Phylogenetic Study of the Neotropical Fish Genera *Creagrutus* Günther and *Piabina* Reinhardt (Teleostei: Ostariophysi: Characiformes), with a Revision of the Cis-Andean Species

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Phylogenetic Study of the Neotropical Fish Genera *Creagrutus* Günther and *Piabina* Reinhardt (Teleostei: Ostariophysi: Characiformes), with a Revision of the Cis-Andean Species

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ABSTRACT

Vari, Richard P., and Antony S. Harold. Phylogenetic Study of the Neotropical Fish Genera *Creagrutus* Günther and *Piabina* Reinhardt (Teleostei: Ostariophysi: Characiformes), with a Revision of the Cis-Andean Species. *Smithsonian Contributions to Zoology,* number 613, 239 pages, 97 figures, 60 tables, 2001.—*Creagrutus* Günther (1864) and *Piabina* Reinhardt (1867) are diagnosed as a monophyletic assemblage on the basis of synapomorphies in various osteological and soft anatomical systems. Synapomorphies in a subset of these systems diagnose each genus and partially resolve the intrageneric phylogeny within *Creagrutus. Piabina* was found to be nonmonophyletic as previously constituted and is restricted herein to its type species, *P. argentea* Reinhardt (1867). *Creagrudite* Myers (1927) and *Creagrutops* Schultz (1944) share the characters diagnostic for *Creagrutus* and are considered junior synonyms of that genus in order to make *Creagrutus* monophyletic. *Piabarchus* Myers (1928), based on a species originally described in *Piabina,* was found to lack the derived features of the *Creagrutus-Piabina* lineage.

A total of 64 species are recognized in *Creagrutus* (including 37 new species), 56 of which occur east of the Andean Cordilleras and are reviewed in this paper. The number of *Creagrutus* species herein recognized represents 337% of the number of species considered valid prior to Harold and Vari (1994).

Contrary to recent taxonomic practice, *Piabina* is recognized as distinct but is limited to a single species, *P. argentea* Reinhardt (1867), distributed in various rivers of eastern Brazil.

Keys are provided to the species of *Creagrutus* and *Piabina* in the major drainage basins within the range of the genera.

Creagrutus nasutus Günther (1876) is considered a synonym of *C. peruanus,* and *Creagrutus boehlkei* Géry (1972) is placed into the synonymy of *C. amoenus. Creagrutus pellegrini* Puyo (1943) is assigned to the characid genus *Chalceus.*

Lectotypes are designated for *Piabina argentea* Reinhardt, *Leporinus muelleri* Günther, *Creagrutus nasutus* Günther, *C. pearsoni* Mahnert and Géry, *Piabina peruana* Steindachner, and *C. phasma* Myers.

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Contents

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Richard P. Vari and
Antony S. Harold

Introduction

Species of the characiform genera *Creagrutus* Günther and *Piabina* Reinhardt inhabit a diversity of freshwater systems across the broad expanse of the Neotropics from Panama to Paraguay. Through that vast region, the more than five dozen species of *Creagrutus* and the single species of *Piabina* are most abundant in moderately to swiftly flowing water bodies. Species-level diversity within *Creagrutus* is greatest in the streams and rivers draining the piedmont of the eastern slopes of the central and northern Andes, the Pacific versant of northern Colombia, the Caribbean slopes of Colombia and Venezuela, the coastal ranges of the northern portions of the Río Orinoco basin in Venezuela, and the uplands of the Brazilian and Guyana shields. Matching this broad distribution of *Creagrutus* is its notable altitudinal range compared to that of most characiform genera, extending from near sea level at various sites on the continent to nearly 1900 m in southeastern Peru. Relatively high elevation distributions of *Creagrutus* species occur along a nearly 3000 km swath of the Andean Cordilleras extending from southern Peru to Venezuela, with the genus being one of the few among characiforms known from above 1000 m elevations at multiple localities along both the Atlantic and Caribbean versants of the Andean Cordilleras (Ortega, 1992:43; Péfaur, 1988:487; Jiménez et al., 1998:24; this paper). *Piabina,* in contrast, has a distribution totally allopatric to that of *Creagrutus,* being limited to low to midlevel elevation localities in the eastern portions of Brazil and northeastern Paraguay.

Creagrutus and *Piabina* are absent, or rare, in ichthyofaunal samples from lentic waters (Galacatos et al., 1996:894) and from low gradient streams and rivers, most notably those in the central portions of the Amazon basin. At least one species of *Creagrutus,* however, has been reported to be capable of surviving in drying pools (Beebe, 1945:84). Neither *Creagrutus* nor *Piabina* are known from the Pacific versant rivers of Ecuador, Peru, and Chile. East of the Andean Cordilleras both genera are apparently absent from Argentina, most of the shorter Atlantic coastal drainages of eastern and southeastern Brazil, and the southern portions of the Río de La Plata basin, including the Río Uruguay and lower sections of the Río Paraguay and Río Paraná.

Distinctive jaw and dentition modifications in *Creagrutus* and *Piabina* permit members of those genera to exploit specialized food items selected from the bottom of water bodies (F. Lima, pers. comm., 1999), in particular small seeds and the aquatic and terrestrial life stages of a variety of insects. Supplementing these food items are phytoplankton, mollusks, crustaceans, and, less commonly, fish scales (Barriga, 1982; pers. obs.) and smaller fishes (Godoy, 1975; Ortaz, 1992; K.O. Winemiller, pers. comm., 1999; pers. obs.).

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TABLE 1.—Nominal species assigned herein to the genera *Creagrutus* and *Piabina* and recognized equivalent species according to the results of this study and that of Harold and Vari (1994). Nominal species are cited as in original description and arranged alphabetically by specific epithet. Species indicated by asterisks occur to the west of Andean Cordilleras in northwestern South American and southern Central America; these were discussed in detail in Harold and Vari (1994).

Nominal species	Assignment herein
Creagrutus affinis Steindachner, 1879*	*Creagrutus affinis*
Creagrutus amoenus Fowler, 1943a	*Creagrutus amoenus*
Creagrutus anary Fowler, 1913	*Creagrutus anary*
Piabina argentea Reinhardt, 1867	*Piabina argentea*
Creagrutus atratus, new species	*Creagrutus atratus*
Creagrutus atrisignum Myers, 1927	*Creagrutus atrisignum*
Creagrutus barrigai, new species	*Creagrutus barrigai*
Creagrutus beni Eigenmann, 1911	*Creagrutus beni*
Piabina beni Pearson, 1924	*Creagrutus pearsoni*[1]
Creagrutus boehlkei Géry, 1972	*Creagrutus amoenus*
Creagrutus bolivari Schultz, 1944	*Creagrutus bolivari*
Creagrutus brevipinnis Eigenmann, 1913*	*Creagrutus brevipinnis*
Creagrutus britskii, new species	*Creagrutus britskii*
Creagrutus calai, new species	*Creagrutus calai*
Creagrutus caucanus Eigenmann, 1913*	*Creagrutus caucanus*
Creagrutus changae, new species	*Creagrutus changae*
Creagrutus cijerri	nomen nudum[2]
Creagrutus cochui Géry, 1964	*Creagrutus cochui*
Creagrutus cracentis, new species	*Creagrutus cracentis*
Creagrutus crenatus, new species	*Creagrutus crenatus*
Creagrutus ephippiatus, new species	*Creagrutus ephippiatus*
Creagrutus figueiredoi, new species	*Creagrutus figueiredoi*
Creagrutus flavescens, new species	*Creagrutus flavescens*
Creagrutus gephyrus Böhlke and Saul, 1975	*Creagrutus gephyrus*
Creagrutus gracilis, new species	*Creagrutus gracilis*
Creagrutus gyrospilus, new species	*Creagrutus gyrospilus*
Creagrutus hildebrandi Schultz, 1944*	*Creagrutus hildebrandi*
Creagrutus holmi, new species	*Creagrutus holmi*
Creagrutus hysginus Harold et al., 1994	*Creagrutus hysginus*
Creagrutus ignotus, new species	*Creagrutus ignotus*
Creagrutus kunturus Vari et al., 1995	*Creagrutus kunturus*
Creagrutus lassoi, new species	*Creagrutus lassoi*
Creagrutus lepidus Vari et al., 1993	*Creagrutus lepidus*
Creagrutus leuciscus Regan, 1913*	*Creagrutus affinis*
Creagrutus londonoi Fowler, 1945c*	*Creagrutus affinis*
Creagrutus machadoi, new species	*Creagrutus machadoi*
Creagrutus magdalenae Eigenmann, 1913*	*Creagrutus magdalenae*
Creagrutus magoi, new species	*Creagrutus magoi*
Creagrutus manu, new species	*Creagrutus manu*
Creagrutops maracaiboensis Schultz, 1944*	*Creagrutus maracaiboensis*
Creagrudite maxillaris Myers, 1927	*Creagrutus maxillaris*
Creagrutus melanzonus Eigenmann, 1909	*Creagrutus melanzonus*
Creagrutus melasma Vari et al., 1994	*Creagrutus melasma*
Creagrutus menezesi, new species	*Creagrutus menezesi*
Creagrutus meridionalis, new species	*Creagrutus meridionalis*
Creagrutus molinus, new species	*Creagrutus molinus*
Creagrutus mucipu, new species	*Creagrutus mucipu*
Leporinus mülleri Günther, 1859	*Creagrutus muelleri*
Creagrutus nasutus Günther, 1876	*Creagrutus peruanus*
Creagrutus nigrostigmatus Dahl, 1960*	*Creagrutus nigrostigmatus*
Creagrutus notropoides Meek and Hildebrand, 1912*	*Creagrutus affinis*
Creagrutus occidaneus, new species	*Creagrutus occidaneus*
Creagrutus ortegai, new species	*Creagrutus ortegai*
Creagrutus ouranonastes, new species	*Creagrutus ouranonastes*
Creagrutus paraguayensis Mahnert and Géry, 1988	*Creagrutus paraguayensis*
Creagrutus paralacus Harold and Vari, 1994*	*Creagrutus paralacus*
Creagrutus pearsoni Mahnert and Géry, 1988[1]	*Creagrutus pearsoni*[1]
Creagrutus pellegrini Puyo, 1943	apparently a *Chalceus* species[3]
Creagrutus peruanus Steindachner, 1875	*Creagrutus peruanus*

Table 1.–Continued.

Nominal species	Assignment herein
Creagrutus petilus, new species	*Creagrutus petilus*
Creagrutus phasma Myers, 1927	*Creagrutus phasma*
Creagrutus pila, new species	*Creagrutus pila*
Piabina piquira	nomen nudum[4]
Creagrutus planquettei Géry and Renno, 1989	*Creagrutus planquettei*
Creagrutus provenzanoi, new species	*Creagrutus provenzanoi*
Creagrutus runa, new species	*Creagrutus runa*
Creagrutus saxatilis, new species	*Creagrutus saxatilis*
Creagrutus seductus, new species	*Creagrutus seductus*
Creagrutus simus Meek and Hildebrand, 1913*	*Creagrutus affinis*
Creagrutus taphorni, new species	*Creagrutus taphorni*
Creagrutus ungulus, new species	*Creagrutus ungulus*
Creagrutus veruina, new species	*Creagrutus veruina*
Creagrutus vexillapinnus, new species	*Creagrutus vexillapinnus*
Creagrutus xiphos, new species	*Creagrutus xiphos*
Creagrutus zephyrus, new species	*Creagrutus zephyrus*

[1]Mahnert and Géry (1988:5) synonymized *Piabina* Reinhardt (1867) into *Creagrutus* Günther (1864), an action that made *Piabina beni* a junior homonym of *Creagrutus beni* Eigenmann (1911). Mahnert and Géry consequently proposed *pearsoni* as a replacement for *beni* of Pearson (1924).

[2] *Creagrutus cijerri*, listed by Bisbal and Sanchez (1997:267) in the listing of holotypes at MHNLS, is a nomen nudum based on a manuscript name of Fernández-Yépez (C. Lasso, pers. comm., 2000).

[3]*Creagrutus pellegrini* Puyo (1943:113) is apparently based on a *Chalceus* species (see "On the status of *Creagrutus pellegrini* Puyo" under "Genus *Creagrutus* Günther").

[4]*Piabina piquira* listed by Eigenmann (1910:434) is apparently a nomen nudum (see "Remarks" under *Piabina argentea*).

Less than 15 decades have passed since the first descriptions of species in the assemblage herein recognized as *Creagrutus* and *Piabina* (Günther, 1859; Reinhardt, 1867, respectively). These dates are unexpectedly recent in light of the externally obvious distinguishing features shared by *Creagrutus* and *Piabina*, the broad distribution of the assemblage consisting of these taxa within South and southern Central America, and the relative abundance of many *Creagrutus* and *Piabina* species in appropriate habitats. Such a tardy recognition of this distinctive assemblage likely reflects the problems in sampling the ichthyofauna of the interior upland areas and the rapidly flowing streams typically inhabited by *Creagrutus* and *Piabina* species.

Previous analyses of intrageneric diversity in *Creagrutus* were often constrained by limited population samples, a problem compounded by the unavailability of type specimens to many researchers. As a consequence, intraspecific variation and interspecific differences within this assemblage were poorly understood. This taxonomic uncertainty contributed to the pervasive confusion concerning the geographic ranges of most species in the genus. Some *Creagrutus* species have been reported from a suspiciously broad swath of the continent (e.g., *C. beni* Eigenmann, which supposedly ranged from northeastern Bolivia to the Trans-Andean and eastern portions of Venezuela). Other nominal forms (e.g., *C. anary* Fowler), alternatively, were known only from their type series and few, if any, subsequent reports. These interlocking limitations made it difficult, if not impossible, to confidently identify most samples of *Creagrutus*.

More than seven decades ago in the last in-depth review of *Creagrutus* and *Piabina*, Eigenmann (1927) dealt with the 15 nominal species described to that time, 10 of which he recognized as valid. Subsequent decades saw an episodic, albeit progressive, description of additional nominal species assigned to each genus. In overviews of *Creagrutus*, *Piabina*, *Creagrudite* Myers, and *Creagrutops* Schultz (the latter two taxa herein considered synonyms of *Creagrutus*), Géry (1964, 1977) recognized 20 of the 26 species described to that time as valid. Two additional species were subsequently described by Mahnert and Géry (1988) and Géry and Renno (1989) for a total of 28 nominal species, 22 of which were then recognized as valid. Three of these 22 species were, in turn, considered junior synonyms by Harold and Vari (1994) in their analysis of the *Creagrutus* fauna to the west of the Andean Cordilleras. As a result, only 19 of the nominal *Creagrutus* species described prior 1994 were recognized as valid in the literature at that time.

The Trans-Andean *Creagrutus* species of northwestern South America and southern Central America were analyzed by Harold and Vari (1994) who recognized eight species, including one previously undescribed form, in that region. The previously unrecognized diversity within *Creagrutus* east of the Andean Cordilleras was partially addressed by Vari et al. (1993, 1994, 1995) and Harold et al. (1994). Those publications, in conjunction with the conclusions reported herein, demonstrate a dramatically higher intrageneric diversity within *Creagrutus* than previously suspected but at the same time necessitate a more restricted concept of *Piabina* than utilized by many prior authors. *Creagrutus*, in the sense of this study, consists of 64 species (Table 1), 37 of which are first described herein and five of which were described in our earlier publications (Harold and Vari, 1994; Harold et al., 1994; Vari et al.,

1993, 1994, 1995). This increase from 19 to 64 species (337%) is symptomatic of the problems that bedeviled earlier attempts at species-level determinations within *Creagrutus*. Such pronounced increase in the recognizable species of *Creagrutus* is undoubtedly paralleled by comparable undetected species diversity in many genera of South American freshwater fishes of small to moderate body sizes, particularly in groups such as *Creagrutus* that inhabit distinct, patchily distributed habitats.

Mirroring the species-level uncertainties within *Creagrutus* and *Piabina* were quandaries in unequivocally diagnosing each genus. Prior faunal and systematic studies included within *Creagrutus* the majority of species herein assigned to that genus. Nonetheless, some species of *Creagrutus*, as diagnosed herein, were assigned to three separate, albeit externally similar and evidently closely related, taxa. The first of these, *Piabina*, was proposed by Reinhardt (1867) for a single species from eastern Brazil. *Piabina* was synonymized into *Creagrutus* by Eigenmann and Eigenmann (1891), resurrected from that synonymy without discussion by Eigenmann (1910), and expanded by Eigenmann (in Eigenmann et al., 1914) and Pearson (1924). One of the nominal *Piabina* species subsequently was shifted to *Piabarchus* by Myers (1928), a genus that was proposed at the same time. More recently, *Piabina* was again returned to the synonymy of *Creagrutus* by Mahnert and Géry (1988), a synonymy not, however, derived from a new phylogenetic perspective. The decision rather was a consequence of the observation that the purported gap in anal-fin ray counts between *Creagrutus* and *Piabina*, the character traditionally used to distinguish the genera, was bridged by the anal-fin ray counts in various nominal *Creagrutus* species and, thus, failed to discriminate the genera.

A third nominal genus allied with *Creagrutus* is *Creagrudite*, which was originally proposed by Myers (1927) for a *Creagrutus*-like species with distinctive dentition in both jaws, most notably the presence of only two distinct rows of teeth on the premaxilla. *Creagrudite* was synonymized into *Creagrutus* by Böhlke and Saul (1975) following their discovery of *C. gephyrus*, a species with oral dentition they considered intermediate between that occurring in *Creagrudite* and that typical for most *Creagrutus* species. That synonymy has not, however, been evaluated within a broader phylogenetic study. Finally, *Creagrutops* was proposed by Schultz (1944) for a diminutive species characterized by apparently reductive features. This genus was synonymized into *Creagrutus* by Harold and Vari (1994). Although providing preliminary justification for their action, Harold and Vari (1994) deferred a definitive statement on the phylogenetic placement of the single nominal species, *Creagrutops maracaiboensis*, within *Creagrutus* pending further studies.

In our review of the Trans-Andean *Creagrutus* species (Harold and Vari, 1994), we neither delved into the questions of the monophyly of *Creagrutus* and generic phylogenetic intrarelationships, nor addressed the problem of the phylogenetic relationships of taxa assigned at various times to *Creagrutus*, *Creagrudite*, *Creagrutops*, and *Piabina*. Vari and Harold (1998) used a subset of the characters discussed in this study to approach the question of the relationships of *Creagrutus* and *Piabina* and of the monophyly of each genus. An analysis of the intrageneric relationships in *Creagrutus* would have been premature in the absence of a thorough review of the recognizable species of that genus occurring east of the Andes, a complex problem first addressed in this paper.

In this paper we provide a revision of all species of *Creagrutus* and *Piabina* known from east of the Andean Cordilleras (see Harold and Vari (1994) for a revision of the Trans-Andean *Creagrutus* species in northwestern South America and southern Central America). Hypotheses on the monophyly of the clade consisting of *Creagrutus* and *Piabina* and of each genus are advanced based both on the characters discussed by Vari and Harold (1998) and those found in other body systems. A hypothesis of the intrageneric phylogenetic relationships within *Creagrutus* is proposed on the basis of shared derived anatomical features.

In the absence of an explicit hypothesis of the placement of *Creagrutus* and *Piabina* within characiforms, our outgroup observations were expanded to include a diversity of characiforms. These focus on the Characidae, with a particular emphasis on the Tetragonopterinae (see discussion under "Character Description and Analysis," below). The intrageneric analysis serves, in turn, as the basis for a discussion of the historical biogeography of the clade formed by *Creagrutus* and *Piabina* and subunits within *Creagrutus*.

Methods and Material

Measurements were made with dial calipers or an ocular micrometer with data recorded to tenths of a millimeter. Counts and measurements were made on the left side of specimens when possible and follow the methods outlined in Harold and Vari (1994:2). During the course of this study one additional useful meristic feature was discovered, the variation in the number of post-anal scales. These are the number of median scales between the posterior rim of the anus and the base of the first anal-fin ray. Counts of scale rows between the lateral line and anal fin do not include the scales in the sheath of scales overlying the base of the anterior rays of the anal fin found in some *Creagrutus* species living east of the Andean cordilleras.

The number, distribution, and form of the premaxillary teeth in characiforms usually are most readily studied by the careful depression of the lower jaw. Various modifications of the lower jaw and associated bones and musculature in well-preserved specimens of most *Creagrutus* species make the depression of the lower jaw difficult, if not impossible, without severe damage to the dentary and/or the dentary teeth. Retraction of the typically fleshy lower lip by careful manipulation allows examination of the premaxillary and maxillary dentition without forcing the lower jaw open or damaging the lower lip. Cleared and stained or counterstained specimens (see below) served as

supplemental sources of information on premaxillary and maxillary dentition and as a primary source of data on dentary teeth.

The first entry under the "Material Examined" section for each species summarizes the total number of specimens examined (with the number in parentheses being the specimens forming the basis for the meristic and morphometric data and the range of standard lengths for those specimens). This entry is followed by a geographically sorted listing of the material examined, including collection locality, institutional abbreviation, catalog number, and number of specimens in the lot (in parentheses, the number of specimens in the lot from which counts and measurements were taken if that number is less than the total number of specimens in the lot, and the range of standard lengths (in mm) of the individuals whose standard length could be accurately determined).

Information on collectors and date of collection are included, when available, only for type series of species described in this paper. As a consequence of limited samples and the poor condition of available juveniles for most species, most presented morphometric ranges do not include juvenile specimens other than when the species is only known from smaller individuals. Mature males were identified by the presence of bony hooks on the anal and sometimes the pelvic fins, with sex confirmed in a subsample via examination of the gonads. The presence and/or relative development of such bony hooks in mature males may vary on a seasonal basis, and an understanding of this variability requires life history studies beyond the scope of this project.

Geographic descriptors are in the sequence of country (small capital letters), state, province, department or district (italicized), followed by specific locality data. Country names are in English, but more specific locality information is in the language of the country in question. References to the Rio Negro basin, which is mostly in Brazil, follow the Portuguese and do not accent Rio. Exceptions involve references to Venezuelan or Colombian localities in which the form Río is used. Latitude and longitude are either taken directly from data associated with the specimens or, if such data was originally lacking, from gazetteers in those instances in which a locality could be unequivocally identified. The locality coordinates for material collected in the Rio Madeira basin by the Expedição Permanente de Amazônia were taken from Heyer (1977). Common names are taken from previously published accounts. In the synonymies for each species, type localities are presented as originally cited, followed by a translation into English when necessary. Other citations are presented in English followed by the modern or corrected equivalents, in parentheses, if those are known to differ.

Ecological and life history information provided for some of the species in this paper are based on diverse sources, including literature information, stomach content analyses conducted during this study, personal communications, catalog databases, and field notes. The co-occurrence of two or more *Creagrutus* species in a sample or at a locality is noted when such information is available. Such occurrence information is not presented for the non*Creagrutus* species at those collecting sites.

Nonpatronymic species names proposed in this study are based on Brown (1956).

INSTITUTIONAL ABBREVIATIONS.—The following abbreviations for institutions and collections are used:

AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences of Philadelphia
BMNH	The Natural History Museum, London, formerly, British Museum (Natural History)
CAS	California Academy of Sciences, San Francisco
CBF	Colección Boliviana de Fauna, La Paz
CM	Carnegie Museum, Pittsburgh (fish collections now mostly at FMNH)
FML	Fundación Miguel Lillo, San Miguel de Tucumán
FMNH	Field Museum of Natural History, Chicago
ICLMA	Instituto de Ciencias e Letras do Medio Araguaia, Universidad Federal do Mato Grosso, Barra da Garças
ICNMHN	Instituto de Ciencias Natural, Museo de Historia Natural, Bogota
INHS	Illinois Natural History Survey, Champaign
IU	Former Indiana University collections (now dispersed to various repositories)
KU	Museum of Natural History, University of Kansas, Lawrence
LACM	Los Angeles County Museum of Natural History
MBUCV	Museo de Biología, Universidad Central de Venezuela, Caracas
MCNG	Museu de Ciencias Naturales, Guanare, Venezuela
MCP	Museu de Ciências e Tecnologia, Pontificia Universidade Católica do Rio Grande do Sul, Porto Alegre
MCZ	Museum of Comparative Zoology, Cambridge
MEPN	Museo, Escuela Politécnica Nacional, Quito
MHNG	Muséum d'Histoire Naturelle, Geneva
MHNLS	Museo de Historia Natural La Salle, Caracas
MNHN	Muséum National d'Histoire Naturelle, Paris
MNHNP	Museo Nacional de Historia Natural del Paraguay, Asunción
MNRJ	Museu Nacional, Rio de Janeiro
MTD	Staatliches Museum für Tierkunde, Dresden
MUSM	Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima
MZUSP	Museu de Zoologia, Universidade de São Paulo, São Paulo
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
NMW	Naturhistorisches Museum Wien, Vienna
NNM	Nationaal Natuurhistorisch Museum, Leiden
NRM	Naturhistoriska Riksmuseet, Stockholm
ORSTOM	Centre ORSTOM de Cayenne, French Guiana
ROM	Royal Ontario Museum, Toronto
SU	Stanford University (fish collections now deposited at CAS)
UF	Florida Museum of Natural History, Gainesville
UMMZ	University of Michigan, Museum of Zoology, Ann Arbor
USNM	Former United States National Museum, collections in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.
ZMA	Instituut voor Systematiek and Populatiebiologie, Amsterdam
ZMH	Zoologisches Institut und Zoologisches Museum, Hamburg
ZMUC	Zoologisk Museum, Copenhagen
ZSM	Zoologische Staatssammlung, Munich

OSTEOLOGICAL PREPARATIONS.—The vast majority of the osteological preparations were cleared and counterstained for

cartilage and bone using a modification of the method outlined by Taylor and Van Dyke (1985). Previously cleared specimens stained solely with alizarin Red-S were supplemental sources of osteological data and are indicated by (AR) in the following listing. The following cleared and stained specimens served as the basis for most observations in the phylogenetic analysis. The number following the catalog number indicates the number of specimens cleared. Standard length is indicated in millimeters. Locality data in the following list are typically abbreviated, with complete information on *Creagrutus* and *Piabina* specimens provided in the species accounts of this paper for the Cis-Andean species and in Harold and Vari (1994) for Trans-Andean *Creagrutus* endemics.

Creagrutus and *Piabina* species

Creagrutus affinis, USNM 78562, 1, 48.7 mm; Panama, Río Boqueron. USNM 310414, 2, 36.7–43.8 mm; Panama, Colon, Río Morti. USNM 293249, 2, 26.7–42.3 mm; Panama, Río Pucuro. ANSP 71619, 1 (AR), 33.3 mm, paratype of *Creagrutus londonoi;* Colombia, Río Magdalena basin, Honda.

Creagrutus amoenus, ANSP 70503, 1 (AR), 47.9 mm, paratype; Colombia, Caquetá, Florencia. USNM 311339, 1, 65.0 mm; Ecuador, Pastaza, Río Danta, tributary to Río Conambo. USNM 164070, 1, 62.4 mm; Ecuador, Napo, Río Tutapishco, near Loreto.

Creagrutus anary, MZUSP 35604, 2, 40.4–44.4 mm; Brazil, Amazonas, Rio Madeira, Cachoeira de Santo Antônio.

Creagrutus atratus, USNM 353867, 2, 47.5–63.4 mm; paratypes, Colombia, Cundinamarca, mouth of Río Saname, Río Meta basin.

Creagrutus atrisignum, USNM 341479, 1, 50.1 mm; Brazil, Goiás, Niquelândia, Ribeirão do Engenho.

Creagrutus barrigai, USNM 340976, 2, 40.8–45.6 mm, paratypes; Ecuador, Sucumbíos, Río Aguarico, upstream of Zancudo.

Creagrutus beni, USNM 340959, 2, 36.4–43.0 mm; Bolivia, Cochabamba, Río Chapare basin, Villa Tunari.

Creagrutus bolivari, ANSP 159831, 2, 40.7–48.2 mm SL; Venezuela, Bolivar, Río Cariapo basin. NRM 16844, 2, 51.7–54.7 mm; Colombia, Meta, Río Meta basin.

Creagrutus brevipinnis, USNM 120148, 2, 44.7–46.8 mm; Colombia, tributary of upper Río Cauca.

Creagrutus britskii, USNM 340952, 2, 35.8–39.3 mm, paratypes; Brazil, Goiás, Iaciara, Ribeirão Macambira.

Creagrutus calai, USNM 353304, 2, 44.8–49.0 mm, paratypes; Colombia, Meta, Caño Emma, Finca El Viento.

Creagrutus caucanus, USNM 79187, 1, 69.2 mm; Colombia, Valle, Paila. USNM 120147, 1, 45.8 mm; Colombia, upper Río Cauca.

Creagrutus changae, USNM 285276, 2, 50.6–55.5 mm, paratypes; Peru, Huanuco, Río San Alejandro.

Creagrutus cochui, MZUSP 28055, 2, 64.2–66.4 mm; Brazil, Amazonas, Rio Içá.

Creagrutus cracentis, USNM 353862, 1, 26.1 mm, paratype; Brazil, Pará, Rio Tapajós, 5 km S of Itaituba.

Creagrutus crenatus, MHNLS 12900, 1, 57.0 mm, paratype; Venezuela, Lara, Quebrada Sanare, in Yay. INHS 28851, 1, 43.6 mm, paratype; Venezuela, Lara, Río Curarigua, Puente Torres.

Creagrutus ephippiatus, MBUCV V-18559, 2, 55.1–55.8 mm, paratypes; Venezuela, Amazonas, upper Río Siapa.

Creagrutus figueiredoi, USNM 292221, 3, 60.7–63.0 mm, paratypes; Brazil, Distrito Federal, Rio Maranhão.

Creagrutus flavescens, USNM 340973, 2, 58.1–58.7 mm; Ecuador, Sucumbíos, Río San Miguel basin, Río La Bermeja.

Creagrutus gephyrus, USNM 324461, 1, 41.3 mm; Ecuador, Napo, Río Napo, at Coca. USNM 340953, 1, 47.4 mm; Ecuador, Napo, Río Napo, approximately 25 km downstream of Coca.

Creagrutus gracilis, USNM 341370, 2, 36.1–42.1 mm, paratypes; Peru, Amazonas, Río Santiago.

Creagrutus gyrospilus, INHS 51282, 2, 51.9–55.8 mm, paratypes; Venezuela, Portuguesa, Río Saguaz.

Creagrutus hildebrandi, USNM 121487, 1, 43.2 mm, paratype; Venezuela, Río Palmar near Totuma. USNM 121484, 2, 26.7–40.5 mm, paratypes; Venezuela, Río San Juan.

Creagrutus holmi, USNM 167816, 3 (AR), 39.4–57.8 mm; Peru, Cajamarca, Balsas. USNM 341368, 1, 55.4 mm, paratype; Peru, Amazonas, Río Marañon basin, Bagua Grande.

Creagrutus hysginus, USNM 326035, 2, 36.1–42.7 mm, paratypes; USNM 326055, 2, 39.5–41.3 mm, paratypes; MBUCV-V 20304, 1, 38.0 mm, paratype; Venezuela, Sucre, Río La Toma. CAS 79623, 1, 41.3 mm, paratype; Venezuela, Sucre, Río Güiria.

Creagrutus ignotus, USNM 326672, 1, 28.1 mm, paratype; Brazil, Mato Grosso, Diamantino.

Creagrutus kunturus, USNM 335147, 1, 68.6 mm, paratype; Peru, Amazonas, Río Comainas basin.

Creagrutus lassoi, MCNG 24685, 2, 41.9–57.6 mm; Venezuela, Yaracuy, Río Tupe, N of Aroa.

Creagrutus lepidus, USNM 325045, 2, 33.0–40.3 mm, paratypes; Venezuela, Yaracuy, Río Aroa basin.

Creagrutus machadoi, MCNG 41717, 1, 44.4 mm; Venezuela, Bolivar, Caño Yumucukena.

Creagrutus magdalenae, USNM 357733, 8, 16.8–45.8 mm; Colombia, Cundinamarca, Apulo.

Creagrutus magoi, USNM 353863, 1, 42.2 mm, paratype; Venezuela, Bolivar, Río Chaviripa.

Creagrutus manu, USNM 326903, 1, 39.3 mm, paratype; Peru, Madre de Dios, Parque Nacional Manu.

Creagrutus maracaiboensis, USNM 121532, 1, 19.0 mm, paratype of *Creagrutops maracaiboensis;* Venezuela, Lago Maracaibo basin, Río Negro. MCNG 126, 2, 22.3–25.0 mm; Venezuela, Zulia, Caño La Raza. USNM 357791, 2, 23.0–23.7 mm; Venezuela, Zulia, Río Negro.

Creagrutus maxillaris, ANSP 161235, 1, 39.8 mm; Venezuela, Amazonas, Río Ventuari, above confluence with Río Orinoco. CAS 151036, 1 (AR), 37.1 mm; Venezuela, Amazonas, Río Orinoco.

Creagrutus melanzonus, ROM 70239, 1, 26.4 mm; Guyana, Mazuruni-Potaro, Mazuruni River. MCNG 1031, 1, 28.5 mm; Venezuela, Bolivar, Río Cuyuni basin.

Creagrutus melasma, MBUCV V-21257, 2, 32.0–32.2 mm, paratypes; USNM 326056, 2, 32.0–32.2 mm, paratypes; Venezuela, Aragua, Río Tuy basin.

Creagrutus menezesi, MZUSP 4970, 2, 23.4–26.5 mm; Brazil, Maranhão, Rio Tocantins, Estreito. USNM 292229, 2, 57.1–61.8 mm, paratypes; Brazil, Goiás, Rio Tocantins basin, Ribeirão Paranoa do Meio.

Creagrutus meridionalis, USNM 341363, 2, 45.2–48.5 mm, paratypes; MZUSP 50547, 50.9 mm, paratype; Brazil, Mato Grosso, Ribeirão Chiqueirão.

Creagrutus mucipu, USNM 350449, 1, 41.4 mm, paratype; Brazil, Goiás, Município de Minaçu/Colinas do Sul, Rio Tocantins.

Creagrutus muelleri, USNM 340984, 2, 45.4–53.3 mm; Ecuador, Pastaza, Río Pastaza. USNM 340983, 1, 75.9 mm; Ecuador, Zamora-Chincipe, Río Zamora.

Creagrutus nigrostigmatus, ICNMHN 989, 1, 19.8 mm; Colombia, Sucre, Tuloviejo, Caño Pechlin.

Creagrutus occidaneus, USNM 326920, 2, 56.0–59.1 mm; Peru, Madre de Dios, Parque Nacional Manu.

Creagrutus ortegai, USNM 340972, 2, 49.0–53.1 mm, paratypes; Peru, San Martin, Río Cainarachi.

Creagrutus ouranonastes, USNM 340988, 1, 52.2 mm, paratype; Peru, Apurimac, Aymaraes, Río Chalhuanca.

Creagrutus paraguayensis, USNM 340958, 2, 48.9–52.5 mm; Paraguay, Alto Paraguay, 5 km N of Bahia Negra.

Creagrutus paralacus, USNM 121502, 2, 50.7–59.0 mm; Venezuela, Tachira, Río Mototán. USNM 121505, 1, 51.3 mm; Venezuela, Merida, Río González at La González.

Creagrutus pearsoni, USNM 263951, 2, 27.6–30.4 mm; Peru, Madre de Dios, Río Tambopata system.

Creagrutus peruanus, USNM 340981, 2, 41.1–44.2 mm; Peru, Junin, Río Mijandari. USNM 340979, 2, 47.0–50.1 mm; Peru, Junin, Chanchamayo, Río Chanchamayo, Mijandari.

Creagrutus petilus, USNM 340957, 2, 44.0–44.4 mm, paratypes; Brazil, Rondônia, Rio Marco Rondon.

Creagrutus phasma, MCNG 21491, 1, 51.4 mm; Venezuela, Bolivar, Salto de Icutu, Río Caura system. MCNG 17961, 2, 40.5–46.2 mm; Venezuela, Apure, Río Cinaruco.

Creagrutus pila, USNM 341367, 2, 46.7–51.3 mm, paratypes; Peru, Ucayali, Río Tahuayo.

Creagrutus provenzanoi, MBUCV V-14547, 2, 46.4–47.1 mm; Venezuela, Bolivar, Río Cataniapo.

Creagrutus runa, MZUSP 29890, 1, 41.5 mm; Brazil, Amazonas, Rio Negro, Cachoeira de São Gabriel. MCNG 23311, 1, 56.3 mm; Venezuela, Amazonas, upper Río Negro.

Creagrutus saxatilis, USNM 341480, 1, 47.6 mm, paratype; Brazil, Distrito Federal, Rio Maranhão.

Creagrutus seductus, USNM 342231, 1, 60.8 mm, paratype; Brazil, Mato Grosso, upper Rio Araguaia basin, Município de Barra do Garças.

Creagrutus taphorni, USNM 357730, 2, 50.7–51.1 mm; Venezuela, Miranda, El Amoladero, Río Guiare. USNM 357729, 3, 40.7–62.7 mm; Venezuela, Río Guaire, near Caracas.

Creagrutus ungulus, USNM 303066, 3, 55.0–53.5 mm, paratypes; Peru, Madre de Dios, Río Alto Madre de Dios.

Creagrutus vexillapinnus, USNM 341361, 1, 42.0 mm; Brazil, Amazonas, Rio Negro, above Barcelos.

Creagrutus zephyrus, ANSP 161236, 2, 25.4–27.5 mm; Venezuela, Amazonas, Río Casiquiare.

Piabina argentea, USNM 311172, 1, 50.2 mm; Brazil, Minas Gerais, Córrego de Julião, N of Lagoa Santa. USNM 292220, 3, 33.8–59.2 mm; Brazil, Distrito Federal, Ribeirão Santana.

The following outgroup characiforms were the basis for the comparisons in this study.

Alestidae

Alestes lateralis Boulenger, USNM 310101, 1, 75.0 mm; Botswana, Xugana.

Alestes longipinnis (Günther), USNM 285665, 3, 44.7–50.5 mm; Togo, Togble-Kope.

Characidae

Bracychalcinus copei (Steindachner), USNM 263862, 2, 32.5–36.8 mm; Peru, Madre de Dios, tributary stream to Río Madre de Dios.

Brycon falcatus Müller and Troschel, USNM 226161, 2, 71.3–78.2 mm; Suriname, Corantijn River.

Bryconamericus brevirostris Günther, USNM 311293, 2, 50.5–53.4 mm; USNM 311329, 12, 35.0–36.7 mm; Ecuador, Los Ríos, Río Vinces.

Bryconamericus hyphessus Eigenmann, USNM 225745, 2, 30.4–33.5 mm; Suriname, Nickerie District, Mataway Creek.

Bryconamericus iheringi Boulenger, USNM 285884, 2, 29.1–54.1 mm; Brazil, Rio Grande do Sul, Arroio Garupa.

Bryconamericus stramineus Eigenmann, USNM 232201, 1, 41.5 mm; Paraguay, Amambay, Río Aquidaban. USNM 285959, 2, 33.4–39.6 mm; Brazil, Rio Grande do Sul, Rio Garupa.

Bryconops affinis (Günther), USNM 225968, 3, 42.8–48.5 mm; Suriname, Nickerie District, Corantijn River.

Chalceus macrolepidotus Cuvier, USNM 231547, 1, 115 mm; aquarium specimen.

Cheirodon affinis (Meek and Hildebrand), USNM 209483, 2, 29.5–33.3 mm; Panama, Río Santa Maria.

Gymnocharacinus bergi Steindachner, USNM 313878, 3, 34.5–44.3 mm; Argentina, Provincia Río Negro, Estancia "El Rincon."

Hemibrycon dariensis Meek and Hildebrand, USNM 293245, 2, 44.0–57.4 mm; Panama, Darien, Río Pucuro.
Hemibrycon metae Myers, USNM 228563, 2, 43.3–48.6 mm; Venezuela, Surce, Clavellino Reservoir.
Hemibrycon sp., USNM 317772, 2, 44.0–59.2 mm; Peru, Madre de Dios, Alto Río Madre de Dios basin.
Hyphessobrycon sp., USNM 345533, 2, 30.0–32.4 mm; Venezuela, Amazonas, Río Negro basin, Caño Urami.
Hyphessobrycon sp., USNM 345532, 4, 22.3–32.8 mm; Venezuela, Amazonas, Río Negro basin, Caño Tremblador.
Lignobrycon myersi (Miranda-Ribeiro), USNM 304497, 1, 84.8 mm; Brazil, Bahia, Rio do Braco.
Moenkhausia cotinho Eigenmann, USNM 272424, 3, 35.9–38.9 mm; Venezuela, Amazonas, upper Río Negro basin.
Odontostilbe paraguayensis Eigenmann and Kennedy, USNM 181422, 2, 30.7–31.6 mm; Paraguay, Río Paraguay, Isla Margarita.
Piabarchus analis (Eigenmann), USNM 326384, 2, 30.6–30.9 mm; Brazil, Mato Grosso, Rio Paraguai, near Capo Grande.
Piabarchus torrenticola Mahnert and Géry, USNM 326536, 5, 24.3–26.7 mm; Brazil, Mato Grosso, Rio Paraguai, 48 km from Porto Esperidião.
Piabucus melanostomus Holmberg, USNM 310907, 2, 61.5–62.8 mm; Brazil, Amazonas, Rio Madeira basin, 5 km E of Humaitá.
Poptella compressa (Günther), USNM 300994, 2, 50.5–57.6 mm; Venezuela, Delta Amacuro, Río Orinoco basin.
Roeboides affinis (Günther), USNM 308781, 6, 28.0–47.7 mm; Brazil, Amazonas, Rio Amazonas, Ilha de Marchantaria.
Roeboides occidentalis Meek and Hildebrand, USNM 293236, 2, 49.9–59.1 mm; Panama, Darien, Río San Antonio basin.
Triportheus angulatus (Spix), USNM 270343, 2, 63.2–74.6 mm; Venezuela, Bolivar, Río Orinoco.
Virilia pabrensis (Roman), USNM 326209, 2, 33.4–37.5 mm; Ghana, Dayi River.

Crenuchidae

Ammocryptocharax elegans Weitzman and Kanasawa, USNM 210691, 3, 36.3–39.8 mm; Brazil, Amazonas, Brazilian-Bolivian border region.
Characidium sp., USNM 100957, 2, 20.2–33.3 mm; Brazil, Minas Gerais, Rio São Francisco, Piraporinha.

Distichodontidae

Nannocharax intermedius Boulenger, USNM 231555, 2, 50.7–63.4 mm; West Africa.
Nannocharax seyboldi Schultz, USNM 193921, 1, 42.1 mm; Liberia, Gbarnga District, tributaries of St. John's River.
Paradistichodus dimidiatus Pellegrin, USNM 231556, 2, 45.6–47.3 mm; Ghana, Dayi River.
Xenocharax spilurus Günther, USNM 227693, 1, 89.3 mm; Gabon, Lac Ezanga.

Hemiodontidae

Anodus elongatus Spix, USNM 231550, 1, 120 mm; Peru, Loreto, Río Ucayali.
Argonectes scapularis Böhlke and Myers, USNM 243224, 1, 125 mm; Brazil, Amazonas, Rio Janauperi.
Bivibranchia velox Vari and Goulding, USNM 268345, 1, 109 mm; Brazil, Pará, Rio Tocantins.
Hemiodus ocellatus Vari, USNM 225593, 1, 99.6 mm SL; Suriname, Nickerie District, Corantijn River.

Parodontidae

Apareidon affinis (Steindachner), USNM 176007, 1, 89.0 mm; Argentina, Río Paraná, Santa Fe.
Apareidon dariensis (Meek and Hildebrand), USNM 345548, 1, 80.5 mm; Colombia, Río Salado.
Parodon suborbitalis Valenciennes, USNM 231552, 2, 55.0–58.1 mm; Colombia, Río Salado.
Saccodon dariensis (Meek and Hildebrand), USNM 208505, 1, 73.3 mm; Panama, Río Membrillo.

TERMINOLOGY.—Osteological terminology is that used by Weitzman (1962) with the following modifications discussed by Vari (1989). Vomer is substituted for prevomer and intercalar for opisthotic as in most recent publications dealing with characiforms. The use of epioccipital rather than epiotic follows Patterson (1975), and the use of the anguloarticular for articular and retroarticular instead of angular follows Nelson (1973). Use of posterior ceratohyal for epihyal and anterior ceratohyal for ceratohyal follows Nelson (1969), and mesethmoid rather than ethmoid follows Fink and Fink (1981).

The concepts of characiform families used in this paper are those of Greenwood et al. (1966) with several modifications. The family Ichthyboridae of Greenwood et al. (1966) is considered to be a subunit of the Distichodontidae following Vari (1979), and the Cynodontidae of those authors is recognized as a tribe within the Characidae, in keeping with the results of Howes (1976), Toledo-Piza (1997), and Lucena and Menezes (1998). *Anodus* Agassiz and *Eigenmannina* Fowler, assigned to the Curimatidae by Greenwood et al. (1966), are rather placed in the Hemiodontidae as proposed by Roberts (1974) and Langeani (1996, 1998). The use of Crenuchidae for taxa previously placed within the Characidae follows Buckup (1998). Old World taxa assigned to the Characidae according to Greenwood et al. (1966) are referred to herein as the Alestidae as proposed by Buckup (1998) and as discussed by Vari and Ortega (1999).

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Character Description and Analysis

Vari and Harold (1998) proposed that *Piabina* is the sister group to *Creagrutus,* but they did not delve into the question of intrageneric relationships within the latter genus. We herein discuss a more extensive series of characters relevant to the hypothesis of a sister-group relationship between *Creagrutus* and *Piabina* along with synapomorphies that diagnose both genera. We also advance a hypothesis of relationships within *Creagrutus.* Proposal of a hypothesis of phylogenetic relationships within *Creagrutus* is complicated by the absence of a rigorous hypothesis of the more inclusive relationships of that genus and *Piabina.* Although various authors (e.g., Géry, 1966:281) cited similarities of *Creagrutus* to other characid genera, these conjectures were derived from the joint possession of characters of undetermined polarity rather than identified synapomorphies. *Creagrutus, Piabina, Creagrudite,* and *Creagrutops* do, however, lack the supraorbital bone, which is an independent ossification of the lateral surface of the skull primitively present anterodorsal or dorsal of the orbit. The derived absence of this ossification is diagnostic of the subfamily Tetragonopterinae within the Characidae (Weitzman and Malabarba, 1998:163), although it also is absent in the characid subfamilies Agoniatinae, Aphyocharacinae, Characinae, Cheirodontinae, Glandulocaudinae, Iguanodectinae, Paragoniatinae, Rhoadsinae, and Stethaprioninae. *Creagrutus* and *Piabina*, however, lack the synapomorphies for the Characininae (Lucena, 1998), Cheirodontinae (Malabarba, 1998), Glandulocaudinae (Weitzman and Menezes, 1998), Iguanodectinae (Vari, 1977), and Stethaprioninae (Reis, 1989) and similarly lack the distinctive specializations of the Agoniatinae, Aphyocharacinae, Paragoniatinae, and Rhoadsinae. As a consequence, we center our comparisons of *Creagrutus* and *Piabina* on the Tetragonopterinae. In the absence of evidence supporting the monophyly of the Tetragonopterinae, our outgroup comparisons were expanded to other characids and in some instances to noncharacid characiforms. General statements about characters in examined

TABLE 2.—Character matrix of 57 characters for the species of Creagrutus and Piabina in the sense of this study. Character numbers correspond to those in the text. Lack of material precluded the inclusion of *C. molinus*, *C. planquettei*, *C. veruina*, and *C. xiphos*.

Taxon	Character					
	1–10	11–20	21–30	31–40	41–50	51–57
Creagrutus						
affinis	1110110111	1110000010	1100111011	0011100000	1110001110	0000100
amoenus	1110110211	1110000010	1100111011	0010110101	0110001110	0001100
anary	1110110111	1110000010	1100111011	0011100100	1110001010	0000100
atratus	1110110111	1110000010	1100111011	0110110101	1110101110	0000101
atrisignum	1110110111	1110000010	1100111011	0011101101	1110101010	0010100
barrigai	1110110111	1110000010	1100111011	0110100100	1110001010	0000100
beni	1110110111	1110000010	1100111011	0011110100	0110001010	0000100
bolivari	1110110111	1110000010	1100111011	0110110100	1110101110	0000001
brevipinnis	1110110111	1110000010	1100111011	0011110101	1110001010	0000100
britskii	1110110111	1110000010	1100111011	0010110101	1110101010	0000100
calai	1110110111	1110000010	1100111011	0010100101	1110001010	0000100
caucanus	1110110111	1110000010	1100111011	0011100101	0110001010	0000100
changae	1110110111	1110000010	1100111011	0011110101	1110001110	0000100
cochui	1110110111	1110000010	1100111011	0010111100	0110101010	0010100
cracentis	0??1011111	1101101111	1100110011	0010000100	0110011010	0100100
crenatus	1110110111	1110000010	1100111011	0010100100	1110001111	0000100
ephippiatus	1110110111	1110000010	1100111011	0010110101	1110001110	0000100
figueiredoi	1110110111	1110000010	1100111011	0010110100	0110101010	0000100
flavescens	1110110111	1110000010	1100111011	0010100101	1110001010	0000100
gephyrus	0110111111	1101101110	1000110011	0110000100	0110001110	0000100
gracilis	1110110111	1110000010	1100111011	0110100100	1110101010	0000100
gyrospilus	1110110111	1110000010	1101111011	0010110101	1111001110	0000100
hildebrandi	1110110111	1110000010	1100111011	0011100101	1110001011	0000100
holmi	1110110111	1110000010	1100111011	0011110101	1110001010	0000100
hysginus	1110110111	1110000010	1100111011	0010110100	0111001110	0000100
ignotus	1110110111	1110000010	1100111011	0010100100	1110001010	0000100
kunturus	1110110211	1110000010	1100111011	0010110101	1110001110	0001100
lassoi	1110110111	1110000010	1101111011	0010100101	0110001110	0001000
lepidus	1110110111	1110000010	1100011110	0010111100	0110001111	0000100
machadoi	1110110111	1110000010	1100111011	0110110100	1110001110	0000000
magdalenae	1110110111	1110000010	1100111011	0110110100	1110001010	0000100
magoi	1110110111	1110000010	1100111011	0010100101	1110001110	0000101
manu	1110110111	1110000010	1100111011	0011110101	1110001010	0000100
maracaiboensis	1000110101	1110000010	1110111002	0000101110	1110001111	1000110
maxillaris	0??1011111	1101101111	1100110011	0010000100	0110011010	0100000
melanzonus	1000110111	1110010010	1100111011	0010100100	1100001010	0000000
melasma	1110110111	1110000010	1100111110	0010100100	1110001011	0000100
menezesi	1110110111	1110000010	1100111011	0010110100	1110001010	0000100
meridionalis	1110110111	1110000010	1100111011	0010100000	1110101110	0000100
mucipu	1110110111	1110000010	0100111011	0110110100	0110001110	0000000
muelleri	1000110101	1110000010	1100111011	0010101101	1110001010	0000100
nigrostigmatus	1000110101	1110000010	1110111011	0000100110	1110001110	1000110
occidaneus	1110110111	1110000010	1100111011	0010110101	0110001010	0000100
ortegai	1110110111	1110000010	1100111011	0011110100	1110001110	0000100
ouranonastes	1000110101	1110000010	1100111011	0010101101	1110001110	0000100
paraguayensis	1110110111	1110000010	1100111011	0010110101	1110101110	0000100
paralacus	1110110111	1110000010	1100111011	0110110101	1111001110	0000100
pearsoni	1110110111	1110000010	1100111011	0011100000	1100001010	0000100
peruanus	1000110101	1110000010	1100111011	0010100101	1110001011	0000100
petilus	1110110111	1110000010	1100111011	0010110100	0110001111	0000000
phasma	1110110111	1110010010	1100111011	0010100100	1110001010	0000000
pila	1110110111	1110000010	1100111011	0111101101	0110001010	0000100
provenzanoi	1110110111	1110000010	1100111011	0010100100	0110001110	0000100
runa	1000110111	1110010010	1100111011	0011100100	1110001010	0000000
saxatilis	1110110111	1110000010	1100111011	0011100100	0110001010	0000000
seductus	1110110111	1110000010	1100111011	0110110101	0110001010	0000100
taphorni	1110110111	1110000010	1100111011	0110110101	1110001110	0000100
ungulus	1110110111	1110000010	1100111011	0010110101	0110001011	0100100
vexillapinnus	1110110111	1110000010	1100111011	0110110100	0110001010	0000100
zephyrus	1110110111	1110000010	1110111011	0111100100	0100001100	0000000
Piabina						
argentea	1000000001	0010000000	1000001000	1000100000	0110000100	0000100

characiform outgroups encompass diverse assemblages, including when appropriate *Xenocharax*, the hypothesized most generalized characiform (Fink and Fink, 1981) and other members of the basal clade formed by the Citharinidae and Distichodontidae.

The character numbers in the text correspond to those in Table 2. Synapomorphy numbers in the "Phylogenetic Reconstruction" sections correspond to that numbering system. Autapomorphic characters are not included in Table 2, are not utilized in the computer analyses, and are not numbered, but they are cited in the diagnosis for the species, if those species are treated in this paper.

PHYLOGENETIC POSITIONS OF *Creagrudite, Creagrutops,* AND *Piabina*.—A subset of the derived characters discussed by Vari and Harold (1998) and in the following sections are congruent with the hypothesis that *Piabina argentea* is the sister lineage to *Creagrutus*. This conclusion differs from traditional taxonomic concepts under which *Piabina argentea* was aligned with a species herein placed in *Creagrutus* (*C. pearsoni* of this study) with which it shares a higher number of branched analfin rays than is typical for most *Creagrutus* species. Our recognition of a separate *Piabina* also runs counter to recent taxonomic practice (e.g., Mahnert and Géry, 1988) under which *Piabina* was considered a junior synonym of *Creagrutus*. *Piabina* (sensu stricto), although outside the scope of a revisionary and intrageneric phylogenetic study of *Creagrutus* as diagnosed herein, is, as the sister group to *Creagrutus*, significant for purposes of the polarization of characters within the latter genus.

Although *Piabina* lies outside the scope of the originally envisioned revisionary study of *Creagrutus*, autapomorphies for *Piabina* have not been previously identified, nor has its single contained species, *P. argentea* Reinhardt, been analyzed across its geographic range. We consequently expanded our revisionary study to include a redescription of *Piabina argentea* and broadened our phylogenetic analysis to identify autapomorphies for that species. Prior to the synonymy of *Piabina* into *Creagrutus* (Mahnert and Géry, 1988), *Piabina* included a second species, *Piabina beni* Pearson (1924), the *Creagrutus pearsoni* Mahnert and Géry (1988) of this study (see comments under "Remarks" for the latter species). The results of the phylogenetic analysis indicate that *Creagrutus pearsoni*, the former *Piabina beni*, is more closely related to components of *Creagrutus* deeply nested within the phylogeny of that genus than it is to *Piabina argentea*.

Myers (1927:117) and Schultz (1944:327) distinguished *Creagrudite* and *Creagrutops*, respectively, from *Creagrutus* based on modifications of the lateral line and dentition. The most parsimonious hypothesis of phylogenetic relationships for the assemblage consisting of *Creagrutus, Creagrudite,* and *Creagrutops* indicates that the diagnostic features proposed for *Creagrudite* and *Creagrutops* are derived, but that each genus constitutes a specialized lineage within what would be a nonmonophyletic *Creagrutus* if *Creagrudite* and *Creagrutops* continue to be recognized. Thus, *Creagrudite* and *Creagrutops* are considered synonyms of *Creagrutus* in order to make the latter genus monophyletic. From this point on, *Creagrutus* is used in this broader sense, including the species formerly placed in *Creagrudite* and *Creagrutops*.

GENERIC ASSIGNMENT OF *Creagrutus molinus, C. planquettei, C. veruina,* AND *C. xiphos*.—Three species described as new in this paper are known only from a holotype (*C. molinus*) or small type series (*C. veruina, C. xiphos*). *Creagrutus planquettei* Géry and Renno, 1989, in turn, was described from a limited type series and evidently has not been collected subsequently. Such restricted samples preclude clearing and staining of specimens of these four species for detailed studies of their osteology. The four species, nonetheless, share the externally obvious characters synapomorphic for *Creagrutus* or subunits of that genus (see "Phylogenetic Position of *C. molinus, C. planquettei, C. veruina,* and *C. xiphos*," below). Given that the vast majority of the characters utilized in the phylogenetic analysis can only be examined in cleared and stained specimens, we exclude these species from the matrix rather than representing them primarily as missing data. Resolution of the exact intrageneric phylogenetic relationships of these species must await the collection of additional material.

The discussion of phylogenetically informative characters is arranged in terms of various major body systems, with diverse residual characters discussed under "Miscellaneous."

JAWS AND ASSOCIATED LIGAMENTS

PREMAXILLA.—The premaxilla in *Piabina argentea* and most *Creagrutus* species approximates an irregular triangle when examined from a ventral view (Figures 1, 2). In these taxa the premaxillary teeth are large both with respect to the size of the upper jaw and relative to the dentigerous surface of the premaxilla. As a consequence, the dentition covers an unusually high proportion of the ventral surface of the premaxilla relative to the condition in most characids. Although an approximately triangular dentigerous surface on the premaxilla also occurs in some species of *Brycon* Müller and Troschel (e.g., *B. dentex* Günther and *B. oligolepis* Regan; see Howes, 1982, figs. 15, 21), the premaxillary dentition in these *Brycon* species is much more dispersed than the densely packed teeth typical of *Piabina* and *Creagrutus* species. Other *Brycon* species have more elongate premaxillae and much different arrangements of premaxillary dentition (e.g., *B. devillei* Castelnau and *B. falcatus* Müller and Troschel; see Howes, 1982, figs. 16, 18). Although *Brycon* is undiagnosed on the basis of synapomorphies, it has been defined by a series of unpolarized characters (Howes, 1982:1), which may either diagnose a natural assemblage or more closely align it with genera such as *Triportheus* Cope, *Chalceus* Cuvier, or *Moojenichthys* Miranda-Ribeiro (see Castro and Vari, 1990:532; Malabarba, 1998:76). Furthermore, studies on a subset of characiform taxa (Buckup, 1998:134) indicated that *Brycon* is not closely related to *Tetragonopterus* Cuvier, the type genus of the Tetragonopterinae that shares with *Creagrutus* and *Piabina* the apomorphic loss of the supraorbital. This evidence supports a hypothesis that the roughly triangular dentigerous surface of the premaxilla in *Brycon* species, such as *B. dentex* and *B. oligolepis*, was achieved independently of that in *Piabina* and *Creagrutus*. Given its re-

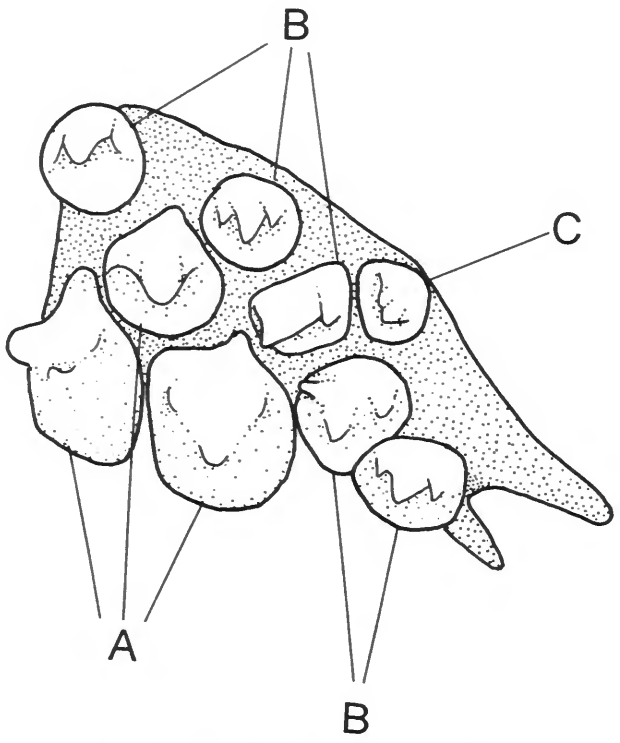

FIGURE 1.—Premaxilla and premaxillary dentition in *Creagrutus muelleri*, USNM 340983, 75.9 mm SL; left side, ventral view, anterior at top. (Abbreviations: A, triangular cluster of teeth; B, primary premaxillary tooth series, and C, single lateral tooth.)

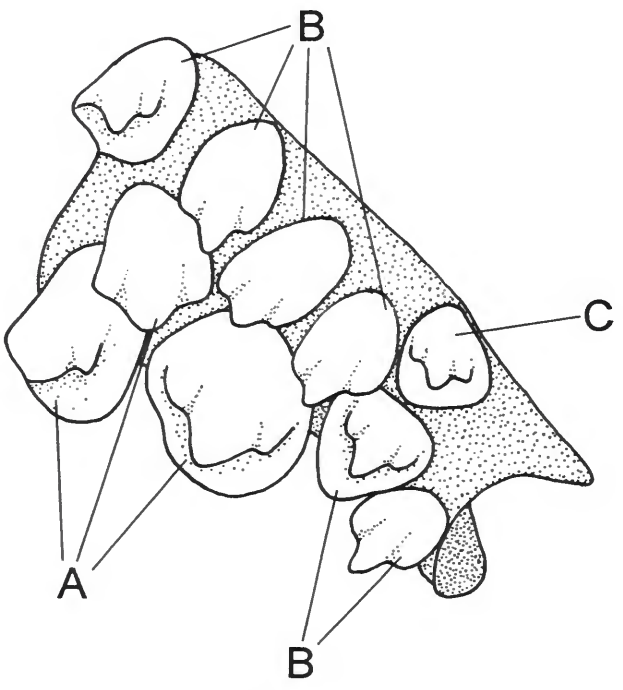

FIGURE 2.—Premaxilla and premaxillary dentition in *Creagrutus hysginus*, USNM 326055, 41.3 mm SL; left side, ventral view, anterior at top. (Abbreviations: A, triangular cluster of teeth; B, primary tooth row; and C, single lateral tooth.)

stricted occurrence among characiforms and its absence in basal characiform taxa, such as the Distichodontidae and Citharinidae, the triangular dentigerous surface of the premaxilla in *Piabina* and *Creagrutus* is considered to be derived.

The form of the dentigerous surface of the premaxilla typical for most members of *Creagrutus* demonstrates only minor intrageneric variations other than in *C. cracentis, C. gephyrus,* and *C. maxillaris.* These three species, rather than having an approximately triangular premaxilla, have a posterolaterally elongate, roughly rectangular premaxillae in a ventral view (Figures 3, 4). The ventral surface of the premaxilla in these three species approximates that in many characid outgroups (e.g., *Paracheirodon innesi* Myers; see Weitzman and Fink, 1983, fig. 23). Nonetheless, such a posteroventrally elongate premaxilla in these three species is considered to be independently derived under the overall most parsimonious hypothesis of phylogenetic relationships in the *Piabina-Creagrutus* assemblage under which the clade formed by *C. cracentis, C. gephyrus,* and *C. maxillaris* is deeply nested within the phylogeny for *Creagrutus* (Figure 17).

CHARACTER 1. State 0: Dentigerous surface of premaxilla longitudinally elongate from ventral view. State 1: Dentigerous surface of premaxilla triangular from ventral view.

PREMAXILLARY TEETH.—Diverse descriptive schemes (e.g., Howes, 1982, for *Brycon*) have been proposed to resolve the homology of components of the premaxillary dentition among various genera in the families Characidae and Alestidae, which together form the major portion of the Characidae of many previous authors. As noted under "Premaxillary Dentition in *Creagrutus* and *Piabina,*" below, these alternative descriptive schemes failed to unequivocally homologize individual teeth or groups of teeth across the major taxonomic groups in these families. Such difficulties are understandable given the diversity of tooth arrangement patterns across the Characidae and Alestidae.

Three general patterns of premaxillary teeth, each with less pronounced internal variation among included species, occur among the species of *Creagrutus,* one of which also is common to the first outgroup, *Piabina* (Figures 1–4). Perusal of these tooth patterns demonstrates the difficulties inherent in homologizing individual teeth even within this limited subunit of the Tetragonopterinae, let alone in addressing the question of tooth homologies across the rest of that subfamily or the entire Characidae. For the purposes of this study we discuss the premaxillary dentition in *Creagrutus* and *Piabina* in terms of the three major components found in all but a few *Creagrutus* species.

One landmark constant to the three patterns of premaxillary dentition in *Piabina* and *Creagrutus* is the large tricuspidate tooth situated at the posterior margin of the premaxillary tooth

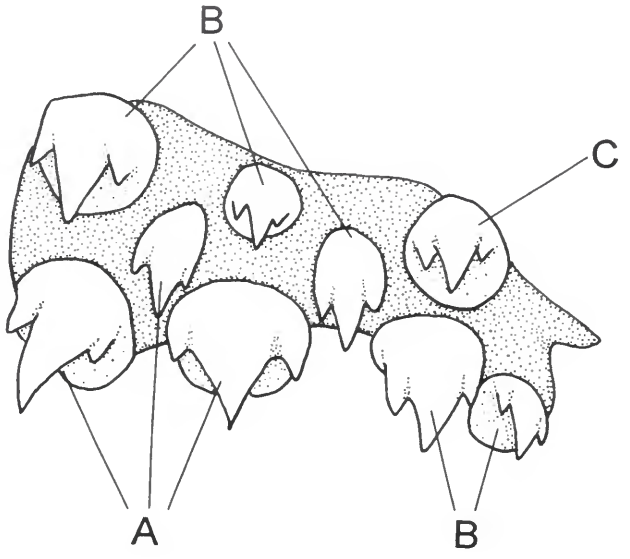

FIGURE 3.—Premaxilla and premaxillary dentition in *Creagrutus gephyrus*, USNM 340953, 47.4 mm SL; left side, ventral view, anterior at top. (Abbreviations: A, triangular cluster of teeth; B, primary tooth tow; and C, single lateral tooth.)

series (Figures 1, 2). That tooth and two other proportionally large teeth, one medial to it and the second anteromedial to it, form a distinct triangular cluster (hereafter termed the triad) situated on the posteromedial portion of the dentigerous surface of the premaxilla. This triad is the first major component of the premaxillary dentition in these genera (note: triad modified in *Creagrutus cracentis* and *C. maxillaris*, see discussion below). Located anterior and lateral to the triad is a series of four to seven, somewhat to distinctly smaller, teeth whose arrangement ranges from a nearly straight line, through an arch, to a sigmoid pattern. Regardless of their exact arrangement or the number of teeth, these four to seven teeth form an identifiable unit herein termed the primary premaxillary tooth series, the second major component of the premaxillary dentition. Lateral to the third to fifth teeth of the primary series (relative position a function of the number teeth in the primary series) is a single, typically tricuspidate, tooth, termed herein the lateral tooth, which is the third component of the pattern (this tooth is absent in a small number of *Creagrutus* species; see discussion below).

Piabina argentea and seven *Creagrutus* species (*C. maracaiboensis, C. melanzonus, C. muelleri, C. nigrostigmatus, C. ouranonastes, C. peruanus, C. runa*) have the gap between the first and second teeth in the primary tooth series distinctly wider than the spaces between the remaining teeth of the series (Figure 1). The separation of those two teeth in these species also is much more pronounced than the gap between homologous teeth in all other *Creagrutus* species, other than *C. cracentis* and *C. maxillaris*, which have highly modified premaxillary dentition. The extent of the gap in *Piabina argentea* and the seven cited *Creagrutus* species approximates the separation between these teeth in other tetragonopterines, and its presence is therefore considered the primitive condition. The primary tooth series found in all *Creagrutus* species, other than for *C. maracaiboensis, C. melanzonus, C. muelleri, C. nigrostigmatus, C. ouranonastes, C. peruanus,* and *C. runa,* differs from the pattern in those seven species in having contact, or near contact (Figure 2), between the two anterior teeth of the primary series rather than a distinct gap in that region, which is a derived condition.

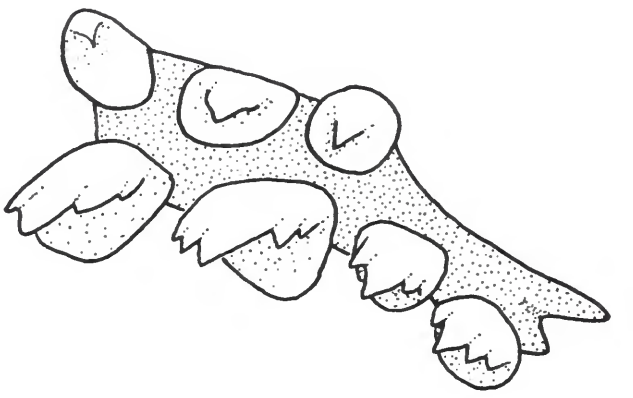

FIGURE 4.—Premaxilla and premaxillary dentition in *Creagrutus maxillaris*, ANSP 161235, 39.8 mm SL; left side, ventral view, anterior at top.

CHARACTER 2. State 0: Primary premaxillary tooth series with gap between first and second teeth distinctly greater than spaces between the remaining teeth in series. State 1: Primary premaxillary tooth series with gap between first and second teeth comparable to those between remaining teeth in that series.

Piabina argentea and seven *Creagrutus* species (*C. maracaiboensis, C. melanzonus, C. muelleri, C. nigrostigmatus, C. ouranonastes, C. peruanus, C. runa*) have the triad of premaxillary teeth positioned immediately posterior to the primary premaxillary series (Figure 1). The anterior position of the triad in conjunction with the distinct separation of the first and second teeth of the primary series results in the anterior tooth of the triad being nestled, to varying degrees, in the gap between the first and second teeth. This proximity between the primary tooth row and the triad and the forward location of the anterior tooth of the triad in these eight species led some authors (e.g., Géry and Renno, 1989:4) to interpret the premaxillary dentition in this assemblage as consisting of two irregular tooth rows, a pattern common to various characids and alestids. Although such a description could be applied to *Piabina* and the seven *Creagrutus* species, we prefer to apply the three component description outlined above to these eight species in order to assure consistency in all descriptions across *Piabina* and *Creagrutus*.

In all *Creagrutus* species, other than *C. maracaiboensis, C. melanzonus, C. muelleri, C. nigrostigmatus, C. ouranonastes,*

C. peruanus, and *C. runa,* the triad of teeth is positioned more posteriorly relative to the primary tooth series than it is in the pattern described above for *Piabina argentea* and these *Creagrutus* species (see also below concerning *C. cracentis* and *C. maxillaris*). As a consequence, the anterior tooth of the triad is positioned distinctly posterior of the main axis through the primary tooth series, being either situated behind the transverse line through the second tooth or posterior to the transverse line extending through the gap between the second and third tooth of the primary series (e.g., *C. planquettei,* Géry and Renno, 1998, fig. 3). This tooth arrangement pattern is unique to this assemblage of *Creagrutus* species among examined characiforms and is thus considered to be derived.

As noted above, the highly modified form of the premaxilla and its tooth arrangement in *Creagrutus cracentis* and *C. maxillaris* constitute the third pattern of premaxillary dentition within *Creagrutus* (Figure 4). The magnitude of the alterations in these two species renders direct comparisons of their tooth patterns and premaxillary form with the conditions in congeners problematic. An evaluation of the homologies of the premaxillary dentition in *C. cracentis* and *C. maxillaris* with those in other *Creagrutus* species is, however, facilitated by an examination of the tooth arrangement in *C. gephyrus* (Figure 3). The latter species has a premaxillary dentition arrangement intermediate between that typical of *Creagrutus* species (Figures 1, 2) and the tooth pattern found in *C. cracentis* and *C. maxillaris* (Figure 4). Although arranged in a more compact and elongate pattern than in most *Creagrutus* species, the premaxillary dentition in *C. gephyrus* retains the three premaxillary dentition components typical for the genus.

Creagrutus cracentis and *C. maxillaris* share the relatively elongate premaxillary form of *C. gephyrus,* with the enlarged posterolateral tooth of the triad in the latter species evidently homologous with the large premaxillary tooth in a comparable position in *C. cracentis* and *C. maxillaris* (Figure 4). The tooth medial to this enlarged tooth in *C. cracentis* and *C. maxillaris* is considered to be homologous with the posteromedial tooth of the triad of teeth in most *Creagrutus* and *Piabina* species; this conclusion is based on its position and proximity to the contralateral tooth of the other maxilla.

More problematic is a determination of the homology between the remaining premaxillary teeth in *C. cracentis* and *C. maxillaris* and those in other *Creagrutus* species. The remaining teeth on the premaxilla of *C. cracentis* and *C. maxillaris* may represent the primary premaxillary tooth row in other *Creagrutus* species, albeit with more space between the anterior teeth than is typical among their congeners. If that is the case, then the anterior tooth of the triad typical for *Creagrutus* and *Piabina* species is absent in *C. cracentis* and *C. maxillaris.* Alternatively, the anterior tooth of the triad may have shifted dramatically anteriorly in these two species to a position along the anterior margin of the premaxilla. Under such a scenario, the anterior tooth of the triad is now a component of what otherwise appears to be the primary tooth series. Such a homology necessitates either the loss of one tooth originally in the primary series or a pronounced posterolateral shift of the second and following teeth in that series to provide space for the anteriorly repositioned anterior tooth of the triangular cluster. This second explanation is more complex and thus less preferable. We consequently assume that the anterior tooth of the triad typical for *Creagrutus* and its sister group, *Piabina,* is lacking in *C. cracentis* and *C. maxillaris.* The overall level of uncertainty with these homologies leads us, however, to score the dentition form in these two species as "?" for both Characters 2 and 3.

CHARACTER 3. State 0: Anterior tooth of premaxillary tooth triad positioned, at least in part, within gap between first and second tooth in primary tooth series. State 1: Anterior tooth of premaxillary tooth triad positioned distinctly posterior of first and second teeth of primary series.

An additional pronounced difference between the premaxillary dentition in *C. cracentis* and *C. maxillaris* and that of other *Creagrutus* species and *Piabina argentea* is the absence of the lateral tooth, the single tooth situated to the side of the primary tooth series. Although the absence of the lateral tooth is hypothesized to be derived for the clade consisting of *C. cracentis* and *C. maxillaris* under the overall most parsimonious hypothesis of relationships, it was apparently lost independently within *Creagrutus* in *C. molinus. Creagrutus molinus* lacks the attenuate form of premaxilla and the highly modified premaxillary triad and primary tooth row typical of *C. cracentis* and *C. maxillaris,* and to a lesser degree *C. gephyrus.* Instead, *C. molinus* retains the overall triangular form of the dentigerous surface of the premaxilla and the arrangement of the triad of teeth and the primary tooth row typical for *Creagrutus* species. Thus, the loss of the single tooth in *C. molinus* is apparently not a function of the dramatic restructuring of the premaxilla, such as occurs in *C. cracentis* and *C. maxillaris. Creagrutus molinus,* is known only from the holotype, rendering detailed anatomical examination impossible. Nonetheless, it lacks the other externally apparent distinguishing features of the clade consisting of *C. cracentis* and *C. maxillaris.* In light of these differences, the secondary loss of the lateral tooth is tentatively considered to be apomorphic for *C. molinus* on the one hand and a shared derived condition for *C. cracentis* and *C. maxillaris* on the other (note: *C. molinus* not included in the data matrix of Table 2).

CHARACTER 4. State 0: Single tooth situated lateral to primary premaxillary tooth row present. State 1: Single tooth situated lateral to primary premaxillary tooth row absent.

MAXILLA.—Two major morphologies of the maxilla occur among *Creagrutus* species. The first of these, limited to *C. cracentis* and *C. maxillaris,* is an overall relatively elongate ossification with a slender anterior process extending dorsally toward the lateral wing of the mesethmoid. Posterior to the premaxilla, the maxilla in these species is a transversely compressed, blade-like ossification with teeth along at least its anterodorsal margin. Such a form of the maxilla also occurs in *Piabina* (Figure 5A), the sister clade to *Creagrutus,* and approximates the form of the bone widespread among characids. It is

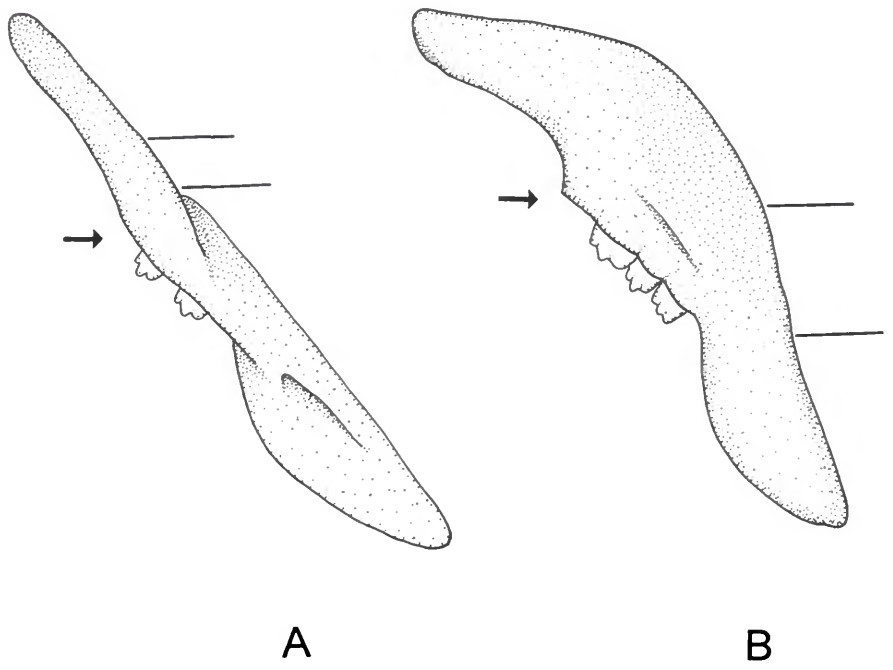

FIGURE 5.—Maxilla in (A) *Piabina argentea*, USNM 292220, 59.2 mm SL; and (B) *Creagrutus atrisignum*, USNM 341478, 50.1 mm SL; left side, lateral view, anterior to left. (Horizontal lines indicate limits of region where primordial ligament attaches to maxilla in each species. Arrows indicate approximate ventral limit of area of contact of premaxilla and maxilla.)

considered to be the plesiomorphic condition for the *Creagrutus* clade, albeit it is hypothesized within the final phylogeny as having been secondarily achieved in *C. cracentis* and *C. maxillaris*.

A proportionally much more robust maxilla occurs in the remaining 62 *Creagrutus* species (Figure 5B). Anteriorly this restructuring is reflected in the distinctly thicker anterior process of the maxilla that extends along the dorsal margin of the premaxilla. Overall maxillary robustness among these species is even more obvious in the distinctly more transversely rotund portion of the bone that extends posterior to the posteroventral corner of the premaxilla. The absence of such a robust form of maxilla in *Piabina argentea*, the proximate outgroup to *Creagrutus*, and in examined characid outgroups is congruent with the hypothesis that the robust form of the maxilla in most *Creagrutus* species is derived.

CHARACTER 5. State 0: Maxilla with anterior process relatively slender and posterior portion transversely compressed. State 1: Maxilla with anterior process thick and posterior portion robust.

Further distinguishing the maxilla in *Creagrutus* from that in *Piabina argentea* and other examined outgroups is the degree of inflection of the main axis of that bone in the region where the maxilla extends past the posterior limit of the premaxilla. The maxilla in *Piabina argentea* is nearly straight along its longest axis (Figure 5B), with only a minor inflection along its primary axis at the point where the bone extends beyond the posterior limits of the premaxilla. *Creagrutus* species have a much more pronounced inflection of the maxilla in that region. The degree of this flexion varies intragenerically within *Creagrutus*, with a moderate angle present in three *Creagrutus* species (*C. gephyrus, C. cracentis,* and *C. maxillaris;* angle somewhat greater in the two latter species) and a pronounced angle along the primary axis of the premaxilla common to all other species of *Creagrutus* (Figure 5B). The increased flexion, regardless of its degree, is considered to be the derived condition.

CHARACTER 6. State 0: Maxilla without distinct flexion in region where it extends past posterior limit of premaxilla. State 1: Maxilla with distinct flexion in region where it extends past posterior limit of premaxilla.

MAXILLARY TEETH.—*Piabina argentea* (Figure 5A), the sister group to *Creagrutus*, has two to five teeth limited to the upper portion of the anterior oral margin of the maxilla. Such a range also is common to all *Creagrutus* species (Figure 5B) other than *C. cracentis, C. gephyrus,* and *C. maxillaris*. These three species have distinctly higher maxillary tooth counts (*C. cracentis,* 8 or 9; *C. gephyrus,* 7 to 11; *C. maxillaris,* 10 to 12), with the dentition extending along nearly the entire oral margin

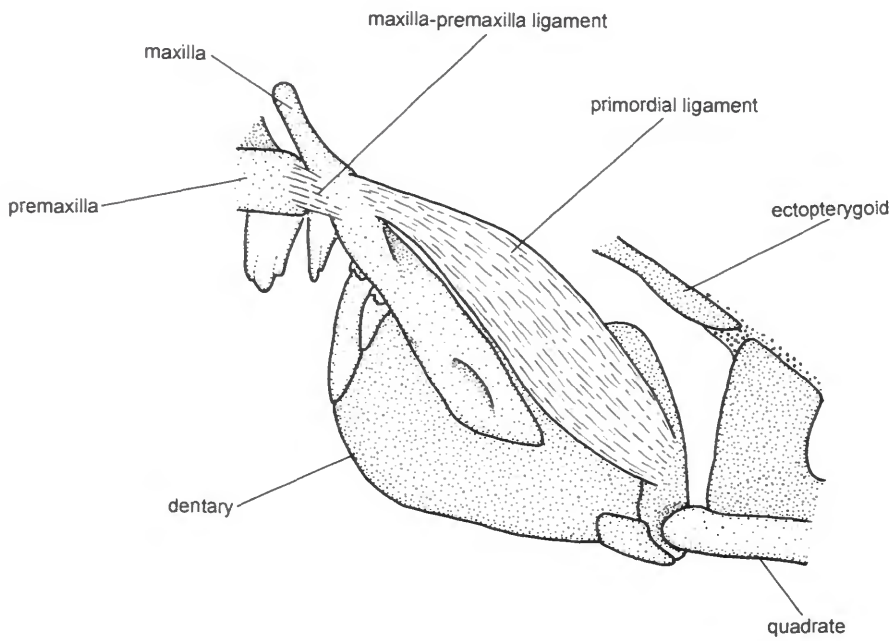

FIGURE 6.—Form of primordial ligament and adjoining bones in *Piabina argentea*, USNM 292220, 59.2 mm SL; left side, lateral view, anterior to left.

of the maxilla rather than being limited to the anteroventral region of the oral margin. Given the broad variation in the number of maxillary teeth in the diverse groups within the Tetragonopterinae, it is not possible to polarize this character.

CHARACTER 7. State 0: Maxilla with 2 to 5 teeth. State 1: Maxilla with 7 to 12 teeth.

PRIMORDIAL LIGAMENT.—Characiforms demonstrate a broad range of modifications of the primordial ligament (sensu Winterbottom, 1974:232; the articular-maxillary ligament of Alexander, 1964:183). These differences involve both the overall form of the ligament and details of its attachment dorsally to the maxilla and ventrally to the lower jaw and portions of the suspensorium. As would be expected, the pronounced restructuring of the jaws in the species of *Creagrutus* is paralleled by distinctive changes both in the morphology of the primordial ligament and of its attachments to the maxilla, lower jaw, and quadrate.

Piabina argentea retains the primordial ligament morphology typical of many outgroup characids in which the ligament is a dorsally attenuating, relatively strap-like connective-tissue band (Figure 6). The primordial ligament in *Creagrutus* species (Figure 5B) is more highly developed than in outgroups, with its greater overall robustness reflected in its proportionally more rounded cross sectional dimensions, a hypothesized derived condition.

Creagrutus also differs from *Piabina* and other examined outgroups in the position of the attachment of the primordial ligament on the maxilla. In *Piabina* the ligament attaches to the posteromedial surface of the ascending process of the maxilla approximately at the horizontal through the region where the anterior surface of the maxilla contacts the posteroventral corner of the premaxilla (Figures 5A, 6). All *Creagrutus* species instead have the ligament attaching onto a broad area of the posterior and, to a lesser degree, the medial and lateral margins of the distal one-half (often one-third) of the maxilla (Figures 5B, 7). As a consequence, the area of attachment of the ligament onto the maxilla in *Creagrutus* is situated distinctly ventral of the posteroventral terminus of the premaxilla, the portion of the maxilla onto which the ligament attaches in *Piabina* and other examined outgroup characids. This ventral shift in *Creagrutus* species is hypothesized to be derived.

