat. (2 males, 54.1-62.3), Rio Purus, Campina, P. E. Vanzolini. MZUSP uncat. (2 males, 107.5-117.4; 2 females, 115.4-116.6), Lago Janauacá and vicinity, September 1976-January 1977, R/V *Alpha Helix* expedition. Para: MZUSP 7862-7874 (5 males, 90.7-110.7; 8 females, 86.2-117.6), Parana Jacarí, municipality of Fars, 13 December 1967, EPA. MZUSP 34417 (25 of 570, 47.5-77.3), Rio Madeira, Calama, shoreline at Caraparu, 13-16 December 1980, M. Goulding. MZUSP 34418 (4, 68.4-75.7), Rio Madeira, Calama, Paraná do Flechal, M. Goulding.

Peru. – ANSP 139065 (male, 59.0), Río Nanay opposite naval base, vicinity of Iquitos, backwater pools about 4 mi above Rio Solimoes, 12 October 1955, C. G. Chaplin et al. CAS 58259 (paratype of *T. alta*, probable female, 104.8), Iquitos, 1922, Morris. CAS-IU 15790 (holotype of *T. alta*; female, 109), Río Maraño, 1920. CAS-SU 58750 (male, 63.0), Yahnas Yacu, near Pebas, 24 July 1941, W. G. Scherer. MZUSP 26268 (male, 66.2; female, 73.6), Province Coronel Portillo, Yarinacocha, Pucallpa, 9 August 1973, H. Ortega. MZUSP 25972 (5, 41.5-75.9), Province Coronel Portillo, Río Ucayali, Masisea, 6 October 1975, H. Ortega. USNM 124918 (3, 64.3-68.2), Shansho Caño, 4 December 1935, W. G. Scherer. USNM 270812 (male, 72.2; female 56.4), Loreto, Pucallpa, Río Ucayali, Tachshitea, 3 October 1984, H. Ortega. MHNG 2394.39 (3 males, 56.5-61.0), confluence of Rio Calleria with Rio Ucayali, Cocha Tachsita, 3 October 1984, P. de Rham and H. Ortega.

Table 8. – Summary of principal meristic characters of *Ageneiosus brevis*.

	NON-TYPES*				PARALECTOTYPE (NMW 47801:2)
	Range	Mode	Mean	N	
Pectoral-fin Rays	9-12	11	10.8	87	11
Anal-fin Rays	29-42	36	34.9	76	34
Branchiostegal Rays	7-10	9	8.6	56	8
Total Gill Rakers	21-32	---	25.5	19	22
Pleural Ribs	5-6	5	5.4	31	5
Total Vertebrae	38-43	40	40.8	68	40
Preanal Vertebrae	13-16	14	14.4	62	14

*Includes 2 syntypes of *A. rondoni* and 15 types of *A. madeirensis*.

Table 9. – Proportional measurements of *Ageneiosus brevis*.

Measurements 2-21 are expressed as thousandths of standard length (SL);
measurements 22-34 are expressed as thousandths of head length (HL).

	LECTOTYPE (NMW 47801:1)	NON-TYPES (N = 11)	
		Range	Mean
1. Standard length (SL, mm)	104	57.5-93.5	----
2. Preadipose length	815	670-828	800
3. Preanal length	633	513-636	592
4. Predorsal length	395	319-405	366
5. Prepelvic length	500	435-526	482
6. Prepectoral length	320	274-338	300
7. Pectoral origin to dorsal origin	232	205-241	227
8. Pelvic origin to dorsal origin	237	195-262	233
9. Pelvic origin to adipose origin	383	354-417	384
10. Dorsal origin to adipose origin	463	433-510	464
11. Adipose origin to anal insertion	130	99-152	134
12. Body depth at dorsal origin	207	178-235	210
13. Caudal peduncle depth	85	66-114	91
14. Caudal peduncle length	113	102-129	117
15. Body width at pectoral origin	221	211-243	227
16. Body width at pelvic origin	111	88-120	103
17. Dorsal spine length	178	141-259	*
18. Pectoral spine length	219	159-231	202
19. Pelvic fin length	160	141-177	158
20. Anal-fin base length	299	264-399	308
21. Head length (HL)	313	264-324	298
22. Head depth at occiput	488	517-715	582
23. Head width at postorbitals	644	628-790	696
24. Dorsal interopercular width	436	433-554	507
25. Anterior internarial distance	337	290-341	328
26. Anterior-posterior narial distance	196	156-200	178
27. Preisthmus length	629	638-828	721
28. Isthmus width	224	270-511	408
29. Snout length	506	393-493	438
30. Gape width	537	508-653	560
31. Upper jaw length	396	326-393	359
32. Lower jaw length	347	295-373	325
33. Eye diameter	175	147-211	189
34. Barbel length	101	110-296	**

*Mean length of dorsal fin spine in prenuptial males = 226 (N = 3); females and non-nuptial males = 185 (N = 6).

**Mean barbel length in nuptial males = 267 (N = 3); females and non-nuptial males = 139 (N = 8).

Fig. 38.—*Ageneiosus brevis*, FMNH 58143 (holotype of *A. madeirensis*), prenuptial male, 102 mm SL.
Redrawn from illustration by Fisher (1917).

Fig. 39. – Geographic distribution of *Ageneiosus brevis*.

Ageneiosus piperatus (Eigenmann), new combination

Fig. 40

Table 10

Tympanopleura piperata Eigenmann 1912:203-204; pl. 10, fig. 3 (original description [type locality: Essequibo River at Crab Falls, British Guiana {=Guyana}]). Henn 1928:75 (holotype listed). Eigenmann and Myers, in Myers 1928:85 (comments on size and comparison with *T. alta*). Eigenmann and Allen 1942:138 (designated type species of genus). Gosline 1945:25 (citation). Fowler 1951:456 (cited as generic type [orthotype]). Ibarra and Stewart 1987:84,86 (holotype and paratype listed). Burgess 1989:286 (citation).

Ageneiosus piperatus: Britski 1972:104, 109 (cited as generic type [orthotype]; new combination). Ferraris 1988:122, 125, 128 (citation; nomenclatural status of *Tympanopleura*).

Diagnosis

Known at present from very few specimens. A diminutive ageneiosid, reaching sexual maturity at less than 50 mm SL. Further distinguished from all other ageneiosids by a combination of its low numbers of ribs (5), pectoral rays (I+9), and branchiostegals (7-8). Posterior processes of epioccipital pronounced, reaching laterally to skin midway between dorsal and pectoral fins. Swimbladder large in adults, lying just beneath posterior epioccipital processes and extending laterally to skin; integument in area of contact with swimbladder bulging slightly outward, forming semi-translucent, ovoid or triangular membranous patch covered partially by dense concentration of chromatophores. Snout very short, eye large, gape small and not greatly recurved in ventral profile. Body profusely speckled with minute melanophores, condensed into a dark patch on the chin and an hourglass-shaped band across the base of the caudal fin.

Description

This is apparently a paedomorphic ageneiosid, inasmuch as adults reach sexual maturity at a very small size and retain a large swimbladder, and have lower meristic counts than other species. All specimens examined range from 39.7 to 47.5 mm SL. Body elongate, markedly compressed and gently tapering to tail. Head flattened but not especially broad, widest at posterior margins of opercula. Eye large, snout short, dentaries extending to just below rear margin of eye. Gape relatively small, lower jaw subequal to upper; mouth nearly linear in ventral profile, only slightly recurved at corners of premaxillae. A single pair of maxillary barbels, small and filamentous except in nuptial males, each lying concealed in a groove at rictus of upper lip. Maxillary barbels in prereproductive males reaching past rictus and ossified over most of length, bearing four to five incipient odontodes in one paratype and one non-type, but otherwise unornamented in remaining specimens. Mental barbels absent, mandibular barbels absent or reduced to minute fleshy vestiges in adults. Anterior nares near tip of snout, just lateral to tips of mesethmoid flanges. Premaxillary and dentary tooth patches thin, only slightly recurved at posterolateral corners; teeth minute, conical, in few rows. One specimen (ANSP 137688) with 7 long, lanceolate gill rakers in outer row of first epibranchial and 12 rakers in outer row of ceratobranchial. Lateral-line dendritic along body, with short ventral and dorsal rami, bifurcated at caudal peduncle and with a branch extending onto base of each caudal lobe. Proportional measurements of the type specimens are listed in Table 10.

Dorsal fin small, spine stout, edentulate on anterior margin and with about 17-20 weak retrorse denticulations along posterior margin in females (and presumably in non-breeding males); posterior margin edentulate, entire anterior margin with weak-to-moderately developed antrorse odontodes in prereproductive

males (numbering 34 in one specimen). Anterior rays of anal fin thickened, coalesced to form incipient gonopodium in nuptial males. Pectoral spine stout, armed with about 13-15 sharp, retrorse odontodes along entire posterior margin; anterior margin smooth or very weakly crenulate. Posterior cleithral process absent. Tail deeply forked.

Meristic counts as follow (number of specimens in parentheses, counts of holotype marked with an asterisk): dorsal rays I+6* (7); pelvic rays i+6* (7); pectoral rays I+9* (4) or I+10 (1); anal pterygiophores 33* (3), 34 (2), or 35 (1); anal rays 35* (3), 36 (2), or 37 (1); principal caudal rays 8+9* (6); upper procurrent caudal rays 17 (2) or 18* (3); lower procurrent caudal rays 14 (1), 15* (2), or 16 (2); pleural ribs 5* (4); preanal vertebrae 15 (3) or 16* (4); total vertebrae 39 (2), 40* (3), or 41 (1).

Swimbladder large, without posterior caecae, longitudinal septum extending posteriorly onto ventromedial surface as stiffened tunica; anterior chamber flexible, lacking complete transverse septum. Lateral margins of swimbladder contacting skin beneath posterior processes of epioccipital, visible externally in region devoid of musculature behind opercula as a large, translucent "lateral cutaneous area" (*sensu* Alexander 1964:425).

Color in Alcohol

Overall background color dusky brown, consisting of minute scattered flecks over dorsum and most of sides (Fig. 40). Paired fins generally hyaline except for scattered spots along outer rays. Dorsal and anal fins with scattered specks along base and anterior rays; adipose with pigment at base only. Base of caudal fin with intense concentration of dense melanophores forming hourglass-shaped band,

narrowest proximally and expanded distally on each lobe of fin, extending posteriorly in some specimens as scattered flecks along longest branched rays.

Melanophores densest on top of head and dorsum of body, gradually diminishing in intensity laterally. Concentrations of pigment forming larger, diffuse spots on top of occiput, across top of snout in front of eyes, on chin, posterolaterally behind postorbitals, and over dorsoanterior half of "tympanum".

Comments

Eigenmann (1912) designated as the holotype a male specimen 64 mm in length (CM 1708), and two males and five females 57-61 mm as paratypes (CM 1707a and IU 12090). One of the specimens has been destroyed or lost, and two others are in poor condition (see comments under nomenclatural status of *Tympanopleura*). Examination of the specimen currently recorded as the holotype indicates that it is probably a female, based on gross and radiographic comparisons of the barbels and anal fin of all specimens. The two largest specimens examined are females, suggesting that Eigenmann erroneously identified the sex of the holotype, that the missing specimen actually represents the holotype, or that some transposition of specimens and data may have occurred during transfer of the type material from the Carnegie Museum and Indiana University. This situation is not redressed by examination of the collection ledgers in the institutions involved. The holotype was listed by Henn (1928) prior to its transfer to the Field Museum.

A more complete understanding of the taxonomic status, morphology, distribution, and ecology of this species will require collection of additional material. Based on its small size at maturity, relative to other ageneiosids, this

species can be added to the preliminary list of miniaturized South American fishes compiled by Weitzman and Vari (1988).

Etymology

From the Latin *piper*, meaning pepper, in reference to the finely stippled pattern of pigmentation on the body.

Distribution

Known only from the type-locality in Guyana and in Brazil from the Rio Negro just downstream from the confluence with the Rio Branco.

Ecology

Nothing published. The smallest male specimen (39.7 mm SL) examined was in nuptial condition, indicating that this species attains sexual maturity at an exceptionally diminutive size.

Material Examined

Type material. – Holotype: FMNH 53243 (female, 47.3), Essequibo River at Crab Falls, British Guiana (= Guyana), 1908, C. H. Eigenmann. Paratypes: 6 specimens, all taken with the holotype; FMNH 53244 (female, 41.7); CAS 58382 (ex IU 12090) (female, 47.5; 2 males, 44.6 and 46.9); MCZ 30189 (female, 46.4); BMNH 1911.10.31.102 (male, 44.8).

Brazil. – Roraima: ANSP 137688 (male, 39.7), near confluence of Rio Negro and Rio Branco, W of Moura, approximately 1° 30' S and 61° 48' W, J. Faughn (R/V *Alpha Helix*).

Table 10. – Proportional measurements of type specimens of *Ageneiosus piperatus*. Measurements 2-21 are expressed as thousandths of standard length (SL); measurements 22-34 are expressed as thousandths of head length (HL).

	HOLOTYPE (Female)	PARATYPES			
		Females (N=3)		Males (N=3)	
		<u>Range</u>	<u>Mean</u>	<u>Range</u>	<u>Mean</u>
1. Standard length (SL, mm)	47.3	41.7-47.5	----	44.6-46.9	----
2. Preadipose length	793	773-806	793	780-821	800
3. Preanal length	529	525-597	568	527-547	535
4. Predorsal length	307	301-336	314	288-305	298
5. Prepelvic length	419	436-463	451	433-437	436
6. Prepectoral length	249	257-266	261	243-244	244
7. Pectoral origin to dorsal origin	195	185-209	196	176-207	195
8. Pelvic origin to dorsal origin	199	218-242	234	241-256	249
9. Pelvic origin to adipose origin	408	374-407	395	404-433	416
10. Dorsal origin to adipose origin	516	459-520	486	507-554	526
11. Adipose origin to anal insertion	135	139-166	155	143-146	145
12. Body depth at dorsal origin	165	183-204	195	194-213	203
13. Caudal peduncle depth	76	82-105	96	94-100	98
14. Caudal peduncle length	125	99-119	111	107-117	112
15. Body width at pectoral origin	182	177-187	182	182-183	183
16. Body width at pelvic origin	----	77-92	84	76-92	83
17. Dorsal spine length	182	157-192	175	181-191	186
18. Pectoral spine length	----	166-168	167	161-166	164
19. Pelvic fin length	154	129-163	150	143-158	151
20. Anal-fin base length	372	319-371	340	356-368	361
21. Head length (HL)	230	232-259	248	222-242	230
22. Head depth at occiput	633	602-682	635	630-683	652
23. Head width at postorbitals	633	583-745	658	657-798	736
24. Dorsal interopercular width	505	536-542	539	537-596	559
25. Anterior internarial distance	----	280-309	294	278-307	292
26. Anterior-posterior narial distance	----	153-200	176	178-185	182
27. Preisthmus length	688	630-818	737	731-752	742
28. Isthmus width	183	167-347	262	267-315	291
29. Snout length	422	398-436	414	370-433	400
30. Gape width	450	389-500	449	472-519	492
31. Upper jaw length	321	322-336	331	317-365	335
32. Lower jaw length	294	287-300	292	277-308	288
33. Eye diameter	284	269-309	289	306-337	320
34. Barbel length	----	155-161	158	278-337	314

Fig. 40.—Holotype of *Ageneiosus piperatus* (= *Tympanopleura piperata* Eigenmann), a 47.3-mm-SL female (FMNH 53243), as redrawn from photograph in Eigenmann (1912). Holotype is presently in poor condition, but most other specimens have retained the body shape and color pattern as illustrated.

Ageneiosus atronasus Eigenmann and Eigenmann

Figs. 1, 6-7, 10, 12, 18, 20, 23, 26, 32, 41-42

Tables 11-12

Ageneiosus atronasus Eigenmann and Eigenmann 1888:119,149-150 (original description [type locality unknown, but probably Amazon River basin; collected by L. Agassiz or field associates during Thayer expedition]); 1890:300, 302-303 (in key; partial synonymy [after Eigenmann and Eigenmann 1888]; description; comparison with *A. brevis*); 1891:35 (citation). Miranda-Ribeiro 1911:402 (diagnosis). Gosline 1945:24 (citation). Fowler 1951:451 (partial synonymy). Britski 1972:105 (citation). Ferraris 1988:124 (citation). Burgess 1989:286 (citation).

Ageneiosus melanopogon Miranda-Ribeiro 1917:51-52 (original description [type locality unknown]). Gosline 1945:25 (citation). Fowler 1951:453 (partial synonymy; distribution). Britski 1972:99, 108 (citation). Ferraris 1988:126 (citation). Burgess 1989:286 (citation).

Tympanopleura nigricollis Eigenmann and Allen 1942:139; plate 5, figs. 2-3; plate 6, fig. 3 (original description [type locality: Iquitos, Peru]). Fowler 1945:67 (citation); 1951:456, fig. 484 (partial synonymy; distribution). Gosline 1945:26 (citation). Ortega and Vari 1986:14 (citation; common name). Burgess 1989:286 (citation).

Ageneiosus nigricollis: Britski 1972:100, 108 (new combination; citation). Ferraris 1988:69, 71-72, 126-128, 151, figs. 5, 45 (citation; diagnosis; morphology of tripus, swimbladder, and elastic spring apparatus; phylogenetic relationships)

Diagnosis

A small species distinguished from all other ageneiosids by a unique combination of the following characters: size small, rarely exceeding 120 mm SL; unusual pigmentation pattern, consisting of a dense semicircular patch of melanophores on the chin, a patch on the flanks above the anal fin, and an elongate stripe radiating from the base of each caudal lobe; relatively low numbers of pectoral fin rays, anal fin rays, and branchiostegals; swimbladder large, unencapsulated, with bilobed anterior chamber and a pair of posterior caecae; snout short, with gape of mouth gently recurved; tooth patches on premaxillae and

dentaries thin, with relatively few, minute teeth. The small body size is shared among congeners only with *A. brevis* and *A. piperatus*. Distinguished from *A. brevis* by differences in pigmentation and a number of meristic counts (see diagnosis of *A. brevis*). Separated from *A. piperatus* by the pigmentation pattern; presence of posterior caecae on the swimbladder; fewer anal-fin rays (23-30 versus 35-37); fewer pectoral-fin rays (7-9 versus 9-10); greater number of preanal vertebrae (17-19 versus 15-16); greater number of branchiostegals (modally 8 versus 7); and, greater number of ribs (modally 7 versus 5).

Description

Morphometrics and diagnostic meristic counts of the species are summarized in Tables 11-12. Dorsal profile of head gently sloping to just behind orbits, then angled upward in a straight line to dorsal fin origin. Ventral profile of head gently curved. Skin on top of head thin, cranial bones moderately textured with ridges, particularly on supraoccipital and nuchal plate. Mouth subterminal, the upper jaw extending only slightly in front of lower jaw. Snout short (37-50% HL), forming a broad arc in dorsal profile (Figs. 1, 6). Premaxillary tooth band crescentic, very narrow and inflected posteriorly near corners of mouth; teeth relatively small and villiform. Dentary tooth patch slightly broader than premaxillary band, recurved at rictus of mouth. Eye large ($\bar{X}$ = 21% HL), covered by thick skin and invested by opaque subepidermal fat deposits on anterior and posterior margins. Fontanelle groove short, deep, bounded by relatively high ridges on central portion of frontals. Anterior nares lateral to distal tip of mesethmoid wings and directed forward; posterior nares remote, not bordering lateral margins of frontals, each with very short flap of skin surrounding entire margin. Posterior tip of dentary reaching to just below middle of eye. Gill membranes fused to isthmus behind plane through

rear margin of orbit. Upper limb of first gill arch with 3-7 (modally 4) thin, weakly crenulate gill rakers in outer row; lower limb with 9-15 (modally 11) rakers. Total number of rakers in outer row of first gill arch 14-23 (modally 16). Maxillary barbels normally small, filiform, concealed in groove above upper lip; barbel of nuptial males elongated, ossified the entire length, and with 4-10 (modally 8) long, sharp, recurved hooks protruding dorsally.

Dorsal profile of body from behind dorsal fin to caudal slightly convex, smooth. Belly slightly rounded from throat to anal fin origin. Ventral contour of body above anal fin angled upward in straight line roughly parallel to dorsal profile of head behind eyes. Caudal peduncle relatively deep ($\bar{X} = 11\%$ SL). Body not markedly compressed at pectoral fin base, but rather gradually tapered to base of tail.

Dorsal spine relatively short, stout, posterior margin armed with about 20-30 ($\bar{X} = 24.5$; $N = 10$) retrorse odontodes in females and nonreproductive males. Dorsal spine of nuptial males greatly elongated (18-43% SL), with about 45-60 ($\bar{X} = 53.2$; $N = 8$) sharp, antrorse odontodes along anterior margin; serrae arranged in an alternating fashion along distal portion of spine, in a single row along midline at base (Fig. 23b). Adipose fin small, with posterior margin free. Anal fin relatively short (23-30 rays), distal margin straight except in breeding males; anterior rays of nuptial males coalesced and lengthened to form copulatory organ. Anal fin pterygiophores 21-27, modally 25. Pectoral fin spine short, stout, with about 12-26 ($\bar{X} = 19.4$; $N = 94$) sharp, retrorse serrae along posterior margin; entire fin not reaching to pelvic fin origin, with 7-9 branched rays.

Color in Alcohol

Top of head and dorsum with a dense cast of slate-gray melanophores, diminishing sublaterally (Fig. 41). The intensity and extent of pigmentation is variable, but never appearing mottled and almost always including dense patches of dusky specks on the chin, the flanks above the anal fin, and an elongate streak in each caudal lobe extending from the base of the hypural plate to the midpoint of the longest caudal rays or beyond. Pigment on the chin ranges from a full semicircle of dense specks extending from the lower lip to the rear margins of the orbits, to a faint crescent overlying the dentaries, and invariably represented by at least traces of subcutaneous flecks scattered between the symphysis of the dentaries. Fresh specimens have deep black on the lips, chin, and flanks above the anal fin, and have streaks through each lobe of the caudal fin. In most specimens there is a diffuse oval patch of minute, superficial melanophores on the flank between the lateral line and the base of the anal fin.

Distribution

Ageneiosus atronassus is distributed throughout the middle and upper Amazon River basin, including the Río Ucayali in Peru, the Río Mamoré in Bolivia, and other major drainages of the Rio Solimões and upper Rio Amazonas in Brazil (Fig. 42). The species has been taken principally from the large main channels and sloughs associated with lowland lotic habitats throughout its range. Of the material examined, the farthest downstream record in the Amazon basin is from the Rio Maica, just below the mouth of the Rio Tapajós, but additional collecting is needed to determine the eastern extent of the species' range.

Ecology

Nothing has previously been published about the ecology of *A. atronasus*. In the moderate amount of material examined, at least 27 prenuptial or nuptial males and 26 gravid females were identified. Based on these specimens, the reproductive period for this species in the middle and upper Amazon basin occurs sometime between mid-to-late October and the end of March. The extended period during which reproductive specimens were available represents temporal and spatial variation in the rainy season. Males exhibited peak nuptial dimorphism in December and January. Reproductive males ranged from 68.7 to 109.9 mm SL ($\bar{x}$ = 87.1), and ripe females ranged from 60.4 to 115.7 mm SL ($\bar{x}$ = 89.7).

Etymology

From the Latin *ater* (neuter *atrum*), meaning black, and *nasus*, the nose, in reference to the intense black pigmentation on the tip of the snout in live and freshly preserved specimens.

Material Examined

Type material. – Holotype: MCZ 27270 (probable male, 72.2), locality unknown, but presumably from the Amazon river basin in Brazil.

Peru. – Loreto: BMNH 1977.3.10.229 (male, 87.6), Bueno Caño Amazonas, near Iquitos, 30 May 1974, M. Chapman. BMNH 1977.3.10.230 (male, 93.3), Lago Yarinococha, 27 March 1974, M. Chapman. CAS 57940 (ex IU 15788, holotype of *T. nigricollis*; male, 88.8), Iquitos, W. R. Allen. CAS 57941 (ex IU 15788, paratypes of *T. nigricollis*; male, 95.9; 2 females, 52.1-91.5), Iquitos, September 1920. CAS 57942 (ex IU 15789, paratype of *T. nigricollis*; female ?, 79.2), Río Ucayali near

Orellana, August 1920, W. R. Allen. FMNH 93488 (3 males, 100.8-109.9),
Yarinococha, January 1977, P. Hocking et al. CAS-SU 34216 (male, 74.7), Río
Ampiyacu near Pebas, 6 March 1937, W. G. Scherer. CAS-SU 34217-34218 (2
males, 97.0-104.7), Río Ampiyacu near Pebas, 1937, W. G. Scherer. CAS-IU 15911
(female ?, 95.3), Pebas, date unknown, Steere. Ucayali: USNM 261396 (2, 72-85.5),
Río Ucayali, Masisea, 31 May 1973, H. Ortega.

Bolivia. – Beni: FMNH 58137 (female, 93.0), Berlin, Río Mamoré, 15
September 1909, J. D. Haseman. FMNH 58138 (female, 94.4), Río Machupo, San
Joaquín, 5 September 1909, J. D. Haseman. FMNH 58139 (female, 69.2), Río
Mamoré below mouth of Río Guaporé, 19 September 1909, J. D. Haseman.
AMNH 56070 (2, 56.3-58.3), Río Mamoré ca. 5 km SE of Limoquije, 6 August 1965,
W. P. MacLean. MZUSP 27804 (male, 107.1; 2 females, 102.9-103.2), Laguna San
José, Trinidad, 3 March 1982, Conv. Pisc. ORSTOM-UTB.

Brazil. – Amazonas: MCZ 52582 (5 females, 88.2-116.5) Paraná de Janauacá,
about 3°25'S, 61°21'W, 7-12 December 1976, W. L. Fink. MCZ 52583 (7 males,
85.1-107.6) Paraná de Janauacá, about 3°25'S, 61°21'W, 7-12 December 1976, W.
L. Fink. MNHN 99-204, 205 (2, 57.7-74.6), Amazon River at Manaus, 1899 ?,
d'Anthonay. MPEG 1.444 (2 males, 68.7-80.6; female, 82.1), Rio Solimões, Ponta
do Catalão, 5 April 1983, R. Barthem and P. Stockman. MZUSP 5920 (male, 77.6),
Lago Jacarí, Rio Solimões, above Manacapuru, 29-31 March 1967, EPA. MZUSP
6338 (109.6), Lago Castro, mouth of Rio Purus, 7-8 November 1967, EPA. MZUSP
6581 (male, 90.1; 2 females, 86.9-88.9), Lago Manacapuru, 12-13 November 1967,
EPA. MZUSP 6997 (2 females 92.0-93.6), Río Madeira 25 km below Nova Olinda
do Norte, 27 November 1967, EPA. MZUSP 7546 (male, 75.8; 2 females, 78.1-
79.5), Paraná do Urucará, Urucará, 9 December 1967, EPA. MZUSP 9283-9284
(male, 89.9; female, 88.5), Rio Solimões, Fonte Boa, 6 October 1968, EPA. MZUSP
9285 (female, 109.0), Itapiranga, Paraná de Urucará, 9-12 September 1968, EPA.

MZUSP 9286 (female, 93.0), Rio Solimões, near Ilha Baruruá, above mouth of Jutai, 15 October 1968, EPA. MZUSP 9287 (male, 96.8), Santo Antônio do Içá, mouth of Rio Içá, 17 October 1968, EPA. MZUSP 26937 (male, 89.5), Lago Janauacá in the vicinity of Manaus, November-December 1976, R/V *Alpha Helix*. MZUSP 27627 (female, 88.9), Costa Japão, Rio Japurá, Tefé, 23 October 1982, L. Portugal. MZUSP 27630 (2 males, 83.1-83.8; 7 females, 78.4-90.5), Rio Solimões, near mouth of Rio Purus, Codajás, 25 October 1982, L. Portugal. MZUSP uncat. (female, 79.2), Benjamin Constant, 25-27 September 1962, K. Jenko. MZUSP uncat. (103.2), Três Bocas, Rio Preta da Eva, near Manaus, 13-28 January 1972, A. Abe. MZUSP uncat. (5 males, 77.8-93.4; 3 females, 80.0-115.2), mouth of Rio Pauini, 11-14 December 1974, P. E. Vanzolini. MZUSP uncat. (6 males, 68.9-80.3; 2 females, 108.6-111.5), Rio Pauini, 15-19 December 1974, P. E. Vanzolini. MZUSP uncat. (male, 86.0), mouth of Rio Pacιά, 23 December 1974, P. E. Vanzolini. MZUSP uncat. (female, 88.7), Canutama, 29 December 1974, P. E. Vanzolini. MZUSP uncat. (male, 105.7), Rio Purus, Santa Luzia, 11 January 1975, P. E. Vanzolini. MZUSP uncat. (7 males, 75.8-82.0; 15 females, 60.4-103.7), Rio Purus, Beruri, 12-13 January 1975, P. E. Vanzolini. MZUSP uncat. (1 male, 61; 2 females, 84.1-91.3), Rio Solimões, Lago Janauacá and vicinity, November 1976-January 1977, R/V *Alpha Helix*. UF uncat. (male, 89.4; 2 females, 91.0-112.5) slough of Rio Amazonas 10 km E of Manaus, 9 October 1985, T. Shepard and M. Barton. Para: MZUSP 7861 (male, 83.1), Paraná Jacarí, Faro, 13 December 1967, EPA. UF 44926 (2, 90.1-105.3), Rio Maica just below mouth of Rio Tapajós, 02°40' S, 54°30' W, 8 December 1986, L. G. Nico.

No Data. – UMMZ 56135 (male, 72.4; female, 102.3), Beal and Steare.

Table 11. – Summary of principal meristic characters of *Ageneiosus atronasus*.

	NON-TYPES				HOLOTYPE (MCZ 27270)
	Range	Mode	Mean	N	
Pectoral-fin Rays	7-9	9	8.8	94	9
Anal-fin Rays	23-30	27	27.3	88	28
Branchiostegal Rays	7-9	8	8.0	46	8
Total Gill Rakers	14-23	16	16.3	25	17
Pleural Ribs	7-8	7	7.3	28	7
Total Vertebrae	40-42	41	41.2	32	40
Preanal Vertebrae	17-19	17	17.5	30	18

Table 12. – Proportional measurements of *Ageneiosus atronasus*.
Measurements 2-21 are expressed as thousandths of standard length (SL);
measurements 22-34 are expressed as thousandths of head length (HL).

	HOLOTYPE (MCZ 27270)	NON-TYPES (N = 43)	
		Range	Mean
1. Standard length (SL, mm)	72.2	56.3-116.5	----
2. Preadipose length	821	743-844	816
3. Preanal length	645	559-678	645
4. Predorsal length	360	299-412	346
5. Prepelvic length	536	492-541	517
6. Prepectoral length	296	256-303	282
7. Pectoral origin to dorsal origin	186	157-209	192
8. Pelvic origin to dorsal origin	249	212-291	261
9. Pelvic origin to adipose origin	325	312-381	350
10. Dorsal origin to adipose origin	479	436-529	489
11. Adipose origin to anal insertion	129	108-165	138
12. Body depth at dorsal origin	151	136-235	199
13. Caudal peduncle depth	102	82-127	107
14. Caudal peduncle length	114	110-151	131
15. Body width at pectoral origin	204	178-229	209
16. Body width at pelvic origin	115	64-131	117
17. Dorsal spine length	229	175-428	*
18. Pectoral spine length	170	133-189	170
19. Pelvic fin length	157	123-177	151
20. Anal-fin base length	233	221-276	247
21. Head length (HL)	296	253-306	285
22. Head depth at occiput	509	482-686	563
23. Head width at postorbitals	724	543-799	705
24. Dorsal interopercular width	458	486-594	540
25. Anterior internarial distance	304	265-333	299
26. Anterior-posterior narial distance	196	37-197	163
27. Preisthmus length	724	664-825	731
28. Isthmus width	341	285-519	397
29. Snout length	421	369-495	445
30. Gape width	533	476-589	548
31. Upper jaw length	341	307-395	354
32. Lower jaw length	322	258-372	322
33. Eye diameter	243	160-278	212
34. Barbel length	243	108-343	**

*Mean dorsal spine length of nuptial males = 305 (N = 16); females = 200 (N = 12).

**Mean barbel length of nuptial males = 311 (N = 16); females = 137 (N = 12).

Fig. 41.—*Ageneiosus atronasus*, UF uncat., non-nuptial male, 89.4 mm SL.

Fig. 42. – Geographic distribution of *Ageneiosus atronasus*.

Ageneiosus pardalis Lütken
Figs. 1, 14, 20, 26, 43-44
Tables 13-14

Ageneiosus pardalis Lütken 1874:190-192 (original description [type locality: Caracas, Venezuela, but herein regarded as questionable]). Steindachner 1878:33-35, pl. 3, fig. 1 (description); 1880:62 (brief description). Eigenmann and Eigenmann 1890:307 (placed in synonymy of *A. dentatus*). Schultz 1944:240 (tentatively in synonymy of *A. caucanus* Steindachner; specific epithet misspelled as *paradalis*). Stigchel 1947:108 (epithet misspelled as *paradalis*; placed in synonymy of *A. dentatus*). Gosline 1945:24 (citation; placed in synonymy of *A. dentatus*). Dahl 1971:64 (species thought to be synonymous with *A. dentatus*; excluded from Colombia). Britski 1972:99, 106 (placed in synonymy of *A. caucanus*). Nielsen 1974:51 (holotype listed). Ferraris 1988:124 (citation).

Ageneiosus caucanus Steindachner 1880:61-62, pl. 6, figs. 1-1a (original description [type locality: Río Cauca, Colombia]). Eigenmann and Eigenmann 1890:300, 306 (in key; citation); 1891:35 (citation). Eigenmann 1909:315 (listed; Río Magdalena drainage). Meek and Hildebrand 1916:245-246 (description; variation in coloration; Río Tuyra [= Tuira]). Eigenmann 1920a:13 (in table; Río Magdalena drainage); 1920c:8, 14 (listed; in table; Río Tuyra [= Tuira] and Río Atrato drainages); 1920d:29 (in table; lower Magdalena drainage). Breder 1927:104-105, 144, 152, 155, 157, 161, 169 (description of coloration; comparison with *A. dentatus*; food habits; in faunal lists; Indian name; in taxonomic key). Hildebrand 1938:236 (distribution). Myers 1942:97 (tributary of Lake Maracaibo). Schultz 1944:240, 242-243 (not *A. caucanus* [Myers]; in key; synonymy in part; comparison with *A. freiei*). Gosline 1945:25 (citation). Miles 1947:75-77 (in taxonomic key; illustrated; brief description; common names). Lundberg and Baskin 1969:7, 30 (in material examined; caudal fin morphology). Mago-Leccia 1970:32 (listed; common name). Dahl 1971:64-65 (common names; illustration of sexes; economic importance; conservation status). Britski 1972:99, 106-107 (citation). Taphorn and Lilyestrom 1984a:17, 29 (listed; common name). Ferraris 1988:124, 151 (citation; ontogenetic variation in Weberian apparatus). Burgess 1989:286 (citation). Curran 1989:418 (in material examined).

Ageneiosus virgo Posada 1909:295 (original description [type locality: Río Magdalena, Colombia]). Ferraris 1988:125 (citation).

Ageneiosus freiei Schultz 1944:240-243 (original description [type locality: Río Agua Caliente 2-3 km above Lago Maracaibo, Venezuela]; in key and comparison with *A. caucanus*). Gosline 1945:25 (citation; *A. caucanus* [not Steindachner] Myers placed in synonymy). Mago-Leccia 1970:32 (listed; common name). Britski 1972:100, 107 (citation). Royero 1987:16 (misspelled *friei*; in material

examined). Ferraris 1988:127 (citation). Burgess 1989:286 (citation; considered possible synonym of *A. caucanus*).

Ageneiosus sp. cf. *madeirensis*: Burgess 1989:629 (photograph [misidentified]).

Diagnosis

Distinguished from all other species that mature at sizes greater than about 150-200 mm SL by the retention of an enlarged, unencapsulated swimbladder. Externally, a combination of the large body size, deeply forked tail, and prominent dorsal mottling pattern separates *A. pardalis* from all congeners except *A. ucayalensis*, *A. valenciennesi*, and *A. vittatus*. Further distinguished from *A. ucayalensis* by a shorter anal fin (35-42 rays, versus 41-50), more ribs (modally 9 versus 8), and fewer branchiostegals (modally 9 versus 10) and gill rakers. Distinguished from *A. valenciennesi* by a combination of the slightly higher mean number of anal rays (37.8 versus 36.6), and modally fewer branchiostegals (9 versus 10) and pectoral rays (12 versus 13), but the ranges of counts overlap too much to allow these species to be identified on meristics alone; however, the difference in the swimbladders, and the distantly allopatric ranges of *A. pardalis* and *A. valenciennesi*, easily serves to separate them. *Ageneiosus vittatus* reaches sexual maturity at a smaller size than *A. pardalis*, and is further distinguished by fewer total vertebrae (45-48 versus 49-51) and the presence of two high-contrast caudal spots.

Description

Ageneiosus pardalis is a large-sized species, reaching a maximum of 440 mm SL in the material examined, with individuals of some populations apparently capable of attaining much greater lengths (see comments). The principal meristic and morphometric characters of the species are summarized in Tables 13-14.

Head strongly depressed and moderately large, 27-31% SL in length, 15-19% SL in breadth at postorbitals. Dorsal profile of head gently raised to dorsal fin origin, more abruptly inflected upward in large specimens; head depth at middle of orbits 7-10% SL, depth at frontal-supraoccipital suture 10-15% SL. Snout relatively long (52-57% HL), broadly parabolic to slightly pointed in dorsoventral profile. Mouth inferior, gape broad, exposing anterior portion of premaxillary tooth patch (Fig. 1). Premaxillary tooth patches broad at midline, strongly recurved and tapered to thin points at corners of mouth. Premaxillary teeth setiform, retrorse. Eyes sublateral, relatively small (8-14% HL), covered by thick skin and invested by fatty tissue, especially in larger individuals. Anterior nares near margin of upper lip, at anterolateral corners of mesethmoid; posterior nares remote from anterior pair. Barbels filiform, inconspicuous in females and nonbreeding males; barbels of nuptial males ossified, with 11 + 10 recurved odontodes in one specimen examined. Cranial bones textured on dorsal surface with weak longitudinal ridges. Fontanelle relatively long, terminating at plane behind orbit, not extending onto nuchal shield. Gill membranes narrowly fused to isthmus at plane passing behind orbits. Branchiostegals 8-9, modally 9. First epibranchial with 3-4 gill rakers in outer row, ceratobranchial with 9-12 rakers; total number of gill rakers 13-16. Gill rakers relatively short, crenulate on medial margin.

Body elongate and strongly compressed behind pectoral fins. Profile of back from dorsal fin to caudal peduncle nearly straight or gently curved. Ventral profile tapering gradually to caudal peduncle. Body depth relatively low at dorsal fin origin (14-19% SL); caudal peduncle very narrow (6-7% SL in depth).

Dorsal-fin spine thin, slightly rugose on anterior margin, with very weak, retrorse serrae along distal half or more of posterior margin. Dorsal spine of nuptial males elongated and hyperossified, with about 40-60 sharp, antrorse serrae along anterior margin. Adipose fin small, strongly constricted at base. Caudal fin

deeply forked, with 8 + 10 principal rays, and about 16-23 upper and 14-18 lower procurrent rays. Anal fin with 35-42 rays and 32-38 pterygiophores. Pectoral fin not reaching to pelvic origin, with 11-14 soft rays. Pectoral spine thin, with about 13-25 relatively short, recurved serrae along distal half to two-thirds of posterior margin.

Total number of vertebrae 49-51, modally 50. Total preanal vertebrae 18-20, modally 18. Pleural ribs 9-10. Swimbladder of adults large, globule-shaped, with an opaque, turgid, external tunica and no posterior caecae (Fig. 20f).

Color in Alcohol

Most specimens are characterized by a heavily mottled pigmentation pattern, concentrated primarily on top of the head and upper half of the body (Fig. 43), but extending over much of the sides of the body in some specimens. Considerable variation is evident in preserved material, and, judging from observations in other species, individuals of *A. pardalis* are probably capable of dramatic coloration changes, depending on ecological and other factors.

Background color generally yellowish or cream-colored. Pigmented areas consisting of dense, irregular brown or black spots and blotches. Top of head with scattered brown spots and dark streaks along the top of each frontal. Upper half of operculum with similar spots. Top of back from dorsal-fin origin to caudal peduncle with a prominent series of irregular, dark brown or black blotches, which tend to be broken into smaller, more discrete spots with increasing SL. Midline of back typically with a thin, unpigmented stripe extending from rear of rayed dorsal fin to upper caudal lobe. Spots or blotches on back diminishing laterally, but extending to or beneath lateral line in some specimens. Sides of body with a midlateral broken stripe, extending to or beyond vertical through pelvic origin, and a sublateral stripe, beginning at the top of the opercular chamber and angled obliquely downward

toward the pelvic fin base. Both stripes on the sides of the body are extremely variable, and may range from relatively few, scattered blotches, to a series of prominent spots extending the length of the body, or, in the case of the sublateral pair, to a point above the pelvic fin base. In heavily pigmented specimens, the entire dorsum and upper half or more of the sides are heavily spotted or reticulated.

Dorsal fin pallid or with a few irregular spots. Adipose fin with scattered brown flecks at base and along distal margin. Caudal fin with a broad band over middle of rays, frequently broken into large, crescentic spots in each lobe, with scattered flecks radiating posteriorly. Pigment at base of upper lobe continuous with pigment on top of caudal peduncle. Anal fin immaculate, or with scattered flecks and a dark marginal band. Paired fins ranging from immaculate to spotted or streaked on upper surface. Venter normally unpigmented.

Distribution

Ageneiosus pardalis is the only trans-Andean species of the family, occurring in western and southern tributaries of Lake Maracaibo, Venezuela, and ranging westward in the major lowland drainages to southern Panama, including the Río Atrato, Río San Juan, Río Magdalena, and Río Cauca (Fig. 44). The significance of the distribution of *A. pardalis* is discussed in greater detail in the section on zoogeography of the family.

Etymology

From the Latin *pardalis*, meaning a female panther, an allusion to the reticulated or spotted pattern of the head and body.

Common Names

Colombia: doncella, señorita, niña, gata, fría, barbul, rollera (Miles 1947, Dahl 1971). Venezuela: doncella (Mago-Leccia 1970, Taphorn and Lilyestrom 1984a).

Ecology

Little is known of the biology or ecology of *A. pardalis*. Most of the available information was provided by Dahl (1971). The species was found to spawn in July in water 3-4 meters deep over a mud bottom. Breder (1927) found that the stomach of one specimen contained fragments of a decapod.

Dahl (1971) commented on the food value and fisheries exploitation of this species. He implicated overfishing in population declines observed during the decade prior to publication of his book, and suggested that the species was in need of legal protection in the form of fishing restrictions. Recent degradation of water quality as a result of human pollution may be responsible for a decline in this species' abundance in portions of the Río Magdalena (A. Acero, personal communication).

Comments

In the original description of *A. pardalis*, Lütken (1874) listed the specimens as having come from Caracas, Venezuela. There is no current evidence that this species occurs near Caracas, however, and the type locality of the species is therefore questionable. It is likely that Lütken received the holotype from material sent to Caracas from a collection made to the west of the easternmost Andean cordilleras in Venezuela or Colombia.

Two specimens were found in the syntypic series of *A. caucanus*. The largest of these is designated the lectotype (NMW 47811:1, male, 395 mm SL) and the smaller the paralectotype (NMW 47811:2, male, 340 mm SL).

The nominal species *A. freiei* was considered by Schultz (1944) to be distinct from *A. caucanus* (= *A. pardalis*), primarily on the basis of differences in pigmentation and pectoral fin rays; *A. freiei* was thought to have two well-defined black stripes on the sides of the body, and an average of 13 pectoral rays, as opposed to 11-12 in *A. caucanus*. In the present study, tremendous variation in pigmentation was noted among all specimens examined, and the number of pectoral rays varied from 11 to 14, with no apparent geographic differences. The degree of variation in pigmentation ranged from specimens having virtually no pigment, other than mottling on the top of the head and dorsum and scattered throughout the fins, to specimens that were strongly mottled on the entire dorsum, with broken lateral stripes on the body, blotches on the tail and anal fin, and scattered flecks over the rest of the body, as in the holotype of *A. freiei* (cf. Schultz 1944: plate 4b). The variation in pigmentation is attributed to ecological, behavioral, or other factors, rather than to taxonomic differences.

The largest specimens of *A. pardalis* examined in this study ranged from 415-460 mm SL. Dahl (1971) reported that specimens reached 70 cm, and possibly more. Individuals from populations draining into the Maracaibo basin have been found to reach a very large size, perhaps over 1.5 meters in length (F. Mago-Leccia, A. Machado-Allison, and F. Provenzano, personal communication). Unfortunately, no individuals of such large size have been adequately preserved in museum collections. Despite a fair degree of ichthyofaunal endemism in the Maracaibo basin, populations of *A. pardalis* from that area are not herein considered to be specifically distinct from populations in more western drainages of Colombia and Panama. For unknown reasons, certain fish (e.g., *Synbranchus*, *Sorubim* n. sp. [an

endemic], and *Sternopygus*) in the Maracaibo basin attain much larger sizes than conspecifics or closely related taxa in other parts of their ranges (D. C. Taphorn, personal communication). Evidently, *A. pardalis* is one such species that exhibits the unique phenomenon of gigantism in this region.

Material Examined

Type material. – Holotype: ZMUC 207 (female?, 415), Venezuela, exact locality unknown.

Venezuela. – Zulia: CAS-SU 36497 (1, 121), river tributary on E side of Lake Maracaibo, 10 km S of Lagunillas, 23 March 1938, F. F. Bond. MCZ 37210 (paratype of *A. freiei*; female ?, 215), Río [ciénega] Agua Caliente 2-3 km above Lake Maracaibo, 1 May 1942. FMNH 41991 (female, 215), Lake Maracaibo, 1911, W. H. Osgood. USNM 121260 (female, 208; holotype of *A. freiei*) and USNM 121261 (female, 230; paratype of *A. freiei*), Río Agua Caliente 2-3 km above Lake Maracaibo, 1 May 1942. USNM 121262 (male, 385; female, 208; paratypes of *A. freiei*), Río Negro below mouth of Río Yasa, 2 March 1942, L. P. Schultz.

Colombia. – Antioquia: FMNH 59355 (male, 325), Río Magdalena at Puerto Berrio, C. H. Eigenmann. NRM-SOK/1989046.5908 (1, 156), Buchadó, Caño Ponelaolla and mouth of Río Guaquandó about 1 km downstream from Buchadó, 28 January 1989, S. O. Kullander et al. Bolivar: FMNH 59351 (male, 425), Río Magdalena at Calamar, C. H. Eigenmann. Choco: CAS 12686 (male, 295), Río Truando, 1913, A. Hern and C. Wilson. CAS 13182 (male, 312), Río Atrato at Quibdo, 1913, C. H. Eigenmann. FMHN 59353 (male, 327) and FMNH 59354 (male, 375), Río Atrato at Quibdo, C. H. Eigenmann. NRM-SOK/1989044.5855 (1, 80), Río Napipí, river bank at village, 26 January 1989, S. O. Kullander et al. USNM 270813 (1, 205), Río Atrato at town of Río Sucio, 9 February 1968, H.

Loftin. State Unknown: MNHN 1786 (1, 338), Magdalena River, 1851, Léwy.
 NMW 47811 (syntypes of *A. caucanus* Steindachner, 2 males, 340-395), Río Cauca.
 FMNH 59352 (male, 272), Soplaviento, C. H. Eigenmann.

Panama. – Darien: AMNH 11398 (female, 91.3), Río Chucunaque at island below Yavisa, 15 March 1924, Darien expdt. CAS 13179 (female, 248), Río Tuira, Marrigante, 8 March 1912, S. E. Meek and S. F. Hildebrand. FMNH 26346-66 (11 males, 145-270; 10 females, 142-300), FMNH 26379-80 (male, 164.9; female, 146.4), Río Tuira, Marrigante, 1912, Darien. UF 15454 (2, 177-178), Río Pirri at El Real, June 1967, J. R. Moore. USNM 78254 (19, 114-380), Río Tuira, Marrigante, 8 March 1912, S. E. Meek and S. F. Hildebrand. USNM 270814 (3 males, 265-325; female, 440), Río Chucanaque, 9°2'N, 78°2'W, 1 March 1967, F. I. Battelle et al. USNM 270815 (2, 153-163), Río Chucunaque just above confluence with Río Tuira, 16-19 February 1985, J. G. Lundberg and B. Chernoff. Exact Locality Unknown: FMNH 55223 (male, 247), Darien Province, 1911-1912, S. E. Meek and S. F. Hildebrand.