Within *Creagrutus* the dorsal portions of the primordial ligament are further developed in *C. amoenus* and *C. kunturus* relative to the condition in their congeners. The attachment of the ligament onto the maxilla extends further laterally than in other *Creagrutus* species and outgroups, and it continues ventrally nearly to the distal tip of the maxilla, a point far ventral of the limit of the attachment of the ligament in the other species of *Creagrutus* and examined outgroup characids. In light of its unique nature, the broadened area of attachment of the primordial ligament in *C. amoenus* and *C. kunturus* is considered to be a shared derived feature.

CHARACTER 8. State 0: Primordial ligament relatively flat transversely and attaching to posteromedial process of ascend-

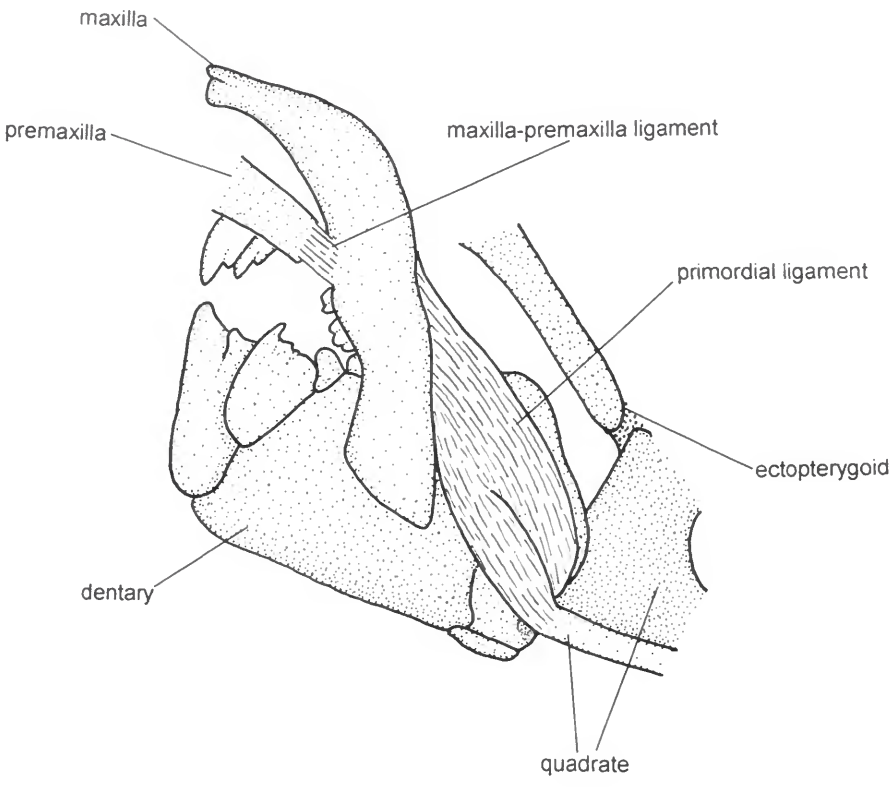

FIGURE 7.—Form of primordial ligament and adjoining bones in *Creagrutus flavescens*, USNM 340973, 58.7 mm SL; left side, lateral view, anterior to left.

ing process of maxilla. State 1: Primordial ligament more rotund in cross section and attaching primarily to distal one-half of maxilla but not to distal portion of that bone. State 2: Primordial ligament distinctly rotund in cross section and extending ventrally nearly to distal tip of maxilla.

Notable variability occurs in the ventral attachments of the primordial ligament among *Creagrutus* species. The simplest form of this attachment within *Creagrutus* occurs in *C. maracaiboensis, C. muelleri, C. nigrostigmatus, C. ouranonastes,* and *C. peruanus* (see also comments below, concerning condition in *C. cracentis* and *C. maxillaris*) in which the primordial ligament has the form ventrally of a single band with an attachment onto the lateral surface of the anguloarticular (Figure 6). Comparable forms of the primordial ligament occur in *Piabina argentea* and other examined outgroup characids and are consequently hypothesized to represent the primitive condition within *Creagrutus*. In the remaining *Creagrutus* species, the ventral portion of the primordial ligament bifurcates ventrally into a larger medial portion and a smaller posteroventral band as it extends distally from the maxilla (Figure 7). The larger medial portion of the primordial ligament in these species attaches ventrally to the lateral surface of the anguloarticular, the area of attachment of the entire ligament in *Piabina argentea, Creagrutus maracaiboensis, C. muelleri, C. nigrostigmatus, C. ouranonastes,* and *C. peruanus*. Given the similarity in form and attachment, we consider this portion of the bifurcate primordial ligament homologous with the ventral portion of the ligament in the five listed species. All *Creagrutus* species other than these five species also have a second, more laterally situated, smaller portion of the primordial ligament extending posteroventrally from the main body of the ligament to an insertion on the lateral surface of the quadrate. The attachment of this smaller component of the primordial ligament on the quadrate is situated slightly posterior of the articular facet on the lateral margin of the shelf-like process, which serves as an area of attachment for the ventral portion of the adductor mandibulae muscle. The attachment of the ligament is often onto a small lateral process extending laterally from the main shelf-like process of the quadrate. Outgroup comparisons lead us to hypothesize that the posterolateral component of the bifurcating *Creagrutus*-form of the ligament is derived from the connective-tissue layers overlying the main portion of the primordial ligament in examined outgroups. If such a homology is correct, the ventrally branched primordial ligament found in the vast ma-

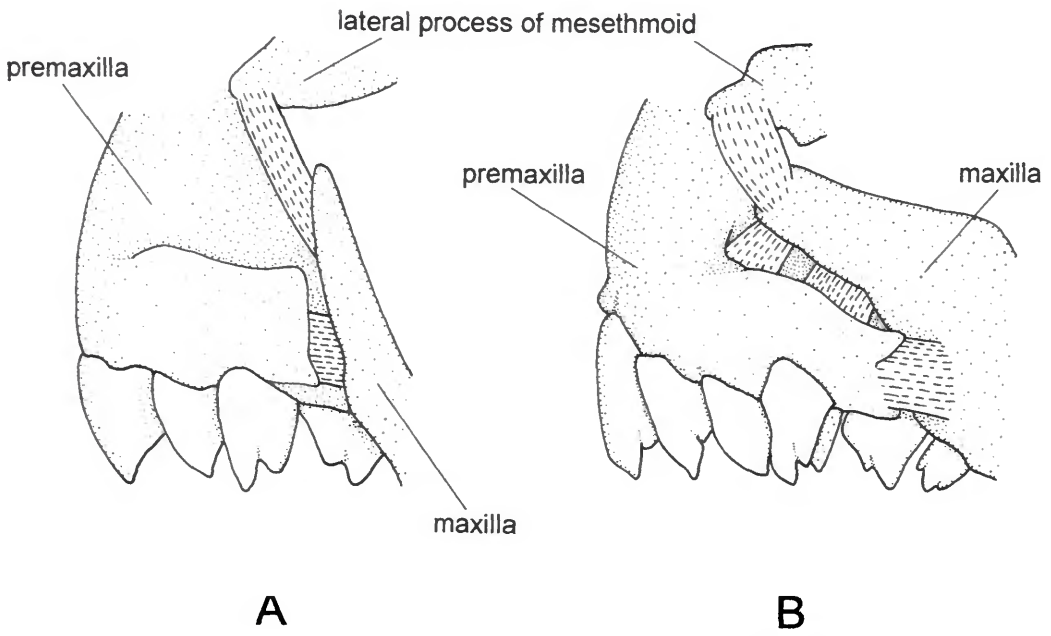

FIGURE 8.—Maxilla, lateral process of mesethmoid, dorsal portion of premaxilla, and associated ligaments in (A) *Piabina argentea*, USNM 292220, 58.3 mm SL; and (B) *Creagrutus hysginus*, USNM 326035, 41.3 mm SL; left side, lateral view, anterior to left.

jority of *Creagrutus* species is of composite origin. Support for this hypothesis is provided by the form of the primordial ligament in *Creagrutus cracentis* and *C. maxillaris*. Although lacking the same form of bifurcation of the primordial ligament, such as occurs in most other members of *Creagrutus*, these two species have a discrete, albeit somewhat less organized, band of connective tissue that extends from the maxilla to the quadrate and that overlies the primordial ligament. This lateral connective-tissue band is apparently homologous, at least in part, with the ventrolateral component of the bifurcated primordial ligament typical of most *Creagrutus* species. Ontogenetic studies may resolve the question of the origin of the lateral portion of the ventrally bifurcating primordial ligament in most *Creagrutus* species. Regardless of its origin, the more complex form of the primordial ligament in all *Creagrutus* species other than *C. maracaiboensis, C. muelleri, C. nigrostigmatus, C. ouranonastes*, and *C. peruanus* is hypothesized to be derived.

CHARACTER 9. State 0: Primordial ligament in form of band with single ventral attachment to lateral surface of anguloarticular. State 1: Primordial ligament ventrally bifurcating with attachments to both the lateral surface of the anguloarticular and the lateral margins of the shelf-like lateral process of the quadrate.

LIGAMENTS ASSOCIATED WITH DORSAL PORTION OF MAXILLA.—*Piabina* and other outgroups to *Creagrutus* have a ligamentous band extending dorsally from the anterodorsal margin of the maxilla to the ventral margin of the distal region of the lateral mesethmoid wing (the lateral ethmoid wing of Weitzman (1962:19) and Roberts (1969:405)). The position of the maxilla relative to the premaxilla is, in turn, further stabilized by connective-tissue bands extending from the posteroventral corner of the premaxilla to the anterior surface of the maxilla at the point where the latter bone extends past the posteroventral corner of the maxilla. Although the just-described pattern of ligament is generalized for characiforms, noteworthy modifications in the system of ligaments connecting the maxilla and premaxilla occur in *Piabina* and *Creagrutus*, which serve to reduce the degree of mobility between these two ossifications.

One of the most noteworthy of these alterations involves the relative size and degree of consolidation of the connective-tissue bands joining the posteroventral corner of the premaxilla to the anterior surface of the midsection of the maxilla. The connective tissues in this region are poorly to moderately developed in examined tetragonopterine outgroups, permitting some mobility of maxilla relative to the premaxilla. In *Piabina argentea* (Figures 6, 8A) and in all species of *Creagrutus* (Figures 7, 8B), the maxilla-premaxilla ligament is rather a highly developed, discrete mass tightly joining the anterior of the maxilla to the vertical or near vertical bony notch on the posteroventral corner of the premaxilla. This expansion of the ligament in *Piabina* and *Creagrutus* compared with the condition in examined outgroups is considered to be derived.

Reductions in the mobility of the maxilla relative to the premaxilla also occurs in other characiforms, most notably the

genera *Belonophago* Giltay, *Eugnatichthys* Boulenger, *Hemistichodus* Pellegrin, *Ichthyborus* Günther, *Mesoborus* Pellegrin, *Microstomatichthyoborus* Nichols and Griscom, *Paraphago* Boulenger, and *Phago* Günther of the African family Distichodontidae (Vari, 1979:273–274, fig. 4). Among these distichodontids, the greatly reduced maxilla lacks the dorsomedial process typical for characiforms and is immovably joined, albeit not fused to the rear of the enlarged premaxilla. This restructuring of the ossification eliminates the mobility between the premaxilla and maxilla permitted by the premaxillary-maxillary ligament in other characiforms and, furthermore, renders it impossible to determine whether that ligament is still present as a discrete body. Among New World characiforms, a significantly restructured maxilla tightly associated with the posterodorsal margin of the premaxilla and lacking an obvious premaxillary-maxillary ligament occurs in *Ctenolucius* Gill and *Boulengerella* Eigenmann, which constitute the family Ctenoluciidae (Vari, 1995:15, fig. 6). Once again it is impossible to identify a discrete maxillary-premaxillary ligament in ctenoluciids. Despite these uncertainties, the cited distichodontids and ctenoluciids are deeply imbedded in clades whose other members have associations of the maxilla and premaxilla generalized for characiforms (Vari, 1979, and 1995, respectively) and have an obvious premaxillary-maxillary ligament. Thus, the adaptations in the cited ctenoluciids and distichodontids are not pertinent to the discussion of modifications of this system discussed above in *Creagrutus*. Various characid taxa (*Iguanodectes* Cope, *Acestrorhynchus* Eigenmann and Kennedy) demonstrate less pronounced alterations of the maxilla than those found in the above-cited distichodontids and ctenoluciids. These taxa, nonetheless, retain the generalized ligamentous attachments of the maxilla to the premaxilla described previously for *Piabina* and *Creagrutus*. In addition, neither of these taxa is closely aligned phylogenetically with the Tetragonopterinae (Buckup, 1998).

CHARACTER 10. State 0: Ligament between posteroventral corner of premaxilla and anterior surface of maxilla moderately developed. State 1: Ligament between posteroventral corner of premaxilla and anterior surface of maxilla well developed.

The degree of mobility between the maxilla and premaxilla within *Creagrutus* is further constrained by additional ligamentous attachments of the anterior portion of the maxilla to proximate ossifications. *Piabina argentea* retains a single, well-developed ligament between the anterodorsal surface of the maxilla and the distal portion of the lateral wing of the mesethmoid (Figure 8A). This condition occurs in outgroup characiforms, and consequently it is hypothesized to be primitive for the order. In the species of *Creagrutus,* the anterodorsal process of the maxilla is, as previously described, both more robust and positioned closer to the posterodorsal surface of the premaxilla than in *Piabina* or other examined outgroup tetragonopterines. The position of the expanded anterodorsal process of the premaxilla relative to the dorsal surface of the maxilla in *Creagrutus* species is maintained, at least in part, by two ligaments that are absent both in *Piabina* and in other examined outgroup tetragonopterines. Anteriorly *Creagrutus* species have a distinct ligament that extends ventrally or anteroventrally from the anteroventral surface of the anterodorsal process of the maxilla to an attachment on the dorsal surface of the premaxilla (Figure 8B). The form of this ligament varies somewhat intragenerically. At one extreme, some *Creagrutus* species have a distinct, approximately cylindrical, ligament with nearly equivalent areas of attachment on the premaxilla ventrally and the maxilla dorsally. In other *Creagrutus* this ligament is triangular from a lateral view, with the extent of its attachment ventrally on the premaxilla distinctly wider than its attachment dorsally on the maxilla.

In nearly all examined, cleared and stained *Creagrutus* specimens, the ligament that extends between the anterior tip of the maxilla and the dorsal surface of the premaxilla is distinct from the ligament linking the anterodorsal portion of the maxilla to the distal portion of the lateral mesethmoid wing. Some smaller examined cleared and stained *Creagrutus* specimens, in contrast, have these dorsally and ventrally directed ligaments partially contiguous along the tip of the anterodorsal process of the maxilla. Such continuity of these ligaments is, however, absent in larger cleared and stained specimens of these species. The partial continuity between the ligaments extending dorsally and ventrally from the anterodorsal portion of the premaxilla in smaller individuals may thus be an ontogenetic stage leading to completely separated ligaments in larger conspecific specimens. The continuity, or lack thereof, between the ligaments and the implication of the increasing ontogenetic separation of the ligaments for hypotheses on the phylogenetic origin of the ligament extending from the anteroventral portion of the maxilla to the dorsal surface of the premaxilla require further ontogenetic study. Regardless, the occurrence of a distinct ligamentous band between the anterior tip of the maxilla and the dorsal surface of the premaxilla is hypothesized to be a derived feature for the species of *Creagrutus* given its absence in examined outgroup characiforms.

CHARACTER 11. State 0: No ligament extending between anterodorsal tip of the maxilla and dorsal surface of premaxilla. State 1: Distinct ligament extending between anterodorsal tip of maxilla and dorsal surface of premaxilla.

The close association between the anterior portion of the maxilla and the dorsal portion of the premaxilla in *Creagrutus* species is further stabilized by a connective-tissue band extending between the ventral margin of the central portion of the anterodorsal portion of the maxilla and the proximate dorsal surface of the premaxilla. This ligamentous band is situated anterior of the region where the large ligament joins the posteroventral corner of the premaxilla to the anterior surface of the maxilla (see discussion above). Within *Creagrutus,* this additional ligament is a longitudinally aligned, band-like sheet of connective tissue extending between the maxilla and premaxilla (Figure 8B). The ligament is present in all examined *Creagrutus* species but is variable in its degree of development.

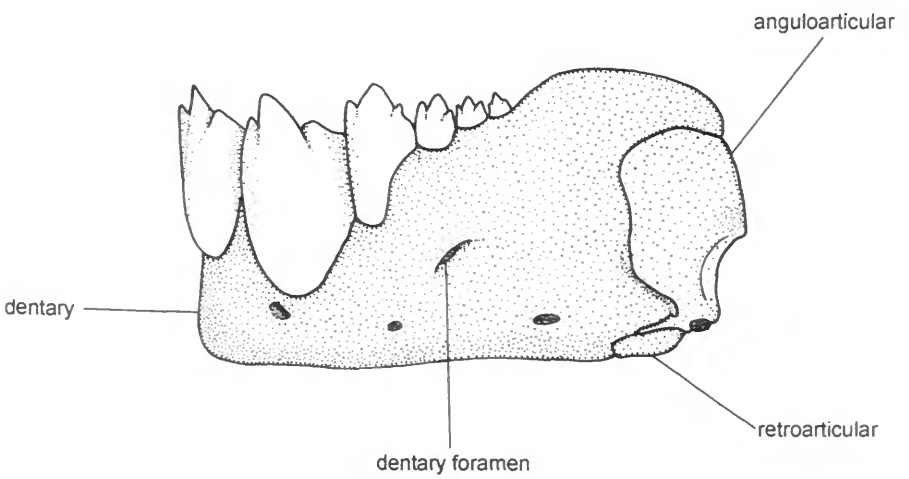

FIGURE 9.—Lower jaw of *Creagrutus amoenus*, USNM 311339, 65.0 mm SL; left side, lateral view, anterior to left.

Given the proximity of these ossifications in *Creagrutus*, it is often difficult to see the ligament from a lateral view without slightly separating the two ossifications. The presence of this additional maxillary-premaxillary ligament is judged to be derived given its absence in *Piabina* and other examined tetragonopterine outgroups.

CHARACTER 12. State 0: Ligament extending between midventral portion of ascending process of maxilla and dorsal surface of premaxilla absent. State 1: Ligament extending between midventral portion of ascending process of maxilla and dorsal surface of premaxilla present.

DENTARY.—The external feature that most readily distinguishes *Piabina argentea* and most *Creagrutus* species from the vast majority of other characids is the distinctly posterior position of the anterior margin of the lower jaw relative to the anterior limit of the upper jaw. As shown in Figure 9, the typical dentary form in these genera is an anteroposteriorly compact structure, a morphology quite different from that in characid outgroups (see Howes, 1982, for figures of lower jaws in various *Brycon* species). Furthermore, the articulation between the quadrate and the anguloarticular in both *Piabina* and *Creagrutus* lies along a vertical line slightly posterior of the blade-like lateral portion of the lateral ethmoid, a position of articulation typical of many characids in which the upper and lower jaws are of approximately equal lengths. This posterior location of the anterior margin of the lower jaw relative to the upper jaw in *Piabina* and *Creagrutus* is considered to be the result of the foreshortened dentary (Figure 9) rather than a posterior shift of the relative position of the articulation of a nonshortened lower jaw with the quadrate, a repositioning that occurs in some other characiforms.

As a consequence of the disparity in the lengths of the upper and lower jaws in the species of *Creagrutus* and *Piabina*, the cutting margins of the anterior dentary teeth on the dentary are significantly shifted posteriorly compared with the condition in numerous characid outgroups. Such a shift results in the insertion of the anterior dentary teeth behind the lingual margins of the two posterior teeth of the triad (see relative position of the teeth as shown in Figure 6), one of the primary components of the premaxillary dentition in both *Piabina* and *Creagrutus*. Functionally, the relative positions of these components of the dentary and premaxillary dentition create a shearing surface between the anterodorsal surface of the anterior dentary teeth and the posterior surface of two posterior teeth of the premaxillary triad. The shearing action between these teeth, which apparently serves as the main cutting area within the jaws in *Creagrutus* and *Piabina*, would account for the chopped up, but not finely ground or crushed, seeds and juvenile and adult insects that are major components of the stomach contents of these genera.

Comparable positions of the upper- and lower-jaw dentition also occur in various New World characids, including some *Brycon* species (e.g., *Brycon dentex;* see Howes, 1982, fig. 13), the serrasalmine characid sister genera *Colossoma* Eigenmann and Kennedy and *Piaractus* Eigenmann (see Machado-Allison, 1983, fig. 6, for an illustration showing relative positions of upper- and lower-jaw teeth in the closed mouth in the latter genus), and some African alestids. All of these outgroup taxa retain a supraorbital, a feature lacking in tetragonopterines, including *Piabina* and *Creagrutus*. Furthermore, at least for *Brycon* and alestids, the phylogenetic evidence indicates that these taxa are not closely related to the Tetragonopterinae (Buckup, 1998). A great disparity in jaw lengths is absent in most characiforms, including basal lineages. Thus, the association of the upper and lower jaws in *Piabina* and *Creagrutus* is hypothesized to be derived.

Functional aspects of the feeding mechanism of the cited taxa with disparate jaw lengths are unknown, with the exception of that of *Colossoma*, which was briefly described by Irish (1983:846). She reported that seeds (experimentally almonds)

"are anchored against the premaxillary teeth while a shearing force is applied by the mandibular [=dentary] teeth. Small pieces are sequentially broken off and sucked back into the orobranchial chamber while the body of the seed is passively held between the fleshy lips." In addition to having comparable relative positions of the teeth in the upper and lower jaws, *Colossoma, Piabina,* and *Creagrutus* species also possess fleshy lips, particularly the lower lip, which may serve to position food items being processed by the jaw teeth. Chopped up seeds, a common item in the stomach contents of *Creagrutus* and *Piabina* species, are a feature of the diet shared with *Colossoma.* Thus, it seems likely that species of *Creagrutus* and *Piabina* may use feeding methods similar to that reported by Irish (1983) for *Colossoma,* or at least do so when dealing with certain relatively hard food items, such as seeds and insect parts.

Distinctly foreshortened lower jaws occur in *Piabina argentea* and all members of *Creagrutus,* with the exception of *C. cracentis, C. gephyrus,* and *C. maxillaris,* which have dramatically restructured upper and lower jaws compared with these systems in other members of these genera. These three species, nonetheless, retain a somewhat foreshortened dentary relative to the upper jaw, with the dorsal portions of the anterior dentary teeth inserting behind the posterior teeth of the premaxilla as in their congeners. The proportional lengthening of the dentary in these species is hypothesized to be a reversal within the context of the overall intrageneric phylogeny.

CHARACTER 13. State 0: Anterior terminus of dentary dentition not distinctly posterior of anterior terminus of premaxillary dentition. State 1: Anterior terminus of dentary dentition distinctly posterior of anterior terminus of premaxillary dentition.

DENTARY FORAMEN.—The dentary in all *Creagrutus* species, *Piabina,* and various other examined characids (*Brycon falcatus, Bryconamericus iheringi, Chalceus macrolepidotus, Moenkhausia cotinho, Lignobrycon* (formerly *Moojenichthys*) *myersi, Triportheus angulatus*) and alestids (*Alestes lateralis, A. longipinnis, Virilia pabrensis*) has a discrete foramen passing through the bone (e.g., *Creagrutus amoenus,* Figure 9) that serves for the passage of the mandibular nerve through the bone.

Laterally this dentary foramen opens onto the medial surface of the dentary approximately lateral to the anterior terminus of the meckelian cartilage. When present, the opening typically transverses the dentary at an oblique angle, necessitating manipulation of the jaw to varying degrees to determine the course of the channel. The opening varies both in form and in position within *Creagrutus.* Most obvious among these conditions is the anteroposteriorly lengthened ovate opening on the lateral surface of the dentary in *C. cracentis, C. gephyrus,* and *C. maxillaris.* Associated with the horizontal lengthening of the opening laterally in these three species is a repositioning of the channel through the bone such that it passes directly transversely through the dentary rather than obliquely through that ossification as is typical of other congeners and many outgroup taxa. As a consequence of this realignment, it is possible from a lateral view in cleared and stained specimens to see through the dentary aperture to the space enclosed by the contralateral dentaries.

Creagrutus species other than *C. cracentis, C. gephyrus,* and *C. maxillaris,* along with *Piabina argentea* and other examined outgroup characids with the channel opening on the midlateral surface of the dentary, have a rotund aperture on the outer surface of the dentary. Such a rotund lateral opening of the dentary foramen occurs even in outgroup characids in which the upper and lower jaws are of approximately the same length, a condition comparable to that in *C. cracentis, C. gephyrus,* and *C. maxillaris.* Dentary elongation does not, per se, result in an anteroposteriorly elongate dentary foramen, such as occurs in these three *Creagrutus* species. Outgroup taxa with the midlateral dentary apertures typically also have posteriorly angled tubular openings extending through the dentary contrary to the transverse orientation of the channel that occurs in *C. cracentis, C. gephyrus,* and *C. maxillaris.* Thus, the horizontal elongation of the lateral aperture and the transverse orientation of the passage in those three species are considered to be derived conditions.

CHARACTER 14. State 0: Dentary foramen obliquely aligned and having rotund lateral opening. State 1: Dentary foramen aligned directly transversely and having horizontally elongate lateral opening.

The midlateral dentary foramen also differs in its medial point of exit. The majority of *Creagrutus* species have the opening situated near the anterodorsal tip of the meckelian cartilage and dorsal to the midline along the long axis of that cartilage. In *C. cracentis, C. gephyrus,* and *C. maxillaris,* the opening on the medial surface of the dentary is rather immediately anterior to the tip of the meckelian cartilage and is aligned along the line through the long axis of that cartilage. A third position of the opening occurs in a small subgroup of *Creagrutus* species (*C. melanzonus, C. phasma, C. runa*) in which the opening of the passage on the medial surface of the dentary is instead located near the anteroventral tip of that cartilage but is distinctly ventral to the line extending through the longitudinal axis of the meckelian cartilage.

In examined outgroup characids with the midlateral dentary foramen, the opening of the passage on the medial surface of the dentary is located anterodorsal to the tip of the cartilage and dorsal to the line through the long axis of the cartilage; thus, it matches the condition common to the majority of *Creagrutus* species and the outgroup *Piabina argentea.* This position of the aperture is consequently hypothesized to be the primitive location of the foramen for *Creagrutus.* The shift in the position of the medial opening to locations either anterior to, or ventral of, the anterodorsal tip of the cartilage in the two groups of *Creagrutus* species (*C. cracentis, C. gephyrus, C. maxillaris,* on the one hand, and *C. melanzonus, C. phasma, C. runa,* on the

other) are considered to be derived and are coded as discrete characters.

CHARACTER 15. State 0: Medial opening of dentary foramen located anterodorsal to tip of meckelian cartilage. State 1: Medial opening of dentary foramen located immediately anterior to tip of meckelian cartilage.

CHARACTER 16. State 0: Medial opening of dentary foramen located anterodorsal to tip of meckelian cartilage. State 1: Medial opening of dentary foramen located distinctly anteroventral to tip of meckelian cartilage.

LATEROSENSORY CANAL SEGMENT IN DENTARY.—The dentary in characiforms typically has a bony canal along its ventrolateral surface that encloses a portion of the laterosensory canal system. In *Piabina argentea* and in all species of *Creagrutus*, with the exception of *C. maracaiboensis*, the canal extends from the region of contact of the anguloarticular anteriorly to a point approximately three-fourths of the distance toward the dentary symphysis, which is the generalized characiform condition (anterior opening of mandibular laterosensory canal segment shown as unlabeled foramen located ventral to large second tooth in Figure 9). *Creagrutus maracaiboensis*, in contrast, lacks the ossified posterior portion of the laterosensory canal segment in the dentary. As a consequence, that species retains only a short, isolated, laterosensory canal segment that extends along approximately the middle one-third of the lateral surface of the dentary. This is a reductive autapomorphy for *C. maracaiboensis*.

DENTARY TEETH.—The number of teeth on each dentary falls into two distinct groups within *Creagrutus*. *Creagrutus cracentis*, *C. gephyrus*, and *C. maxillaris* have a range of 10 to 12 teeth on each dentary. The remaining *Creagrutus* species have four to seven dentary teeth (e.g., *Creagrutus amoenus*, Figure 9), a range that also occurs in *Piabina* and many other outgroup characids and is considered to be plesiomorphic. The increased tooth number in *C. cracentis*, *C. gephyrus*, and *C. maxillaris* is consequently considered to be derived.

CHARACTER 17. State 0: Dentary teeth 4 to 7. State 1: Dentary teeth 10 to 12.

An additional feature common to *Creagrutus cracentis*, *C. gephyrus*, and *C. maxillaris* is their possession of four or five cusps on the anterior dentary teeth in contrast to the three cusps present in the remaining species of *Creagrutus* (e.g., *Creagrutus amoenus*, Figure 9). These one or two additional, very small cusps flank the posterior (when four cusps are present) or anterior and posterior (when five cusps are present) lateral cusps present in other *Creagrutus* species. Recently emerged teeth, as indicated by their sharp cutting edges and in some instances only by their partially ossified basal portions, have these additional cusps quite distinct. Such smaller cusps on these teeth are not apparent on older teeth, as indicated by their rounded cutting edges; their absence is most likely a consequence of mechanical erosion. Although tricuspidate teeth are quite common among tetragonopterines, including *Piabina argentea*, the sister group to *Creagrutus*, various tetragonopterin taxa also have increased numbers of cusps on the dentary teeth. As a consequence of this variation in outgroups, we treat the character as unordered.

CHARACTER 18. State 0: Anterior dentary teeth with 3 cusps. State 1: Anterior dentary teeth with 5 cusps.

ANGULOARTICULAR.—Associated with the foreshortening of the lower jaw in *Piabina* and *Creagrutus* is a reduction in the antero-posterior extent of the anguloarticular. From a lateral view, the anguloarticular appears vertically elongate, rather than having the more horizontal expanse typical of outgroup characids (Figure 9). Examined at the level of the horizontal through the articular socket, which contacts the condylar surface of the quadrate, this antero-posterior shortening is manifested by the near contact of the posterior portion of the dentary and the posterior surface of the laterally expanded articular socket. The three species of *Creagrutus* (*C. cracentis*, *C. gephyrus*, *C. maxillaris*) with secondarily elongated jaws, nonetheless, retain the same overall form of the anguloarticular, albeit with a proportionally slightly increased space between the posterior margin of the dentary and the articular socket of the anguloarticular. The reduced, vertically elongate form of the anguloarticular is coded as derived and is a synapomorphy for *Creagrutus*.

CHARACTER 19. State 0: Anguloarticular not as in 1. State 1: Anguloarticular horizontally foreshortened.

The posterodorsal portion of the anguloarticular in the majority of *Creagrutus* species has a posterior margin that ranges from being nearly vertical to being somewhat convex and extending posterior of the articular facet on that ossification, a morphology that also is present in *Piabina argentea*, the first outgroup to *Creagrutus* (Figure 9). Two *Creagrutus* species, *C. cracentis* and *C. maxillaris*, instead have a distinctly anterodorsally angled dorsal margin of the anguloarticular, a modification considered to be derived in light of its absence in *Piabina* and other examined characid outgroups.

CHARACTER 20. State 0: Margin of posterodorsal portion of anguloarticular vertical to somewhat convex. State 1: Margin of posterodorsal portion of anguloarticular distinctly anterodorsally angled.

The characiform anguloarticular typically has a short laterosensory canal segment positioned ventrally and immediately above its articulation with the retroarticular. This canal segment is uniquely absent in *Creagrutus maracaiboensis* within *Creagrutus*. Although *Creagrutus maracaiboensis* achieves some of the smallest maximum known body sizes within the genus, its diminutive size is not, per se, the explanation for its lack of a sensory canal segment in the anguloarticular. A specimen of *C. nigrostigmatus*, another diminutive species, of comparable size to the examined *C. maracaiboensis* specimens has a fully developed laterosensory canal in the anguloarticular, and the canal segment is present in even smaller individuals of *C. magdalenae*, a species that achieves distinctly larger body sizes as an adult than does *C. maracaiboensis*.

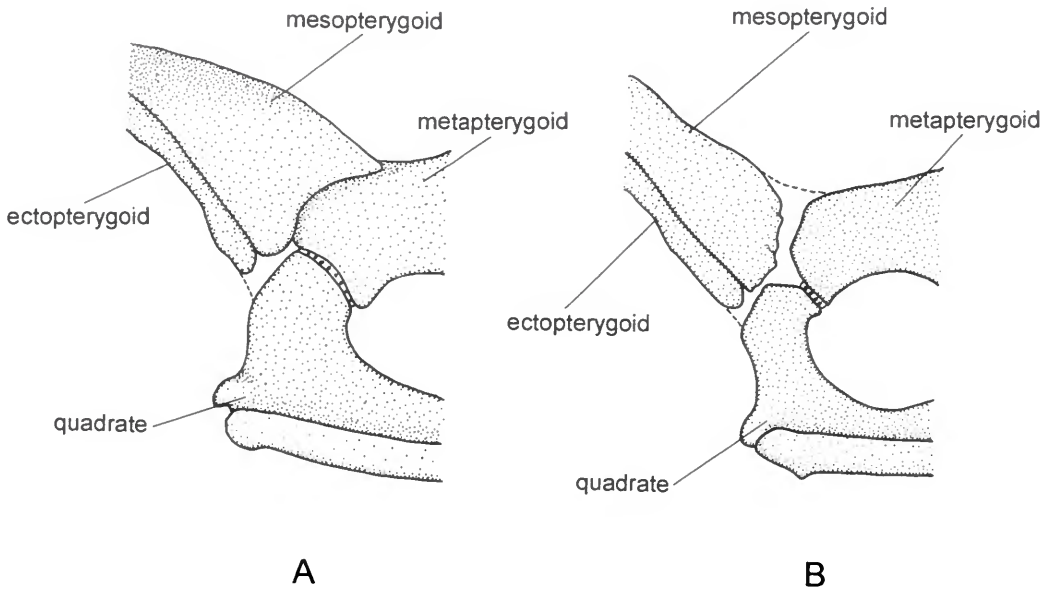

FIGURE 10.—Central portions of suspensorium in (A) *Piabina argentea,* USNM 292220, 59.2 mm SL; and (B) *Creagrutus amoenus,* USNM 311339, 65.0 mm SL; left side, lateral view, anterior to left. (Dashes indicate limits of connective tissue.)

SUSPENSORIUM

RELATIONSHIP OF ECTOPTERYGOID AND QUADRATE.—The ectopterygoid either contacts or overlaps the anterodorsal portion of the quadrate to varying degrees in a most characiform groups. Characiform taxa demonstrating such contact between these two bones include components of the family Characidae (e.g., *Cynopotamus* Valenciennes, *Galeocharax* Fowler, and *Acestrocephalus* Eigenmann, see Menezes, 1976, figs. 11–13; *Brycon,* see Weitzman, 1962, fig. 10), Acestrorhynchidae (*Acestrorhynchus,* see Roberts, 1969, fig. 32), Alestidae (*Alestes* Müller and Troschel, *Chalceus* Cuvier, and *Triportheus* Cope), Anostomidae (*Schizodon* Agassiz, see Roberts, 1973, fig. 12), Curimatidae (*Potamorhina* Cope, see Vari, 1983, fig. 27), Erythrinidae (*Hoplias* Gill, see Roberts, 1969, fig. 29), Hemiodontidae (*Hemiodus* Müller, see Roberts, 1974, fig. 8), Hepsetidae (*Hepsetus* Swainson, see Roberts, 1969, fig. 26), and Lebiasinidae (*Poecilobrycon* Eigenmann, see Weitzman, 1964, fig. 7), and basal family Distichodontidae (*Xenocharax* Günther, see Fink and Fink, 1981, fig. 11).

Species of *Creagrutus,* with the exception of *C. mucipu* along with *Piabina argentea,* differ from this generalized characiform condition in their lack a direct bony contact of the ectopterygoid and the quadrate, although with different degrees of separation of the bones. In *Piabina argentea* the posteroventral margin of the ectopterygoid approaches, but does not contact, the anterodorsal portion of the quadrate (Figure 10A). The species of *Creagrutus* other than *C. mucipu,* in contrast, have a distinct gap between the proximate portions of the ectopterygoid and quadrate (Figures 10B, 11). In the absence of direct ectopterygoid-quadrate contact, both *Piabina* and *Creagrutus* have a relatively thick sheet of connective tissue flexibly extending from the posteroventral margin of the ectopterygoid to the anterodorsal section of the quadrate. *Creagrutus mucipu,* the only member of the genus with contact between these bones, has a slight overlap of the posteroventral portion of the ectopterygoid over the quadrate. The overlap between these bones in *C. mucipu* is less pronounced than in most characiforms and is considered to be a secondary reacquisition of this feature within the context of the overall most parsimonious hypothesis of relationships. Such ectopterygoid-quadrate separation in *Piabina* and nearly all *Creagrutus* species is judged to be derived, given the bony contact of these elements in most characiform outgroups, including the basal family Distichodontidae.

A lack of direct contact between the ectopterygoid and the quadrate occurs in a few other characiforms. Within the Hemiodontidae the ectopterygoid and quadrate are separate in *Anodus* Agassiz (Roberts, 1974, fig. 45; Langeani, 1998, fig. 7). These two ossifications, however, overlap to varying degrees in *Micromischodus* Roberts, the sister group to *Anodus,* and in *Bivibranchia* Eigenmann, *Hemiodus,* and *Argonectes* Böhlke and Myers, the remaining hemiodontid genera that form the sister group to the clade formed by *Micromischodus* and *Anodus* (Langeani, 1998, fig. 22). Thus, the lack of ectopterygoid-quadrate contact in *Anodus* is most parsimoniously hypothesized as homoplastic to this condition in *Creagrutus* and *Pia-*

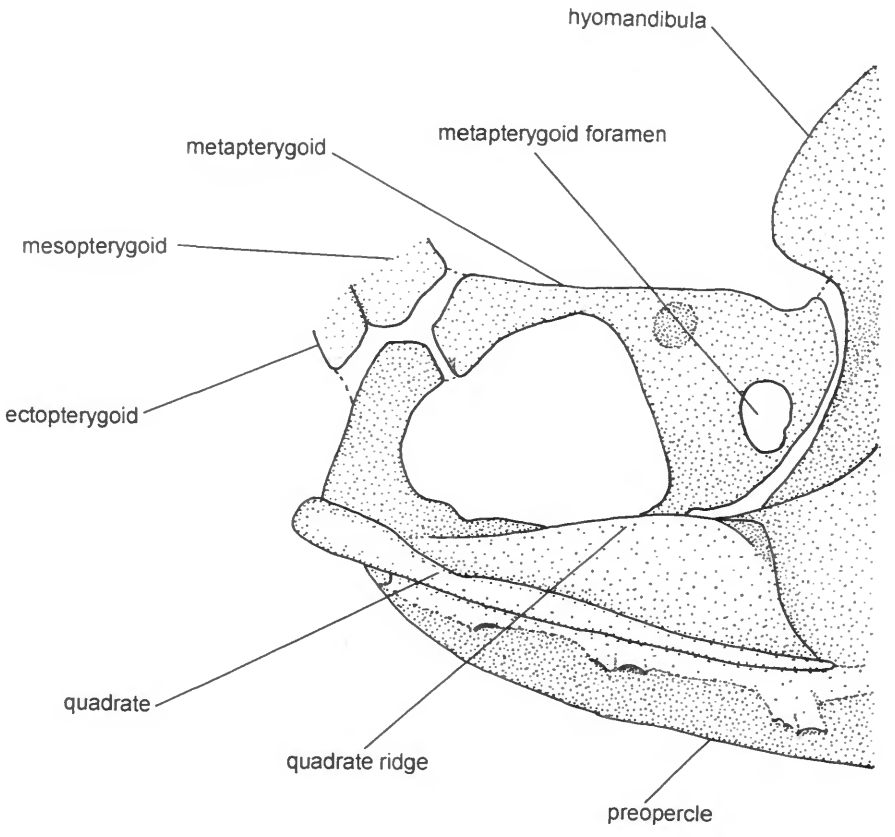

FIGURE 11.—Central portions of suspensorium in *Creagrutus barrigai*, USNM 340976, 45.6 mm SL; left side, lateral view, anterior to left.

bina. The ectopterygoid and quadrate also are separated in *Parodon* Valenciennes of the Parodontidae (see Roberts, 1974, fig. 70), whereas these bones are in contact in *Saccodon* Kner and *Apareidon* Eigenmann, which are the remaining genera of the Parodontidae. Although intrafamilial phylogenetic relationships of parodontids have yet to be critically analyzed, the family is undoubtedly monophyletic (Starnes and Schindler, 1993) and is furthermore phylogeneticaly distant from the Tetragonopterinae (Buckup, 1998). The separation of the ectopterygoid and quadrate in *Parodon* is consequently judged to be homoplastic relative to the lack of contact of those bones in *Piabina argentea* and the species of *Creagrutus*.

CHARACTER 21. State 0: Ectopterygoid and quadrate in contact, typically with distinct degree of overlap. State 1: Ectopterygoid and quadrate not in contact.

RELATIONSHIP OF MESOPTERYGOID AND METAPTERYGOID.—Associated with the loss of direct contact of the ectopterygoid and quadrate in *Creagrutus* and *Piabina* is a change of the relationship of the mesopterygoid and metapterygoid. Outgroup characiforms cited in the previous section all demonstrate a broad overlap of the posteroventral portion of the mesopterygoid onto the anterodorsal portion of the metapterygoid. *Piabina argentea* has a reduction of the posteroventral portion of the mesopterygoid compared to the condition in many outgroup characids but, nonetheless, retains an overlap of that ossification and the metapterygoid (Figure 10A), albeit to a less pronounced degree than in outgroup characid taxa.

Creagrutus species, with the exception of *C. gephyrus*, have a pronounced reduction of the posteroventral portion of the mesopterygoid resulting in a distinct separation of the posterior margin portion of the mesopterygoid from the border of the anterodorsal region of the metapterygoid (Figures 10B, 11). The proximate portions of the metapterygoid and mesopterygoid, in the absence of osseous contact, are joined by a connective-tissue sheet. This sheet is not as well developed as that extending between the separated ectopterygoid and quadrate in *Piabina* and *Creagrutus*. Such a separation of the mesopterygoid and metapterygoid in all *Creagrutus* species other than *C. gephyrus* is hypothesized to be derived given the contact and/or overlap of those two ossifications in examined characiform outgroups.

As noted, the one exception to the general separation of the mesopterygoid and metapterygoid in *Creagrutus* species oc-

curs in *C. gephyrus* in which the degree of overlap of the two ossifications is comparable to that in *Piabina.* Within the context of the final most parsimonious hypothesis of phylogenetic relationships within the genus, the overlap of these elements in *C. gephyrus* is hypothesized to be a reversal of the lack of contact of these ossifications typical for *Creagrutus* species.

The ectopterygoid, mesopterygoid, and palatine in *Creagrutus* species are tightly conjoined by connective tissue and by the elongate band of cartilage that extends along their proximate margins. The resultant tightly joined unit in *Creagrutus* is somewhat mobile relative to the more posterior components of the suspensorium, other than in the case of *C. gephyrus,* which has an apparently inflexible overlap of the mesopterygoid and metapterygoid. The functional significance of the resultant mobility is uncertain, but perhaps it is associated with the shearing action of the anterior dentary teeth and the posterior premaxillary teeth discussed above.

Various degrees of mobility of an anterior element of the suspensorium relative to the more posterior portion of the system also occurs among characiforms in members of the Hemiodontidae and Parodontidae and in the Anostomidae in *Gnathodolus* Myers (see discussion in Vari, 1983:30). In none of these outgroup characiform taxa, however, does the intra-suspensorium mobility involve movement between a unit formed by conjoined ectopterygoid, mesopterygoid, and palatine relative to the posterior components of the suspensorium. Furthermore, the phylogenetic relationships of all of these taxa are distant from the Tetragonopterinae, including *Creagrutus* (Buckup, 1998).

CHARACTER 22. State 0: Mesopterygoid and metapterygoid overlapping along their area of contact. State 1: Mesopterygoid and metapterygoid separate.

METAPTERYGOID.—Nearly all *Creagrutus* species have a distinct transverse foramen located in the posterior portion of the metapterygoid, and such an aperture also is present in *Piabina argentea,* the sister group to *Creagrutus.* This aperture (Figure 11) serves as a channel for a large blood vessel; the posterior margin of the opening is formed by a distinct bony bridge. In two Trans-Andean *Creagrutus* species (*C. maracaiboensis* and *C. nigrostigmatus*) and one Amazonian species (*C. zephyrus*), the passage for the blood vessel rather than being bordered posteriorly by a bony bridge instead opens along the rear margin of the metapterygoid. This is a unique and evidently derived condition within *Creagrutus.*

It is noteworthy that *C. maracaiboensis* and *C. nigrostigmatus* achieve the smallest known maximum adult body sizes in *Creagrutus,* and the cleared and stained specimens of *C. zephyrus* also are relatively small. Comparable incomplete closures of the metapterygoid foramen occur in juveniles of other *Creagrutus* species, the adults of which have a fully enclosed opening in the metapterygoid. Thus, the incomplete enclosure of the foramen in *C. maracaiboensis* and *C. nigrostigmatus* is potentially a consequence of a paedomorphic process reflecting the diminutive adult body sizes of these species, with the incomplete closure of the foramen in the cleared and stained specimens of *C. zephyrus* possibly a function of their size.

CHARACTER 23. State 0: Metapterygoid foramen enclosed within metapterygoid. State 1: Metapterygoid foramen open posteriorly.

Piabina argentea and *Creagrutus* species demonstrate variation in the form of the anteroventral process of the metapterygoid, which extends anteriorly to meet a comparable process from the quadrate situated along the dorsal margin of the symplectic. Some species in these genera have a distinct separation between the tips of these processes, with the intervening gap filled by an elongate cartilage. Other species have a nearly direct contact of the processes, with a relatively limited amount of intervening cartilage. The continuity in the degree of development of this process within this assemblage renders the assignment of species to particular character states problematic, making it impossible to utilize this variation for phylogenetic purposes. Two species with contact of well-developed metapterygoid and quadrate processes, *C. lassoi* and *C. gyrospilus,* have, however, a distinct, vertically expanded region of contact between the adjoining portions of the two processes. The degree of development of the area of contact is such that the joint is slightly expanded dorsally into the ventral portion of the metapterygoid-quadrate fenestra, a unique and derived condition.

CHARACTER 24. State 0: Contact of metapterygoid and quadrate in region dorsal of symplectic either cartilaginous or bony but not vertically expanded. State 1: Contact of metapterygoid and quadrate in region dorsal of symplectic via vertically expanded bony contact.

Nearly all *Creagrutus* species have the anteroventral process of the metapterygoid extending anteriorly to meet a comparable process from the quadrate situated along the dorsal margin of the symplectic. This contact is located approximately at the level of the horizontal through the ventral tip of the hyomandibula. The single exception is *C. lepidus* in which the anteroventral process of the metapterygoid (and the matching process on the quadrate, see "Quadrate," below) is positioned distinctly dorsal of the upper margin of the symplectic and of the horizontal through the ventral tip of the hyomandibula. As a consequence of its dorsal shift, the metapterygoid process and the matching process on the quadrate in *C. lepidus* dorsally delimit an opening that is, in turn, bordered ventrally by the symplectic. This additional fenestra in the suspensorium is situated below the large metapterygoid-quadrate fenestra present in most groups of characiforms. In light of its unique nature among examined characiforms, the aperture is considered to be an autapomorphy for *C. lepidus.*

QUADRATE.—The typical characiform quadrate has a slender posterodorsal process that extends posteriorly above the symplectic and that contacts the anteroventral process of the metapterygoid via an intervening cartilage body. In the typical characiform condition, this posterodorsal quadrate process is smoothly continuous with the slightly more laterally located

proximate portion of the main body of the quadrate. This generalized characid morphology of this portion of the quadrate is present in *Piabina argentea. Creagrutus* species have instead a variably developed vertical ridge or process extending dorsally from the main body of the quadrate in, and posterior to, the region where the posterodorsal process of the quadrate contacts the anteroventral process of the metapterygoid. This dorsally developed process is situated distinctly lateral of the typical posterodorsal process of the quadrate. When well developed, it covers (from a lateral view) the anterodorsal portion of the symplectic and the anteroventral portion of the posterior region of the metapterygoid (Figure 11). In light of its unique nature among examined characiforms, this quadrate process is considered to be a derived condition.

CHARACTER 25. State 0: Not as in state 1. State 1: Quadrate with variably developed vertical ridge or process extending dorsally from main body of the quadrate in, and posterior to, region where posterodorsal process of quadrate contacts anteroventral process of metapterygoid.

The only exception to the general *Creagrutus* form of this process of the quadrate occurs in *C. lepidus* in which the ridge is poorly developed. That reduction in the ridge on the quadrate, in combination with the dorsal shift in the contact of the anteroventral portion of the metapterygoid (see above under "Metapterygoid") and the posterodorsal process of the quadrate, results in those processes being visible in lateral view. The dorsal shift of the posterodorsal process of the quadrate in *C. lepidus* also contributes to the fenestra delimited by that process, the matching process of the metapterygoid, and the symplectic. This modification, unique to *C. lepidus* among the species of *Creagrutus,* was not encountered in examined characid outgroups, so it is considered to be derived.

HYOMANDIBULA.—The hyomandibula is a complex bone with several modifications of interest in *Creagrutus.* When examined in lateral or medial view the most obvious of these modifications is the expansion anteriorly of the anteromedial portion of the ossification (Figure 11). As a consequence, this portion of the hyomandibula extends over the posterodorsal region of the metapterygoid, with the degree of extension variable within *Creagrutus.* This form of hyomandibula differs from the typical characid condition in which the anterior margin of the hyomandibula is straight or even slightly concave (e.g., *Brycon meeki;* see Weitzman, 1962, fig. 10), and its presence in *Creagrutus* species is consequently considered to be a derived condition.

CHARACTER 26. State 0: Anterior margin of hyomandibula straight or slightly concave. State 1: Anterior margin of hyomandibula anteriorly expanded and extending over posterodorsal region of metapterygoid.

The dorsal margin of the hyomandibula also demonstrates a modification involving the association of the ossification with the neurocranium. When examined from a dorsal view, the portion of the hyomandibula that articulates with the cranial hyomandibular fossa in characids is symmetrical about an anteroposterior line and is typically rectangular overall or somewhat pinched midway along its length. The vast majority of species of *Creagrutus* along with *Piabina argentea* have, in contrast, a highly asymmetrical profile of the dorsal articular surface of the hyomandibula when viewed from the dorsal view. In these species the anterior portion of the articular surface of the hyomandibula is distinctly expanded laterally compared with the condition in tetragonopterine outgroups. Underlying this expanded portion of the articular surface is a progressively ventrally attenuating lateral buttress on the hyomandibula, another distinctive feature for this assemblage. Both the lateral expansion of the articular surface and the associated lateral expansion of the adjoining portion of the hyomandibula in *Piabina argentea* and most *Creagrutus* species are thus considered to be derived.

The restructurings of the dorsal portions of the hyomandibula described above are, however, absent in three *Creagrutus* species (*C. cracentis, C. gephyrus, C. maxillaris*). These species have nearly symmetrical articular surfaces on the dorsal margin of the hyomandibula, the generalized tetragonopterine condition. Within the context of the overall phylogenetic analysis this is judged to be a single secondary reversal to the generalized characid condition.

CHARACTER 27. State 0: Dorsal articular surface of hyomandibula nearly symmetrical; hyomandibula without dorsolateral buttress. State 1: Dorsal articular surface of hyomandibula asymmetrical; hyomanibula with dorsolateral buttress.

ANTORBITAL AND INFRAORBITALS

ANTORBITAL.—The typical shape of the antorbital in *Creagrutus* is an elongate, posterodorsally inclined ossification with a slight medial flexure and moderate anteroventral expansion. This condition also is present in *Piabina argentea* and other examined outgroups. In two *Creagrutus* species (*C. lepidus, C. melasma*) the anteroventral portion of the ossification is expanded relative to the condition in congeners. This restructuring results in an anteroposteriorly wider antorbital that in a lateral view is characterized by a distinct posteroventral angle along its longest axis. Given the absence of such an expansion in its congeners or in *Piabina*, the sister group to *Creagrutus*, the antorbital form in *C. lepidus* and *C. melasma* is hypothesized to be a derived condition.

CHARACTER 28. State 0: Antorbital elongate, with slight medial flexure and moderate anteroventral expansion. State 1: Antorbital distinctly wider anteriorly and with distinct angle.

FIRST INFRAORBITAL.—The first infraorbital (IO_1) demonstrates a notable degree of variation in overall form across *Creagrutus*. Continuity across this variation, however, mostly precludes the unequivocal recognition of discrete character states across this morphological variability. The single exception involves the degree of development of the anterior portion of the laterosensory canal segment in the first infraorbital. In *Piabina argentea* the anterior portion of the laterosensory canal seg-

ment in the first infraorbital terminates distinctly posterior of the anterior margin of the plate-like main body of the ossification. *Creagrutus* species, in contrast, have the laterosensory canal segment extending forward as far as, or beyond, the anterior limit of the first infraorbital. This anterior extension of the laterosensory canal segment in the first infraorbital in *Creagrutus* species demonstrates an intrageneric range in form from a discrete tube integral to the plate-like anterior portion of the bone to a distinct ossified tube extending forward of the main, plate-like portion of the bone. Outgroup tetragonopterines have variable degrees of development of the laterosensory canal in the first infraorbital making it impossible to polarize the character.

CHARACTER 29. State 0: Anterior portion of the laterosensory canal segment in first infraorbital terminating distinctly posterior of anterior margin of bone. State 1: Anterior portion of laterosensory canal segment in first infraorbital reaching or extending beyond anterior margin of main body of ossification.

JOINT BETWEEN FIRST AND SECOND INFRAORBITALS.—Two distinct conditions of the joint between the first and second infraorbitals (IO_1 and IO_2, respectively) occur within *Creagrutus*. In two species (*C. lepidus, C. melasma*) the adjoining margins of these ossifications abut without overlap. Other *Creagrutus* species have the posterior portion of the first infraorbital overlapping the anterior portion of the second infraorbital, with variation in the degree of overlap between species. No overlap between the first and second infraorbitals occurs in *Piabina,* the sister group to *Creagrutus.* Given the variability in this feature among other tetragonopterines, we are unable to polarize this feature.

CHARACTER 30. State 0: First and second infraorbitals abutting without overlap. State 1: Posterior portion of first infraorbital overlapping anterior portion of second infraorbital.

The form of the area of contact between the first and second infraorbitals in *C. maracaiboensis,* a diminutive species endemic to the Lago Maracaibo basin, cannot be determined and consequently is coded as "?." In the region anteroventral to the orbit, *C. maracaiboensis* has a single ossification in the space filled by the first and second infraorbitals in the remaining *Creagrutus* species. We are unable to determine whether this ossification represents a fusion of the first and second infraorbitals, or the loss of one of these elements with the subsequent expansion of the remaining infraorbital into the space originally occupied by the lost element. Regardless of its identity, this form of infraorbital, unique within *Creagrutus,* is an autapomorphy for *C. maracaiboensis.*

FOURTH INFRAORBITAL (IO_4).—The fourth infraorbital varies both in form and relative size in the assemblage formed by *Piabina* and *Creagrutus;* however, continuity across this variation renders it mostly impossible to delimit discrete character states. The one exception to that generality involves the form of the ossification in *Piabina argentea,* the single species of the genus. In all *Creagrutus* species the fourth infraorbital is approximately quadrilateral (Figure 12A), the condition present in most characiformes. In *Piabina argentea* the fourth infraorbital is rather triangular with an acute posterior angle (Figure 12B). Smaller specimens of *P. argentea* have the posteriorly tapering portion of the fourth infraorbital contributing to the posterior margin of the infraorbital ring, at least to a limited degree. During ontogeny, *P. argentea* demonstrates a differential expansion of the posterior portions of the third through fifth infraorbitals, with the fourth infraorbital expanding posteriorly to a lesser degree than the third and fifth infraorbitals. This differential development and the resultant contact of the third and fifth infraorbitals along the posterior margin of the infraorbital ring excludes the fourth infraorbital from the posterior infraorbital margin in larger individuals of *P. argentea.* Exclusion of the fourth infraorbital from the posterior margin of the infraorbital series in *P. argentea* contrasts with the situation in all *Creagrutus* species in which the fourth infraorbital contributes to the posterior margin of the infraorbital ring, a condition that also is generalized for most tetragonopterines (e.g., *Hemibrycon* Günther; see Géry, 1962, fig. 5) and indeed characiforms. Retention of contact consequently is judged to be plesiomorphic, whereas the morphology of the fourth infraorbital in *Piabina* is considered to be derived, although not unique among characiforms.

A fourth infraorbital excluded from the posterior margin of the orbital ring also occurs in two clades of the family Ctenoluciidae (Vari, 1995:12, fig. 1). The first clade consists of *Ctenolucius beani* (Fowler) and *C. hujeta* (Valenciennes), and the second consists of *Boulengerella cuvieri* (Agassiz), *B. lucius* (Cuvier), and *B. xyrekes* Vari. One notable difference between the *Piabina* condition of the fourth infraorbital and that in ctenoluciids is the proportionally significantly smaller ossification among ctenoluciids. Such proportional differences do not, a priori, render the reduced fourth infraorbitals in ctenoluciids homoplastic relative to that in *Piabina.* Ctenoluciids are, however, deeply nested within a series of sequential clades that include neither *Creagrutus* nor *Piabina* (Vari, 1995, fig. 15) and that retain a quadrangular fourth infraorbital extending to the posterior margin of the infraorbital series. Consequently, the occurrence of a reduced fourth infraorbital excluded from the posterior rim of the infraorbital series in ctenoluciids is most parsimoniously judged to be homoplastic to the presence of the somewhat similar condition in *Piabina argentea.*

Elsewhere among characiforms, a reduced fourth infraorbital also occurs in the characid *Roeboides* Günther. Lucena (1998:40, fig. 4) reported a posteriorly attenuating triangular fourth infraorbital falling short of the posterior infraorbital margin in larger individuals of *R. dayi* Steindachner, *R. occidentalis* Meek and Hildebrand, *R. bouchellei* Fowler, *R. dientonito* Schultz, and *R. ilsea* Bussing. The remaining *Roeboides* species lack the ossification, as is shown by their possession of only five infraorbitals. In his phylogenetic analysis, Lucena (1998:28) advanced a series of characters that support the hypothesis of the monophyly of *Roeboides* and demonstrated that

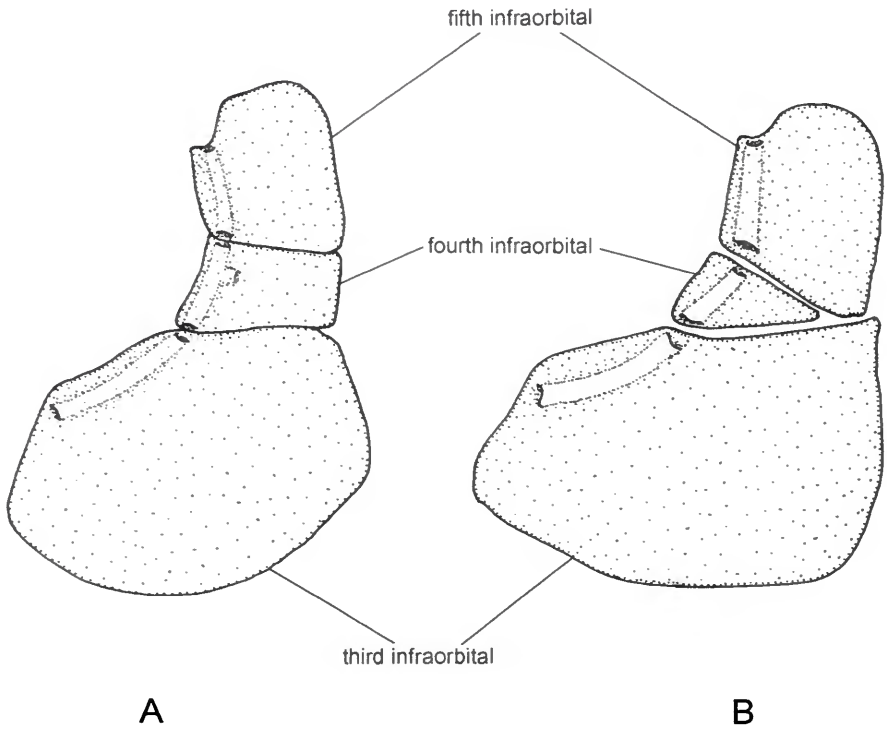

FIGURE 12.—Third through fifth infraorbitals of (A) *Creagrutus menezesi,* USNM, 292229, 61.8 mm SL; and (B) *Piabina argentea*, USNM 292220, 59.2 mm SL; left side, lateral view, anterior to left.

under the most parsimonious hypothesis of relationships the reduced fourth infraorbital in some *Roeboides* species is a reacquisition of the ossification (Lucena, 1998:39–40). In an earlier study Lucena (1993) advanced information indicating that the relationships of *Roeboides* lie with taxa traditionally placed in the subfamily Characinae, an assemblage defined by features absent in *Piabina* and the *Piabina-Creagrutus* clade. Thus, the posteriorly attenuating fourth infraorbital in *R. occidentalis* is consequently hypothesized to be homoplastic to that in *Piabina.*

CHARACTER 31. State 0: Fourth infraorbital approximately quadrangular and contributing to posterior margin of infraorbital series at all sizes. State 1: Fourth infraorbital approximately triangular and excluded from posterior margin of infraorbital series in medium- to large-sized individuals.

FIFTH INFRAORBITAL.—The fifth infraorbital within *Creagrutus* generally has a distinct posterodorsal process (Figure 12) that is situated posterior to the relatively small sixth infraorbital (=dermosphenotic); this condition also is present in the first outgroup, *Piabina argentea. Creagrutus lepidus,* uniquely within the genus, lacks this posterodorsal process of the fifth infraorbital and as a consequence has the sixth infraorbital situated completely dorsal of the fifth infraorbital. Although adult *C. lepidus* attain relatively small body sizes compared to many congeners, their lack of the posterodorsal process of the fifth infraorbital cannot be ascribed to that factor. This posterolateral process of the fifth infraorbital is present in other *Creagrutus* species at body sizes comparable to those of adults of *C. lepidus* in which the process is absent. The absence of the process on the fifth infraorbital is hypothesized to be autapomorphic for *C. lepidus* in light of the broad distribution of such a process within *Creagrutus* and its immediate outgroup, *Piabina.*

BRANCHIAL ARCHES

FOURTH BASIBRANCHIAL TOOTH-PLATE.—The fourth basibranchial (BB_4) is a variably developed median cartilage. Beginning immediately posterior of the partially to completely ossified third basibranchial, the cartilaginous fourth basibranchial extends posteriorly between the medial portions of the contralateral fourth ceratobranchials to terminate at, or beyond, the anterior portions of the fifth ceratobranchials. The dorsal surface of the fourth basibranchial in examined outgroups, includ-

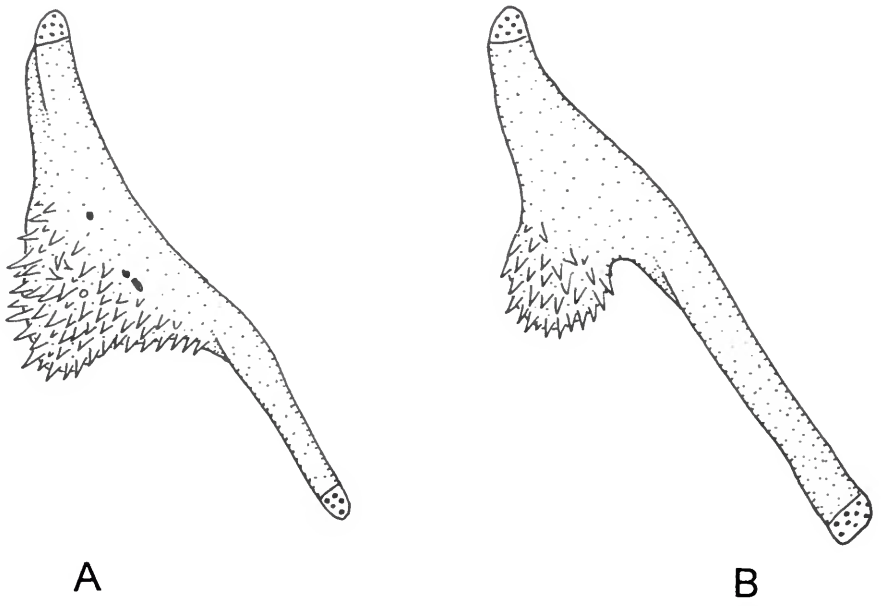

FIGURE 13.—Fifth ceratobranchial of (A) *Piabina argentea*, USNM 292220, 59.2 mm SL; and (B) *Creagrutus magoi*, USNM 292220, 59.2 mm SL; right side, dorsal view, anterior at top, larger stippling represents cartilage.

ing *Piabina argentea*, bears a bony plate. That ossification also is present in all but fourteen *Creagrutus* species (*C. atratus, C. barrigai, C. bolivari, C. gephyrus, C. gracilis, C. machadoi, C. magdalenae, C. mucipu, C. paralacus, C. pila, C. seductus, C. taphorni, C. vexillapinnus, C. zephyrus*). Given the common occurrence of the ossification in outgroups, including *Piabina*, its absence in some *Creagrutus* species is considered to be derived.

CHARACTER 32. State 0: Dorsal surface of fourth basibranchial bearing body plate. State 1: Dorsal surface of fourth basibranchial without body plate.

FIFTH CERATOBRANCHIAL.—The fifth ceratobranchial (C_5) in the Characidae has two primary components when observed from dorsal view. The first is the anteromedially aligned main shaft whose orientation matches the longitudinal alignment of the more anterior ceratobranchials. Medial to this main shaft is a tooth-bearing triangular portion with a patch of teeth covering its dorsal surface (Figure 13). The junction of the posterior margin of the tooth-bearing portion of the fifth ceratobranchial with the main shaft of the bone ranges between a right angle and a distinctly obtuse angle. Along its lateral margin, the fifth ceratobranchial tooth patch extends approximately in parallel with the axis of the main shaft of the bone. Medially the tooth patch extends distinctly forward of the transverse level through the point where the tooth-bearing portion of the bone contacts the main shaft of the fifth ceratobranchial. Such a morphology of the fifth ceratobranchial and its tooth patch occurs in diverse characids (e.g., *Brycon falcatus* Müller and Troschel (see also Weitzman, 1962, fig. 11, for *B. meeki* Eigenmann and Hildebrand), *Bryconamericus iheringi* (Boulenger), *Triportheus angulatus* (Spix), and *Tetragonopterus* sp.) and alestids (e.g., *Alestes lateralis* Boulenger, *Virilia pabrensis* (Roman)).

This generalized characid and alestid arrangement of the fifth ceratobranchial also occurs in *Piabina argentea* (Figure 13A), but within *Creagrutus* it is limited to *C. maracaiboensis* and *C. nigrostigmatus*. The remaining *Creagrutus* species have the tooth-bearing portion of the fifth ceratobranchial relatively reduced and extending not as far anteriorly along the medial margin of the bone (Figure 13B). More notably, the tooth-bearing portion of the fifth ceratobranchial is reduced along its lateral margin, resulting in a distinct concavity along the posterior margin of the fifth ceratobranchial in the region where the tooth-bearing portion of the fifth ceratobranchial meets the main shaft of the bone. This restructuring of the tooth-bearing portion of the fifth ceratobranchial and the associated reduction in the extent of the toothed portion of that ossification in most *Creagrutus* species is considered to be derived, given the condition in examined outgroups.

Among examined outgroup taxa only the iguanodectine characid *Piabucus melanostomus* has a fifth ceratobranchial form somewhat comparable to that in the majority of *Creagrutus* species. Although *Piabucus melanostomus* has a deeply indented posterior margin of the tooth-bearing portion of the bone, the dentition on the fifth ceratobranchial extends along much of the medial margin of that ossification rather than being limited to the posterior portion of the bone. Furthermore, *Piabucus* and its sister genus, *Iguanodectes* (Vari, 1977), which together constitute the subfamily Iguanodectinae, lack the other

derived features common to *Creagrutus* and *Piabina* and also lack the synapomorphies for the species of *Creagrutus*. Thus, the similar form of fifth ceratobranchial in *Piabucus melanostomus* and the majority of *Creagrutus* species are considered homoplastic.

CHARACTER 33. State 0: Dentigerous portion of fifth certobranchial well developed and elongate, meeting main shaft of ossification approximately at a right angle. State 1: Dentigerous portion of fifth certobranchial smaller and rotund, meeting main shaft of ossification approximately at a distinctly acute angle.

THIRD INFRAPHARYNGOBRANCHIAL.—The presence of dentition on the posteroventral portion of the third infrapharyngobranchial (PB_3) is common to diverse characids (e.g., *Brycon falcatus;* see Vari, 1989, fig. 17), although with variation in the form of the tooth patch and number of teeth. Dentition on the third infrapharyngobranchial is absent in *Piabina argentea* but is present in a subset of *Creagrutus* species, including four of the eight members of the genus living to the west of the Andean Cordilleras (*C. affinis, C. brevipinnis, C. caucanus, C. hildebrandi*) and a much smaller percentage of the Cis-Andean species (*C. anary, C. atrisignum, C. beni, C. changae, C. holmi, C. kunturus, C. manu, C. meridionalis, C. ortegai, C. pearsoni, C. pila, C. runa, C. saxatilis, C. zephyrus*). In the absence of information on proximate outgroups to *Creagrutus* beyond *Piabina,* it is not possible to polarize this character.

CHARACTER 34. State 0: Dentition on third infrapharyngobranchial absent. State 1: Dentition on third infrapharyngobranchial present.

CRANIUM

Components of the cranium pertinent to the phylogenetic reconstruction are discussed starting with the dorsal elements in an anterior to posterior direction, followed by more ventral ossifications in the same sequence.

MESETHMOID.—Anteriorly the mesethmoid in characids typically terminates in a conic process that forms the anteriormost portion of the cranium. The anterior portion of the mesethmoid in characids usually extends directly, or nearly directly, forward, typically in the form of an anteriorly tapering, sometimes attenuate, triangle that serves as a broad area of attachment for the median surfaces of the contralateral premaxillae. In *Piabina* and *Creagrutus* this anterior portion of the mesethmoid is expanded ventrally compared with the condition in other examined characids. As a consequence, this portion of the mesethmoid in these genera forms a variably anteroventrally expanded process that extends between the premaxillae nearly as far as the ventral surface of the median suture between those bones (Figure 14). This expansion of the mesethmoid takes two forms within the clade composed of *Piabina* and *Creagrutus.*

Piabina argentea and all *Creagrutus* species other than *C. cracentis, C. gephyrus,* and *C. maxillaris* have the anterior portion of the mesethmoid expanded ventrally into a relatively large, transversely flattened, vertical plate that projects downward from the ventral margin of the main body of the mesethmoid (Figure 14). Ventrally this process, herein termed the anteroventral process of the mesethmoid, ranges from being somewhat rounded to nearly square in lateral view. It extends between the symphyseally expanded premaxillae and nearly separates these contralateral ossifications except for a limited degree of contact along their anterior and ventral margins. This form of ventrally expanded mesethmoid was not encountered in examined characiform outgroups and is consequently considered to be derived.

In *Creagrutus cracentis, C. gephyrus,* and *C. maxillaris* the premaxillae are narrower symphyseally than in their congeners (see comments under "Premaxilla," above). Associated with this proportionally reduced symphyseal contact of the contralateral premaxillae is a restructuring of the ventral portion of the anterior section of the mesethmoid into an anteroventrally oriented triangular process that again mostly separates the medial surfaces of the opposing premaxillae.

Among examined outgroup characids only *Gymnocharacinus bergi* was found to have a form of anterior process of the mesethmoid reminiscent of that in *Creagrutus cracentis, C. gephyrus,* and *C. maxillaris.* The form of the process in the examined *Gymnocharacinus* specimen (USNM 313878) is not as triangular as that illustrated by Miquelarena and Arámburu (1983, fig. 3), which more closely approximates the condition in the three *Creagrutus* species. Furthermore, the overall form of the mesethmoid in *Gymnocharacinus bergi* differs significantly from that in *Creagrutus. Gymnocharacinus bergi* also lacks both the series of distinguishing features of the *Creagrutus-Piabina* clade and the synapomorphies for the clades within *Creagrutus,* which include *C. cracentis, C. gephyrus,* and *C. maxillaris.* These factors in combination lead us to hypothesize that the condition of the anterior process of the mesethmoid in *Gymnocharacinus* is nonhomologous with that in *Creagrutus cracentis, C. gephyrus,* and *C. maxillaris.*

CHARACTER 35. State 0: Anterior portion of mesethmoid not as in 1. State 1: Anterior portion of mesethmoid expanded ventrally into a relatively large, transversely flattened, vertical plate.

The main body of the mesethmoid in numerous characids, including *Piabina* and *Creagrutus*, has a ventromedial lamellar process, which contacts the dorsal surface of main body of the vomer, or a matching lamellar process extending dorsally from the median portion of vomer. This ventral lamellar process on the mesethmoid arises from the ventral surface of a varyingly developed median chamber that extends anteriorly within the mesethmoid to differing degrees. Examined tetragonopterine outgroups, including *Piabina argentea,* along with the majority of *Creagrutus* species, either lack the median chamber within the mesethmoid or have a vertically broad medial lamellar process separating the contralateral nasal capsules. A subset of *Creagrutus* species (*C. amoenus, C. atratus, C. beni, C. bolivari, C. brevipinnis, C. britskii, C. changae, C. cochui, C.*

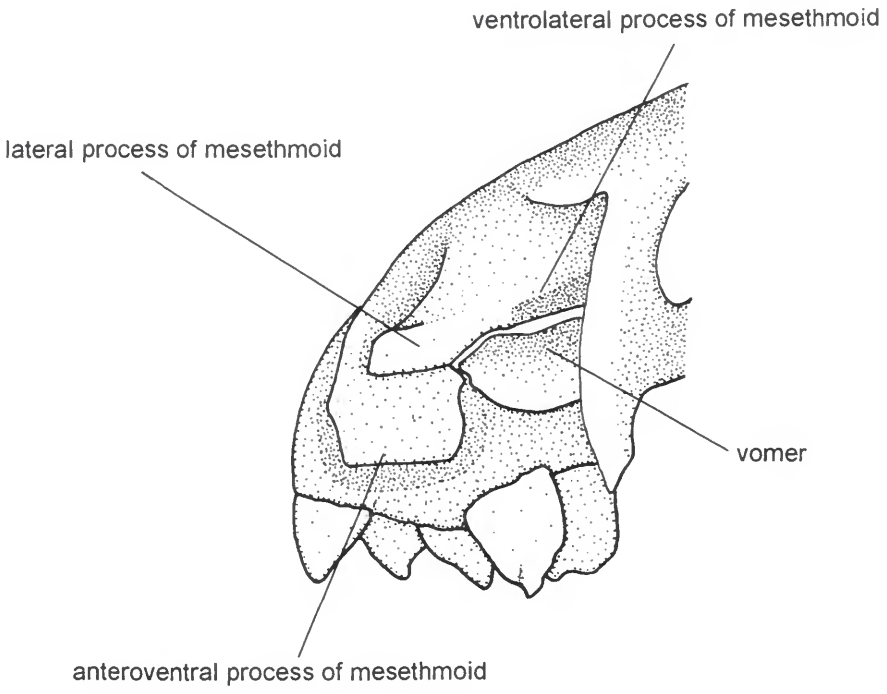

FIGURE 14.—Lateral view of anterior portion of mesethmoid in *Creagrutus amoenus,* USNM 311339, 65.0 mm SL; left premaxilla removed, right premaxilla in place, showing ventral expansion of anteroventral portion of mesethmoid; anterior to left.

ephippiatus, C. figueiredoi, C. gyrospilus, C. holmi, C. hysginus, C. kunturus, C. lepidus, C. machadoi, C. magdalenae, C. manu, C. melasma, C. menezesi, C. mucipu, C. occidaneus, C. ortegai, C. paraguayensis, C. paralacus, C. petilus, C. seductus, C. taphorni, C. ungulus, C. vexillapinnus) has the dorsal portion of the lamellar plate expanded laterally to varying degrees, with the expansion most pronounced posteriorly. The degree of expansion ranges from a limited lateral flaring along the posterior portion of the lamella to a pronounced expansion that extends as far anteriorly as the posterior margin of the lateral mesethmoid wing. Continuity across these different degrees of expansion renders the subdivision of this mesethmoid expansion into different characters impossible, and the expansion, regardless of degree, is considered to be a single derived condition.

CHARACTER 36. State 0: Mesethmoid without lateral expansion of dorsal portion of lamellar plate. State 1: Mesethmoid with lateral expansion of dorsal portion of lamellar plate.

FRONTAL.—The majority of characiforms have the frontals separated to varying degrees by the median fronto-parietal fontanel, with contact between the frontals sometimes limited to the transverse epiphyseal bar that divides the fontanel into anterior and posterior portions. A well-developed fontanel separating the frontals is present in a variety of characiforms, including the basal distichodontid characiform *Xenocharax* (Daget, 1960, fig.7) and including *Piabina argentea,* the proximate sister group to *Creagrutus.* In those taxa, the anterior portions of the frontals are only in contact through the epiphyseal bar. Seven *Creagrutus* species (*C. atrisignum, C. cochui, C. lepidus, C. maracaiboensis, C. muelleri, C. ouranonastes, C. pila*) have, instead, the anteromedial portions of the frontals in broad contact, which reduces the relative longitudinal extent of the anterior portion of the fontanel. In light of its generality within characiforms and its presence in *Piabina,* the more extensive fontanel is considered to be primitive, and the increased contact of the contralateral frontals in the seven cited *Creagrutus* species is considered to be derived.

CHARACTER 37. State 0: Anterior portions of frontals not in contact anterior to fontanel. State 1: Anterior portions of frontals in contact anterior to fontanel.

Contact of the frontals along their medial margins is most pronounced in *C. maracaiboensis* in which the fontanel extends only a short distance anterior to the epiphyseal bar, an autapomorphic modification. This species also has the posterior portion of the fontanel significantly expanded laterally, with the opposing medial margins of the frontals distinctly further separated than in any congener or in *Piabina argentea.* Although *C. maracaiboensis* is one of the most diminutive species in *Creagrutus* in terms of maximum known body size, this frontal separation is apparently not a consequence of its small

size. The separation of the frontals in *C. nigrostigmatus*, a second diminutive species, and juveniles of other *Creagrutus* species comparable in body size to adults of *C. maracaiboensis* lack an increased separation of the frontals lateral to the fontanel. Given its unique nature among *Creagrutus* species and its absence in outgroups, this modification is considered to be an autapomorphy for *C. maracaiboensis*.

The laterosensory canal in the sixth infraorbital (dermosphenotic) of characiforms typically communicates with the supraorbital canal by a large opening in the latter canal located in the region above the dilatator fossa. Two forms of this opening occur in *Creagrutus*. In the first, the opening is located at the junction between the anterior process of the pterotic and the posteroventral portion of the frontal. This condition is considered to be present if the pterotic in any way contributes to the margin of the opening (see Table 2 for listing of species with this condition). In the second condition, the opening into the supraorbital canal is entirely within the frontal, typically being well separated from the region of contact between the frontal and the pterotic along the supraorbital canal (see Table 2 for listing of species with this condition). Variability in this feature among tetragonopterine outgroups makes it impossible to polarize this feature.

CHARACTER 38. State 0: Opening in supraorbital canal for communication with laterosensory canal in sixth infraorbital at junction between anterior process of pterotic and posteroventral portion of frontal. State 1: Opening in supraorbital canal for communication with laterosensory canal in the sixth infraorbital entirely in frontal.

PARIETAL.—The parietal branch of the supratemporal laterosensory canal in characids usually extends from the frontal across the lateral surface of the parietal to terminate on the posterior portion of the parietal; this morphology also is present in *Piabina argentea*, the sister group to *Creagrutus*. All but two *Creagrutus* species share that generalized morphology of the canal, albeit with some variation in the location of the posterior terminus of the canal segment. In *C. maracaiboensis* and *C. nigrostigmatus* the parietal branch is either entirely lacking or is restricted to a very short segment immediately posterior to the junction of the frontal and parietal. *Creagrutus maracaiboensis* and *C. nigrostigmatus* are the smallest members of the genus as adults, and reduced adult body size often is correlated with a decrease in the development of the laterosensory canal system on the head and body (Weitzman and Vari, 1988:445). In *C. maracaiboensis* and *C. nigrostigmatus* the absence of the parietal canal is not apparently directly size-related because the canal is fully developed in juveniles of other *Creagrutus* species at sizes comparable to those of adults of *C. maracaiboensis* and *C. nigrostigmatus*.

CHARACTER 39. State 0: Parietal branch of supratemporal laterosensory canal extending from frontal to posterior portion of parietal. State 1: Parietal branch of supratemporal laterosensory canal either lacking or restricted to short segment immediately posterior to frontal-parietal junction.

Creagrutus maracaiboensis has the parietal portion of the fronto-parietal fontanel distinctly wider than in its congeners or *Piabina argentea*. This increased separation of the medial margins of the parietals is absent in examined outgroups and is considered to be autapomorphic for *C. maracaiboensis*. Although *C. maracaiboensis* is a diminutive among *Creagrutus* species in terms of maximum known body size, this increased separation of the parietals relative to the condition in its congeners is apparently not correlated with small size. Neither the second diminutive *Creagrutus* species, *C. nigrostigmatus*, nor smaller specimens of other *Creagrutus* species have a comparable increased separation of the medial margins of parietals lateral to the fronto-parietal fontanel at body sizes equivalent to those of adults of *C. maracaiboensis*.

DILATATOR GROOVE.—The dilatator groove is a variably developed fossa that extends from the sphenotic spine onto the skull roof and involves, to different degrees, contributions from the sphenotic, frontal, and pterotic in different groups of characiforms (see comments by Weitzman, 1964:139; Roberts, 1969:408). In *Creagrutus* the groove extends onto the lateral surface of the sphenotic and frontal. The extent of the groove is limited dorsally by the ventral margin of the raised posterior portion of the supraorbital canal in the frontal and by the pterotic canal in the pterotic. In *Piabina argentea* and approximately half of the species of *Creagrutus* the groove is not dorsally roofed by either the frontal or the pterotic. Approximately half of the species of *Creagrutus* have ventrolateral plate-like extensions from the lateral margin of the posterior section of the supraorbital canal in the frontal and from the anterior portion of the pterotic canal. These extensions varyingly roof over the dilatator groove dorsolaterally (see Table 2 for listing of species with this condition). The degree of development of these extensions is particularly pronounced in examined specimens of *C. atratus, C. ephippiatus, C. lassoi, C. paralacus, C. taphorni,* and *C. ungulus,* but it is not scored as a further derived condition because of the intraspecific ontogenetic variation in the expression of this feature and because of the range in size of examined specimens of the different species. A roofing over of the dilatator fossa was absent in both *Piabina* and other examined outgroup tetragonopterines, and its presence in a subset of *Creagrutus* species is considered to be derived.

CHARACTER 40. State 0: Dorsolateral portion of dilatator groove not roofed over by processes from frontal and pterotic. State 1: Dorsolateral portion of dilatator groove roofed to varying degrees by processes from frontal and pterotic.