No Data. – CAS-SU 31569

Table 13.--Summary of principal meristic characters of *Ageneiosus pardalis*.

	NON-TYPES				HOLOTYPE (ZMUC 207)
	<u>Range</u>	<u>Mode</u>	<u>Mean</u>	<u>N</u>	
Pectoral-fin Rays	11-14	12	11.8	37	12
Anal-fin Rays	35-42	---	37.8	32	38
Branchiostegal Rays	8-9	9	8.9	19	9
Total Gill Rakers	13-16	15	14.4	14	15
Pleural Ribs	9-10	9	9.2	32	9
Total Vertebrae	49-51	50	50.1	33	47
Preanal Vertebrae	18-20	18	18.4	33	18

Table 14. – Proportional measurements of *Ageneiosus pardalis*.
Measurements 2-21 are expressed as thousandths of standard length (SL);
measurements 22-34 are expressed as thousandths of head length (HL).

	HOLOTYPE (ZMUC 207)	NON-TYPES (N = 14)	
		Range	Mean
1. Standard length (SL, mm)	415	121-425	----
2. Preadipose length	831	802-862	823
3. Preanal length	646	562-627	594
4. Predorsal length	313	292-339	312
5. Prepelvic length	506	431-495	468
6. Prepectoral length	289	270-309	290
7. Pectoral origin to dorsal origin	152	144-173	154
8. Pelvic origin to dorsal origin	231	204-248	227
9. Pelvic origin to adipose origin	349	254-403	368
10. Dorsal origin to adipose origin	487	486-569	531
11. Adipose origin to anal insertion	111	84-113	99
12. Body depth at dorsal origin	142	136-187	159
13. Caudal peduncle depth	63	57-72	65
14. Caudal peduncle length	101	89-131	116
15. Body width at pectoral origin	193	173-198	185
16. Body width at pelvic origin	----	54-105	88
17. Dorsal spine length	142	160-276	*
18. Pectoral spine length	120	120-152	138
19. Pelvic fin length	125	122-154	136
20. Anal-fin base length	270	233-313	289
21. Head length (HL)	296	270-307	287
22. Head depth at occiput	455	338-512	425
23. Head width at postorbitals	585	538-663	588
24. Dorsal interopercular width	----	343-412	387
25. Anterior internarial distance	528	323-371	348
26. Anterior-posterior narial distance	----	102-252	127
27. Preisthmus length	----	661-729	696
28. Isthmus width	----	94-142	119
29. Snout length	496	520-566	535
30. Gape width	528	519-635	552
31. Upper jaw length	----	434-473	453
32. Lower jaw length	----	374-418	395
33. Eye diameter	77	83-142	105
34. Barbel length	----	95-268	**

*Mean dorsal spine length of nuptial males = 234 (N = 2); females and non-nuptial males = 183 (N = 8).

**Mean barbel length of nuptial males = 253 (N = 2); females and non-nuptial males = 150 (N = 9).

Fig. 43.—*Ageneiosus pardalis*, NRM-SOK/1989046.5908, immature male, 156 mm SL.

Fig. 44.—Geographic distribution of *Ageneiosus pardalis*

Ageneiosus vittatus Steindachner
Figs. 1, 2, 5, 21, 23, 30, 45-46
Tables 15-16

Ageneiosus vittatus Steindachner 1908:64-65 (original description [type locality: Rio Purus, Brazil]); 1910:402-403, pl. 9 (brief description). Gosline 1945:25 (citation). Fowler 1951:455, fig. 482 (partial synonymy; distribution). Britski 1972:110 (citation). Ferraris 1988:125 (citation). Burgess 1989:286 (citation).

Ageneiosus sp.: Köpke 1986:393-395 (reproduction in captivity). Royero 1987:16, 130, figs. 38-39 (morphology of dorsal fin).

Ageneiosus sp. cf. *marmoratus*: Burgess 1989:628 (photograph [misidentification]).

Diagnosis

Ageneiosus vittatus is separated from all congeners except *A. n. sp.*, *A. valenciennesi* and *A. pardalis* by its combination of moderate size, deeply forked tail, encapsulated swimbladder, short anal fin (less than 40 rays), and typically mottled coloration. Perhaps most commonly confused with *A. n. sp.*, both species of which have a superficially similar striped pattern, but distinguished from that species by slightly fewer pectoral-fin rays (11-13 versus 12-15); greater numbers of total ($\bar{X}$ = 46.5 versus 45.4) and preanal ($\bar{X}$ = 18.4 versus 17.2) vertebrae; more pleural ribs (8-10 versus 7-8); a more robust head and body; and by significant differences in pigmentation. *Ageneiosus vittatus* is not sympatric with either *A. pardalis* or *A. valenciennesi*, and differs from each of those species by morphological differences presented in their respective diagnoses.

Description

A small to medium-sized species, reaching a maximum of 220 mm SL in the material examined. The principal meristic and proportional measurements are summarized in Tables 15-16.

Top of head gradually sloping upward in a straight line to dorsal fin origin. Underside of head slightly convex. Head profile from above broadly parabolic. Gape broad, gently recurved (Fig. 1); mouth weakly inferior, the upper jaw overhanging lower jaw by less than width of premaxillary tooth band. Head relatively robust, 28-33% SL in length, width at postorbitals 20-23% SL. Eye relatively small, 11-16% HL. Fontanelle moderately short, 28-41% HL, terminating near plane through rear margin of orbits. Premaxillary tooth patch narrow, gently recurved at posterior margins; teeth short, viliform, randomly scattered over premaxillae. Dentary teeth similar to those on premaxillae, the patches on each side of approximately equal width. Anterior nares just above edge of upper lip and lateral to mesethmoid, displaced on very short, valvular, fleshy flaps in anterodorsal position. Each posterior nare situated behind anterior one by distance about equal to width of eye, bordering lateral margin of frontal, surrounded by short flap of skin. Gill membranes fused to isthmus at plane passing behind orbits. Branchiostegal rays 8-11, modally 9. First epibranchial with 3-6 moderately short, weakly crenulate gill rakers in outer row; first ceratobranchial with 9-12 rakers; total number of gill rakers on outside row of first arch 12-18, modally 15. Barbels short, filiform in females and non-breeding males, concealed within rictal groove. Maxillary barbels of nuptial males elongated and ossified, reaching to or slightly beyond front margin of eyes, and with 5-8 sharp odontodes on dorsolateral margin. Mental barbels present in postlarval individuals, reduced to tiny vestiges or completely resorbed in specimens greater than about 50 mm SL.

Body width greatest at pectoral-fin origin (18-24% SL), gradually attenuated to caudal peduncle. Body depth at dorsal-fin origin 16-24% SL. Dorsal profile of body slightly convex, the belly gently rounded. Least caudal peduncle depth 8-11% SL.

Dorsal fin in females and non-nuptial males relatively short (14-20% SL), constricted at base, and with a moderately short spine that is weakly serrated along the distal half or more of the posterior margin. Dorsal spine of nuptial males greatly elongated (23-35% SL), armed along anterior border with about 30-40 sharp, antrorse odontodes (Fig. 23d), smooth on posterior margin. Adipose fin relatively large for the genus, posterior margin free, forming short flap. Caudal fin large and moderately forked, with 8 + 9 principal rays, and about 19-23 ($\bar{X}$ = 21) upper and 14-19 ($\bar{X}$ = 16) lower procurrent rays; tail often frayed and appearing truncate or rounded, as a result of damage inflicted by fin-eating characiforms. Anal fin relatively short, obliquely angled upward toward caudal peduncle, with 32-39 ($\bar{X}$ = 36) fin rays. Anal pterygiophores 29-36, modally 33. Anterior 3-7 anal lepidotrichia enlarged and coalesced to form gonopodium in nuptial males. Pectoral fin triangular, not reaching to pelvic origin. Pectoral spine relatively short and thin, with about 10-22 sharp, retrorse serrae on posterior margin in specimens greater than 100 mm SL; serrae reduced to short, rounded bumps near base (small specimens have fewer serrae, about 6-10, that are proportionally larger relative to the length and diameter of the shaft). Soft pectoral rays 11-13, modally 12.

Total vertebrae 45-48, modally 47. Preanal vertebrae 17-20, modally 18. Pleural ribs 8-10, modally 9. Swimbladder in adults a relatively small bipartite capsule, encased by superficial ossification of the complex centra, with two short, turgid, posterior caecae (Fig. 21a).

Color in Alcohol

Pigmentation in *A. vittatus* is extremely variable and depends, at least in part, on the hydrological characteristics of the water from which specimens were collected. Individuals from turbid waters are much less intensely pigmented than those from clear or tannin-stained waters. The following generalized description is based on the typical condition observed in preserved museum material, supplemented with comments about variation (see section on pigmentation for a detailed discussion).

Background color of head and body dusky white or yellowish. Top of head brownish to black, ranging from relatively uniform, dense speckling, to a rather mottled appearance consisting of large, irregular spots (Fig. 45). Area above fontanelle and over optic and olfactory tracts often pale yellow, with diffuse brown or black specks scattered on skin. In extreme cases of mottling, there are dark brown stripes along the sides of the fontanelle, a broad band across the tip of the snout, and irregular stripes and spots above the occipital shield, extending laterally and downward on upper half of head. Top of back from dorsal fin insertion to caudal fin invariably with a distinctive, unpigmented, cream-colored stripe extending down midline of back, subtended on both sides by sharply contrasting brown or black stripes that begin together in front of the dorsal fin and converge toward the tail. The dorsal stripes extend ventrally to about midway between the center of the back and the lateral line, and may be of nearly uniform color throughout, or, more commonly, appear somewhat mottled. In extreme cases, the dorsal stripes are broken into a series of prominent, large blotches or irregular saddles. Sides of body with a pair of very distinctive brown or black lateral stripes, one beginning above the opercular opening, the other above the pectoral fin base. Midlateral stripe typically longer than the sublateral one, extending along the lateral line to above anal fin

origin or beyond. Sublateral stripe angled obliquely downward and often terminating above pelvic fin base. Both lateral stripes occasionally broken into a series of elongate spots. Midlateral musculature along posterior portion of lateral line often with melanophores deeply embedded beneath superficial epidermis. In extremely dark specimens, the dorsal and lateral stripes form a dense reticulated network of blotches.

Caudal fin with a very prominent pair of large, black or brown spots of much greater contrast than in any other species. Upper spot crescent shaped, contiguous anteriorly with dorsal stripe, extending over middle of upper principal rays. Spot in middle of lower caudal fin lobe oval to crescentic, opposite spot in upper lobe. In lightly pigmented specimens the spots are less discrete, and the lower one may be very small to nearly absent, whereas in very darkly colored specimens both spots merge to form a broad crescentic band. Remainder of caudal fin generally with little or no pigmentation in most specimens. Dorsal fin with diffuse black along leading edge of spine, and occasionally with specks on distal portion of interradi al membranes. Adipose fin pale except at base. Paired fins with scattered brown on upper surface, ranging from very few diffuse specks to one or more stripes along anterior rays. Anal fin typically immaculate or with a few scattered spots at base. Chin, throat, and belly normally unpigmented. In melanistic specimens, the entire body, including the fins, may become heavily mottled and spotted (Fig. 2).

Distribution

Presently known from the Río Orinoco basin of Venezuela, and from the upper Amazon basin in the Río Beni drainage of Bolivia and the Río Napo drainage of Ecuador (Fig. 46). This species is relatively common in the middle Orinoco basin, as revealed by 13 years of recent survey work by Donald C. Taphorn (MCNG)

in the Río Apure drainage. The paucity of specimens available from other river systems, and the widely disjunct gap in the Amazon basin from which no specimens were available, is perhaps due largely to poor collecting efforts in the intervening areas. Presumably, the species is more widespread in the upper reaches of the Amazon basin.

Etymology

From the Latin *vittatus*, meaning bound with a ribbon or striped, alluding to the prominent dorsal and midlateral stripes on the body.

Ecology

Aspects of the ecology of this species have been investigated by Otto Castillo (Estacion de Investigaciones Pesqueras, San Fernando de Apure, Venezuela), but the results of his study have not yet been published. The species feeds predominately on other fishes and invertebrates, especially decapod crustaceans (L. Nico, personal communication).

In the Río Apure of the middle Orinoco basin, seminuptial males (123-168 mm SL) were in reproductive condition, as evidenced by hyperossified barbels, from early March to late May, a period coinciding with the onset of the rainy season in that area.

One collection in the Bení drainage of Bolivia, taken in late August, had 3 seminuptial males ranging in size from 170 to 179 mm SL.

Köpke (1986) described courtship, spawning behavior, and oviposition of internally fertilized eggs in captive individuals of this species.

Comments

This species has occasionally been confused with an undescribed form from the lower and middle Amazon basin. This problem probably results from their superficially similar striped coloration, as well as possible confusion surrounding the type locality of *vittatus*. Steindachner gave the type locality as the mouth of the Rio Purus in Brazil. In the present study, no specimens of *A. vittatus* were found from this area, although the species is known from the upper Amazon basin in Bolivia and Ecuador. Thus, it would appear possible that the species could be, or at one time was present, in the Rio Purus or near its mouth in the Rio Solimões. Conversely, the type locality as given by Steindachner may be erroneous. This possibility cannot be unequivocally refuted, given the fact that there have been occasional mistakes identified with locality records kept by Steindachner (C. R. Gilbert, personal communication).

An unpublished manuscript name has been proposed for this species by colleagues in Venezuela (O. Castillo, A. Machado Allison, and F. Provenzano, personal communication), who are of the opinion that the form in the middle Orinoco basin represents an undescribed species. I have expressed to them my belief that the name *vittatus* applies to the Orinoco form; however, they apparently do not agree, inasmuch as they recently (June 1989) informed me that they intended to proceed with a formal description of this taxon.

Specimens in the limited amount of material from Bolivia and Ecuador have a somewhat more mottled pigmentation pattern than those typically collected from whitewater rivers in the middle Orinoco. In addition, the number of pectoral fin rays in these specimens averages one higher than in specimens from the Orinoco basin. Individuals from the Orinoco, nevertheless, are capable of dramatic coloration changes when collected from, or placed in, clear or dark water (see

section on pigmentation), and strongly resemble the Amazonian specimens when allowed to reach maximum pigmentation intensity. Since both populations are identical in all other morphological respects, they are here considered conspecific, and the difference in pectoral rays, if real, is attributed to infraspecific or geographical variation.

Material Examined

Type Material. – Holotype: NMW 47853 (154), Río Purus, Goldi.

Venezuela. – Apure: MCNG 823, 1272, 1476, 5962 (10, 67-205), Hato el Frio, NW of Mantecal, 2 October 1979, D. C. Taphorn et al. UF 80895 (male, 146), Caño Maporal in isolated section along a dead end road S of UNELLEZ module, 13 February 1979, D. C. Taphorn and C. G. Lilyestrom. UF uncat. (2, 156-157), barrow pit canal on E side of UNELLEZ module, 14 February 1979, D. C. Taphorn et al (DCT79-17). USNM 257551 (3, 113-137), side channel of Río Apure about 3 km W of center of San Fernando, 7°53'N, 67°29'W, 25 January 1983, personnel of Apure Fisheries Station. USNM 258262 (3, 125-134), Río el Canito, where crossed by road from San Fernando to Cunaviche, 7°28'N, 67°39'W, 22 January 1983, San Fernando Fisheries Sta. personnel. Barinas: MCNG 3406 (5, 115-138) Río Apure, flooded zone in front of Bruzual, 6 November 1981, S. Reid et al. MCNG 5508 (8, 101-128), Caño Dora, Reserva Forestal Ticoporo, 9 December 1982, D. C. Taphorn and G. Rios. MCNG 5862 (male, 169), canals near Dolores, 30 May 1980, D. C. Taphorn et al. UF uncat. (male, 165), Río Guasimito, SE of Arismendi, 6 April 1984, D. C. Taphorn et al. Delta Amacuro: USNM 265633 (1, 146), shallow lagoon on N side of river, west of Caño Araguaio, 131 nautical mi from sea buoy, 14 November 1979. Guarico: UF 78146 (4, 137-147), Río Chirgua at log bridge on unpaved road from Guardrinajas to Barbasco, due E of Barbasco, 23 March 1981,

D. C. Taphorn et al. USNM 257562 (5, 104-151), Fundo Masaguaral, Río Caracol where crossed by bridge on ranch, 8°34'N, 67°30'W, 19 January 1983. USNM 260209 (1, 141), caños to W of highway from Calobozo to San Fernando, about 35 km S of Fundo Masaguaral, 20 January 1983. Portuguesa: MCNG 8823 (male, 149), black water channel between Caño Maraca and Guanarito on Guare-Guanarito road, 24 May 1980, D. C. Taphorn and S. Reid. MCZ 59370 (6 females, 123-161), Caño Maraca at bridge on road to Guarito from Guanare, 19 March 1978, D. C. Taphorn.

Bolivia. – Ballivia: USNM 297399 (4, 93.7-117.3), Río Matos below road crossing, 48 km E of San Borgia, 28 August 1987, W. C. Starnes et al. USNM 297400 (14, 90.3-190), Río Curiraba about 10 km NE of El Provenir Biological Station, about 40 air km E of San Borgia, 31 August 1987, W. C. Starnes et al.

Ecuador. – Napo: FMNH 96583 (female, 129), Río Zancudococha about 1 km upstream from mouth at Río Aguarico, 2-3 November 1983, D. J. Stewart et al. FMNH 96584 (female, 220), Río Aguarico at Destacamento Zancudo, mouth of Ibda Zancudococha, approximately 0°33'S, 75°29'W, 26-31 October 1983, D. J. Stewart et al. FMNH 96588 (female, 145), Río Blanco, first creek tributary to Río Tiputini upstream from bridge, 0°44.5'S, 76°53'W, 4 November 1981, D. J. Stewart et al. Pastaza: FMNH 96445 (1, 104), Río Bobonaza at Chicherota, September 1958, A. Proano.

Table 15. – Summary of principal meristic characters of *Ageneiosus vittatus*.

	NON-TYPES				HOLOTYPE (NMW 47853)
	Range	Mode	Mean	N	
Pectoral Fin Rays	11-13	12	11.8	64	13
Anal Fin Rays	32-39	---	35.6	42	37
Branchiostegal Rays	8-11	9	9.5	35	11
Total Gill Rakers	12-18	15	14.1	24	15
Pleural Ribs	8-10	9	8.8	33	---
Total Vertebrae	45-48	47	46.5	38	47
Preanal Vertebrae	17-20	18	18.4	38	18

Table 16. – Proportional measurements of *Ageneiosus vittatus*.
Measurements 2-21 are expressed as thousandths of standard length (SL);
measurements 22-34 are expressed as thousandths of head length (HL).

	HOLOTYPE (NMW 47853)	NON-TYPES (N = 28)	
		Range	Mean
1. Standard length (SL, mm)	145	67-161	----
2. Preadipose length	841	765-824	785
3. Preanal length	700	610-730	638
4. Predorsal length	337	296-361	327
5. Prepelvic length	526	493-549	509
6. Prepectoral length	333	285-339	302
7. Pectoral origin to dorsal origin	198	155-198	177
8. Pelvic origin to dorsal origin	320	250-301	267
9. Pelvic origin to adipose origin	393	314-491	344
10. Dorsal origin to adipose origin	517	421-500	470
11. Adipose origin to anal insertion	138	130-190	168
12. Body depth at dorsal origin	203	167-237	193
13. Caudal peduncle depth	83	81-109	95
14. Caudal peduncle length	114	97-121	107
15. Body width at pectoral origin	241	182-243	223
16. Body width at pelvic origin	----	98-128	113
17. Dorsal spine length	----	132-353	*
18. Pectoral spine length	159	122-173	147
19. Pelvic fin length	----	108-178	145
20. Anal-fin base length	298	230-313	286
21. Head length (HL)	303	278-329	300
22. Head depth at occiput	545	430-615	529
23. Head width at postorbitals	750	653-764	713
24. Dorsal interopercular width	----	396-476	443
25. Anterior internarial distance	414	354-399	379
26. Anterior-posterior narial distance	----	115-155	138
27. Preisthmus length	648	587-702	664
28. Isthmus width	186	108-190	143
29. Snout length	541	501-579	548
30. Gape width	----	593-705	655
31. Upper jaw length	364	433-500	472
32. Lower jaw length	295	392-449	415
33. Eye diameter	145	112-157	135
34. Barbel length	182	109-418	**

*Mean length of dorsal fin spine in nuptial males = 280 (N = 8); females and non-nuptial males = 169 (N = 16).

**Mean barbel length in nuptial males = 324 (N = 8); females and non-nuptial males = 184 (N = 26).

Fig. 45. —*Ageneiosus vittatus*, USNM 297400, 140 mm SL.

Fig. 46. – Geographic distribution of *Ageneiosus vittatus*.

Ageneiosus n. sp.
Figs. 21, 27, 29, 47-48
Tables 17-18

Ageneiosus vittatus: Burgess 1989:629 (photograph [misidentified]; specimen from Rio Tefé).

Diagnosis

Ageneiosus n. sp. is distinguished from all other members of the genus by its unique coloration pattern, predominated by a very discrete brown midlateral stripe that is subtended above and below by unpigmented stripes of nearly equal width. A combination of the forked tail, encapsulated swimbladder, and moderate size separates this species from all others except *A. ucayalensis*, *A. valenciennesi*, *A. pardalis*, and *A. vittatus*. Distinguished from the last three species, however, by a combination of the slightly shorter anal fin, modally fewer ribs and vertebrae, and the absence of mottling or spotting. Confusion between *A. n. sp.* and either *A. valenciennesi* or *A. pardalis* is not likely because of the distantly allopatric distributions of these three species, as well as the pronounced differences in size, coloration, and other morphological characteristics. *Ageneiosus* n. sp. differs from *A. vittatus* in having fewer pairs of ribs (modally 7 versus 9); a slightly shorter vertebral column (44-47 [$\bar{X}$ = 45.4] versus 45-48 [$\bar{X}$ = 46.5] total vertebrae, and 16-18 [$\bar{X}$ = 17.2] versus 17-20 [$\bar{X}$ = 18.4] preanal vertebrae); slightly more branched pectoral fin rays (modally 13 versus 12); a much more flattened head and compressed body; and a considerably different pigmentation pattern. *Ageneiosus* n. sp. is most similar to *A. ucayalensis* in body shape, both species having an extremely flattened head, but distinguished from that species by a shorter anal fin (31-38 rays versus 41-50 in *ucayalensis*), fewer gill rakers (11-18 versus 18-25), fewer total vertebrae (44-47 versus 46-55), and a markedly different pigmentation pattern.

Description

A relatively small-sized species, not exceeding 170 mm SL in the material examined. The principal meristic and morphometric characters are summarized in Tables 17- 18.

Head greatly flattened and spatulate; 27-32% SL in length, 17-20% SL in breadth. Snout elongate (42-51 % HL), broadly rounded along anterior margin. Contour on top of head gradually sloping to dorsal fin origin, slightly inflected upward at nuchal plate; profile above supraoccipital much more acute in breeding males. Skin on top of head very thin; superficial neurocranial bones moderately textured with weak striae. Fontanelle moderately long, extending posteriorly onto supraoccipital as a weak groove. Nuchal plate hourglass-shaped, relatively narrow in middle. Anterior nares directed forward, just above upper lip and lateral to mesethmoid cornua. Posterior nares remote from anterior pair, between frontals and posterolateral margins of lateral ethmoids. Eyes moderately large, 15-20% HL. Maxillary barbels small, filiform, hidden in rictal groove in females and nonbreeding males. Nuptial males with elongate, hyperossified barbels bearing 7-14 sharp, recurved odontodes on dorsal margin of each. Gape moderately curved, mouth inferior. Teeth on premaxillaries numerous, setiform, in moderately broad crescentic bands, tapering gently to corners of mouth; teeth on dentaries similar, forming a weakly upturned knob at symphysis. Gill membranes broadly fused to isthmus at a plane at or behind rear margin of orbit. Branchiostegal rays 8-10, modally 9. Gill rakers moderately long, 3-5 in outer row of first epibranchial, 8-13 on ceratobranchial; total gill rakers in outer row of first arch 11-18 ($\bar{X}$ = 13.4; N = 26).

Body elongate, notably compressed behind pectoral fins; width of body at pectoral-fin origin 17-20%, width at pelvic origin 9-11% SL. Sides of body strongly

compressed behind pectoral fins, gradually tapered to caudal peduncle. Top of back smooth, gently curved to caudal fin. Ventral profile slightly convex from throat to anal fin origin. Caudal peduncle moderately long, 11-15% SL.

Dorsal fin relatively short in nonbreeding individuals (14-19% SL); dorsal spine thin, nearly smooth on anterior border, posterior border with relatively short, sharp, retrorse serrae. Dorsal spine of nuptial males greatly elongated (34-43% SL), smooth on posterior margin; anterior margin with about 35-60 antrorse serrae, alternately angled to each side along distal portion, clustered in a single row and diminishing to short, rounded bumps near base. Adipose fin small, constricted at base, with large portion of posterior margin free. Caudal fin deeply forked, with acutely pointed, symmetrical lobes; principal caudal rays 8 + 9, about 17-25 ($\bar{X}$ = 21) upper and 15-21 ($\bar{X}$ = 18) lower procurrent rays. Anal fin weakly falcate, with 31-38 (modally 34) rays and 29-35 (modally 32) pterygiophores. First few anal rays of nuptial males thickened and elongated into a recurved gonopodium (Fig. 29). Pectoral fin long, reaching beyond pelvic origin, with 12-15 (modally 13) soft rays. Pectoral spine thin, smooth or slightly rugose on anterior margin, with about 18-25 sharp, retrorse serrae on posterior margin in specimens over 100 mm SL. Pelvic fins moderately large, reaching beyond anal fin origin.

Total vertebrae 44-47, modally 44. Preanal vertebrae 16-18, modally 17. Pleural ribs 7-8, modally 7. Swimbladder small, encapsulated by a heart-shaped ossification of the complex centra, with two relatively long, turgid, posterior caecae (Fig. 21b).

Color in Alcohol

Ageneiosus n. sp. is easily distinguished from all other species of the genus by its unique midlateral brown stripe that extends the length of the lateral line and is

bound above and below by unpigmented stripes. Slight variation in coloration pattern is evident in specimens collected from different areas, with the darkest coloration present in individuals from clear or blackwater rivers. Overall coloration dark brown or black, with unpigmented areas appearing white or yellowish in preserved specimens. Top of head nearly uniform brown except for a short, immaculate or weakly pigmented band along the posterolateral margin of each frontal just in front of the supraoccipital. Opercular area uniformly brown. Lips and upper surface of barbels fringed with brown. Chin, throat, and belly often without much pigment, but occasionally with scattered flecks of brown. Top of back from dorsal fin origin to caudal fin with a uniform chocolate brown stripe, extending laterally to about the upper fourth or third of the side. A prominent, sharply delineated stripe extending length of the body over lateral line, bordered above and below by unpigmented white or cream colored stripes; lower unpigmented stripe of nearly equal width as brown stripe, the upper unpigmented stripe slightly narrower than both. Pigment on lower half of sides of body variable, but typically consisting of diffuse, brown specks that extend onto the base of the anal fin.

Dorsal fin with brown streaks along anterior border of spine and over distal portions of branched rays. Adipose fin with scattered brown flecks throughout, concentrated near base. Distal margin of caudal fin unpigmented, but the rest of the fin with dense brown pigment, occasionally appearing slightly striped along the principal rays, but never with distinct round or elliptical spots as in other fork-tailed species. Pectoral and pelvic fins invariably with brown streaks on upper surface, usually concentrated near base and along outermost rays. Anal fin with diffuse brown specks throughout, often darker and more concentrated near base and along distal margin.

Distribution

Ageneiosus n. sp. ranges widely throughout the middle and lower Amazon basin, including substantial portions of the Rio Negro, Rio Trombetas, Rio Purus, and Rio Tapajos (Fig. 48). It is also present in the Rio Amapá, which drains directly into the Atlantic Ocean, north of Ilha de Marajó at the mouth of the Amazon River. Additional collecting is needed to determine the extent of the species' distribution within other coastal drainages and tributaries of the Amazon. With the exception of one specimen taken from the Río Casiquiare drainage in Venezuela, all of the material examined was collected in Brazil.

Ecology

Nothing previously published. The material examined included a preponderance of nuptial males ($N = 45$), ranging in size from 100-147 mm SL, and all collected between February and June. Only one gravid female (168 mm) was found in these collections, suggesting that there might be possible segregation of the sexes, a skewed sex ratio, or gear selectivity during sampling (nuptial males are probably captured more easily with gill nets or similar gear, due to their spiny barbels and dorsal fin). Three other non-gravid females ranged in size from 141-165, indicating that females probably reach a slightly larger size than males.

Comments

Some authors have apparently confused *A. n. sp.* with *A. vittatus*, presumably on the basis of some overall similarity in coloration patterns. The description of *A. vittatus* by Steindachner (1908) was accompanied by a drawing of the holotype, which exhibits a pronounced midlateral stripe similar to that found in *A. n. sp.*

Unlike this species, however, *A. vittatus* has a large spot at the base of each lobe of the caudal fin, as clearly evident in the figure accompanying Steindachner's description (Steindachner 1908; pl. 9), and still observable in the holotype.

Although the coloration pattern of *A. vittatus* is extremely variable, especially the degree of mottling and extent of stripes on the body, this species never exhibits the uniformly striped coloration of *A. n. sp.* Moreover, *A. vittatus* can be distinguished from *A. n. sp.* on the basis of several additional features (see diagnosis).

Material Examined

Brazil. – Amapá: MZUSP uncat. (MG 27141, 27143-27144, 27147-27149, 27151-27153, 27155; 13 males, 119.3-145.8; 1 female, 168.0), Rio Amapá, cachoeira grande, February 1984, M. Goulding. Amazonas: ANSP 131433 (97.0), W of Moura, near junction of Rio Negro and Rio Branco, approximately 1.5°S, 61.8°W, April-June 1967, J. Faughn. MZUSP 6074 (10 males, 105.8-127.9), Rio Preto da Eva, near Manaus, 13 April 1967, EPA. MZUSP 6337 (female), Lago Castro, mouth of Rio Purus, 7-8 November 1967, EPA. MZUSP 9288 (female, 164.5), market in Manaus, 17-19 September 1968, EPA. MZUSP 34360 (male, 127.1), Rio Negro, cataracts at São Gabriel, 18 May 1979, M. Goulding. MZUSP 34361 (female, 165), Rio Marauíá, cataracts at Bicho-açu, 13 October 1979, M. Goulding. MZUSP 34362 (male, 128.5), confluence of Rio Marauíá and Rio Negro, 27 May 1979, M. Goulding. MZUSP 34363 (male, 134.1), confluence of Rio Negro and Rio Cuiuni, 3 June 1979, M. Goulding. MZUSP 34364 (male, 125.6), confluence of Rio Marauíá and Rio Negro, 27 May 1979. MZUSP 34366 (2 males, 99.8-116.7), confluence of Rio Urubaxi and Rio Negro, 4 February 1980, M. Goulding. MZUSP 34367 (9 males, 132.9-146.9), cataracts at São Gabriel, 1 May 1980, M. Goulding. MZUSP uncat. (3 males, 118.6-131.7), Rio Purus, Santa Luzia, 11

January 1975, P. Vanzolini. Para: MZUSP 5479 (male, 124.2), Rio Trombetas, Oriximiná, February-March 1967, EPA. MZUSP 8266 (2 males, 109.0-112.7), Rio Trombetas, Oriximiná, 16-18 December 1967, EPA. MZUSP uncat. (male, 118.5), Lago Paru, Oriximiná, February-March 1969, EPA. Roraima: MZUSP 34365 (2 males, 114.9-119.7), Rio Branco, mouth of Lago Maquari, 8 May 1979, M. Goulding.

State Unknown. MZUSP 34356 (2 females, 141-145), Rio Tapajos, between Itaituba and Sao Luiz, September-October 1983, M. Goulding. MZUSP 34368 (5, 128.4-166.1), Rio Trombetas, Cuminá, October-November 1983, M. Goulding. MZUSP 34369 (female, 128), Rio Tapajos, between Itaituba and São Luiz, September-October 1983, M. Goulding.

Venezuela. - Amazonas: MCNG 6333 (1, 72.3), Acuarico de Valencia, November 1981.

Table 17. – Summary of principal diagnostic meristic characters of *Ageneiosus* n. sp.

	<u>Range</u>	<u>Mode</u>	<u>Mean</u>	<u>N</u>
Pectoral-fin Rays	12-15	13	13.4	55
Anal-fin Rays	31-38	34	34.3	50
Branchiostegal Rays	8-10	9	9.2	40
Total Gill Rakers	11-18	13	13.9	26
Pleural Ribs	7-8	7	7.3	24
Total Vertebrae	44-47	44	45.4	30
Preanal Vertebrae	16-18	17	17.2	30

Table 18. – Proportional measurements of *Ageneiosus* n. sp. (N = 13). Measurements 2-21 are expressed as thousandths of standard length (SL); measurements 22-34 are expressed as thousandths of head length (HL).

	<u>Range</u>	<u>Mean</u>
1. Standard length (SL, mm)	109-147	----
2. Preadipose length	720-883	786
3. Preanal length	532-619	582
4. Predorsal length	291-333	306
5. Prepelvic length	423-480	457
6. Prepectoral length	267-305	285
7. Pectoral origin to dorsal origin	145-173	156
8. Pelvic origin to dorsal origin	189-238	218
9. Pelvic origin to adipose origin	330-449	387
10. Dorsal origin to adipose origin	448-564	492
11. Adipose origin to anal insertion	118-152	136
12. Body depth at dorsal origin	128-181	157
13. Caudal peduncle depth	83-99	92
14. Caudal peduncle length	113-151	131
15. Body width at pectoral origin	167-196	183
16. Body width at pelvic origin	91-115	103
17. First dorsal ray length	143-434	*
18. Pectoral spine length	164-220	195
19. Pelvic fin length	142-249	177
20. Anal-fin base length	270-352	313
21. Head length (HL)	272-315	287
22. Head depth at occiput	378-502	423
23. Head width at postorbitals	601-698	653
24. Dorsal interopercular width	349-384	366
25. Anterior internarial distance	312-384	337
26. Anterior-posterior narial distance	157-177	168
27. Preisthmus length	635-707	671
28. Isthmus width	112-200	152
29. Snout length	421-513	482
30. Gape width	503-589	551
31. Upper jaw length	364-423	399
32. Lower jaw length	333-376	357
33. Eye diameter	164-207	181
34. Barbel length	138-318	**

*Mean length of dorsal fin spine in nuptial males = 398 (N = 11); females and non-nuptial males = 167 (N = 5).

**Mean barbel length of nuptial males = 290 (N = 11); females and non-nuptial males = 176 (N = 5).

Fig. 47.—*Ageneiosus* n. sp., MZUSP uncat. (MG 27356), nuptial male, 146 mm SL.

Fig. 48. – Geographic distribution of *Ageneiosus* n. sp.

Ageneiosus valenciennesi Bleeker

Figs. 1, 13, 21, 26, 49-50

Tables 19-20

Ageneiosus militaris Valenciennes, in Cuvier and Valenciennes 1840:232-239 (not *Silurus militaris* Linnaeus or Bloch; original description [type locality: Buenos Aires, Argentina]). Valenciennes 1847:7, pl. 4, fig. 1 (citation; synonymy [error]; illustration). Eigenmann and Bean 1907:663 (in synonymy of *A. ucayalensis* [error]). Fowler 1951:455 (in synonymy of *A. valenciennesi*). Boeseman 1972:317 (nomenclature of specific epithet).

Ageneiosus valenciennesi Bleeker 1864:82 (replacement name for *A. militaris* Valenciennes; sexual dimorphism). Eigenmann and Eigenmann 1888:150 (citation; Rio Puty [= Rio Poti]; probable misidentification); 1890:300, 304-305 (in key; partial synonymy; description); 1891:35 (citation). Eigenmann and Bean 1907:663 (in synonymy of *A. ucayalensis* [error]; sexual dimorphism). Eigenmann 1909:341, 348 (listed; Rio Paraguay basin and Amazon basin [error]). Fisher 1917:426 (Buenos Aires; authorship of species in error). Pozzi 1945:260, 272, 280 (citation; distribution; common name). Fowler 1951:455, fig. 481 (partial synonymy; distribution). Ringuelet and Aramburu 1961:42 (citation). Miranda-Ribeiro 1962:4 (museum records). Ringuelet et al. 1967:269-272 (in key; synonymy; description; ecology; *A. militaris* and *A. uruguayensis* placed in synonymy). Boeseman 1972:317 (type specimens and historical nomenclature of *A. militaris*). Britski 1972:100-101, 110 (ontogeny of swimbladder encapsulation; citation). Lopez et al. 1984:76 (listed). Lopez et al. 1987:27 (listed). Ferraris 1988:124 (citation; discussion of nomenclature). Burgess 1989:286 (citation).

Ageneiosus militaris: Günther 1864:191 (partial synonymy; description). Perugia 1891:634 (citation; Rio Plata). Holmberg 1893:90 (common name; barbels; Rio Cuyaba).

Ageneiosus Valenciennesi: Lahille 1895:270 (citation; Isla Santiago).

Ageneiosus valenciennes: Eigenmann 1907:149 (citation).

Ageneiosus uruguayensis Devincenzi 1933:3-4, pl. 1 (original description, [type locality: Rio Uruguay in front of Paysandu, Uruguay]; compared with *A. militaris* Valenciennes). Devincenzi and Teague 1942:56 (brief description; seasonal abundance and breeding period; food habits; fisheries). Pozzi 1945:260, 272, 280 (citation; distribution). Fowler 1951:454-455 (partial synonymy; distribution). Achenbach and Bonetto 1957:7 (common names). Ringuelet and Aramburu 1961:42 (citation). Luengo 1966:19, 21 (holotype listed). Olazarri et al. 1970:4 (type specimens listed). Ferraris 1988:126 (citation). Burgess 1989:286 (citation).

Diagnosis

Ageneiosus valenciennesi can be distinguished from all other large (> 200 mm SL) species, except *A. pardalis* and *A. vittatus*, by its deeply forked tail and characteristic coloration pattern. Meristic counts are of limited use in separating *A. valenciennesi* from *A. n. sp.*, *A. pardalis*, and *A. vittatus*. *Ageneiosus valenciennesi* usually has a prominent mottled or grizzled pattern on the head and body, unlike the distinctive striped appearance of *A. n. sp.*, and also reaches a larger size and has a less spatulate head. The reticulated pattern of blotches on the back in *A. valenciennesi* is somewhat irregular and generally confined to the top third of the dorsum, and includes rather discrete stripes and spots on top of the head; similar blotches in *A. vittatus*, when present, are more closely spaced, less sharply contrasted, and often extend over most of the sides of the body. *Ageneiosus valenciennesi* also reaches a larger size (to at least 300 mm SL) than *A. vittatus* (to about 200 mm SL), and the two are physiographically isolated. In terms of the mottled coloration pattern, *A. valenciennesi* is most similar to *A. pardalis*, but it does not attain nearly the size of *pardalis* (> 450 mm SL), and the ranges of these two species are the most widely disjunct of any in the genus.

Description

Ageneiosus valenciennesi is a moderately large species, reaching a maximum size of at least 300 mm SL. Proportional measurements and the principal meristic characters are summarized in Tables 19-20.

Head greatly flattened, body very compressed posterior to pectoral fins. Head relatively large, 26-30% SL in length, 15-20% SL in breadth. Dorsal profile of head smooth, gradually ascending from snout to dorsal fin origin. Dorsal contour of body gently convex from dorsal fin to caudal peduncle. Ventral contour of body

slightly rounded from snout to anal-fin origin, gradually tapered to caudal-fin base. Snout broadly rounded, gape relatively large. Mouth distinctly inferior, the upper jaw extending beyond the lower and exposing the premaxillary tooth patch in ventral profile. Teeth numerous, setiform. Eyes moderately large (10-16% HL), sublateral, invested in thick fatty tissue. Lateral margins of nuchal shield gradually tapered to dorsal-fin origin. Fontanelle relatively large, opaque, lying within a slightly recessed groove formed by the medial margins of the frontals, not extending far onto supraoccipital. Posterior nares remote from anterior pair. Maxillary barbels small, filiform, concealed in rictal groove except in breeding males. Barbels of nuptial males elongate, ossified, modally with 8 (range = 6-14; N = 10) sharp, recurved odontodes on dorsal margin. Longest gill rakers weakly crenulate on inner margin, 3-5 on outer row of first epibranchial, 9-12 on ceratobranchial, totalling 12-17 ($\bar{X}$ = 14.6) (Fig. 13b). Gill membranes fused to isthmus behind margin of eyes; branchiostegal rays on each side 9-11 (modally 10).

Dorsal-fin spine relatively thin, weakly serrated along distal half or two-thirds of posterior margin, with about 14-16 short, retrorse serrae. Nuptial males with hyperossified dorsal spine, elongate and sinuous, armed along anterior margin with a total of about 40-50 sharp, antrorse serrae, in a basal cluster of about 10 laterally directed serrae, followed distally by an alternating series along the remaining distal portion of the spine; posterior edge of spine smooth. Adipose fin small, posterior margin free. Caudal fin deeply forked, with 8 + 9 principal rays and 17-21 procurrent rays in each lobe (upper lobe averaging 2 more than lower lobe). Pectoral fin not reaching to pelvic origin, triangular and constricted at base, with 11-14 branched rays; pectoral spine relatively thin, with 11-18 short, retrorse teeth along distal half of posterior margin (Fig. 26d). Anal fin with 32-37 pterygiophores (modally 34) and 33-39 rays (modally 37).

Color in Alcohol

Dorsum of body slate gray to brown, usually broken into a series of prominent blotches (Fig. 49). Overall background color dusky white to yellow. Top of head with an irregularly mottled pattern consisting of dark brown blotches, normally with a very dark stripe along each margin of the fontanelle, connected anteriorly by a band extending across the top of the mesethmoid. Nape with a number of smaller spots. Areas between blotches on top of head ranging from immaculate to small, diffuse brown specklings. A dark spot at posteroventral margin of eye, but rest of orbit typically without much pigment. Opercular flap with diffuse specks, margin lightly pigmented.

Mottling on back consisting of large blotches, with a light stripe down midline; blotches not extending much down sides. Side of body with a diffuse band just above lateral line, diminishing abruptly below middle of sides. Sides above pectoral fin with a sublateral band of variably intense speckling, generally disappearing before pelvic fin. Belly, chin, and throat immaculate.

Dorsal fin pale, generally without much pigment except for scattered brown flecks. Adipose fin with brown specks at base, otherwise immaculate. Caudal fin with a crescent shaped spot at base of upper lobe, extending about a third onto rays, and confluent with stripe on top of caudal peduncle.

Distribution

Ageneiosus valenciennesi is confined to southern Brazil, Argentina, Paraguay, and Uruguay. It is distributed widely throughout the middle and lower Rio Paraná-Paraguay basin, and in the lower reaches of the Río Uruguay (Fig. 50) Throughout its range the only other species of the genus with which it is sympatric are *A. brevifilis* and *A. ucayalensis*.

Ecology

Devincenzi and Teague (1942) reported that this species was most abundant in August and September, and March and April; gravid females were identified in November and December. These authors also found that fishes and crustaceans were the principal dietary items.

A series of 44 specimens of *A. valenciennesi* (MZUSP 21113) collected between 1977 and 1980, as part of an impact study prior to the impoundment of a reservoir near Sete Quedas, Brazil, contains 2.3 females per male, but it is unknown whether this sample reflects a naturally skewed sex ratio or a sampling bias. Godoy (1986) found that *A. valenciennesi* was a relatively common species in the Rio Parana near Ilha Grande, prior to the construction of a large hydroelectric dam in that area. The impact of the artificial hydrological conditions resulting from these projects on the population biology and conservation status of this species remains to be ascertained.

Etymology

The patronym *valenciennesi* was provided by Bleeker (1864) as a replacement name for *A. militaris* Valenciennes (1840). The complicated history surrounding the use of the name *militaris* is reviewed in greater detail in the Introduction. As discussed there, the epithet *militaris* is unavailable for this species because at the time that it was originally proposed for an ageneiosid it was preoccupied by a marine catfish (*Osteogeneiosus militaris*) in the family Ariidae .

Common Names

Argentina: manduvé, manduvei, manduví, manduví fino, mandubí (Pozzi 1945, Achenbach and Bonetto 1957, Riguelet and Aramburu 1961, Riguelet et al. 1967).

Comments

Three specimens are extant in the Museum National d'Histoire Naturelle (MNHN), Paris, that presumably provided the material on which Valenciennes (in Cuvier and Valenciennes 1840) based his description of *A. militaris*, and thus serve as the syntypic series for which Bleeker (1864) proposed the accepted replacement name. The specimens were collected in 1829 by d'Orbigny in the vicinity of Buenos Aires, Argentina. All three specimens are males, and were in incipient nuptial condition at the time of preservation as judged from the original description and recent examination of the barbels and dorsal fin spines. They are in moderately good condition given their age, although the largest and smallest were previously dissected or eviscerated. The largest specimen in MNHN B.691, a 233-mm-SL male, is in the best condition and is herein designated the lectotype; the remaining two specimens thus become paralectotypes.

In their synonymy, Riguelet et al. (1967) included a number of references that were not available to me; however, considering the mottled coloration pattern and limited distribution of *A. valenciennesi*, it is unlikely that most of the names provided in their synonymy were based on any other species, with the possible exception of misidentifications of *A. ucayalensis*.

Material Examined

Type specimens. – Lectotype: MNHN B.691 (male, 233), Buenos Aires, Argentina, d'Orbigny, 1829. Paralectotypes: MNHN B.690 (male, 298) and MNHN B.691 (male, 207), both apparently collected with the lectotype.

Argentina. – Buenos Aires: CAS-SU 31569 (male, 255), Buenos Aires. FMNH 58050 (2 males, 221-241), Buenos Aires, 20 February 1909, J. D. Haseman. Misiones: MHNG 2120.4 (male, 208), Ao. Aguaray 30 km au sud de San Juan Bautista, 16 October 1982, Expdt. Museum de Geneve. Santa Fe: – MCZ 23699 (male, 217), Rosario, Captain Brooks. MCZ 23702 (male, 222), Rosario, received 1857, Captain Brooks.

Brazil. – Mato Grosso: MZUSP uncat. (2 males, 112-134; 3 females, 131-258; 1 decapitated), Rio Paraná, Ilha Solteira, 25-28 May 1972. MZUSP uncat. (male, 244), Rio Paraná opposite Jupia, November 1964, P. E. Vanzolini. Paraná: MZUSP 21113 (13 males, 175-250; 30 females, 250-305), Rio Paraná, below Sete Quedas, 1977-1980, CETESB. MZUSP 21114 (17 of 20; 9 males, 115-177; 8 females, 125-205), Rio Paraná, below Sete Quedas, 1977-1980, CETESB. MZUSP 21634 (49, 148-245), Rio Paraná, Guaíra, above Sete Quedas, 1977-1980, CETESB. MZUSP uncat. (2 males, 195-208), Rio Paraná, Guará, July-August 1977, CETESB. Rio Grande do Sul: MZUSP uncat. (2 males, 222-275), Itaqui. São Paulo: MZUSP uncat. (male, 212; female, 242), Salto Grande, August 1963, C. M. Machado. MZUSP uncat. (female, 115), Rio Paraná, Ilha Solteira, September 1965.

Table 19. – Summary of principal diagnostic meristic characters of *Ageneiosus valenciennesi*. Syntypic series is a combination of MNHN B.690 (1 specimen) and MNHN B.691 (2 specimens, last three characters).