TEMPORAL FORAMEN.—An opening, the temporal foramen (Weitzman, 1962:24), is present in diverse characids, including *Piabina argentea*. This aperture is situated along the junction of the sphenotic and pterotic in the area ventral to the pterotic portion of the laterosensory canal joint (Figure 15; see also Weitzman, 1962, fig. 3, for opening in *Brycon meeki*). This foramen is present in a subset of *Creagrutus* species, although it exhibits a notable range in relative size (see Table 2 for listing of species with this condition). The opening is lacking in all re-

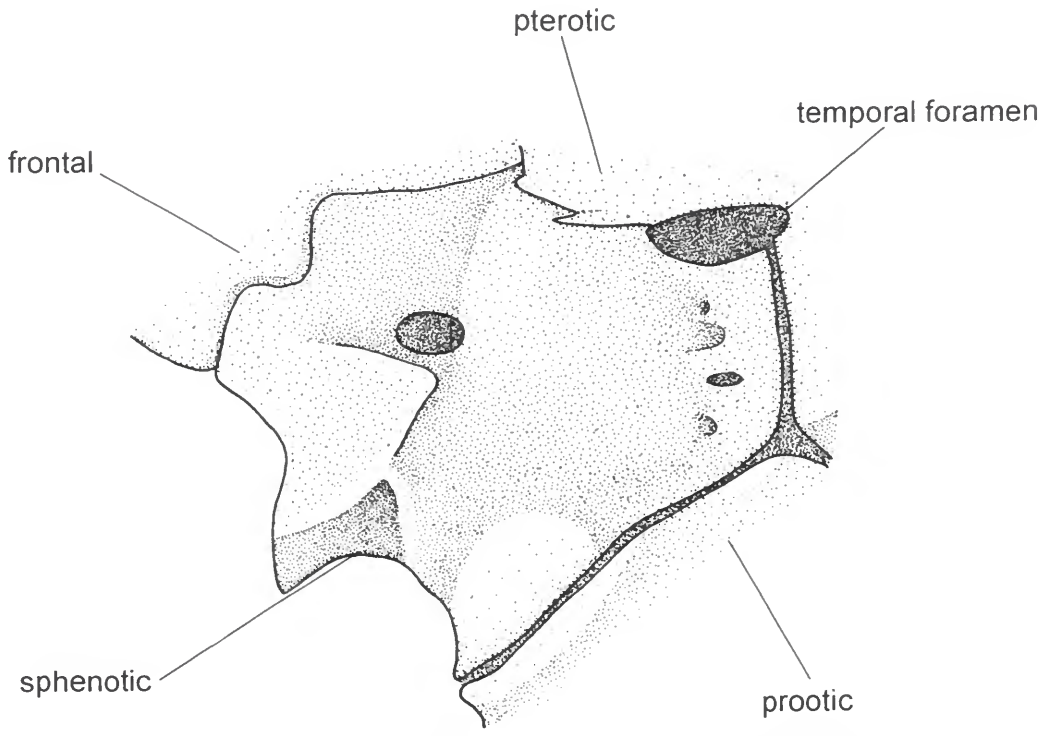

FIGURE 15.—Lateral view of sphenotic and adjoining bones in *Creagrutus hysginus*, USNM 326055, 41.3 mm SL; left side, lateral view, anterior to left.

maining species of *Creagrutus*, an apparently derived condition given the broad occurrence of the temporal foramen in *Piabina*, the sister group to *Creagrutus*, and among examined outgroup tetragonopterines.

CHARACTER 41. State 0: Temporal foramen present. State 1: Temporal foramen absent.

SPHENOTIC.—The ventral portion of the sphenotic that borders the prootic forms the anterior portion of the hyomandibular fossa, which is the region of articulation of the dorsal portion of the hyomandibula with the cranium. Along its dorsal articular margin the hyomandibula in *Piabina* and *Creagrutus* is typically expanded laterally, resulting in a broadened area of contact between that bone and the cranium (see discussion under "Hyomandibula," above). Matching this expanded portion of the hyomandibula is a laterally expanded articular surface on the ventral portion of the sphenotic, with the anterior portion of the hyomandibular fossa mostly formed by the sphenotic (Figure 15). This expansion of the sphenotic contribution to the hyomandibular fossa results from the lateral expansion of the sphenotic in the region dorsal of the anterior portion of the hyomandibula. Associated with this expansion of the sphenotic articular surface is a reorientation of the region of articulation to a more obtuse angle relative to the horizontal plane than occurs in examined characid outgroups. In addition, the plane of the articular surface on the sphenotic is rotated slightly outward. As a consequence, the anterior portion of the hyomandibular fossa on the sphenotic (and also the prootic) is visible in lateral view in both *Piabina* and *Creagrutus*. This contrasts with the typical characid condition in which the hyomandibular fossa is not readily visible in lateral view. The combination of these changes results in a form of the ventral portion of the sphenotic that is not found in examined outgroup characiforms; therefore, this form is judged to be derived.

CHARACTER 42. State 0: Hyomandibular fossa not as in 1. State 1: Hyomandibular fossa visible laterally as a consequence of reorientation of that portion of sphenotic.

In characiforms, the lateral surface of the sphenotic bears a strong sphenotic spine. The spine typically has a blade-like ventral portion that delimits the posterior margin of the orbit. This spine is most often unelaborated in characiforms, but in *Piabina argentea* and in *Creagrutus* species other than *C. melanzonus*, *C. pearsoni*, and *C. zephyrus* the distal portion of the lateral surface of this spine is variously elaborated posteriorly. These extensions of the spine serve for the attachment of aponeurotic tissue sheets associated with adjoining muscles, and the presence of such processes is considered to be derived.

CHARACTER 43. State 0: Sphenotic spine simple. State 1: Distal portion of lateral surface of sphenotic spine variously elaborated posteriorly.

Within the assemblage of species with such elaborated sphenotic spines there is considerable diversity in the degree of development of these processes, both infra- and intraspecifically, and ontogenetically. This variability renders it impossible to unambiguously define discrete characters within most of this variation. Discrete modifications of that process occur in *Creagrutus gyrospilus, C. hysginus,* and *C. paralacus,* which, in addition to having distinct posteriorly directed processes extending from the distolateral margin of the sphenotic spine, also have an anterior lamellar process along the lateral margin of the spine. This process contacts the anteroventral margin of the adjoining portion of the frontal, thereby enclosing a medial space. No such process has been encountered in examined outgroups, and its presence is considered to be derived.

CHARACTER 44. State 0: Anterior margin of sphenotic spine unelaborated. State 1: Anterior margin of sphenotic spine with anterior lamellar process.

In *Creagrutus gephyrus* the sphenotic spine is narrower basally than in congeners and is shifted posterodorsally compared with the typical condition in that genus and in outgroup characids. As a consequence, the base of the spine is distant from, rather than proximate to, the sphenotic component of the hyomandibular fossa. This shift also moves the spine well into the center of the basal portion of the dilatator grove, a condition not encountered elsewhere within *Creagrutus* or examined outgroup characids. The form of the sphenotic spine is hypothesized to be an autapomorphy for the species.

EPIOCCIPITAL.—The vast majority of characiforms are characterized by two pairs of posttemporal fossae situated at the posterolateral and dorsolateral margins of the posterior portion of the cranium (e.g., *Brycon meeki;* see Weitzman, 1962, figs. 3, 5). These two pairs of apertures are present in all *Creagrutus* species, but *C. atratus, C. atrisignum, C. bolivari, C. britskii, C. cochui, C. figueiredoi, C. gracilis, C. meridionalis,* and *C. paraguayensis* also have a third opening enclosed entirely within the epioccipital in the region medial to the tube for the posterior vertical semicircular canal.

Various New and Old World characiforms have a third posttemporal fossa bordered, at least in part, by the epioccipital. An extensive, vertically ovate third posttemporal fossa bordered by both the exoccipital and epioccipital occurs in the New World characid subfamily Cynodontinae (Vari, 1979:289; Toledo-Piza, 1997) and in the African sister families Citharinidae and Distichodontidae (Vari, 1979, fig. 15). Given the contribution of the exoccipital to the fossa in these three families, these apertures are judged to be nonhomologous with those in some species of *Creagrutus.* Phylogenetic information further indicates that neither the Cynodontinae (Lucena and Menezes, 1998, fig. 1; Toledo-Piza, 2000) nor Citharinidae and Distichodontidae (Buckup, 1998:134) are closely related to the Tetragonopterinae, including *Creagrutus.*

A third posttemporal fossa situated entirely within the epioccipital, such as occurs in the cited species of *Creagrutus,* is unknown elsewhere within the Characidae but is present in the Neotropical characiform families Curimatidae (Vari, 1983:37), Parodontidae (Roberts, 1974:425, fig. 59), and Hemiodontidae (Vari, 1979:416, fig. 5). The Curimatidae is most closely related to the Prochilodontidae (Vari, 1983:47–48; Vari, 1989:51–52), with that clade, in turn, most closely related to a clade formed by the Anostomidae plus Chilodontidae (Vari, 1983:50). Prochilodontids, anostomids, and chilodontids all lack a third posttemporal fossa within the epioccipital, so the epioccipital fossa in curimatids is most parsimoniously hypothesized to be homoplastic to that in some species of *Creagrutus.* Buckup (1993:229; 1998:134) proposed that the phylogenetic relationships of the Parodontidae and Hemiodontidae lie with groups other than the subset of characid genera he examined. That evidence and the absence in both *Piabina,* the sister group to *Creagrutus,* and in various outgroup characids of a posttemporal fossa limited to the epioccipital leads us to hypothesize that its presence in a various *Creagrutus* species is derived, albeit homoplastically present in some groups of noncharacid characiforms.

CHARACTER 45. State 0: Third posttemporal fossa within epioccipital absent. State 1: Third posttemporal fossa within epioccipital present.

VOMER.—The vomer in *Creagrutus* has a pair of openings for the passage of a nerve into the oral cavity. The orientation and relative size of this opening differ somewhat within the assemblage formed by these genera, but only in two species, *Creagrutus cracentis* and *C. maxillaris,* do these openings differ dramatically from the condition in their congeners. In these two species the openings are relatively significantly larger and are located distinctly more anteriorly than in *Piabina* and other *Creagrutus* species; these modifications consequently are hypothesized to be derived conditions.

CHARACTER 46. State 0: Not as in state 1. State 1: Openings in vomer for passage of nerve into oral cavity large and anteriorly located.

PECTORAL GIRDLE

MESOCORACOID.—The mesocoracoid in characiforms has a widened base that contacts the scapula and coracoid ventrally and extends slightly dorsolaterally to contact the medial surface of the cleithrum. The contact between the mesocoracoid and the medial surface of the cleithrum is varyingly reinforced by an expansion of the dorsal portion of the mesocoracoid into a broad plate, which is highly variable in form and is tightly joined to the medial surface of the cleithrum. In the basal characiform family Distichodontidae (*Xenocharax spilurus, Nannocharax intermedius, Paradistichodus dimidiatus*) the mesocoracoid is only slightly expanded dorsally. A greater expansion of the dorsal portion of mesocoracoid occurs in various characiforms, including diverse characids, often with a ventral extension of this portion of the ossification along the medial surface of the cleithrum.

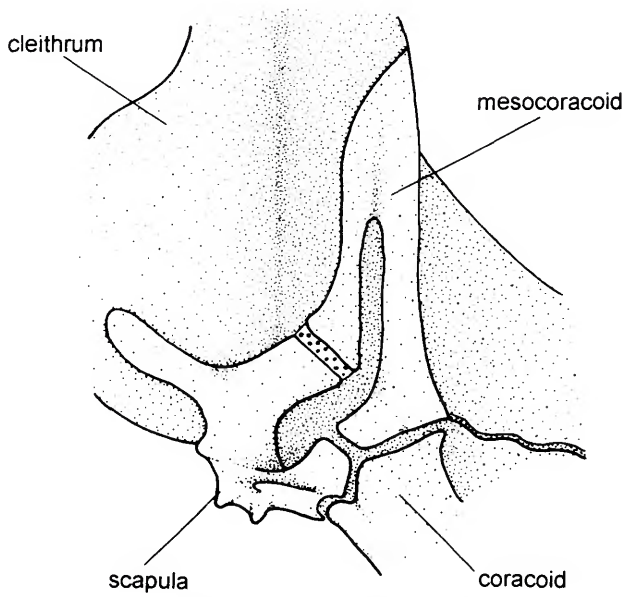

FIGURE 16.—Mesocoracoid, scapula, and adjoining bones in *Creagrutus lepidus*, USNM 325045, 40.3 mm SL; right side, medial view, anterior to right.

This ventral expansion of the mesocoracoid extends towards, but is nearly always separate from, the medial portion of the scapula among examined characids, including *Piabina*. In the species of *Creagrutus*, in contrast, the ventrolateral extension of the mesocoracoid is further developed and contacts the dorsolateral margin of the scapula through a small intervening cartilage (Figure 16). As a consequence, the scapula and mesocoracoid in *Creagrutus* delimit an anteroposteriorly aligned passage through the pectoral girdle and exclude the cleithrum from the border of that opening, contrary to the typical characiform condition. Given the lack of such scapula-mesocoracoid contact in outgroup characiforms the condition in *Creagrutus* is considered to be derived.

Among examined characiform outgroups, only the characid genera *Triportheus* and *Moojenichthys*, sister groups according to Castro and Vari (1990), have contact between the ventrolateral margin of the mesocoracoid and the dorsolateral portion of the scapula. *Moojenichthys* was hypothesized to be most closely related to the monotypic fossil genus *Lignobrycon* and was placed into the synonymy of the latter genus by Malabarba (1998:78). We hereafter refer to *Moojenichthys myersi* as *Lignobrycon myersi*, but we have not examined specimens of the fossil *L. ligniticus* and cannot evaluate the contact, or lack thereof, between the ventrolateral margin of the mesocoracoid and the dorsolateral portion of the scapula in that species. Contact between the ventrolateral margin of the mesocoracoid and the dorsolateral portion of the scapula in the *Lignobrycon-Triportheus* clade is, however, the result of different modifications from those in *Creagrutus*. As noted, contact between these bones in *Creagrutus* is a consequence of a ventral extension of the dorsomedial portion of the mesocoracoid to meet the dorsomedial margin of the scapula. In *Lignobrycon* and *Triportheus* the ventral extension of the dorsomedial portion of the mesocoracoid is absent. Rather, the entire scapula is tilted, bringing its dorsolateral margin into contact with the ventral margin of the mesocoracoid. This form of contact is nonhomologous with that between these bones in *Creagrutus*. The form of mesocoracoid-scapula contact in *Creagrutus* is consequently considered a synapomorphy for the species of that genus.

CHARACTER 47. State 0: Ventrolateral portion of mesocoracoid not contacting dorsolateral margin of scapula. State 1: Ventrolateral extension of mesocoracoid contacting dorsolateral margin of scapula through a small intervening cartilage.

SCAPULAR FORAMEN.—The scapular foramen in many characiforms, including *Xenocharax*, is an opening situated in the anterior portion of the scapula (e.g., *Brycon meeki*, Weitzman, 1962, fig. 20). Anteriorly the border of the scapular foramen is formed by a narrow bony ring that separates the foramen from a more anterior opening delimited by the scapula, cleithrum, and coracoid. Given the broad occurrence of this anterior ring of bone delimiting the anterior portion of the scapular foramen among characids, the possession of such a ring-like process is considered to be plesiomorphic within the assemblage consisting of *Piabina* and *Creagrutus*. The narrow anterior ring of bone forming the anterior portion of the scapular foramen is present in a number of *Creagrutus* species but is absent both in *Piabina argentea* and various *Creagrutus* species (see Table 2 for a listing of the species with each character). The absence of a narrow anterior scapular ring is hypothesized to be the derived condition.

CHARACTER 48. State 0: Scapula with narrow ring-like process forming anterior border of scapular foramen. State 1: Scapula lacking narrow ring-like process forming anterior border of scapular foramen.

CONTACT BETWEEN CORACOID AND CLEITHRUM.—The scapular foramen is separated by a narrow ring of bone from the more anteriorly positioned opening delimited by the scapula, coracoid, and cleithrum (Weitzman, 1962, fig. 5). This distinct anterior opening occurs in diverse examined characids and characiforms, including *Xenocharax*, a member of the basal distichodontid-citharinid clade within characiforms. In *Piabina* and *Creagrutus* the opening situated at the junction of the scapula, coracoid, and cleithrum is eliminated as a consequence of the expansion of the cleithrum and particularly the coracoid into the opening plesiomorphically present in that region. In the species of *Creagrutus* with a narrow anterior ring of the scapula forming the anterior portion of the scapular fossa, the portions of the cleithrum and coracoid immediately proximate to the ring contact and match the form of the anterior margin of the bony ring, consequently forming a concentric bony margin. When the narrow anterior bony ring of the scapula is lacking in *Piabina* and various *Creagrutus* species (see "Scapular Foramen," above) the expanded portions of the cleithrum and coracoid form the anterior margin of the rounded

scapular foramen, with the remainder of the border of the opening formed by the scapula. Such an expansion of the cleithrum and coracoid was not encountered elsewhere in examined characiforms and is considered to be derived.

CHARACTER 49. State 0: Opening delimited by the scapula, coracoid, and cleithrum present anterior to scapular foramen. State 1: Opening delimited by the scapula, coracoid, and cleithrum anterior to scapular foramen lacking.

FIRST POSTCLEITHRUM.—The presence of three postcleithra along the posterior margin of the pectoral girdle is typical for characiforms; however, these ossifications are lost in various combinations within the order. Postcleithrum 1, the dorsalmost of the series, is a variably shaped, flat, ossification located at the posteroventral margin of the supracleithrum and posterior of the cleithrum in *Piabina argentea* and most *Creagrutus* species. This ossification is, however, absent in eight *Creagrutus* species (*C. crenatus, C. hildebrandi, C. lepidus, C. maracaiboensis, C. melasma, C. peruanus, C. petilus, C. ungulus*).

All postcleithra are missing in the Gasteropelecidae (Weitzman, 1954:226), and the first postcleithrum is missing in the African distichodontid characiforms *Nannocharax* Günther and *Hemigrammocharax* Pellegrin (Vari, 1979:311) and in the Neotropical anostomid genera *Synaptolaemus* Myers and Fernández-Yépez and *Sartor* Myers and Carvalho (Winterbottom, 1980:46). The distichodontid and anostomid genera lacking postcleithrum 1 are deeply embedded within the phylogeny of groups otherwise characterized by the presence of that ossification (see Vari, 1979, and Winterbottom, 1980, respectively). Furthermore, available evidence (Vari, 1979; Buckup, 1998) indicates that the relationships of distichodontid and anostomid taxa lie with clades distant from that including *Creagrutus*. The relationships of the Gasteropelecinae within the Characiformes are still uncertain, although Orti and Myer (1997) found that molecular data aligned the subfamily with taxa other than those presently assigned to the Tetragonopterinae. The Gasteropelecinae also lacks the synapomorphies for the *Creagrutus*+*Piabina* clade and for *Creagrutus*. Thus, the absence of postcleithrum 1 in a subset of *Creagrutus* is hypothesized to be derived and homoplastic relative to the lack of this ossification in the cited outgroups.

CHARACTER 50. State 0: First postcleithrum present. State 1: First postcleithrum absent.

SQUAMATION

LATERAL LINE.—*Creagrutus maracaiboensis* is unique among the species of *Creagrutus* in having laterosensory canal pores limited to the anterior eight to 10 scales of the lateral line scale series. This reduction in the extent of lateral line poring contrasts with the completely pored lateral line series in all the remaining species in the clade, which is the typical condition within characiforms. This apomorphic reduction is, however, a common paedomorphic feature associated with miniaturization in various teleostean fishes (Myers, 1958:29; Weitzman and Vari, 1988:445). Paedomorphosis as an explanation for the truncated lateral line in *C. maracaiboensis* is compromised, at least to some degree, by the presence of a completely pored lateral line in *C. nigrostigmatus,* a species with a body size comparable to that in *C. maracaiboensis.*

Harold and Vari (1994:7) noted that two trans-Andean species, *Creagrutus nigrostigmatus* and *C. maracaiboensis,* have unusually low numbers of lateral line scales (30–32, and 29–31 lateral line scales, respectively) that compare with the 33 to 41 scales in their trans-Andean congeners. Those authors tentatively proposed that this low lateral line scale count might represent a synapomorphy for that species pair, but they refrained from a definitive statement pending a thorough examination of that feature in the cis-Andean *Creagrutus* species. Analysis has shown that cis-Andean *Creagrutus* species have 34 to 45 lateral line scales. This range does not overlap that of *C. nigrostigmatus* and *C. maracaiboensis.* Given the higher number of lateral line scales in *Piabina argentea* and in other outgroup taxa, we hypothesize that the lower number of lateral line scales in *C. nigrostigmatus* and *C. maracaiboensis* is derived.

CHARACTER 51. State 0: Possession of 33 or more lateral line scales. State 1: Possession of 29 to 32 lateral line scales.

LATERAL LINE SCALE FORM.—The scales of the lateral line in *Creagrutus caucanus* have a form of the aperture into the sensory pore that is unique in *Creagrutus* and, indeed, that has not been encountered elsewhere among characiforms. In *C. caucanus* there is a lateral lamellar process overlying the sensory pore. This shelf-like process is formed by an abrupt posterior expansion of the posterior ostium on the lateral line canal in each scale (see Harold and Vari, 1994, fig. 3), an autapomorphy for the species.

POST-ANAL SCALES.—The position of the anus relative to the anal-fin origin demonstrates a degree of variation within *Creagrutus.* The vast majority of species within *Creagrutus* have two median scales between the posterior margin of the anus and the point where the anteriormost anal-fin ray exits from the body. This condition also is found in *Piabina* and many other tetragonopterines and is consequently hypothesized to be primitive. *Creagrutus amoenus* and *C. kunturus* have, instead, only one median scale in the region, whereas three species have a higher number of post-anal median scales, which is a derived condition. Four post-anal scales occur in *C. ungulus* and five scales are found along the post-anal midline in *C. cracentis* and *C. maxillaris.* Proximity of the anus and anterior anal-fin rays is typical in characid outgroups, and the increased separation between these structures in these three species is hypothesized to be derived, although the overall most parsimonious hypothesis of intrageneric relationships indicates that the increased number of post-anal scales in *C. cracentis* and *C. maxillaris* was arrived at independently of that in *C. ungulus.*

CHARACTER 52. State 0: Post-anal scales 1 or 2. State 1: Post-anal scales 4 or 5.

PIGMENTATION

Creagrutus species differ in a number of details of pigmentation. Much of this variation, most notably that involving the humeral mark, presents problems both in definition and polarization. Some components of body and fin pigmentation are, however, discrete and phylogenetically informative.

DORSAL-FIN PIGMENTATION.— Although various *Creagrutus* species have some dark pigmentation on the dorsal fin, only *C. vexillapinnus* has a discrete patch of dark pigmentation overlying the central portions of the fin rays. In light of the lack of such pigmentation in its congeners and *Piabina,* such pigmentation is considered to be autapomorphic for *C. vexillapinnus.*

CAUDAL-FIN PIGMENTATION.—The caudal fin among *Creagrutus* species bears varying areas of dark pigmentation. *Creagrutus ouranonastes* is unique within the genus in having the dark caudal-fin pigmentation concentrated into two small, very dark spots bordering the middle ray of the caudal fin. This feature is hypothesized to be an autapomorphy of the species because of its absence in congeners and *Piabina,* the first outgroup to *Creagrutus.*

HUMERAL MARK FORM.—The humeral mark is highly variable within *Creagrutus,* with most members of the genus having a rotund mark or having the mark developed vertically to varying degrees. The intrageneric continuity within the humeral variation renders it impossible to nonarbitrarily discriminate character states, and only the most discrete conditions are incorporated into the phylogenetic analysis. The vertically elongate humeral spot is common to *Piabina,* the majority of *Creagrutus* species, and many outgroup tetragonopterines; therefore, that condition is assumed to be plesiomorphic within *Creagrutus.*

Creagrutus atrisignum and *C. cochui* have horizontally elongate main bodies of the humeral marks. This form is hypothesized to be derived compared with the rotund or vertically elongate form of the mark in most congeners and the immediate outgroup *Piabina.*

CHARACTER 53. State 0: Humeral mark rotund or vertically elongate. State 1: Humeral mark horizontally elongate.

Associated with the horizontal elongation of the main body of the humeral spot in *C. atrisignum* is the presence of a secondary patch of dark pigmentation situated dorsal of the main body of the humeral mark. The degree of development of the dorsal spot varies intraspecifically. In some specimens of *C. atrisignum* there is a vertical component of the dorsal spot that extends ventrally to approach or contact the main body of the humeral spot. The presence of such a secondary component of the humeral mark is unique and is considered to be autapomorphic for *C. atrisignum.*

MIDLATERAL BODY PIGMENTATION.—Among *Creagrutus* species, only *C. mucipu* of the Rio Tocantins basin has midlateral body pigmentation consisting of a series of posteriorly convex, dark, midlateral chevron-shaped spots. Such pigmentation is rare in characiforms. This pattern is hypothesized to be an autapomorphy for *C. mucipu.*

Although many *Creagrutus* species have a stripe of dark pigmentation extending to differing degrees anteriorly from the base of the caudal fin, in only three species does the stripe extend, in at least some individuals, the entire length of the body. Such a midlateral band of dark pigmentation is, however, achieved by two different methods within the genus.

Creagrutus lepidus has a broad, continuous band of dark pigmentation extending between the supracleithrum and the base of the middle caudal-fin rays. The stripe, which apparently subsumes the humeral mark, is well developed in all examined specimens, including those as small as 32.7 mm SL. As noted by Vari et al. (1993:352), this form of midlateral stripe is unique to *C. lepidus* within *Creagrutus.*

The second form of well-developed, dark, midlateral pigmentation occurs in *Creagrutus amoenus* and *C. kunturus.* Although larger individuals of both species have midlateral stripes that are somewhat reminiscent of, albeit not as continuous as, the stripe in *C. lepidus,* such pigmentation patterns are not general for either species. Smaller specimens of *C. amoenus* and *C. kunturus,* which are comparable in size to the known size range of *C. lepidus,* have patterns of dark spots arranged along the midlateral surface of the body. There is a general, although by no means universal, ontogenetic trend of spot coalescence in both *C. amoenus* and *C. kunturus.* In some larger specimens, often those from acidic dark waters, the degree of coalescence is such that a nearly solid midlateral stripe results. Although the midlateral stripe in these species differs from, and thus is considered to be nonhomologous with that in *C. lepidus,* the pattern of a series of dark midlateral spots on the body in *C. amoenus* and *C. kunturus* is unique among *Creagrutus* species, is lacking in *Piabina,* and is atypical among characids and is thus considered to be derived.

CHARACTER 54. State 0: Midlateral body pigmentation not as in State 1. State 1: Midlateral body pigmentation consisting of series of dark spots that progressively coalesce ontogenetically, sometimes forming midlateral stripe in adults.

MISCELLANEOUS

EPURALS.—The number of epurals varies among *Creagrutus* species, although most species have either one or two elements (see Table 2 for listing of species with each count). Rare individual variants of *C. gyrospilus* have three epurals, otherwise the species has two epurals. Available evidence does not permit us to polarize this character in the absence of a definitive secondary outgroup.

CHARACTER 55. State 0: 1 epural present. State 1: 2 or 3 epurals present.

VERTEBRAE.—In their treatment of the Trans-Andean *Creagrutus* species Harold and Vari (1994:7) noted that two species, *C. nigrostigmatus* and *C. maracaiboensis,* had unusually low numbers of vertebrae (32 or 33 in each species), which contrasts with the 34 or more vertebrae in their trans-Andean congeners. Harold and Vari (1994) tentatively proposed that this

low vertebral number might be a synapomorphy for the species pair, but they refrained from a definitive hypothesis pending a thorough examination of the much more speciose cis-Andean assemblage of *Creagrutus* species. Analysis has shown that the cis-Andean species of *Creagrutus* have 34 to 43 vertebrae, which does not overlap that for *C. nigrostigmatus* and *C. maracaiboensis.* Given the high number of vertebrae in cis-Andean *Creagrutus,* in *Piabina argentea* (the immediate outgroup to *Creagrutus*), and in other outgroup taxa, we hypothesize that the lower vertebral numbers in *C. nigrostigmatus* and *C. maracaiboensis* are derived.

CHARACTER 56. State 0: Possession of 34 or more vertebrae. State 1: Possession of 32 or 33 vertebrae.

NOTOCHORDAL MINERALIZATIONS.—The notochord in characiforms, including the species of *Piabina* and *Creagrutus,* extends posterodorsally past the uroneurals (only one pair present in these two genera) for a moderate distance beyond the hypural fan. The distal portion of the notochord is bordered dorsally, distally, and ventrally by the opisthural cartilage. Uniquely among the species of *Creagrutus,* three species, *C. atratus, C. bolivari,* and *C. magoi,* have one or more dense, mineralized bodies embedded within the laterally visible distal portion of the notochord. These structures, which have a granular appearance, irregular margins, and stain deeply with alizarin red, evidently are comparable to the structures that Arratia and Schultze (1992, figs. 13, 21) identified as being a "mineralization of the notochord not forming a chordacentrum." Such mineralizations of the notochord are absent in *Piabina argentea* and in other examined outgroup characiforms, and their presence is thus considered to be derived within *Creagrutus.*

CHARACTER 57. State 0: Notochordal mineralizations absent. State 1: Notochordal mineralizations present.

Phylogenetic Reconstruction

The strict consensus tree for the 61 species included in the analysis (*Piabina argentea* and 60 species of *Creagrutus*) was based on 1531 trees and had a consistency index (CI) of 0.40 and a resolution index (RI) of 0.66. As might be expected given the relatively low CI, the degree of resolution of the tree was relatively poor. The resolution does, however, permit us to address the question of the diagnosable genera within this assemblage. The strict consensus tree is presented in Figure 17. Character numbers in the listing of synapomorphies for the various clades match those in the "Character Description and Analysis," above, and letters on Figure 17 indicate clades discussed in the text.

MONOPHYLY OF THE *Creagrutus* AND *Piabina* CLADE (Figure 17, Clade A).—Some evidence pertinent to the hypothesis of the monophyly of the clade formed by *Creagrutus* and *Piabina* was previously discussed by Vari and Harold (1998). The following list summarizes that information and the additional synapomorphies discovered during this study.

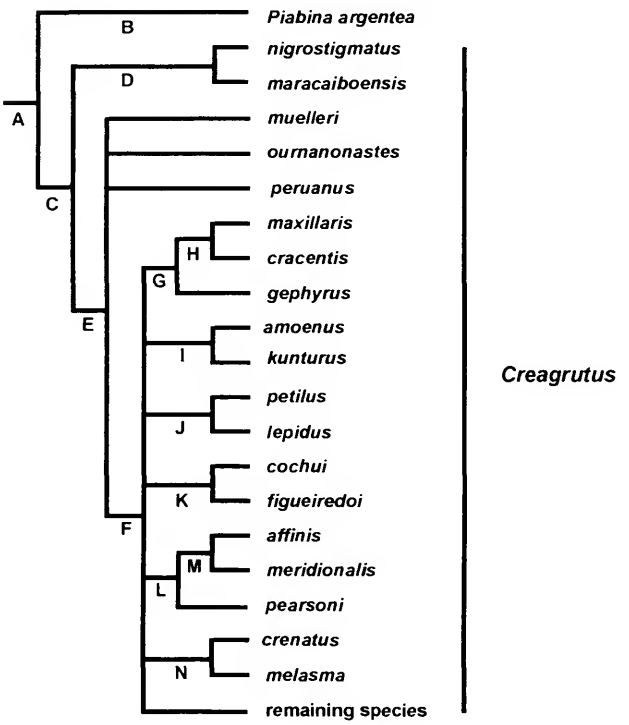

FIGURE 17.—Consensus tree of relationships of the genera *Piabina* and *Creagrutus* and within *Creagrutus.* "Remaining species" represents an unresolved multitomy of 41 *Creagrutus* species not cited in the cladogram. Letters represent nodes of clades discussed in the text.

1. Dentigerous surface of premaxilla triangular from ventral view (character 1). Reversed in clade consisting of *Creagrutus cracentis, C. gephyrus,* and *C. maxillaris;* see synapomorphy 44.
2. Ligament between posteroventral corner of premaxilla and anterior surface of maxilla well developed (character 10).
3. Anterior terminus of dentary dentition distinctly posterior of anterior terminus of premaxillary dentition (character 13). Reversed in clade consisting of *Creagrutus cracentis* and *C. maxillaris;* see synapomorphy 46.
4. Ectopterygoid and quadrate not in contact (character 21). Reversed in *Creagrutus mucipu.*
5. Dorsal articular surface of hyomandibula asymmetrical; hyomandibula with dorsolateral buttress (character 27). Reversed in clade consisting of *Creagrutus cracentis, C. gephyrus,* and *C. maxillaris;* see synapomorphy 51.
6. Anterior portion of mesethmoid expanded ventrally into a relatively large, transversely flattened, vertical plate (character 35). Reversed in clade consisting of *Creagrutus cracentis, C. gephyrus,* and *C. maxillaris;* see synapomorphy 52.

7. Hyomandibular fossa visible laterally as a consequence of the reorientation of that portion of the sphenotic (character 42).
8. Distal portion of the lateral surface of the sphenotic spine variously elaborated posteriorly (character 43). Reversed independently in each of *Creagrutus melanzonus, C. pearsoni,* and *C. zephyrus.*
9. Opening delimited by the scapula, coracoid, and cleithrum anterior to scapular foramen lacking (character 49).
10. Two or 3 epurals present (character 55). Independently reversed to 1 epural in *C. bolivari, C. lassoi, C. machadoi, C. maxillaris, C. melanzonus, C. phasma, C. zephyrus,* and clade formed by *C. lepidus* and *C. petilus;* see synapomorphy 63.

The following are ambiguously optimized for this clade:

11. Anterior portion of the laterosensory canal segment in first infraorbital reaching or extending beyond anterior margin of bone (character 29). Either derived at this level and secondarily lost in *Piabina* or a synapomorphy for the members of *Creagrutus.*
12. Posterior portion of the first infraorbital overlapping the anterior portion of the second infraorbital (character 30). Either derived at this level and secondarily lost in *Piabina* and in three species of *Creagrutus* or a synapomorphy for the members of the latter genus with secondarily loss in those same three species.
13. Opening in supraorbital canal for communication with laterosensory canal in the sixth infraorbital entirely in frontal (character 38). Either derived at this level with secondarily loss in *C. affinis* and *C. meridionalis* and secondarily lost in *Piabina,* or a synapomorphy for the species of *Creagrutus* with secondarily loss in *C. affinis* and *C. meridionalis.*

MONOPHYLY OF *Piabina* (Figure 17, Clade B).—Two derived features were found to diagnose *Piabina,* one of which (synapomorphy 14) is unique to the genus in the *Creagrutus-Piabina* clade and rare among characiforms. The ambiguously optimized characters for *Creagrutus+Piabina* (11–13) also could involve secondarily derived losses for *Piabina.*

14. Fourth infraorbital approximately triangular and excluded from posterior margin of infraorbital series in medium- to large-sized individuals (character 31).
15. Scapula lacking the narrow ring-like process forming the anterior border of the scapular foramen (character 48).

MONOPHYLY OF *Creagrutus* (Figure 17, Clade C).—The following includes both the synapomorphies for the species of *Creagrutus* proposed by Vari and Harold (1998) and additional synapomorphies discovered during this study.

16. Maxilla with anterior process thick and posterior portion robust (character 5). Reversed in clade formed by *C. cracentis* and *C. maxillaris;* see synapomorphy 56.
17. Maxilla with distinct flexion in region where it extends past the posterior limit of the premaxilla (character 6).
18. Primordial ligament variably rotund in cross section and attaching primarily to distal one-half of maxilla (character 8). Further developed in clade consisting of *C. amoenus* and *C. kunturus;* see synapomorphy 41.
19. Distinct ligament extending between the anterodorsal tip of the maxilla and the dorsal surface of the premaxilla (character 11).
20. Ligament extending between midventral portion of ascending process of maxilla and dorsal surface of premaxilla present (character 12).
21. Anguloarticular horizontally foreshortened (character 19).
22. Mesopterygoid and metapterygoid separate (character 22). Reversed in *C. gephyrus.*
23. Quadrate with variably developed vertical ridge or process extending dorsally from the main body of the quadrate in, and posterior to, the region where the posterodorsal process of the quadrate contacts the anteroventral process of the metapterygoid (character 25). Reversed in *C. lepidus.*
24. Anterior margin of hyomandibula anteriorly expanded and extending over posterodorsal region of metapterygoid (character 26).
25. Temporal foramen absent (character 41). Reversed in clade consisting of *C. cracentis, C. gephyrus,* and *C. maxillaris* (synapomorphy 54), clade formed by *C. lepidus* and *C. petilus* (synapomorphy 60), clade consisting of *C. cochui* and *C. figueiredoi* (synapomorphy 64), and independently in some other *Creagrutus* species.
26. Ventrolateral extension of mesocoracoid contacting the dorsolateral margin of the scapula through a small intervening cartilage (character 47).

The following characters are equivocally optimized at this level.

27. Anterior portion of the laterosensory canal segment in first infraorbital reaching or extending beyond anterior margin of bone (character 29). Either derived at this level or at level of *Creagrutus* plus *Piabina.*
28. Posterior portion of the first infraorbital overlapping the anterior portion of the second infraorbital (character 30). Either derived at this level and secondarily lost in some *Creagrutus* or gained at level of *Creagrutus* plus *Piabina* with secondary losses.
29. Scapula lacking narrow ring-like process forming anterior border of scapular foramen (character 48). Also equivocal at level of *Creagrutus* plus *Piabina* with secondarily losses in *Creagrutus.*

INTRAGENERIC RELATIONSHIPS WITHIN *Creagrutus.*—Two basal clades within *Creagrutus* are defined by the characters examined in this study. One consists of *C. maracaiboensis* and *C. nigrostigmatus* (Figure 17, Clade D) and the other clade includes all of the remaining species in the genus (Figure 17,

Clade E). Synapomorphies for *C. maracaiboensis* and *C. nigrostigmatus* (Clade D) are as follows:

30. Metapterygoid foramen open posteriorly (character 23). Feature independently present in *C. zephyrus.*
31. Parietal branch of supratemporal laterosensory canal either lacking or restricted to short segment immediately posterior to frontal-parietal junction (character 39).
32. Scapula lacking narrow ring-like process forming anterior border of scapular foramen (character 48). Independently achieved elsewhere in *Creagrutus* (synapomorphies 58, 61, 68).
33. Possession of 29 to 32 lateral line scales (character 51).
34. Possession of 32 or 33 vertebrae (character 56).

The clade consisting of all other *Creagrutus* species (Clade E) is defined by the following synapomorphies:

35. Dentigerous portion of fifth ceratobranchial smaller and rotund, meeting main shaft of ossification approximately at distinctly acute angle (character 33).
36. Dorsolateral portion of dilatator groove roofed to varying degrees by processes from frontal and pterotic (character 40). Reversed in various species within the clade.

Synapomorphies 35 and 36 define a clade that consists of a multitomy between *C. muelleri, C. ouranonastes,* and *C. peruanus* and a clade (Figure 17, Clade F) that includes the majority of the species of *Creagrutus.* Clade F is defined by the following synapomorphies.

37. Primary tooth row on premaxilla without distinctly larger gap between first and second teeth (character 2). Reversed independently in *C. melanzonus* and *C. runa.* Condition uncertain in *C. cracentis* and *C. maxillaris.*
38. Anterior tooth of premaxillary tooth triad positioned distinctly posterior of first and second teeth of primary series (character 3). Reversed independently in *C. melanzonus* and *C. runa.* Condition uncertain in *C. cracentis* and *C. maxillaris.*
39. Primordial ligament ventrally bifurcating, with attachments ventrally to both the lateral surface of the anguloarticular and lateral margins of the shelf-like lateral process of the quadrate (character 9).
40. Mesethmoid with lateral expansion of dorsal portion of lamellar plate (character 36). Reversed in various species.

The clade defined by characters 37 to 40, which includes the majority of *Creagrutus* species, is poorly resolved internally. Four clades of two species and three clades of three species form a multitomy with the remaining 41 species of *Creagrutus* that are indicated as "Remaining species" in Figure 17. The first of these clades, consisting of *C. cracentis, C. gephyrus,* and *C. maxillaris,* is defined by 11 characters, five of which are uniquely derived. The sister-species pair *C. cracentis* and *C. maxillaris* share five synapomorphies, two of which are unique to that clade. The second clade formed by *C. amoenus* and *C. kunturus* is defined by three synapomorphies, two of which are unique to this lineage. Both of these clades consistently appeared in various analyses, both those involving all the characters and those with the subtraction of various characters with high levels of homoplasy. The remaining four clades are defined by one to four optimized synapomorphies involving both homoplasies and reversals and often are not present when various characters with high levels of homoplasy are excluded from the analysis. The clades and their defining characters are given below.

The first of the clades in this assemblage (Figure 17, Clade G) consists of three species, *C. cracentis, C. gephyrus,* and *C. maxillaris,* that share the following synapomorphies, all of which are either unique to this lineage or are uniquely reversed within *Creagrutus:*

41. Dentigerous surface of premaxilla longitudinally elongate from ventral view (character 1). Reversal of synapomorphy 1.
42. Maxilla with 7 to 12 teeth (character 7).
43. Anterior terminus of dentary dentition not distinctly posterior of anterior terminus of premaxillary dentition (character 13). Reversal of synapomorphy 3.
44. Dentary foramen aligned directly transversely, with horizontally elongate lateral opening (character 14).
45. Medial opening of midlateral dentary foramen located immediately anterior to tip of meckelian cartilage (character 15).
46. Dentary teeth 10 to 12 (character 17).
47. Anterior dentary teeth with 5 cusps (character 18).
48. Dorsal articular surface of hyomandibular nearly symmetrical; hyomandibula without dorsolateral buttress (character 27). Reversal of synapomorphy 5.
49. Anterior portion of mesethmoid not expanded ventrally into a relatively large, transversely flattened, vertical plate (character 35). Reversal of synapomorphy 6.
50. Mesethmoid without lateral expansion of dorsal portion of lamellar plate (character 36).
51. Temporal foramen present (character 41). Reversal of synapomorphy 25.

Within the clade formed by these three species, the subclade (Clade H) consisting of *C. cracentis* and *C. maxillaris* is defined by the following synapomorphies:

52. Single tooth lateral to primary premaxillary tooth row absent (character 4). Independently lost within *Creagrutus* in *C. molinus.*
53. Maxilla with anterior process relatively slender and posterior portion transversely compressed (character 5). Reversal of synapomorphy 16.
54. Margin of posterodorsal portion of anguloarticular distinctly anterodorsally angled (character 20).
55. Openings in vomer for passage of nerve into oral cavity large and anteriorly located (character 46).

56. Post-anal scales 4 or 5 (character 52). Independently present in *Creagrutus* in *C. ungulus*.

The clade consisting of *Creagrutus amoenus* and *C. kunturus* (Clade I) is defined by the following synapomorphies, two of which are unique to these species in the genus:

57. Primordial ligament distinctly rotund in cross section and extending ventrally nearly to distal tip of maxilla (character 8). Further development of synapomorphy 18.
58. Scapula lacking narrow ring-like process forming anterior border of scapular foramen (character 48). Feature independently acquired elsewhere in *Creagrutus* (synapomorphies 32, 61, 68).
59. Midlateral body pigmentation consisting of a series of dark spots that progressively coalesce ontogenetically, sometimes forming a midlateral stripe in adults (character 54).

The *Creagrutus lepidus* and *C. petilus* clade (Clade J) is defined by the following synapomorphies, none of which are unique to this group:

60. Temporal foramen present (character 41). Reversal of synapomorphy 25.
61. Scapula lacking narrow ring-like process forming anterior border of scapular foramen (character 48). Process independently lost elsewhere in *Creagrutus* (synapomorphies 32, 58, 68).
62. First postcleithrum absent (character 50). Also lost independently in some other *Creagrutus* species.
63. 1 epural present (character 55). Reversal of synapomorphy 10.

The clade formed by *C. cochui* and *C. figueiredoi* (Clade K) is defined by two features, neither of which is unique to these species in *Creagrutus:*

64. Temporal foramen present (character 41). Reversal of synapomorphy 25.
65. Third posttemporal fossa within epioccipital present (character 45). Also in other *Creagrutus* species.

The clade formed by *C. affinis, C. meridionalis,* and *C. pearsoni* (Clade L) is defined by the following two synapomorphies, neither of which is unique to this group of species within *Creagrutus.*

66. Opening in supraorbital canal for communication with laterosensory canal in sixth infraorbital at junction between anterior process of pterotic and posteroventral portion of frontal (character 38). Reversal of synapomorphy 13.
67. Dentition on third infrapharyngobranchial present (character 34). Also present independently in other *Creagrutus* species.

Within this clade, *C. affinis* is hypothesized to be sister species of *C. meridionalis* (Clade M) based on the following equivocal synapomorphy:

68. Scapula lacking narrow ring-like process forming anterior border of scapular foramen (character 48). Independently gained elsewhere in *Creagrutus* (synapomorphies 32, 58, 61).

The final clade consisting of *C. crenatus* and *C. melasma* (Clade N) is defined by one synapomorphy:

69. First postcleithrum absent (character 50). Also lost independently in some other *Creagrutus* species.

As noted above, the lineage indicated as "remaining species" on Figure 17 consists of 41 species of unresolved relationships within the consensus tree.

PHYLOGENETIC POSITION OF *Creagrutus molinus, C. planquettei, C. veruina,* AND *C. xiphos.*—Among the numerous previously undescribed species discovered during the course of this study was one very distinctive form from the Rio Tocantins basin, *Creagrutus molinus,* known only from a single specimen herein designated as the holotype for the species. *Creagrutus veruina* and *C. xiphos,* although known from a larger number of specimens, are not represented by a sufficiently large sample size or by specimens in appropriate condition to permit the preparation of cleared and counterstained specimens. *Creagrutus planquettei* was described by Géry and Renno (1989) on the basis of a limited type series, and we have been unsuccessful in locating other specimens of the species. In the absence of additional specimens of these four species that we can clear and counterstain for cartilage and bone, our phylogenetic analysis is limited to the externally obvious features of *C. molinus, C. planquettei, C. veruina,* and *C. xiphos.*

Creagrutus mucipu, C. planquettei, C. veruina, and *C. xiphos* share several externally obvious features diagnostic of the clade consisting of *Piabina* and *Creagrutus* or subunits of *Creagrutus.* In each species, the lower jaw is foreshortened, which is a derived feature diagnostic for the clade consisting of *Piabina* and *Creagrutus* (see discussion under "Dentary," above). Similarly, these four species apparently have the derived broadened form of the premaxilla in ventral view, which is common to *Creagrutus* and *Piabina.* Furthermore, all four species share the arrangement of the primary premaxillary tooth series and the triangular cluster of large teeth lying medial to it, which are characteristic of both *Piabina* and the majority of *Creagrutus* species (see description under "Premaxillary Teeth," above, and see Géry and Renno, 1989, fig. 3, showing arrangement of the premaxillary teeth in *C. planquettei*).

The arrangement of the premaxillary dentition in these four species is further informative at less inclusive phylogenetic levels. All four of these species have the triangular cluster of teeth situated entirely posterior of the primary row of premaxillary teeth, with the anterior teeth of the triangular cluster not entering into a gap in the arch of the primary series (see Géry

and Renno, 1989, fig. 3, for *C. planquettei*). This arrangement of these components of the premaxillary dentition is hypothesized to be derived features (synapomorphies 37, 38) delimiting a subunit within *Creagrutus*.

In summary, *Creagrutus mucipu, C. planquettei, C. veruina,* and *C. xiphos* share three of the synapomorphies for the clade consisting of *Creagrutus* and *Piabina* and share one derived character defining a subunit of *Creagrutus*, but they lack the defining features for *Piabina*. We consequently assign these four species to *Creagrutus*, although we are presently unable to resolve their phylogenetic position within that genus.

COMMENTS ON *Piabarchus* Myers.—Eigenmann (in Eigenmann et al., 1914:8–9) described *Piabina analis* from a single specimen collected at "Caceres" (=São Luiz de Caceves in the upper Río Paraguay basin; Eigenmann and Myers, 1929:432). Eigenmann's brief original description of *Piabina analis* provided scant insight as to the basis for this generic assignment other than describing the species as having a "mouth as in *Creagrutus*, anal [fin] long" and noting that the "scales [are] as in *argenteus*" (=*Piabina argentea*, the type species of *Piabina;* bracketed insertions ours). Myers (1928:90), in a brief discussion, pointed out that *P. analis* "differs from all known species of *Piabina* in the long, anteriorly inserted, anal fin" and commented on the similarity of *P. analis* to "certain *Bryconamericus* species." Myers also noted that *Piabina* had in common with *Creagrutus* "massive dentition," presumably implying that the feature was absent in *Piabina analis*, and he proposed a new genus, *Piabarchus*, for that species. Eigenmann and Myers (1929:432) commented that "*Piabarchus* is certainly more entitled to recognition as distinct from *Piabina* than *Piabina* is from *Creagrutus*" but did not delve further into the question of relationships. Most recently Mahnert and Géry (1988:1) described a second *Piabarchus* species (*P. torrenticola*) and reconsidered the question of the relationships of the genus but were unable to resolve that issue.

Our examination of a series of specimens of *Piabarchus analis* (USNM 326384) and *P. torrenticola* (USNM 326536) revealed that both species lack the derived features for the *Creagrutus-Piabina* lineage. Most notably, neither species has the massive dentition arranged in three series on the premaxilla, the form of dentition common to both *Creagrutus* and *Piabina*, but instead have the premaxillary teeth arranged in the pattern typical of many characids (see Mahnert and Géry, 1988, pl. 1: figs. 4–6, pl. 2: fig. 11, for illustrations of premaxillary dentition in *Piabarchus analis* and *P. torrenticola*, respectively). *Piabarchus* species similarly lack the distinctly foreshortened dentary of *Piabina* and *Creagrutus*. Although the dentary teeth of the two *Piabarchus* are somewhat enlarged anteriorly, such as occurs in various characids, they are not proportionally as massive as are those in *Piabina* and *Creagrutus* (compare Figure 9 herein with illustrations of lower jaw in Mahnert and Géry, 1988, pls. 1, 2). Neither does either of the species of *Piabarchus* possess the other derived features characteristic of the *Piabina-Creagrutus* assemblage. Finally, the species of *Piabarchus* also have a fourth infraorbital that broadly contributes to the posterior margin of the infraorbital ring. This is the plesiomorphic characiform condition, which contrasts with the condition in *Piabina* in which the posteriorly tapering fourth infraorbital is excluded from the posterior margin of the infraorbital series, an autapomorphy for the genus *Piabina*.

Mahnert and Géry (1988:1) were unable to advance a definitive statement on the phylogenetic relationships of *Piabarchus*, noting that its "affinities with the genus *Bryconamericus*...are difficult to determine" (our translation). Our results are no more informative on this matter, but they do indicate that the relationships of *Piabarchus* lie outside of the *Creagrutus-Piabina* assemblage. Indeed, given the form of the jaws and the upper- and lower-jaw dentition in *Piabarchus analis*, which differ significantly from those in *Creagrutus* (and *Piabina*), it is not apparent why Eigenmann (in Eigenmann et al., 1914:8) stated that *Piabina analis* had the "mouth as in *Creagrutus*" and assigned the genus to *Piabina*.

Genus *Creagrutus* Günther

Creagrutus Günther, 1864:339 [type species *Leporinus mülleri* Günther, 1859: 92, by monotypy; gender masculine].

Creagrudite Myers, 1927:117 [type species *Creagrudite maxillaris* Myers, 1927:118, by original designation; gender masculine].

Creagrutops Schultz, 1944:327 [type species *Creagrutops maracaiboensis* Schultz, 1944:327, by original designation; gender masculine].

DIAGNOSIS.—*Creagrutus* is diagnosed on the basis of a series of synapomorphies listed under "Monophyly of *Creagrutus*," above. Externally, the foreshortened lower jaw and the premaxillary teeth arranged in either of the patterns shown in Figures 1–3 combined with a fourth infraorbital whose posterior margin contributes to the posterior margin of the infraorbital series distinguishes the species of *Creagrutus* within characiforms. Two exceptions to this generality are *C. cracentis* and *C. maxillaris*, species with highly derived dentition (Figure 4) but sharing a series of synapomorphies with their congeners and within subclades of *Creagrutus* (Figure 17).

STATUS OF *Creagrutus, Piabina, Creagrudite,* AND *Creagrutops*.—Our introductory remarks detailed the differing opinions concerning the generic limits of *Creagrutus*. During the last century, *Piabina* has variably been recognized as a distinct genus or as a synonym of *Creagrutus* by diverse authors (see "Remarks" under "Genus *Piabina* Reinhardt" for a detailed discussion). Such decisions either were unexplained or were focused on a single character system, the number of anal-fin rays that was purported to distinguish *Piabina* from *Creagrutus*. Mahnert and Géry (1988) demonstrated a continuity in anal-fin ray counts between the two nominal genera, and our more encompassing analysis has found that the anal-fin ray count for *Piabina argentea* (15–18) is continuous with that for several *Creagrutus* species (*C. barrigai, C. manu, C. paraguayensis*), all of which have an upper range of 15 anal-fin

rays. The 15 to 18 anal-fin rays of *Piabina argentea* exactly overlaps that of *C. pearsoni,* a species previously assigned to *Piabina* (as *P. beni*), but which our research has shown to be a member of the *Creagrutus* clade. An analysis of the phylogenetic relationships within the *Creagrutus-Piabina* clade shows that the genera constitute sister groups, with *Creagrutus* diagnosed by a series of synapomorphic features and with *Piabina,* in turn, characterized by an autapomorphic modification of the fourth infraorbital. In order to highlight this sister-group relationship between these genera, and to reflect the diagnostic characters for both *Creagrutus* and *Piabina,* the genus *Piabina* is recognized as distinct, contrary to the action of Mahnert and Géry (1988).

We herein consider two other nominal genera, *Creagrudite* Myers (1927) and *Creagrutops* Schultz (1944), as synonyms of *Creagrutus.* The type species of *Creagrudite, C. maxillaris* Myers (1927), is deeply embedded within the phylogeny of *Creagrutus*, and its continued recognition would render the latter genus nonmonophyletic. *Creagrutops* was proposed by Schultz (1944) for *C. maracaiboensis* Schultz (1944), a diminutive species endemic to the Lago Maracaibo basin. A single feature, the incomplete poring of the lateral line, was used by Schultz to distinguish *Creagrutops* from *Creagrutus* and *Creagrudite.* The phylogenetic analysis has shown that this feature is an autapomorphy for the species and that *C. maracaiboensis* is the sister species to *C. nigrostigmatus.* The clade formed by these two species shares a series of synapomorphies with the rest of the species of *Creagrutus.* The continued recognition of *Creagrutops* as defined by Schultz based on the incomplete poring of the lateral line of *C. maracaiboensis* would render *Creagrutus* nonmonophyletic. Such a course of action is unjustified, and *Creagrutops* is placed into the synonymy of *Creagrutus.*

TYPE SPECIES.—*Creagrutus muelleri* from Ecuador was originally described by Günther (1859:92) as *Leporinus müller*i. Soon thereafter (1864:339), Günther transferred his species to *Creagrutus,* designating it at that time as the type species of the genus. Steindachner (1876:105) subsequently described a second species as *Leporinus mülleri* based on material from a number of Amazonian localities. *Leporinus müller*i Steindachner is, however, a member of the characiform family Anostomidae and is not closely related to the species of the same name described by Günther as the type species of *Creagrutus.*

STATUS OF *Creagrutus pellegrini* PUYO.—Puyo (1943:143) described *Creagrutus pellegrini* based on two specimens from the upper Fleuve Itany and Fleuve Maroni of French Guiana. This generic assignment was briefly critiqued by Myers (1960:210) and was followed by Géry (1964:59). Both authors proposed that Puyo's *C. pellegrini* was a member of the characid genus *Chalceus* Cuvier. A more in-depth discussion herein is appropriate given the original assignment of the species to *Creagrutus.*

Notwithstanding the apparent loss of the type series of various species described by Puyo, presumably including that of *Creagrutus pellegrini* (Géry, 1959:345–346; Géry and Planquette, 1982:68), the information and figures in Puyo's publications (1943, 1949) demonstrate that his assignment of his species to *Creagrutus* was erroneous. Puyo (1943:144; 1949:129) remarked that the scale row immediately dorsal of the lateral line was formed by "very large scales, the largest of all on the body of this fish" (our translation), a feature obvious in the accompanying illustrations (Puyo, 1943, fig. 2; 1949, fig. 66). Myers noted (1960:211) that such scale-size disparity is limited to *Chalceus* among New World characiforms (see Eigenmann, 1912, pl. 55: fig. 1, for illustration showing scale-size disparity in *Chalceus*). We have not discovered such enlarged scales in any *Creagrutus* or *Piabina* species, but we have found that feature in all examined *Chalceus* species.

Puyo (1943:143; 1949:129) furthermore noted that *Creagrutus pellegrini* has "20 conical teeth, with blunt tips, small and implanted along the external border of the upper jaw" (our translation). The small conical teeth with blunt tips reported for *C. pellegrini* contrast with the typically tricuspidate teeth on the maxilla and outer portions of the premaxilla in *Creagrutus.* In addition, the 20 teeth reported along the upper-jaw margin (a count presumably including both premaxillary and maxillary teeth) is higher than in any *Creagrutus* species. The vast majority of *Creagrutus* species have five or six teeth in the primary premaxillary tooth row and a maximum of five maxillary teeth, total numbers distinctly lower than those reported by Puyo for *C. pellegrini.* Even *Creagrutus maxillaris* and *C. cracentis,* species with highly modified dentition and an increased number of teeth, have three or four teeth in the external row of the premaxilla and 10 to 12 maxillary teeth, which result in totals (13–16) lower than the 20 upper-jaw teeth reported by Puyo for *C. pellegrini.* Reference to specimens of *Chalceus* from northeastern South America, the type region for *Creagrutus pellegrini* (USNM 226115), reveal, however, that Puyo's description of the form and number of teeth in *C. pellegrini* corresponds to that of *Chalceus* specimens from that region. Given this similarity in dentition and the distinctive scale-size disparities common to *C. pellegrini* and *Chalceus,* we follow Myers (1960:211) and recognize *Creagrutus pellegrini* as a doubtful species *Chalceus pellegrini* (Puyo), and we do not treat it further in this study.

DISTRIBUTION.—In our introductory comments we alluded to the broad distribution of the species of *Creagrutus* and *Piabina* in the regions east of the Andean Cordilleras. This distribution has proven to be quite uneven, however, when examined at finer levels (Figure 18). Whereas some gaps in the known distribution of these genera in Cis-Andean South America likely represent the absence of the taxa in certain drainage basins, the absence of these genera, in particular *Creagrutus,* from various regions is suspect to varying degrees.

The absence or rarity of *Creagrutus* along the main channel of the central and eastern portions of the Amazon River (Figure

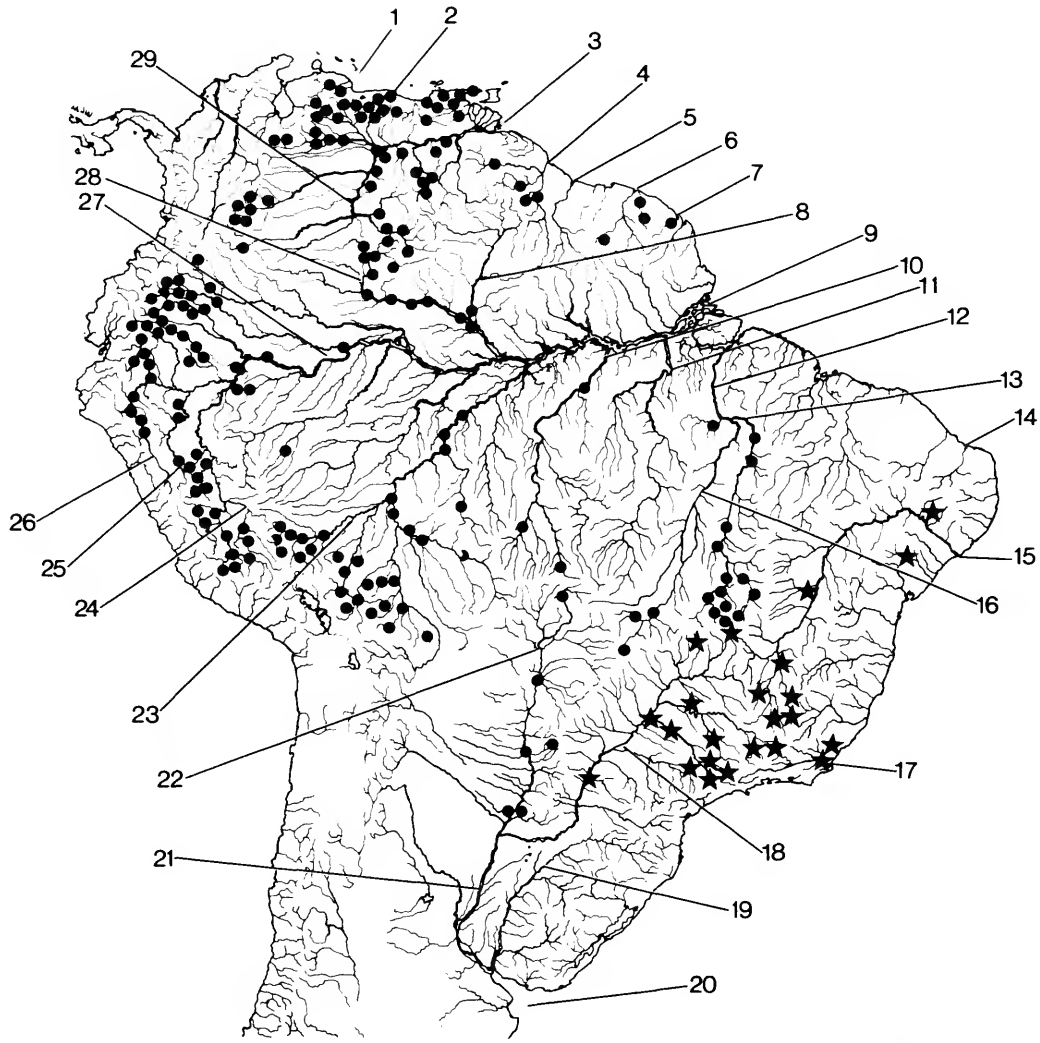

FIGURE 18.—Map of South America showing known occurrence of *Creagrutus* (dots) and *Piabina* (stars) species east of the Andean Cordilleras. Many symbols represent more than one lot of specimens and/or collecting locality. Drainage basins of note relative to discussion in text (mouth of river basin often indicated) are as follows: 1=Río Aroa and Río Yaracuy, 2=Río Tuy, 3=Río Orinoco, 4=Essequibo River, 5=Corantijn River, 6=Maroni or Morawijne River, 7=Fleuve Approuague, 8=Rio Branco, 9=Rio Amazonas, 10=Rio Tapajós, 11=Rio Xingu, 12=lower Rio Tocantins, 13=upper Rio Tocantins, 14=Rio Jaguaribe, 15=Rio São Francisco, 16=Rio Araguaia, 17=Rio Paraíba, 18=upper Rio Paraná, 19=Río Uruguay, 20=mouth of Río de La Plata, 21=lower Río Paraná, 22=Río Paraguay, 23=upper Rio Madeira, 24=Río Ucayali, 25=Río Huallaga, 26=Rio Marañon, 27=upper Rio Amazonas (Rio Solimões), 28=Rio Negro, and 29=upper Río Orinoco.

18, indicated by 9) and lower portions of the main tributary rivers likely reflects the absence in such areas of the prime habitat for both *Creagrutus* and *Piabina*, namely riffles and rocky bottoms with moderate to swift water current. Amazonian records for *Creagrutus* mostly occur peripheral to the central portion of the Amazon basin, typically in uplands where the preferred habitats for most members of the genus are more common. This pattern is particularly apparent in the southeastern, southwestern, and western portions of the basin in the Rio Madeira, Río Ucayali, Río Huallaga, and Río Marañon (Figure 18, rivers 23 through 26). Throughout these regions, ichthyological collecting activities often yield sympatrically occurring *Creagrutus* species, most represented by moderate to sizable population samples. Locality records for *Creagrutus* from central portions of the Amazon, in contrast, nearly invariably represent single species, typically with smaller numbers of specimens from each site. Similarly, in the adjoining Rio Tocantins system (Figure 18, rivers 12, 13, 16) the majority of population sam-

ples originated in the upriver southern portions of the basin.

An examination of the gaps in the known occurrence of *Creagrutus* in Cis-Andean South America within the context of the intensity of ichthyological collecting efforts across that region, raises questions as to the confidence we can place in these gaps as indicative of the actual absence of the genus. In many cases the gaps more likely reflect problems with our overall knowledge of the distribution of all components of the Neotropical freshwater fish fauna (see also comments by Böhlke et al., 1978; Vari and Weitzman, 1990; Vari and Reis, 1995).

The large gap in the known distribution of the *Creagrutus* within the relatively poorly sampled Rio Tapajós system (Figure 18, river 10) is notable, with a single sample of *C. cracentis* from the lower portions of the river and with *C. ignotus* represented by a few samples from two localities in the southern reaches of the basin. More striking is the lack of any *Creagrutus* material that originated in the Rio Xingu basin (Figure 18, river 11) and the extremely limited records from the headwater portions of the series of rivers in the region between the Rio Madeira (Figure 18, river 23) and the upper Amazon (Figure 18, river 27). Both the Rio Xingu and these more westerly rivers contain numerous headland streams with habitat presumably suitable for *Creagrutus*. We suspect that the absence of samples of the genus from these areas is likely a function of the limited available samples of the ichthyofauna from those basins.

Creagrutus is unknown from the various rivers north of the main stream of the Amazon between the mouth of the Rio Negro (Figure 18, river 28) and the mouth of the Amazon (Figure 18, indicated by 9). The only published report of a reasonably thorough ichthyofauna survey within this area is that of Ferreira (1995) who extensively sampled the lower and middle portions of the Rio Trombetas. Ferreira's survey, although including sites of swifter-moving water comparable to those inhabited by *Creagrutus* elsewhere through its range, did not document the presence of the genus within the basin. The remaining left bank tributaries of the Amazon in this region remain inadequately surveyed ichthyologically, making a definitive statement on the absence of the genus in that region impossible. Even within the Rio Negro basin (Figure 18, river 28), the best sampled left bank tributary to the Amazon, the majority of *Creagrutus* samples originated in the upper portions of the basin. The only record from the Rio Branco (Figure 18, river 8), the major left bank tributary of the Rio Negro is from near the mouth of the Rio Branco into the Rio Negro.

Records for *Creagrutus* in the region between the mouths of the Amazon and Orinoco rivers (Figure 18, rivers 9 and 3, respectively) are limited and patchy in distribution. *Creagrutus planquettei* is apparently endemic to the Fleuve Approuague of eastern French Guiana (Figure 18, river 7). *Creagrutus melanzonus*, as defined herein, ranges from eastern Venezuela (Río Cuyuni basin in the Essequibo River system, Figure 18, river 4) east to the central portions of French Guiana (Figure 18, Fleuve Maroni system, river 6), but with a major gap in the central portion of its known distribution in eastern Guyana and most of Suriname. The species has been reported from the Corantijn River (Figure 18, river 5) along the Suriname-Guiana border (Ouboter and Mol, 1993:146), a report we have been unable to confirm. The only confirmed record for *C. melanzonus*, or for that matter *Creagrutus*, from within Suriname is a single record of the species from the Olemari River in the upper reaches of the river basin that forms much of the border between Suriname and French Guiana (Figure 18, river 6). Ichthyological collecting efforts have been carried out on various Surinamese rivers; however, the habitats appropriate for *Creagrutus* are often not readily accessible (pers. obs. RPV) through many of the interior portions of that country. This may account for the virtual absence of records of the genus within Suriname. Similarly, given the limited available samples of the fish fauna from the Brazilian state of Amapá, north of the mouth of the Amazon, it is impossible to determine whether the lack of *Creagrutus* material from that area is significant.

The single species of *Piabina*, as defined in this study (*P. argentea*), is totally allopatric to, and complements, the distribution of *Creagrutus*. *Piabina* is limited to the eastern portions of South America in the basins of the Rio São Francisco (Figure 18, river 15); the Rio Itapicuru, which empties in the Atlantic Ocean about 200 km south of the mouth of the Rio São Francisco; the upper Río Paraná (Figure 18, river 18); the Rio Paraíba (Figure 18, river 17); and the Rio Itapemirim, whose mouth is approximately 70 km north of that of the Rio Paraíba. *Piabina argentea* is the best represented species among those treated in this paper in terms of numbers of samples, reflecting the relatively intensive collecting efforts that have been undertaken within its range, albeit with remaining gaps in its known distribution (Figure 18, stars). The lack of specimens of *Piabina* from the coastal rivers between the Rio Itapicuru and Rio Itapemirim of eastern Brazil and in the areas south of the mouth of the Rio Paraíba (Figure 18, river 17) probably reflects the actual absence of this genus in that region given the extensive, although not exhaustive, sampling of the fishes that has been undertaken in that area.

Neither *Creagrutus* nor *Piabina* are known from the portion of northeastern Brazil east of the Rio Tocantins basin (Figure 18, river 12) and north of the São Francisco drainage (Figure 18, river 15). The single possible exception is a *Creagrutus* specimen (ANSP 164289) in somewhat poor condition, with a stated locality of Russas, on the lower Rio Jaguaribe (Figure 18, river 14), Ceará, Brazil, a site distant from confirmed localities for the genus. This record is questionable for several reasons. First, Fowler (1941) did not cite *Creagrutus*, despite commenting (1941:123) that "descriptions also are given of rare or noteworthy specimens." The first record of *Creagrutus* from northeastern Brazil would have fit the criterion of rare or noteworthy. More notably, the *Creagrutus* specimen was formerly part of ANSP 69531-38, the type series of *Cheirodon macropterus* Fowler (1941:182). Böhlke (1984:50) noted that the type series contained a specimen of *Creagrutus*, lending credence to the possibility that the *Creagrutus* specimen was added to the *Cheirodon macropterus* type series subsequent to

Fowler's description of the latter species. Even if that is not the case, Roberts (1973:213) suggested that some of the specimens that Fowler (1941) cited as coming from northeastern Brazil originated instead in the Amazon basin; a suggestion supported by subsequent studies. Castro (1990:87) demonstrated that *Semaprochilodus squamilentis,* a prochilodontid described by Fowler (1941) with a reported type locality in northeastern Brazil, is, rather, endemic to the Rios Tocantins and Xingu of the Amazon basin. Similarly, Vari (1995:80) noted that the *Boulengerella cuvieri* Agassiz in Spix and Agassiz locality reported by Fowler (1941:194) (Rio Parnahya (=Parnaíba), Therezina (=Teresina), Piauhy (=Piauí)) is a considerable range extension that is unconfirmed by other specimens. That species is, however, widespread within the Rio Tocantins basin (Vari, 1995, fig. 45).

Definitive identification of the *Creagrutus* specimen purportedly from northeastern Brazil is precluded by its condition. Nonetheless, the 39 vertebrae, 12 branched anal-fin rays, overall head and body form, size and form of the infraorbitals, and residual dark body pigmentation match those of *C. seductus,* a Rio Tocantins basin endemic. We therefore propose that the specimen originated in the Rio Tocantins basin, as apparently did other specimens reported by Fowler (1941) as having been collected in northeastern Brazil.

Creagrutus beni was cited from northwestern Argentina by Pozzi (1945:270) and later by Ringuelet and Aramburu (1961: 30) and Ringuelet et al. (1967:134). Pozzi's reported localities in the provinces of Jujuy and Salta lie some 700 km from the nearest known site for *C. beni,* and they are within the Río de La Plata system rather than the upper Rio Madeira basin of the Amazon drainage to which *C. beni* is endemic. The occurrence of *C. beni* in the Río de La Plata basin cannot be confirmed by available specimens, nor were subsequent citations of the species by later authors based on additional specimens. Indeed, we have been unable to locate any *Creagrutus* specimens that originated in northwestern Argentina, and recent collecting efforts in that region failed to reveal the presence of the genus (L. Fernandez, pers. comm., 1999). For these reasons, the record of *C. beni* in northwestern Argentina is considered suspect (see "Remarks" under *C. beni*).

Premaxillary Dentition in *Creagrutus* and *Piabina*

Premaxillary dentition arrangement has served as the primary criterion both for the recognition of *Creagrutus* and *Piabina* and for the discrimination of intrageneric species groups within *Creagrutus* (e.g., Eigenmann, 1927:418; Géry, 1977:406; Géry and Renno, 1989:4). This previous emphasis on the premaxillary dentition of these two genera together with the use of premaxillary tooth patterns in the following keys necessitates a discussion of the system for describing premaxillary dentition utilized herein.

Divergent identification schemes (see comments by Böhlke (1958) and Howes (1982)) have been applied to characiform dentition patterns, with the arrangement of the premaxillary teeth in *Creagrutus* and *Piabina* described within the bauplan of the two rows of premaxillary teeth typical for many characids. That practice, although relatively applicable to two *Creagrutus* species (*C. maxillaris* (Figure 4) and *C. cracentris*) and, to a lesser degree, appropriate for *Piabina argentea* and five *Creagrutus* species (*C. maracaiboensis, C. melanzonus, C. muelleri, C. peruanus, C. runa*), poorly serves as a descriptive framework for the other 57 species of *Creagrutus.* Previous attempts to characterize the dentition of most *Creagrutus* species in terms of two or more tooth rows resulted in complex descriptions of premaxillary tooth patterns (e.g., Eigenmann, 1927:418) that often made it difficult, if not impossible, to visualize the actual tooth pattern and that greatly complicated comparisons of upper-jaw tooth arrangement among species.

Our practice (see also Harold and Vari, 1994:4) analyzes the dentition in *Piabina argentea* and all *Creagrutus* species, other than *C. maxillaris* and *C. cracentis,* in terms of three primary components (see also comments in the phylogenetic discussion of premaxillary dentition concerning potential homologies of different teeth). The first and most generalized pattern within *Creagrutus* (Figure 2) has a primary row of five or six teeth (seven teeth are sometimes present as an individual variant) that form a shallow arch or sigmoid pattern extending from the anterior portion of the premaxillary symphysis to the posterolateral region of the premaxilla. The primary premaxillary tooth row demonstrates two major patterns within *Creagrutus.* Most species have the five to seven sequential teeth of this series either in contact or nearly in contact without a distinctly greater gap between the first and second teeth (the two most medial teeth). A subunit of *Creagrutus* (*C. maracaiboensis, C. melanzonus, C. muelleri, C. nigrostigmatus, C. ouranonastes, C. peruanus, C. runa*) and *Piabina argentea* have a distinct gap between the first and second teeth of that series.

The second component to the premaxillary dentition is a triangular cluster (triad) of three larger teeth (Figure 3). In the majority of *Creagrutus* species the anterior tooth of the three tooth cluster is situated distinctly posterior of the arch of the anterior portion of the primary series. *Piabina argentea* and seven *Creagrutus* species (*C. maracaiboensis, C. melanzonus, C. muelleri, C. nigrostigmatus, C. ouranonastes, C. peruanus, C. runa*), in contrast, have a more anterior position of the medial cluster of three larger teeth. As a consequence, the anterior tooth of the triangular cluster is partially situated in the gap present between the first and second tooth of the primary series in these species.

The final component of the *Piabina-Creagrutus* premaxillary tooth pattern is a single tooth (Figure 2) situated lateral to the third or fourth tooth of the primary series, or in the region lateral to the area of juxtaposition of either the third and fourth or

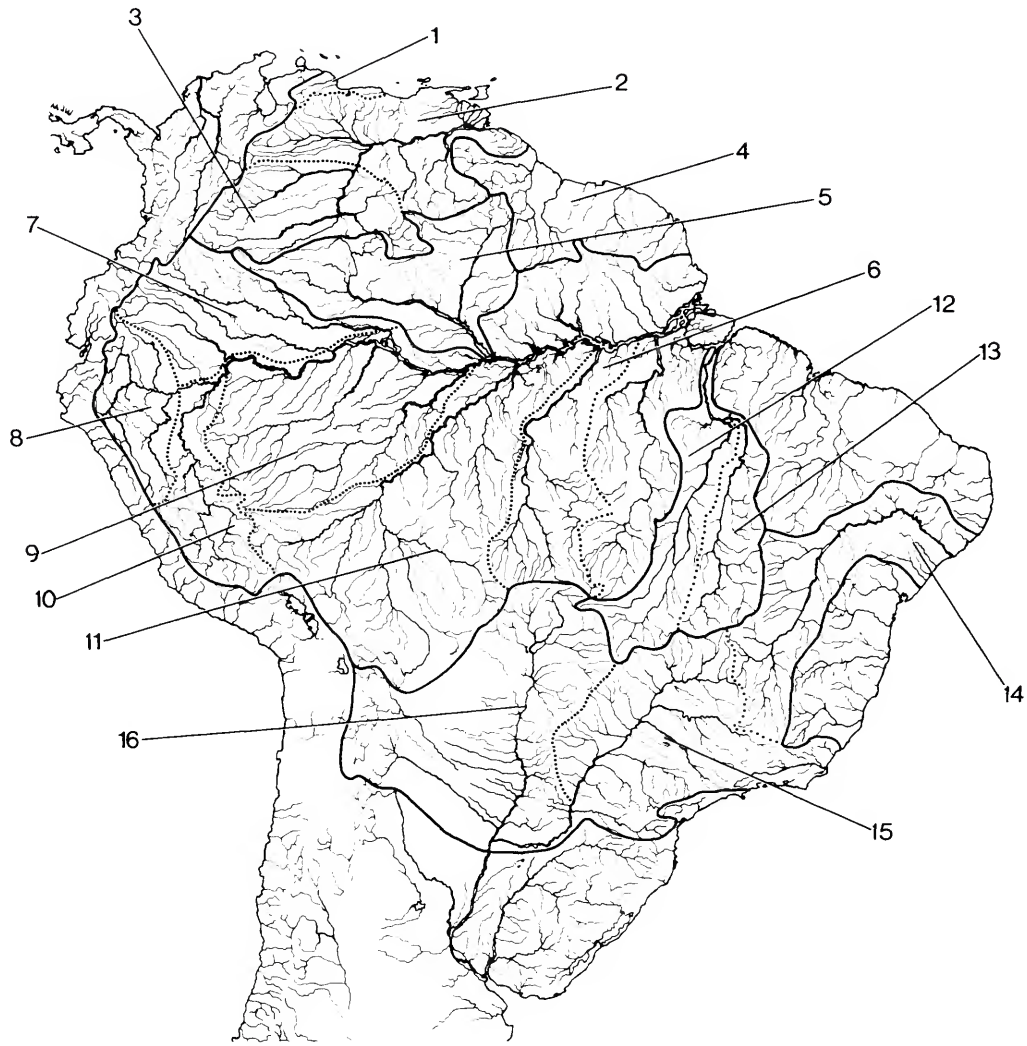

FIGURE 19.—Map of South America with heavy lines delimiting regions of Cis-Andean South America represented by different regional "keys" to species of *Creagrutus* and *Piabina*. Species common to more than one region are dealt with in the key to each of those regions. Dotted lines delimit subunits of each major Cis-Andean region that serve as basis for citation of species occurrences in Table 3. Neither *Creagrutus* nor *Piabina* is known to occur in northeastern Brazil (area east of Rios Tocantins-Araguaia basin, 12 and 13, and north of the Rio São Francisco basin, 14) in coastal rivers of eastern Brazil (area east of Rio São Francisco basin, 14), in Rio Xingu basin (between areas 6 and 12), or north bank tributary rivers draining into lower portion of Rio Amazonas east of mouth of Rio Negro (area 5).

Numbered regions (small capitals) and subregions (when applicable) are as follows: ORINOCO-CARIBBEAN: 1 =Cis-Andean Caribbean versant, 2=lower and middle Río Orinoco basin, and 3 = upper Río Orinoco basin. GUIANAS: 4=Atlantic coastal drainages of Guyana, Suriname, and French Guiana (=Guyane), no subdivisions. RIO NEGRO: 5=Rio Negro basin, including Rio Branco, no subdivisions. AMAZON: 6=Rio Tapajós, 7=far northwestern Amazon basin (Ríos Tigre, Napo, Putomayo, Caqueta and intervening basins), 8=far western Amazon basin (Ríos Marañon and Huallaga), 9=Western Amazon basin (Rios Purus, Jurua, southern tributaries to middle Solimões, and intervening basins), 10=Río Ucayali, 11=Rio Madeira. TOCANTINS: 12=Rio Araguaia, and 13= Rio Tocantins. SÃO FRANCISCO-PARANÃ-PARAGUAY: 14=Rio São Francisco, 15=Rio Paranã and Rio Paraíba, and 16=Río Paraguay. Major areas and basins from which *Creagrutus* or *Piabina* samples are unknown are not identified on map (see Figure 2 for exact distribution of known localities).

TABLE 3.—Occurrence of species of *Creagrutus* and *Piabina* in major regions and included subregions of Cis-Andean South America discussed in text. See Figure 19 for limits of regions and subregions. Numbered regions (small capitals) and subregions (when applicable) are as follows: ORINOCO-CARIBBEAN: 1=Cis-Andean Caribbean versant, 2=lower and middle Rio Orinoco basin, 3=upper Río Orinoco basin. GUIANAS: 4=Atlantic coastal drainages of Guyana, Suriname, and French Guiana (=Guyane), no subdivisions. RIO NEGRO: 5=Rio Negro basin, including Rio Branco, no subdivisions. AMAZON: 6=Rio Tapajós, 7= far Northwestern Amazon basin (Ríos Tigre, Napo, Putomayo, Caqueta, and intervening basins), 8= far Western Amazon basin (Ríos Marañon, Huallaga, and Ucayali), 9=Western Amazon basin (Rio Purus indicated by line) and rivers to the north, to the south bank of the main Amazon (Solimões) and east of the Río Ucayali, 10=Rio Ucayali of Western Amazon subdivision; and 11= Southwestern (Rio Madeira (indicated by line) and rivers to south and east of main-stream Amazon below mouth of the Madeira to divide with Rio Tapajós basin. TOCANTINS: 12=Rio Araguaia, and 13=Rio Tocantins. SÃO FRANCISCO-PARANÃ-PARAGUAY: 13=Rio São Francisco and adjoining costal basins, 14=Upper Rio Paranã and Rio Paraiba, 15=Río Paraná, and 16=Río Paraguay (X=present; -=absent).

Genus and species	Regions and subregions															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Creagrutus																
amoenus	-	-	-	-	-	-	-	x	-	x	-	-	-	-	-	-
anary	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-
atratus	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-
atrisignum	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-
barrigai	-	-	-	-	-	-	x	x	x	-	x	-	-	-	-	-
beni	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-
bolivari	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-
britskii	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-
calai	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-
changae	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
cochui	-	-	x	-	-	-	x	-	-	x	-	-	-	-	-	-
cracentis	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-
crenatus	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ephippiatus	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-
figueiredoi	-	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-
flavescens	-	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-
gephyrus	-	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-
gracilis	-	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-
gyrospilus	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-
holmi	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-
hysginus	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ignotus	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-
kunturus	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-
lassoi	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
lepidus	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
machadoi	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
magoi	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-
manu	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-
maxillaris	-	x	x	-	x	-	-	-	-	-	x	-	-	-	-	-
melanzonus	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-
melasma	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
menezesi	-	-	-	-	x	-	-	-	-	-	-	x	x	-	-	-
meridionalis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x
molinus	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-
mucipu	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-
muelleri	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-
occidaneus	-	-	-	-	-	-	-	-	x	-	x	-	-	-	-	-
ortegai	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
ouranonastes	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
paraguayensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x
pearsoni	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-
peruanus	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
petilus	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-
phasma	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-
pila	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
planquettei	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 3.—Continued.

Genus and species	Regions and subregions															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
provenzanoi	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-
runa	-	-	x	-	x	-	-	-	-	-	-	-	-	-	-	-
saxatilis	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-
seductus	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-
taphorni	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ungulus	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	
veruina	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-
vexillapinnus	-	-	x	-	x	-	-	-	-	-	-	-	-	-	-	-
xiphos	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-
zephyrus	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-
Piabina																
argentea	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	-

the fourth and fifth tooth of the primary series. This tooth is uniquely absent in *Creagrutus molinus* among species with this general arrangement of premaxillary teeth.

Some authors (e.g., Eigenmann, 1927:418) described the premaxillary tooth pattern present in *Piabina argentea* and some *Creagrutus* species (*C. maracaiboensis, C. melanzonus, C. muelleri, C. nigrostigmatus, C. ouranonastes, C. peruanus, C. runa*) as consisting of two irregular tooth rows, and indeed it can be interpreted in that manner. The premaxillary dentition in these species, however, shares the three components generalized for most of the species of *Creagrutus,* and it is this interpretation of that arrangement that facilitates the utilization of premaxillary dentition in keys and diagnoses.

Creagrutus cracentis and *C. maxillaris* have the arrangement of premaxillary teeth highly modified compared with their congeners, with two rows of teeth clearly present (see Figure 4), a much different situation than in all other members of the genus.

Keys to the Species of *Creagrutus* Günther and *Piabina* Reinhardt East of the Andes

Although *Creagrutus* and *Piabina* can be readily distinguished internally by a series of differences in a variety of body systems (see "Monophyly of *Creagrutus,*" above), they are externally quite similar. That factor, the speciose nature of *Creagrutus* east of the Andean Cordilleras, and the limited range of intrageneric morphological variation compared with the intrageneric species diversity would make utilizing an all-inclusive key to the members of the two genera both difficult and tedious, particularly for species at the terminus of a long chain of sequential couplets. Most Cis-Andean *Creagrutus* species have relatively restricted distributions, being typically confined to one of the major regions or drainage basins delimited on Figure 19. It is thus most efficient to present keys for the species known from within each such area.

Five *Creagrutus* species are included in more than one regional key. *Creagrutus menezesi* occurs in both the Amazon and Tocantins basins. *Creagrutus maxillaris, C. runa,* and *C. vexillapinnus* occur in both the upper portions of the Río Orinoco and the Rio Negro systems, the latter a major tributary to the mainstream Amazon. Finally, *C. zephyrus,* although unknown from the Río Orinoco, does occur in the Río Casiquiare proximate to where the upper Río Orinoco bifurcates into the main Río Orinoco and the Río Casiquiare of the upper Rio Negro basin. Given such proximity of *C. zephyrus* to the upper Río Orinoco, the species is likely present in that drainage system and is therefore included in the key to the *Creagrutus* species of that basin.