	NON-TYPES				SYNTYPES
	Range	Mode	Mean	N	Range
Pectoral-fin Rays	11-14	13	12.6	50	12-13*
Anal-fin Rays	33-39	37	36.6	43	34-36*
Branchiostegal Rays	9-11	10	9.9	36	9-10*
Total Gill Rakers	12-17	15	14.6	31	12*-16
Pleural Ribs	8-9	9	8.7	14	9*-10 (2)
Total Vertebrae	48-50	49	49.3	14	50* (2)
Preanal Vertebrae	18-19	19	18.8	13	19*-20 (2)

*Value for the lectotype (MNHN B.691, male, 233 mm SL).

Table 20. – Proportional measurements of *Ageneiosus valenciennesi*. Measurements 2-21 are expressed as thousandths of standard length (SL); measurements 22-34 are expressed as thousandths of head length (HL).

	LECTOTYPE (MNHN B.691)	NON-TYPES (N = 18)	
		Range	Mean
1. Standard length (SL, mm)	233		----
2. Preadipose length	815	767-834	793
3. Preanal length	640	542-640	595
4. Predorsal length	310	260-325	295
5. Prepelvic length	467	430-510	465
6. Prepectoral length	269	247-304	274
7. Pectoral origin to dorsal origin	153	122-221	154
8. Pelvic origin to dorsal origin	190	149-261	234
9. Pelvic origin to adipose origin	348	335-522	366
10. Dorsal origin to adipose origin	510	379-541	502
11. Adipose origin to anal insertion	124	117-150	136
12. Body depth at dorsal origin	129	130-192	161
13. Caudal peduncle depth	68	73-92	83
14. Caudal peduncle length	124	102-135	122
15. Body width at pectoral origin	173	155-205	182
16. Body width at pelvic origin	105	78-116	98
17. Dorsal spine length	175	128-335	*
18. Pectoral spine length	143	117-160	132
19. Pelvic fin length	142	114-164	139
20. Anal-fin base length	276	261-321	290
21. Head length (HL)	276	256-303	279
22. Head depth at occiput	377	425-520	469
23. Head width at postorbitals	548	561-724	618
24. Dorsal interopercular width	414	376-454	415
25. Anterior internarial distance	350	302-376	340
26. Anterior-posterior narial distance	120	120-508	151
27. Preisthmus length	671	568-730	666
28. Isthmus width	153	78-210	127
29. Snout length	516	511-555	530
30. Gape width	534	489-643	553
31. Upper jaw length	455	418-556	456
32. Lower jaw length	396	357-408	386
33. Eye diameter	137	85-157	118
34. Barbel length	174	115-287	**

*Mean dorsal spine length of nuptial males = 314 (N = 5); females = 143 (N = 8).

**Mean barbel length of nuptial males = 257 (N = 5); females = 135 (N = 8).

Fig. 49.—*Ageneiosus valenciennesi*, MZUSP 21634, female, 217 mm SL.

Fig. 50. – Geographic distribution of *Ageneiosus valenciennesi*.

Ageneiosus ucayalensis Castelnau

Figs. 1, 9, 11, 13, 14, 16, 21, 23, 30, 32, 51-52

Tables 21-22

Ageneiosus ucayalensis Castelnau 1855:49, plate 17, fig. 2 (original description [type locality: Río Ucayali, Peru]). Bleeker 1864:83 (sexual dimorphism; comparison with *A. brevifilis* and *militaris*). Eigenmann and Eigenmann 1888:150 (citation); 1890:300, 306-307 (in key; description); 1891:35 (citation). Miranda-Ribeiro 1911:402, 405-406 (in key; description; account possibly based on complex of species). Fisher 1917:425 (records from Amazon River; variability of premaxillary teeth). Eigenmann and Allen 1942:137-138 (partial synonymy; description). Fowler 1945:67 (citation); 1951:454 (partial synonymy; distribution). Gosline 1945:24 (citation). Pozzi 1945:260, 272 (citation; distribution; probable misidentification of *A. valenciennesi*). Stigchel 1947:107-108 (description). Ringuelet and Aramburu 1961:42 (citation; common name). Miranda-Ribeiro 1962:4 (museum records). Ringuelet et al. 1967:269, 272 (in key; synonymy). Britski 1972:99, 110 (citation). Smith 1981:22 (migration; species associates). Lauzanne and Loubens 1985:69, 98 (sexual dimorphism; sexes illustrated; comparison with *A. brevifilis*). Ortega and Vari 1986:14 (citation; common name). Royero 1987:16, 134, 137 (dorsal fin morphology). Ferraris 1988:123, 127, 151, figs. 7d, 21 (citation; swimbladder encapsulation). Burgess 1989:286 (citation).

Ageneiosus dentatus Kner 1858:441-442 (original description [type locality: Surinam]). Eigenmann and Eigenmann 1888:150 (citation; *A. pardalis* placed in synonymy); 1890:300, 307-309 (in key; partial synonymy; description); 1891:35 (citation, after 1888 account). Eigenmann and Bean 1907:663-664 (partial synonymy; sexual dimorphism; account possibly based on composite of species). Eigenmann 1909:322 (listed in table; Surinam). Miranda-Ribeiro 1911:402, 405 (in key; description; account possibly based on complex of species); 1914:12 (*A. ucayalensis* placed in synonymy). Fisher 1917:425-426 (Bolivian records). Eigenmann 1920a:13 (listed in table; Río Magdalena drainage; probably based on *A. pardalis*); 1920d:27, 29 (listed; lower Magdalena drainage; probably based on *A. pardalis*). Gosline 1945:24 (citation; *A. pardalis* placed in synonymy). Pozzi 1945:260, 272 (citation; distribution; probable misidentification of *A. valenciennesi*). Miles 1947:75, 77 (in taxonomic key; *A. pardalis* placed in synonymy). Stigchel 1947:108-109 (description; *A. paradalis* [error in spelling] placed in synonymy). Fowler 1951:452 (partial synonymy; distribution). Miranda-Ribeiro 1962:3-4 (museum records). Ringuelet et al. 1967:269, 272 (in key; synonymy). Chardon 1968:104-109 (anatomy of the Weberian apparatus and associated structures). Britski 1972:99, 107 (citation). Santos et al. 1984:59 (brief description; photograph; comments on migration). Ferraris 1988:123 (citation). Curran 1989:418 (in material examined). Burgess 1989:286 (citation).

Ageniosus dentatus: Günther 1864:192, 432 (partial synonymy; brief description).

Ageneiosus porphyreus Cope 1867:404 (original description [type locality: Surinam]; allied to *A. dentatus*). Eigenmann and Eigenmann 1888:150 (citation); 1890:301, 309 (in key; citation); 1891:35 (citation). Eigenmann 1909:322 (listed in table; Surinam). Fowler 1915:224 (holotype listed; suggested to be synonymous with *A. guianensis*). Gosline 1945:24 (citation). Britski 1972:99, 109 (citation). Ferraris 1988:124 (citation; misspelled *porphyrus*). Burgess 1989:286 (citation).

Ageneiosus parnaguensis Steindachner 1910:399-401 (original description [type locality: Rio Parnagua, Piauí, Brazil]). Gosline 1945:25 (citation). Fowler 1951:453 (partial synonymy; distribution). Britski 1972:99, 109 (citation). Ferraris 1988:125 (citation). Burgess 1989:286 (citation).

Ageneiosus guianensis Eigenmann 1912:204-205, pl. 21, fig. 2 (original description [type locality: Wismar, British Guiana {= Guyana}]). Henn 1928:74 (holotype listed). Gosline 1945:24 (citation). Britski 1972:99, 107 (citation). Ibarra and Stewart 1987:6, 86 (holotype listed). Ferraris 1988:125, 127, 151, figs. 33, 36 (citation; swimbladder encapsulation; gill arch elements; hyoid apparatus). Burgess 1989:286 (citation).

Ageneiosus caucanus: Burgess 1989:628 (photograph [misidentified]).

Diagnosis

Readily distinguished from other species of the genus by a combination of the deeply forked tail, a very elongate, compressed body, a greatly flattened head with a distinctly inferior mouth, and a very long anal fin. Pigmentation variable, the typical pattern, consisting of dark stripes along the cranial fontanelle, an hourglass-shaped patch on the nuchal plate, and a thin middorsal stripe along the back from behind the rayed dorsal fin and extending onto the base of the upper caudal lobe, further serves to distinguish this species from congeners. The high number of anal fin rays (41-50), and numerous (18-25), long, crenulated gill rakers on the first arch separates *A. ucayalensis* from all other species.

Description

Ageneiosus ucayalensis is a medium-sized species, commonly exceeding 200 mm SL and reaching a maximum size of 283 mm SL in the material examined. Diagnostic meristic and morphometrics of the species are summarized in Tables 21-22. Head greatly flattened and narrow, tapering anteriorly into a spatulate profile when viewed from above or below (Fig. 1). Dorsal profile of head smooth, flat to well-behind orbits, gradually raised above nuchal plate to dorsal spine origin. Eyes large (15% HL in horizontal diameter), sublateral, without free margin and covered by opaque flesh in preserved specimens, frequently with thick subepidermal fat deposits filling adjacent areas of orbital socket. Snout elongate, parabolic, the upper jaw greatly overhanging lower jaw. Premaxillary tooth band broad in center, curved and gradually tapering to thin points posteriorly, with numerous long, setiform, recurved teeth; most of tooth patch exposed when mouth is closed. Dentaries with patch of teeth similar to premaxillae. Anterior nares remote from edge of upper lip. Skin on head thin, translucent; superficial bones of neurocranium and dorsal portion of brain and cranial nerves, especially optic and olfactory tracts, often visible through skin. Dorsal neurocranial elements thin and delicate, porous in young individuals and without prominent superficial bumps or ridges. Frontal constricted anteriorly, forming deeply zigzagged suture with lateral ethmoid and contributing to large, open orbital area. Sphenotic small plate-like element articulating along short anteromedial margin with frontal and posteromedially with the supraoccipital. Branchiostegal rays 8-11, modally 10. Gill membranes fused to isthmus at or behind plane passing through rear margin of orbit. First gill arch with 4-8 rakers in outer row of epibranchial, 12-17 on ceratobranchial; total number of rakers 18-25 (mode = 23; N = 39). Gill rakers long, closely spaced, and generally with accessory cusps on inner margin (Fig. 13a). Barbels short, filiform in all but

non-breeding males, concealed in rictal groove; barbels of nuptial males reaching to or beyond front margin of eye, with about 6-12 long, recurved odontodes on upper margin, concentrated distally (Fig. 16b).

Body widest at pectoral origin, tapering sharply to pelvic-fin base, very compressed and elongate posteriorly. Greatest body depth at dorsal fin origin (10-17% SL), least depth at middle of caudal peduncle (6-10% SL). Dorsal profile of body smooth, ventral profile gradually tapering to anal fin insertion.

Dorsal fin small, constricted at base. Dorsal spine thin, with up to about 30 short, sharp serrations along distal half or more of posterior margin. Dorsal spine of nuptial males greatly elongated and thickened, armed with about 25-50 sharp, antrorse odontodes arranged in an alternating serial row along most of anterior margin and with a dense basal cluster oriented laterally; posterior margin smooth, with a thin medial groove toward base. Adipose fin very small, constricted at base, with free posterior margin. Caudal fin deeply forked, with long, symmetrical, acutely pointed lobes; principal caudal rays invariably 8 + 9, with 19-23 upper procurrent rays and 16-21 lower procurrent rays. Hypural plates highly porous in most specimens, more heavily ossified in older individuals. Pectoral fins relatively long, pointed, constricted at base and with 11-15 segmented lepidotrichia; most rays branched except for short, proximal one or two elements. Pectoral-fin spine long, thin, smooth on anterior margin and with 13-31 ($\bar{X} = 21$) short, sharp, recurved serrae along distal two-thirds or more of posterior margin. Pelvic fins large, roughly triangular in shape. Anal fin long, extending nearly to base of caudal, and with 41-50 rays, the first few unbranched; margin of fin straight, or slightly falcate at anterior margin in nuptial males. Anal pterygiophores 38-47, modally 45.

Swimbladder relatively large in specimens under about 50 mm SL, forming teardrop-shaped capsule invested by thin fibrous tunica; in larger specimens, the swimbladder becomes greatly reduced in size and eventually is encapsulated in a

rigid ossification formed from the vertebral complex (Fig. 21d). Total pairs of pleural ribs 7-9, modally 8. Total vertebrae 46-55 ($\bar{X}$ = 50.1); total preanal vertebrae 16-20 ($\bar{X}$ = 18.1)

Color in Alcohol

Ageneiosus ucayalensis is a polymorphic species that exhibits considerable variation in body pigmentation. Coloration patterns range in intensity both within and among populations. Most individuals have an hourglass-shaped patch of melanophores above the occiput that extends laterally with short extensions onto the opercula, and anteriorly as long stripes along the edges of the fontanelle, approaching or joined to a crescentic spot on top of the snout. Scattered melanophores on top of rest of head, a small spot just behind eye, and sometimes over top half of operculum. Chin and belly normally immaculate, except for scattered patches of melanophores at origin of paired fins in some individuals. Dorsum with variable pigmentation down back, from dorsal origin to caudal base, ranging from a discrete pair of stripes with an unpigmented middorsal stripe to a small band of irregular dark saddles or blotches (Fig. 51). Pigment of back usually extending onto adipose as a small patch at base. A crescentic spot of variable intensity at base of upper caudal lobe, often accompanied by a smaller round spot near center of lower lobe; distal margin of caudal fin with black margin, often evident only at tips of longest rays.

Specimens collected from tannin-stained or other dark-water habitats are much more heavily pigmented than described above. Pigmentation in these specimens typically consists of a nearly uniform dense stippling of brown over most of the head and body, diminishing in intensity ventrally to some degree. In addition, the fins often are moderately to deeply pigmented, especially the paired fins, the

anal, and the base of the caudal. Certain populations, especially those occupying rivers draining the Guiana shield, consistently have such a darker pigmentation pattern.

Distribution

Ageneiosus ucayalensis is a widespread species, paralleling *A. brevifilis* in terms of the size of its entire geographic distribution (Fig. 52). It is found throughout most of the major lowland drainages of South America, including the Orinoco and Amazon basins and various river systems draining directly into the Atlantic Ocean in the northeastern portion of the continent. It is not present in any of the trans-Andean rivers of northwestern Venezuela or Colombia, and apparently does not enter the Rio São Francisco of eastern Brazil. It is present, however, in the upper reaches of the Rio Tapajos, as well as in the Rio Paraná drainage.

Etymology

The specific epithet is derived from the Río Ucayali of Peru, where the holotype was collected.

Common Names

Brazil: ximbé, fidalgo, patinha (Smith 1981, Santos et al. 1984). Venezuela: bagre zapato (Novoa 1982 [fig. 43] mislabelled *A. brevifilis*).

Ecology

In many areas *A. ucayalensis* is seasonally abundant and frequently utilized as a food source, largely as a bycatch of fishing efforts for other species.

Smith (1981) reported the presence of *A. ucayalensis* in schools of mixed species that migrate upstream annually in main channels of the Amazon river. These migrations, known locally as piracemas, are dominated by jaraqui (*Semaprochilodus insignis* and *S. taeniurus*), but include many other species (up to 41 according to Smith 1981). The piracemas begin in June when water levels begin to drop, and continue through early October. *Ageneiosus ucayalensis* is most abundant in piracemas at Itacoatiara during June and July.

At Tucuruí on the Rio Tocantins, Brazil, the peak abundance of *A. ucayalensis* during migration occurs from November to January, and the species was reported to comprise about 20% of the catch during that period (Santos et al. 1984). These authors speculated that, prior to the impoundment of a large reservoir in that area, *A. ucayalensis* migrated further upstream to spawn.

In the Orinoco basin, Novoa (1982) provided cursory notes on the ecology; however, it is unclear if his observations applied exclusively to *ucayalensis*, inasmuch as a figure accompanying his account was mislabelled as *A. brevifilis*, and the maximum length reported for *ucayalensis* (54 cm TL) is considerably greater than any of the material examined in this study. Novoa and Ramos (1978) had earlier identified *brevifilis* as *Ageneiosus* sp., so I assume that the account by Novoa (1982) was indeed based on *A. ucayalensis*. Fish remains were identified as the principal dietary items. Individuals in reproductive condition were found in the middle Orinoco in July. The species was not considered by Novoa (1982) to be of significant commercial importance.

Comments

Four specimens were examined from the syntypic series of *A. parnaguensis*, all currently deposited at NMW. The largest of these (NMW 47837), a 233 mm SL male, is designated the lectotype. The remaining specimens, therefore, become paralectotypes (NMW 47832 and NMW 47838 [2]).

Two syntypes of *A. porphyreus* were examined; the largest of these (ANSP 8388, female, 235 mm SL) is designated the lectotype, and the smaller specimen (ANSP 8389, 159 mm SL) the paralectotype.

Material Examined

Type Material. – Holotype: MNHN B.611 (1, 170), Río Ucayali, Peru, collected by F. Castelnau.

Peru. – Loreto. CAS-IU 15784 (2, 90-210), Lago Cashiboya, August 1920, W. R. Allen. CAS-IU 15785 (2, 137-161), Iquitos, September 1920, W. R. Allen. CAS-SU 34212 (1, 250), Río Ampiyacu near Pebas, 6 November 1936, W. G. Scherer. CAS-SU 34213-34214 (2, 115-126), Pebas District, Shansho Caño, 16 January 1937, W. G. Scherer. CAS-SU 34215 (1, 58), Pebas District, Pebas Caño, 22 February 1936, W. G. Scherer. FMNH 93085 (female, 287), Río Marañon, 9 February 1957, C. Kalinowski. MZUSP 26412 (1, 154), Río Ucayali, Pucallpa, H. Ortega. USNM 167848 (2, 209-217), Lago Cashiboya, August 1920, W. R. Allen. USNM 163834 (1, 182), Iquitos market, 5 August 1920, J. C. Bradley. Ucayali: USNM 261454 (1, 144), Río Ucayali, Pucallpa, 29 May 1979, H. Ortega.

Ecuador. – Napo: FMNH 96587 (female, 215), Río Aguarico about 1 km upstream from Destacamento Lagartococha, 0°38'S, 75°18'W, 1-3 November 1983, D. J. Stewart et al.

Colombia. – Meta: ANSP 128224 (2 males, 154-175), Río Metica, approximately 1.5 km E of Rajote, 3°56'N, 73°03'W, 19 February 1973, W. Saul and W. Smith-Vaniz. State Unknown: FMNH 73412 (male, 173), Río Guaviare, approximately 2°45'N, 71'W, December 1957, S. Weinstein.

Venezuela. – Barinas: Río Caparo at Guayabo, approximately 20 river km below Cantón, 21 December 1983, D. C. Taphorn and L. G. Nico. Bolivar: MCNG 10958 (1, 145), Lago Guri Norte, 1978, J. E. Pacheco. USNM 265676 (1, 104), lagoon on south side of Isla Isabela, between Palua and Ciudad Bolívar, 7 November 1979, J. G. Lundberg et al. Amazonas: CAS-SU 57914 (male, 87), Orinoco bifurcation, Playa de la boca del Casiquiare, 22 March 1925, C. Ternetz. CAS-SU 57958 (1, 102), Orinoco bifurcation, Laja Tama Tama, 28 March 1925, C. Ternetz. Delta Amacuro: CAS 58078 (1, 232), Orinoco River, 8°23'N, 62°42'W, 9 November 1979, D. J. Stewart (R/V *Eastward*). CAS 58082 (2), Orinoco River near Curiapo, river km 60, 8°35'N, 60°59'W, 23 February 1978, J. N. Baskin & J. G. Lundberg (R/V *Eastward*). CAS 58086 (1, 109), Río Orinoco on bottom of deep channel, 8°29'N, 61°18'W, 22 February 1978, (R/V *Eastward*). CAS 58088 (1, 78), Orinoco River downstream from Cano Paloma, river km 91, 8°29'N, 61°25'W, 21 February 1978, J. Baskin and J. Lundberg (R/V *Eastward*). CAS 58155 (3, 61-88), Orinoco River at Curiapo, 8°35'N, 60°59'W, 23 February 1978, J. Baskin and J. Lundberg (R/V *Eastward*). USNM 265666 (female, 62), channel of Río Orinoco below mouth of Río Arature, 52 nautical miles upstream from sea buoy, 8°36'N, 60°54'W, 24 February 1978, J. G. Lundberg and J. N. Baskin. USNM 265681 (1, 85), Río Orinoco, Brazo Imataca, deep channel, 80 nautical miles upstream from sea buoy, 22 February 1978, J. G. Lundberg and J. N. Baskin. USNM 265683 (2, 107-114), channel of Río Orinoco below mouth of Río Arature, 53 nautical miles upstream from sea buoy, 24 February 1978, J. G. Lundberg and J. N. Baskin. USNM 265690-265691 (4, 80-92; 1 c/s), Río Orinoco, river channel downstream

from mouth of Caño Paloma, 8°29'N, 61°25'W, 21 February 1978, J. G. Lundberg and J. N. Baskin. USNM 265693 (4, 75-81), Río Orinoco, Brazo Imataca, 8°28'N, 61°17'W, 22 February 1978, J. G. Lundberg and J. N. Baskin. USNM 265695 (2, 73-83), Río Orinoco, February 1978, J. G. Lundberg and J. N. Baskin. USNM 265700 (1, 80), Boca Grande, shallow river mouth 29 nautical miles from sea buoy, 8°35'24''N, 60°31'48''W, 19 November 1979, J. G. Lundberg et al. USNM 265704 (1, 60), channel of Río Orinoco below mouth of Río Arature, 8°36'N, 60°54'W, 24 February 1978, J. G. Lundberg and J. N. Baskin. USNM 265712 (3, 70-87), channel of Río Orinoco below Barrancas, 8°24'N, 62°07'W, 17 February 1978, J. G. Lundberg and J. N. Baskin. USNM 265715 (2, 53-60), channel of Río Orinoco near Curiapo, 8°35'N, 60°59'W, 23 February 1978, J. G. Lundberg and J. N. Baskin. USNM 265717 (4, 68-89), Río Orinoco, Brazo Imataca, 8°28'N, 61°17'W, 22 February 1978, J. G. Lundberg and J. N. Baskin. State Unknown: CAS-SU 58845 (2, 98-155), Río Orinoco, 8 May 1925, C. Ternetz.

Guyana. – AMNH 12950 (male, 141), Demerara River at Malali, Great Falls, December 1934, A. S. Pinkus. AMNH 13656 (2, 44-74), Demerara River, April 1936, A. S. Pinkus. BMNH 1934.9.12.377 (1, 115), Mazaruni River. CAS 53525 (2, 70-99), locality unknown, July 1976-September 1977. FMNH 53247 (holotype of *A. guianensis*; female, 139), Wismar, 1908, C. H. Eigenmann.

Surinam. – AMNH 54737 (6, 100-131), Corintijn River, km 65, 4 December 1979, R. P. Vari et al. AMNH 54740 (1, 124), Corintijn River, island opposite Camp MacClemmen, 4 December 1979, R. P. Vari et al. UF 16278 (male, 153), vicinity of Paramaribo, 20 June 1968, W. Greenhood. ANSP 8388, 8389 (2, 159-235; syntypes of *A. porphyreus*), exact locality unknown. ZMUC 146-148X (4, 85-132), 13 July 1842, no other data. USNM 226054 (1, 131), Corantijn River, approximately 5°50'N, 57°07'W, 14 May 1980, H. M. Madarie. USNM 226065 (3, 47-82),

Corantijn River about 5 km N of Camp MacClemmen Landing, approximately 5°35'N, 57°11'W, 5 September 1980, R. P. Vari.

Brazil. – Amapá: MZUSP uncat. (2, 200-210), Rio Cupisci, January 1984, M. Goulding. MZUSP uncat. (3, 175-200), Rio Amapá, February 1984. Amazonas: FMNH 58134 (female, 206), Manaus, 16 November 1909, J. D. Haseman. FMNH 58161 (female, 217), Manaus, 28 November 1909, J. D. Haseman. MCZ 7609 (1, 205), vicinity of Teffé, December 1865, Thayer expedition. MZUSP 5767 (2, 156-162), mouth of Paran de Uruc, 15-16 March 1967. MZUSP 5784-5788 (10, 137-283), Paran de Uruc, Itapirang, 16 March 1967, EPA. MZUSP 5873 (male, 154), mouth of Lago Preto, 25 March 1968, EPA. MZUSP 5965 (1, 258), mouth of Rio Purus, 1-5 April 1967, EPA. MZUSP 5966 (2 males, 203-218), mouth of Rio Purus, 1-5 May 1967, EPA. MZUSP 6159 (3 males, 142-160), Rio Negro, above Manaus, 22-25 April 1967, EPA. MZUSP 6201 (10 males, 134-152), Rio Negro, Iq. Jakaqui, 22-24 April 1967, EPA. MZUSP 6399 (1, 185), Rio Purus, Lago Beruri, 8-9 November 1967, EPA. MZUSP 6580-6583 (11, 149-212), Lago Manacapuru, 12-13 November 1965, EPA. MZUSP 6996 (34, 97-163), Rio Madeira, 25 km below Nova Olinda, 27 November 1967, EPA. MZUSP 7613 (1, 151), Paran do Mocambo near Parintins, 10 December 1967, EPA. MZUSP 9289 (4, 142-205), near Ilha Bararu, above mouth of Rio Jutai, 15 October 1968, EPA. MZUSP 13501, 13531 (2, 209-228), Itacoatiara, July 1977, N. J. H. Smith. MZUSP 27635 (3, 64-78), Rio Negro, mouth of Rio Ja, Ayrao Velho, 7 November 1982, L. Portugal. MZUSP 27640 (1, 146), Rio Negro, Pedra do Gvo, Moura, 13-14 November 1982, L. Portugal. MZUSP 34401 (male, 131), Rio Madeira at mouth of Rio Aripuan, M. Goulding. MZUSP 34409 (male, 159; female, 140), Rio Negro, Rosa Maria, 24 October 1979, M. Goulding. MZUSP 34410 (male, 148), Rio Negro, Anavilhanas, mouth of Rio Maraj, M. Goulding. MZUSP 34413 (2 males, 139-145), Rio Negro, Anavilhanas, Lago do Prato, October 1980, M. Goulding. MZUSP 34414 (male, 154), Rio Negro,

Anavilhanas, Igapó, July 1980, M. Goulding. MZUSP 34416 (4 males, 130-163), Rio Negro, São Gabriel da Cachoeira Igapó, 18 May 1979, M. Goulding. MZUSP 36104 (1, 163), Paraná do Lago Castanho, mouth of Rio Japurá, 27 August 1984, R. Barthem. MZUSP uncat. (1, 248), Igarapé Manduacu, Para ná de Inpiá, NW of Fonte Boa, 8-9 October 1968, EPA. MZUSP uncat. (11 males, 160-180; 1 female, 210), Lago de Rei, Ilha Canini, 19 October 1968, EPA. MZUSP uncat. (male, 178; female, 199), Lago do Puco, opposite Santo Antonio do Iça, 18 October 1968, EPA. MZUSP uncat. (male, 163), mouth of Rio Pauini, 11-14 December 1974, P. E. Vanzolini. MZUSP uncat. (4, 112-177), Rio Pauini, 15-19 December 1974, P. E. Vanzolini. MZUSP uncat. (4 males, 158-174), mouth of Ituxi, 22 December 1974, P. E. Vanzolini. MZUSP uncat. (1, 243), Rio Purus, Cassia, 3 January 1975, P. E. Vanzolini. MZUSP uncat. (1, 272), Rio Purus, Campina, 10 January 1975, P. E. Vanzolini. MZUSP uncat. (7 males, 178-230), Rio Purus, Santa Luzia, 11 January 1975, P. E. Vanzolini. MZUSP uncat. (MG 27271) (1, 196), Rio Negro, cataracts at São Gabriel, April-May 1980, M. Goulding. MZUSP uncat. (MG 27287) (1, 182), Rio Marauíá, cataracts at Bicho Açú, 13 October 1979, M. Goulding. MZUSP uncat. (MG 27310) (1, 190), Rio Negro, Anavilhanas, 20 November 1979, M. Goulding. MZUSP uncat. (MG 27362), upper Rio Negro, São Pedro, confluence with Igarapé do Ibará, 23 May 1979, M. Goulding. MZUSP uncat. (MG 28640-28647: 7 males, 175-190; 1 female, 225), confluence of Rio Negro and Rio Marauíá, 27 May 1979, M. Goulding. MZUSP uncat. (1, 150), Rio Arirará, October 1979, M. Goulding. Maranhão: MZUSP uncat. (10, 220-225), Rio Parnaíba (?), R. A. Braga, 1971. Mato Grosso do Sul: MZUSP 27195 (male, 244), Rio Paraguai, Ilha de Taiaimã, 1-7 December 1980, A. S. Soares. Pará: AMNH 3844 (4, 118-221), Para, E. C. Starks. AMNH 3876 (4, 120-149), Para, E. C. Starks. CAS 6572 (3, 121-154), Santarem, 4 August 1924, C. Ternetz. CAS 6591 (2, 166-203), Santarem, 4 July 1924, C. Ternetz. CAS 6597 (1, 150), Rio Tapajos, Santarem, May 1924, C. Ternetz.

CAS 6613 (1, 121), CAS 6627 (1, 200), CAS 6634 (5, 102-200), fish market in Belem, May 1924, C. Ternetz. CAS 6644 (4, 110-153), CAS 6701 (1, 113), Amazon River at mouth of Rio Trombetas, 7 June 1924, C. Ternetz. CAS 6645 (4, 160-159), Rio Tapajos at Santarem, June 1924, C. Ternetz. CAS-SU 22177 (11, 109-213), CAS-SU 22473 (9, 110-232), Para, E. C. Starks. CAS-SU 58830 (2, 165-172), Rio Tapajos, Santarem, 14 June 1924, C. Ternetz. CAS uncat. (1, 211), Santarem market, September 1924, C. Ternetz. FMNH 58135 (7, 140-177), Pará (=Belém), 27 December 1909-22 January 1910, J. D. Haseman. MCZ 7601-7606 (14, 114-225; 1 c/s), Pará (=vicinity of Belém), September 1865, Thayer expedition. MCZ 7608 (3, 103-121), Rio Tocantins at Cametá, February 1866, Thayer expedition. MZUSP 3716 (2 females, 129-208), Lago Irari, 1944, I. Campos. MZUSP 5478, 5480-5481 (14 males, 159-198; 1 female, 214), Rio Trombetas, Oriximiná, February-March 1967, EPA. MZUSP 5650-5652 (20 males, 140-172; 2 females, 189-246), Lago Paru, Oriximiná, February-March 1967, EPA. MZUSP 5678 (1, 192), Rio Trombetas, mouth of Lago Paru, Oriximiná, 5-8 March 1967, EPA. MZUSP 5720 (6, 90-159), Rio Tapajos, Santarem, February-March 1967, EPA. MZUSP 5740-5742 (3, 189-238), Paraná do Armador, Obidos, 12 March 1967, EPA. MZUSP 9198 (male, 178), Rio Maicá, Santarem, 19-27 October 1971, EPA. MZUSP 9480 (7, 128-183), Rio Amazonas, Breves, 3 August 1968. MZUSP 9519 (1, 185), Rio Tapajós, Averio, 19 August 1968, EPA. MZUSP 15825 (1, 202), Rio Trombetas, flooded shoreline at mouth of Lago Jacaré, Reserva Biológica de Trombetas, 26 July 1979, R. M. Castro. MZUSP 25509 (male, 90), Santo Antonio (Pau Rosa), bank of Rio Tapajos, km 83 on BR 230, Parna, 10-13 January 1979, J. C. de Oliveira. MZUSP uncat. (9, 158-200), Taperinha, 21 October 1970, EPA. MZUSP uncat. (MG 27233-27238, 27240-27243) (10, 155-200), on bank of Rio Trombetas, 20 km above the mouth, October-November 1983, M. Goulding. MZUSP uncat. (MG 27252-27255) (4, 155-190), bank of Rio Trombetas, Cuminá, October-November 1983, M. Goulding. MZUSP

uncat. (MG 31070) (1, 200), on bank of Rio Tapajós, between Itaituba and São Luiz, September-October 1983, M. Goulding. MZUSP uncat. (7, 153-191), Rio Tapajós, no other data. USNM 52544 (2 males, 148-155; 3 females, 161-221; 1 c/s), Amazon River from Para (=Belém) to Manaus, 1901, J. B. Steere. Piauí: ANSP 95837 (1, 262), Rio Parnahyba, Therezina (= Teresina), 1936, R. Ihering. MCZ 7610 (male, 255), Rio Poti at Teresina, December 1865, Thayer expedition. MZUSP 36608 (4 males, 214-241; 1 female, 257), market in Teresina, 22 November 1985, H. A. Britski. NMW 47832 (1, 220), NMW 47837(1, 233), and NMW 47838 (2, 177-212) (all syntypes of *A. parnaguensis* Steindachner), Paranagua, 1903. Rondônia: MZUSP 34070 (5, 82-156), Rio Madeira, Calama, December 1980, M. Goulding. MZUSP uncat. (MG 27364: male, 180), Rio Madeira, Calama, March 1980, M. Goulding. Roraima: MZUSP 34408(4 males, 128-159), Rio Branco, Lago Maquari, 8 May 1979, M. Goulding. MZUSP uncat. (MG 28635-28639: 4 males, 148-172; female, 270), between mouths of Rio Branco and Rio Xeriuni, 9 May 1979, M. Goulding. No Data: CAS-IU 4247 (1, 117), locality unknown.

Argentina. – Misiones: MHNG 2394.35 (female, 258), Río Paraná at Candelaria, 26 September 1986, C. Dlouhy. MHNG 2394.36 (3 males, 210-218), Río Paraná at El Dorado, 10 February 1987, C. Dlouhy.

Table 21. – Summary of principal meristic characters of *Ageneiosus ucayalensis*.

	NON-TYPES				HOLOTYPE (MNHN B.611)
	Range	Mode	Mean	N	
Pectoral-fin Rays	11-15	13	13.3	117	14
Anal-fin Rays	41-50	45	45.2	63	47
Branchiostegal Rays	8-11	10	9.9	77	10
Total Gill Rakers	18-25	23	21.4	39	24
Pleural Ribs	7-9	8	7.9	56	8
Total Vertebrae	46-55	---	50.9	71	54
Preanal Vertebrae	16-20	18	18.1	66	19

Table 22. – Proportional measurements of *Ageneiosus ucayalensis*.
 Measurements 2-21 are expressed as thousandths of standard length (SL);
 measurements 22-34 are expressed as thousandths of head length (HL).

	HOLOTYPE (MNHN B.611)	NON-TYPES (N = 120)	
		Range	Mean
1. Standard length (SL, mm)	170	44-289	----
2. Preadipose length	----	809-887	833
3. Preanal length	557	508-615	557
4. Predorsal length	283	252-354	290
5. Prepelvic length	441	398-492	444
6. Prepectoral length	262	224-309	266
7. Pectoral origin to dorsal origin	116	115-164	133
8. Pelvic origin to dorsal origin	191	183-253	208
9. Pelvic origin to adipose origin	430	377-471	419
10. Dorsal origin to adipose origin	574	500-620	555
11. Adipose origin to anal insertion	----	86-136	113
12. Body depth at dorsal origin	105	101-171	134
13. Caudal peduncle depth	62	63-100	80
14. Caudal peduncle length	116	88-146	110
15. Body width at pectoral origin	158	127-189	166
16. Body width at pelvic origin	----	61-116	94
17. Dorsal spine length	----	84-344	*
18. Pectoral spine length	----	106-171	143
19. Pelvic fin length	----	108-182	142
20. Anal-fin base length	335	305-464	345
21. Head length (HL)	----	222-320	269
22. Head depth at occiput	287	326-578	413
23. Head width at postorbitals	464	458-686	569
24. Dorsal interopercular width	----	320-442	381
25. Anterior internarial distance	304	288-389	317
26. Anterior-posterior narial distance	----	114-175	143
27. Preisthmus length	622	666-785	730
28. Isthmus width	125	74-265	174
29. Snout length	428	461-570	507
30. Gape width	----	385-558	488
31. Upper jaw length	----	382-500	439
32. Lower jaw length	----	318-439	370
33. Eye diameter	139	89-209	145
34. Barbel length	64	66-259	**

Fig. 51.—*Ageneiosus ucayalensis*, nuptial male, ANSP 128224, 175 mm SL.

Fig. 52. – Geographic distribution of *Ageneiosus ucayalensis*.

Ageneiosus polystictus (Steindachner)

Fig. 13, 21, 53-54

Table 23

Ageneiosus polystictus Steindachner 1915:217-218 (original description [type locality: mouth of Rio Negro, Brazil]).

Ageneiosus polystictus: Steindachner 1917:84-86, pl. 7, figs. 1-3 (expanded description of 1915 account; generic name corrected). Gosline 1945:24 (citation). Fowler 1951:453 (partial synonymy; distribution). Britski 1972:99,109 (citation). Ferraris 1988:126 (citation). Burgess 1989:286, 629 (citation; photograph of live specimen [pl. 147], misidentified as *Ageneiosus* sp. cf. *guianensis*).

Diagnosis

Ageneiosus polystictus is the only member of the genus having a weakly forked to strongly emarginate tail with broadly rounded lobes in adult individuals. Further distinguished from all congeners by its unique coloration, consisting of dark black spots and reticulations over most of the head and body. In its general body shape *A. polystictus* most closely resembles *A. brevifilis*, but is distinguished from that species by its slightly forked tail, versus an obliquely truncate one in *brevifilis*, and by the lower numbers of pectoral-fin rays (averaging 13.6, versus 14.6 in *brevifilis*), ribs (9-10 versus 10-12), preanal vertebrae (19-20 versus 20-23), and total vertebrae (51-53 versus 55-58).

Description

A moderately large species, commonly exceeding 350 mm SL and reaching up to 450 mm SL. Head fairly blunt (26-31% SL in length, 18-22 % SL in width), body moderately elongate. Dorsal profile of head smoothly sloping in a straight line to dorsal-fin origin. Contour on top of body nearly straight or very slightly convex

from dorsal fin to caudal peduncle. Chin and throat gently curved, giving the head a roughly triangular appearance. Belly typically rounded or swollen to anal-fin origin. Ventral profile of trunk angled upward to relatively narrow caudal peduncle. Morphometrics of the species are summarized in Table 23. Frequencies of meristic counts are in parentheses in the following description, and the values for the holotype are denoted with asterisks.

Mouth subterminal, the upper jaw extending beyond the lower by width of the premaxillary tooth patch. Gape moderately wide, parabolic and slightly pointed at tip of snout in ventral profile. Premaxillary tooth patch relatively narrow, teeth long, setiform. Dentary tooth patch similar to that on premaxillary, except symphysis of dentaries with a prominent upturned knob that is concealed just behind anterior tip of premaxillaries when the mouth is closed. Gill membranes fused to isthmus at plane passing through rear margin of orbits. Branchiostegal rays 10* (9) or 11 (1). Gill rakers relatively short and conical; 3-4 rakers in outer row of first epibranchial, 15-19 rakers on ceratobranchial, total gill rakers 19 (1), 21* (3), 22 (1), 23 (1), or 24 (1). Skin on top of head relatively thick, smooth; bones on top of head (especially the frontals and supraoccipital) textured with weak ridges. Nuchal plate relatively narrow, with slightly convex lateral margins. Anterior nares posterolateral to tips of mesethmoid; posterior nares remote from anterior pair, at margins of frontals.

Swimbladder of adults forming a small, pyriform bulb encapsulated by superficial ossification of the complex centra (Fig. 21e).

Caudal fin weakly forked to strongly emarginate, with distal tip of each lobe broadly rounded, asymmetrical, and the upper lobe longer and narrower than the lower lobe. Principal caudal-fin rays 8 + 9, with about 21-25 upper and 19-21 lower procurent rays.

Pectoral fin long, extending beyond origin of the pelvic fin. First pectoral element forming a very weak spine, ossified at base but filamentous, segmented, and not forming a sharp tip distally; spine moderately flexible, anterior margin smooth, without prominent teeth along posterior margin. Branched pectoral-fin rays 13 (7), 14 (7), or 15* (2). Pelvic fin moderately large, triangular in shape. Anal fin weakly falcate in nonbreeding individuals, with 34* (2), 35 (1), 36 (6), 37 (2), or 39 (1) rays. Anal pterygiophores 32* (1), 34 (3), 35 (2), or 36 (1). Pairs of pleural ribs either 9 (4) or 10 (2). Total vertebrae 51* (2), 52 (4), or 53 (1). Preanal vertebrae 19 (3) or 20* (4).

Color in Alcohol

Overall background color slate-gray to light brown on sides, deep brown or nearly black on dorsum. Live and freshly preserved specimens with a steel-blue cast. Top of body and head of nearly uniform darkness, often with obscure traces of spots. Sides of body below lateral line with a characteristic strongly spotted pattern (Fig. 53). Profuse black or purple spots on head and sides of body formed from dense aggregations of minute specks, becoming more diffuse in intervening areas. Spotting pattern irregular and somewhat variable; in some specimens the spots form elongate, anastomosing reticulations. Belly and throat with considerable pigmentation on a yellowish background, but generally more diffuse and not forming discrete spots as on rest of body. Pigmentation on underside of head most heavily concentrated as thin stripe along lower lip, along leading edge of dentary, as broken spots over brachiostragals, and as diffuse submarginal band along free portion of opercular flap. Skin over eye and small patch above cranial fontanelle unpigmented.

Spinous dorsal fin darkly pigmented, appearing slightly spotted or streaked in some specimens due to lightly pigmented areas of interradial membranes. Adipose fin uniformly black throughout, except for unpigmented thin band along posterior margin. Caudal fin dark brown, spotted at base, uniformly dark throughout lobes, except for broad, unpigmented distal margin, which appears yellowish in preserved specimens. Paired fins heavily pigmented, slightly mottled, with black band along distal margin. Anal fin heavily spotted or mottled at base, pigment extending throughout fin as irregular spots. The intense, dark coloration of this species is attributed in part to its occurrence in the clear and blackwater habitats prevalent throughout its range.

Distribution

Ageneiosus polystictus is found only in the Rio Negro drainage of Brazil, including at least the lower reaches of the Rio Branco (Fig. 54). Some specimens have been taken from near Manaus, Brazil, in the vicinity of the mouth of the Rio Negro. However, the species does not apparently enter the Rio Amazonas proper. The extent of its distribution in the upper Rio Negro and upper Rio Branco is not known because of poor collecting efforts in these areas. Presumably, it may enter the Rio Casiquiare in northern Brazil and southern Venezuela.

Ecology

Nothing is known about the ecology of *A. polystictus*. Since this species appears to be confined to the Rio Negro, draining the southwestern portion of the Guiana shield, it presumably is in some way adapted for the nutrient-poor, blackwater hydrology characteristic of that system. The Rio Negro has a fair degree

of ichthyofaunal endemism, and *A. polystictus* can be added to the preliminary list of species compiled by Goulding et al. (1988:99). At present it is impossible to speculate about any ecological factors that limit *A. polystictus* to this blackwater system, or prevent it from dispersing into the main Amazon river channel or whitewater tributaries.

Etymology

From the Greek *poly*, neuter singular of *polys*, meaning many, and *stiktos*, meaning dotted, in reference to the characteristic spotted pigmentation pattern of this species.

Material Examined

Type Material. – Holotype: NMW 47839 (male, 185), mouth of Rio Negro, J. D. Haseman.

Brazil. – Amazonas: MZUSP 6160 (female, 255), Rio Negro, above Manaus, 22-25 April 1967, EPA. MZUSP 6200 (male, 345), Ig. Jaraqui, m. esq. do Rio Negro, above Manaus, 22-24 April 1967, EPA. MZUSP uncat. (MG 27249-27251; 3 males, 210-230), Rio Daraá, cataract of Aracú, 10 February 1979, M. Goulding. MZUSP uncat. (MG 27264; female, 385), confluence of Rio Negro and Rio Marauia, 27 May 1979, M. Goulding. MZUSP uncat. (MG 27265-27267; 3 females, 285-310), Rio Negro, Anavilhanas, Igapó, July 1980, M. Goulding. MZUSP uncat. (MG 27268; female, 270), Rio Negro, Anavilhanas, September 1980, M. Goulding. MZUSP uncat. (MG 27269; male, 230), Rio Negro at confluence with Rio Arirará, 8 October 1979, M. Goulding. MZUSP uncat. (MG 27270; female, 360), Rio Negro, Anavilhanas, Igapó, July 1980, M. Goulding. MZUSP uncat. (MG 27273; male,

215), Rio Negro, Anavilhanas, Igapó, July 1980, M. Goulding. MZUSP uncat. (MG 27285-27286, 27322; 3 females, 260-315), Rio Marauia, cataract pools of Bicho-Açu, 13 October 1979, M. Goulding. MZUSP uncat. (MG 27288-27292; 3 males, 210-235; 2 females, 285-370), confluence of Rio Negro and Rio Cuiuni, 3 June 1979, M. Goulding. MZUSP uncat. (MG 27307; male, 255), Rio Negro, Anavilhanas, Igapó, May 1980, M. Goulding. MZUSP uncat. (MG 27300-27301, MG 27303-27306, MG 27308; 4 males, 205-230; 3 females, 258-365), Rio Negro, Ilha de Tamaquaré, 10-11 October 1979, M. Goulding. MZUSP uncat. (MG 27309; female, 310), Rio Negro, Anavilhanas, 20 November 1979, M. Goulding. MZUSP uncat. (MG 27311-12, 27314-27316; 4 males, 275-298; 3 females, 330-380), Rio Negro, Anavilhanas, Igapó, March-April 1980, M. Goulding. MZUSP uncat. (MG 27318-27319, 27321, 27323; 2 males, 245-250; 2 females, 230-360), Rio Marié, Lago Curua-muru, 17 October 1979, M. Goulding. MZUSP uncat. (MG 27328; male, 242), confluence of Rio Negro and Rio Cuiuni, 3 June 1979, M. Goulding. MZUSP uncat. (MG 27329-27333; 3 males, 304-306; 2 females 370-420), Rio Negro, Anavilhanas, Igapó, January 1981, M. Goulding. MZUSP uncat. (MG 27334-27337; 3 males, 290-320; female, 385), Rio Negro, Anavilhanas, January 1981, M. Goulding. MZUSP uncat. (MG 27339-27340; 2 females, 253-270), Rio Negro at confluence with Rio Arirará, 8 October 1979, M. Goulding. MZUSP uncat. (MG 27341; male, 218: MG 28622-28626; 3 males, 325-340; 2 females, 280-350), Rio Negro, at confluence with Rio Arirará, 6 October 1979, M. Goulding. MZUSP uncat. (MG 27345; male, 330), Rio Negro at confluence with Rio Mandiquié, 8 October 1979, M. Goulding. Roraima: MZUSP uncat. (MG 27281; male, 348: MG 27296; female, 318: MG 27327; male, 217: MG 28634; male, 177), Rio Branco, between mouths of Rio Branco and Rio Xeriuni, 9 May 1979, M. Goulding.

No Data. – MZUSP uncat. (2 males, 210-238).

Table 23. – Proportional measurements of *Ageneiosus polystictus*.
Measurements 2-21 are expressed as thousandths of standard length (SL);
measurements 22-34 are expressed as thousandths of head length (HL).

	HOLOTYPE (NMW 47839)	NON-TYPES (N = 12)	
		Range	Mean
1. Standard length (SL, mm)	185	205-270	----
2. Preadipose length	755	702-785	739
3. Preanal length	580	560-626	585
4. Predorsal length	265	263-311	278
5. Prepelvic length	431	429-500	453
6. Prepectoral length	278	269-325	286
7. Pectoral origin to dorsal origin	153	136-157	146
8. Pelvic origin to dorsal origin	233	218-250	237
9. Pelvic origin to adipose origin	348	322-430	354
10. Dorsal origin to adipose origin	511	330-492	450
11. Adipose origin to anal insertion	256	160-180	169
12. Body depth at dorsal origin	162	147-187	163
13. Caudal peduncle depth	85	78-91	84
14. Caudal peduncle length	127	122-149	135
15. Body width at pectoral origin	181	158-216	190
16. Body width at pelvic origin	---	107-124	116
17. Dorsal spine length	---	148-336	205
18. Pectoral spine length	183	168-220	187
19. Pelvic fin length	---	153-186	170
20. Anal-fin base length	292	268-329	303
21. Head length (HL)	275	258-306	277
22. Head depth at occiput	439	470-568	509
23. Head width at postorbitals	665	607-788	698
24. Dorsal interopercular width	---	364-414	394
25. Anterior internarial distance	380	347-409	381
26. Anterior-posterior narial distance	---	121-155	145
27. Preisthmus length	473	565-704	640
28. Isthmus width	151	89-171	119
29. Snout length	535	489-662	585
30. Gape width	590	562-694	633
31. Upper jaw length	520	474-581	528
32. Lower jaw length	412	441-548	488
33. Eye diameter	186	102-187	145
34. Barbel length	227	148-289	218

Fig. 53.—*Ageneiosus polystictus*, MZUSP uncat. (MG 27306), female, 258 mm SL.