Table 3 details the known distribution of the species of *Creagrutus* in a series of drainage systems in Cis-Andean South America as an aid to determining the composition of the *Creagrutus* fauna within a particular region. In some instances the major regions utilized in the keys are subdivided in Table 3 to provide finer-scale distributional information (see descriptions of the major regions and their subregions in legend for Figure 19). Although no single, all inclusive, key for the species of *Creagrutus* is presented, each species diagnosis details the combination of features that discriminate the species from both Cis- and Trans-Andean congeners.

The reader is cautioned that 73% of the Cis-Andean *Creagrutus* species recognized herein are first proposed in this study or were described after 1995. Furthermore, many species are known from limited samples, sometimes only from a holotype. Those factors and the patchy ichthyological collecting efforts in many Cis-Andean drainages make it likely that additional *Creagrutus* species remain undiscovered. Indeed, a significant percentage of the diversity in the genus still may be unknown. Similarly, the distribution of some known forms likely will be extended to varying, perhaps considerable, degrees by future collecting efforts, such as has been the case in other groups of Neotropical fishes, including not only small-sized species but also many medium- and large-sized forms (see examples in Vari and Blackledge, 1996; Vari and Reis, 1995; Vari and Ortega, 1997).

Key to the Species of *Creagrutus* in the Amazon Basin Other Than the Rio Negro

1. Premaxilry teeth in 2 distinct rows with outer row consisting of 3 teeth and inner row of 4 teeth on each side [Figure 3]; dentary with 10 to 12 teeth; 5 median scales between posterior margin of anus and anal-fin origin; third infraorbital well developed 2

   Premaxillary teeth in 3 series as typical for *Creagrutus*; usually with 5 or 6, rarely 7 teeth in primary row on each side [Figure 2]; dentary with 4 to 6 teeth; typically 1 or 2, rarely 4, median scales between anus and anal-fin origin, if 4 median scales present between posterior margin of anus and anal-fin origin, then third infraorbital relatively small with posterior and ventral margins falling distinctly short of vertical and horizontal limbs of preopercle 3

2. Postorbital portion of head 36.8%–38.0% of HL; orbital width 37.0%–40.0% of HL; pectoral-fin length 17.9%–20.0% of SL ..... ***C. cracentis,*** new species (lower Rio Tapajós basin)

   Postorbital portion of head 40.6%–46.8% of HL; orbital width 28.7%–34.6% of HL; pectoral-fin length 15.1%–18.2% of SL ..... ***C. maxillaris*** (Río Orinoco, upper Rio Negro, and upper Rio Madeira basins)

3. Maxilla with 7 to 11 teeth along anteroventral margin; dentary with 10 or 11 teeth ..... ***C. gephyrus*** (northwestern Amazon basin)

   Maxilla with 2 to 5 teeth along anteroventral margin; dentary with 4 to 7 teeth (4 teeth very rare) 4

4. Midlateral surface of body with series of separate dark spots arranged in longitudinal series; spots sometimes coalescing longitudinally, more so on posterior portion of body in larger specimens, particularly those with darker overall pigmentation; posterior margin of anus and anal-fin origin separated by 1 median scale 5

   Midlateral surface of body lacking series of separate dark spots, or if midlateral pigmentation present taking form of continuous stripe; posterior margin of anus and anal-fin origin separated by 2 to 4 median scales 6

5. Lateral line scales 35 to 39; vertebrae 36 to 39, rarely 39; depth of caudal peduncle 12.2%–13.8% of SL; distance from dorsal-fin origin to anal-fin origin 33.8%–38.8% of SL ..... ***C. amoenus*** (northwestern Amazon basin)

   Lateral line scales 39 to 43; vertebrae 38 to 41, typically 39 or 40; depth of caudal peduncle 11.1%–12.1% of SL; distance from dorsal-fin origin to anal-fin origin 30.9%–33.5% of SL ..... ***C. kunturus*** (northwestern Amazon basin)

6. Distinct gap present between first and second teeth of primary tooth row of premaxilla on each side, gap partially filled posteriorly by anterior portion of anterior tooth of triangular cluster of posteromedial premaxillary teeth [Figure 1] 7

   First and second teeth of primary tooth row of each premaxilla in contact, anterior tooth of triangular cluster of posteromedial premaxillary teeth situated posteromedially of primary row of premaxillary teeth [Figure 2] 9

7. Predorsal scales 13 to 15; dentary teeth 7; scale rows between lateral line and dorsal-fin origin 6; vertebrae 40 to 43 ..... ***C. ouranonastes,*** new species (western Amazon basin)

   Predorsal scales 10 to 13, rarely 13; dentary teeth 5 or 6; scale rows between lateral line and dorsal-fin origin 4 or 5; vertebrae 38 to 40 8

8. Third infraorbital very well developed, wider than diameter of pupil; ventral margin of third infraorbital approaching (smaller specimens) or in contact (larger specimens) with horizontal limb of preopercle; posterior margin of third infraorbital ap-

proaching vertical limb of preopercle; anal-fin length 15.3%–17.8% of SL ..... ***C. muelleri***
(western Amazon basin)

Third infraorbital relatively slender; ventral and posterior margins of third infraorbital distinctly separated from horizontal and vertical limbs of preopercle; posteroventral margin of third infraorbital concentric with rim of orbit; anal-fin length 18.4%–20.0% of SL ..... ***C. peruanus***
(western Amazon basin)

9. Humeral mark horizontally elongate, lying within midlateral stripe ..... ***C. cochui***
(western Amazon basin)

Humeral mark vertically elongate to varying degrees, extending distinctly above and below midlateral stripe on body when stripe present 10

10. Branched anal-fin rays 13 to 18 11

Branched anal-fin rays 9 to 12 13

11. Distinct midlateral stripe on posterior one-half to two-thirds of body; distance from snout to anal-fin origin 63.5%–66.4% of SL; anal-fin length 20.4%–21.8% of SL ..... ***C. manu,*** new species
(southwestern Amazon basin)

No distinct midlateral stripe on body; distance from snout to anal-fin origin 58.5%–63.4% of SL; anal-fin length 15.6%–20.7% of SL 12

12. Branched anal-fin rays 13 to 15; scale rows between lateral line and dorsal-fin origin 4; distance from snout to dorsal-fin origin 45.4%–49.2% of SL; anal-fin length 18.0%–20.7% of SL; postorbital head length 34.2%–41.9% of HL ..... ***C. barrigai,*** new species
(northwestern and west central portions of Amazon basin)

Branched anal-fin rays 15 to 18 (15 very rare); scale rows between lateral line and dorsal-fin origin 5 or 6; distance from snout to dorsal-fin origin 49.4%–52.9% of SL; anal-fin length 15.6%–17.4% of SL; postorbital head length 41.0%–45.1% of HL ..... ***C. pearsoni***
(southwestern Amazon basin)

13. Post-anal median scales to anal-fin origin 4; third infraorbital very narrow, with posteromedial margin concentric with margin of orbit ..... ***C. ungulus,*** new species
(southwestern portions of Amazon basin)

Post-anal median scales to anal-fin origin 2; third infraorbital moderately to well developed, when moderately developed posteroventral margin of third infraorbital not concentric with bony margin of orbit 14

14. Basal portions of middle caudal-fin rays with distinct spot of dark pigmentation ..... ***C. anary***
(middle portions of Rio Madeira basin)

Basal portions of middle caudal-fin rays without distinct spot of dark pigmentation, sometimes with scattered chromatophores 15

15. Anterior and posterior margins of humeral mark distinct and regular, either nearly vertical or approaching vertical; forming either a vertical bar or a ventrally, gradually attenuating, vertically elongate triangle 16

Shape of humeral mark variable, sometimes with margins quite defuse (*C. holmi*); overall form of mark rotund, anteriorly concave, or somewhat rhomboidal 19

16. Gill rakers on lower limb of first gill arch 11 to 13, scales above lateral line to dorsal-fin origin 3 or 4; bony orbital diameter 32.6%–37.9% of HL; lateral line scales 36 to 38; anal-fin length 15.9%–19.5% of SL; anteroventral portion of third infraorbital approaching or contacting horizontal limb of preopercle ..... ***C. occidaneus,*** new species
(western portions of Amazon basin)

Gill rakers on lower limb of first gill arch 8 to 10; scales above lateral line to dorsal-fin origin 4 to 6; if 4 then bony orbital diameter 29.5%–32.7% of HL (*C. beni*) or lateral line scales 38 to 43; anal-fin length 19.3%–22.7% of SL; and anteroventral portion of third infraorbital falling distinctly short of horizontal limb of third infraorbital (*C. pila*) 17

17. Lateral line scales 35 to 37; scale rows between lateral line and anal-fin origin 3; teeth on each dentary 5; distance from snout to pectoral-fin insertion 25.7%–28.5% of SL; pelvic-fin length 16.4%–19.6% of SL; anal-fin length 19.3%–22.7% of SL ... ***C. pila,*** new species (western portions of Amazon basin)

Lateral line scales 38 to 43, 38 uncommon; scale rows between lateral line and anal-fin origin 3 or 4; if 38 lateral line scales or 3 scale rows between lateral line and anal-fin origin present, then 6 teeth present on each dentary; distance from snout to pectoral-fin insertion 21.2%–26.0% of SL; pelvic-fin length 13.9%–16.8% of SL; anal-fin length 19.3%–22.7% of SL 18

18. Width of orbit 8.7%–10.3% of SL; width of orbit equals or exceeds horizontal distance from posterior margin of orbit to posterior margin of opercle; 5 teeth present on each dentary ..... ***C. changae,*** new species (western portions of Amazon basin)

Width of orbit 7.1%–8.4% of SL; width of orbit less than horizontal distance from posterior margin of orbit to posterior margin of opercle; 6 teeth present on each dentary ..... ***C. beni*** (southwestern portions of Amazon basin)

19. Humeral mark rhomboidal [Figure 71] ..... ***C. ortegai,*** new species (western portions of Amazon basin)

Humeral mark diffuse, rounded, or anteriorly concave 20

20. Ventral margin of third infraorbital in adults contacting horizontal limb of preopercle 21

Ventral margin of third infraorbital in adults not contacting horizontal limb of preopercle 23

21. Humeral mark diffuse and distinctly wider dorsally [Figure 46] ..... ***C. holmi,*** new species (western portions of Amazon basin)

Humeral mark distinct and anteriorly curved 22

22. Distance from dorsal-fin origin to hypural joint 53.3%–55.4% of SL; distance from dorsal-fin origin to anal-fin origin 26.9%–30.5% of SL; distance from dorsal-fin origin to pelvic-fin insertion 21.5%–25.4% of SL; distance from dorsal-fin origin to pectoral-fin insertion 28.5%–30.7% of SL; caudal peduncle depth 9.3%–10.7% of SL ..... ***C. ignotus,*** new species (Rio Tapajós basin)

Distance from dorsal-fin origin to hypural joint 55.5%–61.9% of SL; distance from dorsal-fin origin to anal-fin origin 32.4%–40.4% of SL; distance from dorsal-fin origin to pelvic-fin insertion 30.2%–35.1% of SL; distance from dorsal-fin origin to pectoral-fin insertion 32.0%–36.6% of SL; caudal peduncle depth 11.5%–13.7% of SL ..... ***C. flavescens,*** new species (western portions of Amazon basin)

23. Primary tooth row of premaxilla with 5 teeth; 8 to 10 gill rakers on upper and 11 to 13 gill rakers on lower limb of first gill arch; 39 to 43 lateral line scales ..... ***C. gracilis,*** new species (western portions of Amazon basin)

Primary tooth row on premaxilla with 6 teeth; 5 or 6 gill rakers on upper and 9 to 11 gill rakers on lower limb of first gill arch; 36 to 39 lateral line scales ..... ***C. petilus,*** new species (southwestern portions of Amazon basin)

Key to the Species of *Creagrutus* in the Rio Negro Basin

1. Premaxillary teeth in 2 distinct rows [Figure 4]; outer row consisting of 3 teeth and inner row of 4 teeth; maxilla elongate, with 10 to 12 tricuspidate teeth along anteroventral margin; each dentary with 10 to 12 teeth; 5 scales between posterior margin of anus and anal-fin origin ..... ***C. maxillaris*** (Río Orinoco, upper Rio Negro, and upper Rio Madeira basins)

   Premaxillary teeth in 3 series typical for *Creagrutus* species, with 4 to 7 teeth in primary row of each side [Figure 2]; maxilla of moderate length, with 2 or 3 tricuspidate teeth along margin; each dentary with 4 to 6 teeth; 2 scales between posterior margin of anus and anal-fin origin 2

2. Branched anal-fin rays 12 to 14; dorsal fin with distinct patch of black pigmentation on middle portion of last unbranched and first six branched rays ..... ***C. vexillapinnus,*** new species (middle and upper Rio Negro and upper Río Orinoco basins)

   Branched anal-fin rays 9 to 11; dorsal fin lacking distinct patch of black pigmentation on middle portion of last unbranched and first six branched rays 3

3. Primary series of premaxillary dentition consisting of 4 teeth ..... ***C. runa,*** new species (upper Rio Negro and upper Río Orinoco basins)

   Primary series of premaxillary dentition with 5 to 7 teeth 4

4. Basal portions of middle caudal-fin rays without dark pigmentation ..... ***C. menezesi,*** new species (Rio Negro basin and Rio Tocantins basin)

   Basal portions of middle caudal-fin rays with dark pigmentation 5

5. Primary series of premaxillary teeth with 5 teeth; humeral mark in form a distinctly arcuate stripe; dark pigmentation on caudal fin horizontally elongate mark on midportion of middle caudal-fin rays ..... ***C. phasma*** (upper portion of Río Negro, Río Orinoco basin)

   Primary series of premaxillary teeth with 6, rarely 5 teeth; humeral mark vertically elongate, but not distinctly arched; caudal-fin pigmentation, when present, either a rounded spot on basal portions of middle caudal-fin rays or extending along length of middle caudal-fin rays 6

6. Postorbital head length 43.7%–47.4% of HL; bony orbital diameter 31.3%–35.7% of HL; predorsal scales 10 to 12; caudal pigmentation, when present, extending along length of middle caudal-fin rays ..... ***C. ephippiatus,*** new species (Río Siapa, upper Río Negro basin)

   Postorbital head length 35.1%–41.0% of HL; bony orbital diameter 36.9%–40.3% of HL; predorsal scales 8 or 9; caudal pigmentation, when present, a rounded spot on basal portions of middle caudal-fin rays ..... ***C. zephyrus,*** new species (upper Río Negro and Río Casiquiare)

Key to the Species of *Creagrutus* in the Rio Tocantins Basin

1. Premaxillary lacking single tooth typically lying lateral to fourth or fifth tooth of primary series in most *Creagrutus* species; distance from dorsal-fin origin to pelvic-fin insertion 21.5% of SL; distance from dorsal-fin origin to pectoral-fin insertion 27.8% of SL ..... ***C. molinus,*** new species (upper Rio Araguaia basin)

Premaxillary with single tooth typically lying lateral to fourth or fifth tooth of primary series [Figures 1–3]; distance from dorsal-fin origin to pelvic-fin insertion 28.2%–35.0% of SL; distance from dorsal-fin origin to pectoral-fin insertion 29.6%–35.8% of SL 2

2. Scale rows between dorsal-fin origin and lateral line 5 3
   Scale rows between dorsal-fin origin and lateral line 4 4
3. Humeral mark dark, horizontally elongate in larger specimens; secondary pigmented region located slightly dorsal of primary humeral mark, sometimes joined to it by vertical patch of less densely concentrated melanophores; gill rakers on upper portion of first arch 7 or 8, usually 8 ..... ***C. atrisignum*** (upper Rio Tocantins basin)

   Humeral mark moderately pigmented, rotund or vertically elongate (more so in larger individuals); without distinct secondarily pigmented region slightly dorsal of primary humeral mark; when humeral mark vertically elongate, intensity of pigmentation fading dorsally; gill rakers on upper portion of first arch 6 or 7, most often 6 ..... ***C. britskii,*** new species (upper Rio Tocantins basin)
4. Branched anal-fin rays 9 or 10 5
   Branched anal-fin rays 11 to 13 6
5. Premaxilla with 5 teeth in primary series; humeral mark approximating form of inverted comma [Figure 40] with distinctly anteriorly concave margin; region of mark immediately dorsal of lateral line distinctly darker than remaining portions of mark ..... ***C. figueiredoi,*** new species (upper Rio Tocantins andupper Rio Araguaia basins)

   Premaxilla with 6, rarely 7, teeth in primary series; humeral mark vertically elongate and ventrally tapering, with anterior margin straight or barely concave; intensity of pigmentation not varying along length of mark ..... ***C. menezesi,*** new species (upper Rio Araguaia basin, Rio Tocantins, Rio Negro)
6. Body with series of dark chevron-shaped marks on midlateral surface in larger specimens [Figure 68], with dorsal branch of chevron more pronounced in medium-sized individuals; distal margin of caudal fin with dusky band separated by hyaline region from basal dusky portion of fin; 5 teeth in primary premaxillary tooth series; gill rakers 6–7 + 9–11 ..... ***C. mucipu,*** new species (upper Rio Tocantins basin)

   Body lacking series of dark chevron-shaped marks on midlateral surface; caudal pigmentation lacking distinct distal band; 6 or 7, rarely 5 teeth in primary premaxillary tooth series (5 teeth rarely present in *C. saxatilis,* which has 8–10 + 13–14 gill rakers) 7
7. Lateral line scales 37 to 39; vertebrae modally 37, rarely 36 or 38; interorbital distance 31.6%–36.4% of HL; depth of caudal peduncle 11.3%–12.2% of SL; gill rakers on upper limb of first arch 8 to 10, rarely 8; gill rakers on lower limb of first arch 11 to 13, rarely 13 ..... ***C. saxatilis,*** new species (upper Rio Tocantins basin)

   Lateral line scales 39 to 41; vertebrae 38 or 39; interorbital distance 28.4%–31.9% of HL; depth of caudal peduncle 10.6%–11.2% of SL; gill rakers on upper limb of first arch 7 or 8; gill rakers on lower limb of first arch 13 or 14 ..... ***C. seductus,*** new species (upper Rio Araguaia basin)

Key to the Species of *Creagrutus* in the Guianas, including the Río Cuyuni

Primary tooth row of premaxilla usually with 5 teeth; body shallow and fusiform; dentary teeth 6 or 7; humeral mark a short vertical crescent with slight anterior concavity; lat-

eral line scales 35 to 38; gill rakers on lower limb of first gill arch 10 to 12; orbital diameter 34.8%–42.9% of HL; 35 to 37 vertebrae ..... ***C. melanzonus***
(Essequibo River drainage, Guyana and eastern Venezuela to Fleuve Sinnamary, central French Guiana)

Primary tooth row of premaxilla usually with 6 teeth; body deep and laterally compressed; dentary teeth 5; humeral mark ovate, horizontally elongate; lateral line scales 38 to 40; gill rakers on lower limb of first gill arch 12 to 13; orbital diameter 29.2%–36.7% of HL; 38 or 39 vertebrae ..... ***C. planquettei***
(Fleuve Approuague, eastern French Guiana)

Key to the Species of *Creagrutus* in the Río Orinoco Basin and Cis-Andean Caribbean Versant Drainages

1. Premaxillary dentition in 2 distinct rows [Figure 4]; outer tooth row consisting of 3 teeth and inner row of 4 teeth; maxilla elongate, with 10 to 12 teeth along anteroventral margin; each dentary with 10 to 12 teeth ..... ***C. maxillaris***
(Río Orinoco, upper Rio Negro, and upper Río Madeira basins)

   Premaxillary dentition with 3 components typical for *Creagrutus* species, with 4 to 6 teeth in primary row of each premaxilla [Figure 2]; maxilla of moderate length, with 2 to 7 teeth along margin; each dentary with 5 to 8 teeth 2

2. Primary row of premaxillary teeth with 6 teeth 3

   Primary row of premaxillary teeth with 4 or 5, usually 5, teeth 15

3. Humeral mark in the form of a circular blotch 4

   Humeral mark in the form of a vertical bar of various shapes 5

4. Third infraorbital well developed, its ventral margin approaching or contacting horizontal limb of preopercle; 4, occasionally 5, horizontal scale rows between lateral line and dorsal-fin origin; bony orbital diameter 25.8%–31.7% of HL; maxillary teeth usually 3 or 4, rarely 2 ..... ***C. gyrospilus,*** new species
(upper portions of northern tributaries of Río Apure)

   Third infraorbital relatively small with a broad gap separating its ventral margin from horizontal limb of preopercle; 5 horizontal scale rows between lateral line and dorsal-fin origin; bony orbital diameter 28.5%–36.1% of HL; maxillary teeth usually 4 or 5 ..... ***C. hysginus***
(rivers draining into Golfo de Paria, northeastern Venezuela)

5. Humeral mark not very wide, in the form of a narrow, vertical to anteriorly concave bar; horizontal scale rows between lateral line and anal-fin origin 2 or 3; anal-fin ray hooks, when present, on first branched ray only; postorbital head length 35.1%–41.0% of HL 6

   Humeral mark well developed, in the form of a broad, vertical to anterodorsally tapered bar with maximum width immediately dorsal of lateral line; horizontal scale rows between lateral line and anal-fin origin 3 to 5; anal-fin ray hooks, when present, on first 2 to 5 branched rays; postorbital head length 38.4%–53.5% of HL 7

6. Small, diffuse spot of dark pigmentation on anterior portion of middle caudal-fin rays; caudal peduncle depth 9.7%–10.9% of SL; 2 or 3, usually 3, horizontal scale rows between lateral line and dorsal-fin origin; vertebrae 38 or 39 ..... ***C. zephyrus,*** new species
(upper Rio Negro and Río Casiquiare drainages)

   No spot of dark pigmentation on anterior portion of middle caudal-fin rays; caudal peduncle depth 10.8%–11.7% of SL; 4 horizontal scale rows between lateral line and dorsal-fin origin; vertebrae 36 or 37 ..... ***C. xiphos,*** new species
(Río Mato, Río Caura basin)

7. Body somewhat tubular; branched anal-fin rays 9 to 13; interorbital distance 34.0%–37.9% of HL ..... ***C. atratus,*** new species (upper Río Meta)

Body slightly compressed, not tubular; branched anal-fin rays 8 to 12; interorbital distance 26.1%–35.4% of HL 8

8. Third infraorbital bone well developed, its ventral margin approaching or contacting horizontal limb of preopercle; humeral mark distinctly expanded anteriorly and posteriorly directly dorsal of lateral line, tapered and/or curved anterodorsally behind head 9

Third infraorbital bone small, with a broad gap separating its ventral margin from horizontal limb of preopercle; humeral mark a uniform vertical bar or a bar with a slight expansion dorsal of lateral line 11

9. Gill rakers on upper portion of first gill arch 9 to 11; gill rakers on lower portion of first gill arch 13 or 14; interorbital distance 30.2%–34.3% of HL; lower lip not pigmented ..... ***C. magoi,*** new species (Río Chaviripa)

Gill rakers on upper portion of first gill arch 7 to 9; gill rakers on lower portion of first gill arch 11 to 13; interorbital distance 27.4%–32.0% of HL; lower lip pigmented . 10

10. Elongate dark pigment spot along middorsal portion of body immediately posterior of head; dentary teeth 6 or 7; humeral mark attenuated ventrally, appearing overall as an inverted comma; bony orbital diameter 33.2%–39.0% of HL; caudal peduncle depth 9.9%–11.3% of SL; pectoral-fin rays 12 to 14; dentary teeth 6 or 7 ..... ***C. provenzanoi,*** new species (Río Cataniapo)

No dark elongate dark pigment spot along middorsal portion of body posterior of head; dentary teeth 5; humeral mark not attenuated ventrally, appearing as a centrally expanded vertical bar; bony orbital diameter 31.1%–35.6% of HL; caudal peduncle depth 10.4%–12.2% of SL; pectoral-fin rays 13 to 15; dentary teeth 5 ..... ***C. calai,*** new species (upper Río Meta)

11. Branched anal-fin rays 8 to 10; maxillary teeth 2 to 4; anal-fin ray hooks, when present, on first 1 or 2 branched rays; interorbital distance 26.1%–33.3% of HL; snout to dorsal-fin origin 45.0%–50.9% of SL; predorsal median scales 8 to 10 12

Branched anal-fin rays 10 to 12; maxillary teeth 2 to 5; anal-fin ray hooks, when present, on first 2 to 4 branched rays; interorbital distance 28.6%–35.4% of HL; snout to dorsal-fin origin 47.5%–53.6% of SL; predorsal median scales 8 to 13 . 13

12. Bony orbital diameter 33.5%–43.0% of HL; interorbital distance 26.1%–30.0% of HL; postorbital head length 38.4%–43.8% of HL; caudal-peduncle depth 9.9%–11.2% of SL ..... ***C. machadoi,*** new species (upper Río Caura)

Bony orbital diameter 28.2%–36.6% of HL; interorbital distance 28.0%–33.3% of HL; postorbital head length 41.4%–49.5% of HL; caudal peduncle depth 10.9%–13.2% of SL ..... ***C. bolivari*** (lower tributaries and near main channel of Río Orinoco to upper Río Meta)

13. Dorsal-fin origin at, or slightly posterior of, vertical through pelvic-fin insertion; dark, narrow median line of pigmentation on predorsal surface of body, pigmentation often restricted to anterior one-half of that region; pectoral-fin rays 11 or 12; interorbital distance 29.3%–33.5% of HL; postorbital head length 46.7%–53.5% of HL; snout to pelvic-fin insertion 41.9%–51.1% of SL; snout to dorsal-fin origin 47.5%–53.6% of SL ..... ***C. lassoi,*** new species (Ríos Aroa and Yaracuy, Caribbean versant of northern Venezuela)

Dorsal-fin origin at, or slightly anterior of, vertical through pelvic-fin insertion; no median line of dark pigmentation on predorsal surface; pectoral-fin rays 11 to 13; interorbital distance 28.6%–35.4% of HL; postorbital head length 45.1%–51.9% of HL; snout to pelvic 44.2%–49.0% of SL; snout to dorsal-fin origin 47.8%–51.7% of SL 14

14. Humeral mark even vertical bar; gap between infraorbitals 4 through 6 and vertical limb of preopercle approximately constant in width; posterior margins of many scales on flank undulate to crenate; lower jaw and lip unpigmented; pelvic-fin ray hooks, when present, on both medial and lateral surfaces of branched rays, most highly developed on medial 2 or 3 rays; predorsal median scales 8 to 11; lateral line scales 37 to 39; gill rakers on upper limb of first gill arch 5 to 7 ..... ***C. crenatus,*** new species
(Caribbean versant drainages of Estado Lara, northern Venezuela)

Humeral mark a vertical bar, somewhat expanded anteriorly and posteriorly immediately dorsally of lateral line; gap between infraorbitals 4 through 6 and vertical limb of preopercle decreasing in width dorsally; posterior margins of many scales on flank smooth to slightly undulate; lower jaw, dorsally, and lip, pigmented; pelvic-fin ray hooks, when present, on medial surfaces of branched rays only; predorsal median scales 9 to 13; lateral line scales 36 to 38; gill rakers on upper limb of first gill arch 6 to 8 ..... ***C. taphorni,*** new species
(Río Orinoco basin, north central Venezuela, and Río Tuy of Caribbean versant of northern Venezuela)

15. Scale rows between lateral line and dorsal-fin origin 5 or 6; scale rows between lateral line and anal-fin origin 4 or 5; lateral line scales 34 to 37; humeral mark either obscured by lateral stripe or a straight, vertical to slightly oblique, bar angled from anteroventral to posterodorsal; body transversely compressed 16

Scale rows between lateral line and dorsal-fin origin 4; scale rows between lateral line and anal-fin origin 2 or 3, rarely 4; lateral line scales 38 to 43; humeral mark a short vertical bar or an anteriorly concave shallow crescent; body shallow and fusiform 17

16. Humeral mark absent; solid, dark lateral stripe along entire length of body, obscuring humeral mark; hooks on anal-fin rays, when present, on up to first 10 branched rays; lateral line scales 36 or 37; gill rakers on upper limb of first gill arch 6 or 7 ..... ***C. lepidus***
(Ríos Aroa and Urama, Caribbean versant of northern Venezuela)

Humeral mark present, a straight, vertical to slightly oblique, bar angled from anteroventral to posterodorsal; lateral stripe anteriorly diffuse, as in most *Creagrutus* species, extending from slightly posterior of humeral mark to base of caudal fin; hooks on anal-fin rays, when present, on up to first 3 to 5 branched rays; lateral line scales 34 to 36; gill rakers on upper portion of first gill arch 3 to 6 ... ***C. melasma***
(upland tributaries of northern portion of Río Orinoco, and Ríos Tuy and Neverí of Caribbean versant of northern Venezuela)

17. Branched anal-fin rays 11; horizontal scale rows between anal-fin origin and lateral line 2; central caudal-fin rays diffusely pigmented, with no obvious spot or stripe; maxillary teeth 3 or 4 ..... ***C. veruina,*** new species
(Río Cataniapo)

Branched anal-fin rays 9 or 10; horizontal scale rows between anal-fin origin and lateral line 2 to 4, usually 3; central caudal-fin rays with distinct dark stripe restricted to anterior one-half of fin; maxillary teeth 4 to 7 ..... ***C. phasma***
(upper Río Orinoco and Río Casiquiare drainages)

Key to the Species of *Creagrutus* and *Piabina* in the Río de La Plata and Rio São Francisco Basins and Rivers of Southeastern Brazil

1. First and second teeth of primary premaxillary tooth row separated by distinct gap [Figure 1]; dorsal-fin origin to hypural joint 48.5%–52.7% of SL; caudal-peduncle depth 9.0%–10.9% of SL; branched anal-fin rays 15 to 18 ..... ***Piabina argentea*** (Rio São Francisco, Rio Itapicuru, upper Río Paraná, Rio Paraíba and Rio Itapemirim basins)

   First and second teeth of primary premaxillary tooth row in contact along their adjoining margins [Figure 2]; dorsal-fin origin to hypural joint 52.5%–59.8% of SL; caudal-peduncle depth 10.5%–12.5% of SL; branched anal-fin rays 11 to 15 2

2. Snout to anal-fin origin 62.1%–66.4% of SL; scale rows between lateral line and dorsal-fin origin 4; branched anal-fin rays 11 to 13 ..... ***Creagrutus meridionalis,*** new species (middle and upper portions of Río Paraguay basin)

   Snout to anal-fin origin 55.3%–61.0% of SL; scale rows between lateral line and dorsal-fin origin 5; branched anal-fin rays 13 to 15 ..... ***Creagrutus paraguayensis*** (middle portions of Río Paraguay basin)

Species Accounts

To facilitate the location of, and cross reference between, accounts for the different species, the species descriptions are arranged alphabetically within *Creagrutus* regardless of their region(s) of occurrence. These are followed by the description of *Piabina argentea.*

Creagrutus amoenus Fowler, 1943

FIGURES 20–22, TABLE 4

Creagrutus amoenus Fowler, 1943a:239, fig. 18 [type locality: Colombia (Caquetá), Florencia, Río Ortuguasa (=Orteguaza); one paratype=*C. flavescens*]; 1948:82, fig. 86 [literature record based on Fowler, 1943a]; 1975:25 [literature compilation].—Géry, 1977:407 [in key].—Wilkens, 1977:156 [paratype despository].—Böhlke, 1984:42 [type depository].—Castro and Arboleda, 1988:8 [Colombia, Río Caqueta].—Vari et al., 1995:289 [comparisons with *C. kunturus; C. boehlkei* Géry (1972) tentatively placed as synonym of *C. amoenus* Fowler].—Román-Valencia and Cala, 1996:145 [discussion of species based on literature information].

*Creagrutus müller*i [not of Günther, 1859].—Böhlke, 1958:30, tab. 3, pl. 3: fig. 1 [misidentification] [Ecuador (Napo), Río Tutapischo, Río Villano, headwaters of Río Arajuno].

Creagrutus boehlkei Géry, 1972:63, tab. 5, pl. iv: fig. 2 [type locality: Ecuador, "Oriente del Ecuador" (eastern portion of Ecuador); also Río Conambo, Río Capotazo, Río Villano]; 1977:407 [in key].—Wilkens, 1977:156 [paratype depository].—Stewart et al., 1987:26 [Ecuador, Río Napo].—Ibarra and Stewart, 1989:369 [Ecuador, upper Río Napo basin].—Barriga, 1991:17 [literature compilation; eastern portion of Ecuador; based on Géry, 1972].—Vari et al., 1995:289 [*C. boehlkei* tentatively placed as synonym of *C. amoenus*]. [New synonymy.]

Creagrutus muelleri [not of Günther, 1859].—Saul, 1975:106 [misidentification] [Ecuador: Napo (now in Sucumbíos), Santa Cecilia, Río Conejo; ecology and stomach contents].

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a pronounced gap between the first and second teeth of the primary premaxillary tooth series, 2 to 4 maxillary teeth, the typical possession of 6 teeth in the primary premaxillary tooth series, 1 post-anal medial scale to the anal-fin origin, 4 scale rows between the lateral line and the dorsal-fin origin, the pigmentation pattern of a series of dark spots along the midlateral line on the body that ontogenetically coalesce, sometimes resulting in a solid stripe in larger individuals, the lack of a distinct patch of pigmentation on the middle portions of the dorsal fin, and the absence of a distinct, vertically elongate humeral mark distinguishes *C. amoenus* from all congeners with the exception of *C. kunturus. Creagrutus amoenus* can be separated from *C. kunturus*, the only other member of the genus with comparable pigmentation on the body and one post-anal scale, by the combination of the number of lateral line scales (35–39 in *C. amoenus* versus 39–43 in *C. kunturus*), total vertebrae (36–39, rarely 39, in *C. amoenus* versus 38–41, typically 39–40, in *C. kunturus*), the depth of the caudalpeduncle (12.2%–13.8% of SL in *C. amoenus* versus 11.1%–12.1% of SL in *C. kunturus*), and the distance from the dorsal-fin origin to the anal-fin origin (33.8%– 38.8% of SL in *C. amoenus* versus 30.9%–33.5% of SL in *C. kunturus*).

DESCRIPTION.—Morphometric and meristic data for *C. amoenus* in Table 4. Head and body relatively robust. Greatest body depth at dorsal-fin origin in smaller individuals, variably at, or somewhat anterior of, that line in larger individuals. Dorsal profile of head from tip of snout to rear of supraoccipital spine, ranging from smooth and slightly convex in some specimens to distinctly convex with irregular profile above nostrils in other individuals. Interorbital region distinctly convex. Predorsal profile of body with variably evident change in alignment relative to that of head; slightly convex in smaller specimens, typically distinctly so in larger individuals. Dorsal

TABLE 4.—Morphometrics and meristics of *Creagrutus amoenus:* (A) holotype of *C. amoenus,* ANSP 70499; (B) holotype of *C. boehlkei,* ZSM 28428; and (C) all other specimens of *C. amoenus* from which counts and measurements were taken (n=59). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B	C
		Morphometrics	
Standard length	66.5	91.2	35.4–91.2
1. Snout to anal-fin origin	68.6	66.2	62.6–70.8
2. Snout to pelvic-fin insertion	49.5	49.5	45.9–50.2
3. Snout to pectoral-fin insertion	26.6	27.8	23.7–29.5
4. Snout to dorsal-fin origin	48.7	48.3	47.1–51.7
5. Dorsal-fin origin to hypural joint	55.3	55.1	53.5–58.8
6. Dorsal-fin origin to anal-fin origin	34.0	36.7	33.8–38.8
7. Dorsal-fin origin to pelvic-fin insertion	29.9	32.9	29.0–35.6
8. Dorsal-fin origin to pectoral-fin insertion	33.1	35.5	32.8–38.4
9. Caudal peduncle depth	12.8	13.0	12.2–13.8
10. Pectoral-fin length	22.3	21.2	19.5–22.9
11. Pelvic-fin length	16.5	16.8	15.6–18.9
12. Dorsal-fin length	23.8	21.5	20.1–24.5
13. Anal-fin length	17.3	17.4	16.0–22.3
14. Head length	26.9	28.0	25.3–29.9
15. Postorbital head length	43.6	48.2	41.7–49.3
16. Snout length	24.8	27.8	24.4–32.1
17. Bony orbital diameter	29.6	29.4	29.3–34.0
18. Interorbital width	29.6	29.4	25.7–33.0
		Meristics	
Lateral line scales	37	37	35–39
Scale rows between dorsal-fin origin and lateral line	4	4	4
Scale rows between anal-fin origin and lateral line	3	3	3
Predorsal median scales	9	10	9–10
Branched dorsal-fin rays	8	8	7–8
Branched anal-fin rays	11	11	10–12[1]
Branched pelvic-fin rays	7	7	6–7[2]
Pectoral-fin rays	11	11	10–14
Vertebrae	37	37	36–39[3]

[1]Eleven branched dorsal-fin rays typical, 10 or 12 rays present in fewer than 5% of examined specimens.
[2]Seven branched pelvic-fin rays typical.
[3]Thirty-nine vertebrae present in only one examined paratype.

profile of body inclined at dorsal-fin base, ranging from nearly straight between posterior insertion of dorsal fin and caudal peduncle to slightly convex in region of adipose fin. Ventral profile of head with variably obtuse angle at anteroventral corner of dentary, gently curved from that region to isthmus. Ventral profile of body convex to anal-fin origin, convexity more pronounced in deep-bodied individuals.

Head obtusely pointed in lateral view, distinctly pointed in dorsal view. Upper jaw distinctly longer than, and overhanging, lower jaw. Anterior portion of snout fleshy, with scattered papillae. Papillae more concentrated along ventral margin of upper lip and on fleshy folds and plicae extending between outer and medial premaxillary teeth and along dorsal margin of lower lip.

Infraorbital series moderately developed, proportionally more extensive posteriorly in larger specimens. Ventral margin of third infraorbital curved, deepest region of infraorbital contacting, or nearly contacting, horizontal limb of preopercle. Posterior margins of third through fifth infraorbitals distinctly separated from vertical limb of preopercle.

Premaxillary dentition in three series: primary row slightly curved or sigmoid, typically with 6 teeth (5 teeth present on one side of head in one specimen) without pronounced gap between first and second tooth of series and with medial tooth separated from its equivalent tooth of contralateral series by distinct gap; triangular cluster of 3 larger teeth; and single tooth of form similar to that of primary series occurring lateral to fourth tooth of primary premaxillary row (2 teeth present in this region of one premaxilla in one, apparently anomalous, specimen). Maxilla with 2 to 4 teeth; teeth all tricuspidate when 2 or 3 teeth present, fourth tooth often with irregular, but not distinctly tricuspidate, distal margin. Dentary typically with 6 teeth, 5 teeth present on dentary on one side of jaws in several specimens. Three anterior dentary teeth distinctly larger than remaining teeth and tricuspidate, with central cusp largest; second tooth largest, about twice as large as first tooth and three times as large as third tooth. Three posterior dentary teeth gradually becoming smaller, with approximately equal and distinct cusps (teeth 4 and 5) or barely apparent cusps (tooth 6, when present).

FIGURE 20.—*Creagrutus amoenus*, ANSP 145981, 81.0 mm SL; Ecuador, Napo, tributary to Río Napo, approximately15 mi (23 km) downstream of Missahuali (0°56′N, 77°30′W).

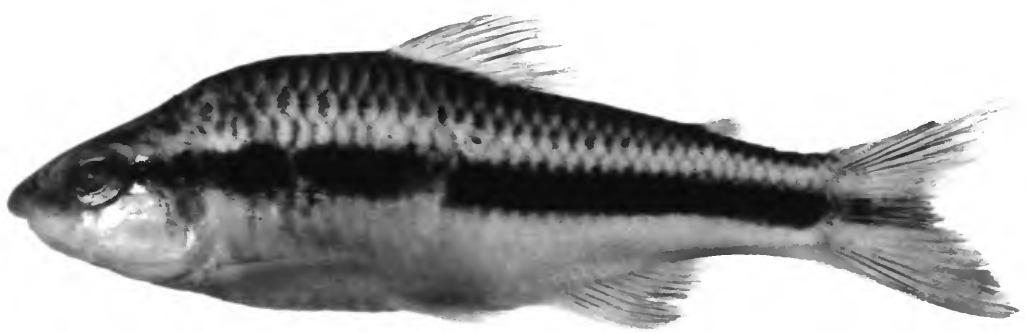

FIGURE 21.—*Creagrutus amoenus*, MEPN 4626, 76.0 mm SL; Ecuador, Napo, Río Cowi (0°08′10″S, 76°15′18″W).

Dorsal-fin rays typically ii,8, rarely ii,7. Dorsal-fin origin approximately at vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin straight to very slightly concave. Anal-fin rays ii–iii,10–12. Profile of distal margin of anal fin straight to slightly concave. Hooks typically present on anal-fin rays in mature males of many *Creagrutus* species not present in examined specimens. Pectoral-fin rays i,9–13; relative length of fin somewhat variable, tip extending posteriorly into area slightly to distinctly short of vertical through pelvic-fin insertion. Pelvic-fin rays i,6,i in some small specimens, i,7 in majority of examined individuals. Tip of pelvic fin falling slightly to distinctly short of anus. Hooks typically present on pelvic-fin rays in mature males of many *Creagrutus* species not present in examined specimens.

Gill rakers of first arch relatively short on epibranchial, elongate on ceratobranchial; 7–8 + 9–11.

COLORATION IN LIFE (based on a transparency of an aquarium specimen provided by H.-G. Evers and the examination of recently collected specimens still in formalin at MEPN).—Overall coloration silvery, more so midlaterally and ventrally. Region above midlateral line with pronounced yellow tint. Yellow coloration most concentrated immediately above midlateral silvery stripe that overlies darker midlateral stripe seen in preserved specimens lacking guanine. Dorsal surface of head yellow. Dorsal fin yellowish, with yellow pigmentation most concentrated along most of length of anterior rays and central portions of remaining rays. Caudal-fin lobes yellow, more so basally, with distal portions having only faint yellow pigmentation. Anal fin with patch of intense yellow pigmentation overlying central portions of all rays, pigmentation more intense an-

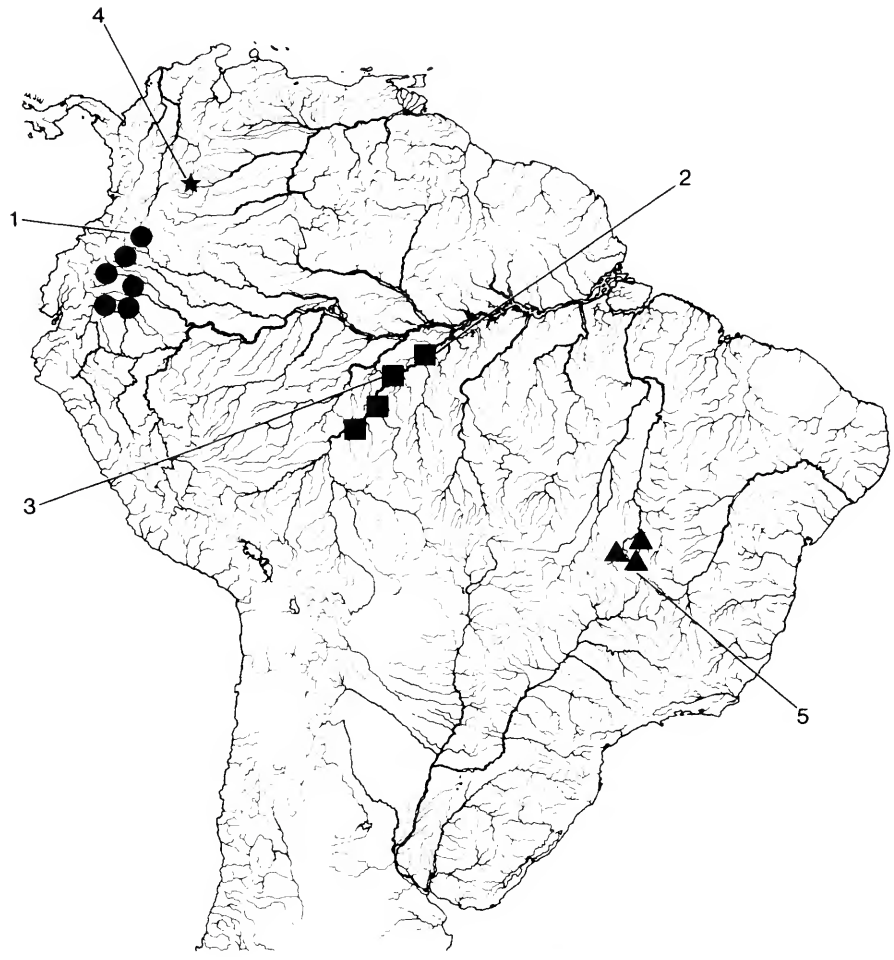

FIGURE 22.—Map of central and northern South America showing geographic distribution of *Creagrutus amoenus* (dots, 1=type locality), *Creagrutus anary* (squares, 2=type locality based on information in original species description; 3=type locality according to Böhlke, 1955), *Creagrutus atratus* (star, 4=type locality), and *Creagrutus atrisignum* (triangles, 5=type locality) (some symbols represent more than one locality or lot of specimens).

teriorly. Pelvic fin with intense yellow pigmentation on central portions of all but lateralmost rays. Lateralmost pelvic-fin rays with distinct white coloration in photographs of live aquarium specimen. Pectoral fin with broad region of yellow pigmentation; yellow color less obvious on distal portions of rays and on medial rays of fin.

COLORATION IN ALCOHOL.—Overall ground coloration of relatively freshly collected specimens light tan. Dorsal surface of head with dense field of small dark chromatophores, giving region distinctly dusky appearance. Intensity of pigmentation more noticeable over brain, evidently as consequence of deeplying pigmentation. Dense surface pigmentation continuing anteriorly over snout and upper lip. Denser patch of pigmentation present anterior to nares. Specimens with darker overall head and body pigmentation having region immediately ventral to and posterior to orbit with pigmentation field interrupted by patch of faintly pigmented laterosensory canal segments. Dorsal region of preopercle and infraorbitals with numerous small dark chromatophores. Variably developed pattern of dark pigmentation present posterior to orbit; pattern ranging in form from discrete spot positioned along posterior margin of fourth and fifth infraorbitals, through irregular horizontal band limited to lateral surface of infraorbitals, to distinct stripe extending from posterior margin of orbit to rear of opercle.

Scales of dorsolateral portion of body with small dark chromatophores concentrated along posterior scale margin, giving overall reticulate pattern to body pigmentation in that region. Development of humeral mark highly variable. Overall form of

mark vertically elongate, with rotund, intensely pigmented region centered immediately dorsal of lateral line. Intensely pigmented region typically flanked ventrally and dorsally by less pigmented areas. Darkly pigmented region dorsal of humeral mark more apparent in smaller individuals and in larger specimens with less intense overall body pigmentation; pigmentation field anterodorsally sloping and dorsally attenuate. Maximum height of humeral mark approximately equal to that of two scales in that region. Ventral extension of main portion of humeral mark usually less obvious, pigmentation extending about one scale width ventral of main body of mark in form of ventrally attenuating patch of scattered chromatophores. Dark pigmentation along midlateral portion of body highly variable both ontogenetically and between comparably sized individuals. Midlateral pigmentation consisting of two components, midlateral band of dark deep-lying chromatophores and regions of dark surface pigmentation. Surface pigmentation ranging from discrete, widely separated spots approximately size of pupil of eye, through variously coalesced spots and stripe segments, to uninterrupted dark band extending from region of rear of opercle to base of middle caudal-fin rays. Highly developed midlateral stripe subsumes humeral mark. Stripe continuous anteriorly with horizontal stripe extending from rear of orbit to rear of opercle.

Dorsal fin with membranes and margins of fin rays overlain by small dark chromatophores, particularly on distal two-thirds of dorsal-fin rays; intensity of dark pigmentation increasing ontogenetically, with number of rays with such pigmentation also increasing with body size. Basal portions of anal-fin rays outlined by small dark chromatophores in medium-sized individuals, rays nearly completely outlined in larger specimens. Caudal fin with fin rays and membranes overlain by small dark chromatophores, particularly in larger individuals. Distinct band of dark pigmentation on middle caudal-fin rays; band most intense basally where it forms irregular spot in many specimens. Basal portion of rays bordering middle caudal-fin rays less intensely pigmented. Distal portions of middle caudal-fin rays and of rays dorsal and ventral to them with margins more intensely pigmented. Pelvic and pectoral fins nearly hyaline in smaller individuals, dusky in larger specimens.

ECOLOGY.—Saul (1975:106) reported that in the Río Conejo, northeastern Ecuador, *Creagrutus amoenus* (identified therein as *C. muelleri*) was taken "in swift current over sand, gravel, or bedrock bottom. A few fish (4) were seined in a slow-flowing effluent of the lower lake." His analysis of stomach contents revealed that *C. amoenus* feeds on plant debris, insect debris, fish eggs, dragonfly nymphs, beetle larvae, caddisfly larvae, and fly larvae, including those of chironomids, with fly larvae the most abundant. The smallest mature female examined was a gravid 69.7 mm specimen with 0.9 mm ova captured in mid-June. At one locality in the Río San Miguel basin, northeastern Ecuador, *C. amoenus* was captured sympatrically with *C. flavescens* (USNM 340973 and USNM 340986, respectively).

DISTRIBUTION.—*Creagrutus amoenus* occurs in rivers of the Andean foothills of eastern Ecuador and southeastern Colombia (Figure 22, dots).

REMARKS.—Fowler (1943a:239) described *Creagrutus amoenus* on the basis of a holotype and three paratypes. One of the paratypes of the species (ANSP 70500, 62.8 mm SL) is a specimen of *C. flavescens*.

Géry (1972:66) noted in his original description of *Creagrutus boehlkei* that "there exists a species from the Río Ortuguesa in Colombia, *C. amoenus* Fowler, 1943, in which the overall appearance, particularly of the anterior head region, greatly resembles that of *C. boehlkei* sp. nov. *C. amoenus* has only 34 or 35 scales in total along the lateral line, however, and a different coloration" (our translation). Géry's citation of lateral line scales for *C. amoenus* was based on data presented in the original description of that species by Fowler (1943a:239) who evidently used different criteria for his lateral line scale counts than did Géry (1972). Examination of the holotypes of *C. amoenus* and *C. boehlkei* did not reveal differences in lateral line scale counts (Table 4). Similarly, the evident differences in pigmentation between the two nominal species noted by Géry (1972) fall within the range of variation for this feature within population samples from the type regions of each nominal species. Given the evident absence of differences between these nominal species, *C. boehlkei* is herein placed as a synonym of *C. amoenus*.

Böhlke (1958:30) reported *Creagrutus mülleri* from various Ecuadorian localities, noting, however, that the material might represent another, possibly undescribed species. Géry (1972:65) identified Böhlke's material as *C. boehlkei*. These specimens are *C. amoenus*, with the exception of one specimen, which is *C. flavescens* (ANSP 70500, in part).

MATERIAL EXAMINED.—347 specimens (59, 35.4–91.2).

COLOMBIA. *Caquetá:* Florencia (approximately 1°45′N, 75°35′W), Río Ortuguasa (=Orteguaza), ANSP 70499, 1 (66.5; holotype of *Creagrutus amoenus*); ANSP 70500–70502, 2 (54.4–68.0; paratypes of *Creagrutus amoenus*, third paratype in lot is *C. flavescens*, see "Remarks," above); ANSP 70503, 1 (paratype of *Creagrutus amoenus*, specimen cleared and stained for bone); USNM 100762, 1.

ECUADOR. "Oriente del Ecuador" (=eastern Ecuador), ZSM 28428, 1 (91.2, holotype of *Creagrutus boehlkei*); ZSM 28429, 2 (75.9–88.6, paratypes of *Creagrutus boehlkei*); ANSP 136915, 1 (76.5). *Pastaza:* Río Conambo, tributary of Río Tigre, ZMH 1757, 1 (81.0, paratype of *Creagrutus boehlkei*). Río Danta, tributary to Río Conambo (1°45′03″S, 76°47′04″W), USNM 311297, 2 (64.2–68.0); USNM 311339, 3 (1, 65.0; 1 specimen cleared and counterstained for cartilage and bone); MEPN 6608, 4; MEPN 6602, 3; MEPN 6607, 27. Río Capotazo, tributary of upper Río Pastaza (approximately 2°07′S, 77°27′W), ZMH 1758, 4 (62.5–70.0, paratypes of *Creagrutus boehlkei*); MCNG 2183.35, 2 (paratypes of *Creagrutus boehlkei*). Río Villano, ZMH 1868, 1 (68.5, paratype of *Creagrutus boehlkei*). Río Villano, near Villano (1°30′S, 77°29′W),

ANSP 75910, 1 (76.0); USNM 164045, 5; MEPN uncataloged, 7. Río Tiguino basin, estero of Tiguino No. 3 (unnamed tributary of Río Tiguino; 1°07′35″S, 76°56′52″W), MEPN 4599, 1; MEPN 6288, 5. Río Landayacu, Moretecocha (01°35′12″S, 77°24′18″W), MEPN 7194, 12. Río Metzera (=Río Palora; 1°51′S, 77°49′W), MEPN 5357, 2. Río Jandiayacu, MEPN 9649, 17. *Napo:* Río Yasuni, Estero Triniti, 45 minutes by boat from Rocafuerte, USNM 311341, 4; MEPN 6497, 3. Río Tutapishco, near Loreto (0°38′S, 77°19′W), ANSP 75909, 1; ANSP 75908, 1; USNM 164070, 4 (2, 62.4–83.1; 1 specimen cleared and counterstained for cartilage and bone). Stream tributary to Río Napo, approximately 15 mi (23 km) downstream of Missahuali (0°56′S, 77°30′W), ANSP 145981, 1 (81.0). Río Cowi, near camp of oil drilling site in "Bloque 16 Pozo Cowi-Conoco" (0°08′10″S, 76°15′18″W), MEPN 4626, 27 (10, 51.3–76.5); USNM 340985, 4. Quebrada Yaucanoyacu, tributary to Río Payamino, downstream from Río Tiquino (0°25′36″S, 77°19′24″W), FMNH 102997, 28 (10, 37.4–48.8). Quebrada Aulayacu, tributary to Río Payamino (0°25′36″S, 77°19′24″W), FMNH 102998, 11. Quebrada to Río Misahualli, in front of church at Cotundo (0°52′18″S, 77°50′12″W), FMNH 102979, 5. Río Napo, near Puerto Francisco de Orellana (=Coca; 0°28′S, 76°58′W), USNM 340987, 6. Quebrada Yaucanayacu, tributary of Río Payamino, 1 river km below mouth of Río Tiquino (0°25′36″S, 77°19′24″W), MEPN 5267, 50. Quebrada Aulayacu, tributary of Río Payamino, 0.8 river km below mouth of Río Tiquino (0°25′36″S, 77°19′24″W), MEPN 5255, 10. *Sucumbios:* Río Conejo, at bridge on road from Lago Agrio to Lumbaqui, near Santa Cecilia (0°3′30″N, 77°02′W), MEPN 5265, 13. Río Shushufindi, tributary to Río Aguarico (0°10′S, 76°40′W), ANSP 137626, 4 (65.5–82.3). Santa Cecilia, Río Conejo (approximately 0°03′N, 76°58′W), 1 km N of town, KU 13457, 7. Río Bahita, 0.5 mi (0.8 km) N of Santa Cecilia, KU 13454, 6. Río Coca drainage basin, headwater tributary of Río Dashino, approximately 9 km SW of Lumbaqui (by road) and 0.3 km S (0°0′3″S, 77°23′48″W), FMNH 102984, 46 (15, 35.4–53.7). Río San Miguel basin, Río La Bermeja, in front of Communidad Shuor Chari (approximately 0°10′N, 76°25′W), MEPN 4640, 6; USNM 340986, 4.

Creagrutus anary Fowler, 1913

FIGURES 22, 23, TABLE 5

Creagrutus anary Fowler, 1913:552, fig. 16 [type locality: Brazil, Madeira River (=Rio Madeira), approximately 200 miles (=320 km) E of longitude 62°20′W; see also under "Remarks," below, concerning reported locality]; 1948:82, fig. 87 [literature compilation]; 1975:25 [literature compilation].—Eigenmann, 1927:423 [Madeira River, based on Fowler, 1913].—Géry, 1964:62 [in key]; 1977:407 [Rio Madeira, *C. hildebrandi* Schultz cited as possible junior synonym].—Böhlke, 1984:42 [holotype reported missing, paratype cited as cleared and stained].—Cala, 1990:92 [as possible synonym of *C. hildebrandi* following Géry, 1977].—Chang and Ortega,1995:2 [Peru, Department of Madre de Dios].—Chang, 1998:22 [southeasternPeru].

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three ecomponents generalized for most species of *Creagrutus* without a pronounced gap between the first and second teeth of the primary tooth series of the premaxilla, 6 teeth in the primary series of each premaxilla, 2 to 4 maxillary teeth, 4 or 5 teeth on each dentary, 8 or 9 median predorsal scales, 40 to 43 lateral line scales without a lamellar process over each pore, 4 scale rows between the dorsal-fin origin and the lateral line, 10 to 12 branched anal-fin rays, 7 or 8 gill rakers on the upper limb of the first gill arch, the distance from the snout to the pectoral-fin insertion (21.0%–23.8% of SL), the snout length (24.9%–26.4% of HL), the bony orbital diameter (33.9%–37.4% of HL), the interorbital width (30.7%–33.0% of HL), the lack of contact between

TABLE 5.—Morphometrics and meristics of *Creagrutus anary*: (A) paratype of *C. anary*, ANSP 39291 (specimen in poor condition and holotype of the species is apparently lost; see "Remarks" within species account); and (B) all other specimens of *C. anary* from which counts and measurements were taken (n= 10). Dashes indicate values that could not be determined because of damage to paratype.

Characters	A	B
	Morphometrics	
Standard length	~25.0	25.0–44.5
1. Snout to anal-fin origin	–	60.7–64.5
2. Snout to pelvic-fin insertion	–	44.3–47.5
3. Snout to pectoral-fin insertion	–	21.0–23.8
4. Snout to dorsal-fin origin	–	44.0–48.3
5. Dorsal-fin origin to hypural joint	–	54.0–58.3
6. Dorsal-fin origin to anal-fin origin	–	28.5–32.3
7. Dorsal-fin origin to pelvic-fin insertion	–	24.1–27.5
8. Dorsal-fin origin to pectoral-fin insertion	–	30.5–32.6
9. Caudal peduncle depth	–	9.7–11.4
10. Pectoral-fin length	–	18.9–19.4
11. Pelvic-fin length	–	14.8–16.2
12. Dorsal-fin length	–	21.8–23.5
13. Anal-fin length	–	18.4–19.5
14. Head length	–	23.5–26.1
15. Postorbital head length	–	39.4–42.5
16. Snout length	–	24.9–26.4
17. Bony orbital diameter	–	33.9–37.4
18. Interorbital width	–	30.7–33.0
	Meristics	
Lateral line scales	–[1]	40–43
Scale rows between dorsal-fin origin and lateral line	–[2]	4
Scale rows between anal-fin origin and lateral line	–[3]	3
Predorsal median scales	–[4]	8–9
Branched dorsal-fin rays	8[5]	8
Branched anal-fin rays	12[6]	10–12
Branched pelvic-fin rays	7[7]	6–7
Pectoral-fin rays	13[8]	12–14
Vertebrae	39	38–40

[1]Reported by Fowler (1913) as 40 in paratype and 42 in holotype.
[2]Reported by Fowler (1913) as 5 in both paratype and holotype.
[3]Reported by Fowler (1913) as 3 in paratype and 4 in holotype.
[4]Reported by Fowler (1913) as 9 in paratype and 8 in holotype.
[5]Same value reported by Fowler (1913) for holotype.
[6]Reported by Fowler (1913) as 11 in both paratype and holotype.
[7]Same value reported by Fowler (1913) for holotype.
[8]Same value reported by Fowler (1913) for holotype.

the ventral margin of the third infraorbital and the horizontal limb of the preopercle, the possession of a distinct spot of dark pigmentation at the base of the middle caudal-fin rays, the moderately vertically elongate humeral mark without a secondary, dorsally situated patch of pigmentation, the absence of a distinct patch of pigmentation on the dorsal fin, and the lack of a series of dark spots along the midlateral surface of the body distinguishes *Creagrutus anary* within the clade formed by *Creagrutus* and *Piabina*.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus anary* in Table 5. Head and body moderately robust, body more so in larger females. Greatest body depth at vertical through dorsal-fin origin in most individuals, shifted distinctly anteriorly in specimens with distended abdomens. Dorsal profile of head convex from margin of upper lip to vertical through anterior margin of orbit, nearly straight from that point to tip of supraoccipital spine. Interorbital region distinctly convex transversely. Predorsal profile slightly convex, without obvious change in alignment relative to that of head. Predorsal region of body with obtuse median ridge proximate to dorsal-fin origin. Ventral profile of head slightly convex anteriorly, with barely obvious obtuse angle at anteroventral corner of dentary (angle in ventral profile of dentary not apparent in fig. 16 of Fowler, 1913); head profile nearly straight from that point to isthmus. Profile of prepelvic region of body variably convex, more so in larger specimens. Prepelvic region of body distinctly flattened transversely.

Head obtusely pointed in lateral view, moderately compressed in dorsal view. Upper jaw slightly longer than, and overhanging, lower jaw. Anteromedial portion of snout fleshy with scattered papillae. Scattered papillae distributed over lateral surface of jaw with papillae more concentrated along ventral margin of jaw anteriorly and on plicae and folds extending between outer and medial premaxillary teeth. Lower lip fleshy, with papillae concentrated along dorsal margin and scattered papillae anteromedially.

Infraorbital series relatively well developed. Ventral margin of third infraorbital contacting or nearly contacting horizontal limb of preopercle. Posterior margins of third and fourth infraorbitals falling slightly short of vertical limb of preopercle; posterior margin of fifth infraorbital in, or nearly in, contact with vertical limb of preopercle.

Premaxillary dentition in three series: primary row slightly sigmoid, with 6 teeth, without pronounced gap between first and second tooth of series and with medial teeth of contralateral series distinctly separated; triangular cluster of 3 larger teeth with medial teeth of contralateral clusters nearly in contact; and single tooth of form similar to that of primary series occurring lateral to or slightly anterolateral to fourth tooth of premaxillary row. Maxilla with 2 to 4 tricuspidate teeth. Dentary with 4 or 5 teeth; 3 anterior teeth distinctly larger and tricuspidate with middle cusp much larger; second tooth about twice as high and wide as first tooth and three times as high and four times as wide as third tooth; fourth and fifth teeth (when 5 teeth present) graded in size, fourth always tricuspidate, fifth tricuspidate or with small posterior cusp missing.

Dorsal-fin rays ii,8 in all examined specimens. Dorsal-fin origin at, or approximately at, vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin slightly concave. Anal-fin rays ii or iii,10–12. Anal-fin hooks present on first branched anal-fin ray in mature males. Pectoral-fin rays i,11–13. Tip of pectoral fin extending approximately two-thirds to three-fourths of distance to pelvic-fin insertion. Pelvic-fin rays i,6,i or i,7. Tip of pelvic fin extending to anus or to anal-fin origin.

Gill rakers 7–8 + 10–11.

COLORATION IN ALCOHOL.—Ground coloration of specimens yellow-tan. Dorsal surface of the head with few surface dark chromatophores scattered over anterodorsal region of head and over snout, otherwise without surface pigmentation. Series of very dark, deep-lying stellate chromatophores overlying dorsal portion of brain. Anterior portion of brain overlain by contralateral, horizontally elongate patches of dark chromatophores. Region anterior to nostrils with crescent-shaped patch of dark chromatophores. Anteroventral region of orbit outlined by variably obvious narrow series of dark chromatophores. This series not continuous with chromatophore field anterior to nostrils, nor continuing around ventral and dorsal margins of orbits as in many congeners. Sixth infraorbital and proximate portion of opercle with few scattered dark chromatophores.

Scales of anterodorsal portion of body outlined by single series of dark chromatophores. Middorsal region with field of scattered chromatophores. Obscure midlateral stripe formed of scattered dark chromatophores extending from approximately vertical through dorsal-fin origin to caudal peduncle. Humeral mark moderately obvious and vertically elongate, with variable anterior and posterior margins. Ventral margin of humeral mark extending approximately to lateral line; dorsal margin less discrete, with variably developed series of scattered dark chromatophores extending dorsally from main body of mark.

Dorsal fin with anterior margin of second unbranched ray outlined by dark chromatophores and with membranes between distal one-half to two-thirds of anterior branched rays with scattered chromatophores. Anal-fin rays with chromatophores at base of anterior branched rays. Middle caudal-fin rays with obscure horizontal stripe; stripe most concentrated anteriorly, giving appearance of distinct spot. Pectoral and pelvic fins hyaline.

ECOLOGY.—Stomach contents of two specimens prepared for clearing and staining consisted mostly of parts of small seeds, with limited amounts of insect parts and insect larvae.

DISTRIBUTION.—*Creagrutus anary* is known from the middle portions of Rio Madeira basin in Brazil (Figure 22, squares). The species also has been reported from further upstream in the Department of Madre de Dios, Peru (Chang and Ortega, 1995:2).

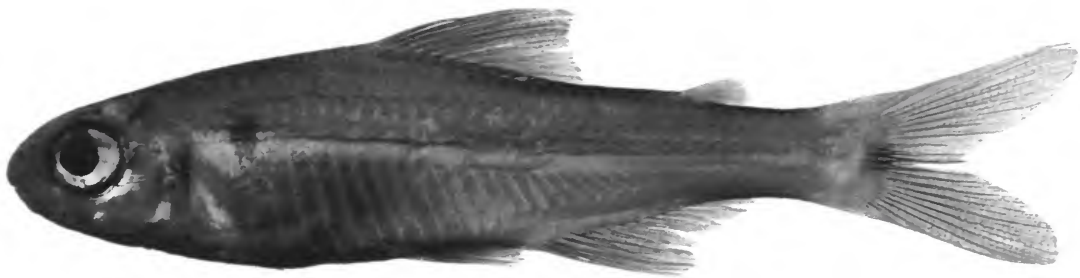

FIGURE 23.—*Creagrutus anary,* MZUSP 35604, 44.5 mm SL; Brazil, Rondônia, Rio Madeira, Cachoeira de Santo Antônio (8°43′S, 63°55′W).

COMPARISONS.—In addition to *Creagrutus anary,* only one other *Creagrutus* species, *C. petilus,* is known to occur in the central portions of the Rio Madeira basin. *Creagrutus anary* and *C. petilus* are readily distinguishable in overall appearance, number of lateral line scales, and head length, snout length, and interorbital width (compare Tables 5 and 46).

REMARKS.—Fowler's description (1913:552) of *Creagrutus anary* was based on a holotype and single paratype collected together with it in the Rio Madeira system (see discussion below with respect to problematic reported type locality). Böhlke (1984:42) reported that the holotype (ANSP 39290) was missing and that the single paratype (ANSP 39291) had been cleared and stained for bone. Examination reveals that the paratype apparently had desiccated at some point prior to being stained. Whether it also had been cleared is uncertain, but if it was so prepared, the residual soft tissues have subsequently darkened to a degree that precludes the examination of internal features.

Despite the evident loss of the holotype and the limited degree of information available from the paratype, the data available from the latter specimen (Table 5) plus information from the original description lead us to equate the material herein considered to be *C. anary* with that species. These specimens agree with the data provided in the original description of the species and demonstrate the unusual dark pigmentation at the base of the middle caudal-fin rays characteristic of *C. anary.*

Type locality and collector for *Creagrutus anary* were reported by Fowler (1913:554) as "Madeira River, about 200 miles east of Long[itude]. W. 62°2′, Brazil" by E.A. Smith. This approximate locality lies in the lower portions of the Rio Madeira. Böhlke (1955:8–12) discussed the problems with various localities cited by Fowler for the specimens collected by Smith. Based on the evidence, Böhlke reasonably proposed that the actual distance was 20 rather than 200 miles east of longitude 62°20′W. Such an interpretation shifts the type locality for *C. anary* further upstream along the Rio Madeira and places it significantly closer to the other collecting sites with exact locality information provided by the collector, E.A. Smith. All nontype material of *C. anary* examined in this study originated in the middle portions of the Rio Madeira basin in the area proximate to where the majority of Smith specimens were collected, a distribution in agreement with Böhlke's suggestion that the type locality cited in the original description of the species was problematic.

Fowler (1913:555) reported the paratype of *C. anary* as "length 34 mm." As noted by Böhlke (1984:42), this was probably total length. The paratype (ANSP 39291) is instead approximately 25 mm SL.

Géry (1977:407), presumably based mostly on information in the literature, proposed that *Creagrutus hildebrandi,* described by Schultz (1944:330) from the Lago Maracaibo basin of northern Venezuela, was as a possible synonym of *C. anary,* which was originally described a considerable distance away in the Rio Madeira basin. Cala (1990:92) followed Géry in this tentative synonymy. Although the pigmentation patterns of the two species are quite similar, *C. hildebrandi* is endemic to the Lago Maracaibo basin and adjoining independent Caribbean versant coastal drainages of northwestern Venezuela (Harold and Vari, 1994, fig. 13). The two species differ in a series of features, most notably in the numbers of lateral line scales (34 to 37 in *C. hildebrandi* versus 40 to 43 in *C. anary*) and vertebrae (35 to 37 in *C. hildebrandi* versus 38 to 40 in *C. anary*).

MATERIAL EXAMINED.—19 specimens (10, 25.0–44.5).

BRAZIL. *Amazonas:* Madeira River (=Rio Madeira), approximately 200 miles (=320 km) E of longitude 62°20′W (see under "Remarks," above, concerning the reported locality), ANSP 39291, 1 (approximately 25 mm, paratype of *Creagrutus anary;* specimen stained for bone and perhaps cleared, in poor condition). Mouth of Igarapé Puruzinho (7°24′S, 63°00′W), MZUSP 35590, 1. Rio Madeira, Ilha do Puruzinho (7°24′S, 63°00′W), MZUSP 35615, 5 (1, 30.5). *Rondônia:* Rio Madeira, Calama (8°04′S, 62°52′W), MZUSP 30575, 4 (1, 29.0). Rio Madeira, Paraná do Caraparu, Calama (8°04′S, 62°52′W), MZUSP 31875, 2 (1, 25.0). Rio Madeira, Cachoeira de Santo Antônio (8°43′S, 63°55′W), MZUSP 35604, 6 (34.1–44.5; 2 specimens cleared and counterstained for cartilage and bone).

Creagrutus atratus, new species

FIGURES 22, 24, 25, TABLE 6

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth in the primary series, typically 6 teeth in primary series of each premaxilla, 3 or 4 maxillary teeth, 5 or 6 teeth on each dentary, 10 to 13 median predorsal scales, 38 to 42 lateral line scales without a lamellar process over each pore, 4, rarely 5, scale rows between the dorsal-fin origin and the lateral line, 3 or 4 scale rows between the anal-fin origin and the lateral line, 9 to 13 branched anal-fin rays, 6 to 8 gill rakers on the upper limb and 8 to 10 gill rakers on the lower limb of the first gill arch, 38 or 39 vertebrae, the postorbital head length (45.5%–52.8% of HL), the bony orbital diameter (24.4%–32.0% of HL), the interorbital width (34.0%–37.9% of HL), the caudal peduncle depth (12.1%–13.6% of SL), the two post-anal median scales to the anal-fin origin, the contact or near contact between the ventral margin of the third infraorbital and the horizontal limb of the preopercle, the lack of a distinct spot of dark pigmentation at the base of the middle caudal-fin rays, the vertically elongate, ventrally tapering humeral mark without a secondary, dorsally situated patch of pigmentation, the absence of a distinct patch of pigmentation on the dorsal fin, and the lack of a series of dark spots along the midlateral surface of the body distinguishes *Creagrutus atratus* within the clade formed by *Creagrutus* and *Piabina*.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus atratus* in Table 6. Head and body relatively robust, increasingly so in larger specimens. Greatest body depth at dorsal-fin origin in specimens of up to about 35 mm SL, shifted anteriorly approximately to midway between pectoral- and pelvic-fin insertions in larger specimens with more rotund prepelvic profiles. Dorsal profile of head distinctly convex from margin of upper lip to vertical through anterior margin of eye, straight or very slightly convex from that point to tip of supraoccipital spine. Interorbital region distinctly rounded overall transversely, but with some median flattening in larger specimens. Dorsal profile of body nearly straight from tip of supraoccipital spine to dorsal-fin origin in specimens smaller than approximately 35 mm SL, increasingly convex in larger specimens, with distinct change in profile relative to that of the head. Predorsal region of body with obtuse median ridge proximate to dorsal-fin origin. Ventral profile of head with obtuse angle at anteroventral corner of dentary, approximately straight from that angle to isthmus. Prepelvic region of body slightly convex in specimens smaller than 30 mm SL, convexity increasing in larger specimens.

Head obtusely pointed in lateral view and somewhat compressed in dorsal view. Upper jaw longer than, and overhanging, lower jaw. Papillae in some individuals much more broadly distributed than in many congeners. Smaller specimens with papillae scattered ove dorsal portion of head, snout, and upper and lower lips. Larger individuals with papillae field more extensive. Some individuals with papillae on dorsal and lateral surfaces of head, including infraorbitals and opercular series, with papillae also present on upper lip and jaw, on folds and plicae extending between outer and medial premaxillary teeth, and on anterior and lateral surfaces of lower jaw. Occasionally papillae extending onto scales of anterodorsal portions of body. Variation in degree of development of papillae field not correlated with any externally obvious sexual differences. No correlation found between numbers of papillae and body size, with comparable-sized specimens collected at same time and location showing significant differences in the extent of papillae fields. Papillae fields poorly developed in

TABLE 6.—Morphometrics and meristics of *Creagrutus atratus*, new species: (A) holotype of *C. atratus*, ICNMHN 4158; and (B) paratypes of *C. atratus* (n =49). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	86.4	35.4–91.5
1. Snout to anal-fin origin	60.5	60.2–67.6
2. Snout to pelvic-fin insertion	48.0	47.0–54.0
3. Snout to pectoral-fin insertion	22.6	22.3–27.6
4. Snout to dorsal-fin origin	45.8	44.8–49.5
5. Dorsal-fin origin to hypural joint	57.1	54.3–59.2
6. Dorsal-fin origin to anal-fin origin	31.1	29.6–35.3
7. Dorsal-fin origin to pelvic-fin insertion	27.9	27.4–34.0
8. Dorsal-fin origin to pectoral-fin insertion	33.4	32.3–36.2
9. Caudal peduncle depth	12.2	12.1–13.6
10. Pectoral-fin length	19.6	18.4–21.3
11. Pelvic-fin length	13.7	13.3–16.7
12. Dorsal-fin length	21.2	19.6–23.5
13. Anal-fin length	15.9	15.5–20.9
14. Head length	24.5	25.5–28.1
15. Postorbital head length	50.0	45.5–52.8
16. Snout length	28.3	26.6–31.6
17. Bony orbital diameter	25.9	24.4–32.0
18. Interorbital width	35.4	34.0–37.9
	Meristics	
Lateral line scales	41	38–42
Scale rows between dorsal-fin origin and lateral line	4	4–5[1]
Scale rows between anal-fin origin and lateral line	3[2]	3–4[2,3]
Predorsal median scales	12	10–13
Branched dorsal-fin rays	8	8
Branched anal-fin rays	12	9–13[4]
Branched pelvic-fin rays	6	5–7[5]
Pectoral-fin rays	12	11–14
Vertebrae	38	38–39

[1]Five scale rows above lateral line present in only 5 of 49 paratypes.

[2]Larger specimens with short sheath of small scales along anterior portion of base of anal fin, giving appearance of an additional row of scales.

[3]Four scale rows below lateral line present in only 4 of 49 paratypes.

[4]Nine anal-fin rays present in only 3 of paratypes, one of these 3 with distinct gap within anal-fin ray series.

[5]Five branched rays present in 1 paratype; 7 branched rays present in 1 paratype.

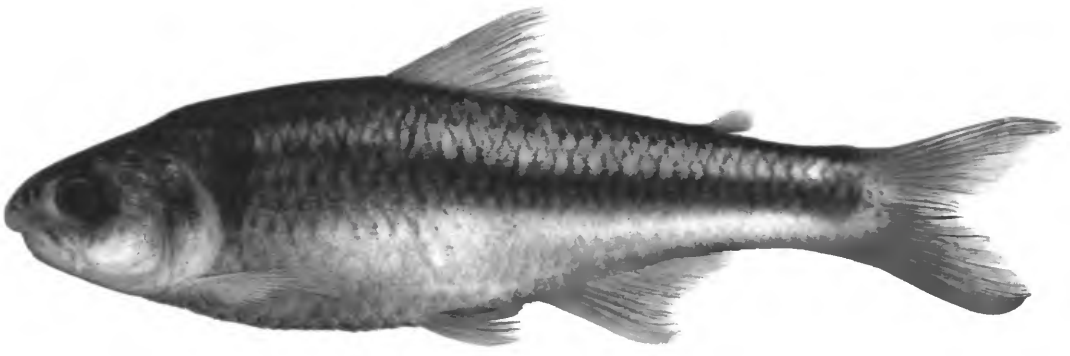

FIGURE 24.—*Creagrutus atratus*, new species, holotype, ICNMHN 4158, 86.4 mm SL; Colombia, Cundinamarca, Río Caqueza, tributary to Río Negro, about 2 km upstream of village of Caqueza.

FIGURE 25.—*Creagrutus atratus*, new species, USNM 353865, 69.5 mm SL; Colombia, Cundinamarca, Río Meta basin, mouth of Río Caqueza.

some available population samples, perhaps reflecting seasonality in their presence.

Infraorbital series relatively well developed. Ventral margin of third infraorbital varyingly curved, deepest portion of third infraorbital contacting, or nearly contacting, horizontal limb of preopercle. Posterior margins of third through fifth infraorbitals distinctly separated from vertical limb of preopercle.

Premaxillary dentition in three series: primary series straight to slightly curved, typically with 6 tricuspidate teeth, but with 5 teeth present as variant on one, or rarely both, premaxillae in some specimens, without pronounced gap between first and second tooth of series but with medial tooth separated from contralateral series by distinct gap; triangular cluster of 3 tricuspidate teeth, all somewhat to distinctly larger than those of primary tooth row; and single tooth comparable in form and size to those of primary series occurring lateral to fourth tooth of primary premaxillary row (when 6 teeth present in primary row) or in area of contact of third and fourth teeth (when 5 teeth present in primary row); second tooth lateral to primary premaxillary row present on one side of head in one specimen. Maxilla with 3 tricuspidate teeth in smaller individuals, with 3 or 4 teeth in larger specimens. Dentary with 5 or 6 teeth. Three anterior dentary teeth distinctly larger and tricuspidate with central cusp largest. Second tooth slightly longer vertically than first tooth and about twice as high as third tooth. Fourth and fifth or sixth teeth slightly tricuspidate and graduated in size.

Dorsal-fin rays typically ii,8; iii,8 in one specimen. Dorsal-fin origin slightly anterior to vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin straight to slightly concave, concavity typically more pronounced in larger individuals. Anal-fin rays ii,9–13 or iii,11–13. Profile of distal margin of anal fin concave, with slight anterior lobe developed in

some specimens. Anal-fin hooks present in mature males of many congeners not present in any of examined specimens of present species. Pectoral-fin rays i,10–13. Tip of pectoral fin reaching posteriorly approximately two-thirds of distance to pelvic-fin insertion. Pelvic-fin rays i,5–7, typically i,6. Tip of pelvic fin reaching posteriorly to anal-fin insertion in some smaller individuals, falling 2 or 3 scales short of that point in larger specimens. Pelvic-fin hooks present in mature males of many congeners not present in any of examined specimens.

Body scales sometimes with papillae (see above); scales extending onto basal region of central portions of each caudal lobe.

Gill rakers 6–8 + 8–10. Some larger individuals have gill rakers on lower portion of first gill arch forked distally.

COLORATION IN ALCOHOL.—Overall dark pigmentation highly variable between samples and within certain lots. Ground coloration tan. Small specimens with light overall head and body coloration having dense field of dark chromatophores overlying brain and less concentrated chromatophore field over anterodorsal portion of head. Other small individuals with more intense overall pigmentation with nearly solid dark pigmentation field on dorsal surface of head. Larger specimens with continuous chromatophore field on dorsal surface of head, but with overall darkness function of intensity of individual chromatophores. Lighter specimens showing crescent-shaped darker chromatophore field anterior to nostril and posteroventrally angled band of dark chromatophores extending from under nostrils to below anteroventral portion of orbit. Both of these pigmentation patterns subsumed into darker head pigmentation in individuals with overall darker coloration. Dispersed dark chromatophores on dorsal portions of first and second infraorbitals, dorsal portion of third infraorbitals, and over fourth and fifth infraorbitals; chromatophore field extending more ventrally on first to third infraorbitals in larger specimens. Region of cheek between posterior margin of third infraorbital and vertical limb of preopercle with vertically elongate chromatophore field continuous dorsally with dark pigmentation situated posterior of orbit. Opercle pigmented other than along its posteroventral one-third in some specimens; pigmentation forming variably shaped, vertically elongate dark mark; spot more extensive in individuals with overall darker pigmentation.

Scales of dorsolateral portion of body with dark chromatophores concentrated along margin of scales and forming reticulate pattern. Humeral mark vertically elongate and ventrally tapering. Mark extending from about one scale ventral of lateral line to one and one-half scales from dorsal midline. Humeral mark distinct in lightly colored specimens, especially smaller individuals, somewhat less distinct, albeit still obvious, in most darker specimens, and nearly completely subsumed into overall body pigmentation in very dark individuals. Broad midlateral stripe extending from posterior margin of humeral mark to rear of caudal peduncle. Pigmentation of stripe consisting both of band of deep-lying, diffuse, dark coloration and of discrete, dark chromatophores overlying scales.

Distal one-fourth to two-thirds of dorsal-fin rays with small dark chromatophores outlining rays and ray segments; scattered chromatophores over intervening membranes, usually not extending as far basally as pigmentation located along ray margins. Specimens with particularly dark overall pigmentation having dusky region extending across middle portion of dorsal fin. Caudal-fin rays outlined by chromatophores, giving fin dusky appearance; pigmentation more intense in overall darker specimens, with middle caudal-fin rays darker than remainder of fin, albeit not forming discrete stripe; ventral lobe of caudal fin usually more intensely pigmented than dorsal lobe, but with difference less obvious in very dark specimens. Anal fin ranging from hyaline to having distal one-half to two-thirds of rays outlined by small dark chromatophores with scattered chromatophores on intervening membranes. Individuals with particularly dark overall pigmentation with region of dusky pigmentation extending along middle section of anterior half of fin. Pelvic fin ranging from hyaline to having rays outlined by small, dark chromatophores. Pectoral-fin rays outlined by chromatophores, more so in darker individuals.

ETYMOLOGY.—The specific name, *atratus,* from the Latin for dressed in black, refers to the dark coloration of the type series and many of the available specimens.

ECOLOGY.—*Creagrutus atratus* occurs with *C. bolivari* at least in two localities, as shown by some examined lots.

DISTRIBUTION.—*Creagrutus atratus* occurs in the western portions of the Río Orinoco basin in the foothills of the eastern Cordillera of the Andes (Figure 22, stars).

MATERIAL EXAMINED.—97 specimens (55, 35.4–91.5).

HOLOTYPE.—COLOMBIA. *Cundinamarca:* Río Meta basin, Río Caqueza, tributary to Río Negro, about 2 km upstream of village of Caqueza (latter at 4°25′N, 73°57′W), collected by A.M.C. Silfvergrip, 5 Dec 1987, ICNMHN 4158, 1 (86.4).

PARATYPES.—49 specimens (49, 35.4–91.5).

COLOMBIA. *Cundinamarca:* Río Meta basin, Río Caqueza, tributary to Río Negro, about 2 km upstream of village of Caqueza (latter at 4°25′N, 73°57′W), collected with holotype, NRM 16842, 19 (48.5–89.3); USNM 353866, 5 (51.3–80.8). Río Meta basin, backwater of Río Negro, at Caqueza (4°27′N, 73°53′W), collected by J.E. Böhlke et al., 4 Apr 1975, ANSP 134080, 5 (49.3–69.6). Río Meta basin, Río Sanane, where emptying into Río Negro (approximately 4°20′N, 73°52′W), collected by A.M.C. Silfvergrip, 19 Dec 1987, NRM 16843, 15 (35.4–91.5); USNM 353867, 5 (47.5–67.7; 2 specimens cleared and counterstained).

NONTYPE SPECIMENS.—47 specimens (5, 46.3–70.1).

COLOMBIA. *Cundinamarca:* Río Meta basin, mouth of the Río Caqueza, where emptying into Rio Negro, NRM 16841, 32; USNM 353865, 5 (46.3–70.1). *Meta:* Río Meta basin, Río Guayuriba, where crossed by road between Villavicencio and Acacías, NRM 16852, 2; NRM 16851, 5. Río Meta basin, Río Guayuriba, approximately 4 km south of village of Santa Rosa, NRM 16850, 3.

Creagrutus atrisignum Myers, 1927

FIGURES 22, 26, TABLE 7

Creagrutus beni [not of Eigenmann, 1911].—Eigenmann, 1927:421 [misidentification] [in part, citation of species in Rio Tocantins basin; specimen from Brazil, Rio Tocantins, Cachoeira de Valpa de Rio Nova, near Piabana; not citations of *C. beni* from other regions of South America].

Creagrutus atrisignum Myers, 1927:116 [type locality: [Brazil], Goyaz (= Goiás), upper Rio Maranhão (upper Rio Tocantins basin)].—Eigenmann and Myers, 1929:549 [based on Myers, 1927].—Fowler, 1948:83 [literature compilation]; 1975:25 [literature compilation].—Géry, 1977:407, 410 [in key, drawing of paratype].

DIAGNOSIS.—The form of the dark humeral mark in *Creagrutus atrisignum* consisting of a primary variably horizontally elongate central portion and a distinct, smaller, secondary dorsal component, with the two components joined in some individuals by a narrow band of dark chromatophores is autapomorphic within the assemblage consisting of *Creagrutus* and *Piabina*. *Creagrutus atrisignum* is further distinguished in the clade consisting of *Creagrutus* and *Piabina* by the combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a pronounced gap between the first and second teeth of the primary series, 2 to 4 maxillary teeth, 4 teeth in each dentary, 9 to 11 median predorsal scales, 5 scale rows between the dorsal-fin origin and the lateral line, 9 or 10 branched anal-fin rays, 2 post-anal scales anterior to the anal-fin origin, the well-developed third infraorbital with its ventral margin contacting the horizontal limb of the preopercle, the lack of a series of dark spots along the midlateral surface of the body, the discrete humeral marks whose two components, although encompassing a vertically elongate area, do not form a vertical bar, and the lack of a discrete patch of dark pigmentation on the anterior portion of the middle of the dorsal fin.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus atrisignum* in Table 7. Head and body moderately robust (Figure 26). Greatest body depth at, to somewhat anterior of, dorsal-fin origin; typically more anterior in larger specimens. Dorsal profile of head smoothly convex from margin of upper lip to vertical through posterior nostril, straight from that point to tip of supraoccipital spine. Interorbital region smoothly convex transversely. Anterior portion of predorsal region of body continuing profile of posterior portion of head; profile becoming more curved posteriorly but without pronounced change in alignment relative to that of head in most specimens. Predorsal region of body somewhat flattened transversely anteriorly, with median ridge proximate to dorsal-fin origin. Ventral profile of head with variably obvious obtuse angle at anteroventral corner of dentary, nearly flat from angle to isthmus. Prepelvic profile of body convex, more so in many larger specimens.

Head obtusely pointed in lateral view, less so in dorsal view. Upper jaw distinctly longer than, and overhanging, lower jaw. Anteromedial portion of snout fleshy with scattered papillae. Papillae more concentrated on fleshy upper lip, especially along ventral margin of lip and on folds and plicae extending between outer and medial premaxillary teeth. Lower lip very fleshy with numerous papillae distributed over dorsal and anterior surfaces.

Infraorbital series well developed. Ventral margin of third infraorbital contacting horizontal limb of preopercle. Posterior margins of third through fifth infraorbitals slightly separated from vertical limb of preopercle.

Premaxillary dentition in three series: primary row curved, usually with 6, occasionally 5, tricuspidate teeth without pronounced gap between first and second tooth of series but with medial tooth separated from medial tooth of contralateral series by distinct gap; triangular cluster of 3 teeth distinctly larger than those of primary series; and single tooth of form similar to that of primary series occurring lateral to fourth tooth of primary premaxillary row (when 6 teeth present in primary series) or lateral to gap between third and fourth teeth (when 5 teeth present in primary series). Maxilla with 2 to 4 tricuspidate teeth. Dentary with 4 tricuspidate teeth, anterior and posterior cusps barely apparent on posteriormost tooth; second tooth dis-

TABLE 7.—Morphometrics and meristics of *Creagrutus atrisignum:* (A) holotype of *C. atrisignum*, CAS 41339 (formerly IU 17679); and (B) all other specimens of *C. atrisignum* from which counts and measurements were taken (n= 30). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	46.0	37.2–55.2
1. Snout to anal-fin origin	64.6	61.5–68.0
2. Snout to pelvic-fin insertion	49.1	45.4–49.6
3. Snout to pectoral-fin insertion	23.9	22.9–26.2
4. Snout to dorsal-fin origin	51.1	47.5–51.3
5. Dorsal-fin origin to hypural joint	56.5	52.9–56.9
6. Dorsal-fin origin to anal-fin origin	32.6	29.3–32.8
7. Dorsal-fin origin to pelvic-fin insertion	28.5	25.7–28.9
8. Dorsal-fin origin to pectoral-fin insertion	33.9	31.2–35.0
9. Caudal peduncle depth	12.2	11.2–12.3
10. Pectoral-fin length	20.9	19.1–21.9
11. Pelvic-fin length	16.1	14.8–17.4
12. Dorsal-fin length	22.6	20.6–23.5
13. Anal-fin length	16.4	16.4–19.4
14. Head length	27.0	25.5–28.0
15. Postorbital head length	44.4	44.1–45.8
16. Snout length	28.6	28.4–31.7
17. Bony orbital diameter	32.3	31.4–37.1
18. Interorbital width	30.6	30.4–33.3
	Meristics	
Lateral line scales	37	36–38
Scale rows between dorsal-fin origin and lateral line	5	5
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	9	9–11
Branched dorsal-fin rays	8	8
Branched anal-fin rays	10	9–10
Branched pelvic-fin rays	6	6
Pectoral-fin rays	12	12–13
Vertebrae	36	35–37

tinctly larger than first and about twice as high as third; fourth tooth distinctly smaller than third.

Dorsal-fin rays ii,8 in all specimens. Dorsal-fin origin approximately at vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin straight to very slightly concave. Anal-fin rays ii,9–10 or iii,9. Profile of distal margin of anal fin straight to slightly concave. Mature males with hooks typically present on anterior 3 or 4 branched rays, hooks rarely present on fifth branched anal-fin ray. Pectoral-fin rays i,11–12. Tip of pectoral fin extending approximately two-thirds distance to pelvic-fin insertion. Pelvic-fin rays i,6,i in all specimens. Tip of pelvic fin extending to anal-fin origin in smaller specimens, falling short of that point and extending posteriorly only to anus in larger individuals. Mature males with hooks present on all branched pelvic-fin rays.

Gill rakers 7–8+11–13.

COLORATION IN ALCOHOL.—Head and body of specimens retaining guanine on scales somewhat silvery. Ground coloration of specimens lacking guanine on scales tan. Dorsal surface of head with scattered, dark, small chromatophores. Large stellate chromatophores overlying membranes of dorsal surface of brain. Dorsal surface of snout and upper lip with field of dense chromatophores; chromatophore field more concentrated anterior to nostrils, but only forming discrete crescent-shaped dark pigment patch in larger specimens. Region anteroventral to nostrils with field of chromatophores, but this pigmentation not continuing around ventral and posterior margins of orbit as in many congeners. Dorsal portions of opercle and infraorbital series with patch of chromatophores forming irregular horizontal stripe behind orbit.

Scales of dorsolateral surface of body in specimens over approximately 35 mm SL with basal patch of dark chromatophores and irregular series of chromatophores along distal margin. Region between chromatophore fields hyaline. Overall pigmentation of scales most prominent immediately ventral of dorsal-fin base, and somewhat less so middorsally. Humeral mark dark at all examined sizes, shape ontogenetically variable, rotund in specimens of approximately 20–30 mm SL, slightly horizontally elongate in some specimens of approximately 35 mm SL, and distinctly horizontally elongate and usually wider along its posterior one-half in larger individuals. Variably present series of dark chromatophores less concentrated than those of main body of humeral mark extending ventrally from main portion of mark in larger individuals. Second patch of concentrated chromatophores situated approximately one scale dorsal of anterior portion of main humeral mark. Secondary patch of humeral pigmentation absent in specimens of 20–30 mm SL, slightly developed in specimens of approximately 35 mm SL, and obvious in larger specimens. Two areas of dark humeral pigmentation ranging from completely separated to joined by a thin vertical band of dark chromatophores. Midlateral body stripe formed by both surface and deep-lying chromatophores. Anterior portion of stripe diffuse, extending anteriorly approximately to under middle of dorsal fin in smaller individuals, nearly to posterior margin of humeral mark in larger specimens. Stripe typically most intense on posterior one-half of body and extending onto basal portions of middle caudal-fin rays.

Dorsal fin with last unbranched and anterior branched rays overlain with dark chromatophores and with distal one-half of following 3 or 4 branched rays with scattered, dark chromatophores. Membranes of pigmented rays with numerous dark chromatophores anteriorly and scattered chromatophores posteriorly. Chromatophores on rays and membranes in combination form a diffuse, but obvious, dark spot. Basal portions of anal-fin rays outlined with small dark chromatophores. Caudal-fin rays outlined with small dark chromatophores, giving fin overall dusky appearance. Dense concentration of chromatophores on basal portions of middle caudal-fin rays forming irregular spot variably continuous with midlateral stripe, spot particularly prominent in smaller individuals. Pectoral and pelvic fins typically hyaline, sometimes with few scattered, dark chromatophores.

ECOLOGY.—Stomach contents of specimens prepared for clearing and counter staining consisted solely of parts of larval insects.

DISTRIBUTION.—*Creagrutus atrisignum* is apparently limited to the Rio Maranhão basin, a tributary of the upper Rio Tocantins (Figure 22, triangles).

REMARKS.—A portion of the paratype series of *Creagrutus atrisignum* is a lot of seven specimens (CAS 41340). One paratype is not *Creagrutus* but rather an individual of *Bryconamericus* or a similar genus.

The type series and many of the other examined lots of *Creagrutus* were collected by Carl Ternetz in the Rio Maranhão system, an upper tributary of the Rio Tocantins in the state of Goiás, Brazil. Although it impossible to determine the exact location of many of the collecting sites report by Ternetz, the available information indicates that they all lie within the Rio Maranhão basin.

MATERIAL EXAMINED.—130 specimens (30, 37.2–55.2).

BRAZIL. *Goiás:* Rio Maranhão "into Rio Tocantins," upper Rio Tocantins basin, CAS 41339, 1 (46.0, holotype of *Creagrutus atrisignum,* formerly IU 17679). Córrego do Monjolo, tributary of Rio Maranhão, CAS 69260, 7 (6, 45.4–51.2, paratypes of *Creagrutus atrisignum,* formerly IU 17680, in part; see under "Remarks," above, concerning identity of other specimen in lot); MCZ 31571, 1 (47.5, paratype of *Creagrutus atrisignum*). Rio Arial-Velho "into Rio Maranhão" (approximately 15°20′S, 47°58′W), CAS 69241, 1 (37.2). Rio Maranhão, at Aqua Quente, CAS 69504, 1 (42.5). Rio Bom-Jesus "into Rio Maranhão," CAS 69240, 3 (1, 44.6). Salobro "Brook" (?=Córrego Salobro, 15°13′S, 48°08′W), CAS 69260, 3 (50.5–55.2). Niquelândia, Rio do Peixe, right bank tributary of Rio Maranhão (14°28′S, 48°45′W), MNRJ 12662, 16 (14, 37.8–53.5), USNM 341516, 2 (41.4–49.8). Município de Niquelândia, Ribeirão do Engenho, along road from Niquelândia to Codemin, 29 km S of Codemin (14°25′S, 48°28′W),

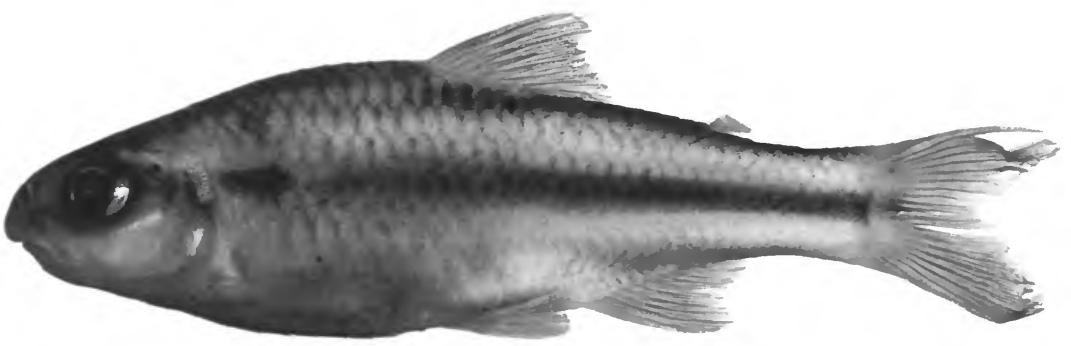

FIGURE 26.—*Creagrutus atrisignum*, MNRJ 12662, 52.7 mm SL; Brazil, Goiás, Niquelândia, Rio Maranhão basin, Rio do Peixe (14°28′S, 48°45′W).

MCP 15929, 54; USNM 341479, 3 (1 specimen cleared and counterstained for cartilage and bone). Município de Niquelândia, Rio Bacalhau, along road from Niquelândia and Colinas (14°32′S, 48°23′W), MCP 15944, 18. Município de Niquelândia, Córrego Fundo, along road from Niquelândia and Colinas (14°28′S, 48°18′W), MCP 15960, 20.

Creagrutus barrigai, new species

FIGURES 27, 28, TABLE 8

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 2 or 3 maxillary teeth, 5 teeth on each dentary, 36 to 38 vertebrae, 13 to 15 branched anal-fin rays, 8 to 10 predorsal scales, 4 scale rows between the lateral line and the dorsal-fin origin, 6 to 8 gill rakers on the upper limb of the first gill arch, the well-developed third infraorbital contacting the horizontal limb of the preopercle, the postorbital head length (34.2%–40.9% of HL), the bony orbital diameter (36.2%–42.0% of HL), the lack of a series of dark midlateral spots on the body, the vertically elongate humeral mark, and the laterally compressed, relatively deep body distinguish *C. barrigai* from all congeners other than *C. manu* and *C. pearsoni*. *Creagrutus barrigai* can be separated from *C. manu* by the distance from the snout to the anal-fin origin (58.5%–63.4% of SL versus 63.5%–66.4% of SL, respectively) and the absence in *C. barrigai* of the dark midlateral stripe present in *C. manu*. *Creagrutus barrigai* can, in turn, be discriminated from *C. pearsoni* by differences in the distance from the snout to the dorsal-fin origin (45.4%–49.2% of SL versus 49.4%–52.9% of SL, respectively), the anal-fin length (18.0%–20.7% of SL versus 15.6%–17.4% of SL, respectively), the postorbital head length (34.2%–40.9% of HL versus 41.0%–45.1% of HL, respectively), and the number of scale rows between the lateral line and dorsal-fin origin (4 versus 5 or 6, respectively).

DESCRIPTION.—Morphometric and meristic data for *Creagrutus barrigai* in Table 8. Head and body relatively compressed compared with other members of genus, degree of compression somewhat more pronounced in larger specimens. Body depth relatively greater than in most other *Creagrutus* species; greatest body depth at dorsal-fin origin at all sizes. Dorsal profile of head moderately convex from tip of snout to vertical through nostrils, nearly straight from that point to tip of supraoccipital spine. Dorsal profile of body very slightly convex predorsally, without distinct change in alignment relative to that of head. Predorsal surface of body with obtuse median ridge proximate to dorsal-fin origin. Ventral profile of head with obvious obtuse angle at anteroventral corner of dentary, very slightly convex from that angle to isthmus. Prepelvic profile of body convex; convexity more pronounced in larger individuals. Prepelvic region obtusely flattened transversely, more obviously so in larger specimens.

Head obtusely rounded in lateral view, relatively compressed in dorsal view. Upper jaw somewhat longer than, and overhanging, lower jaw. Snout slightly fleshy anteromedially, with papillae scattered over anterior portions. Papillae common on lateral surface of upper jaw and on folds and plicae extending between outer and medial premaxillary teeth. Lower lip fleshy anteriorly with numerous papillae on dorsal surface and scattered papillae anteriorly and anteroventrally.

Infraorbital series relatively well developed and nearly covering cheek. Third infraorbital horizontally elongate, with ventral margin contacting horizontal limb of preopercle. Posterior margins of third through fifth infraorbitals nearly in contact with vertical limb of preopercle.

Premaxillary dentition in three series: primary row curved, with 5 or 6 teeth without pronounced gap between first and second teeth, but with medial tooth separated from anterior tooth

TABLE 8.—Morphometrics and meristics of *Creagrutus barrigai*, new species: (A) holotype of *C. barrigai*, MEPN 4621; (B) paratypes of *C. barrigai* (n=32); and (C) all Ecuadorian and Peruvian samples of *C. barrigai* from which counts and measurements were taken (n=7; see comments under "Remarks," concerning samples of the species from western Brazil). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B	C
		Morphometrics	
Standard length	46.9	19.1–46.5	19.1–53.3
1. Snout to anal-fin origin	59.1	58.5–63.3	58.5–63.4
2. Snout to pelvic-fin insertion	45.8	45.2–48.9	45.2–48.9
3. Snout to pectoral-fin insertion	23.7	22.9–25.3	22.9–25.3
4. Snout to dorsal-fin origin	46.3	45.4–49.0	45.4–49.2
5. Dorsal-fin origin to hypural joint	56.9	54.4–59.4	54.4–59.4
6. Dorsal-fin origin to anal-fin origin	35.4	32.6–39.3	32.6–39.3
7. Dorsal-fin origin to pelvic-fin insertion	31.8	29.1–36.4	29.1–36.4
8. Dorsal-fin origin to pectoral-fin insertion	35.0	33.5–37.5	33.0–37.5
9. Caudal peduncle depth	11.5	11.0–12.9	11.0–13.1
10. Pectoral-fin length	19.6	18.6–21.5	18.5–21.5
11. Pelvic-fin length	16.0	14.2–17.5	13.7–17.5
12. Dorsal-fin length	24.7	24.4–27.0	24.4–27.3
13. Anal-fin length	18.5	18.0–20.7	18.0–20.7
14. Head length	24.5	24.4–26.4	24.4–26.4
15. Postorbital head length	39.1	34.2–39.9	34.2–40.9
16. Snout length	24.3	23.6–28.2	23.3–28.2
17. Bony orbital diameter	40.0	36.2–41.7	36.2–42.0
18. Interorbital width	32.2	31.6–34.6	30.9–34.6
		Meristics	
Lateral line scales	39	36–39	36–39
Scale rows between dorsal-fin origin and lateral line	4	4	4
Scale rows between anal-fin origin and lateral line	3	3	3
Predorsal median scales	10	8–10	8–10
Branched dorsal-fin rays	8	8	8
Branched anal-fin rays	15	13–15	13–15
Branched pelvic-fin rays	6	6	6
Pectoral-fin rays	12	12–14	12–14
Vertebrae	38	36–38	36–38

of contralateral series by distinct gap; triangular cluster of 3 larger teeth; and single tooth of form similar to that of primary series occurring lateral to fourth tooth, or lateral to area of contact of third and fourth teeth of primary row. Maxilla with 3, rarely 2, tricuspidate teeth. Dentary with 5 tricuspidate teeth; first and second distinctly larger than remaining teeth; second tooth slightly larger than first and both of these teeth approximately three times size of third tooth. Fourth and fifth teeth graded in size, more compressed than anterior teeth.

Dorsal-fin rays ii,8 in all specimens. Dorsal-fin origin approximately at vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin moderately concave. Anal-fin rays ii,13–15 or iii,14–15; first anal-fin ray short when three rays present. Profile of distal margin of anal fin distinctly concave, anterior anal-fin rays forming distinct lobe. Mature males with hooks present on first, or first and second, branched anal-fin rays. Pectoral-fin rays i,11–13. Tip of pectoral fin extending posteriorly slightly over three-fourths of distance to pelvic-fin insertion. Pelvic-fin rays i,6,i in all specimens. Tip of pelvic fin extending posteriorly to, or slightly beyond, anus. Mature males with hooks typically present on all branched pelvic-fin rays, or with hooks rarely absent on lateralmost branched ray.

Gill rakers 6–8+9–13.

COLORATION IN ALCOHOL.—Ground coloration tan. Dorsal surface of head with scattered, dark chromatophores slightly more concentrated on posterior portion of head and over snout. Deep-lying field of dark chromatophores overlying brain. Chromatophore field anterior to nostrils slightly more concentrated, forming indistinct crescent. Ventral and dorsal margins of orbit outlined by variably obvious narrow band of dark chromatophores. Scattered, dark chromatophores variably present posteriorly on dorsal portions of infraorbital series and proximate region of lateral surface of head.

Scales of dorsal portion of body with small dark chromatophores concentrated along posterior scale margin. Deeper-lying series of chromatophores under scales aligned with series of chromatophores along margins of overlying scale, with two chromatophore fields together giving overall reticulate appearance to that portion of body. Scales of midlateral region of body with scattered chromatophores without definite pattern. Humeral mark somewhat indistinct. Anterior and posterior

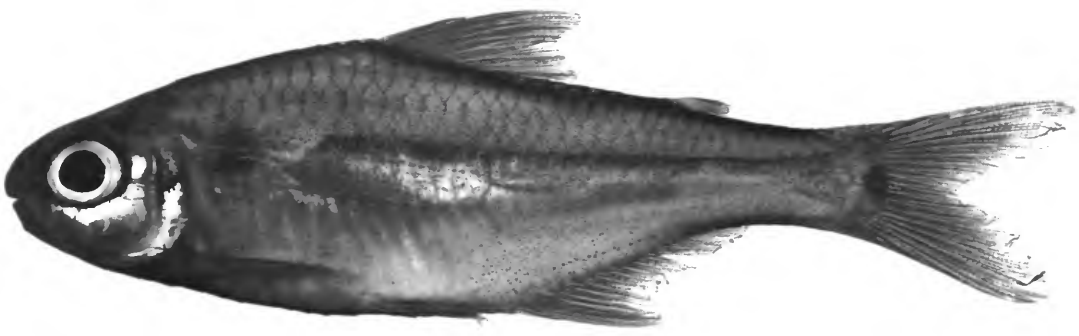

FIGURE 27.—*Creagrutus barrigai,* new species, holotype, MEPN 4621, 46.9 mm SL; Ecuador, Sucumbíos, Río Aguarico, near San Pablo de Kantesiya (0°15′18″S, 76°25′30″W).

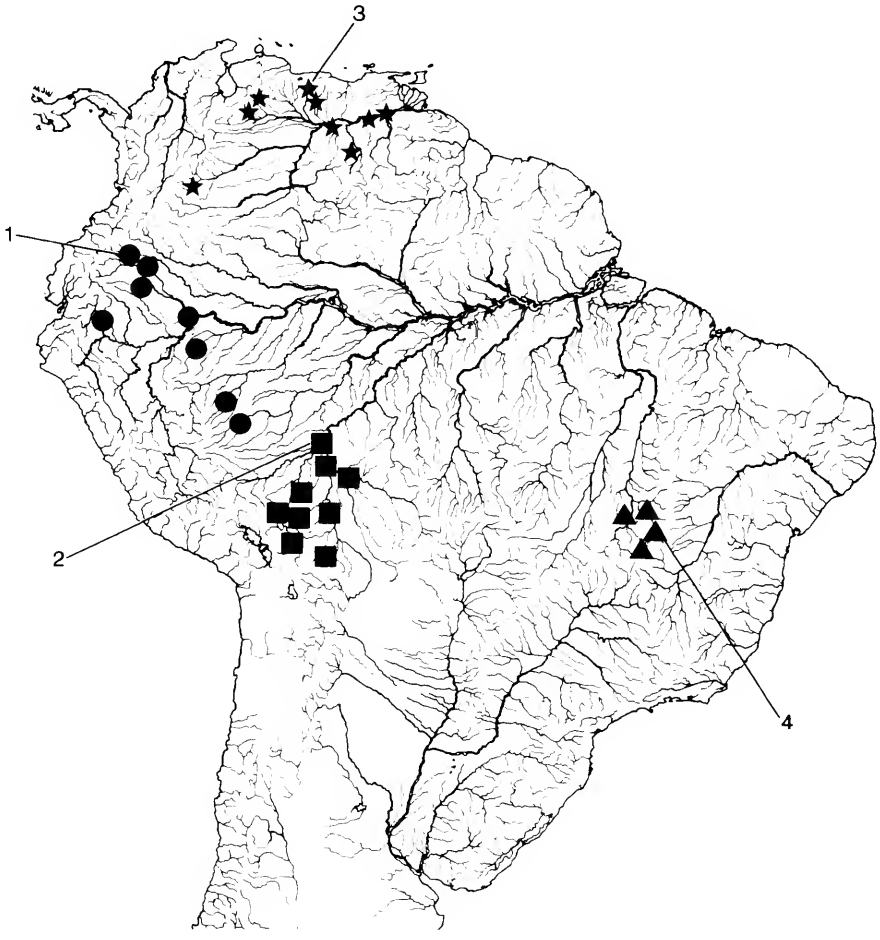

FIGURE 28.—Map of central and northern South America showing geographic distribution of *Creagrutus barrigai* (dots, 1=type locality), *Creagrutus beni* (squares, 2=type locality), *Creagrutus bolivari* (stars, 3=type locality), and *Creagrutus britskii* (triangles, 4=type locality) (some symbols represent more than one locality or lot of specimens).

margins of mark ranging from straight to somewhat bowed both anteriorly and posteriorly. Dorsal region of humeral mark merging into chromatophore field of dorsal portion of body, with ventral portion of mark sometimes continued ventrally as variably developed field of scattered, dark chromatophores. Faint lateral stripe formed mostly of dark surface chromatophores present approximately one scale dorsal of lateral line; stripe beginning slightly anterior of vertical through dorsal-fin origin and extending onto caudal peduncle.

Dorsal fin with anterior unbranched ray and basal portions of second unbranched rays and anterior branched rays outlined with small, dark chromatophores. Membranes of distal two-thirds of dorsal fin with scattered, dark chromatophores. Anal-fin membranes with scattered chromatophores; chromatophores less common on membranes of anterior and posterior rays. Caudal-fin rays with scattered chromatophores; chromatophores typically most concentrated on basal portions of middle caudal-fin rays, giving dusky appearance to that region. Some individuals with faint horizontal stripe along middle caudal-fin rays. Pectoral and pelvic fins ranging from hyaline in smaller specimens to having scattered, dark chromatophores in larger individuals.

ETYMOLOGY.—The species name, *barrigai,* is in honor of Ramiro Barriga of the Universidad Politecnica, Quito, Ecuador, in recognition of his many contributions to our knowledge of the freshwater fishes of Ecuador and of his assistance to the authors in this and other projects.

ECOLOGY.—Two juvenile, nontype specimens collected in the Río Aguarico basin along the Ecuador-Peru frontier (USNM 329815) came from a slow-moving, clear-water stream. Mature males, as indicated by the presence of well-developed anal and pelvic-fin hooks, range from 32.1 to 41.2 mm SL, whereas females collected with those specimens reach notably larger sizes, 40.7–53.3 mm SL.

Examination of the stomach contents of two specimens prepared for clearing and staining indicated that they fed exclusively on insects.

DISTRIBUTION.—*Creagrutus barrigai* occurs in the western portions of the Amazon basin in northeastern Peru, northeastern Ecuador, and western Brazil (Figure 28, dots).

GEOGRAPHIC VARIATION.—*Creagrutus barrigai* is known from scattered localities in the western portion of the Amazon basin. Most examined samples originated in the Río Napo system, with the majority being from the Río Aguarico basin of northeastern Ecuador. Distinctly separated from those collections geographically are samples herein considered to be that species from the Río Santiago system of northeastern Peru, the upper portions of the Rio Juruá and Rio Purus in Acre, Brazil, and the Río Javari in western Amazonas, Brazil (see, however, comments below concerning the Brazilian samples). No differences were found between the population samples of *C. barrigai* from various localities in Ecuador and Peru.

One specimen in poor condition (NRM 16860) from the Rio Javari along the Brazilian-Peruvian frontier, and three specimens from the Rio Tarauacá in the upper portions of the Rio Juruá in Acre, Brazil, apparently represent a major range extension to the southeast for *C. barrigai* beyond the core distribution of the species in Ecuador and Peru. Although agreeing with the Peruvian and Ecuadorian samples of this species in pigmentation and the vast majority of meristic and morphometric features, the limited Brazilian samples of *C. barrigai* for which radiographs are available, differ in having 36 or 37 vertebrae with 36 vertebrae most common (36, n=5; 37, n=2). Samples of the species from Peru and Ecuador, in contrast, have 36 to 38 vertebrae, but with a mode of 37 vertebrae (36, n=6; 37, n=82; 38, n=18). The proportional postorbital head length of these Brazilian samples (37.5%–42.9% of HL) also is at the upper range of this proportion for the species, and extends slightly beyond the highest value for that feature in the Peruvian and Ecuadorian samples (34.2%–40.9% of HL). Additional samples from throughout the western portions of the Amazon are necessary to determine the significance, if any, of these differences.

MATERIAL EXAMINED.—216 specimens (40, 19.1–53.3).

HOLOTYPE.—ECUADOR. *Sucumbíos:* Río Aguarico, near San Pablo de Kantesiya (0°15′18″S, 76°25′30″W), collected by D.J. Stewart et al., 23 Nov 1983, MEPN 4621, 1 (46.9).

PARATYPES.—32 specimens (32, 19.1–46.5).

ECUADOR. *Sucumbíos:* Río Aguarico, near San Pablo de Kantesiya (0°15′18″S, 76°25′30″W), collected with holotype, MEPN uncataloged, 10 (31.6–45.4); USNM 340977, 4 (33.6–46.4). Río Aguarico, near Destacamento Militar Cuyabeno and mouth of Río Cuyabeno in the Río Aguarico (0°15′30″S, 75°53′30″W), collected by R. Barriga et al., MEPN 5252, 7 (19.1–34.7); USNM 340978, 3 (23.0–33.6). Río Aguarico, near mouth of stream draining from Laguna Zancudo Cocha, upstream of Zancudo (0°33′S, 75°30′W), USNM 340976, 8 (40.3–46.5; 2 specimens cleared and counterstained for cartilage and bone).

NONTYPE SPECIMENS.—183 specimens (7, 27.8–53.3).

BRAZIL. *Amazonas:* Rio Javari basin, right bank sand playa immediately downstream of confluence of Rio Jaquirana and Rio Gálvez (approximately 5°10′S, 72°53′W), NRM 16860, 1. *Acre:* Tarauacá, Rio Tarauacá (approximately 8°10′S, 70°40′W), MZUSP 30573, 4 (3, 33.7–48.8); MZUSP 30574, 30. Rio Acre between Seringal Paraiso and Lago Amapá, MZUSP 49761, 35. Rio Acre, Seringal Floresta, 10 minutes above Boca do Acre (latter at 8°45′S, 67°23′W), MZUSP uncataloged ex. MZUSP 49600, 1.

ECUADOR. *Napo:* Río Napo near Pompeya (0°26′30″S, 76°28′12″W), MZUSP 38678, 10. Río Jivino, lower 4 km to approximately 0.6 km upstream from mouth (between the two "ports" for Limonococha, FMNH 106030, 43.

PERU. *Amazonas:* Río Santiago at La Poza (4°01′S, 77°47′W), LACM 39913-16, 49 (4, 27.8–53.3). *Loreto:* Provincia Maynas, Puesto de Vigilancia Arcadia, Quebrada Isla, Río Napo (approximately 1°00′S, 75°18′W), USNM 328575, 3. Río Napo, mouth of Río Mazan, INHS 36601, 7.

Creagrutus beni Eigenmann, 1911

FIGURES 28, 29, TABLE 9

Creagrutus beni Eigenmann, 1911:172, pl. 6: fig. 2 [type locality: Villa Bella on Río Beni (=Bolivia, El Beni, Río Beni, Villa Bella); not specimen from Cachoeira de Velha de Rio Nova, Brazil, cited in footnote]; 1927:421, pl. 58: fig. 3, pl. 93: fig. 4 [Bolivia (El Beni), Río Beni, Villa Bella; not remaining cited specimens or reported distribution of species in Colombia and Venezuela; not pl. 93: figs. 5, 7].—Henn, 1928:63 [presence of holotype in Carnegie Museum].—Pearson, 1937b:108 [Bolivia, Río Beni and Mamoré basins; not cited occurrence of species in Amazon basin outside Río Beni system or citation of species in Río Magdalena, Colombia].—Eigenmann and Allen, 1942:228 [Bolivia, Río Beni; not listed specimens or cited distribution of species outside of Río Beni basin].—Fowler, 1945a:148 [literature compilation; not citations for Río Marañon, Peru, or cited distribution outside Bolivia]; 1948:83, fig. 88 [literature compilation; not citations of occurrence of species outside Bolivia]; 1975:26 [listing].—Géry, 1964:60 [in key, not cited occurrence of species in Peru, [Río] Meta of Columbia, and Venezuela].—Terrazas-Urquidi, 1970:25 [listing in fishes of Bolivia].—Lauzanne and Loubens, 1985:110 [Bolivia: Río Mamoré basin].—Ibarra and Stewart, 1987:28 [holotype depository].—Lauzanne et al., 1991:66 [Bolivia: Río Chapare and Río Boopi].—Not Eigenmann, 1920:12; 1921, pl. 93: fig. 7; 1922:238.—Not Pearse, 1920:12, 25, 43.—Not Fowler, 1931:408; 1942:134; 1943a:238; 1945b:102.—Not Pearson, 1937a:92.—Not Beebe, 1945:84; 1948:149.—Not Pozzi, 1945:270.—Not Fernández-Yépez, 1952: 43.—Not Luengo, 1963:326.—Not Mago-Leccia, 1967:233; 1970:70.—Not Géry, 1972:66.—Not Saul, 1975:106.—Not Cala, 1977:7.—Not Ortega and Vari, 1986:8.—Not Stewart et al., 1987:26.—Not Marrero and Machado-Allison, 1990:66.—Not Barriga, 1991:17.—Not Lowe-McConnell, 1991: 68.—Not Pavlov et al., 1995:233.

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 6 (rarely 5) teeth in the primary tooth row of the premaxilla, 2 to 4 teeth on each maxilla, 6 teeth on each dentary, 38 to 42 lateral line scales without a lamellar process over each pore, 9 to 12 median predorsal scales, 3 or 4 rows of scales between the lateral line and the anal-fin origin, 2 postanal scales to the anal-fin origin, 9 to 11 branched anal-fin rays, 6 or 7 gill rakers on the upper limb of the first gill arch, 8 to 10 gill rakers on the lower limb of the first gill arch, the distance from the snout to the pelvic-fin insertion (44.0%–47.8% of SL), the postorbital head length (44.6%–50.1% of HL), the bony orbital diameter (29.5%–32.7% of HL), the snout length (22.6%–28.9% of HL), the interorbital width (29.7%–32.7% of HL), the caudal peduncle depth (11.4%–12.9% of SL), the well-developed third infraorbital whose ventral margin approaches or contacts the horizontal limb of the preopercle, the lack of a series of dark spots along the midlateral surface of the body, the discrete, vertically elongate humeral mark, and the lack of a distinct patch of dark pigmentation on the middle portions of the anterior dorsal-fin rays distinguishes *Creagrutus beni* from all congeners with the exception of *C. changae*. Those two species can be discriminated by the number of dentary teeth (6 on each dentary in *C. beni* versus 5 in *C. changae*) and by differences in the bony orbital diameter (7.1%–8.4% of SL, less than horizontal distance from posterior margin of orbit to posterior margin of opercle in *C. beni* versus 8.7%–10.3% of SL, equaling or exceeding horizontal distance from posterior margin of orbit to posterior margin of opercle in *C. changae*).

TABLE 9.—Morphometrics and meristics of *Creagrutus beni*: (A) holotype of *C. beni*, FMNH 54585, formerly CM 3216 (specimen apparently dried out at some point and in poor condition, thus morphometric values not directly comparable to those of other specimens. See also "Remarks" under species description concerning differences between several characters in the holotype and information on those features presented in original description of the species); and (B) all other specimens of *C. beni* from which counts and measurements were taken (n=60). Standard length is expressed in mm; measurements 1 to 14 =percentages of standard length; 15 to 18=percentages of head length. Dashes indicate values for holotype that could not be accurately determined as a consequence of the poor condition of the specimen.

Characters	A	B
	Morphometrics	
Standard length	40.4	33.6–73.3
1. Snout to anal-fin origin	61.0	59.8–66.2
2. Snout to pelvic-fin insertion	44.1	44.0–47.8
3. Snout to pectoral-fin insertion	21.3	21.2–26.0
4. Snout to dorsal-fin origin	46.7	46.6–50.7
5. Dorsal-fin origin to hypural joint	58.3	53.9–59.4
6. Dorsal-fin origin to anal-fin origin	34.5	29.9–34.7
7. Dorsal-fin origin to pelvic-fin insertion	30.0	27.1–30.7
8. Dorsal-fin origin to pectoral-fin insertion	31.9	32.0–35.9
9. Caudal peduncle depth	11.9	11.4–12.9
10. Pectoral-fin length	–	18.4–22.1
11. Pelvic-fin length	–	13.9–16.8
12. Dorsal-fin length	–	20.1–25.1
13. Anal-fin length	–	16.8–20.1
14. Head length	24.3	24.7–27.2
15. Postorbital head length	42.9	44.6–50.1
16. Snout length	26.5	22.6–28.9
17. Bony orbital diameter	36.7	29.5–32.7
18. Interorbital width	33.7	29.7–32.7
	Meristics	
Lateral line scales	39	38–42
Scale rows between dorsal-fin origin and lateral line	4	4–5[1]
Scale rows between anal-fin origin and lateral line	3	3–4
Predorsal median scales	8?	9–12
Branched dorsal-fin rays	8	8
Branched anal-fin rays	11	9–11
Branched pelvic-fin rays	–	5–7[2]
Pectoral-fin rays	–	12–14
Vertebrae	38	37–39

[1]Five scale rows between dorsal-fin origin and lateral line typical, 4 scales less common.

[2]Five branched pelvic-fin rays present in only one specimen.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus beni* in Table 9. Head relatively robust in all specimens larger than 25 mm SL, body more robust anteriorly, more so in specimens larger than 30 mm SL. Greatest body depth at dorsal-fin origin in smaller specimens, shifted slightly anteriorly in some larger individuals. Dorsal profile of head smoothly convex from tip of snout to vertical through center of orbit in all specimens, profile from that point to rear of supraoccipital

spine ranging from slightly convex to slightly concave. Predorsal profile continuous with that of head in smaller individuals, with variably evident change in alignment relative to that of head in larger specimens. Ventral profile of head ranging from smoothly convex to having variably obvious obtuse angle at anteroventral corner of dentary, angle typically more obvious in larger individuals. Ventral profile of body smoothly convex from isthmus to anal-fin origin, convexity usually more pronounced in larger individuals.

Head obtusely pointed in lateral view, but more compressed laterally from dorsal view. Upper jaw distinctly longer than, and overhanging, lower jaw. Anterior portion of snout somewhat fleshy, with numerous small papillae. Papillae more concentrated on fleshy upper lip, fleshy folds, and plicae extending between outer and medial premaxillary teeth, and on lateral surface of maxillae. Papillae also common in many specimens on dorsal margin of lower lip, with scattered papillae over ventral surface of lip.

Infraorbital series moderately developed. Third infraorbital variably developed, with ventral margin contacting, or nearly contacting, ventral limb of preopercle in some individuals, but falling short of that point in other specimens. Posterior margins of third through fifth infraorbitals falling distinctly short of vertical limb of preopercle (see under "Remarks," below, concerning discrepancy in this feature between data in original species description and condition in putative holotype).

Premaxillary dentition in three series: primary row moderately curved, more so anteriorly, typically consisting of 6 teeth, with approximately 5% of specimens with only 5 teeth in series, without pronounced gap between first and second tooth of series but with medial tooth of series distinctly separated from matching tooth of contralateral series; triangular cluster of 3 teeth with posterolateral tooth somewhat larger and with medial teeth on contralateral clusters in contact; and single tooth of form similar to that of primary series lying lateral to fourth tooth of primary premaxillary series or lateral to space between third and fourth tooth of that series. Maxilla with 2 to 4, typically 3, teeth, teeth all tricuspidate or fourth tooth, when present, sometimes with straight distal margin. Dentary with 6 teeth; 3 anterior teeth distinctly larger and tricuspidate with middle cusp larger, middle cusp of third tooth posteriorly recurved; first and second teeth largest and subequal, larger than third; fourth to sixth teeth graded in size, tricuspidate or last tooth sometimes conical.

Dorsal-fin rays typically ii,8, iii,8 in one examined specimen with very short first unbranched ray. Dorsal-fin origin slightly posterior of vertical thorough pelvic-fin insertion. Profile of distal margin of dorsal fin straight in smaller specimens, becoming convex in larger individuals, with slight indication of anterior lobe. Anal-fin rays ii,9–11. Profile of distal margin of anal fin distinctly concave, with slightly developed anterior lobe. Mature males with hooks on last unbranched and anterior 3 to 6 branched anal-fin rays. Pectoral-fin rays i,11–13. Pectoral fin extending posteriorly somewhat more than three-fourths of distance to pelvic-fin insertion. Pelvic-fin rays typically i,6,i; i,7 in approximately 15% of specimens, i,5,i in one individual. Mature males with pelvic-fin hooks present on all branched rays of some specimens and also on medial unbranched ray in one specimen. Tip of pelvic fin extending to anus.

Gill rakers 6–7 + 8–10.

COLORATION IN ALCOHOL.—Specimens retaining guanine on scales silvery, more so in region overlying midlateral body stripe and over lateral surface of head. Dorsal surface of head with field of small, dark chromatophores, more so posteriorly. Chromatophore field continuing anteriorly, but less concentrated over snout and upper lip. Region immediately anterior to nares with dark chromatophores somewhat more concentrated; chromatophore field in that region continuous with curved band of chromatophores ventral and posterior to orbit. Dorsal portions of infraorbital series and opercle with scattered, large, dark chromatophores.

Scales of dorsal portion of body with small, dark chromatophores concentrated over anterior portion of exposed section of scales and with band of dark chromatophores along posterior margin of scales. Two pigmented regions separated by hyaline crescent. Humeral mark well developed in all specimens larger than 25 mm SL, variably masked in specimens retaining guanine on scales; vertically elongate with slightly irregular borders, vertical extent of humeral mark greater in larger individuals. Intensity of pigmentation usually even across humeral mark, slightly less developed dorsally and ventrally in some individuals. Obscure midlateral body stripe formed by deep-lying and surface chromatophores extending from under dorsal fin to rear of caudal peduncle. Stripe vertically expanded on caudal peduncle, but not extending onto caudal-fin base.

Dorsal fin with margins of rays and membranes overlain with small dark chromatophores on distal two-thirds of fin; pigmentation most developed on anterior one-half of fin. Anal fin with anterior margins of rays outlined by series of small dark chromatophores, anterior rays with chromatophores extending over basal two-thirds of rays; extent of chromatophore series along rays becoming progressively reduced posteriorly. Anal-fin ray membranes with scattered, dark chromatophores, more so in larger individuals. Caudal-fin rays outlined by series of dark chromatophores. Pelvic and pectoral fins hyaline or with scattered, dark chromatophores.

ECOLOGY.—Little information is available about the ecology of *Creagrutus beni,* but examined specimens come from a noteworthy range of elevations. The type locality (Villa Bella on the Río Beni) and other sites from which population samples are available, are at less than 200 m elevations, whereas some lots from the Department of Cochabamba and La Paz originated at sites of above 1000 m elevation.

A 55.0 mm SL female from the Río Mamoré (MCNG 23913) was filled with numerous eggs. Mature males, as evidence by hooks on the anal and pelvic fins, are typically smaller than simultaneously collected, larger, presumably female, specimens.

FIGURE 29.—*Creagrutus beni*, USNM 340959, 48.0 mm SL; Bolivia, Cochabamba, Río Chapare basin, Villa Tunari (16°55'S, 65°22'W).

DISTRIBUTION.—*Creagrutus beni* is endemic to the upper portions of the Río Madeira system in northeastern Bolivia (Figure 28, squares).

REMARKS.—Eigenmann's original description (1911:172) of *Creagrutus beni* was based on a single specimen described as being "53 mm" and as having the "second suborbital [=third infraorbital] in contact with the preopercle below, but not behind." The specimen, now cataloged as the holotype (FMNH 54585, formerly CM 3216), does not match the original description in either of these details. Evaluation of the differences between the details in the original species description and the purported holotype is complicated by the fact that the specimen is extremely stiff with sunken eyes and body, indicating that it was desiccated at some point. The specimen, furthermore, lacks the left maxilla, has a badly damaged lower jaw, and has lost most of its fin rays.

The specimen identified as the holotype of *C. beni* is approximately 40.4 mm SL, contrary to the 53 mm cited by Eigenmann (1911) who failed, however, to specify whether he was reporting standard or total length. Both standard and total lengths were utilized by Eigenmann in some of his publications (e.g., Eigenmann and Ogle, 1907), but he more typically cited total rather than standard length (e.g., holotype of *Stethaprion crenatus* cited by Eigenmann (1916:80) as being 96 mm, whereas Reis (1989:57) reported it as 76.7 mm SL, and holotype of *Acestrorhynchus nasutus* Eigenmann (1912:411) cited by that author as being 79 mm, whereas Menezes (1969:120) reported it as 66 mm SL). Based on the proportion of standard versus total length apparent in the figure accompanying the original description of *C. beni* and subsequently reproduced by Eigenmann (1927, pl. 58: fig. 3), the standard length of the specimen would be about 44 mm, approximately 10% longer than that of the putative holotype. It is impossible to determine the degree to which the difference between this estimated standard length for the holotype and the actual standard length of the specimen cited as the holotype might be explained by the desiccation that the specimen experienced at some point.

More problematic than the possible discrepancy in standard length are the differences between the degree of development of the third infraorbital reported in the original description by Eigenmann (1911) and that occurring in the putative holotype of *C. beni*. The third infraorbital in the putative holotype is continuously in contact along both its ventral and posterior margins, respectively, with the horizontal and vertical limbs of the preopercle. In contrast, Eigenmann (1911:172) describes the third infraorbital (the "second suborbital" under the terminology utilized by Eigenmann) as not in contact with the preopercle "behind" [=posteriorly]. Again, it is uncertain whether the pronounced dissection that the specimen experienced at some point accounts for the discrepancy between the original description and the condition in the putative holotype.

Only two species of *Creagrutus* are known from the region of the type locality of *C. beni*. The first of these is *Creagrutus pearsoni* (=*Piabina beni* of authors prior to Mahnert and Géry (1988:5)), originally described from the Río Beni basin in the upper portion of the Rio Madeira system. *Creagrutus pearsoni* differs in numerous features from the values reported by Eigenmann (1911) for *C. beni*, most notably in the number of branched anal-fin rays and in overall body form (see Table 44 and compare Figures 29 and 76), and indeed was removed by Pearson (1924) to another genus. The second *Creagrutus* species represented in available material from the Bolivian portion of the upper Rio Madeira matches the original description of *C. beni* in both the number of branched anal-fin rays and overall body form. All of the specimens of this *Creagrutus* species, however, lack any contact between the posterior margin of the third infraorbital and the vertical limb of the preopercle contrary to the situation in the specimen identified as the holotype of *C. beni* in which such contact occurs. These population samples also demonstrate variation as to extent to which the ventral margin of the third infraorbital approaches the horizontal limb of the preopercle. These differences raise questions as to whether the specimen now identified as the holotype of *Creagrutus beni* is the individual described by Eigenmann (1911). It

is, nonetheless, possible that these discrepancies may be a consequence of the desiccation that the specimen underwent at some point in the past.

Although we are unable to resolve these discrepancies at this time, the information in the original description of *Creagrutus beni* is mostly congruent with range of values found in this second of the two *Creagrutus* species known from the type region of *C. beni.* The name is applied herein to that form that served as the basis for the redescription of the species in this paper.

Subsequent to its description by Eigenmann (1911) from northeastern Bolivia, *Creagrutus beni* has been reported from a broad range of localities throughout South America extending north along the eastern slope of the Andean Cordilleras (Eigenmann, 1927:421; Pearson, 1937a:92; Saul, 1975:106) into the Río Orinoco basin (Eigenmann, 1912:12, 1922: 238, 1927:422; Pearse, 1920:12; Fowler, 1943a:238) as far east as the mouth of that river system (Fowler, 1931:408). *Creagrutus beni* has also been reported from Argentina (Pozzi, 1945:270; Ringuelet and Aramburu, 1961:30; Ringuelet et al., 1967:134), the western slope of the Andes (Eigenmann, 1927:421), the rivers draining into Lago Maracaibo of northwestern Venezuela (Schultz, 1944:336), coastal rivers of the Caribbean versant of northern Venezuela (Schultz, 1944:336; Fernández-Yépez, 1952:43; 1972, fig. 1), and the Río Tocantins system of eastern Brazil (Eigenmann, 1911:172; 1927:43). Cala (1990:92), however, questioned this broad distribution, proposing rather that *C. beni* probably forms a "complex" requiring a revisionary study.

The known distribution of *C. beni* is in actuality significantly more restricted than indicated in the literature, encompassing only the upper portion of the Río Madeira system in eastern Bolivia. Reports of *Creagrutus beni* from the Río Tocantins were based on material of *C. atrisignum* (footnote by G.S. Myers in Eigenmann, 1927:421; Myers, 1927:116). Material reported as *C. beni* from the eastern slopes of the Andes in Peru (Pearson, 1937a:92; Fowler, 1945a:148) is rather *C. holmi* (see "Remarks" under that species), and specimens cited as *C. beni* from eastern Ecuador (Saul, 1975:106) are *C. flavescens* (see "Remarks" under that species). Citations of *C. beni* from the Lago Maracaibo basin (Schultz, 1944:336) were based on samples of forms that were later described as *C. paralacus* Harold and Vari (1994:14), those from the Río Orinoco basin on samples of *C. melasma* Vari et al. (1994:90), *C. hysginus* Harold et al. (1994:975), *C. bolivari* (see "Remarks" under that species), and *C. taphorni* (see "Remarks" under that species). Citations of *C. beni* from the Caribbean versant of Venezuela were based on specimens of *C. lassoi* (see "Remarks" under that species), *C. lepidus* Vari et al. (1993:354), and *C. taphorni* (see "Remarks" under that species).

The report of *C. beni* from the provinces of Jujuy and Salta in Argentina by Pozzi (1945:270) was later reiterated by Ringuelet and Aramburu (1961:30) and Ringuelet et al. (1967:134), evidently without the examination of additional specimens. These reports represent either a major range extension for the genus, perhaps being of one of the species of the two other species of the genus endemic to the Río de La Plata basin, or a misidentification at the generic level. Our examinations of specimens indicate that the Argentinean provinces of Jujuy and Salta lie outside the known range of *Creagrutus.*

In addition, numerous other authors have reported *Creagrutus beni* from portions of South America beyond the known range of the species as confirmed by specimens examined for this study (see listing of authors at the end of the synonymy for *C. beni*). In light of the extralimital origin of these specimens, these citations are judged to be misidentifications of *C. beni.* The absence, or unavailability, of voucher specimens associated with many of these citations makes it impossible to determine the identity of this material.

Mahnert and Géry (1988:5) synonymized *Piabina* Reinhardt (1867) into *Creagrutus* Günther (1864), an action that made *Piabina beni* Pearson (1924) a secondary homonym of *Creagrutus beni* Eigenmann (1911). Mahnert and Géry consequently proposed *pearsoni* as a replacement name for *beni* Pearson within *Creagrutus.*

MATERIAL EXAMINED.—161 specimens (60, 33.6–73.3).

BOLIVIA. *El Beni:* Villa Bella (10°23′S, 65°24′W), FMNH 54585, 1 (40.4, holotype of *Creagrutus beni;* formerly CM 3216). Río Mamoré, Laguna de Cristal Mayo (not located), MCNG 23913, 1 (55.0). Provincia Ballivian, Territorio Indigena Reserva de la Biosfera Pilón-Lajas, mouth of Río Suapi (approximately 14°47′S, 67°38′W), 20 (15, 44.5–73.3). Provincia Ballivian, Río San Bernardo, at road from Yucumo to Rurrenbaque (approximately 13°38′S, 65°23′W), CBF 2366, 15 (9, 45.3–68.5). Provincia Cervado, Río Ibare, 5 km N of Puerto Almacén (latter locality at 14°53′S, 64°57′W), UF 82519, 1. Ox-bow lagoon approximately 96 m from Río Itenez, 9 km S of Costa Marques, Brazil (12°32′24″S, 64°12′42″W), UMMZ 204418, 5. Río Mamoré, Isla Nicolas Suarez, between Guayaramerín, Bolivia, and Guajará Mirim, Brazil (approximately 10°48′S, 65°23′W), AMNH 40189, 20. *Cochabamba:* Río Chapare basin, Villa Tunari (16°55′S, 65°22′W), MNHN 1989-1473, 5 (39.5–58.6); USNM 340959, 11 (6, 35.2–48.0; 2 specimens cleared and counterstained for cartilage and bone); MZUSP 27808, 5 (40.6–52.1); CBF 82, 3 (2, 51.3–55.1). Villa Tunari, Río Juntas de Caroni (approximately 16°55′S, 65°22′W), MCNG 23912, 3. Confluence of Río Chapare and Río Coni (approximately 16°51′S, 65°08′W), MHNG 2227.69, 1 (59.7). *La Paz:* Provincia Sud Yungas, upper Río Beni, at San Miguel de Huachi (15°40′S, 67°15′W), MHNG 2227.68, 1 (38.0). Provincia Sud Yungas, upper Río Beni, Río Boopi, San Miguel de Huachi (15°40′S, 67°15′W), CBF 59, 2 (60.4–67.9). Río Iniqui, tributary of Río Beni, approximately one-half distance between Huachi (?=San Miguel de Huachi) and Rurrenbaque, CAS 69287, 19 (5, 52.0–67.0). Provincia Iturralde, unnamed arroyo, 14 km W of Ixiamas (latter at 13°45′S, 68°09′W), CBF 02364, 3. Provincia Iturralde, Río Yariapu system of Río Beni basin, unnamed arroyo, 4 km S de Tumupasa (latter at 14°09′S, 67°55′W), CBF 2365, 6. Provincia Iturralde, Tumupasa (14°09′S, 67°55′W), USNM 86802, 15 (5,

45.0–54.8; formerly IU 17310, in part). Río Iniqui, upper Río Beni system, USNM 86840, 5 (formerly IU 17313, in part). Provincia Nor Yungas, Río San Miguel, upper Río Beni basin, Tomachi (15°26′S, 67°45′W), CBF 02361, 5. Río Popoi, upper Río Beni system, USNM 86771, 5 (2, 33.6–42.3; formerly IU 17311, in part). Río Colorado, lower Río Bopi system, USNM 86839, 5. Río Coroico, Caranavi, INHS 36969, 4.

Creagrutus bolivari Schultz, 1944

FIGURES 28, 30, TABLE 10

Creagrutus beni [not of Eigenmann, 1911].—Eigenmann, 1922:238 [Colombia: Río Guadrigua, Río Roncador]; 1927:421 [in part, specimens from Colombia: Río Guadrigua, Río Roncador and perhaps Quebrada Cramalote, Villavicencio], pl. 93: fig. 7 [illustrated specimen *C. bolivari*, not *C. beni*].

Creagrutus bolivari Schultz, 1944:334, fig. 49, tabs. 22, 23 [type locality: Venezuela, Estado de Aragua, Río Guárico and tributaries between San Sebastián and San Casimiro].—Myers and Roberts, 1967:249 [*C. bolivari* as a possible synonymy of *C. phasma* Myers, 1927].—Mago-Leccia, 1970:70 [footnote; *C. bolivari* as a possible synonym of *C. phasma*, following Myers and Roberts, 1967].—Fowler, 1975:26 [in list of nominal *Creagrutus* species].—Géry and Renno, 1989:3 [as a possible synonym of *C. phasma*].—Vari and Howe, 1991:15 [location of type specimens].—Taphorn, 1992:170, figs. 40a, 109, 110 [occurrence in Río Apure system, Venezuela; ecology, common name].—Machado-Allison and Moreno, 1993:85–94, tabs. 1, 2, 5, 7 [ecology and distribution in Venezuela, Estado Guarico, Río Orituco].—Machado-Allison et al., 1993:66, 69 [Venezuela, Ríos Aguaro and Guariquito; ecology].—Machado-Allison et al., 1993:133 [Venezuela: low Llanos of Río Orinoco basin].—Taphorn et al., 1997:71 [cited for Venezuela].—Marrero et al., 1997:76 [rivers of Llanos of Venezuela].

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 2 to 4 teeth on the maxilla, 6, rarely 5, teeth in the primary tooth row of the premaxilla, 5 dentary teeth, 37 to 40 lateral line scales without a lamellar process over each pore, 8 to 10 predorsal scales, 4 scale rows between the dorsal-fin origin and the lateral line, 35 to 37 vertebrae, 8 to 10 branched anal-fin rays, 2 post-anal median scales to the anal-fin origin, the distance from the snout to the dorsal-fin origin (45.0%–50.3% of SL), the bony orbital diameter (28.2%–36.6% of HL), the interorbital width (28.0%–33.3% of HL), the 5 to 9 gill rakers on the upper limb and 9 to 12 gill rakers on the lower limb of the first arch, the moderately developed third infraorbital whose ventral margin falls distinctly short of horizontal limb of preopercle, the lack of a series of dark midlateral spots on the body, the humeral mark in the form of a vertically elongate bar of nearly uniform width, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus bolivari* within the clade composed of *Creagrutus* and *Piabina*.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus bolivari* in Table 10. Body relatively deep and compressed. Greatest body depth at, or immediately anterior of, dorsal-fin origin. Dorsal profile of head distinctly convex from margin of upper lip to vertical through posterior margin of posterior nares, straight from that point to posterior tip of supraoccipital spine. Dorsal profile of body slightly and symmetrically convex to dorsal-fin origin, straight to slightly concave from that point to base of adipose fin, slightly concave from rear of adipose-fin base to caudal-fin base. Ventral profile of head with obtuse angle approximately midway between margin of lower lip and posterior of dentary, straight to slightly convex from that angle approximately to pectoral-fin insertion; slightly convex between pectoral- and pelvic-fin insertions; slightly concave from anal-fin origin to caudal peduncle.

Upper jaw longer than, and overhanging, lower jaw. Anterior portion of snout quite fleshy, with many minute papillae on anteromedial portion of snout, papillae continuing ventrally onto upper lip and into mouth on fleshy flaps between premaxillary teeth. Lower lip distinctly fleshy anteriorly, with papillae concentrated on lip and decreasing in number ventrally and laterally; papillae also present on isthmus.

Infraorbital series relatively poorly developed, with ventral margin of third infraorbital distinctly separated from horizontal and vertical limbs of preopercle, gap between posterior margin of third infraorbital and vertical limb of preopercle at most one-third width of orbit; posterior and ventral margins of third infraorbital distinctly and smoothly curved. Posterior margins of fourth and fifth infraorbitals vertical and distinctly separated from vertical limb of preopercle by broad gap equal to approximately one-half of width of fourth infraorbital.

Premaxillary dentition in three series: primary row slightly curved, without pronounced gap between first and second tooth of series, typically with 6 teeth, although rarely 5 teeth, present on one premaxilla, and 7 teeth present on both premaxillae in one specimen; triangular cluster of 3 larger teeth with posteromedial tooth distinctly larger; and single tooth of form similar to that of primary series typically lying lateral to fourth tooth of primary row, or lateral to region where fourth and fifth teeth of that row contact. Maxilla with 2 to 4 tricuspidate teeth. Dentary with 5 tricuspidate teeth; second largest, about one and one-half times size of first tooth and twice height of third tooth but much more massive. Fourth and fifth dentary teeth distinctly smaller than third tooth in series.

Dorsal-fin rays ii,8. Dorsal-fin origin located anterior of vertical through pelvic-fin insertion by distance equal to width of one or two midlateral scale rows. Distal margin of dorsal fin slightly concave, with slightly elongate anterior lobe. Anal-fin rays ii,8–10 or iii,8–10. Anal fin with hooks, when present, on segments of first branched ray of mature males (first two rays in 1 out of 5 hook-bearing specimens). Distal margin of anal fin slightly to markedly sinusoidal, with elongate anterior lobe followed by concavity. Pectoral-fin rays i,10–12. Pectoral fin relatively short, tip not extending to pelvic-fin insertion. Pelvic-fin rays i,6,i or i,7. Tip of pelvic fin approaching or extending to anteriormost unbranched anal-fin ray. Mature males with pelvic-fin hooks on segmented and unsegmented portions of all 7

TABLE 10.—Morphometrics and meristics of *Creagrutus bolivari:* (A) holotype of *C. bolivari,* USNM 121497; (B) paratypes of *C. bolivari,* USNM 121498 (n=9); (C) nontype specimens of *C. bolivari* from the central portions of Orinoco basin in Venezuela (n=17); and (D) nontype specimens of *C. bolivari* from the western portions of the Orinoco basin in Colombia (n=37) from which measurements were taken. Standard length is expressed in mm; measurements 1 to 14=proportions of standard length; 15 to 18=proportions of head length.

Characters	A	B	C	D
		Morphometrics		
Standard length	50.2	35.7–48.3	37.8–52.3	26.3–61.0
1. Snout to anal-fin origin	2.7	61.3–66.1	63.4–70.0	62.0–66.7
2. Snout to pelvic-fin origin	47.0	45.7–50.4	47.4–52.4	45.8–50.6
3. Snout to pectoral-fin origin	25.1	24.4–26.8	25.1–28.6	23.7–26.0
4. Snout to dorsal-fin origin	48.2	45.0–48.6	47.1–50.9	46.4–50.3
5. Dorsal-fin origin to hypural joint	56.2	55.1–57.4	55.5–60.3	55.1–60.3
6. Dorsal-fin origin to anal-fin origin	32.9	30.4–33.3	29.4–39.5	30.6–36.4
7. Dorsal-fin origin to pelvic-fin origin	30.1	24.6–28.6	24.2–34.6	26.6–34.5
8. Dorsal-fin origin to pectoral-fin origin	34.3	29.9–33.7	31.8–37.6	32.0–35.3
9. Caudal peduncle depth	12.4	11.1–12.3	10.9–13.2	11.7–12.7
10. Pectoral-fin length	20.3	18.8–20.6	17.8–22.4	18.5–21.3
11. Pelvic-fin length	17.3	14.6–16.8	14.6–17.9	15.0–17.7
12. Dorsal-fin length	16.9	20.0–23.8	19.9–24.0	20.7–23.5
13. Anal-fin length	18.1	16.5–20.1	16.6–20.3	16.0–19.7
14. Head length	26.5	25.1–26.8	25.9–29.4	24.9–27.4
15. Postorbital head length	45.9	42.1–47.7	43.3–49.5	41.4–47.8
16. Snout length	28.6	23.1–31.1	27.2–32.2	24.3–30.6
17. Bony orbital diameter	33.1	32.2–36.4	28.2–36.6	29.9–35.5
18. Interorbital width	32.3	30.7—33.1	28.0–32.4	28.6–33.3
		Meristics		
Lateral line scales	38	37–40	38–40	37–40
Scale rows between dorsal-fin origin and lateral line	4	4	4	4
Scale rows between anal-fin origin and lateral line	3	3	3	3
Predorsal median scales	8	8–9	8–9	8–10
Branched dorsal-fin rays	8	8	8	8
Branched anal-fin rays	9	8–10	8–10	8–10
Branched pelvic-fin rays	7	6–7[1]	7	6–7[1]
Pectoral-fin rays	13	11–13	11–13	11–13
Vertebrae	37	35–37	35–37	36–38

[1]Medialmost pelvic-fin ray unbranched in some specimens.

branched rays or 6 branched rays and on medial unbranched ray.

Gill rakers 5–9+9–12.

COLORATION IN ALCOHOL.—Dorsal surface of head with uniform diffuse pattern of small, dark chromatophores, larger and darker chromatophores present on lateral portions of frontals and on dorsal surface of brain. Smaller dark chromatophores continuing anteriorly onto snout. Distinct small crescent of dark chromatophores immediately in front of anterior nares. Band of scattered, dark chromatophores extending from posterior wall of nares around ventral and posterior margin of orbit, and forming dense patch located anteroventral to eye. Pigmentation on ventral surface of head restricted to transverse band of small, dark chromatophores on lower lip. Pigmentation on lateral surface of head confined to widely scattered, large, light to dark brown chromatophores on dorsalmost portion of cheek and area covering upper portions of infraorbital series and opercle. Body with pigmentation most concentrated dorsally, particularly at dorsal-fin base and in narrow middorsal band extending from dorsal-fin base to procurrent caudal-fin rays, and over center of exposed surface of scales on dorsolateral surface of body. Humeral mark in form of vertically elongate bar of approximately uniform width with one-fourth of its length ventral of lateral line and remainder dorsal of that structure. Pigmentation in mark most concentrated immediately dorsal of lateral line. Overall form of humeral mark relatively straight ventrally and extending towards center of pectoral-fin base; dorsal portion of mark with distinctive anterior concavity and extending towards third or fourth predorsal scale. Humeral bar diffuse in smaller specimens, becoming vertically elongate between 23 and 27 mm SL. Little or no dark pigmentation on body ventral to lateral line. Some individuals with small, dark chromatophores delineating myosepta in region immediately dorsal to anal fin. Variably distinct predorsal stripe present; stripe formed by deep-lying, stellate, dark chromatophores. Chromatophores most concentrated anteriorly near supraoccipital spine in some specimens. Midlateral stripe located entirely

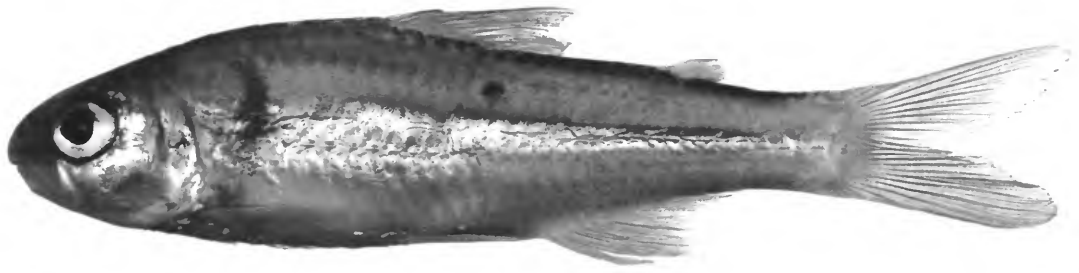

FIGURE 30.—*Creagrutus bolivari*, paratype, USNM 121498, 42.3 mm SL; Venezuela, Aragua, Río Guárico and tributaries between San Sebastion and San Casimiro (latter locality at 10°00′N, 67°01′W).

above lateral line except on caudal peduncle, becoming denser posteriorly and expanding slightly over hypurals.

Caudal-fin membranes invested with dark pigmentation delineating rays, pigmentation darkest on ventral lobe and especially concentrated on central fin-rays; entire distal margin of caudal fin with a band of small, dark chromatophores. Unbranched anal-fin rays unpigmented, anterior margins of branched rays delineated by dark pigmentation. Dorsal fin with patch of dark pigmentation covering distal one-half of last unbranched and two anterior branched rays, becoming narrower and confined to fin margin posteriorly; seventh and eight branched rays unpigmented. Pectoral fin with scattered, large, light brown chromatophores. Pelvic fin unpigmented.

ECOLOGY.—Taphorn (1992:171) summarized the conditions inhabited by *Creagrutus bolivari* as "flowing waters" over rocky substrates in the Andean piedmont and the Llanos (savannahs) of the Río Orinoco basin. The diet of the species consists of drifting or benthic organisms. *Creagrutus bolivari* is moderately abundant in portions of the Río Orituco system in the central portion of its range (Machado-Allison and Moreno, 1993). Ortaz (1997:1147) reported on the reproductive cycle of a species cited as *Creagrutus bolivari* from the Río Orituco in north central Venezuela. That author utilized Schultz (1944) and Géry (1977) as the basis for that identification. Unfortunately the keys provided by those two authors do not discriminate *C. bolivari* from the two other species that occur in the Río Orituco basin, *C. melasma* and *C. taphorni*. It is therefore impossible to ascertain which of the three species was studied by Ortaz (1997). In the western portions of its range *C. bolivari* was captured together with *C. atratus*.

COMMON NAME.—Venezuela, Río Apure system: "Diente-frio, buck-toothed tetra" (Taphorn, 1992:171).

DISTRIBUTION.—*Creagrutus bolivari* is widely distributed in an arc across the Río Orinoco basin from the Río Metica, which is a component of the Río Meta basin in Colombia in the west, through northern Venezuela, to somewhere within Estado de Monagas, Venezuela, in the east (Figure 28, stars; exact coordinates of the Estado de Monagas record could not be determined).

COMPARISONS.—*Creagrutus bolivari* is a quite distinctive species with a steeply sloping predorsal region of the body and an elongate, arcuate humeral bar; these attributes were well represented in the original description (Schultz, 1944:334). The distribution of the species overlaps those of a number of its congeners in the main portion of the Orinoco basin, but it can be readily distinguished by the just-cited characters and the features noted in "Key to Species of *Creagrutus* in the Río Orinoco Basin."

GEOGRAPHIC VARIATION.—Population samples of *Creagrutus bolivari* examined during this study mostly originated in the central and eastern portions of the Río Orinoco basin in Venezuela (Figure 28). A series of samples from the upper portions of the Río Meta basin in the western portions of the basin in Colombia also are identified herein as *C. bolivari* as they agree with the more eastern samples in all meristic and morphometric features, other than for having a shift in the range of the total number of vertebrae. Within the central and eastern portions of the Orinoco basin, *C. bolivari* has 35 to 38, rarely 38, vertebrae, whereas the Colombian population samples have 36 to 38, typically 37 or 38, vertebrae. Further collections from intervening areas are necessary to determine whether this variation demonstrates any discrete pattern.

REMARKS.—Eigenmann (1921, pl. 93: fig. 7; 1922:38; 1927: 421) reported *Creagrutus beni* from various localities along the eastern slope of the Colombian Andean Cordilleras (Río Guadrigua, Río Roncador, and Quebrada Cramalote, Villavicencio) in the western portions of the Río Orinoco basin. Examined specimens from two of those localities (Río Guadrigua, Río Roncador) have proved to be *Creagrutus bolivari*. Although we have not examined the specimens from Quebrada Cramalote, Villavicencio, their locality and the available information on the distribution of *Creagrutus* species in that region indicate that those specimens are also *C. bolivari*.

Myers and Roberts (1967:249) stated that *Creagrutus bolivari* is probably a synonym of *C. phasma* Myers (1927). This view was reiterated by Mago-Leccia (1970:70) in a footnote. We have examined the types and other material of both species and found that they are distinct in various features, including

premaxillary dentition (*C. bolivari,* typically with 6 teeth in the primary premaxillary series versus 5 teeth in that series in *C. phasma*), body shape (deeper in *C. bolivari,* compare Figures 28 and 79), and form of the humeral mark (dorsally arcuate and ventrally vertical in *C. bolivari,* compared with gently arcuate overall in *C. phasma*).

Some differences exist between our observations on *Creagrutus bolivari* and those reported by Schultz (1944) in the original description of the species. The number of gill rakers in the species was reported by Schultz (1944:335) to be "about 5 +9," whereas 5+10 was the lowest count we obtained in our survey of the type series and other material of the species. There are usually 6 or 7 gill rakers on the upper limb and 10 or 11 on the lower limb of the first gill arch. In addition, Schultz (1944) stated that with the exception of the dorsal fin, the fins were unpigmented. As described above, we found that only the pelvic fins are unpigmented in *C. bolivari.*

Schultz (1944:336) commented that *Creagrutus bolivari* differs from all other species in the genus, except *C. brevipinnis,* in having a low number of (branched) anal-fin rays (8 or 9 in *C. bolivari* reported by Schultz; 8–10 found in the present study; versus 9 or 10 in *C. brevipinnis,* Harold and Vari, 1994). Among the *Creagrutus* species described prior to Schultz's paper, however, similarly low counts also occur in *C. magdalenae* Eigenmann (9–11; Harold and Vari, 1994:17, table 5), *C. atrisignum* (9 or 10), *C. beni* (9–11), and *C. peruanus* (9–11) (see species accounts in this paper for data on the latter three species). Schultz (1944) also stated that *C. brevipinnis* has a deeper body and is less elongate than *C. bolivari.* We measure body depth as the distance from the dorsal-fin origin to the lateral base of the pelvic fin. The range for this value in the two species (*C. brevipinnis* and *C. bolivari*) shows pronounced overlap with the range in *C. brevipinnis* and extends only slightly above that of *C. bolivari. Creagrutus brevipinnis,* however, has a shallower caudal peduncle, giving it a more elongate appearance posteriorly, which, in turn, makes the relative body depth appear greater (Harold and Vari, 1994:18, fig. 10). This might account for Schultz' comment. *Creagrutus magdalenae,* the second Trans-Andean species with which Schultz (1944) compared *C. bolivari,* is quite distinct from that species, with a uniquely deepened body and caudal area (Harold and Vari, 1994:16, fig. 9). *Creagrutus bolivari* differs from the other Cis-Andean species listed above in various features or combinations of features listed in the "Diagnosis" of the species (see above).

One specimen from the Río Guarapiche, in the Estado de Monagas in the region north of the delta of the Río Orinoco (USNM 163155), appears similar to *C. bolivari* but clearly differs from it in the configuration of the anal fin. The specimen is tentatively identified as *C.* aff. *bolivari.* The location where the specimen was collected lies at the eastern extreme of the known distribution of the species (Figure 28). A detailed treatment of this specimen and an evaluation of the significance of the difference in the anal-fin form must await the collection and examination of additional material from the eastern portions of the Río Orinoco basin.

MATERIAL EXAMINED.—579 specimens (64, 26.3–61.0).

COLOMBIA. Río Roncador, E slope of Cordillera Oriental, E of Bogotá, CAS 69302, 2 (formerly IU 13179). Río Guadrigua, E slope of Cordillera Oriental, E of Bogotá, CAS 69301, 3 (formerly IU 13174). *Meta:* Río Metica, approximately 1.5 km E of Rajote (3°56′S, 73°03′W), ANSP 134160, 50 (9, 38.6–50.2). Río Meta basin, Río Ocoa, approximately 15 km E of Villavicencio, NRM 16847, 11 (6, 26.3–61.0). Río Meta basin, Caño Union, tributary to Río Ocoa, where crossed by road between Villavicencio and Acacias, NRM 16844, 22 (29.4–54.7). Río Meta basin, Caño Candelaria, tributary to Río Negro, approximately 20 km SW of Villavicencio, NRM 16846, 3. Río Meta basin, Río Manacasias, Restrepo, MHNG 2183.39, 4. Río Metica, approximately 3 km SE of Hacienda Mozambique (3°57′N, 73°02′W), ANSP 134081, 50.

VENEZUELA. *Aragua:* Río Carmen de Cura, 5 km SE of Carmen de Cura (latter locality at 9°48′N, 66°50′W), MHNLS 525, 21 (10, 36.7–44.4). Río Guárico and tributaries between San Sebastion and San Casimiro (latter locality at 10°00′N, 67°01′W), USNM 121497, 1 (50.2, holotype of *Creagrutus bolivari*); USNM 121498, 82 (paratypes of *Creagrutus bolivari;* 9, 35.7–48.3). *Barinas:* Río Santo Domingo, S of city of Barinas (approximately 8°38′N, 70°12′W), MCNG 7432, 9. *Bolivar:* Río Orocopiche, on road from Caicara to Ciudad Bolivar (approximately 8°07′N, 63°39′W), MBUCV V-18110, 5. Pools and beaches in front of Salto de Icutu, Río Nichare system, Río Caura basin (5°53′00″N, 64°51′W), MCNG 21492, 20 (5, 37.8–46.0). Río Matuanta, 12 km E of Ciudad Bolivar, MHNLS 518, 48. Río Cuchivero, at Cuchivero ferry crossing (7°29′N, 65°35′W), ANSP 159830, 43; MBUCV V-18065, 6 (2, 40.2–52.3). Río Cariapo, at bridge along highway from Caicara to Ciudad Bolivar (7°53′N, 63°49′42″W), MBUCV V-18037, 29; ANSP 159833, 1; ANSP 159831, 83. *Guárico:* Río Orituco, along road from Calabozo, below bridge, MBUCV V-21432, 3; MBUCV V-21449, 1. Río Orituco, bridge at road from Calabozo to Cazorla, MBUCV V-21933, 1. Río Orituco, 15 km SSE of Calabozo on Cazorla Road (8°48′N, 67°26′W), ANSP 139534, 3. Río Orituco, MBUCV V-21508, 4. Guariquito Creek, Río Orinoco basin, 6 km E of San Jose, INHS 69458, 4. Río San Jose on W boundary of Aquaro-Guariquito National Park, INHS 69530, 8. *Monagas:* Río Arco, MHNLS 9251, 2. *Portuguesa:* Río Boconó, in front of "Sun-Sun," MBUCV V-8378, 8; USNM 327935, 2. Río Boconó, Puerto Sun-Sun, in front of port, MBUCV V-9464, 15. Río Ospino, at Ospino (9°18′N, 69°27′W), MBUCV V-8404, 3. Río Tucupido, immediately above junction with Río Guanare, just behind the Santuario de la Coromoto, approximately 1.7 km SW of Guanare (latter locality at 9°03′N, 69°45′W), just above junction with Río Guanare, UF 32318, 31.

The following lot, discussed above (see "Remarks"), is tentatively assigned to *C. bolivari.*

VENEZUELA. *Monagas:* Río Guarapiche, Caicara, USNM 163155, 1.

Creagrutus britskii, new species

FIGURES 28, 31, TABLE 11

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 2 or 3 teeth on the maxilla, typically 6 teeth in the primary series on the premaxilla, 4 or 5 teeth on each dentary, 36 to 39 lateral line scales without a lamellar process over each pore, 9 to 11 predorsal median scales, 5 scales rows between the dorsal-fin origin and the lateral line, 9 to 11 branched anal-fin rays, 36 or 37 vertebrae, the 6 or 7 gill rakers on the upper and 10 to 12 gill rakers on the lower limb of the first gill arch, the distance from the dorsal-fin origin to the pelvic-fin insertion (25.4%–32.6% of SL), the postorbital head length (38.1%–45.6% of HL), the snout length (28.3%–33.3% of HL), the interorbital width (30.3%–34.1% of HL), the depth of the caudal peduncle (11.4%–13.9% of SL), the well-developed third infraorbital with the ventral margin of its anterior portion contacting the preopercle in larger specimens, the moderately vertically elongate humeral mark not in the form a ventrally tapering vertical bar and lacking a distinct extension ventrally or a secondary patch of pigmentation dorsal to the primary mark, the lack of a series of dark spots along the midlateral surface of the body, and the lack of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguish *C. britskii* from the other species in the clade composed of *Creagrutus* and *Piabina*.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus britskii* in Table 11. Head relatively robust. Body proportionally moderately more elongate in smaller individuals, progressively more robust anteriorly with increasing body size. Greatest body depth at, or barely anterior to, dorsal-fin origin in individuals up to approximately 45 mm SL, shifted anteriorly in most larger specimens, particularly those with distended abdomens. Dorsal profile of head distinctly convex from margin of upper lip to vertical through posterior nostril, straight from that point to tip of supraoccipital spine in all specimens larger than 20 mm SL. Interorbital region gently convex. Predorsal profile of body continuing that of posterior portion of head and nearly straight to dorsal-fin origin in specimens up to approximately 35 mm SL, becoming progressively more convex in larger individuals. Predorsal region of body in preserved specimens transversely flattened anteriorly in all specimens larger than 20 mm SL, transversely flattened region extending nearly to dorsal-fin origin in smaller specimens, limited to anterior one-half of predorsal region in larger specimens that, in turn, have medial middorsal ridge along posterior one-third of predorsal region. Ventral profile of head gently convex overall anteriorly, with barely apparent obtuse angle at anteroventral corner of dentary, nearly straight from that region to isthmus. Ventral profile of body nearly straight up to approximately 35 mm SL, increasingly convex in larger individuals.

TABLE 11.—Morphometrics and meristics of *Creagrutus britskii*, new species (A) holotype of *C. britskii*, MZUSP 40537; and (B) paratypes of *C. britskii* (n=56). Standard length expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	52.5	27.3–47.5
1. Snout to anal-fin origin	67.9	59.6–68.1
2. Snout to pelvic-fin insertion	47.2	43.3–52.3
3. Snout to pectoral-fin insertion	26.3	22.9–27.2
4. Snout to dorsal-fin origin	51.4	45.1–52.0
5. Dorsal-fin origin to hypural joint	52.6	52.1–58.0
6. Dorsal-fin origin to anal-fin origin	35.5	28.2–36.0
7. Dorsal-fin origin to pelvic-fin insertion	30.9	25.4–32.6
8. Dorsal-fin origin to pectoral-fin insertion	35.0	30.1–35.8
9. Caudal peduncle depth	13.3	11.4–13.9
10. Pectoral-fin length	22.4	17.1–22.4
11. Pelvic-fin length	18.7	13.7–17.9
12. Dorsal-fin length	24.8	20.5–24.8
13. Anal-fin length	18.7	17.0–20.2
14. Head length	27.5	23.7–27.5
15. Postorbital head length	45.2	38.1–45.6
16. Snout length	31.3	28.3–33.3
17. Bony orbital diameter	35.4	30.1–38.2
18. Interorbital width	32.6	30.3–34.1
	Meristics	
Lateral line scales	38	36–39
Scale rows between dorsal-fin origin and lateral line	5	5
Scale rows between anal-fin origin and lateral line	3	3–4
Predorsal median scales	11	9–11
Branched dorsal-fin rays	8	8
Branched anal-fin rays	9	9–11
Branched pelvic-fin rays	6	6
Pectoral-fin rays	13	11–13
Vertebrae	36	36–37

Head obtusely pointed in lateral view, more compressed laterally in dorsal view. Upper jaw longer than, and overhanging, lower jaw. Snout fleshy anteroventrally, with scattered papillae proximate to margin of upper lip. Lateral surface of upper lip with scattered papillae. Ventral margin of upper lip and fleshy folds and plicae extending between outer and medial premaxillary teeth with numerous papillae. Lower lip very fleshy with numerous papillae along anterodorsal margin and scattered papillae anteroventrally.

Infraorbital series moderately developed. Anterior portion of ventral margin of third infraorbital falling distinctly short of horizontal limb of preopercle in smaller specimens, progressively approaching that bone ontogenetically, and in contact with that portion of the preopercle in larger individuals. Posterior margins of third through fifth infraorbitals falling distinctly short of vertical limb of preopercle.

Premaxillary dentition in three series: primary row curved or very slightly sigmoid, typically with 6 teeth (only 5 teeth present on one premaxilla in one examined specimen) without pronounced gap between first and second tooth of series; triangular cluster of 3 larger teeth with posterolateral tooth largest and medial teeth of contralateral clusters in contact; and single

FIGURE 31.—*Creagrutus britskii*, new species, holotype, MZUSP 40537, 52.5 mm SL; Brazil, Goiás, Iaciara, Ribeirão Macambira, near bridge on highway GO 112 (approximately 14°20′S, 46°45′W).

tooth of form similar to that of primary series lying lateral to fourth tooth of primary premaxillary tooth row, or lateral to region of contact of fourth and fifth teeth. Maxilla with 2 or 3 tricuspidate teeth. Dentary with 4 or 5 teeth, anterior three teeth largest; first and second subequal and distinctly larger than third tooth; latter, in turn, notably larger than fourth tooth. Teeth all tricuspidate (when 4 teeth present) or last tooth conical, or nearly so (when 5 teeth present).

Dorsal-fin rays typically ii,8, rarely iii,8 (in only 3 examined specimens). Dorsal-fin origin at, to slightly posterior of, vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin slightly concave. Anal-fin rays ii,9–11. Profile of distal margin of anal fin slightly concave. Mature males with many hooks on at least first and second branched anal-fin rays, some specimens with few hooks also present on third branched anal-fin ray. Pectoral-fin rays i,10–12. Tip of pectoral fin falling distinctly short of pelvic-fin insertion in smaller individuals, extending to, or occasionally surpassing, that point in largest individuals. Pelvic-fin rays i,6,i in all examined specimens. Tip of pelvic fin extending posteriorly to anus or anal-fin insertion. Mature males with hooks on all branched pelvic-fin rays.

Gill rakers 6–7 + 10–12.