Fig. 54. – Geographic distribution of *Ageneiosus polystictus*.

Ageneiosus brevifilis Valenciennes
Figs. 1, 8, 22, 23, 25-27, 30, 55-56
Tables 24-25

Silurus militaris: Bloch 1794:19-21, pl. 362 (description; junior primary homonym of *Silurus* [= *Osteogeneiosus*] *militaris* Linnaeus)].

Ageneiosus armatus Lacepède 1803:132-135 (original description [type locality: Surinam]; based on composite of two species).

Ageneiosus brevifilis Valenciennes, in Cuvier and Valenciennes 1840:242-243 (original description [type locality: Surinam]). Bleeker 1958:206, 359 (Guyana). Kner 1858:438-441, fig. 28 (description; sexual dimorphism; coloration; illustration of swimbladder). Cope 1878:676 (see reference in Fowler). Eigenmann and Eigenmann 1890:301, 309-311, fig. 57 (synonymy; description; in taxonomic key; figure of dentition; Serpa, Villa Bella [Thayer expedition]); 1891:35 (reference; distribution). Lahille 1895: (listed, after Perugia). Eigenmann 1907:149 (citation); 1909:322, 341 (listed in table); 1910:397 (reference); 1912:205-206 (synonymy; description). Steindachner 1910:403, pl. 7 (description); 1911:403, pl. 8 (distribution). Fowler 1915:224-225 (size comparisons; tentative synonymization with *A. ogilviei* and *A. marmoratus*; Peru); 1945:67 (literature compiled, in part; Peru); 1941:144 (distribution); 1951:451-452 (synonymy; references; general distribution). Fisher 1917:426 (collection records). Eigenmann and Allen 1942:138 (partial synonymy; distribution). Schultz 1944:240, 243 (partial synonymy; in key; common name). Gosline 1945:25 (citation). Stigchel 1947:106-107 (synonymy; description). Puyo 1949:92-93 (synonymy; description; habitat). Santos 1954:123-124 (brief description; value as food; cursory notes on ecology). Ringuet and Aramburu 1961:42 (citation). Miranda-Ribeiro 1962:3 (museum records). Ringuet et al. 1967:269-270 (in key; synonymy; common names; description; ecology). Mago-Leccia 1970:32 (listed; common name). Boeseman 1972:303-304 (record of holotype; error in type locality). Britski 1972:106 (in part), figs. 38-39 (compiled; in taxonomic key; morphology; taxonomic comparisons; swimbladder encapsulation; status of *Pseudogeneiosus*). Portus et al. 1982:708-709 (electrophoretic mobility of hemoglobin; comparison with other neotropical catfishes). Reid 1983:33 (listed). Santos et al. 1984:59 (description; photograph). Swing and Ramsey 1984:80 (citation). Thatcher and Boeger 1984:505-510 (parasitic copepod). Lauzanne and Loubens 1985:69 (distinguished from *A. ucayalensis*). Godoy 1986:69 (dorsal spine of males; photograph). Ortega and Vari 1986:14 (citation; common name). López et al. 1987:27 (citation). Royero 1987: 16, 134, 137, 194, fig. 32 (in material examined; mental barbels). Burgess

1989:285-286 (habitat; diet; behavior in captivity; citation). Curran 1989:418 (in material examined).

Hypothalmus dawalla Schomburgk 1841:191-192, pl. 9 (original description [type locality: junction of Rupununi and Essequibo rivers, British Guiana {Guyana}]). Eigenmann and Eigenmann 1890:309 (placed in synonymy of *Ageneiosus dawalla*).

Hypophthalmus davalla: Bleeker 1858:64 (unjustified emendation; type of genus *Davalla*); 1862:14 (citation); 1863:108 (citation).

Davalla schomburgkii: Bleeker 1858:64 (replacement name for *Hypothalmus dawalla* Schomburgk, error in spelling). Boeseman 1972:306-307 (historical nomenclature).

Pseudogeneiosus brevifilis Bleeker 1862:14 (designation as type species of *Pseudogeneiosus*); 1863:108 (repeat of 1862 account); 1864:82-84, pl. 16, fig. 2 (diagnosis of genus; redescription of *brevifilis*; Surinam). Miranda-Ribeiro 1911:16, pl. 52, fig. 2 (Brazil); 1914:12 (sexual dimorphism); 1918:735 (Itaqui, Rio Grande do Sul). Pozzi 1945:260, 272, 280 (citation; distribution; common name). Achenbach and Bonetto 1957:7 (citation; common names).

Ageneiosus brevifilis: Günther 1864:192, 431 (description); 1871:1 (listed; Xeberos [= Peru]). Perugia 1891:634 (Rio Durazno). Boulenger 1896:27 (Paraguay). Goeldi 1898:481 (listed; Rio Capim). Steindachner 1910:403, pl. 8 (Rio Purus [see Fowler 1915]). Bertoni 1914:6 (Paraguay); 1939:51 (Paraguay). Magalhães 1931:135-136 (description; common name). Alexander 1965 (1966):90 (listed in material examined; functional morphology; comparisons of *Ageneiosus* with other siluriforms).

Ageneiosus sebæ: Günther 1864:192 (replacement name for *A. inermis* Valenciennes; brief description). Eigenmann and Eigenmann 1890:309 (in synonymy of *Ageneiosus dawalla*).

Ageneiosus axillaris Günther 1864:431-432 (original description [type locality: Surinam]). Eigenmann and Eigenmann 1890:301, 311 (in key; description). Eigenmann 1909:322 (listed in table). Gosline 1945:25 (citation). Burgess 1989:286 (citation).

Ageneiosus (Pseudogeneiosus) axillaris: Eigenmann and Eigenmann 1888:151 (citation); 1891:35 (after 1888 account).

Ageneiosus (Pseudogeneiosus) brevifilis: Eigenmann and Eigenmann 1888:150 (listed; Serpa); 1891:35 (citation, after 1888 account). Berg 1897:265-266 (synonymy; distribution; coloration; fin ray counts).

Ageneiosus dawalla: Eigenmann and Eigenmann 1888:150 (citation; *A. inermis* Valenciennes and *A. sebæ* placed in synonymy); 1891:35 (after 1888 account). Eigenmann 1909:322 (listed in table). Steindachner 1910:401-402, pl. 10 (nomenclature; description). Gosline 1945:25 (citation; *A. inermis* [not Linnaeus] Cuvier and Valenciennes and *A. sebæ* Günther placed in synonymy). Miranda-Ribeiro 1911:404-405 (description; comparison with *A. valenciennesi*). Miranda-Ribeiro 1962:3 (museum records). Burgess 1989:286 (citation).

Ageneiosus therezinae Steindachner 1909:341-342 (original description [type locality: Rio Puti {Poti}, and Rio Parnahyba {=Parnaíba}, Therezina {=Teresina}, Brazil]. Gosline 1945:25 (citation). Fowler 1951:454 (partial synonymy; distribution). Burgess 1989:286 (misspelled as *therezine*).

Ageneiosus ogilviei Fowler 1914:266 (original description [type locality: Rupununi River, Guyana]; comparison with *A. brevifilis*). Gosline 1945:25 (citation). Burgess 1989:286 (citation).

Pseudogeneiosus brevifilis: Delsman 1941:70 (Rio Amazonas, Santa Julia).

Pseudoageneiosus brevifilis: Devincenzi and Teague 1942:56-57, fig. 4 (description; coloration; photograph; ecology; Rio Uruguay).

Ageneiosus sp.: Novoa and Ramos 1978:105, fig. 39 (ecology; fisheries).

Diagnosis

Ageneiosus brevifilis is distinguished from all other species of the genus except *A. marmoratus* by a combination of the robust body form; an obliquely truncate caudal fin with 8 + 10 principal rays; a high number of pectoral fin rays (13-16); a very reduced, encapsulated swimbladder; and the first pectoral element not forming a stiffened, serrated spine. The species reaches a much greater length (to at least 45 cm) and lacks the distinctive mottling pattern characteristic of *A. marmoratus*.

Further distinguished from large congeners by the high numbers of branchiostegals (modally 11), pleural ribs (10-12), preanal vertebrae (20-23), total vertebrae (55-58), and numerous ($\bar{X}$ = 25) gill rakers that are short, conical, and lack the crenulated

medial margin present in most other species. Some specimens from dark waters have superficial spots on the head and dorsum similar to *A. polystictus*, but can be readily separated on the basis of the obliquely truncate caudal fin, versus a moderately forked to strongly emarginate fin with white or yellow tips of the lobes in *polystictus*.

Description

A large species, commonly exceeding 30 cm SL and reaching a maximum size of 47 cm SL in the material examined during this study; reportedly reaching as large as 55 to 70 cm (Devincenzi and Teague 1942; Ringuelet et al. 1967). Principal meristics and morphometrics of the species are summarized in Tables 24-25.

Dorsal profile of body smooth, top of head gently sloping from snout to dorsal fin origin. Flesh on top of head relatively thick and not exposing the rigid dorsal neurocranial elements. Supraoccipital and nuchal shield extending as broad plate to dorsal origin. Epaxial musculature of nape and anterior trunk well-developed in larger specimens. Breeding males with swollen epaxial musculature surrounding base of dorsal fin, with slope of dorsal profile over supraoccipital much more convex than in females and non-nuptial males. Head blunt and broad, 27-33% SL in length and 19-25% SL in width. Shape of snout broadly parabolic when viewed from above. Mouth large, weakly inferior, the premaxillaries extending slightly in front of the dentaries. Eyes moderately large (horizontal diameter averaging 10% HL), sublateral, equally visible from below or above. Gill membranes broadly fused to isthmus at plane about even with rear margin of eyes. Gill rakers short, conical, without crenulations on medial margin; first gill arch with 3-7 ($\bar{X}$ = 4.3; N = 21) rakers on outside row of epibranchial, 13-25 ($\bar{X}$ = 19.8) on

ceratobranchial, totalling 17-31 ($\bar{X} = 24.6$). Body gently tapered posteriorly, caudal peduncle relatively deep. Belly gently curved or slightly distended. Width of body broadest at base of pectoral fins, gradually tapered from pectoral fin insertion to origin of pelvic fins, markedly compressed posterior to pelvic fin base.

Paired fins large, variably and often darkly pigmented on upper surface.

Pectoral fin with 13-16 rays, modally 15. Postcleithral spine absent. Dorsal fin short in nonbreeding individuals, constricted at base. First pectoral and dorsal fin lepidotrichia unbranched, segmented, flexible, and not forming stiff, serrated spines as in other species. Breeding males with a greatly elongated, stiffened dorsal-fin spine, smooth on posterior margin but heavily armed with about 30-60 ($\bar{X} = 37$; $N = 21$) odontodes on anterior margin; distally the serrae are arranged in a biserial row of sharp antrorse hooks that alternately are directed slightly to each side of the spine, typically followed by a hiatus of no hooks toward the base, and with a swollen, fleshy base with long, curved hooks that are laterally directed opposite to each other (Fig. 23a). Adipose fin large, ovoid, and with a large central black spot. Caudal fin obliquely truncate, the upper lobe longer and more pointed than the gently rounded lower lobe, with 8 + 10 principal rays, about 22-25 upper procurrent rays, and about 18-19 lower procurrent rays; lowermost principal caudal ray articulating with expanded flange on penultimate hemal spine (Fig. 30a). Distal tips of last 5-6 hemal spines enlarged; last three with laminar ossifications confused with each other and the hyperossified lower hypural plate (PU+1+2). Secondary hypurapophysis of caudal fin forming a prominent shelf that extends onto the upper portion of the lower hypural plate. Anal fin of females and nonbreeding males moderate in length, with 33-41 rays; margin nearly straight except near origin, where longer, unbranched anterior rays form a weakly falcate profile. First 6-7 anterior rays of anal fin in

breeding males thickened, elongated, and coalesced into a stiff, slightly recurved gonopodium. Anal-fin pterygiophores 33-39 ($\bar{X} = 35.4$; $N = 14$).

Total vertebrae ranging from 55 to 58, modally 56. Preanal vertebrae 20 to 23, modally 21. Total pairs of ribs 10 to 12. Branchiostegal rays on each side 10-12.

Swimbladder large in juveniles, progressively reduced in size and encapsulated by superficial ossification of the fourth vertebral centrum during ontogeny; reduced to a tiny, bilobed capsule in specimens greater than about 100 mm SL (Fig. 8).

Color in Alcohol

General coloration of body slate-gray to steel-blue dorsally, gradually diminishing in intensity on lower sides and belly. Pigment consisting of very dense, minute gray specks, appearing overall as dusky countershading on top half of head and body (Fig. 55). General pigmentation of body and fins somewhat variable, differing mainly in intensity, degree, and pattern of mottling. The description here is a composite based on the general pattern found in most preserved material.

Top of head typically dark gray to purplish, nearly uniform over most of cranium except for darker areas on occiput in front of dorsal fin, a dark band across the front of the snout over the premaxillae, and a light opaque region above the cranial fontanelle. Top of head occasionally appears lightly mottled. Edge of upper lip often with a thin, dark gray or black margin except at corners of the mouth. Upper surface of barbel often with scattered, light gray specks, darkest basally; lower surface typically unpigmented. Rictal groove immaculate or occasionally with light gray specks. Melanophores on sides of head diminishing on lower half, extending as thin, subocular crescent that merges behind the eye with a broad,

diffuse band extending across the preoperculum and operculum above the lower margin of the eye. Upper half of operculum with dense, weakly-defined submarginal band and a diffuse, light yellow margin. Underside of head generally unpigmented except for scattered melanophores on skin over posterior edges of lateral branchiostegals, and a series of 15-20 star-like clusters surrounding irregular, superficial lateralis canals and pores on chin overlying dentary (Fig. 1).

Specimens collected in clear- or blackwater rivers are much darker than individuals from more turbid habitats. In these specimens the coloration on the dorsum may be steel-blue to nearly black, and the dark pigmentation extends over a much greater portion of the body than in whitewater specimens. The top and sides of the head and the upper half of the body may also have a number of small, round, black spots similar to those found in *polystictus*.

Günther (1864) remarked that young specimens have brown spotting on the body. Some smaller specimens in the present study were observed to have irregular, rather faint blotches (FMNH 58136, USNM 247251). There were no recently collected juvenile specimens in the material examined during this study, hence no detailed information can be provided concerning possible ontogenetic differences in coloration pattern (see comments in *A. marmoratus* account).

Live specimens sometimes have blood red pigment in the fins and on the venter; adequate information on life colors was not available to me, and it remains unknown whether the red pigment, occasionally mentioned in the literature (Steindachner 1910, Puyo 1949), is present year round or only seasonally.

Distribution

Ageneiosus brevifilis is the most widespread species of the genus, occurring throughout most of the major lowland rivers of South America (Fig. 56). It is widespread and relatively common throughout both the Amazon and Orinoco rivers and their major tributaries. In the Amazon at least, there are more records of the species in the middle and lower portions of the basin, although this may reflect more intense fishing exploitation and collecting efforts rather than actual abundance or distribution. The species is widespread and relatively common in rivers draining the northern and eastern section of the Guiana shield, and it is also present in the Rio Negro drainage. To the south, *A. brevifilis* is present in the large north flowing rivers that drain into the Amazon, including the rios Madeira, Tapajos, Xingu, and Araguaia. The species is also distributed widely throughout the Rio Paraná-Paraguay basin, where it and *A. ucayalensis* are the only sympatric congeners of *A. valenciennesi*.

Etymology

From the Latin *brevis*, meaning short or small, and *filum*, meaning a thread or string, in reference to the maxillary barbels, the small size of which was erroneously believed to be characteristic of both sexes of the species by early authors, who failed to observe ossification of the barbels in nuptial males. The subgenus *Pseudogeneiosus*, from the combined form *pseudes*, meaning false, and the stem of the genus, further emphasizing reduction of the barbels.

Common Names

Argentina: manduvé, manduvei, manduví cabezón , manduví, mandubá, manduvá, mandubí (Berg 1897, Pozzi 1945, Achenbach and Bonetto 1957d, Ringuelet and Aramburu 1961, Ringuelet et al. 1967). Brazil: mandubé, mandubé bagre, mandi-leiteiro, palmito, fidalgo, bocudo (Goeldi 1898, Santos et al. 1984, Godoy 1986). Uruguay: manduvá (Devincenzi and Teague 1942). Venezuela: doncella, bagre zapato, chancletas (Mago-Leccia 1970, Novoa 1982, L. Nico, personal communication).

Ecology

Devincenzi and Teague (1942) reported that the diet of *A. brevifilis* consisted primarily of fishes and crustaceans, that the species was most common from November to March, and that reproduction occurred in December and January in the Río Uruguay. Ringuelet (1967) repeated the information presented by Devincenzi and Teague, and also noted that individuals in the Rio Paraná reached 550 mm in length, 2.38 kg, and lived at least five years.

Novoa and Ramos (1978) found that *Ageneiosus* sp. (= *brevifilis* according to their photograph), captured from the main channels of the Río Orinoco, ranged in size from 27 to 54 cm TL and fed predominately on smaller fishes, and that females were gravid during June.

Reid (1983) discovered that juveniles of *A. brevifilis*, together with many other fishes, associated with juveniles of the large pimelodids *Pseudoplatystoma tigrinum* and *P. fasciatum*. I have not examined the material on which Reid based his observations, but there is a significant possibility that they may have been or

included specimens of *A. vittatus*, which is relatively common in the area of his study.

Thatcher and Boeger (1984) described a copepod that parasitizes the nasal capsule of *A. brevifilis*.

Comments

Boeseman (1972) reported on two specimens in Leiden (RMNH 2975) and concluded that the larger of the two (240 mm SL) was the specimen on which Valenciennes based his description, and thus represents the holotype. There was no reference to the smaller specimen in the original description. It was presumably retained by C. J. Temminck, former director of RMNH, in the event the holotype was lost. Eigenmann (1912) stated that the figure by Bleeker (1864) was of the smaller specimen, a conclusion apparently based on pigmentation of the fins. Boeseman (1972) also noted an apparent error in the type locality, commonly cited as Cayenne (French Guiana). The specimens were collected by H. H. Dieperink, presumably in the vicinity of Paramaribo, Surinam. Neither specimen was examined in the present study.

Material Examined

Bolivia. – Beni: AMNH 39724 (male, 271), Río Iténez, opposite Costa Marques, Brazil, 1-5 September 1964, R. M. Bailey.

Peru. – Loreto: CAS 18283 (2, 146-258), Rio Solimões at Iquitos, September 1920, W. R. Allen. CAS 18287 (1, 350), Lago Cashiboya, August 1920, W. R. Allen. CAS 18293 (1, 330), Iquitos, 1920, W. R. Allen. CAS 18377 (1, 220), Iquitos,

September 1920, W. R. Allen. CAS-IU 15955 (2, 180-266), Iquitos, September 1920, W. R. Allen. CAS-IU 15959 (2, 159-197), Iquitos, 1920, P. Morris. CAS-IU uncat. (male, 168), Iquitos, bought in market in Brazil (?), 5 August 1920, J. C. Bradley. USNM 86831 (1, 225), Iquitos, September 1920, W. R. Allen. USNM 86289 (1, 202), Iquitos, ca. 1920, W. R. Allen. USNM 124948 (1, 295), Río Ampiyacu, 14 December 1935, W. G. Scherer. USNM 261449 (1, 201), mouth of Río Napo, 25 September 1982, H. Ortega. Ucayali: MZUSP 26411, Río Ucayali, Pucallpa, 29 April 1976, H. Ortega. State Unknown: ANSP 21166 (1, 178), 1873, J. Orton.

Ecuador. – Napo: FMNH 96586 (head only), Quebrada Zancudococha, about 1 km upstream from mouth in Río Aguarico, 2-3 November 1983, D. J. Stewart et al.

Colombia. – Leticia: ANSP 103928 (female, 382), market on Amazon River, 8 July 1968, Huggins. Meta: ANSP 103985 (male, 305) and 103987 (male, 302), Río Negrito at bridge on road between Puerto Lopez and Villavicencio, 4°03'N, 73°04'W, 15 March 1973, J. E. Böhlke et al. ANSP 103986 (male, 310), NE side of Laguna Mozambique at Mozambique ranch, 3°58'N, 73°04'W, 19 March 1973, J. E. Böhlke et al. ANSP 135829 (female, 450), same locality as ANSP 103986, 26 March 1975, J. E. Böhlke et al.

Venezuela. – Apure: MCNG 11334 (2 males, 305-310), Caño Maporal next to the UNELLEZ module, 15-16 November 1984, D. C. Taphorn et al. MCNG 11335 (male, 325), same locality as MCNG 11334, 23-24 March 1984, L. G. Nico. MCNG 11336 (male, 360), Caño Caicara next to the UNELLEZ module, 16 November 1984, D. C. Taphorn et al. Barinas: MCNG 11075 (female, 450), Río Suripá near mouth of Río Tucupido, 22 December 1983, D. C. Taphorn and L. G. Nico. Bolivar: ANSP 135822 (4, 240-250), Caño Chuapo about 20 min downstream from Jabillal, on Río Caura, 7°07'N, 65°00'W, W. G. Saul et al. MCNG 11333 (1,

264), Caño Raro Claro (?), beneath bridge on road to Isla Amacoco, 2 km west of Alcabala, 13 August 1979, D. C. Taphorn et al. Delta Amacuro: USNM 265630 (1, 198), Río Orinoco, SE end of Isla Portuguesa, 117 nautical mi upstream from sea buoy, 8°36'N, 61°48'W, 20-21 February 1978, J. G. Lundberg and J. N. Baskin.

Guyana. – ANSP 39343 (male, 157.5), holotype of *A. ogilviei*, Rupununi River, 1911-1912, J. Ogilvie. BMNH 1974.5.22:518 (1, 422), Rupununi River, R. Lowe-McConnell. FMNH 59277 (male, 365), Mahaica River, Lama stop-off, 1908, C. H. Eigenmann.

Surinam. – AMNH uncat. (1, 284), Mazuruni-Potaro District, Whyape Creek about 0.5 mi from Cuyuni River, 23 June 1986, R. Schmidt. BMNH 1864-6.2:2 (female, 253), holotype of *A. axillaris*, specific locality unknown, Kappler. ZMUC 145 (male, 263), specific locality unknown, 13 July 1842.

French Guiana. – MNHN B.217 (367), MNHN B.219 (270) and MNHN B.220 (193), Cayenne, 1877, 1855 and 1876, Mélinon. MNHN B.218 (2, about 335), "Cotes Fermes", 1841, Beupershius.