COLORATION IN ALCOHOL.—Overall ground coloration of relatively recently collected specimens tan. Dorsal surface of head with scattered surface chromatophores posteriorly, with chromatophore field becoming denser anteriorly, particularly over snout. Field of deep-lying, dark chromatophores on membranes overlying brain, chromatophore field most intense posterior of epiphyseal bar, degree of intensity of overall pigmentation variable between individuals. Region anterior to nostrils with crescent-shaped field of denser chromatophores sometimes continuous with narrow band of chromatophores along ventral and posterior margins of orbit. Region posterior of orbit with scattered chromatophores on infraorbitals and opercle.

Scales of posterodorsal portion of body with marginal series of dark chromatophores separated from basal patch of chromatophores by hyaline region. Pigmentation more intense anteriorly in smaller specimens and darker overall in larger individuals. Humeral mark vertically elongate, pigmentation most intense in central portion of mark. Central region sometimes expanded horizontally compared with remainder of mark. Dorsal portion of mark less intensely pigmented, with nearly vertical margins, or more often slightly arching anteriorly. Dorsal portion of mark merging into overall darker pigmentation of dorsal portion of body. Ventral portion of humeral mark below intensely pigmented region tapering ventrally. Midlateral stripe formed mostly by deep-lying, dark chromatophores; stripe extending posteriorly from slightly behind humeral mark to caudal peduncle, most obvious on posterior two-thirds of body.

Dorsal fin with last unbranched and first branched rays often outlined with dark chromatophores. Distal portions of membranes between anterior branched rays with scattered, large, dark chromatophores. Anterior two-thirds of branched anal-fin rays outlined basally by dark pigmentation; pigmentation extending further along rays on anterior rays. Caudal-fin rays, particularly central, dorsalmost, and ventralmost rays outlined by dark chromatophores. Basal portions of middle rays with diffuse concentration of darker chromatophores, giving appearance of indistinct spot in some specimens. Pectoral and pelvic fins hyaline.

ETYMOLOGY.—The species name, *britskii*, is in honor of Heraldo Britski, Museu de Zoologia of the Universidade de São Paulo, Brazil, in recognition of his many contributions to our understanding of South American freshwater fishes and of his assistance to the senior author over the years.

ECOLOGY.—Two of the paratype lots of *Creagrutus britskii* (USNM 292226, 292214) were collected in small upland rivers, 6–25 m in width, with bottoms formed by rubble, gravel, bedrock, and silt. Turbidity was moderate, and current ranged from slow to swift.

DISTRIBUTION.—*Creagrutus britskii* is known only from the southeastern portions of the Rio Tocantins basin (Figure 28, triangles).

MATERIAL EXAMINED.—126 specimens (57, 27.3–52.5).

HOLOTYPE.—BRAZIL. *Goiás*: Iaciara, Ribeirão Macambira (approximately 14°20′S, 46°45′W), near bridge on highway

GO 112, collected by J.C. de Oliveira and W.J.M. Costa, 14 Sep 1988, MZUSP 40537, 1 (52.5).

PARATYPES.—56 specimens (56, 27.3–47.5).

BRAZIL. *Goiás:* Iaciara, Ribeirão Macambira (approximately 14°20′S, 46°45′W), near bridge on highway GO 112, collected with holotype, MZUSP 50540, 12 (33.7–43.5); USNM 340952, 4 (34.8–42.7; 2 specimens cleared and counterstained for cartilage and bone). Iaciara, Rio Prata above bridge on highway GO 112 (approximately 14°20′S, 46°45′W), collected by J.C. de Oliveira and W.J.M. Costa, 14 Sep 1988, MZUSP 46546, 18 (31.2–41.0). Rio Tocantins basin, Ribeirão Cangalha, at road, 14 air km NNE of Formosa (15°24′S, 47°17′W), collected by W.C. Starnes et al., 13 Nov 1984, USNM 292214, 3 (42.4–46.8). Ribeirão Paranoa do Meio, at road crossing, 11 air km NNE of Formosa (approximately 15°25′S, 47°18′W), collected by W.C. Starnes et al., 13 Nov 1984, USNM 292226, 13 (27.3–46.6). Minaçu, tributary of Córrego Lageado, left bank tributary of Rio Tocantins, along road to Porto Rubião (approximately 13°38′S, 48°19′W), collected by D.F. Moraes, Jr. et al., 16 Jan 1988, MNRJ 13048, 6 (39.9–47.5).

NONTYPE SPECIMENS.—69 specimens.

BRAZIL. *Goiás:* Ribeirão Angélicu, above entrance to Caverna da Angélicu, São Domingos (approximately 13°36′S, 46°24′W), MZUSP 40629, 2. Município de Monte Alegre de Goiás, Rio Bezerra, right bank tributary of Río Paraná, MZUSP 40702, 3. Iaciara, Ribeirão Macambira (approximately 14°20′S, 46°45′W), near bridge on highway GO 112, MZUSP 50541, 63 (collected with holotype); MZUSP 40534, 1.

Creagrutus calai, new species

FIGURES 32, 33, TABLE 12

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, typically 6 teeth in the primary series of each premaxilla, 3 maxillary teeth, 5 teeth on each dentary, 9 to 11 median predorsal scales, 37 to 41 lateral line scales without a lamellar process over each pore, 4, rarely 5, scale rows between the dorsal-fin origin and the lateral line, 2 post-anal scales to the anal-fin origin, 10 to 12 branched anal-fin rays, 7 to 9 gill rakers on the upper limb and 11 to 13 gill rakers on the lower limb of the first gill arch, the head length (24.3%–27.5% of SL), the postorbital head length (41.2%–46.1% of HL), the interorbital width (28.8%–32.3% of HL), the contact between the ventral margin of the third infraorbital and the horizontal limb of the preopercle in larger specimens, the presence of a horizontally elongate, darkly pigmented, middorsal mark immediately posterior of the head, the lack of a distinct spot of dark pigmentation at the base of the middle caudal-fin rays, the overall vertically elongate, irregularly shaped, humeral mark most intensely pigmented in the area above the lateral line and without a secondary, dorsal patch of pigmentation, the absence of a distinct patch of pigmentation on the dorsal fin, and the lack of a series of dark spots along the midlateral surface of the body distinguishes *Creagrutus calai* within the clade formed by *Creagrutus* and *Piabina*.

TABLE 12.—Morphometrics and meristics of *Creagrutus calai*, new species: (A) holotype of *C. calai*, ANSP 130527, and (B) paratypes of *C. calai* (n=58). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	54.2	33.0–66.0
1. Snout to anal-fin origin	62.4	61.2–66.0
2. Snout to pelvic-fin insertion	45.4	45.1–48.1
3. Snout to pectoral-fin insertion	24.0	23.1–26.8
4. Snout to dorsal-fin origin	45.6	44.4–49.2
5. Dorsal-fin origin to hypural joint	57.7	54.1–59.5
6. Dorsal-fin origin to anal-fin origin	31.2	28.8–34.2
7. Dorsal-fin origin to pelvic-fin insertion	26.0	25.6–29.0
8. Dorsal-fin origin to pectoral-fin insertion	30.8	30.5–34.1
9. Caudal peduncle depth	10.9	10.4–12.2
10. Pectoral-fin length	18.6	17.9–22.0
11. Pelvic-fin length	18.4	14.6–18.6
12. Dorsal-fin length	19.2	18.8–22.6
13. Anal-fin length	16.4	15.0–18.5
14. Head length	24.5	24.3–27.5
15. Postorbital head length	41.4	41.2–46.1
16. Snout length	29.3	26.4–31.7
17. Bony orbital diameter	35.4	31.1–35.6
18. Interorbital width	32.0	28.8–32.3
	Meristics	
Lateral line scales	39	37–41[1]
Scale rows between dorsal-fin origin and lateral line	4	4–5[2]
Scale rows between anal-fin origin and lateral line	3	3–4[3]
Predorsal median scales	10	9–11
Branched dorsal-fin rays	8	8
Branched anal-fin rays	11	10–12
Branched pelvic-fin rays	6	6–7[4]
Pectoral-fin rays	14	13–15
Vertebrae	37	36–39

[1]Thirty-seven and 41 lateral line scales each present in only 1 paratype.

[2]Five scale rows between dorsal-fin origin and lateral line present in only 1 paratype.

[3]Four scale rows between anal-fin origin and lateral line present in only 1 paratype; larger paratypes with sheath of much smaller scales along base of anterior anal-fin rays.

[4]Seven branched anal-fin rays present only in some larger paratypes.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus calai* in Table 12. Head and body relatively slender in smaller specimens, becoming increasingly robust in larger specimens. Greatest body depth approximately at dorsal-fin origin in specimens up to 40 mm SL, falling between dorsal-fin origin and vertical midway between pectoral- and pelvic-fin insertions in larger specimens. Dorsal profile of head distinctly convex from margin of upper lip to vertical through posterior

FIGURE 32.—*Creagrutus calai*, new species, holotype, ANSP 130527, 54.2 mm SL; Colombia, Meta, Rancho El Viento, across Río Meta from Puerto Lopez (4°08′N, 72°39′W).

nostril, straight from that point to tip of supraoccipital spine. Interorbital region somewhat flattened transversely. Predorsal profile of body straight to slightly convex. Predorsal surface of body with obtuse median ridge posteriorly. Ventral profile of head with variably obvious obtuse angle at anteroventral corner of dentary, straight to very gently convex from angle to isthmus. Prepelvic profile of body convex, increasingly so in larger individuals. Prepelvic region of body obtusely flattened transversely.

Head obtusely flattened in lateral view and moderately compressed laterally in dorsal view. Upper jaw longer than, and overhanging, lower jaw. Anterior portion of snout fleshy with scattered papillae. Papillae more concentrated along ventral surface of upper lip and on fleshy folds and plicae extending between outer and medial premaxillary teeth. Anterior and particularly dorsal surfaces of lower lip with numerous papillae.

Infraorbital series moderately well developed in all specimens larger than 35 mm SL, proportionally somewhat more extensive posteriorly in larger individuals. Ventral margin of third infraorbital contacting, or nearly contacting, horizontal limb of preopercle. Posterior and ventral margins of third infraorbital approximately at right angles, with posteroventral corner of bone slightly rounded. Posterior margins of third through fifth infraorbitals separated from vertical limb of preopercle; gap between infraorbitals and preopercle progressively decreasing dorsally.

Premaxillary dentition in three series: primary row slightly curved to slightly sigmoid, typically with 6 teeth (5 teeth present on one side of head in two individuals), without pronounced gap between first and second tooth of series but with medial tooth separated from comparable tooth of contralateral series; triangular cluster of three somewhat to distinctly larger teeth; and single tooth of form similar to that of primary series occurring lateral to primary series; when 6 teeth present in primary series, single tooth of form similar to that of primary series located lateral to fourth tooth of primary series or lateral to area of contact of fourth and fifth teeth of primary series, when 5 teeth present in primary series, single tooth of form similar to that of primary series located lateral to third tooth of primary series. Maxillary teeth 3, tricuspidate. Dentary teeth 5, first two teeth largest, with first tooth about two-thirds height of second tooth and distinctly narrower. Third dentary tooth about one-third height of second tooth. Remaining dentary teeth half as high as third tooth and tricuspidate.

Dorsal-fin rays ii,8 in all specimens. Dorsal-fin origin approximately at vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin straight to slightly concave. Anal-fin rays ii,10–12 or iii,10–12, with first unbranched ray very short when three unbranched rays present. Distal profile of anal-fin concave, more so in larger individuals. Anal-fin hooks present on first and second or first through third rays in mature males. Pectoral-fin rays i,12–14. Tip of pectoral fin reaching posteriorly to within 2 or 3 scales of pelvic-fin insertion. Pelvic-fin rays i,6,i or i,7; i,7 occurs only in larger specimens. Tip of pelvic fin reaching posteriorly to, or nearly to, anal-fin origin. Mature males with pelvic-fin hooks present on all branched rays (6 or 7 rays depending on number of branched rays in an individual).

Gill rakers 7–9+11–13.

COLORATION IN ALCOHOL.—Overall ground coloration of specimens tan. Dorsal surface of head with deep-lying larger stellate chromatophores and smaller surface chromatophores; chromatophore concentration greater in larger individuals. Chromatophore field extending onto snout, upper lip, and region anterior and anteroventral to orbit. Region anterior to nostrils with more intensely pigmented, crescent-shaped field of dark chromatophores. Smaller and medium-sized individuals with posteroventrally angled stripe of dark chromatophores extending from under nostril to anteroventral margin of eye; stripe subsumed into overall darker pigmentation in that region in larger individuals. Fourth and fifth infraorbitals, dorsal portion of third infraorbital, and dorsal portion of opercle with dispersed dark chromatophores in juveniles; chromatophore field more concentrated in larger individuals, with dark chromato-

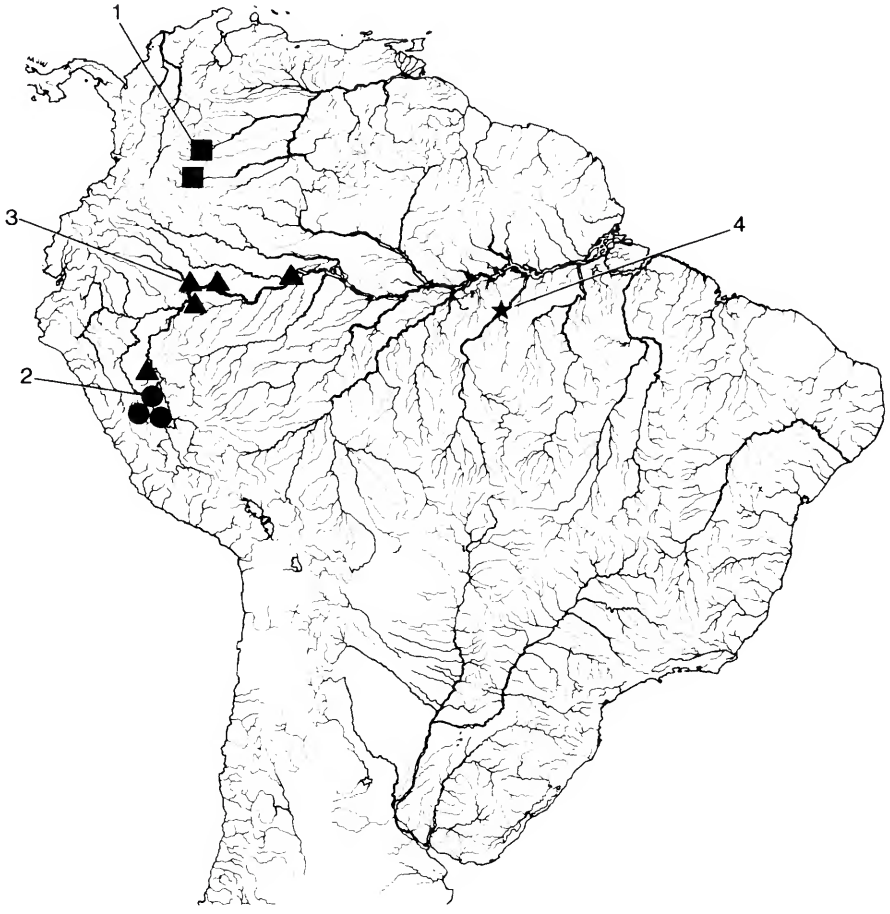

FIGURE 33.—Map of central and northern South America showing geographic distribution of *Creagrutus calai* (squares, 1=type locality), *Creagrutus changae* (dots, 2=type locality), *Creagrutus cochui* (triangles, 3=type locality), and *Creagrutus cracentis* (star, 4=type locality) (some symbols represent more than one locality or lot of specimens).

phores on cheek posterior to third infraorbital, lower portion of opercle, and along subopercle. Lower jaw with field of small dark chromatophores anteriorly.

Scales of dorsolateral portion of body with dense field of small dark chromatophores and distal pattern of larger, more diffuse chromatophores; chromatophore fields separated by hyaline or less pigmented region. Less pigmented areas apparent as reticulate pattern on dorsolateral region of body. Scales ventral to that area with irregular pattern of scattered, dark chromatophores slightly more concentrated along scale margins dorsal to lateral line. Humeral mark vertically elongate; most intensely pigmented in area immediately dorsal of lateral line. Intensely pigmented region of humeral mark more developed horizontally than regions dorsal and ventral to it. Humeral mark continuing ventrally from intensely pigmented region as more diffuse ventrally attenuating region of dark pigmentation. Portion of mark dorsal to central section less intensely pigmented, typically somewhat anteriorly arching and extending one to one and one-half scales dorsally from central region. Midlateral stripe well developed but less intensely pigmented anteriorly, falling 3 or 4 scales short of posterior margin of humeral spot in specimens smaller than approximately 40 mm SL; stripe extending anteriorly to posterior margin of humeral mark; anterior portion somewhat masked by guanine in some specimens.

Dorsal-fin rays outlined by dark chromatophores and with scattered, dark chromatophores on distal portions of anterior rays. Anal fin with small chromatophores outlining basal portions of anterior rays and scattered chromatophores on distal portions of anterior branched rays. Middle caudal-fin rays more intensely pigmented than remainder of fin; pigmentation forming faint stripe in specimens of approximately 40 mm SL, and distinct stripe in larger individuals. Remaining caudal-fin rays outlined by chromatophores, with greater intensity of pigmen-

tation on dorsalmost and ventralmost portions of fin. Pectoral and pelvic fins with rays lightly outlined by series of dark chromatophores.

ETYMOLOGY.—The specific name, *calai,* is in honor of Plutarco Cala, Universidad Nacional de Colombia, in recognition of his many contributions to our understanding of Colombian freshwater fishes, and for his assistance to the authors.

ECOLOGY.—Stomach contents of two specimens of *Creagrutus calai* prepared for clearing and staining in this study consisted of chopped-up seeds and insect parts.

DISTRIBUTION.—*Creagrutus calai* occurs in the western portions of the Río Meta basin in eastern Colombia (Figure 33, squares).

MATERIAL EXAMINED.—66 specimens (59, 33.0–66.0).

HOLOTYPE.—COLOMBIA. *Meta:* Unnamed stream on Rancho El Viento, across Río Meta from Puerto Lopez (4°08′N, 72°39′W), collected by J.E. Böhlke and N.R. Foster, 20 May 1969, ANSP 130527, 1 (54.2).

PARATYPES.—58 specimens (58, 33.0–66.0).

COLOMBIA. *Meta:* Unnamed stream on Rancho El Viento, across Río Meta from Puerto Lopez (4°08′N, 72°39′W), collected with holotype, ANSP 177718, 12 (40.7–58.0); USNM 353307, 4 (42.0–56.1). Rancho El Viento, Caño Emma (4°08′N, 72°39′W), collected by J.E. Böhlke and N.R. Foster, 18 Mar 1973, ANSP 139149, 18 (33.0–65.3); USNM 353304, 4 (42.9–59.5; 2 specimens cleared and counterstained). Río Meta basin, Caño Candelaria, tributary to Río Negro, approximately 20 km SW of Villavicencio, collected by A.M.C. Silfvergrip, 10 Jan 1988, NRM 43015, 2 (64.1–66.0). Río Meta basin, Caño Quenane, tributary to Río Negro, where crossed by road between Villavicencio and Puerto López (4°02′N, 73°10′W), collected by A.M.C. Silfvergrip, 7 Jan 1988, NRM 16849, 10 (46.3–60.0); USNM 353868, 2 (46.6–56.2). Río Meta basin, Caño Quenane, tributary to Río Negro, where crossed by road between Villavicencio and Puerto López (4°02′N, 73°10′W), collected by A.M.C. Silfvergrip, 7 Jan 1988, NRM 16848, 1 (53.9). Río Meta basin, Caño Union, tributary to Río Ocoa, where crossed by road between Villavicencio and Acacías, collected by A.M.C. Silfvergrip, 7 Jan 1988, NRM 43016, 5 (40.6–58.4).

NONTYPE SPECIMENS.—7 specimens.

COLOMBIA. *Meta:* Cordillera Macarena, small brook into Río Guayabero, 5 mi (8.0 km) below El Refugio, elev. 900 ft (approximately 274 m), CAS 153758, 6. Villavicencio, Río Meta basin (4°09′N, 73°39′W), USNM 100790, 1.

Creagrutus changae, new species

FIGURES 33, 34, TABLE 13

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 6 teeth in the primary series of each premaxilla, 3 or 4 teeth on each maxilla, 5 teeth on each dentary, 39 to 43 lateral line scales without a lamellar process over each pore, 9 to 11 median predorsal scales, 5 or 6 rows of scales between the lateral line and the dorsal-fin origin, 4 rows of scales between the lateral line and the anal-fin origin, 2 post-anal scales to the anal-fin origin, 10 or 11 branched anal-fin rays, 37 to 39 vertebrae, 6 or 7 gill rakers on the upper limb and 9 or 10 gill rakers on the lower limb of the first arch, the interorbital width (27.7%–31.3% of HL), the well-developed third infraorbital approaching, or contacting, the horizontal limb of the preopercle, the lack of a series of dark spots along the midlateral surface of the body, the discrete, distinctly vertically elongate humeral mark, and the lack of a discrete patch of dark pigmentation on the anterior rays of the dorsal fin distinguishes *Creagrutus changae* from all members of the clade composed of *Creagrutus* and *Piabina.*

TABLE 13.—Morphometrics and meristics of *Creagrutus changae,* new species: (A) holotype of *C. changae,* MUSM 8858; and (B) paratypes of *C. changae* (n=50). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	75.5	35.9–66.9
1. Snout to anal-fin origin	64.1	61.1–66.3
2. Snout to pelvic-fin insertion	46.2	44.2–50.1
3. Snout to pectoral-fin insertion	25.2	23.5–28.1
4. Snout to dorsal-fin origin	47.5	46.9–50.6
5. Dorsal-fin origin to hypural joint	56.4	53.6–57.9
6. Dorsal-fin origin to anal-fin origin	34.0	31.0–35.1
7. Dorsal-fin origin to pelvic-fin insertion	28.6	26.8–31.1
8. Dorsal-fin origin to pectoral-fin insertion	34.0	31.6–36.7
9. Caudal peduncle depth	12.7	11.7–13.5
10. Pectoral-fin length	20.8	18.9–23.1
11. Pelvic-fin length	16.7	15.0–17.6
12. Dorsal-fin length	22.7	21.9–25.3
13. Anal-fin length	17.6	17.2–20.7
14. Head length	26.6	25.2–29.5
15. Postorbital head length	46.0	42.7–49.0
16. Snout length	28.4	25.3–30.9
17. Bony orbital diameter	31.8	31.0–36.4
18. Interorbital width	30.3	27.7–31.3
	Meristics	
Lateral line scales	40	39–43
Scale rows between dorsal-fin origin and lateral line	5	5–6
Scale rows between anal-fin origin and lateral line	4	4
Predorsal median scales	11	9–11
Branched dorsal-fin rays	8	7–8[1]
Branched anal-fin rays	11	10–11
Branched pelvic-fin rays	7	6–7
Pectoral-fin rays	14	13–14
Vertebrae	38	37–39

[1]Seven branched dorsal-fin rays present in only 2 paratypes.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus changae* in Table 13. Head and body relatively robust in all specimens larger than 30 mm SL. Greatest body depth at, or

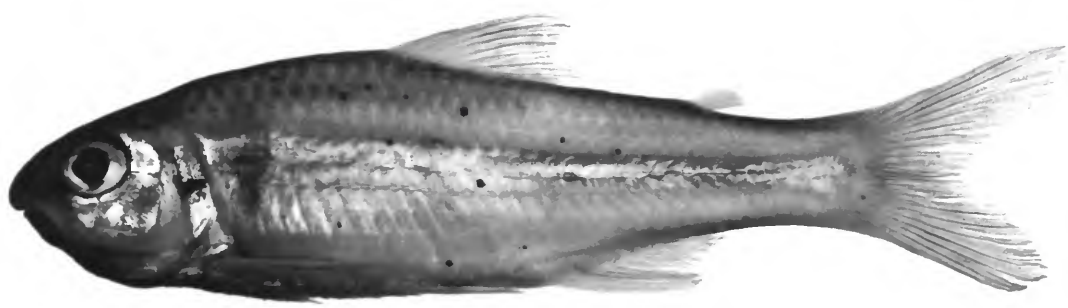

FIGURE 34.—*Creagrutus changae*, new species, holotype, MUSM 8858, 75.5 mm SL; Peru, Huanuco, Provincia Pachitea, Río San Alejandro, a tributary of Río Sungarayacu, just above junction with Río Sungarayacu (approximately 9°23'S, 75°11'W).

more rarely, slightly anterior of dorsal-fin origin. Dorsal profile of head smoothly convex from tip of snout to vertical through posterior nostril, straight or very slightly convex from that point to tip of supraoccipital spine. Interorbital region slightly convex. Dorsal profile of body nearly straight anteriorly; continuous with profile of head in smaller specimens, slightly convex with moderate change in alignment relative to that of head in larger individuals. Profile slightly angled at dorsal-fin base in relatively shallow-bodied individuals, angle more pronounced in deep-bodied specimens. Dorsal surface of body with predorsal median ridge proximate to dorsal fin in all individuals larger than 30 mm SL. Ventral profile of head with slightly to moderately obvious obtuse angle at anteroventral corner of dentary, slightly convex from that angle to isthmus. Ventral profile of body slightly convex in most specimens, more convex in ripe females. Prepelvic region of body obtusely flattened transversely.

Head pointed in both lateral and dorsal views. Upper jaw distinctly longer than, and overhanging, lower jaw. Anterior portion of snout fleshy with numerous papillae; papillae more concentrated along ventral margin of fleshy upper lip, and on fleshy folds and plicae extending between outer and medial premaxillary teeth. Lower lip very fleshy, with numerous papillae on dorsal margin and anteromedial region.

Infraorbital series moderately developed. Ventral margin of third infraorbital falling distinctly short of horizontal limb of preopercle. Posterior margins of third through fifth infraorbitals distinctly separated from vertical limb of preopercle.

Premaxillary dentition in three series: primary row curved and slightly sigmoid medially, consisting of 6 teeth, without pronounced gap between first and second tooth of series but with medial tooth distinctly separated from anterior tooth of contralateral series; triangular cluster of 3 larger teeth, and single tooth of form similar to that of primary series occurring lateral to fourth tooth of premaxillary row. Maxilla with 3 or 4 tricuspidate teeth. Dentary with 5 tricuspidate teeth; first and second teeth subequal and approximately twice height of third tooth; fourth and fifth teeth much smaller and graded in size, compressed.

Dorsal-fin rays typically ii,8, rarely ii,7. Dorsal-fin origin approximately at vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin slightly concave. Anal-fin rays typically ii,10–11, rarely iii,10. Profile of distal margin of anal fin nearly straight in smaller specimens, increasingly concave in larger individuals. Anal fin in mature males with hooks occasionally present on last unbranched and anterior 3 to 6 branched rays. Pectoral-fin rays i,12–13. Pectoral fin extending posteriorly to, or falling slightly short of, pelvic-fin insertion. Pelvic-fin rays i,6,i or i,7; branching of medial pelvic-fin ray limited to larger individuals. Hooks of mature males, when present, occurring on all branched pelvic-fin rays.

Gill rakers 6–7+9–10.

COLORATION IN LIFE.—(Description based on a transparency of recently collected specimen from the Río Yuyapichis (= Llullapichis), Río Pachitea basin, Peru, provided by E. Holm, ROM.) Overall coloration bright silver, with guanine deposits particularly well developed on first through third infraorbitals, opercle, and central region of exposed portions of scales other than on anterodorsal and posterodorsal sections of lateral surface of body. Vertically elongate humeral mark prominent. Midlateral stripe obvious but not to degree as humeral mark. Region of eye dorsal to pupil blood red. Anterior anal-fin rays and lateral pelvic-fin ray white. Dark pigmentation on head, body, and fins as in alcohol-preserved specimens.

COLORATION IN ALCOHOL.—Overall ground coloration of most specimens tan. Dorsal surface of head with scattered, small, dark chromatophores extending onto snout and upper lip. No indication of larger deep-lying dark chromatophores overlying brain as in some *Creagrutus* species. Slight concentration of chromatophores present anterior to nostril in specimens of approximately 30 to 40 mm SL, but region without obvious concentrations of chromatophores in larger individuals. Small dark chromatophores more concentrated anteroventral to orbit, concentration more obvious in smaller specimens. Irreg-

ular band of chromatophores outlining remaining portions of ventral and posterior orbital margins. Scattered chromatophores over dorsal portions of infraorbital series and opercle.

Scales of dorsal portion of body with dense chromatophore field over basal portion of exposed section of scales and with scattered chromatophores along margin of scales. Darkly pigmented regions separated by hyaline crescent. Humeral mark vertically elongate, darkly pigmented in some, usually smaller, specimens, but diffuse in larger individuals. Mark extending approximately 1.5 scales ventral of, and 2 scales dorsal of, lateral line, with distinct dorsal limits in few specimens with prominent marks, but more typically merging imperceptibly into darker pigmentation of dorsal portion of body in specimens with more diffuse marks.

Dorsal fin with anterior margin of first unbranched ray and distal margins of branched rays outlined with dark chromatophores. Basal one-fourth to two-thirds of branched anal-fin rays outlined with chromatophores. Caudal-fin rays variably outlined and overlain by small dark chromatophores, giving fin overall dusky appearance. Pectoral fin ranging from hyaline to rays variably outlined by dark chromatophores. Pelvic fin hyaline.

ETYMOLOGY.—The specific name, *changae,* is in honor of the late Fonchii Chang of the Museo de Historia Natural, Lima, in recognition of her contributions to our understanding of Peruvian fishes and her assistance to the authors prior to her untimely death.

ECOLOGY.—The holotype and three of the paratype lots were collected in the middle of the main channel of the Río San Alejandro over sand bottoms and rocky riffles. Three of the examined lots from the Río Pachitea basin (ROM 55853, ROM 56084, MUSM 8859) were collected in 3 to 7 m wide streams with rubble, silt, sand, gravel, and clay bottoms. Water velocity ranged from slow to fast in pools, across riffles, and in the main channel.

Examination of the stomach contents of two specimens prepared for clearing and staining for this study indicates that the species feeds on adult and larval insects. At one locality in the Río Chanchamayo, Department of Junin, Peru, *C. changae* was collected along with *C. peruanus.*

SEXUAL DIMORPHISM.—Mature males, as shown by the possession of hooks on the anal-fin and pelvic-fin rays, were all smaller than 63 mm SL. Some of the larger examined specimens, larger than 65 mm SL, are females with well-developed eggs.

DISTRIBUTION.—*Creagrutus changae* occurs in various western tributaries of the Río Ucayali in the departments of Junin, Pasco, and Huanuco, Peru (Figure 33, dots).

REMARKS.—Steindachner (1882a) reported *Creagrutus peruanus* without further comment from the Río Huambo. Only *Creagrutus changae* is known from that basin, and Steindachner's report may refer to that species.

MATERIAL EXAMINED.—245 specimens (62, 35.9–75.5).

HOLOTYPE.—PERU. *Huanuco:* Provincia Pachitea, Río San Alejandro, a tributary of Río Sungarayacu, just above junction with Río Sungarayacu (approximately 9°23′S, 75°11′W), collected by D.W. Greenfield et al., 31 Jul 1975, MUSM 8858, 1 (75.5).

PARATYPES.—50 specimens (50, 35.9–66.9).

PERU. *Huanuco:* Provincia Pachitea, Río San Alejandro, a tributary of Río Sungarayacu, just above junction with Río Sungarayacu (approximately 9°23′S, 75°11′W), collected with holotype, USNM 285276, 14 (42.6–66.7; 2 specimens cleared and counterstained for cartilage and bone); FMNH 84265, 10 (49.8–61.0; collected with holotype). Provincia Pachitea, Río Huambo, at its mouth in Río Pachitea (approximately 9°36′S, 74°56′W), collected by E. Holm et al., 28 Jul 1988, ROM 72378, 10 (56.7–66.9); MUSM 8859, 16 (35.9–58.9).

NONTYPE SPECIMENS.—194 specimens (11, 36.4–60.8).

PERU. *Junin:* Provincia Satipo, Río Satipo, 4 km downstream from Satipo (latter locality at 11°16′S, 74°37′W), MUSM 8860, 1 (60.8). Provincia Satipo, Satipo, Río Coviriali (11°16′S, 74°37′W), MUSM 8861, 1 (51.3). Provincia Satipo, Río Ene basin, Río Negro, MUSM 8862, 4 (38.0–51.23). *Pasco:* Provincia Oxampampa, Iscozacin, Río Chuchurras, Villa America (approximately 10°04′S, 75°07′W), MUSM 8863, 13 (3, 36.4–49.6). Provincia Oxampampa, Río Iscozacin, 39 km NNE of Oxampampa, LACM 37362–4, 2. Provincia Oxampampa, Quebrada Sachavaca, tributary of Río Palcazú, MUSM 10761, 6. *Huanuco:* Provincia Pachitea, Río San Alejandro, a tributary of Río Sungarayacu, just above junction with Río Sungarayacu (approximately 9°23′S, 75°11′W), FMNH 105273, 37 (formerly FMNH 84265, in part). Provincia Pachitea, Río Llullapichis (=Yuyapichis), approximately 2 km upstream from mouth into Río Pachitea (approximately 9°37′S, 74°57′W), ROM 55853, 11 (2, 47.4–48.0). Provincia Pachitea, Río Huambo, at its mouth in Río Pachitea (approximately 9°36′S, 74°56′W), ROM 70107, 9. *Cusco:* La Convencion, Echarata Sagakiato, Quebrada Pagonpirintsi, USNM 358006, 6. La Convencion, Echarata Sagakiato, Quebrada Prokigiato, USNM 358005, 3. La Convencion, Echarata Sagakiato, Quebrada Tigonkavi, USNM 358003, 10. La Convencion, Echarata Sagakiato, Quebrada Matiariroate, USNM 358015, 12. La Convencion, Echarata Sagakiato, Quebrada Kemariatoi, USNM 358011, 2. La Convencion, Echarata Sagakiato, Quebrada Porocari, USNM 358007, 8. La Convencion, Echarata Sagakiato, Quebrada Otsitiari, USNM 358012, 1. La Convencion, Echarata Peruanita, Quebrada Igoripato, USNM 358002, 3. La Convencion, Echarata Shivangorani-Camisea, Quebrada Kapoparoari, USNM 358004, 20. La Convencion, Echarata Shivangorani-Camisea, Quebrada Kapiroshambia, USNM 358010, 14. La Convencion, Echarata Shivangorani-Camisea, Quebrada Songarinsiatoi, USNM 358009, 16. La Convencion, Echarata Malvinas, Quebrada Kamagatiniatoi, USNM 358014, 6. La Convencion, Echarata Malvinas, Quebrada Yaririato, USNM 358013, 2. La Convencion, Echarata Malvinas, Río Urubamba, USNM 358008, 2. La Convencion, Echarata Parvanita, Quebrada Kayonaroata, USNM 357992, 5.

Creagrutus cochui Géry, 1964

FIGURES 33, 35, TABLE 14

Creagrutus cochui Géry, 1964:56, fig. 12 [type locality: Peru (Loreto), "Upper Amazon region surrounding Iquitos"]; 1977:393, 407 [species included in key, life photo].—Ortega and Vari, 1986:8 [Peru; common name].—Géry and Renno, 1989:5 [comparison with *C. planquettei*].—Vari and Howe, 1991:15 [holotype depository].—Román-Valencia and Cala, 1996:148 [Colombia, Río Loreto-Yacú, Río Amazonas basin].

DIAGNOSIS.—The presence of a horizontally elongate, but distinct, main body of the humeral mark is unique to *Creagrutus cochui* within the genus, being approximated only by larger specimens of *C. atrisignum*, an endemic of the Rio Tocantins basin. The latter species, however, has a secondary humeral mark situated dorsal to the horizontally elongate primary mark; this additional patch of dark pigmentation is absent in *C. cochui*. Other features, which in combination separate *C. cochui* from the other members of the clade composed of *Creagrutus* and *Piabina*, are the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, typically 6 teeth in the primary premaxillary tooth row, 2 or 3 teeth on the maxilla, 5 teeth on each dentary, 38 to 41 lateral line scales without a lamellar process over each pore, 4 scale rows between the dorsal-fin origin and the lateral line, 9 or 10 predorsal scales, 2 post-anal scales anterior to the anal-fin origin, 11 to 13 branched anal-fin rays, the head length (24.1%–26.5% of SL), the interorbital width (27.8%–32.5% of HL), the relatively shallow and transversely rotund body, the well-developed third infraorbital contacting the horizontal limb of the preopercle, the lack of a series of midlateral dark marks on the body, the horizontally elongate humeral mark, and the absence of a discrete patch of dark pigmentation on the middle portions of the anterior dorsal-fin rays.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus cochui* in Table 14. Greatest body depth at, or slightly anterior of, vertical through pelvic-fin insertion. Dorsal profile of head gently convex from tip of snout to vertical through posterior nostril, nearly straight from that point to tip of supraoccipital spine. Predorsal profile of body gently convex in all examined specimens. Postdorsal profile of body straight to slightly convex. Ventral profile of head with obtuse angle at anteroventral corner of dentary, straight from that point to isthmus. Ventral profile of body convex, more so in larger individuals.

Head obtusely pointed in both dorsal and lateral views. Upper jaw longer than, and overhanging, lower jaw. Snout somewhat fleshy. Papillae concentrated on anterior portion of snout and upper lip, particularly along ventral margin of lip and on folds and plicae extending between outer and medial premaxillary teeth. Lower lip fleshy anteriorly, with papillae concentrated on dorsal surface.

TABLE 14.—Morphometrics and meristics of *Creagrutus cochui*: (A) holotype of *C. cochui*, USNM 200426; and (B) all specimens of *C. cochui* from which counts and measurements were taken (n=19). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length. Dashes indicate values that could not be determined because of damage to the holotype.

Characters	A	B
	Morphometrics	
Standard length	68.3	44.2–79.3
1. Snout to anal-fin origin	64.1	61.3–65.9
2. Snout to pelvic-fin insertion	46.0	44.5–48.3
3. Snout to pectoral-fin insertion	24.0	22.6–25.2
4. Snout to dorsal-fin origin	43.3	42.9–46.1
5. Dorsal-fin origin to hypural joint	59.0	57.8–60.5
6. Dorsal-fin origin to anal-fin origin	32.4	29.9–33.7
7. Dorsal-fin origin to pelvic-fin insertion	24.4	24.0–27.1
8. Dorsal-fin origin to pectoral-fin insertion	29.1	28.9–31.7
9. Caudal peduncle depth	11.4	10.3–11.8
10. Pectoral-fin length	–	18.7–21.0
11. Pelvic-fin length	15.6	15.6–18.0
12. Dorsal-fin length	–	20.0–24.7
13. Anal-fin length	–	17.5–20.3
14. Head length	24.2	24.1–26.5
15. Postorbital head length	42.4	39.0–44.3
16. Snout length	27.3	26.8–30.4
17. Bony orbital diameter	36.3	33.3–39.0
18. Interorbital width	32.1	27.8–32.5
	Meristics	
Lateral line scales	39	38–41
Scale rows between dorsal-fin origin and lateral line	4	4
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	9	9–10
Branched dorsal-fin rays	8	8
Branched anal-fin rays	13	11–13
Branched pelvic-fin rays	7	7
Pectoral-fin rays	13	12–14
Vertebrae	37	37–39

Infraorbital series well developed. Anterior one-half of ventral margin of third infraorbital contacting horizontal limb of preopercle. Posterior margins of third to fifth infraorbitals not contacting vertical limb of preopercle, gap between posterior margins of infraorbitals and preopercle progressively decreasing dorsally.

Premaxillary dentition in three series: primary row slightly curved, typically with 6 teeth, 5 teeth present on one premaxilla in one specimen, without pronounced gap between first and second tooth of series but with anterior teeth of contralateral series distinctly separated; triangular cluster of three tricuspidate teeth; and single tooth of form similar to that of primary series lying lateral to fourth tooth of primary premaxillary series. Maxilla with 2 or 3 tricuspidate teeth. Dentary with 5 teeth, first three teeth distinctly larger, with first and second teeth particularly large. Fourth tooth slightly smaller than third tooth. All teeth tricuspidate, with central cusp proportionally much larger on first three teeth and all cusps nearly equal on fifth tooth.

Dorsal-fin rays ii,8. Dorsal-fin origin slightly anterior to vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin concave, more so in larger individuals. Anal-fin rays ii,11–13, rarely iii,12–13. Profile of distal margin of anal fin distinctly concave, with last branched and first 2 or 3 branched rays forming anterior lobe. Mature males with paired hooks present on posterior margins of main shaft of ray and on posterior branches of first through third branched rays; 1 or 2 hooks sometimes present on fourth ray. Pectoral-fin rays i,11–13. Pectoral fin extending posteriorly approximately three-fourths of distance to pelvic-fin insertion. Pelvic-fin rays i,7. Mature males with hooks present on posterior margin of unsegmented and posterior main branch of segmented portions of all branched rays. Hooks also present on all branches except lateralmost branched pelvic-fin ray. Tip of pelvic fin extending posteriorly to anal-fin origin.

Gill rakers 7–8 + 11–14.

COLORATION IN LIFE.—(based on life photo of a paratype of the species in an aquarium, Géry, 1964, fig. 12a; 1977:393). Overall coloration of body brown with guanine highlights on scales, opercle, and infraorbitals. Horizontally elongate, dark humeral mark very obvious. Lighter patch of dark pigmentation extending dorsally from main portion of humeral mark. Distal portion of anterior rays of dorsal fin apparently dark. Dark pigmentation present on basal portions of middle caudal-fin rays. Anterior margin of anal fin white. Light highlights present along rays of dorsal fin.

COLORATION IN ALCOHOL.—Overall ground coloration tan. Smaller specimens with dorsal surface of brain covered by relatively large, dark chromatophores, this pigmentation obscured by thicker bones and surface pigmentation in larger individuals. Dorsal surface of head with scattered, small, dark chromatophores; chromatophore field more concentrated over snout, particularly anterior to nares where pigmentation forms discrete crescent. Posteroventrally inclined band of chromatophores under anterior margin of adipose eyelid. Narrow band of dark chromatophores bordering ventral and posterior margins of orbit in many *Creagrutus* species absent. Surface of fourth and fifth infraorbitals with scattered, small, dark chromatophores. Distinct patch of large dark chromatophores on dorsal portion of opercle, sometimes also extending anteriorly onto posterior portion of infraorbital series; when well developed chromatophore field forming horizontal dark band posterior of orbit.

Dorsal and dorsolateral surfaces of body with scattered, small, dark chromatophores; chromatophore fields more concentrated over center of scales. Midlateral dark stripe extending from supracleithrum to caudal-fin base. Humeral mark lying within midlateral stripe; main portion of mark consisting of horizontally elongate patch of dark pigmentation. Main portion of humeral mark flanked dorsally by very faint to moderately pigmented anterodorsally angled patch. Some specimens with limited area of scattered, dark chromatophores ventral of main body of humeral mark.

Dorsal fin with interradial membranes between distal portions of last unbranched and anterior 4 to 6 branched rays with vertically elongate patches of dark pigmentation. Interradial pigmentation most intense between last unbranched and first branched and between first and second branched rays. Remainder of dorsal fin with small dark chromatophores outlining rays. Anal fin ranging from hyaline to having distal portions of middle rays somewhat dusky. Caudal fin with variably apparent basal spot formed by chromatophores as large as, and continuous with, those of midlateral stripe. Middle caudal-fin rays and associated membranes with scattered, dark chromatophores, giving region dusky appearance. Pectoral and pelvic fins hyaline to slightly dusky.

ECOLOGY.—Examination of the stomach contents of two specimens prepared for clearing and staining in this study revealed parts of seeds, larval and adult insects, and in one case a portion of the head of a small fish.

In the southern portions of its range *Creagrutus cochui* was captured sympatrically with *C. pila* within the Río Neshuya, a tributary of the Río Aguaytia (MUSM 8887 and 5240; MUSM 8885 and 8876, respectively).

COMMON NAME.—Peru: "Majorita" (Ortega and Vari, 1986:8).

DISTRIBUTION.—*Creagrutus cochui* occurs in the western portions of Amazon basin in Peru, Brazil, and perhaps Colombia (see below, under "Remarks," concerning latter locality; Figure 33, triangles).

GEOGRAPHIC VARIATION.—The pigmentation in the region of the humeral mark in the samples (MUSM 8885, 8886, 8887) from the southern portion of the species' range in the Río Aguaytia basin of the Department of Ucayali, Peru, differs sightly from that in samples from further to the north. The dark pigmentation situated dorsal of the main body of the humeral mark, which is faint in more northerly population samples, is more obvious in the Río Aguaytia sample. The portion of the midlateral stripe contiguous with the humeral mark in the Río Aguaytia sample also is more heavily pigmented than the remainder of the stripe and the humeral mark. This contrasts with the situation in populations further to the north in which the humeral mark and stripe are equally dark. Additional samples from intervening regions are necessary to determine whether this variation is significant.

REMARKS.—One specimen from a Colombian location (UF 33678) may represent the most northerly record for this species. The specimen's poor condition precludes a definitive identification.

MATERIAL EXAMINED.—149 specimens (19, 44.2–79.3).

BRAZIL. *Amazonas:* Rio Içá, Igarapé Boa Vista, MZUSP 28035, 53 (15, 44.2–73.9; 2 specimens cleared and counterstained for cartilage and bone). Caiauá, Igarapé da Cachoeira, along margin of Rio Içá, MZUSP 17536, 3 (1, 79.3). Igarapé Açu, 7 km below Santo Antonio do Içа (3°05′S, 40°49′W), MZUSP 17574, 63. Igarapé tributary to Rio Içа, 17.4 km downstream of Santo Antonio do Içа, USNM 342927, 10.

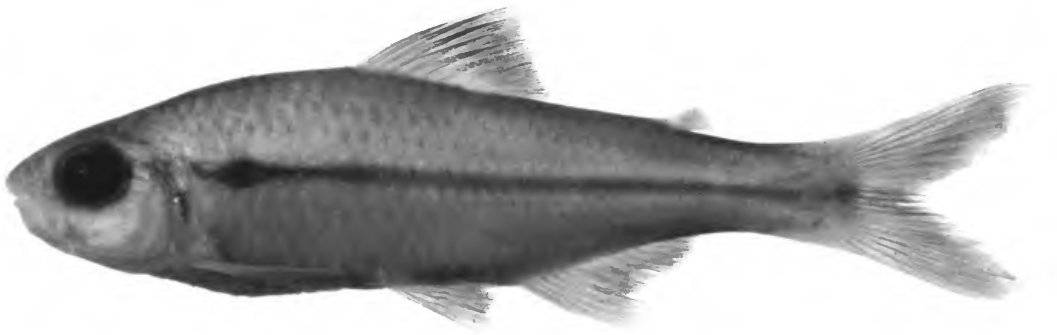

FIGURE 35.—*Creagrutus cochui*, MZUSP 28035, 65.5 mm SL; Brazil, Amazonas, Rio Içá, Igarapé Boa Vista.

COLOMBIA. *Meta:* Roadside pond and stream 48 km NNE of Vistahermosa (Río Guaviare basin), UF 36678, 1 (see under "Remarks," above, concerning this specimen).

PERU. *Loreto:* Upper Amazon [Río Amazonas], near Iquitos, USNM 200426, 1 (68.3, holotype of *Creagrutus cochui*); MHNG 2183.36, 1 (54.8, paratype of *Creagrutus cochui*). Quebrada Carahuayte at km 20 on road between Jenaro Herrera and Colonia Angamos, NRM 26306, 1; NRM 26307, 3 (1, 61.5). Río Ampiyacu, near Pebas (3°20'S, 71°49'W), CAS 160723 (formerly SU 60723), 6. Ramón Castilla, Beirut, MUSM 194, 1. *Ucayali:* Provincia Padre Abad, Río Tahuayo, km 72 on road from Pucallpa to Tingo Mario, MUSM 8887, 1. Provincia Coronel Portillo, Río Aguaytia basin, Río Neshuya (mouth of river at 8°17'S, 75°03'W), MUSM 8885, 3; MUSM 8886, 2.

Creagrutus cracentis, new species

FIGURES 33, 36, TABLE 15

DIAGNOSIS.—The presence of two distinct rows of premaxillary teeth, the very elongate, moderately sloping maxilla compared with the condition in most congeners, and the five median scales between the posterior margin of the anus and the anal-fin origin distinguish *Creagrutus cracentis* from all congeners with the exception of *C. maxillaris*, a species known from the upper portions of the Rio Negro and Río Orinoco of northern Brazil and southern Venezuela and the upper Rio Madeira basin along the Bolivian-Brazilian border. These two species can be differentiated by the postorbital head-length (36.8%–38.0% of HL in *C. cracentis* versus 40.6%–46.8% of HL in *C. maxillaris*), the orbital width (37.0%–40.0% of HL in *C. cracentis* versus 28.7%–34.6% of HL in *C. maxillaris*), and to a lesser degree on the pectoral-fin length (17.9%–20.0% of SL in *C. cracentis* versus 15.1%–18.2% of SL in *C. maxillaris*).

DESCRIPTION.—Morphometric and meristic data for *Creagrutus cracentis* in Table 15. Overall appearance of head and body distinctly elongate compared to most congeners; elongation particularly pronounced in smaller paratypes. Greatest body depth at vertical through dorsal-fin origin. Dorsal profile of head smoothly rounded from margin of upper jaw approximately to vertical through posterior nostril in specimens of all examined sizes; nearly straight from that point to rear of su-

TABLE 15.—Morphometrics and meristics of *Creagrutus cracentis*, new species: (A) holotype of *C. cracentis*, MCP 15213; and (B) paratypes of *C. cracentis* (n=5). Standard length is expressed in mm; measurements 1 to 14= percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	38.3	21.5–33.3
1. Snout to anal-fin origin	66.5	63.7–67.3
2. Snout to pelvic-fin insertion	46.2	46.3–48.3
3. Snout to pectoral-fin insertion	23.2	23.4–25.1
4. Snout to dorsal-fin origin	46.2	46.4–47.0
5. Dorsal-fin origin to hypural joint	54.0	51.2–54.1
6. Dorsal-fin origin to anal-fin origin	28.7	26.6–28.2
7. Dorsal-fin origin to pelvic-fin insertion	19.1	16.5–20.1
8. Dorsal-fin origin to pectoral-fin insertion	28.1	25.6–27.8
9. Caudal peduncle depth	9.2	9.2–9.9
10. Pectoral-fin length	19.3	17.9–20.0
11. Pelvic-fin length	13.8	13.5–15.0
12. Dorsal-fin length	19.5	18.0–19.5
13. Anal-fin length	15.7	14.6–16.2
14. Head length	26.1	25.9–26.8
15. Postorbital head length	38.0	36.8–38.0
16. Snout length	26.0	25.7–28.1
17. Bony orbital diameter	37.0	38.0–40.0
18. Interorbital width	25.0	25.2–27.1
	Meristics	
Lateral line scales	39	39–40
Scale rows between dorsal-fin origin and lateral line	4	4
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	9	9
Branched dorsal-fin rays	8	8
Branched anal-fin rays	10	9–10
Branched pelvic-fin rays	7	6–7
Pectoral-fin rays	14	13–14
Vertebrae	37	38–39

FIGURE 36.—*Creagrutus cracentis*, new species, holotype, MCP 15213, 38.3 mm SL; Brazil, Pará, Rio Tapajós, sandy beaches on island 5 km S of Itaituba (latter locality at 4°17'S, 55°59'W).

praoccipital spine. Interorbital region slightly convex or flat. Dorsal profile of body straight to slightly convex from tip of supraoccipital spine to dorsal-fin origin, barely angled at dorsal-fin base. Ventral profile of head and body gently convex from isthmus to anal-fin origin.

Head pointed anteriorly in lateral view and more so in dorsal view. Upper jaw slightly longer than, and slightly overhanging, lower jaw. Anterior portion of mouth nearly horizontal. Ventral margin of upper jaw gently curved and relatively longer than in all congeners with exception of *Creagrutus maxillaris*. Anterior surface of snout not as fleshy as in all congeners other than *C. maxillaris;* with numerous minute papillae over anterior surface. Papillae also along ventral margin of upper lip, dorsal margin of lower lip, and anterior and anterolateral surfaces of lower jaw. Plicae and fleshy flaps extending between outer and medial premaxillary teeth of most *Creagrutus* species absent. Lower lip not as fleshy anteriorly as in other *Creagrutus* species.

Infraorbital series well developed. Third infraorbital well developed, with ventral margin nearly in contact with horizontal limb of preopercle. Posterior margins of third through fifth infraorbitals nearly in contact with vertical limb of preopercle.

Premaxillary dentition unusual for *Creagrutus* species, with only two distinct rows of teeth. Outer row consisting of 3 teeth arranged in slightly irregular series. First and third teeth of outer row unicuspidate, middle tooth with very weak lateral cusps. Inner tooth row on premaxilla consisting of 4 teeth, all with middle cusp distinctly more developed; medial and two lateral teeth tricuspidate, second tooth in series penticuspidate with very small lateral cusps. Elongate maxilla with 8 or 9 tricuspidate teeth with central cusp longer and typically somewhat posteroventrally curved. Dentary teeth 10 to 12; anterior 3 teeth largest and following teeth progressively smaller. Two anterior dentary teeth quadricuspidate, with second cusp distinctly larger than others; third through ninth teeth tricuspidate, with central cusp stronger and varyingly posteriorly recurved; tenth through twelfth teeth conical (when 11 or 12 teeth present).

Dorsal-fin rays ii,8. Dorsal-fin origin anterior to vertical through pelvic fin-insertion. Profile of distal margin of dorsal fin slightly concave. Anal-fin rays ii,9–10. Profile of distal margin of anal fin concave. Mature males with hooks on anal-fin rays limited to posterior margin of basal and middle segments of the first and second branched rays. Pectoral-fin rays i,12–13. Tip of pectoral fin reaching posteriorly approximately one-half of distance to pelvic-fin insertion. Pelvic-fin rays i,6,i or i,7. Larger mature males with hooks on all branched rays other than medialmost ray. Tip of pelvic fin extending posteriorly approximately two-thirds of distance to anus.

Gill rakers 6–7 + 10–11.

COLORATION IN ALCOHOL.—Overall coloration light tan. Dorsal surface of head with superficial small dark chromatophores. Surface of brain covered with larger, deep-lying, stellate, dark chromatophores, latter pigmentation masked by thicker bones and adipose deposits in larger individuals. Snout and upper jaw with scattering of small, dark chromatophores slightly more concentrated anterior to nares. Scattered chromatophores on lower jaw and on dorsal portions of opercle and infraorbital series. Distinct concentration of chromatophores anterior to nares and along ventral and posterior margins of orbit present in other *Creagrutus* species not apparent in *C. cracentis*. Lateral and dorsolateral portion of body with scattered chromatophores. Faint band formed by small dark chromatophores on midlateral surface of body of smaller specimens; distinction between midlateral band and dorsolateral pigmentation on body becoming increasingly obscure anteriorly with increasing size such that midlateral band is only discrete on posterior one-third of body in specimens of greater than approximately 25 mm SL. Humeral mark vertically elongate, very slightly anteriorly concave, extending from slightly above horizontal through pectoral-fin insertion to approximately one scale width from dorsal midline. Pigmentation of humeral mark most intense in region centered along lateral line, variably less intense in its dorsal and ventral portions.

Dorsal-fin ray margins and membranes with small dark chromatophores. Basal portions of anterior branched anal-fin rays outlined by chromatophores. Caudal fin with dark horizontal stripe formed by superficial chromatophores over middle caudal-fin rays; stripe more intense basally. Stripe on middle caudal-fin rays flanked dorsally and ventrally by 2 or 3 relatively unpigmented rays. Remaining caudal-fin rays with few scattered, dark chromatophores; chromatophores somewhat more

concentrated along ray margins. Pectoral and pelvic fins with only few scattered, small, dark chromatophores.

ETYMOLOGY.—The specific name, *cracentis,* from the Latin for slender or graceful, refers to the slender body form of the species.

ECOLOGY.—The type series was collected on a sandy beach in slow water current with no bottom or floating vegetation and limited vegetation along the shoreline.

DISTRIBUTION.—*Creagrutus cracentis* is known only from the type locality in the lower portions of the Rio Tapajós (Figure 33, star).

COMPARISONS.—The only other *Creagrutus* species known from the Rio Tapajós basin is *C. ignotus,* which has been collected in the upper portions of that drainage basin. *Creagrutus cracentis* and *C. ignotus* differ in numerous features, most obviously in their dentition (see "Key to the Species of *Creagrutus* in the Amazon Basin").

REMARKS.—This is one of the few records for a *Creagrutus* species proximate to the main channel of the lower portions of the Amazon River.

MATERIAL EXAMINED.—6 specimens (5, 21.5–38.3).

HOLOTYPE.—BRAZIL. *Pará:* Rio Tapajós, sandy beaches on an island located 5 km S of Itaituba (latter locality at 4°17′S, 55°59′W), collected by C.A.S. Lucena et al., 8 Dec 1991, MCP 15213, 1 (38.3).

PARATYPES.—5 specimens (4, 21.5–33.3).

BRAZIL. *Pará:* Rio Tapajós, sandy beaches on an island located 5 km S of Itaituba (latter locality at 4°17′S, 55°59′W), collected with holotype, MCP 22018, 3 (2, 21.5–26.3; other specimen with damaged snout), USNM 353862, 2 (26.1–33.3; 1 specimen cleared and counterstained for cartilage and bone).

Creagrutus crenatus, new species

FIGURES 37, 38, TABLE 16

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 3 to 5 teeth on the maxilla, 6, very rarely 5, teeth in the primary tooth row of the premaxilla, 5 dentary teeth, 37 to 39 lateral line scales without a lamellar process over each pore, 8 to 11 predorsal median scales, 3 or 4 scale rows between the dorsal-fin origin and the lateral line, 2 postanal scales to the anal-fin origin, 36 or 37 vertebrae, 10 to 12 branched anal-fin rays, the postorbital length (45.1%–50.4% of HL), the bony orbital diameter (25.2%–34.5% of HL), the interorbital width (31.3%–34.9% of HL), the poorly developed third infraorbital whose ventral margin falls distinctly short of the horizontal limb of the preopercle, the approximately equally wide gap between the posterior margins of the fourth through sixth infraorbitals and the vertical limb of the preopercle, the lack of a series of dark midlateral spots on the body, the bar-like, moderately elongate humeral mark, the absence of a narrow middorsal line of dark pigmentation in the predorsal region, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus crenatus* within the clade composed of *Creagrutus* and *Piabina.*

TABLE 16.—Morphometrics and meristics of *Creagrutus crenatus,* new species: (A) holotype of *C. crenatus,* MHNLS 505; and (B) paratypes of *C. crenatus* from which measurements and counts were taken (n=11). Standard length is expressed in mm; measurements 1 to 14=proportions of standard length; 15 to 18=proportions of head length.

Characters	A	B
	Morphometrics	
Standard length	66.1	41.9–70.2
1. Snout to anal-fin origin	61.1	59.4–64.1
2. Snout to pelvic-fin insertion	45.4	44.4–49.0
3. Snout to pectoral-fin insertion	25.1	25.1–28.7
4. Snout to dorsal-fin origin	49.2	48.7–51.7
5. Dorsal-fin origin to hypural joint	54.9	53.5–57.0
6. Dorsal-fin origin to anal-fin origin	29.7	27.4–32.6
7. Dorsal-fin origin to pelvic-fin insertion	28.0	26.8–31.8
8. Dorsal-fin origin to pectoral-fin insertion	34.9	32.6–36.9
9. Caudal peduncle depth	11.5	11.3–13.1
10. Pectoral-fin length	19.7	18.4–23.2
11. Pelvic-fin length	15.1	14.8–17.7
12. Dorsal-fin length	19.8	18.1–23.9
13. Anal-fin length	16.2	15.6–19.5
14. Head length	26.3	26.1–28.3
15. Postorbital head length	50.0	45.1–50.4
16. Snout length	31.6	27.7–32.7
17. Bony orbital diameter	25.3	25.2–34.5
18. Interorbital width	32.2	31.3–34.9
	Meristics	
Lateral line scales	37	37–39
Scale rows between dorsal-fin origin and lateral line	4	3–4
Scale rows between anal-fin origin and lateral line	4	4
Predorsal median scales	11	8–11
Branched dorsal-fin rays	8	8
Branched anal-fin rays	12	10–12
Branched pelvic-fin rays	6	6–7[1]
Pectoral fin rays	12	11–13
Vertebrae	37	36–37

[1]Seven branched pelvic-fin rays less common.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus crenatus* in Table 16. Body moderately deep and compressed. Greatest body depth between 1 and 3 scale rows anterior of pelvic-fin insertion. Dorsal profile of head distinctly convex from margin of upper lip to vertical between nares, straight from that point to posterior tip of supraoccipital spine. Dorsal profile of body slightly and smoothly convex to dorsal-fin origin, straight from that point to caudal peduncle. Ventral profile of head with obtuse angle (shallow convexity in some specimens) approximately midway between margin of lower lip and posterior of dentary. Ventral profile of head and body slightly convex from that point approximately to pelvic-fin insertion; slightly concave from anal-fin origin to caudal peduncle. Most external surfaces of head covered with minute papil-

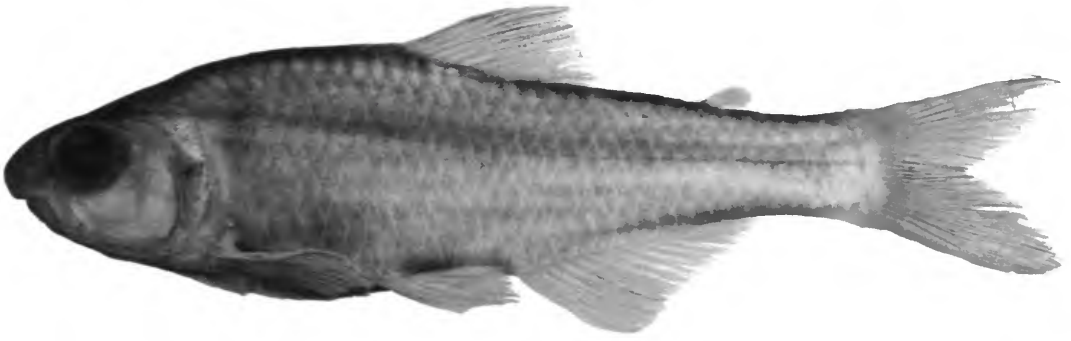

FIGURE 37.—*Creagrutus crenatus*, new species, holotype, MHNLS 505, 66.1 mm SL; Venezuela, Lara, Quebrada Sanare, in Yay (9°45'N, 69°43'W).

lae. Upper jaw longer than, and overhanging, lower jaw. Anterior portion of snout quite fleshy, with many minute papillae continuing from upper lip into mouth on fleshy flaps between premaxillary teeth. Lower lip distinctly fleshy anteriorly, inner surfaces of lower lip highly convolute.

Infraorbital series poorly developed, with ventral margin of third infraorbital broadly separated from ventral limb of preopercle. Posterior margin of third infraorbital distinctly separated from vertical limb of preopercle by space between one-third and one-half width of orbit; posterior and ventral margins of third infraorbital broadly rounded and with greater curvature than orbit. Posterior margins of fourth and fifth infraorbitals separated from vertical limb of preopercle by broad gap approximately equal to width of fourth infraorbital.

Premaxillary dentition in three series; primary row forming gentle curve with teeth all aligned with margin of premaxilla, typically with 6 teeth (5 teeth present on only one premaxilla in 1 of 13 specimens examined for this feature) without pronounced gap between first and second teeth of series; all teeth rounded and tricuspidate with secondary cusps poorly developed in fifth and sixth teeth; triad of three distinctly larger teeth with posterior teeth anteroposteriorly elongate and posterolateral tooth very large; and single tooth of form similar to that of primary series lying lateral to fourth tooth of primary series. Maxilla with 3 to 5 compressed, tricuspidate teeth. Dentary with five tricuspidate teeth; anterior two teeth largest, with second tooth only slightly higher, but obviously larger, than first tooth and more than twice as high as distinctly smaller third tooth. Remaining dentary teeth progressively decrease in size posteriorly.

Dorsal-fin rays ii,8 in all specimens. Dorsal-fin origin located at, or slightly posterior to, vertical through pelvic-fin insertion. Distal margin of dorsal fin nearly straight, very slightly concave as result of slight elongation of first 2 or 3 rays. Anal-fin rays ii,10–12 or iii,10–12. Anal fin in mature males with hooks on segments of anterior 3 to 5 branched rays; hooks present on posterior unbranched ray in one specimen. Distal margin of anal fin nearly straight, anterior rays slightly elongate. Tip of pectoral fin approaching, or extending beyond, pelvic-fin insertion, at most two scale rows separating tip of pectoral fin from pelvic-fin base. Pelvic-fin rays typically i,6,i, less commonly i,7 (in 3 of 13 specimens); one specimen with 7 branched rays and medial unbranched ray. Tip of pelvic fin approaching, or extending to, anal-fin origin. Pelvic-fin rays in mature males with hooks on medial and in some specimens medial and lateral surfaces of segmented and unsegmented portions of all rays medial of lateral unbranched element.

Posterior margin of body scales undulate to crenate. This scale form most obvious in lateral line scales that tend to be smaller than immediately adjacent series of scales in both dorsal and ventral directions.

Gill rakers 5–7 + 7–12.

COLORATION IN ALCOHOL.—Dorsal surface of head with diffuse pattern of small dark chromatophores most concentrated on snout and over frontal portion of fontanel. Distinct small crescent of dark chromatophores present immediately in front of anterior nares. Thin dark longitudinal stripe between nares and dorsal midline extending anteriorly onto snout in some specimens. Band of scattered, dark chromatophores extending from immediately lateral of nares posteroventrally under orbit, and continuing along ventral margin of orbit; band darkest and most concentrated along anteroventral portion of orbit, narrowing and continuing around posterior margin of orbit. Lips and ventrolateral surface of head unpigmented; reflective guanine well developed on opercle and cheek. Dark body pigmentation most concentrated dorsally, particularly along dorsal midline as diffuse longitudinal stripe; stripe darkest at dorsal-fin base, and in transverse band over center of exposed surface of scales. Humeral mark poorly developed, most concentrated immediately dorsal of lateral line and becoming dif-

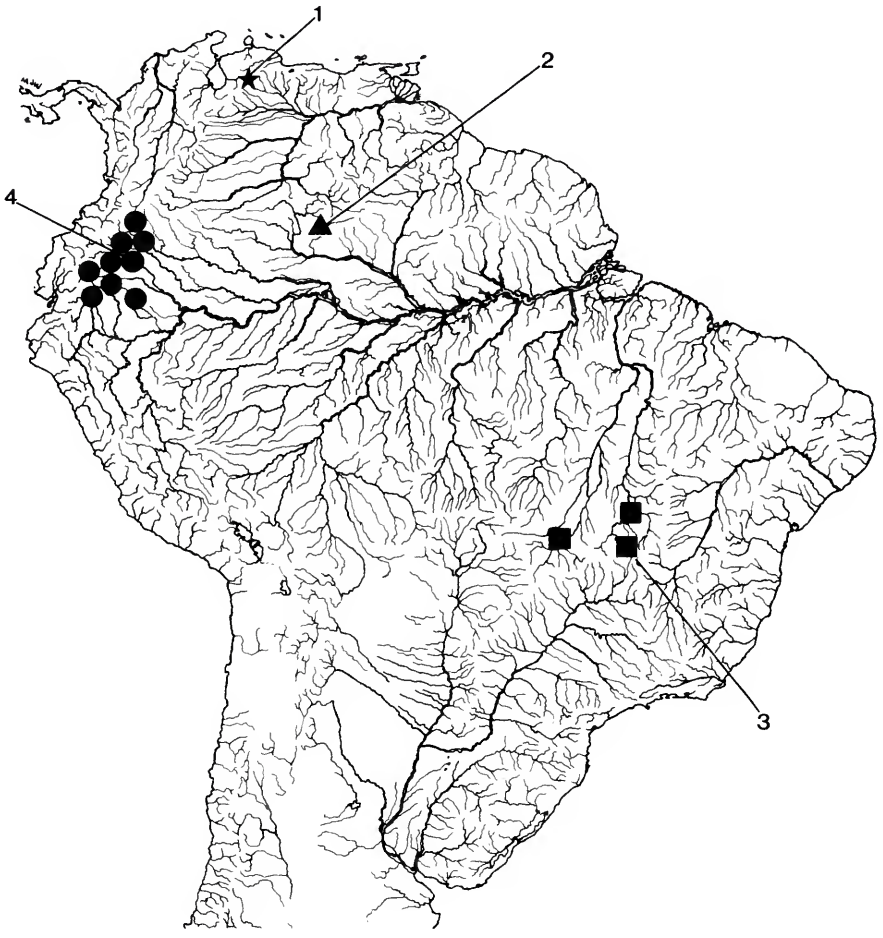

FIGURE 38.—Map of central and northern South America showing geographic distribution of *Creagrutus crenatus* (star, 1=type locality), *Creagrutus ephippiatus* (triangle, 2=type locality), *Creagrutus figueiredoi* (squares, 3=type locality), and *Creagrutus flavescens* (dots, 4=type locality) (some symbols represent more than one locality or lot of specimens).

fuse and irregular two scale rows towards dorsum. Mark attenuated ventrally and only present in second scale row below lateral line as scattered chromatophores. Dark pigmentation on lateral surface of body, other than for humeral bar, restricted to area dorsal of lateral line in some individuals, other specimens with pigmentation along posterior margins of scales above pectoral fin. Region of body immediately dorsal of anal-fin base usually with 10 to 20 scattered chromatophores directly dorsal of anal-fin base. Smaller specimens (INHS 28851, 41.9–48.2 mm SL) showing concentration of chromatophores in association with bases of anterior anal-fin rays. Midlateral stripe becoming denser and somewhat wider posteriorly on caudal peduncle where stellate chromatophores form broad triangular pigmented area. Smaller, better-preserved specimens showing concentration of reflective guanine in central portion of midlateral stripe.

Caudal-fin rays all delineated by dark pigmentation most intense on central and ventral rays. Unbranched anal-fin rays unpigmented except for small number of dark chromatophores near base, branched rays delineated by dark pigmentation; pigmentation darkest on anterior margins of fin rays. Dorsal-fin membranes with dark chromatophores most concentrated on distal one-half of rays, unbranched rays darkly pigmented. Rays of lateral one-half of pectoral fin delineated by large chromatophores in large specimens; smaller specimens (INHS 28851) with few scattered chromatophores. Pelvic fin hyaline.

ETYMOLOGY.—The species name, *crenatus*, from the Latin meaning notched or bearing rounded projections, is in reference to the form of the exposed posterior margins of many of the scales.

ECOLOGY.—One lot (INHS 28851) was collected in a clear rocky stream with considerable current.

DISTRIBUTION.—*Creagrutus crenatus* is known only from three collections that originated in the upper portions of the Rio Tocuyo, an isolated system that drains to the Caribbean Sea, Estado de Lara, north central Venezuela (Figure 38, star).

COMPARISONS.—*Creagrutus crenatus* is similar to *C. taphorni* and *C. lassoi,* two species from the region immediately to the east of the Río Tocuyo system in northern Venezuela. These three species share a moderately deep body, 10 to 12 branched anal-fin rays, and a somewhat diffuse, slightly elongate humeral mark. Two of these species, *C. crenatus* and *C. lassoi,* share the distinctive features of undulate to crenate posterior scale margins and biuncinate pelvic-fin ray segments. *Creagrutus crenatus* is most similar to *C. lassoi,* especially with regard to meristics and fin-ray hook morphology. These two species differ in the straight posterior opercular margin in *C. crenatus* compared with the concave posterior opercular margin in *C. lassoi,* the modally higher number of branched anal-fin rays and lateral line scales in *C. crenatus* versus *C. lassoi,* and the crenate posterior scale margins, especially along the midlateral surface of the body in *C. crenatus* in comparison to the typically smooth scale margins in *C. lassoi.*

MATERIAL EXAMINED.—13 specimens (13, 31.0–70.2).

HOLOTYPE.—VENEZUELA. *Lara:* Quebrada Sanare in Yay (9°45′N, 69°43′W), collected by "Yepez and Martin" (?=A. Fernández-Yépez and F. Martin), 28 Dec 1954, MHNLS 505, 1 (66.1).

PARATYPES.—11 specimens (11, 41.9–70.2).

VENEZUELA. *Lara:* Quebrada Sanare in Yay (9°45′N, 69°43′W), collected with holotype, MHNLS 12900, 6 (55.9–70.2; 1 specimen cleared and counterstained for cartilage and bone). Río Tocuyo drainage, Río Curarigua, Puente Torres (10°12′N, 69°54′W), between Carora and Barquisimeto, collected by D.C. Taphorn et al., 6 Jan 1993, INHS 28851, 5 (41.9–48.2).

NONTYPE SPECIMENS.—1 specimen (31.0).

VENEZUELA. *Lara:* Río Tocuyo drainage, Río Curarigua, Paso San Antonio, Pozo (swamp) La Jaguara near Cuqurizzio, USNM 219617, 1 (31.0).

TABLE 17.—Morphometrics and meristics of *Creagrutus ephippiatus,* new species: (A) holotype of *C. ephippiatus,* MBUCV V-29068; and (B) paratypes of *C. ephippiatus* (n=34). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	47.6	27.4–58.4
1. Snout to anal-fin origin	60.7	60.5–64.5
2. Snout to pelvic-fin insertion	45.3	44.3–48.0
3. Snout to pectoral-fin insertion	22.5	22.8–24.7
4. Snout to dorsal-fin origin	46.9	46.8–49.8
5. Dorsal-fin origin to hypural joint	55.9	54.0–57.9
6. Dorsal-fin origin to anal-fin origin	28.6	27.8–29.7
7. Dorsal-fin origin to pelvic-fin insertion	25.4	23.1–25.7
8. Dorsal-fin origin to pectoral-fin insertion	32.4	30.7–33.6
9. Caudal peduncle depth	11.3	10.7–12.0
10. Pectoral-fin length	20.2	18.1–21.3
11. Pelvic-fin length	16.4	14.0–16.7
12. Dorsal-fin length	22.1	19.5–22.4
13. Anal-fin length	16.8	15.5–18.5
14. Head length	25.6	24.3–27.0
15. Postorbital head length	44.3	43.7–47.4
16. Snout length	28.7	27.3–31.6
17. Bony orbital diameter	33.6	31.3–35.7
18. Interorbital width	30.3	29.7–33.7
	Meristics	
Lateral line scales	39	38–41[1]
Scale rows between dorsal-fin origin and lateral line	4	4–5[2]
Scale rows between anal-fin origin and lateral line	3	3–4[3]
Predorsal median scales	10	10–12
Branched dorsal-fin rays	8	8
Branched anal-fin rays	11	10–11
Branched pelvic-fin rays	7	5–7[4]
Pectoral-fin rays	12	11–13
Vertebrae	38	38–40[5]

[1]Forty-two lateral line scales present in only 1 specimen.

[2]Five scale rows between dorsal-fin origin and lateral line present in only 3 paratypes.

[3]Four scale rows between anal-fin origin and lateral line present in only 2 paratypes.

[4]Five branched pelvic-fin rays present in only 1 paratype; 7 branched rays present only in larger paratypes.

[5]Forty vertebrate present in only 1 paratype.

Creagrutus ephippiatus, new species

FIGURES 38, 39, TABLE 17

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus*and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 6, occasionally 5, teeth in the primary series of each premaxilla, 3 or 4 maxillary teeth, 6, less commonly 7, teeth on each dentary, 10 to12 predorsal median scales, 38 to 41 lateral line scales without a lamellar process over each pore, 4, rarely 5, scale rows between the dorsal-fin origin and the lateral line, 3 or 4 scale rows between the anal-fin origin and the lateral line, 10 or 11 branched anal-fin rays, 38 to 40 vertebrae, 6 or 7 gill rakers on the upper limb and 11 or 12 gill rakers on the lower limb of the first gill arch, the caudal peduncle depth (10.7%–12.0% of SL), the distance from the dorsal-fin origin to the anal-fin origin (27.8%–29.7% of SL), the distance from the dorsal-fin origin to the pelvic-fin insertion (23.1%–25.7% of SL), the distance from the dorsal-fin origin to the pectoral-fin insertion (30.7%–33.6% of SL), the postorbital head length (43.7%–47.4% of HL), the interorbital width (29.7%–33.7% of HL), the contact between the ventral margin of the third infraorbital and the horizontal limb of the preopercle in larger specimens, the spot of dark pigmentation at the base of the middle caudal-fin rays, the vertically elongate, ventrally attenuating humeral mark extending to the middorsal line, without a secondary, dorsal patch of pigmentation, the absence of a distinct patch of pigmentation on the dorsal fin, the dark pigmen-

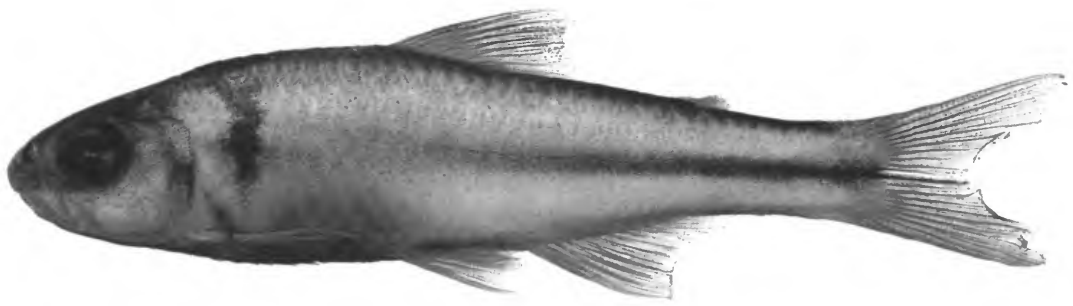

FIGURE 39.—*Creagrutus ephippiatus*, new species, holotype, MBUCV V-29068, 47.6 mm SL; Venezuela, Amazonas, upper Río Siapa, Campamento Siapa.

tation on the basal portions of the middle caudal-fin rays, and the lack of a series of dark spots along the midlateral surface of the body distinguishes *Creagrutus ephippiatus* within the clade formed by *Creagrutus* and *Piabina*.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus ephippiatus* in Table 17. Head and body moderately robust, more so in anterior portion of body in larger specimens. Greatest body depth at, to slightly anterior of, dorsal-fin origin. Dorsal profile of head distinctly convex from margin of upper lip to vertical through posterior nostril, slightly convex from that point to tip of supraoccipital spine; convexity in this region less pronounced in larger individuals. Interorbital region transversely rounded. Dorsal profile of body slightly convex from tip of supraoccipital spine to dorsal-fin origin, but without distinct change in alignment relative to dorsal profile of head. Dorsal surface of body with obtuse middorsal ridge; ridge more obvious posteriorly. Ventral profile of head with obtuse angle at anteroventral corner of dentary, angle variably obvious; profile slightly convex from angle to isthmus. Prepelvic profile of body slightly convex in smaller individuals, somewhat more convex in some larger specimens. Prepelvic region of body transversely rounded.

Head obtusely pointed in lateral view, somewhat more compressed in dorsal view. Upper jaw somewhat longer than, and overhanging, lower jaw. Anterior of snout, particularly anteromedial portion with numerous papillae. Papillae more concentrated on fleshy upper lip, especially along ventral lip margin and on folds and plicae extending between outer and medial premaxillary teeth. Lower lip with numerous papillae on dorsal surface and scattered papillae anteriorly.

Infraorbital series well developed in all specimens larger than about 30 mm SL, with ventral margin of third infraorbital falling slightly short of horizontal limb of preopercle in smaller specimens, but contacting that bone in larger individuals. Posterior margins of third through fifth infraorbitals distinctly separated from vertical limb of preopercle in all specimens; gap decreasing proportionally ontogenetically, but still distinct in larger individuals.

Premaxillary dentition in three series: primary series sigmoid, with 6, occasionally 5, tricuspidate teeth, without pronounced gap between first and second tooth of series but with medial tooth separated from matching tooth of contralateral series by distinct gap; triangular cluster of 3 teeth, larger than those of primary series; and single tooth of form similar to that of primary series occurring lateral to fourth tooth of primary series or in the region slightly anterolateral to area of contact of third and fourth teeth of primary premaxillary row. Maxilla with 3 or 4 tricuspidate teeth, 3 teeth typically present in smaller individuals. Dentary with 6, less commonly 7, tricuspidate teeth, with seventh tooth, when present, having barely apparent cusps; second tooth more massive than and about one-fourth longer than first tooth; second tooth about 1.5 times as high as third tooth; third tooth twice as high as fourth tooth; fourth through sixth or seventh teeth progressively smaller.

Dorsal-fin rays ii,8 in all specimens. Dorsal-fin origin approximately at vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin slightly concave. Anal-fin rays iii,10–11 or ii,10. Profile of distal margin of anal fin concave. Mature males with hooks on distal margins of first 4 or 5 branched anal-fin rays, and occasionally on last unbranched ray; number of hooks decreasing posteriorly and progressively limited to increasingly more distal portions of fin ray. Pectoral-fin rays i,10–12, typically i,11. Tip of pectoral fin falling 1 to 2 scales short of pelvic-fin insertion. Pelvic-fin rays i,5–6,i or i,7; typically i,6,i; i,7 in some larger specimens. Tip of pelvic fin falling 1 to 2 scales short of anal-fin origin. Mature males with hooks on all branched pelvic-fin rays, including medial ray, if branched, and sometimes on medial ray when unbranched; hooks, when present on medial unbranched ray, usually less dense than those on branched rays.

Gill rakers 6–7 + 11–12.

COLORATION IN ALCOHOL.—Ground coloration tan. Dorsal surface of head in smallest specimens with dense pigmentation

overlying brain and scattered, dark chromatophores on snout. Specimens greater than 30 mm SL with entire dorsal surface of head covered with dense field of small, dark chromatophores extending anteriorly to margin of upper lip and posteriorly to anterior margin of orbit. Density of chromatophore field somewhat less on upper lip in some individuals. Region anterior to nostrils with pigmentation somewhat more intense, forming distinct crescent-shaped patch in smaller specimens; patch not apparent in medium-sized to larger individuals. Smaller individuals with narrow band of dark pigmentation extending from under nostrils to region anteroventral or ventral of orbit; band subsumed into overall darker pigmentation in that region in larger specimens. Region posterior to orbit along with dorsal portion of opercle with scattered, dark chromatophores in smaller specimens, chromatophore field expanding further ventrally and somewhat more dense, especially along posterior margin of orbit in larger individuals.

Scales of posterolateral surface of body with series of dark chromatophores along posterior margin in smaller individuals; chromatophore field becoming progressively wider in larger individuals, but with basal portions of scales lacking chromatophores and forming regular pattern of lighter colored regions. Humeral mark obvious and vertically elongate in specimens of all sizes. Mark comma-shaped and limited to lateral portion of body in smaller individuals, midlaterally centered main body darkest with anterior arching patch of more diffuse dark chromatophores extending dorsally from its dorsal portion of dorsal midline. Contralateral humeral marks meet middorsally and form horizontally elongate dark middorsal stripe that extends about 3 scales along predorsal region; stripe extending approximately one scale posterior of margin of humeral mark. Main portion of mark becoming more intensely pigmented and vertically elongate with increasing size. Humeral mark extending ventrally by more diffuse, typically ventrally tapering patch of chromatophores; in largest specimens humeral mark extending to about one scale dorsal of horizontal through pectoral-fin insertion. Middorsal scales posterior to humeral marks with patches of dark pigmentation in larger specimens. Dark midlateral stripe limited to posterior two-thirds of body, pigmentation more intense posteriorly. Midlateral stripe merging anteriorly into overall dark pigmentation on lateral surface of the body in larger individuals.

Dorsal fin with first unbranched ray and distal portions of second unbranched rays covered with dark stellate chromatophores. Membranes of all but one or two posteriormost branched fin rays with dispersed, dark, irregularly shaped chromatophores. Chromatophore field becoming progressive shorter on distal portions of successive fin membranes. Distal portion of second and third unbranched and first and sometimes second branched anal-fin rays unpigmented; otherwise fin rays outlined by small dark chromatophores, with scattered chromatophores on intervening portions of fin membranes. Middle caudal-fin rays more intensely pigmented than rest of fin, with remaining fin rays outlined, to varying degrees, by small dark chromatophores. Pectoral and pelvic fins hyaline, or with some scattered, small, dark chromatophores in larger specimens.

ETYMOLOGY.—The specific name, *ephippiatus,* from the Latin, ephippium, meaning saddle, refers to the saddle-like humeral marks that meet along the dorsal midline.

ECOLOGY.—One of the nontype lots (AMNH 93144) was collected on a small sandy beach over a sand and mud bottom with detritus. A second lot (AMNH 93147) was captured at the upper end of rapids in the Río Siapa over a gravel and boulder bottom.

COMPARISONS.—*Creagrutus ephippiatus* is somewhat similar to *C. provenzanoi* of the Río Cataniapo, a tributary of the upper Río Orinoco. The two species can, however, be distinguished on the basis of the more arcuate dorsal portion of the humeral mark that extends further dorsally in *C. ephippiatus* compared to the mark in *C. provenzanoi,* the number of rows of scales above the lateral line (4, rarely 5, in *C. ephippiatus* versus 5, rarely 4, in *C. provenzanoi*), and less discretely in the distance from the snout to the pectoral-fin insertion (22.5%–24.7% of SL versus 24.4%–27.3% of SL, respectively).

Creagrutus ephippiatus is rather similar in terms of overall meristics and morphometrics to *C. magoi* of the central portions of the Río Orinoco basin. The species differ, however, in overall body form that is best reflected in the distance from the dorsal-fin origin to the anal-fin origin (27.8%–29.7% of SL in *C. ephippiatus* versus 29.2%–33.8% of SL in *C. magoi*), details of dark pigmentation (form of humeral mark and pigmentation of middle caudal-fin rays). The species also have a pronounced modal shift in the number of total vertebrae (*C. ephippiatus:* 38 (34), 39(10), 40(1) versus *C. magoi:* 36(6), 37(38), 38(2)).

DISTRIBUTION.—*Creagrutus ephippiatus* is only known from the Río Siapa, a southern tributary of the Río Casiquiare, upper Río Negro basin, in southern Amazonas State, Venezuela (Figure 38, triangle), and is the only member of the genus known from that river system.

MATERIAL EXAMINED.—56 specimens (35, 27.4–58.4).

HOLOTYPE.—VENEZUELA. *Amazonas:* Upper Río Siapa, Campamento Siapa (Siapa Base Camp), collected by R. Royero et al., 26 Mar 1988, MBUCV V-29068, 1 (47.6).

PARATYPES.—34 specimens (34, 27.4–58.4).

VENEZUELA. *Amazonas:* Upper Río Siapa, Campamento Siapa (Siapa Base Camp), collected with holotype, MBUCV V-29069, 24 (27.4–51.0); MBUCV V-18623, 3 (33.9–58.4); USNM 355116, 7 (33.3–47.0; 2 specimens cleared and counterstained for cartilage and bone).

NONTYPE SPECIMENS.—21 specimens.

VENEZUELA. *Amazonas:* Upper Río Siapa, below Camp 1, MBUCV V-19187, 4. Upper Río Siapa, at Siapa Base Camp, small beach on right bank, AMNH 93144, 13. Upper Río Siapa, Yanomani Village, upper end of rapids on left bank, AMNH 93147, 4.

Creagrutus figueiredoi, new species

FIGURES 38, 40, TABLE 18

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 2 or 3 teeth on the maxilla, 5 teeth in the primary tooth row of the premaxilla, 5 or 6 dentary teeth, 36 to 38 lateral line scales without a lamellar process over each pore, 8 to 11 predorsal scales, 4 scale rows between the dorsal-fin origin and the lateral line, 35 to 37 vertebrae, 9 or 10 branched anal-fin rays, 2 post-anal median scales to the anal-fin origin, the distance from the snout to the pectoral-fin insertion (22.6%–26.6% of SL), the distance from the snout to the anal-fin origin (31.4%–33.6% of SL), the distance from the dorsal-fin origin to the pectoral-fin insertion (30.6%–34.0% of SL), the postorbital head length (41.2%–45.1% of HL), the snout length (28.3%–33.1% of HL), the bony orbital diameter (33.6%–38.1% of HL), the dorsal-fin length (19.4%–22.3% of SL), the anal-fin length (15.6%–18.5% of SL), the caudal peduncle depth (11.2%–12.6% of SL), the well-developed third infraorbital approaching, but not contacting, the horizontal limb of the preopercle, the lack of a series of dark midlateral spots on the body, the discrete, wide, vertically elongate humeral mark shaped like an inverted comma, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus figueiredoi* within the clade composed of *Creagrutus* and *Piabina*.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus figueiredoi* in Table 18. Head moderately robust at all sizes. Body becoming increasingly robust anteriorly with increasing size. Greatest body depth at vertical through dorsal-fin origin in smaller specimens, at that point or shifted somewhat anteriorly in larger individuals. Dorsal profile of head gently convex from margin of upper lip to vertical through posterior nostril, straight from that point to tip of supraoccipital spine in smaller specimens, becoming slightly convex in larger individ-

TABLE 18.—Morphometrics and meristics of *Creagrutus figueiredoi*, new species: (A) holotype of *C. figueiredoi*, MZUSP 50542; (B) paratypes of *C. figueiredoi* (n=27); and (C) nontype specimens of *C. figueiredoi* from Rio Araguaia basin, USNM 342235 (n=2). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B	C
		Morphometrics	
Standard length	63.3	37.6–55.5	41.7–52.1
1. Snout to anal-fin origin	65.4	60.8–65.6	64.5–64.9
2. Snout to pelvic-fin insertion	47.1	44.2–48.2	47.4
3. Snout to pectoral-fin insertion	23.5	22.6–26.6	22.8–24.3
4. Snout to dorsal-fin origin	46.1	44.6–48.1	46.8–47.0
5. Dorsal-fin origin to hypural joint	59.7	55.8–59.9	55.8–58.3
6. Dorsal-fin origin to anal-fin origin	33.1	31.4–33.5	33.1–33.6
7. Dorsal-fin origin to pelvic-fin insertion	28.0	25.5–27.8	28.7–29.6
8. Dorsal-fin origin to pectoral-fin insertion	32.1	30.6–32.8	32.6–34.0
9. Caudal peduncle depth	12.4	11.2–12.6	11.7–12.2
10. Pectoral-fin length	19.7	18.4–20.5	19.4
11. Pelvic-fin length	16.4	14.6–17.3	15.6–15.9
12. Dorsal-fin length	20.2	19.4–21.8	21.6–22.3
13. Anal-fin length	18.6	16.6–18.5	15.6–17.5
14. Head length	26.1	24.2–27.1	25.2–27.5
15. Postorbital head length	44.2	41.2–45.1	42.9–44.1
16. Snout length	30.9	28.3–33.1	28.2–29.4
17. Bony orbital diameter	34.5	33.6–38.1	33.8–38.1
18. Interorbital width	30.3	29.6–34.3	29.7–30.1
		Meristics	
Lateral line scales	38	36–38	38
Scale rows between dorsal-fin origin and lateral line	4	4	4
Scale rows between anal-fin origin and lateral line	3	3	3
Predorsal median scales	9	8–11	9–10
Branched dorsal-fin rays	8	8–9[1]	8
Branched anal-fin rays	10	9–10	10[2]
Branched pelvic-fin rays	7	6–7	6
Pectoral-fin rays	13	12–14	13
Vertebrae	36	35–37	35

[1]Nine branched dorsal-fin rays present in only 1 paratype.

[2]Anal-fin ray count uncertain in one specimen with damaged anal fin.

uals. Interorbital region distinctly convex. Dorsal profile of body very slightly convex, without evident change in alignment relative to that of head in smaller specimens, convex with distinct change in alignment relative to that of head in larger individuals. Predorsal surface of body somewhat flattened transversely in region of supraoccipital spine; with middorsal ridge proximate to dorsal-fin origin in larger specimens. Ventral profile of head with distinct obtuse angle at anteroventral corner of dentary, straight or gently curved from that point to isthmus. Ventral profile of body very slightly convex in smaller specimens, more so in larger individuals. Prepelvic region of body obtusely flattened transversely.

Head obtusely pointed in lateral and dorsal views. Upper jaw distinctly longer than, and overhanging, lower jaw. Snout not very fleshy, with few scattered papillae anteromedially. Papillae more concentrated along fleshy margins of lips and particularly on fleshy folds and plicae extending between outer and medial premaxillary teeth. Lower lip moderately fleshy anteriorly, with numerous papillae along dorsal margin and with scattered papillae anteromedially.

Infraorbital series well developed. Ventral margin of third infraorbital approaching, but falling slightly short of, horizontal limb of preopercle even in larger specimens. Posterior margins of third through fifth infraorbitals falling short of vertical limb of preopercle.

Premaxillary dentition in three series: primary row curved, consisting of 5 teeth, occasionally with gap between third and fourth teeth but without gap between first and second teeth of series and with medial tooth of primary series separated from anterior tooth of contralateral series by distinct gap; triangular cluster of 3 larger teeth with posterolateral tooth largest; and single tooth of form similar to that of primary series situated lateral to space between third and fourth teeth of primary premaxillary row. Maxilla with 2 or 3 tricuspidate teeth. Dentary with 5 or 6 teeth; first two teeth subequal and distinctly larger than third; third tooth, in turn, much larger than fourth and fifth teeth. Dentary teeth all tricuspidate (when 5 teeth present) or last tooth conical (when 6 teeth present). Central cusp very well developed proportionally in first through third teeth, less so in fourth and fifth teeth.

Dorsal-fin rays ii,8–9. Dorsal-fin origin anterior to vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin slightly concave. Anal-fin rays ii,9–10. Profile of distal margin of anal fin distinctly concave, with last unbranched and anterior branched rays forming distinct lobe. Mature males with hooks present on first and second branched anal-fin rays and occasionally on second unbranched anal-fin ray. Pectoral-fin rays i,11–13. Tip of pectoral fin extending posteriorly approximately three-fourths of distance to pelvic-fin insertion. Pelvic-fin rays i,6,i or i,7. Tip of pelvic fin extending posteriorly approximately to anus. Mature males with hooks present on all branched anal-fin rays.

Gill rakers 6–7 + 10–11.

COLORATION IN ALCOHOL.—Overall ground coloration tan. Dorsal surface of head with scattered surface chromatophores overlying more concentrated chromatophores located on membranes of brain. Surface chromatophores more concentrated on snout and in region between and anterior to nostrils. Region immediately anterior to nostrils without more concentrated region of chromatophores forming dark crescent-shaped patch as in many congeners, or patch barely apparent in some specimens. Series of dark chromatophores extending posteroventrally from under nostrils to join curved band of chromatophores along ventral and posterior borders of orbit. Scattered, dark chromatophores on postorbital portion of head located on dorsal one-half to two-thirds of infraorbital series and opercle.

Scales of dorsolateral and dorsal portions of body with dark chromatophores concentrated along distal margin and on basal section of exposed portion of scale, scale pigmentation most intense on dorsal region of body. Diffuse midlateral stripe formed by dark surface chromatophores extending from slightly posterior of humeral mark to posterior portion of caudal peduncle, somewhat more concentrated posteriorly in some individuals. Humeral mark vertically elongate, with densely pigmented portion immediately dorsal of lateral line. Diffuse, ventrally attenuating series of chromatophores extending slightly ventral of densely pigmented portion of mark. Dorsal portion of humeral mark consisting of variably shaped, vertically elongate patch of chromatophores extending one and one-half to two scales dorsal of dark central portion of mark. Dorsal portion of mark ranging from distinctly lighter than central portion of mark to nearly as dark as that region. Anterior margin of mark ranging from straight to distinctly concave.

Dorsal fin with unbranched rays outlined by dark chromatophores, and distal two-thirds of membranes of anterior 4 or 5 rays with numerous larger chromatophores. Anal fin with anterior margins of first 4 to 7 rays variably outlined with chromatophores and with scattered chromatophores on distal portions of membranes of anterior rays. Caudal-fin rays variably outlined with chromatophores, giving fin overall dusky appearance. Pelvic fin mostly hyaline. Pectoral-fin rays variably delimited by small dark chromatophores.

ETYMOLOGY.—The species name, *figueiredoi,* is in honor of José Lima de Figueiredo, Museu de Zoologia of the Universidade de São Paulo, in recognition of his contributions to South American ichthyology and of his assistance to the senior author over the years.

ECOLOGY.—The type locality is an upland river, approximately 30 m wide, with fast to moderate flowing, moderately turbid water, over a rocky and sand bottom. In the upper Rio Araguaia basin *Creagrutus figueiredoi* has been captured together with *C. menezesi* and *C. seductus.* During the filling of the Serra da Mesa reservoir in the upper Rio Tocantins basin, congeners collected with *C. figueiredoi* along the developing lake margin were *C. menezesi* and *C. saxatilis.*

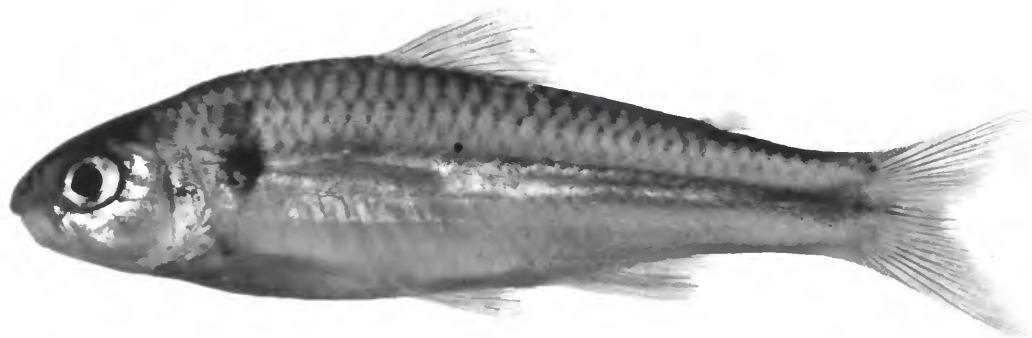

FIGURE 40.—*Creagrutus figueiredoi,* new species, holotype, MZUSP 50542, 63.3 mm SL; Brazil, Distrito Federal, Rio Maranhão, approximately 35 air km N of Brasilia (approximately 15°32′S, 47°49′W).

DISTRIBUTION.—*Creagrutus figueiredoi* occurs in the Rio Tocantins drainage system in both the upper Rio Tocantins and Rio Araguaia basins (Figure 38, squares).

GEOGRAPHIC VARIATION.—The majority of the available specimens of *C. figueiredoi* come from the type locality in the Rio Maranhão basin of the Rio Tocantins system in the region of the type locality (Figure 38, square indicated by 3). Five specimens were collected approximately 400 river km to the north of the type locality along the margins of the Serra da Mesa reservoir in the upper Rio Tocantins during the filling of the impoundment (MNRJ 17334, 17339). These specimens fit within the range of variation for meristic and morphometric values for species from the holotype locality and are designated as paratypes (Table 18).

Two specimens from the Município de Barra do Garças, in the upper portions of the Rio Araguaia (USNM 342235) are tentatively identified as *C. figueiredoi* and are the only known specimens of the species from that portion of the greater Rio Tocantins basin. The Rio Araguaia sample differs from the upper Rio Tocantins samples in proportional values reflecting the depth of the body (dorsal-fin origin to pelvic-fin insertion, dorsal-fin origin to pectoral-fin insertion; Table 18, numbers 7 and 8) and to a lesser degree in the length of the dorsal-fin (Table 18, number 12). Furthermore, the two specimens from the Rio Araguaia have 35 vertebrae. Although this count falls within the range for specimens of upper Rio Tocantins basin (35 to 37 vertebrae), 35 vertebrae are relatively rare in available specimens from the upper Rio Tocantins (frequency of vertebrae in *C. figueiredoi* samples from that region: 35 (3), 36 (21), 37 (3)).

The Rio Araguaia sample is limited to two specimens, and both individuals are apparently ripe females with expanded abdomens. Such increased proportional body depth would account for the greater relative dorsal-fin origin to pelvic-fin insertion distance and would partially contribute to the increased proportional dorsal-fin origin to pectoral fin insertion distance found in this sample in comparison to the samples from the upper Rio Tocantins. Furthermore, more than 2500 river km separate the collection locality of the two specimens from the Rio Araguaia from the nearest known locality for *C. figueiredoi* in the upper Rio Tocantins basin. Intraspecific geographic variation in meristic and morphometric values is often the case across such great distances and is found at shorter geographic distances in other *Creagrutus* species. Thus, the differences in proportional distance from the dorsal-fin origin to the pectoral-fin insertion and the relative length of the dorsal-fin between the Rio Araguaia and upper Rio Tocantins samples are possibly a function of a clinal shift in these features across the range of a single species.

Shifts in modal vertebral counts also occur intraspecifically within various *Creagrutus* species (e.g., *C. flavescens*) and other characiforms (e.g., *Ctenolucius beani* and *Boulengerella maculata,* Vari, 1995:55, 66), which suggests that the modal shift in vertebral counts between population samples from the upper Rio Tocantins and the limited Rio Araguaia sample is a function of their geographic separation. Other recently analyzed species (e.g., *Pituna compacta;* see Costa, 1998:147) have similar disjunct known distributions between the upper portions of the Tocantins and Araguaia basins. Given these factors, and the massive gap in the known distribution of the species, we tentatively identify the Rio Araguaia samples as *C. figueiredoi.* Further samples from the upper Rio Araguaia and throughout intervening localities in the greater Rio Tocantins basin are necessary to resolve whether such variation should be recognized taxonomically.

MATERIAL EXAMINED.—33 specimens (33, 37.6–63.3).

HOLOTYPE.—BRAZIL. *Distrito Federal:* Rio Maranhão, upper Rio Tocantins basin, approximately 35 air km N of Brasilia (approximately 15°32′S, 47°49′W), collected by W.C. Starnes et al., 14 Nov 1984, MZUSP 50542, 1 (63.3).

PARATYPES.—27 specimens (27, 37.6–55.5).

BRAZIL. *Distrito Federal:* Rio Maranhão, upper Rio Tocantins basin, approximately 35 air km N of Brasilia (approximately 15°32′S, 47°49′W), collected with holotype, MZUSP 50543, 9 (40.2–53.1); MNRJ 14482, 2 (42.8–49.6); USNM 292221, 11 (40.1–55.5). *Goiás:* Minaçu/Colinas do Sul, Rio Tocantins, pools formed below the dam of Usina Hidroelectica (UHE) de Serra da Mesa after closure of dam to fill, collected by D.F. Moraes et al., 28 Oct to 3 Nov 1996, MNRJ 17334, 2 (38.8–52.2); MNRJ 17339, 3 (37.6–48.6).

NONTYPE SPECIMENS.—5 specimens (5, 41.7–63.0).

BRAZIL. *Distrito Federal:* Rio Maranhão, upper Rio Tocantins basin, approximately 35 air km N of Brasilia (approximately 15°32′S, 47°49′W), USNM 292221, 3 (60.7–63.0; specimens cleared and counterstained for cartilage and bone). *Mato Grosso:* Município de Barra do Garças, Córrego Fundo (approximately 15°53′S, 52°15′W), USNM 342235, 2 (41.7–52.1; see comments under "Geographic Variation," above, concerning this lot).

Creagrutus flavescens, new species

FIGURES 38, 41, TABLE 19

Creagrutus muelleri [not of Günther, 1859].—Boulenger, 1887:281 [misidentification] [Ecuador (Pastaza) Canelos].

Creagrutus amoenus, Fowler, 1943a:239 [in part, only one of three paratypes; Colombia, (Caquetá), Río Ortuguasa (Orteguaza), Florencia].

Creagrutus beni [not of Eigenmann, 1911].—Saul, 1975:106 [misidentification] [specimens from Ecuador, Napo (now in Sucumbíos), Río Aguarico, at Santa Cecilia].

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 2 or 3 teeth on the maxilla, 6 teeth in the primary tooth row of the premaxilla, 5 teeth on each dentary, 37 to 40 lateral line scales without a lamellar process over each pore, 9 or 10 predorsal median scales, 4 scale rows between the dorsal-fin origin and the lateral line, 36 to 39 vertebrae, 9 to 12 branched anal-fin rays, 2 post-anal median scales to the anal-fin origin, the well-developed third infraorbital contacting the horizontal limb of the preopercle in larger specimens, the distance from the dorsal-fin origin to the pelvic-fin insertion (30.0%–35.1% of SL), the distance from the dorsal-fin origin to the anal-fin origin (34.4%–40.4% of SL), the distance from the dorsal-fin origin to the pelvic-fin insertion (30.0%–35.1% of SL), the distance from the dorsal-fin origin to the pectoral-fin insertion (32.0%–36.6% of SL), the caudal peduncle depth (11.5%–13.7% of SL), the dorsal-fin length (22.8%–26.5% of SL), the postorbital head length (38.3%–45.5% of HL), the bony orbital diameter (33.3%–40.6% of HL), the lack of a series of dark midlateral spots on the body, the possession of a discrete, vertically elongate, anteriorly curved humeral mark, the absence of a distinct dark spot on the basal portions of the caudal fin, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus flavescens* from all species within the clade composed of *Creagrutus* and *Piabina* with the exception of *C. ignotus*. These two species can be distinguished by the distance from the dorsal-fin origin to the hypural joint (55.5%–61.9% of SL *C. flavescens* versus 53.3%–55.4% of SL in *C. ignotus*), the distance from the dorsal-fin origin to the anal-fin origin (34.4%–40.4% of SL versus 26.9%–30.5% of SL, respectively), the distance from the dorsal-fin origin to the pelvic-fin insertion (30.0%–35.1% of SL versus 21.5%–25.4% of SL, respectively), the distance from the dorsal-fin origin to the pectoral-fin insertion (32.0%–36.6% of SL versus 28.5%–30.7% of SL, respectively), and the caudal peduncle depth (11.5%–13.7% of SL versus 9.3%–10.7% of SL, respectively).

DESCRIPTION.—Morphometric and meristic data for *Creagrutus flavescens* in Table 19. Head and body moderately robust, with body deep. Greatest body depth at dorsal-fin origin in individuals up to 50 mm SL, located at that point or shifted somewhat anteriorly in larger specimens, particularly those with distended abdomens. Dorsal profile of head moderately convex from margin of upper lip to point slightly anterior of vertical through anterior nostril; nearly straight from that point to tip of supraoccipital spine. Predorsal profile of body continuing that of head and straight to slightly convex in smaller specimens. Dorsal profile notably convex, with distinct change in alignment relative to that of head in larger individuals. Predorsal surface of body with distinct median ridge proximate to dorsal-fin origin, ridge more prominent in larger individuals. Ventral profile of head with distinct obtuse angle at anteroventral corner of dentary, nearly straight from that angle to isthmus at all sizes. Prepelvic region of body slightly convex in smaller specimens, more curved in larger individuals, being notably convex from populations in the Peruvian lowlands (see comments concerning these populations under "Remarks," below); indistinctly flattened transversely in specimens larger than 30 mm SL. Caudal fin with scales extending onto basal portions of each lobe in larger specimens.

Head obtusely pointed in lateral view, somewhat laterally compressed in dorsal view. Upper jaw longer than, and slightly overhanging, lower jaw. Snout slightly fleshy anteromedially, with papillae on ventral margin of upper lip and on plicae and folds extending between outer and medial premaxillary teeth. Papillae concentrated along margin of upper lip.

Infraorbital series well developed. Ventral margin of third infraorbital barely falling short of horizontal limb of preopercle in specimens of approximately 40 mm SL, in contact with that bone in larger specimens. Posterior margins of third through fifth infraorbitals falling slightly short of vertical limb of preopercle.

Premaxillary teeth in three series: primary row of 6 teeth gently curved in small- to medium-sized specimens, with anterior tooth somewhat displaced laterally and giving series slightly sigmoid appearance in larger specimens, but without pronounced gap between first and second tooth of series. Me-

TABLE 19.—Morphometrics and meristics of *Creagrutus flavescens*, new species: (A) holotype of *C. flavescens*, MEPN 4622; (B) paratypes of *C. flavescens* (n=26); and (C) all specimens of *C. flavescens* from which counts and measurements were taken (n=82). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B	C
		Morphometrics	
Standard length	88.0	43.7–93.8	30.7–93.8
1. Snout to anal-fin origin	62.9	62.2–66.3	60.5–67.6
2. Snout to pelvic-fin origin	45.3	45.1–48.1	45.1–48.1
3. Snout to pectoral-fin insertion	23.2	21.7–24.0	21.7–26.3
4. Snout to dorsal-fin insertion	43.8	44.1–48.4	43.8–48.4
5. Dorsal-fin origin to hypural joint	61.5	56.7–61.9	55.5–61.9
6. Dorsal-fin origin to anal-fin origin	37.8	35.0–37.9	34.4–40.4
7. Dorsal-fin origin to pelvic-fin insertion	32.5	30.0–32.6	30.2–35.1
8. Dorsal-fin origin to pectoral-fin insertion	34.4	32.8–35.6	32.0–36.6
9. Caudal peduncle depth	13.0	11.9–13.7	11.5–13.7
10. Pectoral-fin length	19.0	18.4–22.3	18.0–23.3
11. Pelvic-fin length	16.6	16.5–18.6	15.3–19.5
12. Dorsal-fin length	24.0	24.0–26.5	22.8–26.5
13. Anal-fin length	18.8	17.1–21.0	17.1–22.2
14. Head length	24.3	23.1–25.2	23.1–26.7
15. Postorbital head length	44.4	38.3–45.5	38.3–45.5
16. Snout length	24.5	24.4–30.1	24.4–30.1
17. Bony orbital diameter	35.0	34.5–40.6	33.3–40.6
18. Interorbital width	34.6	28.1–35.0	28.0–35.0
		Meristics	
Lateral line scales	40	37–40	37–40
Scale rows between dorsal-fin origin and lateral line	4	4	4
Scale rows between anal-fin origin and lateral line	3	3	3
Predorsal median scales	9	9–10	9–10
Branched dorsal-fin rays	8	8	8
Branched anal-fin rays	12	10–12	9–12[1]
Branched pelvic-fin rays	6	6–7	6–7
Pectoral-fin rays	13	12–13	12–13
Vertebrae	38	36–39	36–39

[1]Nine branched anal-fin rays present in only 1 of 108 examined type and nontype specimens.

dial tooth of primary series separated from anteriortooth of contralateral series by distinct gap filled by fleshy fold, fold more elaborate in larger individuals; triangular cluster of 3 large teeth, with posterolateral tooth larger; and single tooth of form similar to that of primary series located lateral to fourth tooth of primary premaxillary tooth row. Maxilla with 2 or 3 tricuspidate teeth. Dentary with 5 teeth; first and second teeth distinctly larger than others, with second tooth slightly larger than first and approximately twice height of third; fourth and fifth teeth much smaller and compressed.

Dorsal-fin rays ii,8 in all specimens. Dorsal-fin origin slightly anterior to vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin distinctly concave. Anal-fin rays ii,9–12 (9 very rare). Profile of distal margin of anal fin distinctly concave, with last unbranched and anterior two branched rays forming lobe. Mature males with hooks present on anterior 2 to 4 branched anal-fin rays. Pectoral-fin rays i,11–12. Tip of pectoral fin extending posteriorly two-thirds to three-fourths of distance to pelvic-fin insertion. Pelvic-fin rays i,6,i or i,7; mature males with hooks on all branched pelvic-fin rays. Tip of pelvic fin extending posteriorly to anus.

Gill rakers 7–9 + 10–13.

COLORATION IN LIFE.—In life, species with overall yellowish cast to the head, body, and fins (R. Barriga, pers. comm., 1996). Recently collected specimens, in formalin for less than one week, with body and head silvery overall, with the silvery sheen much more pronounced on the portions of the body ventral of the midlateral body stripe, midlateral body stripe itself overlain by a dense silvery stripe. Portion of body dorsal of midlateral stripe with yellowish tint. Dorsal surface of head yellowish.

Dorsal fin yellow with darker markings apparent in specimens in alcohol quite obvious, yellow pigmentation most intense on unbranched and anterior branched rays and continuing posteriorly as yellow band along central portions of rays and membranes of remaining branched rays. Caudal fin yellow, more so basally, with distal portions of rays less intensely pigmented. Anal fin with patch of intense yellow pigmentation overlying central portions of unbranched rays and all but poste-

rior most branched rays, patch slightly posterodorsally angled and tapering in height posteriorly. Pelvic fin with intense yellow pigmentation on central portions of all but lateralmost rays. Pectoral fin with yellow patch over central portion.

COLORATION IN ALCOHOL.—Specimens retaining guanine on scales and relatively recently collected individuals silvery with ground coloration yellowish. Ground coloration of specimens in alcohol for longer than several months light tan. Dorsal surface of head with field of relatively concentrated small, dark surface chromatophores underlain by larger chromatophores located on surface of brain. Field of surface chromatophores continuing anteriorly over snout, with pigmentation more concentrated dorsal and anterior to nostrils. Denser field of chromatophores proximate to nostrils continuous, with stripe of dark chromatophores extending posteriorly around ventral and posterior margins of orbit. Dorsal portions of opercle and infraorbitals posterior to orbit with field of scattered, dark chromatophores.

Scales of dorsal surface of body with chromatophores concentrated along scale margin and over basal portion of exposed portion of scale; fields of dark chromatophore separated by hyaline region. Intensity of dark pigmentation more pronounced along dorsal midline and gradually decreasing ventrally. Predorsal region of many specimens, typically larger individuals or those with darker overall pigmentation, with distinct, narrow middorsal stripe in region situated dorsal of humeral mark. Humeral mark in specimens of 25 to 45 mm SL distinctly vertically elongate, extending from about one scale row above horizontal through pectoral-fin insertion to one scale row ventral of middorsal line. Anterior margin of mark nearly straight in smaller individuals, becoming more arched with increasing body size. Density of pigmentation within humeral mark not notably variable in smaller individuals. Ventral portion of mark becoming progressively less intensely pigmented in larger specimens. Larger individuals with anterior and, to lesser degree, posterior expansion of portion of mark centered along horizontal through middle of orbit. This expansion, in combination with reduction in intensity of pigmentation in ventral portion of marks, results in dark humeral mark in form of inverted comma in adults. Larger specimens with only scattered, dark chromatophores in region occupied by ventral portion of mark in smaller individuals. Midlateral portion of body with dark horizontal stripe formed by deep-lying and surface chromatophores. Stripe diffuse anteriorly and not continuous with humeral mark; more dense in central portion and extending posteriorly onto caudal peduncle; becoming diffuse posteriorly on caudal peduncle.

Dorsal fin with series of small, dark chromatophores along anterior margin of first and second unbranched rays. Membranes of branched rays with fields of small chromatophores extending over distal two-thirds of fin in smaller individuals, and nearly to fin-base in larger specimens, giving fin overall dusky appearance. Anal-fin membranes with small, dark chromatophores along distal one-half to two-thirds of fin. Caudal fin with rays outlined and sometimes overlain by small dark chromatophores, giving it slightly dusky appearance. Pectoral and pelvic fins hyaline or with few small, dark, chromatophores along fin-ray margins.

ETYMOLOGY.—The specific name, *flavescens,* from the Latin flavus, for golden yellow, refers to the life coloration of the species.

ECOLOGY.—Mature males, as shown by the presence of hooks on the rays of the anal and pelvic fins, are all less than 70 mm SL; all larger individuals evidently are females. One of the females, captured in early May, had large numbers of well-developed eggs.

Saul (1975:106) reported that this species (cited as *C. beni*) occurs "primarily in the swift waters of the Río Aguarico. Specimens were taken along sandbars where a solid sand or mud bottom was present. Large rocks were lacking or widely scattered. One specimen was seined over bedrock at the mouth of a small stream during high water." Comparable conditions also are common to a number of other localities in which *C. flavescens* has been captured (R. Barriga, pers. comm., 1996).

Examination of the stomach contents of two specimens of *C. flavescens* prepared for clearing and staining in this study revealed primarily parts of adult insects along with a small number of chopped up seeds. Saul (1975:106), in his analysis of stomach contents for *C. flavescens* (his *C. beni*), found seeds, plant debris, insect debris, mayfly larvae (Ephemeroptera), stonefly nymphs (Plecoptera), caddisfly larvae (Trichoptera), beetle larvae (Coleoptera), fly larvae (Diptera, Chironomidae), ants (Hymenoptera, Formicidae), and a spider (Araneida). Ants and chironomid larvae were most abundant.

In the Río La Bermeja of the Río San Miguel basin, northeastern Ecuador, *C. flavescens* was captured together with *C. amoenus* (USNM 340973 and 340986, respectively).

DISTRIBUTION.—*Creagrutus flavescens* occurs on the eastern slopes of the Andean piedmont in Ecuador (Figure 38, dots).

GEOGRAPHIC VARIATION.—The holotype of *Creagrutus flavescens* and paratypes collected with it from the southern portions of the species range in Department of Pastaza, Ecuador, have 37 to 39 vertebrae. Of these, only one specimen has 39 vertebrae and a nearly equal number of individuals have 37 and 38 vertebrae, for an overall mean of 37.6 vertebrae. Nontype specimens from lower elevation Peruvian localities in the Río Tigre system, which originates in the Department of Pastaza, Ecuador, have 38 or 39 vertebrae with a mean of 38.2. Specimens of *C. flavescens* from the central and northern portions of the known range of the species (Departments of Napo and Sucumbíos) have a range of 36 to 38 vertebrae with a strong modal value of 37 vertebrae and a mean of 36.99 vertebrae.

Paralleling this variation in the range of modal values of the vertebrae are differences in the range and modal values for lateral line scales. The population sample from the type locality (Department of Pastaza) has 38 to 40 scales and a mean value of 39.0 scales, whereas the more numerous samples from the central and northern portions of Ecuador have a range of 37 to 40 scales with a mean of 38.4 scales. These minor differences do not permit the recognition of more than one species within what is herein identified as *C. flavescens* and may simply re-

FIGURE 41.—*Creagrutus flavescens*, new species, holotype, MEPN 4622, 88.0 mm SL; Ecuador, Pastaza, Río Tiguino basin, Río Tiguino No. 3 (unnamed tributary of Río Tiguino; 1°07′35″S, 76°56′52″W).

flect the limited sample sizes from the southern portions of the species range.

Two lots of *C. flavescens* from the Río Tigre system in the Department of Loreto, Peru, agree with Ecuadorian populations of the species in the vast majority of features but are relatively deeper bodied than is typical for Ecuadorian samples of the species. The three larger specimens in these lots (NRM 26380, 2 of 8 specimens; NRM 26372, 1 specimen) consequently are at the upper limit for the proportional values that reflect body depth. In these Río Tigre specimens the distance from the dorsal-fin origin to the anal-fin origin is 37.0%–40.3% of SL versus a range of 32.4%–37.9% of SL in Ecuadorian samples. Similarly, the distance from the dorsal-fin origin to the pelvic-fin insertion is 32.0%–35.1% versus 28.2%–32.8% of SL, and the distance from the dorsal-fin origin to the pectoral-fin insertion is 34.5%–36.6% versus 32.0%–35.6% of SL for the Peruvian versus Ecuadorian samples, respectively. Further samples from Peru and intervening regions are necessary to determine whether the differences should be recognized taxonomically or only represent geographic or ecophenotipic variation.

REMARKS.—Fowler (1943a:239) described *Creagrutus amoenus* on the basis of a holotype and three paratypes. One of the paratypes of *C. amoenus* (ANSP 70500, 62.8 mm SL) is actually a specimen of *C. flavescens*.

Boulenger (1887:281) reported *Creagrutus muelleri* from Canelos, a town on the Río Bobonaza of eastern Ecuador. Although that locality lies within the general distributional range of *C. muelleri*, the specimen that apparently served as the basis of that report (BMNH 1880.12.8:116) lacks the arrangement of premaxillary dentition typical of that species. The specimen is in somewhat poor condition and lacks pigmentation, thereby precluding a definitive identification, but it is tentatively considered to be an individual of *C. flavescens* based on where it was collected and the available meristic and morphometric evidence.

Saul (1975:106) reported *C. beni* from the Río Aguarico of eastern Ecuador, using the broad concept of that species common at that time. Analysis has shown that his specimens are *C. flavescens*.

MATERIAL EXAMINED.—689 (82, 30.7–93.8).

HOLOTYPE.—ECUADOR. *Pastaza:* Río Tiguino basin, Río Tiguino No. 3 (unnamed tributary of Río Tiguino; 1°07′35″S, 76°56′52″W), collected by R. Barriga, 21 Apr 1989, MEPN 4622, 1 (88.0).

PARATYPES.—26 specimens (26, 43.7–93.8).

ECUADOR. *Pastaza:* Rio Tíguino basin, Río Tiguino No. 3 (unnamed tributary of Río Tiguino; 1°07′35″S, 76°56′52″W), collected with holotype, MEPN 4642, 7 (43.7–82.3); USNM 340974, 8 (61.7–90.7). *Napo:* Estero Yampuna, 300 m from Campamento Petrolano Yampuna, collected 18 Dec 1988, by R. Barriga et al., MEPN 6380, 7 (53.9–93.8); USNM 340975, 4 (55.5–88.6).

NONTYPE SPECIMENS.—652 specimens (55, 30.7–88.7).

COLOMBIA. *Caquetá:* Florencia, Río Orteguasa (=Orteguaza; approximately 1°45′N, 75°35′W), ANSP 70500, 1 (62.8, paratype of *Creagrutus amoenus*). Río Caquetá basin, Morelia (1°29′N, 75°44′W), ANSP 166592, 3. Río Orteguaza basin, small oxbow stream across Río Orteguaza from Tres Esquinas (0°43′N, 75°61′W), CAS 150658, 3. *Putomayo:* Rumiyaco (1000 m elevation), NRM 26424, 3.

PERU. *Loreto:* Río Tigre drainage, San Jacinto, quebrada at km 53 (2°32′S, 75°44′W), NRM 26372, 1 (78.1). Río Corrientes drainage, Teniente López, quebrada tributary to Río Corrientes, at military camp (approximately 3°43′S, 74°45′W), NRM 26380, 8 (2, 50.2–71.9).

ECUADOR. *Napo:* Río Punino, tributary of Río Payamino, above Coca (=Puerto Francisco de Orellana; approximately 0°27′S, 77°08′W), MCZ 51493, 32 (15, 54.5–65.6). Río Blanco, first tributary N of Río Tiputini, above bridge on road

to Coca (=Puerto Francisco de Orellana) (0°44′30″S, 76°53′W), MEPN 5248, 10. Quebrada Capihuara, northern tributary of Río Payamino, 6.5 river km below mouth of Río Tutapischo (approximately 0°30′S, 77°14′30″W), MEPN 5249, 20; FMNH 106029, 32. Quebrada Tiuyacu, first upstream tributary of Río Churuyacu, near mouth of latter in Río Payamino (approximately 0°29′30″S, 77°18′W), MEPN 5253, 9. Rio Tiputini basin, Estero Culiyacu (0°43′08″S, 76°50′12″W), MEPN 6611, 4; MEPN 6374, 1. In cave near Archidona (approximately 0°55′S, 77°48′W), ZMA 119.151, 1. Small stream tributary to Río Payamino, approximately 1.6 km from mouth of river, MCZ 51495, 2. Río Copataza (=Copotaza), BMNH 1981.1.5:341–354, 14. Estero Culiyacu, left margin of Río Tiputini (mouth of river at 0°48′S, 76°33′W), USNM 311356, 13. Río Napo at Puerto Misahuali (1°2′30″S, 77°39′12″W), FMNH 106033, 18. *Pastaza:* Canelos (Río Bobonaza system, 1°35′S, 77°45′W), BMNH 1880.12.8:116, 1 (65.3). Río Bobonaza, near settlement of Montalvo (2°04′S, 76°58′W), MEPN 4639, 8. Río Tiguino basin, Río Tiguino No. 3 (unnamed tributary of Río Tiguino; 1°07′35″S, 76°56′52″W), MEPN 9621, 43. Río Tigrillo, tributary of Río Conambo, Pozo Tigrillo, Tenneco camp (exact locality uncertain), MEPN 6609, 18. Río Pastaza, near Puyo (approximately 1000 m elevation; 01°30′S, 78°00′W), UMMZ 203872, 1. *Sucumbíos:* Río Aguarico basin, mouth of Río Shushifindi, ANSP 137613, 12 (10, 58.0–88.7). Río San Miguel basin, Río La Bermeja, in front of Commmunidad Shuor Chari (approximately 0°10′N, 76°25′W), MEPN uncataloged, 15 (30.7–81.1); USNM 340973, 10 (38.5–75.8; 2 specimens cleared and counterstained for cartilage and bone). Río Aguarico, several km by river above mouth of Río Eno (approximately 0°11′S, 76°30′W), MEPN 5258, 8. Río Aguarico, Guarumo (0°01′S, 76°37′30″W), MEPN 5273, 150; MEPN 9836, 10. Northern tributary of Río Aguarico, 2–3 river km upstream of mouth of Río Pushino (0°03′N, 76°56′W), MEPN 5261, 100. Río Aguarico, beach above mouth of Río Dué (0°04′30″N, 77°22′24″W), MEPN 5250, 10. Río Duguno, approximately 1 km S of Communa Cafán del Duguno (0°02′10″S, 77°05′18″W), MEPN uncataloged, 1. Río Aguarico, at Santa Cecilia (00°06′N, 76°51′W), ANSP 130466, 7 (formerly KU 13444); ANSP 130470, 8; KU 13447, 18; ANSP 130468, 10. Río Aguarico, just upstream from Lago Agrio at Cancha (0°3′30″N, 76°53′W), FMNH 106035, 47.

Creagrutus gephyrus Böhlke and Saul, 1975

FIGURES 42, 43, TABLE 20

Creagrutus gephyrus Böhlke and Saul, 1975:25, figs. 1–4 [type locality: Ecuador, Napo (now in Sucumbíos), Río Aguarico, at Santa Cecilia].—Saul, 1975:106 [Ecuador, Napo (now in Sucumbíos), Río Aguarico, at Santa Cecilia; ecology and habitat].—Böhlke, 1984:47 [depository of holotype and portion of paratype series].—Stewart et al., 1987:26 [Ecuador, Río Napo basin].—Barriga, 1991:17 [tropical eastern Ecuador; common name].—1994:29 [Ecuador, Parque Nacional Yasuní].

DIAGNOSIS.—The combination of the three standard components of premaxillary dentition typical for most *Creagrutus* species (see "Premaxillary Dentition in *Creagrutus* and *Piabina*"), and the possession of 7 to 10 maxillary teeth and 10 or 11 dentary teeth in adult specimens discriminates *Creagrutus gephyrus* from all congeners and *Piabina argentea*, all of which either have two irregular rows of premaxillary dentition (*C. maxillaris* and *C. cracentis*) or 2 to 5 maxillary teeth and 5 to 7 dentary teeth (*Piabina argentea* and all remaining *Creagrutus* species). *Creagrutus gephyrus* also is characterized by a autapomorphic modification of the sphenotic spine (see "Sphenotic," under "Character Description and Analysis").

TABLE 20.—Morphometrics and meristics of *Creagrutus gephyrus:* (A) holotype of *C. gephyrus*, ANSP 130516; and (B) all other specimens of *C. gephyrus* from which counts and measurements were taken (n=25). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length. Dash indicates measurement that could not be taken as a consequence of damage to specimen.

Characters	A	B
	Morphometrics	
Standard length	64.9	29.5–64.6
1. Snout to anal-fin origin	66.9	61.4–67.7
2. Snout to pelvic-fin insertion	49.9	46.9–50.6
3. Snout to pectoral-fin insertion	24.2	23.1–26.7
4. Snout to dorsal-fin origin	49.5	46.2–49.6
5. Dorsal-fin origin to hypural joint	53.0	52.2–57.0
6. Dorsal-fin origin to anal-fin origin	30.8	27.8–31.0
7. Dorsal-fin origin to pelvic-fin insertion	25.9	22.7–26.2
8. Dorsal-fin origin to pectoral-fin insertion	32.0	27.8–32.5
9. Caudal peduncle depth	11.1	10.5–11.6
10. Pectoral-fin length	17.7	16.1–18.6
11. Pelvic-fin length	14.9	13.7–15.5
12. Dorsal-fin length	–	19.6–22.0
13. Anal-fin length	16.2	15.5–17.7
14. Head length	28.0	26.0–28.2
15. Postorbital head length	41.0	41.0–46.0
16. Snout length	29.0	24.0–29.4
17. Bony orbital diameter	27.7	28.4–36.0
18. Interorbital width	25.6	25.4–28.9
	Meristics	
Lateral line scales	39	37–39
Scale rows between dorsal-fin origin and lateral line	4	3–4
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	10	9–10
Branched dorsal-fin rays	8	8
Branched anal-fin rays	11	10–11
Branched pelvic-fin rays	6	6
Pectoral-fin rays	13	13–14
Vertebrae	37	37

DESCRIPTION.—Morphometric and meristic data for *Creagrutus gephyrus* in Table 20. Overall appearance of head and body elongate compared with many congeners. Maximum body depth at vertical through dorsal-fin origin in specimens without distended abdomens, somewhat anterior of that point in ripe females and specimens with full stomachs. Dorsal profile of head smoothly convex between margin of upper lip and vertical through posterior margin of posterior nares. Snout tip somewhat more blunt in larger specimens. Dorsal profile of head posterior to vertical through posterior nares posterodorsally inclined and straight to slightly convex. Dorsal profile of

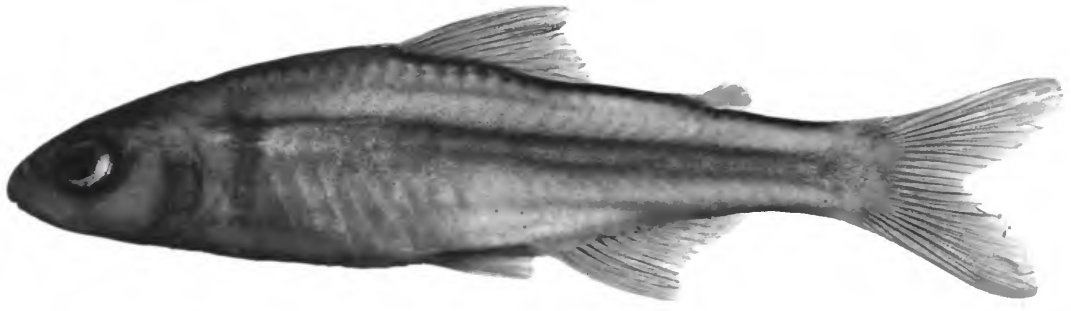

FIGURE 42.—*Creagrutus gephyrus*, USNM 324461, 40.7 mm SL; Ecuador, Napo, Río Napo, at Coca (=Puerto Francisco de Orellana; latter locality at 0°28′S, 80°22′W).

posterior portion of head continued without interruption onto slightly convex predorsal region of body. Dorsal profile of body between dorsal-fin origin and caudal peduncle straight or more typically somewhat convex in region of adipose fin. Ventral profile of head smoothly rounded, without obtuse angle at anteroventral region of dentary. Profile of abdominal region typically straight in smaller individuals, varyingly convex in larger specimens. When abdominal profile straight, abdomen somewhat transversely flattened.

Upper jaw longer than, and overhanging, lower jaw, but with difference in length of jaws less pronounced than in most *Creagrutus* and *Piabina* species. Anterior surface of snout fleshy, albeit less so than in many congeners. Papillae limited to anterior portion of snout, upper lip, and outer fleshy flaps and plicae extending between outer and medial premaxillary teeth. Lower lip somewhat fleshy anteriorly, although less so than in most *Creagrutus* species, with few scattered papillae.

Infraorbital series well developed, covering approximately two-thirds of check in specimens of approximately 17 mm SL; extending over nearly all of that region of head in larger individuals. Ventral margin of third infraorbital contacting horizontal limb of preopercle. Posterior margins of third through fifth infraorbitals falling slightly short of vertical limb of preopercle.

Premaxillary dentition in three series: nearly straight primary row typically with 5, rarely 6, tricuspidate teeth (see under "Geographic Variation," below, concerning this intraspecific difference), with medial teeth of contralateral series distinctly separated; triangular cluster of three larger teeth with posterolateral tooth slightly larger; and single tricuspidate tooth with posteriorly recurved central cusp, tooth located lateral to region between third and fourth teeth of primary premaxillary row. Maxilla with 7 to 11 tricuspidate teeth; 3 anterior maxillary teeth largest with teeth posterior to these becoming progressively smaller. Middle teeth of maxillary series with middle cusp posteriorly recurved. Dentary with 10 or 11 teeth. Anterior 3 teeth distinctly larger and angled anterodorsally or anterolaterally depending on position in jaw. Fourth to last teeth in series gradually decreasing in size. Two anteriormost dentary teeth with 4 cusps, fourth cusp very small, on posterior margin of tooth. All other dentary teeth tricuspidate other than for posteriormost 1 or 2 conical teeth (number of conical teeth depending on whether 10 or 11 dentary teeth present). Central cusps of first and second teeth nearly straight, those of remaining teeth posteriorly recurved to varying degrees.

Dorsal-fin rays ii,8. Dorsal-fin origin at, or slightly anterior to, vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin slightly concave. Anal-fin rays ii,10–11. Profile of distal margin of anal fin distinctly convex, with posterior unbranched and 3 anterior branched rays forming distinct lobe. Single, bilaterally paired hooks present on anterior 2 branched anal-fin rays in mature males (observed in only 2 of 20 specimens). Hooks restricted to posterolateral surface of main shaft. Pectoral-fin rays i,12–13. Tip of pectoral fin extending posteriorly approximately two-thirds of distance to pelvic-fin insertion. Pelvic-fin rays i,6,i. Tip of pelvic fin falling somewhat short of anus. Mature males with pelvic-fin hooks, when present, on basal unsegmented portions and most segments other than distalmost ones on all branched rays. Mature males with hooks also present on segmented portion of medial unbranched pelvic-fin rays, again with exception of distal portion of ray.

Gill rakers 6–7 + 9–11; those of first arch, especially first ceratobranchial, relatively long.

COLORATION IN ALCOHOL.—Dorsal surface of head with smaller dark chromatophores on surface and larger, deep-lying dark chromatophores, particularly over membranes on brain. Field of surface chromatophores extending anteriorly over snout and upper lip. Chromatophore field anterior to nares continuous posteroventrally with band of dark chromatophores continuing posteroventrally to ventral margin of eye and then around posterior margin of orbit. Dorsal portions of opercle and infraorbital series with pattern of scattered, dark chromatophores. Margin of upper lip dark medially. Scales of dorsal portion of body underlain by series of chromatophores in regions where scales overlap; dark pigmentation forming somewhat re-

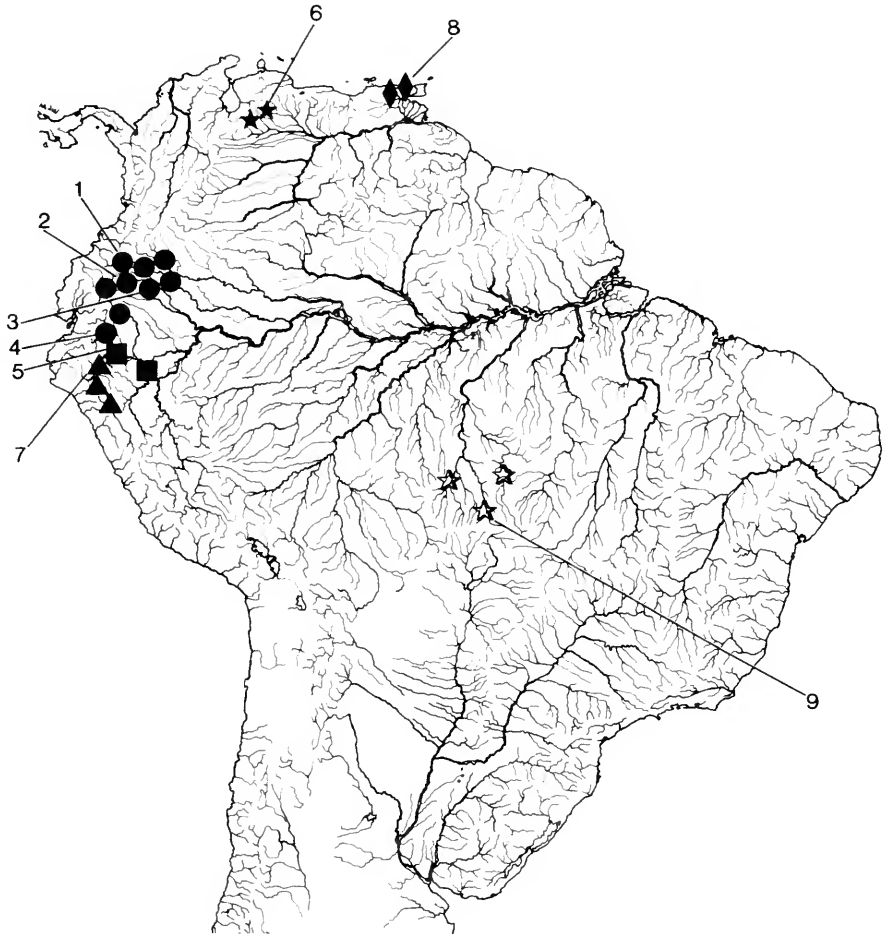

FIGURE 43.—Map of central and northern South America showing geographic distribution of *Creagrutus gephyrus* (dots, 1=type locality, 2 and 3=areas where both *C. gephyrus* and *C. gracilis* occur, 4=area where both *C. gephyrus* and *C. holmi* occur), *Creagrutus gracilis* (squares, 5=type locality; *C. holmi* also collected in this area, see also under *C. gephyrus*), *Creagrutus gyrospilus* (solid stars, 6=type locality), *Creagrutus holmi* (triangles, 7=type locality, see also under *C. gephyrus* and *C. gracilis*), *Creagrutus hysginus* (diamonds, 8=type locality), and *Creagrutus ignotus* (open stars, 9=type locality) (some symbols represent more than one locality or lot of specimens).

ticulate pattern. Reticulate pattern merges into continuous field of chromatophores along dorsal midline.

Humeral mark appearing as vertically elongate pigment patch extending from slightly above horizontal of pectoral-fin insertion, across lateral line, to approximately one scale ventral of middorsal line. Anterior and posterior margins of humeral mark somewhat irregular, but mark typically tapers somewhat ventrally. Body with dark midlateral band formed by surface and deep-lying chromatophores. Deep-lying stripe of dusky pigmentation extending from under dorsal fin posteriorly to rear of caudal peduncle in medium-sized individuals and farther anteriorly, nearly to humeral mark, in larger specimens. Deep-lying stripe overlain by diffuse, wider band of small dark surface chromatophores extending posteriorly from humeral mark to rear of caudal peduncle.

Dorsal fin with margin of longest unbranched ray and distal one-half of anterior branched rays and associated membranes with dark chromatophores; scattered, dark chromatophores on posterior portion of fin. Most branched anal-fin rays with all but distal portions delimited by dark chromatophores. Caudal- and pectoral-fin rays outlined by dark chromatophores. Pelvic fin with scattered chromatophores.

ECOLOGY.—Saul (1975:106) reported that *Creagrutus gephyrus* was captured most often in the main portion of the Río Aguarico of eastern Ecuador over a packed sand and mud bottom, but some individuals occurred in a sluggish backwater of

the river. The specimens examined by Saul had fed on fish and insect larvae. The single specimen prepared for clearing and staining in this study and examined for stomach contents had fed exclusively on insect larvae.

COMMON NAME.—Ecuador: "Sardina" (Barriga, 1991:17).

DISTRIBUTION.—*Creagrutus gephyrus* occurs across the Andean piedmont rivers of eastern Ecuador and northeastern Peru (see "Geographic Variation," below, concerning latter population sample; Figure 43).

GEOGRAPHIC VARIATION.—The southern-most record for *Creagrutus gephyrus* is based on three lots of specimens from Amazonas province of northeastern Peru (LACM 36357-56, 39908-3, 42114-10). These specimens agree with the Ecuadorian samples of the species in all features other than for having 6 rather than 5 teeth in the primary premaxillary row. Given the limited size of the *C. gephyrus* sample from northeastern Peru and the intraspecific variation in the number of teeth in the primary premaxillary tooth row in some other *Creagrutus* species, we prefer to not recognize the specimens from that region as a separate species at this time. If further samples prove that this is an invariant difference between the populations, it may warrant taxonomic recognition.

MATERIAL EXAMINED.—93 specimens (33, 29.5–64.9).

ECUADOR. *Sucumbios:* Tributary of Río Aguarico, at Santa Cecilia (0°06′N, 76°51′W), ANSP 130516, 1 (64.9, holotype of *Creagrutus gephyrus*); ANSP 130517, 1 (60.3, paratype of *Creagrutus gephyrus*); ANSP 130519, 1 (paratype of *Creagrutus gephyrus*); ANSP 130520, 1 (paratype of *Creagrutus gephyrus*); ANSP 130521, 1 (35.8, paratype of *Creagrutus gephyrus*); ANSP 130522, 1 (35.7, paratype of *Creagrutus gephyrus*); KU 13468, 2 (37.4–40.9, paratypes of *Creagrutus gephyrus*). Río Aguarico at Destacamento Militar Santa Cecilia, FMNH 103011, 6. Río Aguarico, approximately 1 river km upriver of confluence with Río Shushufindi (0°17′N, 76°25′W), MEPN 4629, 5. Río Aguarico near Destacamento Militar Cuyabeno and confluence of Río Cuyabeno and Río Aguarico (0°15′30″S, 75°53′30″W), FMNH 103008, 1; MEPN uncataloged, 13 (10, 42.0–47.3). Río Aguarico, slightly below mouth of Río Pushino (0°2′36″N, 76°54′24″W), MEPN uncataloged, 5. Río Aguarico, S of Shushufindi, USNM 352933, 3. Río San Miguel at Tapischa (0°12′30″N, 76°13′W), FMNH 103006, 5. Río Aguarico, 1 km above mouth of Río Lagartococha, beaches on both shores (0°38′S, 75°18′W), MEPN uncataloged, 3. *Napo:* Río Napo, at Coca (=Puerto Francisco de Orellana; 0°28′S, 80°22′W), USNM 324461, 4 (3, 29.5–40.7; 1 specimen cleared and counterstained for cartilage and bone). Río Napo, near Coca (=Puerto Francisco de Orellana; latter locality at 0°28′S, 80°22′W), USNM 343879, 2 (45.3–49.7). Río Napo, tributary stream approximately 25 km downstream of Coca (=Puerto Francisco de Orellana; latter locality at 0°28′S, 80°22′W), USNM 340953, 6 (4, 41.8–49.6; 1 specimen cleared and counterstained for cartilage and bone). Río Napo at Puerto Misahualli (1°2′30″S, 77°39′12″W), FMNH 103002, 10. Río Jatunyacu at Puerto Napo (1°03′S, 77°47′W), FMNH 103004, 1. Quebrada Capihuara, tributary to Río Payamino (0°30′S, 77°14′30″W), FMNH 103009, 7. *Pastaza:* Río Tiguino basin, Río Tiguino No. 3 (unnamed tributary of Río Tiguino; 1°07′35″S, 76°56′52″W, collected with holotype), MEPN uncataloged, 3. Río Tiguino basin, Tiguino No. 1 (unnamed tributary of Río Tiguino), MEPN 9580, 3.

The following specimens are tentatively identified as *Creagrutus gephyrus* (see discussion under "Geographic Variation," above, with respect to their identification).

PERU. *Amazonas:* Río Cenepa, vicinity of Huampani (4°28′S, 78°10′W), LACM 36357-56, 1 (64.6). Río Caterpiza (3°55′S, 77°42′W), LACM 39908-3, 6 (1, 31.6); LACM 42114-10, 1 (48.6).

Creagrutus gracilis, new species

FIGURES 43, 44, TABLE 21

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 3 or 4 teeth on the maxilla, 5 teeth in the primary tooth row of the premaxilla, 5 or 6 dentary teeth, 39 to 43 lateral line scales without a lamellar process over each pore, 9 or 10 predorsal median scales, 4 scale rows between the dorsal-fin origin and the lateral line, 3 scale rows between the anal-fin origin and the lateral line, 38 to 40 vertebrae, 10 or 11 branched anal-fin rays, 2 post-anal median scales to the anal-fin origin, 8 to 10 gill rakers on the lower limb of the first gill arch, 11 to 14 gill rakers on the upper limb of the first gill arch, the snout length (24.7%–28.6% of HL), the well-developed third infraorbital contacting the horizontal limb of the preopercle in larger individuals, the lack of a series of dark midlateral spots on the body, the discrete, vertically elongate, somewhat posterodorsally angled, ovoid, humeral mark without straight anterior and posterior margins, but not in the shape of an inverted comma, the lack of a spot of distinct pigmentation on the basal portions of the middle caudal-fin rays, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus gracilis* within the clade composed of *Creagrutus* and *Piabina.*

DESCRIPTION.—Morphometric and meristic data for *Creagrutus gracilis* in Table 21. Head and body relatively slender at all sizes. Greatest body depth slightly anterior to vertical through pelvic-fin insertion. Dorsal profile of head distinctly convex from margin of lower lip to vertical through anterior nostril, slightly convex, or more usually straight, from that point to rear of supraoccipital spine. Interorbital region obtusely flattened transversely. Dorsal profile of body very slightly convex from rear of head to dorsal-fin origin, convexity slightly more pronounced in larger specimens. Predorsal surface of body with slight middorsal ridge, ridge more developed proximate to dorsal-fin origin. Ventral profile of head with distinct obtuse angle at anteroventral corner of dentary, profile nearly straight from that angle to isthmus. Prepelvic re-

TABLE 21.—Morphometrics and meristics of *Creagrutus gracilis*, new species: (A) holotype of *C. gracilis*, LACM 41724-27; and (B) paratypes of *C. gracilis* (n=40). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	55.8	22.3–58.6
1. Snout to anal-fin origin	63.3	61.0–66.4
2. Snout to pelvic-fin insertion	47.1	45.4–49.6
3. Snout to pectoral-fin insertion	24.4	22.5–25.0
4. Snout to dorsal-fin origin	46.2	43.9–46.6
5. Dorsal-fin origin to hypural joint	60.0	53.7–60.2
6. Dorsal-fin origin to anal-fin origin	31.9	30.2–33.8
7. Dorsal-fin origin to pelvic-fin insertion	26.2	25.2–28.5
8. Dorsal-fin origin to pectoral-fin insertion	30.1	29.8–32.6
9. Caudal peduncle depth	10.9	10.6–12.4
10. Pectoral-fin length	19.7	17.6–20.6
11. Pelvic-fin length	15.7	13.7–16.6
12. Dorsal-fin length	23.2	19.5–24.9
13. Anal-fin length	17.0	15.9–18.9
14. Head length	25.8	23.3–26.6
15. Postorbital head length	45.5	38.0–45.8
16. Snout length	27.8	24.7–28.6
17. Bony orbital diameter	32.3	32.0–36.7
18. Interorbital width	27.6	27.6–32.0
	Meristics	
Lateral line scales	42	39–43
Scale rows between dorsal-fin origin and lateral line	4	4
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	9	9–10
Branched dorsal-fin rays	8	8
Branched anal-fin rays	11	10–11
Branched pelvic-fin rays	6	6–7
Pectoral-fin rays	13	12–14
Vertebrae	39	38–40

gion of body nearly straight in smaller specimens and slightly convex in larger individuals within Peruvian samples; distinctly convex in sample from Río Napo basin, eastern Ecuador (ANSP 134499) in which specimens are all larger than examined Peruvian samples.

Head moderately obtusely pointed in lateral view, less so than in many congeners; obtusely pointed in dorsal view. Upper jaw longer than, and overhanging, lower jaw. Snout fleshy, more so anteriorly, papillae scattered over anterior portion of snout and lateral surface of maxilla, more concentrated along anterior and ventral margin of upper lips and fleshy folds and plicae extending between outer and medial premaxillary teeth, particularly medially. Lower lip very fleshy with numerous papillae on dorsal and anterior margins; scattered papillae on ventromedial region of lip.

Infraorbital series moderately developed. Third infraorbital moderately large and horizontally elongate, with its ventrally convex lower margin falling short of contact with horizontal limb of preopercle in specimens up to approximately 50 mm SL. Central portion of ventral margin of third infraorbital approaching or barely contacting the horizontal limb of preopercle in individuals larger than approximately 50 mm SL. Posterior margins of third through fifth infraorbitals separated by narrow gap from vertical limb of preopercle.

Premaxillary dentition in three series: primary row slightly sigmoid, with 5 teeth in all specimens, without pronounced gap between first and second tooth of series but with medial tooth separated from contralateral equivalent by gap filled by fleshy fold; triangular cluster of 3 larger teeth lying medial to primary row, with posterolateral tooth somewhat larger than others; and single tooth of form similar to that of primary series occurring lateral to third tooth of primary premaxillary series, or lateral to area of contact of third and fourth teeth. Maxillary with 3 or 4, usually 4, tricuspidate teeth. Dentary with 5 or 6 tricuspidate teeth; first and second teeth distinctly larger than others, subequal or second slightly larger; both approximately twice height of third tooth; fourth and fifth or sixth teeth (when 6 teeth present) distinctly smaller and compressed.

Dorsal-fin rays ii,8 in all specimens. Dorsal-fin origin slightly anterior to vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin concave. Anal-fin rays ii,10–11 or iii,10 (only one specimen). Profile of distal margin of anal fin concave, with last unbranched and anterior 2 or 3 branched rays forming distinct lobe. Hooks on anal-fin rays present in mature males of many *Creagrutus* species not found in examined specimens. Pectoral-fin rays i,11–13. Tip of pectoral fin extending one-half to two-thirds of distance to pelvic-fin insertion. Pelvic-fin rays i,6,i or i,7 (typically i,7 in larger individuals). Pelvic-fin length somewhat variable, tip of fin extending posteriorly nearly to anal-fin origin in some individuals, or falling up to 2 scales short of that point in some specimens. Hooks of pelvic-fin rays present in mature males of many *Creagrutus* species not found in examined specimens.

Gill rakers 8–10 + 11–14 (14 in only 1 specimen).

COLORATION IN ALCOHOL.—Nontype specimens retaining guanine on scales silvery golden; guanine layer variably masking dark pigmentation of humeral mark and midlateral stripe of body. Specimens lacking guanine on scales with ground coloration light tan. Dorsal surface of head with field of small, dark surface chromatophores and series of deep-lying, larger, dark chromatophores on membranes overlying brain. Field of small surface chromatophores extending anteriorly over snout and upper lip. Region anterior to nares without dense concentration of dark chromatophores found in many *Creagrutus* species. Anterior portion of lower lip with scattered, small, dark chromatophores. Region anteroventral of orbit with region of concentrated chromatophores comparable to that in many congeners, but this patch not continued along ventral and posterior margins of orbit as in many other *Creagrutus* species. Dorsal infraorbitals and central and dorsal portions of opercle covered with scattered chromatophores.

Scales of dorsal portion of body with fields of chromatophores along posterior margin; width of field greater dorsally, nearly forming continuous area of chromatophores along middorsal portions of body, more so anterodorsally. Midlateral portion of body with indistinct stripe extending from slightly pos-

FIGURE 44.—*Creagrutus gracilis,* new species, holotype, LACM 41724-27, 55.8 mm SL; Peru, Amazonas, Provincia Condorcanqui, Río Santiago, at La Poza (4°01′S, 77°47′W).

terior of humeral mark to rear of caudal peduncle. Stripe formed by field of scattered, small, dark, surface chromatophores and larger, deep-lying, dark chromatophores; latter more concentrated along dorsal margin of stripe. Humeral mark prominent, main portion roughly ovoid, vertically elongate, with slightly anteriorly directly dorsal and ventral extensions.

Anterior margin of dorsal fin with series of small, dark chromatophores; distal portions of membranes with scattered, dark chromatophores; intensity of pigmentation more pronounced anteriorly and increasing overall ontogenetically. Anal-fin rays outlined with series of small dark chromatophores, more so on distal one-half of central rays. Caudal fin with membranes and margins of rays delimited by small, dark chromatophores. Intensity of caudal-fin pigmentation greater in larger individuals, giving fin dusky overall appearance in those specimens. Pectoral and pelvic fins mostly hyaline, with scattered, dark chromatophores.

ETYMOLOGY.—The specific name, *gracilis,* from the Latin for slender or gracile, refers to the relatively shallow body of this species compared to many congeners.

ECOLOGY.—Nothing is known about the ecology of *Creagrutus gracilis,* but all examined specimens originated in regions of less than 500 m elevation.

DISTRIBUTION.—*Creagrutus gracilis* is known from Amazonas and Loreto states of Peru and various localities along the eastern slope of the Andean Cordilleras in Ecuador (Figure 43, squares).

MATERIAL EXAMINED.—191 specimens (43, 22.3–77.0).

HOLOTYPE.—PERU. *Amazonas:* Provincia Condorcanqui, Río Santiago, at La Poza (4°01′S, 77°47′W), collected by D.J. Stewart, 20 Mar 1982, LACM 41724-27, 1 (55.8).

PARATYPES.—40 specimens (40, 22.3–58.6).

PERU. *Amazonas:* Provincia Condorcanqui, Río Santiago, at La Poza (4°01′S, 77°47′W), collected with holotype, LACM 41724-32, 10 (27.2–49.5); USNM 341370, 10 (23.3–42.1; 2 specimens cleared and counterstained for cartilage and bone); MUSM 8864, 10 (22.3–36.6). *Loreto:* Provincia de Alto Amazonas, Río Huallaga, mouth of Río Paranapura, at Yurimaguas (5°54′S, 70°05′W), collected by I. Samanez, 26 Apr 1995, MUSM 10760, 6 (39.2–58.6); USNM 344534, 4 (52.3–54.4).

NONTYPE SPECIMENS.—150 specimens (12, 42.0–77.0).

ECUADOR. *Sucumbíos:* Río Aguarico, 1 km above mouth of Río Lagartococha, beaches on both shores (0°38′S, 75°18′W), MEPN 4620, 2 (42.0–43.8). Río Aguarico, few km upstream from mouth of Río Eno (0°11′S, 76°30′W), FMNH 106031, 24. Río Napo basin, near mouth of Río Panayacyu, at elevation of 230–250 m (approximately 00°25′S, 76°07′W), ANSP 31311, 1 (53.4). *Napo:* Río Napo, sand bank opposite Coca (=Puerto Francisco de Orellana; 0°28′S, 76°58′W), ANSP 134499, 9 (59.0–77.0).

PERU. Nevate (locality not located in gazetteers), LACM 47268-1, 1. *Amazonas:* Provincia Condorcanqui, Río Santiago, at La Poza (4°01′S, 77°47′W; collected with holotype), LACM 41724-33, 113.

Creagrutus gyrospilus, new species

FIGURES 43, 45, TABLE 22

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 6 teeth in the primary series of each premaxilla, 3 or 4, rarely 2, maxillary teeth, 5 or 6 teeth on each dentary, 10 to 12 median predorsal scales, 36 to 39 lateral line scales without a lamellar process over each pore, usually 4 scale rows between the dorsal-fin origin and the lateral line, 2 post-anal scales to the anal-fin origin, 3 scale rows between the anal-fin origin and lateral line, usually 10 or 11 branched anal-fin rays, 5 to 8 gill rakers on the upper limb and 9 to 11 gill rakers on the lower limb of the first gill arch, 35 to 37 vertebrae, the caudal peduncle depth (11.3%–13.2% of SL), the postorbital length (45.0%–50.6% of HL), the bony diameter (25.8%–32.7% of

TABLE 22.—Morphometrics and meristics of *Creagrutus gyrospilus*, new species: (A) holotype of *C. gyrospilus*, INHS 69479; (B) paratypes of *C. gyrospilus* (n=40); and (C) nontypes of *C. gyrospilus* (n=3). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B	C
		Morphometrics	
Standard length	47.7	44.4–62.3	46.3–60.0
1. Snout to anal-fin origin	59.7	59.5–64.8	61.2–65.0
2. Snout to pelvic-fin insertion	44.0	44.5–48.3	44.6–49.9
3. Snout to pectoral-fin insertion	24.8	22.8–24.8	24.1–27.3
4. Snout to dorsal-fin origin	47.5	47.6–51.3	49.1–52.8
5. Dorsal-fin origin to hypural joint	57.9	54.3–57.7	52.3–56.4
6. Dorsal-fin origin to anal-fin origin	31.0	29.6–33.0	32.0–32.6
7. Dorsal-fin origin to pelvic-fin insertion	28.1	26.9–30.4	30.2–31.2
8. Dorsal-fin origin to pectoral-fin insertion	32.8	33.1–35.9	34.9–36.0
9. Caudal peduncle depth	12.6	11.3–13.0	12.6–13.2
10. Pectoral-fin length	20.0	18.2–22.2	20.4–21.9
11. Pelvic-fin length	15.6	13.9–16.9	15.8–16.1
12. Dorsal-fin length	23.9	19.4–25.4	21.9–23.5
13. Anal-fin length	18.9	16.5–20.5	18.1–18.4
14. Head length	25.8	24.1–26.6	25.2–28.5
15. Postorbital head length	45.0	45.7–50.6	45.7–50.1
16. Snout length	26.2	26.9–32.3	27.2–29.9
17. Bony orbital diameter	32.7	25.8–31.7	28.6–31.7
18. Interorbital width	30.4	30.2–34.7	29.1–31.3
		Meristics	
Lateral line scales	36	36–39	38
Scale rows between dorsal-fin origin and lateral line	4	4–5[1]	4
Scale rows between anal-fin origin and lateral line	3	3	3
Predorsal median scales	9	10–12	10–11
Branched dorsal-fin rays	8	8	8–9[2]
Branched anal-fin rays	10	9–11[3]	10–11
Branched pelvic-fin rays	6[4]	6–7[4]	7
Pectoral-fin rays	11	11–13[5]	11–12
Vertebrae	35	35–37	36–37

[1]Five scales between dorsal-fin origin and lateral line present in only 1 paratype.
[2]Nine branched dorsal-fin rays present in only 1 nontype specimen.
[3]Nine branched anal-fin rays present in only 1 paratype.
[4]Medial pelvic-fin ray unbranched when 6 branched rays present, branched when 7 branched rays present.
[5]Thirteen pectoral-fin rays present in only 1 paratype.

HL), the interorbital width (29.1%–34.7% of HL), the contact, or near contact, of the ventral margin of the third infraorbital and the horizontal limb of the preopercle, the lack of a distinct spot of dark pigmentation at the base of the middle caudal-fin rays, the vertically rotund humeral mark without a secondary, dorsal patch of pigmentation, the absence of a distinct patch of pigmentation on the dorsal fin, and the lack of a series of dark spots along the midlateral surface of the body distinguishes *Creagrutus gyrospilus* within the clade formed by *Creagrutus* and *Piabina*.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus gyrospilus* in Table 22. Body relatively deep and compressed. Greatest body depth within one or two scale rows anterior of base of anteriormost dorsal-fin ray. Dorsal profile of head distinctly convex from margin of upper lip to vertical through posterior margin of anterior nares; straight from that point to posterior tip of supraoccipital spine; smoothly convex from that point posteriorly to anterior of dorsal-fin base, or with inflection point or slight hump two to three scale rows posterior of supraoccipital. Profile of body straight and slightly inclined along dorsal-fin base, straight to slightly convex from base of posterior dorsal-fin ray to anterior procurrent caudal-fin ray, with slight dorsal inflection comprising sheath scales at adipose-fin base. Ventral profile of head with broadly rounded obtuse angle approximately midway between margin of lower lip and posterior extremity of dentary, slightly convex from that point to isthmus. Ventral profile of body slightly curved from isthmus to pelvic-fin insertion; then concave from anteriormost anal-fin ray to anterior ventral procurrent caudal-fin ray.

Anterior profile of head rounded in lateral view. Upper jaw longer than, and overhanging, lower jaw by distance about equal to up to one-half of orbital diameter. Anterior portion of snout relatively soft and fleshy, with concentration of soft tissues; minute papillae concentrated on snout and upper lip, continuing into mouth on fleshy flaps and plicae extending be-

FIGURE 45.—*Creagrutus gyrospilus*, new species, holotype, INHS 69479, 47.7 mm SL; Venezuela, Portuguesa, Río Saguaz, Río Guanare-Apure drainage, bridge near park on road to Chabasquén (=Paraíso de Chabasquén; 9°23′30″N, 70°00′30″W).

tween outer and medial premaxillary teeth. Lower jaw distinctly fleshy anteriorly, with concentrated papillae. Inner surfaces of lower lip convolute and papillose, with fleshy flaps extending into mouth. Concentrations of papillae also present over lower jaw, isthmus, and cheek.

Elements of infraorbital series somewhat reduced, with ventral margin of third infraorbital usually contacting, or nearly contacting, ventral limb of preopercle. Posterior and posteroventral margins of third infraorbital separated from vertical limb of preopercle by gap equal to at most one-half width of third infraorbital; posterior and posteroventral margin of infraorbital series describing broad arc approximately concentric with margin of orbit.

Premaxillary teeth in three distinct series: primary series arched, with 6 weakly tricuspidate teeth, without pronounced gap between first and second of series, lateral cusps of anterior 4 teeth usually indistinct; triangular cluster of 3 large tricuspidate teeth, posterior 2 teeth largest and with most highly developed cusps; and single outer weakly tricuspidate tooth positioned approximately lateral to fourth tooth in primary premaxillary series. Maxilla usually with 3 or 4, rarely 2, tricuspidate teeth. Dentary with 5 or 6 unicuspidate or tricuspidate teeth; anterior two teeth largest and with most highly developed secondary cusps, third tooth smaller than first two teeth, with cusps less prominent; 2 or 3 posteriormost teeth relatively small, with weakly developed cusps.

Dorsal-fin rays ii,8 in most individuals, ii,9 in one nontype specimen. Dorsal-fin origin at, or slightly posterior of, vertical through pelvic-fin origin. Distal margin of dorsal fin slightly concave as result of elongation of second unbranched ray, anterior three branched rays, and posterior two branched rays. Anal-fin rays ii-iii,9–11; 9 branched rays less common. Anal-fin hooks, when present, occurring on anteriormost 2 or 3 branched rays. Distal margin of anal fin slightly sigmoidal, with second unbranched and anterior 3 branched rays forming variously developed slightly elongate lobe, outline of posterior 5 or 6 branched rays concave. Pectoral-fin rays i,10–12, 12 branched rays less common. Pectoral fin short in some individuals, reaching to within two scale rows of pelvic-fin origin, longer in presumptive males (as indicated by presence of pelvic- and anal-fin ray hooks) and reaching to, or nearly reaching, pelvic-fin base. Pelvic-fin rays i,6,i or i,7. Pelvic-fin hooks, when present, located on medial surfaces of segmented and unsegmented portions of main shaft and medial and branches of all rays medial of the lateral unbranched element; additional weak hooks present on medial surfaces of lateral secondary branches of medial 3 or 4 rays. Tip of pelvic fin not reaching anal-fin origin in males (as indicated by presence of pelvic- and anal-fin ray hooks); in other specimens tip of pelvic fin reaching within 1 or 2 scale rows of that point. Scales on posterior margin of body generally smoothly rounded.

Gill rakers 5–8 + 9–11.

COLORATION IN ALCOHOL.—Overall pigmentation dusky, with well-developed dark humeral spot and lateral stripe; ground color light brown, with chromatophores ranging from dark brown over much of body to nearly black in areas of higher concentration. Dorsal surface of head with high concentration of small, dark brown, punctate chromatophores, chromatophores most concentrated over snout and medial portions of upper lip, including vertical crescent-shaped area immediately anterior of anterior nares. Pigmentation continuing posteriorly across interorbital area, covering frontal fontanel. Patch of scattered, dark chromatophores extending laterally from snout along dorsal portion of maxilla. Dorsal surface of parietal portions of cranium and area immediately dorsal of eye pigmented with scattered, relatively large, dark brown, stellate chromatophores. Band of small, dark brown chromatophores extending from immediately lateral of nares posteroventrally and continuing around ventral and posterior margins of orbit. Dark, stellate chromatophores scattered over dorsal half of

opercle in region posterior to orbit. Lower lip and ventrolateral surface of head unpigmented.

Body pigmentation most concentrated in region dorsal of lateral line; pigmentation in form of broad vertical crescents in association with anteriormost exposed portion of each scale. Scattered, very dark chromatophores present along dorsal midline, especially well developed along anterior half of predorsal area, in region immediately lateral of dorsal-fin base, and along middorsal area between dorsal and adipose fins. Humeral mark rounded to somewhat vertically ovoid blotch located in lateral line scale row and scale row immediately dorsal to it. Pigmentation on lateral surface of body ventral to lateral line, other than for that associated with humeral spot, mostly restricted to small, dark chromatophores delineating hypaxial myosepta immediately dorsal of anal-fin base. Midlateral body stripe relatively diffuse anteriorly, becoming denser and somewhat wider approximately at vertical through dorsal-fin origin and extending well ventral of lateral line and posteriorly onto caudal peduncle. Intensity of midlateral stripe pigmentation greatest in region from directly ventral of dorsal fin posteriorly to area overlying hypurals.

Dorsal-fin membranes with small number of moderately dark chromatophores associated with distal one-half of second unbranched and anterior 5 or 6 branched rays; basal portions of shafts of all, or nearly all, fin rays with scattered, dark chromatophores. Anal fin mostly unpigmented, with dark chromatophores located along bases of each ray along approximately anterior one-half of its length. Small, nearly black chromatophores scattered over distal portions of anal-fin ray membranes. Caudal-fin rays delineated by small, dark chromatophores, with greatest concentrations along dorsalmost rays and over much of ventral lobe. Darkest caudal-fin pigmentation confined to proximal portions of central 4 branched rays, appearing as small, interrupted, slightly horizontally elongate dark spot. Pectoral-fin pigmentation confined to dark line of chromatophores along lateral unbranched ray and in association with up to four adjacent branched rays. Pelvic fin hyaline.

ETYMOLOGY.—The specific name, *gyrospilus,* from the Latin gyro, meaning circular, and spilus, meaning spot, in reference to the form of the humeral spot in the species.

ECOLOGY.—The type locality (INHS 69479, INHS 51282, and USNM 359486) and the locality from which the nontype specimens (INHS 61329) originated were both clear rocky streams with considerable current.

DISTRIBUTION.—*Creagrutus gyrospilus* is known only from two localities in the western portions of the Río Orinoco basin (Figure 43, solid stars).

COMPARISONS.—*Creagrutus gyrospilus* is most similar to the sympatric *C. taphorni* with respect to body shape, meristic character values, and the relative development of the infraorbital series. The two species differ, however, in the form of the humeral mark (compare Figures 45 and 88). Other similar species, occurring in other drainage systems, include *C. crenatus* and *C. lassoi,* which have vertically elongate humeral marks contrary to the rounded mark in *C. gyrospilus.* These species also differ in various meristic and morphometric features.

REMARKS.—The species, which we herein recognize as *Creagrutus gyrospilus,* represents a component of the variation reported for *C.* cf. *beni* by Taphorn (1992:18, 167), who noted that the humeral mark is usually a rounded blotch, but in some specimens extended above and below the region of the lateral line. The results of our studies indicated that the material identified as *Creagrutus* cf. *beni* by Taphorn (1992) included both *C. taphorni,* which has a vertically elongate humeral mark, and *C. gyrospilus,* which has a noticeably rounded humeral mark.

MATERIAL EXAMINED.—77 specimens (44, 44.4–62.3).

HOLOTYPE.—VENEZUELA. *Portuguesa:* Río Saguaz, Río Guanare-Apure drainage, bridge near park on road to Chabasquén (=Paraíso de Chabasquén; 9°23′30″N, 70°00′30″W), collected by D.C. Taphorn et al., 16 Jan 1986, INHS 69479, 1 (47.7; male).

PARATYPES.—40 specimens (40, 44.4–62.3).

VENEZUELA. *Portuguesa:* Río Saguaz, Río Guanare-Apure drainage, bridge near park on road to Chabasquen (=Paraíso de Chabasquén; 9°23′30″N, 70°00′30″W), collected with holotype, INHS 51282, 32 (48.6–62.3); USNM 359486, 8 (44.4–61.6).

NONTYPE SPECIMENS.—36 specimens (3, 46.3–60.0).

VENEZUELA. *Barinas:* Tributary of Río Santo Domingo, Río Apure drainage, 10 km NW Barinitas (latter locality at 8°45′N, 70°45′W), INHS 61329, 6 (3, 46.3–60.0). *Lara:* Río Claro, in town of Río Claro (9°55′30″N, 69°21′20″W), MCNG 13392, 30.

Creagrutus holmi, new species

FIGURES 43, 46, TABLE 23

Creagrutus beni [not of Eigenmann, 1911].—Pearson, 1937a:92 [misidentification] [Peru (Departmento Cajamarca): Balsas, Tingo de Pauca on Río Marañon, Paipay on Río Crisnejas].