Brazil. – Amapá: MZUSP uncat. (MG 27078-27101, 27103-27104, 27186-27204, 27206-27227, 27246-27248: 52 males, 225-315; 18 females, 205-315), Rio Araguari, Ferreira Gomes, January-February 1984, M. Goulding. MZUSP uncat. (MG 2254-2258: 3 males, 232-345; 2 females, 250-260), Rio Amapá, February 1984, M. Goulding. MZUSP uncat. (MG 2463-2467, 2470-2473. 2475-2477: 7 males, 300-375; 5 females, 290-470), Rio Cupixi, January 1984, M. Goulding. Amazonas: CASIU 15786 (1, 233), Rio Amazonas at Manaus, 1920, W. R. Allen. FMNH 58051 (4, 240-296), Rio Amazonas at Manaus, 15-28 November 1909, J. D. Haseman. MCZ 7606 (female, 442), Serpa, (Rio Amazonas at Itacoatiara), 1865, Thayer expedition. MCZ 23415 (female, 358), Villa Bella, (Rio Amazonas at Paratins), 1865, Thayer expedition. MCZ 52584 (4 males, 266-307), Paraná de Janauacá, 3°25'S, 61°21'W,

7-12 December 1976, W. L. Fink. MZUSP 5768 (male, 305), mouth of Paraná de Urucará, 15-16 March 1967, EPA. MZUSP 6103 (male, 280), Lago Puraqueqara, mouth of Rio Puraqueqara, 17-19 April 1967, EPA. MZUSP 6400 (male, 232; 5 females, 238-320), Rio Purus, Lago Berurí, 8-9 November 1967, EPA. MZUSP 9384 (male, 77.1), cataracts at Igarapé, Cuminá, border of Rio Ica, 60 km above the mouth, 18 October 1968, EPA. MZUSP 13551-13554 (2 males, 335-340; 2 females, 400-410), Itacoatiara, 1977, N. J. H. Smith. MZUSP 36110 (1, 215), Igarapé Ubi, Lago Anamá, above mouth of Rio Japurá, 13 October 1979, R. Barthem. MZUSP 37879 (1, 171), Igarapé Beem, Humaitá, July 1975. MZUSP uncat. (male, 270), market in Manaus, 17-18 September 1968. MZUSP uncat. (1, 355), Lago Puraqueqara, 31 October-1 November 1969, EPA. MZUSP uncat. (male, 295), Rio Purus, Santa Luzia, 11 January 1975, P. E. Vanzolini. MZUSP uncat. (3 males, 320-335; 1 female, 390), Lago Janauacá and vicinity, November 1976-January 1977, R/V *Alpha Helix*. MZUSP uncat. (MG 27228-27232: 5, 247-285), Rio Trombetas, Cuminá, October-November 1983, M. Goulding. MZUSP uncat. (MG 27293, 27344: 2, 267-325), Rio Tefé, 30 July 1979, M. Goulding. Mato Grosso: MZUSP 36932 (5, 255-340) and MZUSP 37484 (1, 285), Rio Alegre, tributary of Rio Guaporé, about 30 km above Vila Bela da Santíssima Trindade, 28-30 September 1984, J. C. Garavello. MZUSP 37424 (1, 250), Rio Branco, tributary of Rio Guaporé na altura da Ponte da BR 364 Cuiabá-Porto Velho, Pontes e Lacerda, 10 October 1984, J. C. Garavello. Mato Grosso do Sul: MZUSP 27194 (2, 275-325), Ilha de Taiamã, Rio Paraguai, 1-7 December 1980, A. S. Soares. MZUSP 27726 (male, 335), Rio Taquari, Coxim, 22 October-2 November 1983, A. Carvalho. Para: CAS-SU 58844 (1, 224), Santarem market, September 1924. MZUSP 3720 (male, 275), Belem, 1944, A. Capos. MZUSP 5040 (7, 178-232), cataracts at Arari, Isla de Marajó (?), 12 June 1966. MZUSP 5483 (female, 350), Rio Trombetas. MZUSP

5531, Lago Jacupá, Oriximiná, February 1967, EPA. MZUSP 5532 (300-325), Lago Jacupá, February 1967. MZUSP 5653 (3 females, 320-370), Lago Paru, Oriximiná, 8 February-5 March 1967, EPA. MZUSP 5654 (9 males, 260-295; female, 325; 2 decapitated), Lago Paru, Oriximiná, February-March 1967. MZUSP 9197 (male, 275; 2 females, 205-255), Rio Maicá, Santarem, 19-27 October 1971, EPA. MZUSP 9444 (2 males, 338-360), mouth of Cuminá, near Oriximiná, 20-27 January 1968, EPA. MZUSP 36863 (2, 355-430), cataracts at Espelho, Rio Xingú, 23-26 October 1986, P. E. Vanzolini. MZUSP uncat. (280-312), Rio Amazonas at Para (= Belem). MZUSP uncat. (male, 170), Rio Trombetas, Oriximiná, 28 August 1968. MZUSP uncat. (female, 265), Lago Jacarí, Rio Trombetas, 7-11 October 1969, EPA. MZUSP uncat. (MG 27178-27184: 4 males, 295-355; 3 females, 275-350), Rio Tapajós, between Itaituba and São Luis, September-October 1983, M. Goulding. MZUSP uncat. (MG 27160-27175: 4 males, 285-365; 12 females, 195-340), Rio Xingu, Belo Monte, July-August 1983, M. Goulding. MZUSP uncat. (MG 27244-27245, 27256: 3, 245-345), Rio Itacaiunas, June-July 1983 (?), M. Goulding.

Paraná: MZUSP 21112 (male, 450), Rio Paraná, below Sete Quedas, 1977-1980, CETESB. Piauí: MZUSP 5116 (female, 280), market in Teresina, 19-22 June 1966. NMW 47840 (2, 268-292) and NMW 47841 (1, 150), all syntypes of *A. therezinae* Steindachner (see comments), Rio Parnaíba at Teresina. Rio Grande do Sul: FMNH 58052 (female, 364), Mato Grosso, Buenos Aires (?), 20 February 1909, J. D. Haseman. MZUSP 2315 (male, 310; female, 465), Itaquí, 1914, Garbe. MZUSP uncat. (ex MZUSP 2275) (male, 255), Rio Uruguay, Itaquí. Rondonia: MZUSP uncat. (MG 27274, 27275-27279: 4 males, 292-340; 2 females, 270-323), Rio Madeira, Calama, April-May 1980, M. Goulding. MZUSP uncat. (MG 27338, 27346-27347: 3, 285-415), Rio Madeira, Calama, Biribá, August 1980, M. Goulding.

Roraima: MZUSP uncat. (MG 27342-27343: 265-275), Rio Branco, Marará, 28

October 1979, M. Goulding. MZUSP uncat. (MG 27280, 27282, 27284, 27294-27295, 27297-27299, 27324-27326: 7 males, 315-350; 4 females, 335-460), Rio Branco, between mouths of Rio Branco and Rio Xeriuni, 9 May 1979, M. Goulding.
State Unknown: ANSP 95833 (1, 290), Forteleza-Ceara, 1937, R. Ihering. FMNH 59800 (male, 212), Bastos, 26 January 1909, J. D. Haseman.

Paraguay. – MHNG 2352.97 (2, 238-242), Río Negro 6 km de Chaco-i, 17-18 March 1985, Expdt. Zool. Mus. Geneve. UMMZ 205824 (2 skel, 304-333), Asuncion, Dept. Central, purchased in Pettirossi Street Mercado Cuatro, 6 June 1979, R. M. Bailey and J. N. Taylor. UMMZ 207464 (female, skel, 345), Rio Parana about 2 km E of Ayolas, 25-26 August 1979, J. N. Taylor and G. Smith. USNM 52607 (1, 290), no specific locality or date, T. J. Page. USNM 181701 (1, 176), Río Paraguay near Asuncion, 20 December 1956, C. J. D. Brown.

Locality unknown. – ANSP 81729 (male, 325; female, 33), 1937, R. Ihering. MNHN A.8899 (1, 355), Brazil.

Table 24. – Summary of principal diagnostic meristic characters of *Ageneiosus brevifilis*.

	<u>Range</u>	<u>Mode</u>	<u>Mean</u>	<u>N</u>
Pectoral-fin Rays	13-16	15	14.6	39
Anal-fin Rays	33-41	36	37.5	33
Branchiostegal Rays	10-12	11	10.9	21
Total Gill Rakers	17-31	---	24.6	23
Pleural Ribs	10-12	10	10.8	16
Total Vertebrae	55-58	56	56.5	17
Preanal Vertebrae	20-23	21	21.0	16

Table 25. – Proportional measurements of *Ageneiosus brevifilis* (N = 29). Measurements 2-21 are expressed as thousandths of standard length (SL); measurements 22-34 are expressed as thousandths of head length (HL).

	<u>Range</u>	<u>Mean</u>
1. Standard length (SL, mm)	159-442	----
2. Preadipose length	685-765	738
3. Preanal length	546-645	606
4. Predorsal length	275-344	301
5. Prepelvic length	446-524	487
6. Prepectoral length	272-337	310
7. Pectoral origin to dorsal origin	143-173	160
8. Pelvic origin to dorsal origin	224-277	251
9. Pelvic origin to adipose origin	271-361	319
10. Dorsal origin to adipose origin	416-473	449
11. Adipose origin to anal insertion	151-207	173
12. Body depth at dorsal origin	150-210	179
13. Caudal peduncle depth	72-93	84
14. Caudal peduncle length	119-147	133
15. Body width at pectoral origin	176-244	209
16. Body width at pelvic origin	96-135	119
17. First dorsal ray length	144-292	*
18. First pectoral ray length	146-209	178
19. Pelvic fin length	123-190	151
20. Anal-fin base length	52-311	272
21. Head length (HL)	268-330	294
22. Head depth at occiput	394-646	524
23. Head width at postorbitals	661-828	736
24. Dorsal interopercular width	378-454	414
25. Anterior internarial distance	362-419	397
26. Anterior-posterior narial distance	108-138	121
27. Preisthmus length	558-699	641
28. Isthmus width	67-292	134
29. Snout length	605-698	638
30. Gape width	614-748	685
31. Upper jaw length	553-630	583
32. Lower jaw length	502-578	540
33. Eye diameter	68-128	98
34. Barbel length	101-314	**

*Mean length of first principal dorsal ray in nuptial males = 252 (N = 5); females and non-nuptial males = 166 (N = 21).

**Mean barbel length of nuptial males = 259 (N = 5); females and non-nuptial males = 159 (N = 24).

Fig. 55.—*Ageneiosus brevifilis*, USNM 265630, 198 mm SL.

Fig. 56. – Geographic distribution of *Ageneiosus brevifilis*.

Ageneiosus marmoratus Eigenmann

Fig. 57

Table 26

Ageneiosus marmoratus Eigenmann 1912:206, pl. 22, fig. 1 (original description [type locality: creek below Potaro Landing, British Guiana { = Guyana}]). Henn 1928:74 (holotype listed). Shelden 1937:26, 30-32, 50-54, 71, 77-89 (osteology and myology of pelvic girdle; evolutionary relationships with other families). Gosline 1945:25 (citation). Britski 1972:99, 108 (citation). Ibarra and Stewart 1987:6, 86 (holotype listed). Ferraris 1988:64, 69, 71, 125, 127, 151 (citation; presence of cleithral spine in juvenile; ontogenetic change of tripus and elastic spring apparatus). Burgess 1989:286 (citation).

Ageneiosus dawala: Puyo 1949:93-94, fig. 51 (synonymy [based at least in part on *A. brevifilis*]; description; color in life; habitat).

Ageneiosus barranquerensis Risso and Risso 1964:10-12, 27 (original description [type locality: Río Negro, Riacho Barranqueras, Argentina]). Ferraris 1988:127 (citation).

Diagnosis

A handsome catfish distinguished from all other species by its striking coloration pattern, consisting of large, irregular, and sharply contrasting black blotches on the head, body, and fins. Further characterized by a combination of its large, robust head; a broad, parabolic snout and wide gape; an emarginate tail with 8 + 10 principal caudal rays; the first dorsal and pectoral lepidotrichia flexible, segmented, and unserrated; short, conical gill rakers; and high numbers of pectoral rays, branchiostegals, and ribs.

Description

Size comparatively small, all known specimens less than 185 mm SL.

Proportional measurements of the species are summarized in Table 26.

Body relatively short, robust, and compressed posteriorly, but fairly broad at base of the pectoral fins. Head large, its mean length comprising 34% SL and its mean width 25% SL. Mouth subterminal, the upper jaw not greatly extending in front of lower; gape gently curved and parabolic. Nuchal shield broad, smoothly contoured on dorsal surface. Fontanelle short, evident as an opaque ellipse at midline in front of orbits. Eye large (15% HL), sublateral, covered by thin unpigmented skin. Anterior nares remote from margin of upper lip, above posterolateral edge of maxillary. Posterior nares well separated from anterior pair, bordering lateral edges of frontals and about even with anterior point of each groove above upper lip. Maxillary barbels short and filiform, not reaching past rictus, and ossified only at base in all specimens examined. Top of head with numerous short, dendritic acousticolateralis canals terminating at surface as small pores. Premaxillary and dentary tooth bands thin, equal in width at midline as along remaining portions. Teeth long, sharp, recurved. Gill membranes fused to isthmus at a point even with or just behind a plane passing through the center of the eye. Gill rakers short and conical.

First principal lepidotrichium of dorsal fin very weak, segmented, unbranched, and unserrated, not forming a stiffened osseous spine. Pectoral fin large, broadly rounded on distal margin, reaching to or beyond origin of pelvic fin. First pectoral lepidotrichium like that of dorsal fin, unserrated and flexible. Postcleithral process absent (Ferraris [1988] reported a spine in one juvenile individual, but none of the specimens examined in this study had one). Pelvic fins large, roughly triangular, reaching past front of anal fin. Base of anal fin short, distal margin of fin straight, rounded at ends of anterior and posterior rays. Caudal fin distinctly emarginate, asymmetrical, with 8 + 10 principal rays, 18-20 upper procurrent rays (modally 20), and 17-19 lower procurrent rays (modally 17).

Swimbladder small, encapsulated by pyriform ossifications of the complex centrum as in *A. brevifilis*.

Additional meristics of the species are as follows (number of specimens in parentheses, holotype marked with an asterisk): pectoral fin rays I + 14 (2), I + 15* (3), I + 16 (1), or I + 17 (1); anal fin rays 31* (1), 37 (2), 39 (2), 40 (1), or 41 (1) (the unusually low number of anal rays in the holotype is due to an apparent injury or teratological deformity in several pterygiophores, and is not considered typical of the species); anal fin pterygiophores 28* (1), 36 (2), 37 (1), 38 (1), or 40 (1); branchiostegals 10 (1) or 11* (5), pleural ribs 10 (1) or 11* (4); total vertebrae 55 (1), 56* (4), or 58 (2); preanal vertebrae 20 (1), 21 (4), or 22* (1); gill rakers on upper limb of first arch 4* or 5 (modally 4), on lower limb of arch 15 to 21; total gill rakers on outer row of first arch 20 (1), 22 (1), 23 (1), 24* (1), 25 (2), or 26 (1).

Color in Alcohol

Characterized by a distinctive color pattern consisting of bold dark brown or black marbling on a yellowish background (Fig. 57). The top of the head is deep brown or black, and is slightly spotted or mottled due to variation in intensity of pigmentation. Opercular flap with a characteristic white or yellowish submarginal band, extending as a faint white band across nuchal plate just in front of dorsal fin. Edge of opercular flap with a few elongate brown spots. Margin of both lips dusky. Pigment on chin, throat, and belly variable, but often with several large, dark patches and some diffuse, brown specks. Sides of body with a series of prominent brown or black blotches, interspersed with yellow, unpigmented areas. Blotches extend over entire sides of body, and form asymmetric saddles across back. Dorsal fin mostly black, in some specimens with a thin immaculate distal margin, a large oval yellow spot in the center, and an unpigmented band at the base of the

unbranched rays. Adipose fin with a large, round, black spot in the center, occasionally extending over most of fin. Caudal fin with a broad wishbone-shaped spot beginning at the base and extending onto each lobe, often merging with a broad black submarginal band in each lobe, thus giving the appearance of being mostly black except for the fin margins and a triangular whitish or yellow spot in the center. Anal fin with a series of smaller brown spots similar to, and in some cases contiguous with, those on the sides of the body. Paired fins very deep black, generally uniform in intensity except for a thin, yellowish distal margin on unbranched (outermost) ray, but distinctly mottled in some specimens.

Distribution

Known at present only from isolated localities in the Essequibo and Corantijn Rivers, Guyana and Surinam, the upper Amazon basin in Peru, and the middle Paraná River in Argentina. These widely disjunct records are presumably indicative of a widespread distribution throughout central and northeastern South America. The low number of voucher specimens deposited in collections may reflect a combination of natural rarity, poor collecting efforts in appropriate habitats, or, possibly, inadequate collections of juvenile *A. brevifilis* as discussed below.

Ecology

No ecological information about *A. marmoratus* has been published. The following notes were provided by R. E. Schmidt (personal correspondence) concerning collection of a single specimen of *A. marmoratus* from Whyape Creek, Guyana, near its confluence with the Cuyuni River. At the point where this

specimen was collected the creek is relatively small (approximately 30 ft wide), but subject to strong freshwater tidal fluctuation of about a 4 ft vertical magnitude.

During the tidal periods the current is very strong. The specimen was taken in a shallow, muddy cove of the river near the bank, shaded by forest vegetation. Other fishes collected in this area included *Ageneiosus brevifilis*, *A. ucayalensis*, *Bryconops caudomaculatus*, *Leporinus frederici*, *Hoplias* sp., and *Serrasalmus rhombeus*.

Etymology

From the Latin *marmor*, neuter gender, meaning marble, in reference to the strongly mottled coloration pattern on the head, body, and fins.

Comments

Fowler (1915) suggested that *A. marmoratus* (and also *A. ogilviei*) was very close, and possibly identical to *A. brevifilis*. He did not explicitly state his reason for this conclusion; however, it is probable that Fowler's implication was based on similarities in body shape and meristics, particularly anal fin rays. In the present study, *A. marmoratus* could not be reliably separated from *A. brevifilis* on the basis of meristics.

It is possible that *A. marmoratus* is synonymous with *A. brevifilis*, and that the bold coloration pattern is characteristic of juveniles and subadults. This possibility seems even more likely, given the fact that all specimens of *marmoratus* examined are of a relatively small size (45-183 mm), whereas the majority of specimens of *brevifilis* examined exceed this length considerably. Furthermore, no nuptial male specimens of *marmoratus* were observed, although the sample size was very limited. The relatively large holotype of *marmoratus* (148.5 mm) has the characteristic

marbled pattern, although it is somewhat faded from long term preservation in alcohol. The smallest specimens of *brevifilis* examined generally show little trace of marbling and resemble larger specimens in coloration. However, a few specimens of *brevifilis* (ANSP 39343 [holotype of *A. ogilviei*], FMNH 58136, and USNM 247251) have an unusual, somewhat intermediate coloration pattern consisting of small, irregular spots and blotches on the dorsum, and, particularly, on the sides in the form of one midlateral row and a shorter sublateral row above the paired fins. These specimens, as well as the majority of other *brevifilis* material examined, also have strongly mottled paired fins and a large ovoid spot in the adipose fin, similar to *marmoratus*. Moreover, *brevifilis* is widely distributed and occurs at the few localities where *marmoratus* has been collected; one record from Argentina is based on the description of *A. barranquerensis*, the holotype (presumably deposited at MACN) of which was not examined in this study. *Ageneiosus barranquerensis*, however, is tentatively placed in the synonymy of *marmoratus* on the basis of illustrations accompanying the original description (Risso and Risso 1964:plate 2), which clearly show the strong mottling pattern found in no other species. Because the amount of material of *marmoratus* and small specimens of *brevifilis* currently deposited in museum collections is inadequate to elucidate possible ontogenetic changes in coloration, I choose to recognize these two taxa as distinct species pending further studies. The solution to this problem will require collections of complete growth series, similar to the study by Lundberg et al. (1989), in which it was shown that the large pimelodid *Sorubimichthys planiceps* undergoes pronounced coloration changes during development.

Material Examined

Type material. – Holotype: FMNH 53245 (female, 148.5), Guyana, Potaro Landing, 1908, Shideler.

Guyana. – AMNH 56068 (1, 44.8), Kartabo, 1930's, W. Beebe. AMNH uncat. (1, 104.9), Mazaruni-Potaro District, Whyape Creek about 0.5 mi from Cuyuni River, 21 June 1986, R.G. Schmidt et al. BMNH 1972-10.17:300 (1, 165.1), Potaro River, Amatuk, 25 October 1959, R. Liley.

Surinam. – USNM 226066 (1, 101.9), Nickerie District, Mataway Creek approximately 8 km from its confluence with Corantijn River, 4°47'N, 57°45'W, 11 September 1980, R.P. Vari.

Peru. – CAS-SU 58749 (1, 126.4), Rio Ampiyacu near Pebas, 28 November 1941, W.G. Scherer.

Ecuador. – FMNH 96585 (1, 82.7), Río Aguas Negras about 1-2 km upstream from road, 1 December 1983, D. J. Stewart et al.

No Data. – AMNH 19441 (female, 183). CAS uncat. (1, 129.3), specimen from Steinhart Aquarium, 1964-1965.

Table 26. – Proportional measurements of *Ageneiosus marmoratus*.
 Measurements 2-21 are expressed as thousandths of standard length (SL);
 measurements 22-34 are expressed as thousandths of head length (HL).

	HOLOTYPE (FMNH 53245)	NON-TYPES (N = 6)	
		<u>Range</u>	<u>Mean</u>
1. Standard length (SL, mm)	148.5	44.8-165.1	----
2. Preadipose length	754	710-774	756
3. Preanal length	666	566-650	618
4. Predorsal length	315	309-355	337
5. Prepelvic length	513	455-523	496
6. Prepectoral length	319	309-377	350
7. Pectoral origin to dorsal origin	160	150-181	168
8. Pelvic origin to dorsal origin	238	194-252	233
9. Pelvic origin to adipose origin	308	257-327	293
10. Dorsal origin to adipose origin	431	379-504	426
11. Adipose origin to anal insertion	138	147-179	166
12. Body depth at dorsal origin	172	147-214	173
13. Caudal peduncle depth	88	56-85	76
14. Caudal peduncle length	137	110-132	121
15. Body width at pectoral origin	224	190-231	209
16. Body width at pelvic origin	123	96-126	107
17. First dorsal ray length	153	139-194	172
18. First pectoral ray length	139	159-196	180
19. Pelvic fin length	168	145-190	166
20. Anal-fin base length	257	246-295	274
21. Head length (HL)	312	303-371	337
22. Head depth at occiput	492	407-626	479
23. Head width at postorbitals	726	658-948	747
24. Dorsal interopercular width	419	366-422	393
25. Anterior internarial distance	397	386-416	401
26. Anterior-posterior narial distance	127	124-134	128
27. Preisthmus length	680	600-881	681
28. Isthmus width	134	96-150	122
29. Snout length	609	590-666	613
30. Gape width	678	602-802	679
31. Upper jaw length	587	545-620	585
32. Lower jaw length	540	526-584	552
33. Eye diameter	140	112-187	146
34. Barbel length	218	194-380	248

Fig. 57.—Composite illustration of *Ageneiosus marmoratus*. Specimen outline was redrawn from figure of holotype by Eigenmann (1912), FMNH 53245, female, 148.5 mm SL. General pigmentation pattern reconstructed from a combination of specimens.

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BIOGRAPHICAL SKETCH

Stephen J. Walsh was born on 8 September 1957 in Denver, Colorado. He developed an early interest in biology and natural history, kindled by many family outings and boy scout camping trips throughout the Rocky Mountains and western plains. He fondly recalls many visits to the Denver Museum of Natural History, where the exhibits captivated his attention for hours at a time.

In 1971 he moved with his family to Edwardsville, Illinois, a small town just east of St. Louis, Missouri. Immediately after graduating high school in 1975, he enrolled as a liberal arts major at Saint Louis University. There he fostered his long-standing interest in biology and received a bachelor of arts degree with honors in 1979. As an undergraduate, he became interested in a variety of subdisciplines, but it was not until his senior year that he became obsessed with the study of fishes.

In the fall of 1979 he received a fellowship at Southern Illinois University at Carbondale, where he enrolled as a graduate student in zoology. There he further developed his keen interest in fish biology and pursued a variety of research topics that resulted in extensive fieldwork throughout Illinois, Missouri, Kentucky, and Tennessee. In 1982 he received a Master of Arts degree, based on his research of pygmy sunfish ecology in the swamps of western Kentucky.

In 1983 he moved to Gainesville, where he enrolled in the Ph.D. program in zoology at the University of Florida. There he pursued additional studies on fishes and nurtured a special interest in catfish biology and systematics. In 1987 he relinquished graduate support in the form of teaching and research assistantships, and began working as a biologist in the fish collection of the Florida State Museum

(now the Florida Museum of Natural History) while continuing to pursue his doctoral degree. His graduate studies and employment in Florida has resulted in field work, museum visits, travel, and attendance at scientific conferences throughout Florida and various areas of the U.S., Canada, and Brazil.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Carter R. Gilbert, Chair
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

David H. Evans
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Frank G. Nordlie
Professor of Zoology

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Jonathan Reiskind
Associate Professor of Zoology

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William Seaman, Jr.
Associate Professor of
Forest Resources and
Conservation

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August 1990

Dean, Graduate School

UNIVERSITY OF FLORIDA

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