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 3 to 5 teeth on the maxilla, 6, very rarely 5, teeth in the primary tooth row of the premaxilla, 5 dentary teeth, 37 to 40 lateral line scales without a lamellar process over each pore, 9 to 11 predorsal median scales, 4 scale rows between the dorsal-fin origin and the lateral line, 36 to 38 vertebrae, 9 to 11 branched anal-fin rays, 2 post-anal median scales to the anal-fin origin, 6 to 8 gill rakers on the upper limb of the first gill arch, 9 to 12 gill rakers on the lower limb of the first gill arch, the distance from the dorsal-fin origin to the anal-fin origin (32.2%–38.5% of SL), the postorbital head length (43.9%–50.0% of HL), the interorbital width (28.6%–34.5% of HL), the well-developed third infraorbital closely approaching or contacting the horizontal limb of the preopercle in larger individuals, the lack of a series of dark

TABLE 23.—Morphometrics and meristics of *Creagrutus holmi*, new species: (A) holotype of *C. holmi*, MUSM 5670; and (B) paratypes of *C. holmi* (n=38). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	81.9	45.1–92.0
1. Snout to anal-fin origin	66.4	62.6–69.4
2. Snout to pelvic-fin insertion	48.0	45.0–52.1
3. Snout to pectoral-fin insertion	23.7	22.2–26.5
4. Snout to dorsal-fin origin	47.9	45.5–50.4
5. Dorsal-fin origin to hypural joint	56.5	54.1–60.1
6. Dorsal-fin origin to anal-fin origin	34.7	32.2–38.5
7. Dorsal-fin origin to pelvic-fin insertion	35.3	28.1–35.4
8. Dorsal-fin origin to pectoral-fin insertion	34.8	32.5–36.4
9. Caudal peduncle depth	11.7	11.5–13.7
10. Pectoral-fin length	20.0	18.5–23.4
11. Pelvic-fin length	15.1	14.9–20.0
12. Dorsal-fin length	20.7	20.6–24.5
13. Anal-fin length	17.2	17.0–20.7
14. Head length	25.3	24.0–28.3
15. Postorbital head length	46.9	43.9–50.0
16. Snout length	28.5	24.6–30.5
17. Bony orbital diameter	29.3	29.2–34.1
18. Interorbital width	30.9	28.6–34.5
	Meristics	
Lateral line scales	39	37–40
Scale rows between dorsal-fin origin and lateral line	4	4[1]
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	10	9–11
Branched dorsal-fin rays	8	8
Branched anal-fin rays	10	9–11
Branched pelvic-fin rays	6	6[2]
Pectoral-fin rays	13	12–14
Vertebrae	37	36–38

[1]Five scales between dorsal-fin origin and lateral line present in only 1 nontype specimen.

[2]Five branched rays present in 1 nontype specimen and 7 branched rays present in 3 nontype specimens.

midlateral spots on the body, the possession of a diffuse, vertically elongate rotund humeral spot, the lack of a distinct dark spot at the base of the middle caudal-fin rays, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus holmi* within the clade composed of *Creagrutus* and *Piabina*.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus holmi* in Table 23. Head and body robust, body proportionally more robust in larger individuals of some populations and in females with well-developed ovaries. Greatest body depth at dorsal-fin origin in most specimens, shifted slightly anterior of that point in ripe females. Dorsal profile of head convex from tip of snout to vertical through posterior nostril, straight or slightly convex anteriorly from that point to tip of supraoccipital spine. Interorbital region distinctly convex. Dorsal profile of body gently curved, with anterior portion continuing alignment of profile of rear portion of head in specimens up to approximately 45 mm SL, more convex with distinct change in alignment relative to that of head in many larger individuals. Dorsal surface of body with obtuse median ridge between tip of supraoccipital spine and dorsal-fin origin. Ventral profile of head with obtuse, but distinct, angle at anteroventral corner of dentary, profile ranging from nearly straight to gently convex from that point to isthmus. Ventral profile of body ranging from slightly to distinctly convex, latter condition typical of ripe females. Prepelvic region of body obtusely flattened transversely.

Head obtusely rounded in both lateral and dorsal views. Upper jaw longer than, and overhanging, lower jaw. Snout slightly fleshy anteroventrally with scattered papillae anteriorly. Upper lip fleshy, with papillae along anterior and ventral margins; papillae continue onto plicae extending between outer and medial premaxillary teeth. Lower lip moderately fleshy with papillae moderately concentrated along dorsal surface and with scattered papillae anteroventrally.

Infraorbital series moderately developed overall. Third infraorbital well developed; ventral margin falling distinctly short of horizontal limb of preopercle in specimens of up to approximately 50 mm SL, but approaching, or in contact with, that bone in larger individuals. Posterior margins of third through fifth infraorbitals falling short of vertical limb of preopercle.

Premaxillary dentition in three series: primary series with 6, very rarely 5, teeth arranged in curved or very slightly sigmoid arch without pronounced gap between first and second tooth of series but with median tooth distinctly separated from its contralateral tooth; triangular cluster of 3 somewhat larger teeth; and single tooth of form similar to that of primary series lying lateral to fourth tooth, or to space between third and fourth teeth, of primary premaxillary series. Maxilla with 3 to 5 tricuspidate teeth. Dentary with 5 tricuspidate teeth; first and second teeth distinctly larger than others and subequal, somewhat less than twice height of third tooth; fourth and fifth teeth distinctly smaller than anterior teeth and compressed.

Dorsal-fin rays ii,8 in all specimens. Dorsal-fin origin approximately at vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin ranging from straight to very slightly concave. Anal-fin rays ii,9–11, rarely iii,10. Profile of distal margin of anal fin straight to very slightly concave with anterior rays forming barely obvious lobe. Anal-fin hooks present in relatively few of examined specimens, perhaps reflecting pronounced seasonality in their presence in mature males; hooks, when present, limited to anterior 2 or 3 branched anal-fin rays. Pectoral-fin rays i,11–13. Tip of pectoral fin extending posteriorly slightly beyond three-fourths of distance to pelvic-fin insertion. Pelvic-fin rays most commonly i,6,i, but one specimen with i,5,i and another with i,7. Tip of pelvic fin extending posteriorly approximately 1 scale short of anus. Pelvic-fin hooks present in relatively few of the examined specimens, perhaps reflecting pronounced seasonality in their presence in mature males; hooks, when present, located on all branched pelvic-fin rays.

Gill rakers 6–8 + 9–12.

COLORATION IN LIFE.—(Descriptions based on slides of recently captured specimens provided by E. Holm, ROM). Ground coloration ranging from tan to purplish gray. Guanine covering scales more obvious over midlateral body stripe in smaller specimens. Midlateral body stripe obvious, but more pronounced in specimens with darker overall pigmentation. Humeral mark variably obvious, most distinct in some specimens with lighter overall head and body coloration. Caudal fin with reddish tint on rays in some specimens. Anterior rays of anal fin sometimes white.

COLORATION IN ALCOHOL.—Ground coloration of specimens light tan. Dorsal surface of head with dense field of small, dark chromatophores extending anteriorly onto snout, upper lip, and region anterior to orbit. No indication of deep-lying dark chromatophores overlying brain. Variably denser concentration of dark chromatophores anterior to nostrils forming crescent-shaped patch. Posterior margin of maxilla and adjoining region of snout with somewhat increased concentration of dark chromatophores. Chromatophore concentration somewhat greater anteroventral of orbit, but without discrete pattern of chromatophores surrounding ventral and posterior margins of orbit as occurs in some congeners. Scattered, dark, surface chromatophores located ventral and posterior of orbit. Variably present denser concentration of dark chromatophores on middle of opercle, with scattered chromatophores on dorsal portion of opercle.

Scales of dorsolateral portion of body with field of dark chromatophores on basal portion of exposed scales and along distal margins, with chromatophore fields on each scale separated by hyaline region. Midlateral body stripe formed of deep-lying chromatophores extending from slightly posterior of humeral mark to posterior portion of caudal peduncle. Humeral mark vertically elongate, but variable in both intensity and form. Mark ranges from barely obvious, vertically elongate patch of chromatophores merging into surrounding pigmentation to obvious but diffuse dark patch. Some specimens with central region of humeral mark distinctly darker. Darker central region of mark in such specimens with less pronounced fields of chromatophores extending from dorsal and ventral margins. Dorsal portion of humeral mark arched somewhat anteriorly, with anterodorsal section forming distinct anterior process. Ventral portion of mark typically ventrally tapering.

Dorsal fin with rays outlined by small dark chromatophores and with fields of chromatophores over distal one-half of fin membranes. Anal fin with basal one-half to three-fourths of fin rays outlined by dark chromatophores. Caudal fin somewhat dusky. Pectoral and pelvic fins hyaline or with few scattered chromatophores.

ETYMOLOGY.—The species name, *holmi,* is in honor of Erling Holm of the Royal Ontario Museum, Toronto, who collected many of the specimens that served as the basis for the species description along with numerous other series of *Creagrutus* specimens valuable to this study and who has been of great assistance to the authors in this and other studies.

ECOLOGY.—The collection locality for the majority of the paratypes of *Creagrutus holmi* (MUSM 8866, ROM 55331, USNM 341369) was at an elevation of 850 m in a rapidly flowing (1 m/sec), 5 m wide, clear water stream over a substrate composed predominantly of boulders (30%), rubble (30%), and gravel (30%), with the remainder sand (10%). The habitat was approximately 90% riffles and the remainder was pools. The canopy over the water was 80% partially open and the rest was totally open. One other sample (ROM 52247) came from generally comparable habitats, although one lot (ROM 52248) came from an area with silt bottoms and only 10% riffles. *Creagrutus holmi* appears to be limited to upland regions with the reported elevations ranging between 800 and 1158 m.

Stomach content analysis of four specimens prepared for clearing and staining in this study showed that the species had been feeding on seeds, larval insects, and in one case on a small characid.

DISTRIBUTION.—*Creagrutus holmi* is limited to the Río Marañon basin above Pongo de Manseriche, in northeastern Peru (Figure 43).

COMPARISONS.—This is the only *Creagrutus* species known from the Río Marañon basin, and it achieves some of the highest elevations of any member of the genus.

GEOGRAPHIC VARIATION.—Although this species has a relatively limited distributional range, there is a notable, but continuous, degree of variation between different population samples. Some specimens collected in the Río Utcubamba basin are somewhat deeper bodied than those from some other localities, with, however, a notable degree of overlap with the range of values for this feature in other population samples. The humeral mark also shows notable variation in intensity among examined specimens, ranging from being effectively absent to very distinct. To a degree, this variation is a function of the size of the specimens, but the features demonstrate a considerable range within and between population samples. Despite this variation, we did not discover any discrete differences that would justify the recognition of more than one species within the material that is herein identified as *Creagrutus holmi.*

REMARKS.—Pearson (1937a:92) reported *Creagrutus beni* from several locations in the upper Río Marañon valley in the southern portions of the Department of Cajamarca, Peru. Examination of material from two of the three localities (Balsas, USNM 167816, formerly IU 17600; Tingo de Pauca, CAS 69292, formerly IU 17601) has shown that it is *C. holmi* rather than *C. beni. Creagrutus beni,* as delimited in this study, is endemic to northern Bolivia and southeastern Peru, a region distant from the known distribution of *C. holmi.* Although specimens from Paipay, the third locality in the upper Río Marañon valley cited by Pearson (1937a:92), have not been examined, *C. holmi* is the only *Creagrutus* species discovered during this study in that river system. Thus, all of Pearson's (1937a) records of *C. beni* are considered herein to refer to *C. holmi.*

FIGURE 46.—*Creagrutus holmi*, new species, holotype, MUSM 5670, 81.9 mm SL; Peru, Amazonas, Provincia Utcubamba, Bagua Grande, San Antonio, Quebrada Jaimito (approximately 5°47′S, 78°23′W).

MATERIAL EXAMINED.—315 specimens (97, 39.8–92.0).

HOLOTYPE.—PERU. *Amazonas:* Provincia Utcubamba, Bagua Grande, San Antonio, Quebrada Jaimito (approximately 5°47′S, 78°23′W), collected by P. Baltazar, 14 Apr 1988, MUSM 5670, 1 (81.9).

PARATYPES.—38 specimens (38, 45.1–92.0).

PERU. *Amazonas:* Provincia Utcubamba, Bagua Grande, San Antonio, Quebrada Jaimito (approximately 5°47′S, 78°23′W), collected with holotype, MUSM 8865, 7 (45.1–59.5); USNM 341368, 6 (47.2–76.5; 1 specimen cleared and counterstained for cartilage and bone). *Cajamarca:* Tributary to Río Huancabamba, approximately 74 km W of road going N to Jaen, between Pucara and Guabel (approximately 5°56′S, 79°15′W), collected by E. Holm and J. Patalas, 8 Jul 1986, MUSM 8866, 5 (51.3–80.7); USNM 341369, 5 (53.5–92.0); ROM 55331, 5 (45.3–91.7); ROM 72379, 10 (61.5–85.8).

NONTYPE SPECIMENS.—276 specimens (58, 39.8–91.7).

PERU. *Amazonas:* Quebrada Pusac, Huancabamba, approximately 16 km by road upstream from Balsas (approximately 6°53′S, 78°01′W), ROM 52247, 10 (39.8–85.2). Balsas (6°50′S, 78°01′W), at 3500 ft (=1067 m), USNM 167816, 7 (41.5–64.5; formerly IU 17600, in part; 3 specimens cleared and stained for bone). Tingo de Pauca, at mouth of Río Crisnejas into Río Marañon (7°21′S, 77°50′W), at approximately 3800 ft (=1158 m), CAS 69292, 12 (formerly IU 17601). Tributary of Río Marañon, at Tsutshunha, near Tutumbertos, downstream from Aramango, at Aguarani Indian Village, ROM 55328, 17 (10, 46.4–66.3). Río Santiago basin, 1 km from Caterpiza (latter locality at approximately 3°55′S, 77°42′W), LACM 41991-7, 6 (63.6–88.7). Río Santiago basin, 3 km from Caterpiza (latter locality approximately 3°55′S, 77°42′W), LACM 41993-13, 5 (44.5–76.8). Quebrada Pastazillio (not located), LACM 39337-9, 7 (40.9–67.0). Río Cenepa, vicinity of Huampani (4°28′S, 78°10′W), LACM 36357-53, 2 (1, 74.0). Río Cenepa basin, Río Huampani, at Huampani (approximately 4°28′S, 78°10′W), LACM 39645-5, 5 (64.9–65.8). Río Cenepa basin, Chigkan entse (=Quebrada Chigkan; approximately 4°28′S, 78°11′W), LACM 39681-2, 1 (80.7). Río Marañon, few km upstream from Puerto Balsas (6°51′S, 78°02′W), ROM 55326, 3 (1, 59.0). Río Marañon, 14 km upstream from Balsas (6°57′S, 78°01′W), ROM 52248, 17. *Cajamarca:* Tributary to Río Huancabamba, approximately 74 km W of road going N to Jaen, between Pucara and Guabel (approximately 5°56′S, 79°15′W), ROM 55331, 5 (45.3–91.7), ROM 52252, 179.

Creagrutus hysginus Harold, Vari, Machado-Allison, and Provenzano, 1994

FIGURES 43, 47, TABLE 24

Creagrutus beni [not of Eigenmann, 1911].—Fowler, 1931:408 [misidentification] [Venezuela (Sucre) Yarapa River].—Beebe, 1945:84 [Venezuela, Monagas, Río San Juan basin, south of Caripito; survival in drying stream; life coloration].—Marrero and Machado-Allison, 1990:66 [in part, citation of Fowler, 1931:408 in synonymy].—Taphorn et al., 1997:71 [cited for Venezuela].

Creagrutus hysginus Harold et al., 1994:975, fig.1 [type locality: Venezuela, Estado Sucre, Río Güiria, near La Toma].

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 4 or 5 teeth on the maxilla, 6 teeth in the primary series of the premaxilla, 6 dentary teeth, 35 to 38 lateral line scales without a lamellar process over each pore, 9 to 11 predorsal median scales, 5 scale rows between the dorsal-fin origin and the lateral line, 36 or 37 vertebrae, 9 or 10 branched anal-fin rays, 2 post-anal median scales to the anal-fin origin, the distance from the dorsal-fin origin to the pelvic-fin insertion (27.5%–33.1% of SL), the distance from the dorsal-fin origin to the pectoral-fin insertion (32.1%–36.8% of SL), the caudal peduncle depth (10.7%–12.9% of SL), the head length (27.3%–30.8% of SL), the length of the postorbital portion of head (44.1%–52.6% of HL), the snout length (21.1%–28.8% of HL), the moderately developed third infraorbital distinctly sep-

TABLE 24.—Morphometrics and meristics of *Creagrutus hysginus*: (A) holotype of *C. hysginus*, MBUCV V-20310; and (B) all other specimens of *C. hysginus* from which counts and measurements were taken (n=28). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	44.9	30.3–55.6
1. Snout to anal-fin origin	66.4	61.7–67.5
2. Snout to pelvic-fin insertion	50.9	46.9–51.6
3. Snout to pectoral-fin insertion	27.7	26.7–31.9
4. Snout to dorsal-fin origin	51.2	48.1–54.6
5. Dorsal-fin origin to hypural joint	54.3	51.4–56.9
6. Dorsal-fin origin to anal-fin origin	33.2	28.3–33.4
7. Dorsal-fin origin to pelvic-fin insertion	31.1	27.5–33.1
8. Dorsal-fin origin to pectoral-fin insertion	36.0	32.1–36.8
9. Caudal peduncle depth	11.7	10.7–12.9
10. Pectoral-fin length	19.5	18.1–22.5
11. Pelvic-fin length	16.2	15.1–17.0
12. Dorsal-fin length	22.5	19.8–24.5
13. Anal-fin length	19.2	14.8–20.4
14. Head length	29.9	27.3–30.8
15. Postorbital head length	49.0	44.1–52.6
16. Snout length	25.5	21.1–28.8
17. Bony orbital diameter	32.5	28.5–36.1
18. Interorbital width	28.2	25.7–35.0
	Meristics	
Lateral line scales	37	35–38
Scale rows between dorsal-fin origin and lateral line	5	5
Scale rows between anal-fin origin and lateral line	3	3–4
Predorsal median scales	10	9–11
Branched dorsal-fin rays	8	8
Branched anal-fin rays	10	9–10
Branched pelvic-fin rays	7	7
Pectoral-fin rays	12	11–12
Vertebrae	36	36–37

arated from the horizontal limb of the preopercle, the lack of a series of dark midlateral spots on the body, the absence of a distinct spot of dark pigmentation on the basal portions of the middle caudal-fin rays, the rotund to slightly vertically elongate humeral mark, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus hysginus* within the clade composed of *Creagrutus* and *Piabina*.

The brilliant red life coloration of the adipose fin of *C. hysginus* is not known to occur in any of the few other *Creagrutus* species for which we have life coloration information. Further life coloration information is necessary to determine whether such adipose-fin pigmentation is unique to, and thus an autapomorphy for, *C. hysginus*.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus hysginus* in Table 24. Body slightly rotund abdominally in profile compared with most species in the genus. Maximum body depth approximately one-half of distance between insertions of pectoral and pelvic fins. Anterior profile of snout and dorsal profile of head meeting in rounded obtuse angle near vertical through point midway between nares. Dorsal profile of head posterior to that line inclined and straight to slightly convex. Predorsal profile of body with notable change in alignment relative to that of head, asymmetrically convex, with convexity most pronounced in anterior one-third of region but with some specimens (e.g., holotype, Figure 47) having pronounced curvature immediately posterior to occiput; presence of pronounced curvature not related to sex. Dorsal profile of body straight between dorsal-fin origin and caudal peduncle. Ventral profile of head and body slightly convex from anterior margin of lower jaw to pelvic-fin origin, or with ventral surface of head and abdomen each with distinctly rounded profile. Rounded obtuse angle delimiting anteroventral angle of dentary, angle variably apparent among specimens depending on state of preservation.

Upper jaw longer than, and overhanging, lower jaw. Anterior surface of snout fleshy, with numerous minute papillae over surface; greatest concentration of papillae on upper lip, margin of upper jaw, and in mouth on fleshy flaps and plicae extending between outer and medial premaxillary teeth. Lower lip with thick, fleshy anterior region and numerous papillae on anterodorsal surface.

Infraorbital series moderately well developed, covering approximately two-thirds of cheek. Ventral margin of third infraorbital separated from horizontal limb of preopercle by space equal to approximately one-half width of that infraorbital. Curvature of posteroventral margin of third infraorbital approximately concentric with margin of orbit. Third through fifth infraorbitals distinctly separated posteriorly from vertical limb of preopercle.

Premaxillary dentition in three series: primary series straight, consisting of 6 tricuspidate teeth with rounded to well-developed cusps, without pronounced gap between first and second tooth of series; triangular cluster of 3 larger teeth with medialmost tooth asymmetrical and nearly contacting contralateral tooth of other side; and single tooth similar in form to those of primary premaxillary row, occurring lateral to fourth tooth of primary series. Maxilla with 4 or 5 tricuspidate teeth. Dentary 6 tricuspidate teeth; anterior 3 teeth largest, second tooth about one-third higher than first tooth and nearly twice as high as third tooth; following teeth successively shorter and compressed.

Dorsal-fin rays ii,8. Dorsal-fin origin at vertical through pelvic-fin origin. Profile of distal margin of dorsal fin with slight concavity. Anal-fin rays ii,9–10 or iii,9–10. Profile of distal margin of anal fin nearly straight, with anterior branched rays slightly elongate. Single, bilaterally paired hooks present on 2 or 3 anterior branched anal-fin rays of mature males (hooks observed on only 3 of 20 examined specimens). Mature males with hooks restricted to posterolateral surface of main shaft and posterior, secondary branch of each ray. Pectoral-fin rays i,11–12. Tip of pectoral fin extending posteriorly to pelvic-fin base in mature males as shown by presence of anal- and pelvic-fin hooks; other specimens with pectoral fin extending posteriorly approximately three-fourths of distance between pecto-

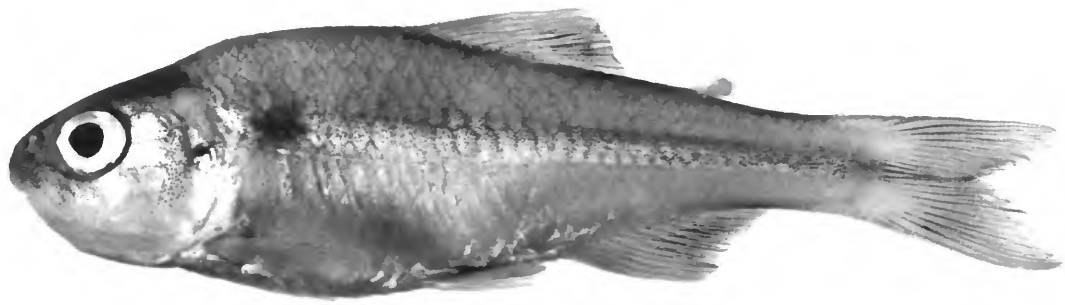

FIGURE 47.—*Creagrutus hysginus*, holotype, MBUCV V-20310, 44.9 mm SL; Venezuela, Sucre, Río Güiria, near La Toga.

ral- and pelvic-fin insertions. Pelvic-fin rays i,7. Tip of pelvic fin approaching or, especially in well-developed mature males, extending to anal-fin origin; with distal portion turned medially in some individuals, giving fin slightly cupped shape. Pelvic-fin hooks in mature males, when present, occurring on all portions of all branched rays, except the smallest, distal branches.

Gill rakers 5–7 + 8–10.

COLORATION IN LIFE.—Adipose fin brilliant red. Less intense orange-red pigmentation present in broad horizontal band through central part of dorsal fin and distal portion of outer caudal-fin rays. Lateral 2 or 3 rays of pelvic and pectoral fins pale orange. Anal fin hyaline. Dorsal surface of eye with bright red patch overlying reflective guanine pigment. Based on the collecting locality, it is likely that the specimens cited as *Creagrutus beni* by Beebe (1945:84) are *C. hysginus*. Beebe reported that the species was "Greenish-yellow with silvery sheen, two more or less blue body bands; a very broad oxidized silver lateral band ... much of the dorsal, anal and caudal fins is scarlet, as is the iris." Nocturnal coloring was noted by Beebe as "all body pigment bands and most of the red color disappear at night."

COLORATION IN ALCOHOL.—Dorsal surface of head with light brown, shallow chromatophores and dark brown to black, deep chromatophores. Deep chromatophores small, punctate, lining interior surfaces of frontal, obscured in midline by connective tissue in fontanel. Shallow chromatophores small to large, stellate, present over entire dorsal surface of head, most concentrated on medial one-half of upper jaw and snout, continuing posterolaterally from snout to nares and posterodorsally to point above center of orbit and overlying fontanel. Small crescent of dark pigmentation often present anterior to nares in other *Creagrutus* species present and continuous with snout pigmentation. Band of scattered, light and dark chromatophores extending from pigmentation on snout and upper jaw posteriorly across cheek around margin of orbit and almost to distal margin of infraorbital bones, and joining body of scattered chromatophores of various sizes posterior to orbit. Scattered, large, brown, stellate chromatophores arranged in dorsoventrally elongate band on cheek between infraorbitals and preopercle.

Scales of dorsal portion of body with small dark chromatophores concentrated in area medial to scale center and with larger stellate, lighter chromatophores arranged in arc on lateral surface of posterior field. Overall appearance of dorsal pigmentation faintly reticulate, but some specimens having irregularly arranged scales with very darkly pigmented central fields. Small black chromatophores along dorsal midline of body and along margin of dorsal-fin base, forming longitudinal stripe from occiput to caudal peduncle. Humeral mark usually appearing as irregular blotch or rounded mark immediately dorsal to lateral line, but occasionally extending anterodorsally and diffusely, giving overall appearance of inverted comma. Diffuse midlateral stripe present, extending posteriorly from area behind humeral mark onto, and slightly expanding on, caudal-fin base. Deep-lying pigmentation of midlateral stripe mostly obscured by overlying guanine in examined specimens. Stripe most sharply defined ventrally and posteriorly. Region of body between midlateral stripe and anal-fin base with very small, dark chromatophores delineating myosepta. Anal-fin base only diffusely pigmented, without dark triangular pigmentation patches present in some congeners.

Small, dark chromatophores present on caudal-fin membranes; greatest concentration of chromatophores in association with central rays, appearing as disjunct extension of midlateral stripe, and on dorsal and ventral branched rays and procurrent rays. In juveniles (approximately 20–22 mm SL), pigmentation of middle caudal-fin rays concentrated basally and appearing as small spot. Ventral lobe of caudal fin much more densely pigmented overall than dorsal lobe. Small dark chromatophores on distal one-half of anal-fin membranes, some specimens showing great enlargement of these chromatophores, giving appearance of dark spot in central portion of fin. Diffuse dark pigmentation in narrow bands immediately adja-

cent to anterior surfaces of basal, unsegmented portions of rays and mainly restricted to narrow bands immediately adjacent to all portions of fin rays. Distal portions of unbranched and anterior two branched anal-fin rays unpigmented. Dark chromatophores of various sizes present across dorsal-fin membranes; pigmentation often darkest and densest in posterior one-half of fin in distal one-half of membrane. Pectoral fin hyaline except for single line of small dark chromatophores on basal one-half of lateral, unbranched ray. Pelvic fin hyaline.

ECOLOGY.—*Creagrutus hysginus* is quite abundant in the Ríos Bautista and Güiria. These are small rivers of crystal-clear water that descend from the mountains of the central Peninsula de Paria, northeastern Venezuela. The substrate of both rivers is coarse, ranging mainly from gravel to large stones with small amounts of sand present. *Creagrutus hysginus* occurs in fast-flowing current as well as quiescent backwater areas. The surrounding forest contributes large amounts of allochthonous material to the streams, including leaves, flowers and fruit, and terrestrial insects. Examination of gut contents of *C. hysginus* revealed that the species feeds on this material as well as aquatic dipteran larvae.

Beebe (1945:84) reported that *C. hysginus* (cited as *C. beni*; see under "Remarks," below) was one of the species surviving in the mixture of damp mud and decaying vegetation at the bottom of a drying creek-bed in Río San Juan basin south of Caripito in the state of Monagas, Venezuela.

DISTRIBUTION.—The known distribution of *Creagrutus hysginus* is restricted to several rivers draining into the Golfo de Paria in the coastal states of Sucre and Monagas, northeastern Venezuela (Figure 43, diamonds). In the Peninsula de Paria, *C. hysginus* has been collected in the upland portions of the Ríos Bautista, Güiria, Irapa, and Yoco. *Creagrutus* species were absent in the 20 collections of freshwater fishes from the lowland region near the base of the peninsula as reported by Fernández-Yépez (1969). The species also occurs in upland tributaries of the Río San Juan of Sucre and Monagas states that flows into the western portions of the Golfo de Paria.

REMARKS.—In a report on fishes collected in Venezuela by L. Wehekind, Fowler (1931:408) attributed material of *Creagrutus hysginus* (ANSP 53383-6) to *C. beni* Eigenmann; however, *C. hysginus* is distinguished from *C. beni* by the shape of the humeral mark (essentially round in *C. hysginus* versus vertically elongate in *C. beni*), the number of branched anal-fin rays (9 or 10 in *C. hysginus* versus 11 to 13 in *C. beni*), and the number of vertebrae (36 or 37 in *C. hysginus* versus 37 to 39 in *C. beni*). Furthermore, *Creagrutus beni,* as recognized in this paper, is endemic to the upper portions of the Río Madeira basin in northeastern Bolivia.

Fowler (1931:408) reported *Creagrutus beni* (material herein ascribed to *C. hysginus*) from the Río Yarapa, Estado de Sucre, in eastern Venezuela. We have been unable to locate such a drainage in examined gazetteers or maps, a problem also encountered by Fernández-Yépez (1969). On the basis of the date cited by Fowler for the collection of these specimens, and locality and collection-date data of other collections from that expedition reported by Fowler (1931), we conclude that those *Creagrutus* specimens (ANSP 53383-6) were most likely collected in an upland tributary of the Río San Juan, a tributary of the western portion of the Golfo de Paria.

Beebe (1945:84) cited *Creagrutus beni* from the upper portions of the Río San Juan, perhaps following Fowler (1931). We have been unable to locate the specimens that were the basis for that citation, but given that *C. beni* is endemic to northern Bolivia and southeastern Peru and that *C. hysginus* is the only *Creagrutus* species we have examined that originated in the Río San Juan basin, it is likely that Beebe's citation of *C. beni* is a misidentification of *C. hysginus.*

MATERIAL EXAMINED.—667 specimens (28, 30.3–55.6).

VENEZUELA. *Sucre:* Río Güiria, near La Toga, MBUCV V-20310, 1 (44.9, holotype of *Creagrutus hysginus*); CAS 79623, 9 (33.2–43.0, paratypes of *Creagrutus hysginus;* 1 specimen cleared and counterstained for cartilage and bone); MBUCV V-24002, 20 (paratypes of *Creagrutus hysginus*); USNM 326055, 10 (34.1–44.5, paratypes of *Creagrutus hysginus;* 2 specimens cleared and counterstained for cartilage and bone); MBUCV V-24003, 186. Río Bautista, Sector Río above last Carretera, MBUCV V-20304, 12 (4, 30.3–37.6, paratypes of *Creagrutus hysginus;* 1 specimen cleared and counterstained for cartilage and bone). Río La Toga, 6 km N of road 9, approximately 4 km W of Güiria, CAS 80270, 10 (paratypes of *Creagrutus hysginus*); MCNG 19691, 148 (paratypes of *Creagrutus hysginus*); USNM 326035, 10 (paratypes of *Creagrutus hysginus;* two specimens cleared and counterstained for cartilage and bone). Río Yarapa (locality uncertain; see comments under "Remarks," above), ANSP 53383–6, 4 (45.4–55.6; 1 specimen cleared and counterstained for cartilage and bone). Río Güiria, NE of Güiria, MBUCV V-20288, 3. Río Yoco, sector Chaguaramas, NW of Yoco, MBUCV V-20295, 25. Río Irapa, MCNG 16174, 5. Río Güiria, west of Güiria, MCNG 16768, 5. Caño E of Campo Claro, MCNG 16776, 21. Río Yoco, near Güiria, MHNLS 9715, 14. Quebrada El Mango, tributary to Río Capiricual (Río San Juan system), MHNLS 9832, 31. *Monagas:* Río Cocollar, Río Guarapiche tributary (Río San Juan system), MHNLS 9830, 7. Río Capiricual, tributary to Río Guarapiche (Río San Juan system), S of El Arbolito, MHNLS 9831, 146.

Creagrutus ignotus, new species

FIGURES 43, 48, TABLE 25

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 2 or 3 teeth on the maxilla, 6, very rarely 5, teeth in the primary tooth row of the premaxilla, 6 dentary teeth, 37 to 40 lateral line scales without a lamellar process over each pore, 9 to 11 predorsal medianscales, 4 scale rows between the dorsal-fin origin and the lateral line, 36 to 38 vertebrae, 9 to 11 branched anal-fin rays, 2 post-anal median

TABLE 25.—Morphometrics and meristics of *Creagrutus ignotus*, new species: (A) holotype of *C. ignotus*, MZUSP 45310; and (B) paratypes of *C. ignotus* (n=14). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	41.1	26.8–41.8
1. Snout to anal-fin origin	66.2	61.3–65.9
2. Snout to pelvic-fin insertion	51.8	45.0–51.9
3. Snout to pectoral-fin insertion	25.3	23.8–26.7
4. Snout to dorsal-fin origin	48.9	46.3–49.6
5. Dorsal-fin origin to hypural joint	54.7	52.9–55.4
6. Dorsal-fin origin to anal-fin origin	29.4	26.9–30.5
7. Dorsal-fin origin to pelvic-fin insertion	22.1	21.5–25.4
8. Dorsal-fin origin to pectoral-fin insertion	29.2	28.5–31.7
9. Caudal peduncle depth	9.5	9.3–11.0
10. Pectoral-fin length	19.5	18.6–22.4
11. Pelvic-fin length	17.0	14.9–17.5
12. Dorsal-fin length	19.3	18.7–21.3
13. Anal-fin length	16.7	14.5–18.0
14. Head length	27.7	24.9–28.9
15. Postorbital head length	43.9	36.8–45.8
16. Snout length	32.5	28.7–33.9
17. Bony orbital diameter	30.7	30.4–34.9
18. Interorbital width	25.4	25.3–28.9
	Meristics	
Lateral line scales	38	37–40
Scale rows between dorsal-fin origin and lateral line	4	4
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	11	9–11
Branched dorsal-fin rays	8	8
Branched anal-fin rays	11	9–11
Branched pelvic-fin rays	6	6
Pectoral-fin rays	12	11–13
Vertebrae	36	36–38

scales to the anal-fin origin, 6 to 8 gill rakers on the upper limb of the first gill arch, 9 to 11 gill rakers on the lower limb of the first gill arch, the distance from the dorsal-fin origin to the hypural joint (52.9%–55.4% of SL), the distance from the dorsal-fin origin to the anal-fin origin (26.9%–30.5% of SL), the distance from the dorsal-fin origin to the pelvic-fin insertion (21.5%–25.4% of SL), the distance from the dorsal-fin origin to the pectoral-fin insertion (28.5%–31.7% of SL), the caudal peduncle depth (9.3%–11.0% of SL), the interorbital width (25.3%–28.9% of HL), the well-developed third infraorbital contacting the horizontal limb of the preopercle in larger specimens, the lack of a series of dark midlateral spots on the body, and the slightly anterodorsally arched, vertically elongate humeral mark without straight anterior and posterior margins distinguishes *Creagrutus ignotus* from all species within the clade composed of *Creagrutus* and *Piabina*.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus ignotus* in Table 25. Head and body relatively elongate across limited size range of available specimens. Greatest body depth at, or slightly anterior of, dorsal-fin origin. Dorsal profile of head distinctly convex anteriorly from margin of upper lip to vertical through posterior nostril, slightly convex from that point to tip of supraoccipital spine in smaller individuals, straight in that region in largest available specimens. Interorbital region nearly flat transversely, noticeably more so in larger specimens. Predorsal profile of body slightly convex, some larger specimens showing barely apparent change in alignment of predorsal profile relative to that of head. Predorsal surface of body slightly flattened transversely proximate to tip of supraoccipital spine, with obtuse median ridge posteriorly proximate to dorsal-fin origin. Ventral profile of head gently curved from margin of lower lip to isthmus in smaller available specimens; with increasingly obvious obtuse angle at anteroventral corner of dentary with increasing body size, and straight from that point to isthmus in larger specimens. Prepelvic profile of body nearly straight, or gently convex, in all specimens. Prepelvic region obtusely flattened transversely in larger specimens.

Head obtusely pointed in lateral view and more compressed laterally in dorsal view. Upper jaw distinctly longer than, and overhanging, lower jaw. Snout slightly fleshy, with scattered papillae anteromedially. Papillae more concentrated along ventral margin of lip and on fleshy folds and plicae extending between outer and medial premaxillary teeth. Lower lip fleshy anteriorly, with numerous papillae along dorsal margin.

Infraorbital series moderately developed. Ventral margin of third infraorbital falling short of horizontal limb of preopercle in smallest specimens, contacting that ossification in larger individuals. Posterior margins of third through fifth infraorbitals falling distinctly short of vertical limb of preopercle in specimens of all sizes.

Premaxillary dentition in three series: primary row slightly curved, typically consisting of 6 teeth (one paratype with only 5 teeth in primary row of each premaxillary), without distinct gap between first and second tooth of that series, but with medial tooth separated from anterior tooth of contralateral series by distinct gap; triangular cluster of 3 large teeth; and single tooth of form similar to that of primary series occurring lateral to fourth tooth of primary premaxillary tooth row. Maxilla with 2 or 3 tricuspidate teeth. Dentary with 6 teeth; anterior three teeth tricuspidate, fourth through sixth conical (in a 28.1 mm SL cleared and counterstained specimen); first and second dentary teeth distinctly largest, with second tooth slightly larger than first and slightly more than two times height of third; fourth through sixth teeth compressed and distinctly smaller than third tooth.

Dorsal-fin rays ii,8. Dorsal-fin origin approximately at vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin slightly concave. Anal-fin rays ii,9–11. Profile of distal margin of anal fin concave, with last unbranched and 2 anteriormost branched rays forming anterior lobe. Hooks typically present on anal-fin rays in mature males of many *Creagrutus* species not present in limited available population samples. Pectoral-fin rays i,10–12. Tip of pectoral fin extending posteriorly to point approximately 2 scales before pelvic-fin insertion. Pelvic-fin rays i,6,i. Hooks typically present on pelvic-fin rays in mature males of many *Creagrutus* species not present in lim-

FIGURE 48.—*Creagrutus ignotus*, new species, holotype, MZUSP 45310, 41.1 mm SL; Brazil, Mato Grosso, Riacho (small stream) 1, tributary to Rio Preto at road to San Francisco, Município de Diamantino (Rio Arinos basin).

ited number of available specimens. Tip of pelvic fin extending posteriorly nearly to anal-fin origin.

Gill rakers 6–8 + 9–11.

COLORATION IN ALCOHOL.—Overall ground coloration ranging from yellow to tan in available specimens, all collected within last six years. Dorsal surface of head with numerous scattered, stellate, dark chromatophores. Chromatophore field either uniformly intense or with chromatophore concentration in field reduced over posterior fontanelle. Deeper-lying dark chromatophores covering membranes of brain. Chromatophore field on dorsal surface of head continuing anteriorly onto snout and upper lip. Chromatophores in this region more concentrated anterior, anterodorsal, and anteroventral to anterior nostril and forming nearly semicircular arch. Arch continuous posteroventrally, with series of dark chromatophores anteroventral to orbit continuing to varying degrees around ventral and posterior margins of orbit. Relatively dense pattern of stellate chromatophores covering most of opercle and dorsal portions of infraorbital series.

Scales of dorsolateral portion of body with exposed portions covered with stellate chromatophores. Chromatophore field more concentrated basally on each scale, giving somewhat reticulate pattern to that portion of body. Humeral mark variably vertically elongate, with somewhat irregular margins. Darker main portion of mark typically centered slightly above lateral line. Dorsal portion of mark formed of less concentrated field of chromatophores arranged in anteriorly arching pattern. Midlateral body stripe extending from suprapreopercle to rear of caudal peduncle, with humeral mark included within stripe anteriorly. Stripe very diffuse anteriorly, particularly in smaller specimens, and becoming increasingly prominent posteriorly.

Dorsal fin with dark pigmentation along margins of most finrays and large chromatophores scattered on distal one-half of anterior two-thirds of rays, chromatophore field most concentrated in center of that region. Anal-fin rays variably outlined with dark pigmentation and with scattered chromatophores on distal one-half to two-thirds of membranes of anterior branched rays in some individuals. Caudal-fin rays variably outlined by dark chromatophores. Dark pigmentation most intense on three portions of caudal fin; middle rays and dorsalmost and ventralmost rays; these more pigmented regions separated by hyaline or less pigmented areas on middle rays of each caudal-fin lobe. Dark pigmentation of middle caudal-fin rays most intense basally, forming very distinct spot in some larger specimens. Pectoral and pelvic fins hyaline.

ETYMOLOGY.—The specific name, *ignotus*, from the Latin for unknown, refers to the previous absence of any records for *Creagrutus* from the upper portions of the Rio Tapajós basin.

ECOLOGY.—Stomach contents of a single examined specimen of *Creagrutus ignotus* prepared for clearing and staining in this study consisted solely of parts of larval insects.

DISTRIBUTION.—*Creagrutus ignotus* is known only from the upper portions of the Rio Tapajós basin, central Brazil (Figure 43, open stars).

COMPARISONS.—*Creagrutus ignotus* is the only member of *Creagrutus* known from the upper portions of the Rio Tapajós system and one of only two *Creagrutus* species known from that drainage basin. *Creagrutus ignotus* is readily discriminated from *C. cracentis*, the second species known from the Rio Tapajós basin, in numerous features, most notably the arrangement of premaxillary dentition and numbers of teeth in the upper jaw (see "Key to the Species of *Creagrutus* in the Amazon Basin").

MATERIAL EXAMINED.—23 specimens (23, 26.8–53.0).

HOLOTYPE.—BRAZIL. *Mato Grosso:* Riacho (small stream) 1, tributary to Rio Preto at road to San Francisco, Município de Diamantino (Rio Arinos basin), collected by N.A. Menezes et al., 24 Oct 1992, MZUSP 45310, 1 (41.1).

PARATYPES.—14 specimens (14, 26.8–41.8).

BRAZIL. *Mato Grosso:* Riacho (small stream) 1, tributary to Rio Preto at road to San Francisco, Município de Diamantino (Rio Arinos basin), collected with holotype, MZUSP 50165, 2 (32.9–34.1); USNM 340960, 3 (32.6–41.8). Riacho (small stream) 3, tributary to Rio Preto at road to San Francisco, Município de Diamantino (Rio Arinos basin), collected by N.A. Menezes et al., 24 Oct 1992, MZUSP 45349, 3 (27.7–32.9); USNM 326672, 3 (26.8–30.5; 1 specimen cleared and counterstained for cartilage and bone). Rio Juína, 31 km along road be-

tween Juína and Fontanilhas, collected by S.O. Kullander et al., 13 Oct 1989, MZUSP 42456, 3 (32.7–41.0).

NONTYPE SPECIMENS.—8 specimens (8, 31.7–53.0).

BRAZIL. *Mato Grosso:* Creek crossing on highway BR-163, 54 km from Sinop, Mato Grosso in direction of Santarém, Pará, tributary of Rio Teles-Pirez, upper Rio Tapajos system, USNM 353153, 4 (33.2–53.0); MZUSP 53244, 4 (31.7–43.0).

Creagrutus kunturus Vari, Harold, and Ortega, 1995

FIGURES 49–51, TABLE 26

Creagrutus mülleri [not of Günther, 1859].—Böhlke, 1958:30 [misidentification] [specimens from Ecuador (Pastaza), Río Arajuno].

Creagrutus kunturus Vari et al., 1995:290, figs. 1, 2 [type locality: Peru, Amazonas, Provincia Condorcanqui, Cordillera del Condor, upper Río Comainas, 20 km upriver of Puesto de Vigilancia no. 22, 3°56′30″S, 78°24′20″W; comparisons with *C. amoenus*].—Roman-Valencia and Cala, 1996:147 [similarity to *C. amoenus*, based on Vari et al., 1995].

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 2 or 3 teeth on the maxilla, 6, rarely 5, teeth in the primary tooth row of the premaxilla, 5 or 6 dentary teeth, 39 to 43 lateral line scales without a lamellar process over each pore, 12 predorsal median scales, 38 to 41 vertebrae, 11 to 13 branched anal-fin rays, 1 post-anal median scale to the anal-fin origin, 9 to 11 gill rakers on the lower limb of the first gill arch, the absence of a discrete secondary component dorsal to the main body of the humeral mark, the possession of a series of dark spots along the midlateral surface of the body that ontogenetically coalesce in variable patterns, sometimes resulting in a solid dark stripe in larger individuals, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus kunturus* from all species within the clade composed of *Creagrutus* and *Piabina* with the exception of *C. amoenus*. *Creagrutus kunturus* can be separated from *C. amoenus* by the combination of the number of lateral line scales (39–43, rarely 39, in *C. kunturus* versus 35–39, rarely 39, in *C. amoenus*), total vertebrae (38–41, typically 39 or 40, in *C. kunturus* versus 36– 39, rarely 39, in *C. amoenus*), the depth of the caudal peduncle (11.1%–12.1% of SL in *C. kunturus* versus 12.2%–13.8% of SL in *C. amoenus*), and the distance from the dorsal-fin origin to the anal-fin origin (30.8%–34.0% of SL in *C. kunturus* versus 33.8%–38.8% of SL in *C. amoenus*).

DESCRIPTION.—Morphometric and meristic data for *Creagrutus kunturus* in Table 26. Head and anterior portion of body relatively robust; region of body posterior of vertical through anal-fin origin more slender. Greatest body depth at, or slightly anterior of, vertical through dorsal-fin origin. Dorsal profile of head from tip of snout to rear of supraoccipital spine smoothly convex, some specimens with profile disrupted by irregular processes in region above nares. Interorbital region distinctly convex transversely. Predorsal profile of body slightly convex, with variably evident inflection of profile of head at rear of supraoccipital spine (compare Figures 49 and 50). Ventral profile of head in many individuals with obtuse angle at anteroventral corner of dentary, gently curved from that region to isthmus. Ventral profile of body convex to anal-fin origin and slightly concave from anal-fin insertion to caudal fin.

Head obtusely pointed in lateral view and distinctly pointed in dorsal view. Upper jaw distinctly longer than, and overhanging, lower jaw. Anterior portion of snout fleshy, with scattered papillae. Papilla more concentrated along ventral margin of upper lip and on fleshy folds and plicae extending between outer and medial premaxillary teeth. Lower lip fleshy anteriorly with papillae along dorsal margin.

Infraorbital series moderately developed. Central portion of ventral margin of third infraorbital contacting horizontal limb of preopercle. Posterior margins of third through fifth infraorbitals distinctly separated from vertical limb of preopercle, gap decreasing gradually dorsally.

Premaxillary dentition in three series: primary row slightly curved, typically with 6 teeth, 5 teeth present on both premaxil-

TABLE 26.—Morphometrics and meristics of *Creagrutus kunturus:* (A) holotype of *C. kunturus*, MUSM 5667; and (B) all specimens of *C. kunturus* from which counts and measurements were taken (n=31). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	84.1	53.2–96.0
1. Snout to anal-fin origin	64.8	61.4–65.3
2. Snout to pelvic-fin insertion	46.6	44.2–49.1
3. Snout to pectoral-fin insertion	24.6	22.3–28.0
4. Snout to dorsal-fin origin	47.3	45.5–50.5
5. Dorsal-fin origin to hypural joint	56.2	53.9–60.3
6. Dorsal-fin origin to anal-fin origin	33.5	30.8–34.0
7. Dorsal-fin origin to pelvic-fin insertion	28.7	27.9–31.6
8. Dorsal-fin origin to pectoral-fin insertion	33.0	32.2–35.1
9. Caudal peduncle depth	11.4	11.1–12.1
10. Pectoral-fin length	20.9	18.6–21.9
11. Pelvic-fin length	15.3	14.7–17.2
12. Dorsal-fin length	20.7	20.1–24.8
13. Anal-fin length	15.8	15.4–19.0
14. Head length	25.1	24.2–29.1
15. Postorbital head length	44.3	40.9–47.1
16. Snout length	28.1	27.3–32.3
17. Bony orbital diameter	28.1	26.7–32.5
18. Interorbital width	28.1	24.9–31.2
	Meristics	
Lateral line scales	41	39–43
Scale rows between dorsal-fin origin and lateral line	5	4–5
Scale rows between anal-fin origin and lateral line	4	3–4
Predorsal median scales	12	12
Branched dorsal-fin rays	8	7–8
Branched anal-fin rays	12	11–13
Branched pelvic-fin rays	7	6–7
Pectoral-fin rays	13	12–14
Vertebrae	39	38–41

lae in one specimen and 7 teeth on one premaxilla in one specimen, without pronounced gap between first and second tooth of series but with anteromedial tooth separated from contralateral equivalent by distinct gap filled by fleshy fold; triangular cluster of 3 larger teeth lying medial to primary row; and single tooth of form similar to that of primary series occurring lateral to fourth tooth of primary premaxillary row. Maxilla with 2 or 3 tricuspidate teeth. Dentary with 5 or 6 tricuspidate teeth; first and second dentary teeth distinctly larger than remaining teeth and subequal, approximately 1.7 times height of third tooth; fourth through fifth or sixth teeth distinctly smaller and compressed.

Dorsal-fin rays typically ii,8, rarely iii,8 or ii,7. Dorsal-fin origin ranging from anterior of, to posterior to, vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin straight to very slightly concave. Anal-fin rays ii,11–13 or iii,11–13. Profile of distal margin of anal fin straight. Hooks typically present on anal-fin rays in mature males of many *Creagrutus* species not found in examined specimens. Pectoral-fin rays i,11–13. Relative length of pectoral fin somewhat variable, ranging from falling slightly short of vertical through pelvic-fin insertion to extending to beyond that line. Pelvic-fin rays i,6,i or i,7 with higher number of branched rays typical of larger individuals. Tip of pelvic fin extending posteriorly to, or falling slightly short of, anus. Hooks typically present on pelvic-fin rays in mature males of many *Creagrutus* species not found in examined specimens.

Gill rakers 7–8 + 9–11.

COLORATION IN ALCOHOL.—Overall ground coloration of relatively freshly collected specimens light tan. Dorsal surface of head with dense field of small dark chromatophores, giving the region distinctly dusky appearance. Intensity of dark pigmentation more noticeable over brain, presumably as consequence of deep-lying pigmentation overlying membranes of that organ in most *Creagrutus* species. Dense surface pigmentation continuing anteriorly over snout and upper lip. Crescent-shaped patch of denser pigmentation anterior to nares obvious in smaller specimens; not distinct from remaining dark pigmentation anterior to orbit in larger individuals. Regions immediately ventral and posterior to orbit with pigmentation field interrupted by unpigmented laterosensory canal segments. Lower portion of cheek lacking dark chromatophores in all but largest individuals, which have scattered chromatophores in that region. Variably developed pattern of dark pigmentation posterior to orbit; pigmentation ranging in form from diffuse, irregular band, through overall diffuse band, to vertically elongate spot overlying portion of preopercle and margins of fourth and fifth infraorbitals, to distinct band with irregular dorsal and ventral borders extending from rear margin of orbit to rear margin of opercle.

Scales of dorsal portion of body with small dark chromatophores concentrated along posterior scale margin, forming overall reticulate pattern. Humeral mark vertically elongate, with most intensely pigmented region centered immediately dorsal of lateral line. Small ventrally attenuating, less densely pigmented region extending ventrally from main body of humeral mark as far as one scale row ventral of lateral line. Distinct, anteriorly concave, more diffuse area of dark pigmentation extending approximately two scale rows anterodorsally from dorsal margin of region of darkest pigmentation. Midlateral body pigmentation highly variable both ontogenetically and between comparably sized individuals, formed of two components: band of dark deep-lying chromatophores and overlying patches of dark surface pigmentation. Surface pigmentation ranging from discrete, widely separated spots of approximately size of pupil of eye, through variously coalesced spots, to nearly continuous dark band extending from near posterior margin of humeral mark posteriorly to base of middle caudal-fin rays.

Dorsal fin with membranes and margins of fin rays with small dark chromatophores, particularly on distal two-thirds of fin; intensity of pigmentation increasing ontogenetically. Basal portions of anal-fin rays outlined by small dark chromatophores in medium-sized individuals, rays nearly completely outlined in larger specimens. Caudal fin with rays and membranes with associated small dark chromatophores, particularly in larger individuals. Distinct band of dark pigmentation on middle caudal-fin rays; band most intense basally. Pelvic and pectoral fins nearly hyaline in smaller individuals, dusky in larger specimens.

ECOLOGY.—The collecting localities of the holotype and paratype series are at an altitude of 850–900 m, along the Cordillera del Condor. In that region the Río Comainas is shallow with clear water for most of the year, but it becomes torrential with white waters during, and after, heavy rains. The river varies from 8 to 20 m in width, with the main channel during low water periods being 30 to 190 cm deep over a bottom of rocks, pebbles, sand, and clay. The nontype specimens collected at Chigkan entse (=Quebrada Chigkan) (LACM 39681-1) also came from a relatively shallow stream approximately 4 m wide with moderate current. The single specimen cleared and counterstained, which was collected during late July, had very well-developed testes and had fed on larval and adult insects.

DISTRIBUTION.—*Creagrutus kunturus* is distributed through the upper Río Marañon in northeastern Peru and through the upper Río Pastaza to the southwestern portion of Río Napo in southeastern Ecuador (Figure 51, dots).

COMPARISONS.—*Creagrutus amoenus,* a species very similar to *C. kunturus* (see "Diagnosis," above), also occurs in the Río Pastaza and Río Napo basins, but the two species are not known to be syntopic. In both the Río Pastaza and Río Napo basins and throughout its range, *C. amoenus* occurs in regions of somewhat lower altitude than does *C. kunturus* (compare Figures 22 and 51).

REMARKS.—Böhlke (1958:30) identified a series of specimens from eastern Ecuador as *Creagrutus mülleri* and these were, in turn, considered to be *C. boehlkei* by Géry (1972:63) in his original description of the latter species. The series re-

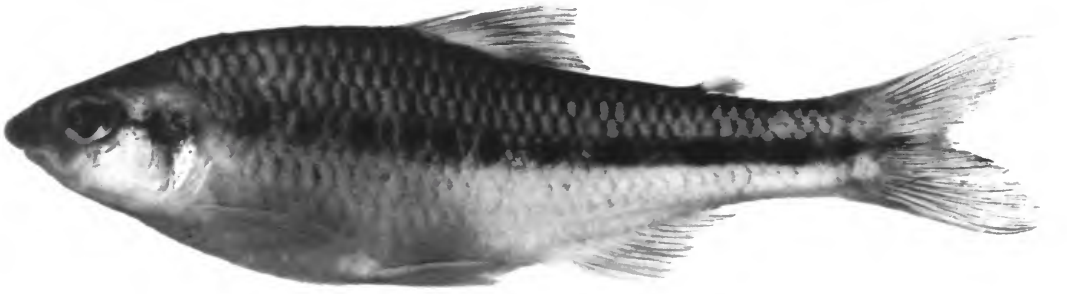

FIGURE 49.—*Creagrutus kunturus*, holotype, MUSM 5667, 84.1 mm SL; Peru, Amazonas, Condorcanqui, Cordillera del Condor, upper Río Comainas, 20 m upriver of Puesto de Vigilancia No. 22 (3°56′30″S, 78°24′20″W).

FIGURE 50.—*Creagrutus kunturus*, KU 19977, 82.5 mm SL; Ecuador, Pastaza, Río Alpayacu, 1 km E of Mera (1°28′S, 78°07′W).

ported on by Böhlke has proven to be complex, consisting mostly of *C. amoenus* (the senior synonym of *C. boehlkei*), but with two lots (USNM 164066 and presumably ANSP 75911, which was removed from it) being specimens of *C. kunturus*.

MATERIAL EXAMINED.—43 specimens (31, 53.2–96.0).

PERU. *Amazonas:* Provincia Condorcanqui, Cordillera del Condor, upper Río Comainas, 20 m upriver of Puesto de Vigilancia No. 22 (3°56′30″S, 78°24′20″W), MUSM 5667, 1 (84.1, holotype of *Creagrutus kunturus*); MUSM 6593, 1 (77.5, paratype of *Creagrutus kunturus*); USNM 335146, 1 (82.3, paratype of *Creagrutus kunturus*). Provincia Condorcanqui, Cordillera del Condor, Quebrada no. 1, tributary of Río Comainas, PV 22, MUSM 5669, 3 (62.2–64.5). Provincia Condorcanqui, Cordillera del Condor, Río Comainas, 30 m down river of Puesto de Vigilancia No. 22 (3°56′30″S, 78°24′20″W), MUSM 5665, 2 (57.3–58.0, paratypes of *Creagrutus kunturus*); USNM 335148, 2 (63.8–65.3, paratypes of *Creagrutus kunturus*). Provincia Condorcanqui, Cordillera del Condor, Río Comainas, 40 m upriver of Puesto de Vigilancia No. 22 (3°56′30″S, 78°24′20″W), MUSM 5663, 1 (90.3, paratype of *Creagrutus kunturus*). Provincia Condorcanqui, Cordillera del Condor, Quebrada no. 3, tributary of Río Comainas, Puesto de Vigilancia No. 22 (3°56′30″S, 78°24′20″W), MUSM 5668, 2 (64.2–75.6, paratypes of *Creagrutus kunturus*); USNM 335147, 2 (64.3–68.6, paratypes of *Creagrutus kunturus;* 1 specimen cleared and counterstained for cartilage and bone). Río Cenepa, Chigkan entse (=Quebrada Chigkan) tributary to Río Cenepa (4°28′S, 78°10′W), LACM 39681-1, 3 (72.0–92.0). Río Alto Comainas, vicinity of Shaim (04°15′S, 78°22′W), LACM 39686-15, 1.

ECUADOR. *Pastaza:* Río Alpayacu, 1 km E of Mera (1°28′S, 78°07′W); KU 19977, 3 (65.5–82.5). Upper portion of Río Arajuno, few km NE of El Puyo, Río Napo basin (approximately 1°24–26′S, 77°50–55′W), USNM 164066, 2 (75.2–

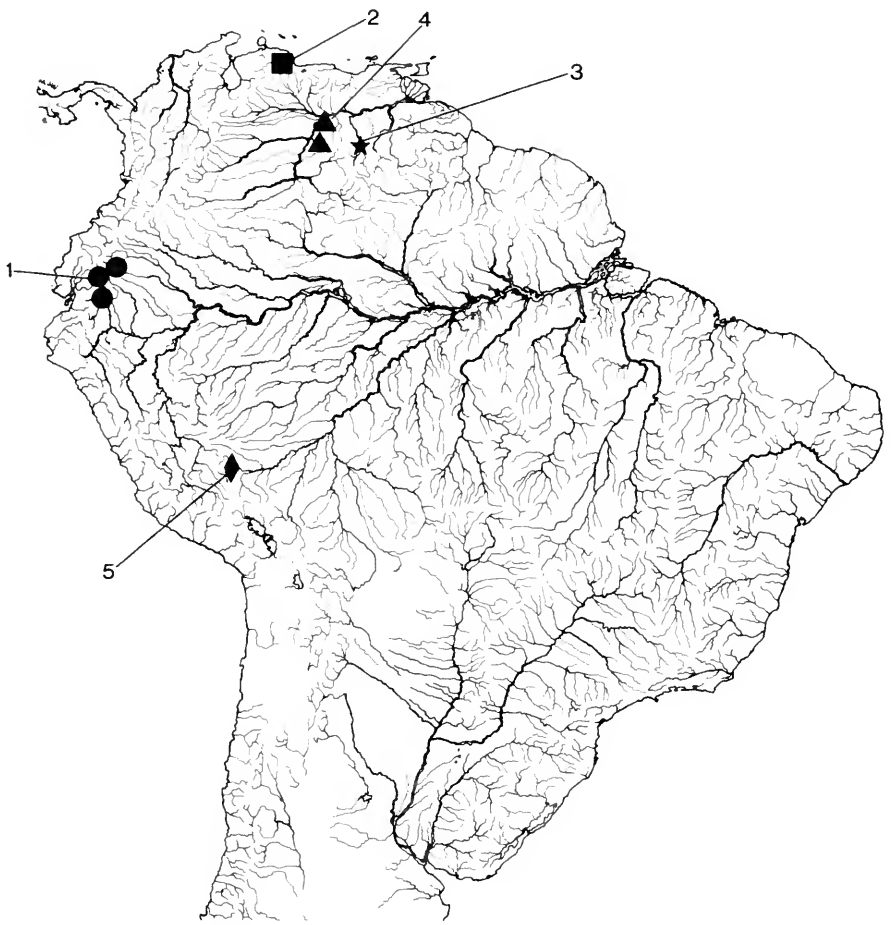

FIGURE 51.—Map of central and northern South America showing geographic distribution of *Creagrutus kunturus* (dots, 1=type locality), *Creagrutus lassoi* (square, 2=type locality, same area as type locality of *C. lepidus*), *Creagrutus lepidus* (square, 2=type locality, same area as type locality of *C. lassoi*), *Creagrutus machadoi* (star, 3=type locality), *Creagrutus magoi* (triangles, 4=type locality), and *Creagrutus manu* (diamond, 5=type locality) (some symbols represent more than one locality or lot of specimens).

96.0); ANSP 75911, 1. Río Pundo Grande, Puyo, MEPN 9838, 1. Río Conambo, at the settlement of Moretecocha (0°36′S, 77°24′W), MEPN 4635, 11 (8, 53.2–71.4); USNM 340956, 6.

Creagrutus lassoi, new species

FIGURES 51, 52, TABLE 27

Creagrutus beni [not of Eigenmann, 1911].—Fernández-Yépez, 1972, pl. 14: fig. 1 [misidentification] [Río Yaracuy].—Géry and Renno, 1989:5 [identification of population identified as *C. beni* by Fernández-Yépez, 1972, questioned].

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 2 to 5 teeth on the maxilla, 6 teeth in the primary tooth row of the premaxilla, 4 dentary teeth, 36 to 38 lateral line scales without a lamellar process over each pore, 9 to 11 predorsal median scales, 4 scale rows between the dorsal-fin origin and the lateral line, the lack of crenation on the scales of the posterior margin of many scales on the lateral surface of the body, 35 or 36 vertebrae, 10 to 12 branched anal-fin rays, 1 or 2 post-anal median scales to the anal-fin origin, the bony orbital diameter (23.3%–32.3% of HL), the postorbital length (46.7%–53.5% of HL), the poorly developed third infraorbital distinctly separated from the horizontal limb of the preopercle, the lack of a series of dark midlateral spots on the body, the humeral mark nearly vertical or slightly posterodorsally to anterodorsally inclined, the presence of a narrow medial predorsal line of dark pigmentation, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dor-

sal-fin rays distinguishes *Creagrutus lassoi* within the clade composed of *Creagrutus* and *Piabina*.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus lassoi* in Table 27. Body moderately deep and compressed. Greatest body depth ranging from slightly anterior of pelvic-fin insertion anteriorly as far as one-half of distance to pectoral-fin insertion. Large specimens much deeper and more compressed than smaller individuals. Dorsal profile of head distinctly convex from margin of upper lip to vertical between nares, straight from that point to rear of supraoccipital spine or with very slight concavity above eye. Dorsal profile of body slightly convex to dorsal-fin origin, inclination of predorsal region greatest in large specimens and in some individuals accentuated by hump-like inflection point immediately posterior to supraoccipital spine. Dorsal profile typically straight from dorsal-fin origin to caudal peduncle. Ventral profile of head with obtuse angle approximately midway between margin of lower lip and posterior of dentary, slightly to highly convex from that point approximately to pelvic-fin insertion; distinctly concave from anal-fin origin to caudal peduncle.

Upper jaw longer than, and overhanging, lower jaw. Anterior portion of snout quite fleshy, with many minute papillae on anteromedial portion of snout, papillae continuing ventrally onto upper lip and into mouth on fleshy flaps between premaxillary teeth. Continuous field of papillae covering most of head, evidently well developed in both sexes. Lower jaw distinctly fleshy anteriorly, with papillae most concentrated on lip and decreasing in number ventrolaterally, but extending posteroventrally in large numbers to isthmus and posteriorly over scales of anterior portion of abdomen.

Infraorbital series poorly developed, with ventral margin of third infraorbital rounded and roughly concentric with posteroventral margin of orbit. Ventral and posterior margins of third infraorbital separated from horizontal and vertical limbs of preopercle by gaps equal in width to approximately one-fourth of orbital diameter; large posteroventral gap approximately equal in width to diameter of pupil separates third infraorbital from inflection of preopercle. Posterior margins of fourth and fifth infraorbitals separated from vertical limb of preopercle by broad gap equal in width to approximately one-half that of respective infraorbital; gap slightly decreasing in width dorsally.

Premaxillary dentition in three series: primary row gently curved along line of premaxillary margin, without pronounced gap between first and second tooth of series, typically with 6 tricuspidate teeth, occasionally 5 teeth present on one premaxilla; anterior 4 teeth large and similarly developed, fifth and sixth teeth smaller with relatively reduced secondary cusps; triad of larger teeth with relatively prominent secondary cusps especially developed on posterior two teeth with posterolateral tooth largest; and single tooth of form similar to that of primary row lateral to fourth tooth of primary series. Maxilla with 2 to 5 tricuspidate teeth, 3 or 4 teeth most common. Dentary with 5 teeth, all tricuspidate except for conical last tooth in series; anterior two teeth largest with second tooth somewhat higher and distinctly wider than first tooth and more than twice as high as third tooth. Remaining dentary teeth becoming progressively smaller posteriorly.

TABLE 27.—Morphometrics and meristics of *Creagrutus lassoi*, new species: (A) holotype of *C. lassoi*, INHS 60094; and (B) paratypes of *C. lassoi* from which measurements and counts were taken (n=18). Standard length is expressed in mm; measurements 1 to 14=proportions of standard length; 15 to 18=proportions of head length.

Characters	A	B
	Morphometrics	
Standard length	47.5	40.5–75.4
1. Snout to anal-fin origin	61.7	59.5–66.9
2. Snout to pelvic-fin origin	44.4	41.9–51.1
3. Snout to pectoral-fin origin	26.5	24.4–27.3
4. Snout to dorsal-fin origin	51.6	47.5–53.6
5. Dorsal-fin origin to hypural joint	53.5	51.8–57.4
6. Dorsal-fin origin to anal-fin origin	31.2	28.9–34.1
7. Dorsal-fin origin to pelvic-fin insertion	31.6	27.4–33.1
8. Dorsal-fin origin to pectoral-fin insertion	37.7	33.9–40.1
9. Caudal peduncle depth	14.1	11.3–13.8
10. Pectoral-fin length	22.5	19.3–22.3
11. Pelvic-fin length	17.1	14.1–17.3
12. Dorsal-fin length	22.1	19.1–22.7
13. Anal-fin length	18.1	15.5–20.6
14. Head length	28.0	25.7–30.4
15. Postorbital head length	47.4	46.7–53.5
16. Snout length	27.1	26.5–33.5
17. Bony orbital diameter	31.6	23.3–32.3
18. Interorbital width	29.3	29.5–33.5
	Meristics	
Lateral line scales	37	36–38
Scale rows between dorsal-fin origin and lateral line	4	4
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	11	9–11
Branched dorsal-fin rays	8	7–8
Branched anal-fin rays	11	10–12
Branched pelvic-fin rays	7	7–8[1]
Pectoral-fin rays	12	11–12
Vertebrae	36	35–36

[1]Eight branched pelvic-fin rays present in only 1 specimen.

Dorsal-fin rays ii,7 or 8. Dorsal-fin origin located at, to slightly posterior of, vertical through pelvic-fin insertion. Distal margin of dorsal fin slightly concave; elongation of anterior lobe barely noticeable. Anal-fin rays ii or iii,10–12. Anal fin in mature males with hooks on segments of anterior two to four branched rays; hooks, if present on fourth ray, usually poorly developed. Distal margin of anal fin sinusoidal, with slightly elongate anterior lobe approximately twice as long as posteriormost branched ray. Pectoral-fin rays i,10 or 11. Tip of pectoral fin approaching or extending past pelvic-fin insertion. Pelvic-fin rays i,7, rarely i,8 or i,6,i. All pelvic-fin rays branched, except medial ray in most examined specimens (unbranched in 13 of 19 specimens). Tip of pelvic fin extending posteriorly to anal-fin origin in mature males, in other specimens fin-tip usually separated from anal-fin origin by distance equal to approx-

imately one scale. Pelvic fin in mature males with hooks on segmented and unsegmented portions of all branched rays and medial ray if unbranched, some specimens with hook on both lateral and medial surfaces of segments, especially on medial three rays. Posterior margin of body scales slightly undulate to crenate; scale striae clearly visible.

Gill rakers 5–8 + 9–11.

COLORATION IN LIFE.—(Observations based on specimens from the Río Tupe, Estado de Yaracuy (MCNG 24685), fixed in formalin and stored in ethanol for three years but retaining some life colors). All unbranched and anterior two branched anal-fin rays, lateral unbranched and first branched pelvic-fin rays, and lateral pectoral-fin rays bright yellow. Both lobes of caudal fin bright yellow, pigmentation most intense in membranes associated with outer 2 or 3 rays; distal one-half of ventral caudal-fin lobe orange. Unbranched dorsal-fin rays yellow but pigmentation less intense than in other fins. Anterodorsal surface of eye orange-red, with overlying layer of reflective guanine.

COLORATION IN ALCOHOL.—Dorsal surface of head with diffuse pattern of small dark chromatophores continuing anteriorly onto snout and medial portions of upper jaw, with distinct small crescent of dark chromatophores immediately in front of anterior nares; pattern of chromatophores more irregular and diffuse laterally proximal to eye. Band of scattered, dark chromatophores extending from snout onto dorsal surface of cheek and continuing around posterior margin of orbit; noticeable concentration of pigmentation anteroventral of eye. Lateral surface of head with scattered stellate chromatophores on dorsal one-half of cheek and covering area behind eye and upper one-half of opercle; remainder of head without pronounced pigmentation pattern.

Body with pigmentation most concentrated dorsally, particularly at dorsal-fin base and below center of exposed surface of scales in broad, vertical, anteriorly concave band; extreme posterior margins of scales outlined by fine, dark pigment. Middorsal stripe, especially visible in mature males, consisting of concentrated dark chromatophores present below scales on anterior one-half of middorsal region and between bases of dorsal and adipose fins. Humeral mark most highly pigmented immediately dorsal of lateral line, extending ventrally one scale row below lateral line and dorsally three rows; overall form of mark bar-like, ranging from vertical to somewhat posterodorsally to anteroventrally oblique. Bar somewhat diffuse in large specimens. Pigmentation on lateral surface of body, other than for that associated with humeral bar, restricted to area dorsal of lateral line except for weakly delineated myosepta dorsal of anal-fin base. Midlateral body stripe diffuse anteriorly, becoming more densely pigmented and somewhat wider posteriorly on caudal peduncle. Reflective guanine layer very well developed, especially in association with, and mostly masking, midlateral stripe.

Caudal-fin rays all delineated by dark pigment, pigmentation darkest on ventral one-half of fin; membranes of ventral one-half of fin covered with diffuse dark chromatophores and extending to distal margin. Unbranched anal-fin rays unpigmented, branched rays delineated by small, dark chromatophores, pigmentation especially developed basally where chromatophores slightly enlarged. Anterior portion of anal fin in some specimens with scattered, large, dark chromatophores on distal membranes. Dorsal-fin membrane and ray margins with many dark chromatophores, except near base and on last two branched rays where pigmentation poorly developed or absent. Pectoral-fin rays delineated by dark chromatophores along their medial surfaces. Pelvic fin hyaline.

ETYMOLOGY.—The specific name, *lassoi,* is in honor of Carlos A. Lasso of the Museo de Historia Natural La Salle, Caracas and the Asociación Amigos de Doñana, Seville, in recognition of his many contributions to our knowledge of the fishes of Venezuela and his assistance to the authors.

ECOLOGY.—*Creagrutus lassoi* is sympatric, and possibly syntopic, with *C. lepidus* in the Quebrada El Charal, Río Aroa system. The general habitat for this low elevation water body was described by Vari et al. (1993) and is repeated under "Ecology" in the *C. lepidus* account herein. Fernández-Yépez (1972) found *C. lassoi* (identified therein as *C. beni*) at three of the eleven collecting locations in the Río Yaracuy drainage. These collections also may have included *C. taphorni* because both forms were at that time included in the rather broad conception of *C. beni* applied by previous authors. Fernández-Yépez (1972, pl. 14) noted that *C. lassoi* (identified by that author as *C. beni*) inhabits clear waters and feeds on algae from submerged stones and logs.

COMMON NAME.—Venezuela: "Pico de Loro" (Fernández-Yépez, 1972, pl. 14).

DISTRIBUTION.—*Creagrutus lassoi* occurs only in the Río Aroa and Río Yaracuy systems, Caribbean versant drainages of north central Venezuela (Figure 51, square).

COMPARISONS.—Reflective guanine is highly developed on the lateral surfaces of the body in *Creagrutus lassoi,* a feature that distinguishes it from all other congeners in rivers of the Caribbean versant and through the Río Orinoco basin. *Creagrutus lassoi* occurs with *C. lepidus* in the Río Aroa system of the Carribean slope. The two species are readily distinguishable on the basis of pigmentation and overall body form (compare Figures 51 and 53). *Creagrutus lassoi* is distinguished from *C. taphorni,* a similar species from that region and with which it co-occurs in the Río Yaracuy, by the undulate to crenate posterior margins of midlateral scales and by the occasional presence of a hook on both the medial and lateral surface pelvic-ray segments, features absent in *C. taphorni. Creagrutus crenatus* is most similar to *C. lassoi,* especially with regard to meristics and fin-ray hook morphology. These two species differ in the straight posterior opercular margin in *C. crenatus* compared with the concave posterior opercular margin in *C. lassoi,* the modally higher number of branched anal-fin rays and lateral line scales in *C. crenatus* versus *C. lassoi,* and the crenate posterior scale margins, especially along the midlateral

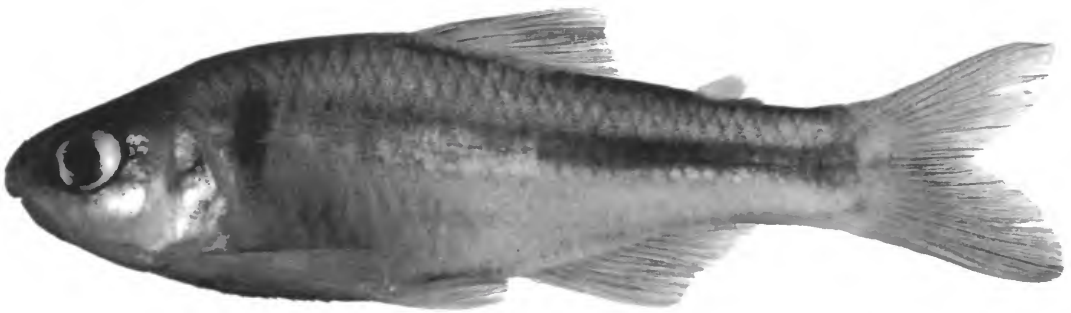

FIGURE 52.—*Creagrutus lassoi,* new species, holotype, INHS 60094, 47.5 mm SL; Venezuela, Yaracuy, Río Tupe, Río Aroa drainage, approximately 12 km N of Aroa, on Highway 3 (10°30′19″N, 68°52′33″W).

surface of the body in *C. crenatus* in comparison to the typically smooth scale margins in *C. lassoi.*

GEOGRAPHIC VARIATION.—Three specimens from the Río Mayorica, Río Yaracuy drainage (INHS 34937) that represent the only documented occurrence of *C. lassoi* outside of the adjacent Río Aroa drainage, have most of the diagnostic features of the species. The body in the Río Mayorica sample is proportionally a little shallower and less compressed, giving the specimens a slightly more rotund appearance. In addition, hooks observed on the pelvic rays are confined to the medial surface of the fin, a feature also observed in many of the smaller mature males from the Río Aroa drainage.

REMARKS.—*Creagrutus lassoi* is one of several forms that we recognize from Venezuela that were previously regarded as components of a wide ranging and variable *C. beni* by Eigenmann (1927), Schultz (1944), and a series of other authors. A photograph of *C. lassoi* was published by Fernández-Yépez (1972, pl. 14: fig. 1) who, however, clearly included this material from the Río Yaracuy with other "*C. beni,*" which he considered to occur across northern Venezuela from the Andean piedmont to the Río Orinoco delta, although noting (text associated with pl. 14) that *C. beni,* in the sense that it was then utilized, might subsume other species. Géry and Renno (1989:5) noted that the material identified by Fernández-Yépez (1972) as *C. beni* differed from specimens of the latter species from its type region in details of pigmentation and squamation. This "forme vénézuélienne," as it was cited by Géry and Renno (1989), included, however, two *Creagrutus* species: *C. taphorni* (the Lago de Valencia populations cited by those authors) and *C. lassoi* (the Río Yaracuy population of those authors).

MATERIAL EXAMINED.—81 specimens (15, 40.5–75.4).

HOLOTYPE.—VENEZUELA. *Yaracuy:* Río Tupe, Río Aroa drainage, approximately 12 km N of Aroa, on Highway 3 (10°30′19″N, 68°52′33″W), collected by L.M. Page et al., 31 Dec 1990, INHS 60094 (47.5).

PARATYPES.—77 specimens (14, 40.5–75.4).

VENEZUELA. *Yaracuy:* Río Tupe, Río Aroa drainage, approximately 12 km N of Aroa, on Highway 3 (10°30′19″N, 68°52′33″W), collected with holotype, INHS 51283, 22; USNM 359487, 5. Río Tupe, N of town of Aroa, E of San Jose (10°30′31″N, 68°52′55″W), collected by D.C. Taphorn et al., 31 Dec 1990, MCNG 24685, 29 (10, 40.5–61.4). Caño Caripial, Río Aroa drainage, 13 km SE of Yumare (10°33′42″N, 68°37′37″W), collected by D.C. Taphorn et al., 21 Jan 1995, INHS 34917, 2. Río Crucito, Río Aroa drainage, Guyamiro (10°29′08″N, 68°39′40″W), collected by D.C. Taphorn et al., 7 Jan 1993, INHS 28890, 1. Quebrada El Charal, Finca El Jaguar, Sierra de Aroa (approximately 10°32′N, 68°32′W), collected by C. Lasso and J. Medina, MHNLS 4143, 18 (4, 47.5–75.4), 24 Jul 1985.

NONTYPE SPECIMENS.—3 specimens.

VENEZUELA. *Yaracuy:* Río Mayorica, Río Yaracuy basin, 9 km N of Alberico at Highway 3 (10°25′42″N, 68°40′47″W), INHS 34937, 3.

Creagrutus lepidus Vari, Harold, Lasso, and Machado-Allison, 1993

FIGURES 51, 53, TABLE 28

Creagrutus lepidus Vari et al., 1993:351, fig. 1 [type locality: Venezuela, State of Yaracuy, Río Aroa basin, Quebrada El Charal, Finca El Jaguar, Sierra de Aroa, approximately 10°32′N, 68°32′W].—Evers 1996:7, color cover photo [northern Venezuela; see "Remarks," below, concerning exact locality].—Johannes, 1996:13 [Venezuela, Carabobo, Río Urama].—Taphorn et al., 1997: 71 [cited for Venezuela].—Lasso et al., 1997:41 [type specimen listing].

DIAGNOSIS.—*Creagrutus lepidus* can be distinguished readily from all congeners and *Piabina* by the autapomorphic presence of a very dark midlateral stripe extending posteriorly from the pectoral girdle to the baseof the central caudal-fin rays in specimens of all sizes. This stripe apparently subsumes the dark humeral mark typical of *Creagrutus* species, with the humeral mark consequently not apparent across the size range of examined specimens. The species also is unique within the

TABLE 28.—Morphometrics and meristics of *Creagrutus lepidus:* (A) holotype of *C. lepidus,* MHNLS 9659; and (B) all specimens of *C. lepidus* from which counts and measurements were taken (n=46). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	37.9	24.5–47.1
1. Snout to anal-fin origin	61.7	60.6–64.8
2. Snout to pelvic-fin insertion	46.4	45.8–49.2
3. Snout to pectoral-fin insertion	26.1	26.0–28.3
4. Snout to dorsal-fin origin	50.7	47.6–52.4
5. Dorsal-fin origin to hypural joint	56.5	54.6–57.3
6. Dorsal-fin origin to anal-fin origin	33.8	32.4–36.1
7. Dorsal-fin origin to pelvic-fin insertion	32.7	31.3–35.6
8. Dorsal-fin origin to pectoral-fin insertion	35.8	35.8–37.6
9. Caudal peduncle depth	12.7	10.8–13.7
10. Pectoral-fin length	21.1	20.1–23.0
11. Pelvic-fin length	19.5	17.8–20.3
12. Dorsal-fin length	29.8	26.4–31.2
13. Anal-fin length	23.7	22.1–25.5
14. Head length	26.4	25.5–27.7
15. Postorbital head length	48.0	44.4–48.5
16. Snout length	32.0	27.1–31.9
17. Bony orbital diameter	32.0	30.9–35.8
18. Interorbital width	30.0	27.8–31.9
	Meristics	
Lateral line scales	36	36–37
Scale rows between dorsal-fin origin and lateral line	6	5–6
Scale rows between anal-fin origin and lateral line	4	4–5
Predorsal median scales	11	10–12
Branched dorsal-fin rays	8	8
Branched anal-fin rays	11	11–13
Branched pelvic-fin rays	7	7
Pectoral-fin rays	12	10–13
Vertebrae	35	34–35

Creagrutus-Piabina lineage in having a reduced fifth infraorbital situated completely ventral of the sixth infraorbital. In addition, the combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 3 or 4 teeth on the maxilla, 5 teeth in the primary tooth row of the premaxilla, 6 dentary teeth, 36 or 37 lateral line scales without a lamellar process over each pore, 10 to 12 predorsal median scales, 5 or 6 scale rows between the dorsal-fin origin and the lateral line, 34 or 35 vertebrae, 11 to 13 branched anal-fin rays, the poorly developed third infraorbital distinctly separated ventrally from the horizontal limb of the preopercle, the presence of a distinct midlateral stripe along the entire length of the body, the absence of a distinct humeral mark, which is apparently subsumed into the midlateral stripe, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus lepidus* within the clade composed of *Creagrutus* and *Piabina.*

DESCRIPTION.—Morphometric and meristic data for *Creagrutus lepidus* in Table 28. Body moderately deep compared with most congeners. Greatest body depth approximately at vertical through pelvic-fin insertion. Anterior profile of snout and dorsal profile of head meeting in rounded obtuse angle near vertical line immediately anterior of nares. Dorsal profile of head posterior of that line straight and distinctly posterodorsally inclined. Predorsal profile of body with notable change in alignment relative to that of head; asymmetrically convex, with convexity most pronounced in anterior one-fourth of that region. Dorsal profile of body nearly straight from dorsal-fin origin to caudal peduncle. Ventral profile of head and body smoothly convex from margin of lower lip to pelvic-fin insertion; rounded obtuse angle on ventral surface of lower jaw at anteroventral corner of dentary typical of many *Creagrutus* species not apparent.

Upper jaw distinctly longer than, and overhanging, lower jaw. Anterior portion of snout fleshy, with minute papillae distributed over anterior of snout and continuing onto upper lip, margin of upper jaw, and into mouth on fleshy folds between inner and outer rows of premaxillary teeth. Lower lip distinctly fleshy, particularly anteriorly, with papillae most numerous on dorsal surface of lip and continuing in decreasing numbers posteroventrally.

Infraorbital series weakly developed, covering approximately one-half of cheek. Ventral margin of third infraorbital distinctly separated from horizontal limb of preopercle. Posterior margins of third through fifth infraorbitals well separated from vertical limb of preopercle. Posteroventral margin of infraorbital series rounded and nearly concentric with posteroventral margin of orbit.

Premaxillary dentition in three series: primary row with 5 rounded, unicuspidate to tricuspidate teeth with second through fifth teeth in straight row, and first tooth displaced somewhat medially relative to rest of series, but without distinct gap between first and second teeth of series accommodating anterior tooth of triad of large teeth; triangular cluster of 3 larger teeth with more prominent cusps located medial to primary row; and single tooth similar in morphology to those of primary row, occurring lateral to third or fourth tooth of that series. Maxilla with 3 or 4 conical to tricuspidate teeth. Dentary with 6 teeth; 4 anterior teeth large and tricuspidate, followed by 2 small conical teeth.

Dorsal, anal, and pelvic fins relatively elongate compared with those of other *Creagrutus* species. Dorsal-fin rays ii,8 or iii,8; when 3 unbranched rays present, first sometimes well developed (e.g., Figure 53). Dorsal-fin origin slightly posterior of vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin nearly straight, but with anterior rays slightly elongate. Anal-fin rays ii,11–13 or iii,11–13. Mature males with hooks on anterior 9 or 10 branched anal-fin rays; hooks proximally directed, with one hook per segment on posterior branched and segmented portion of main shaft of rays. Pectoral-fin rays i,10–13. Tip of pectoral fin extending posteriorly

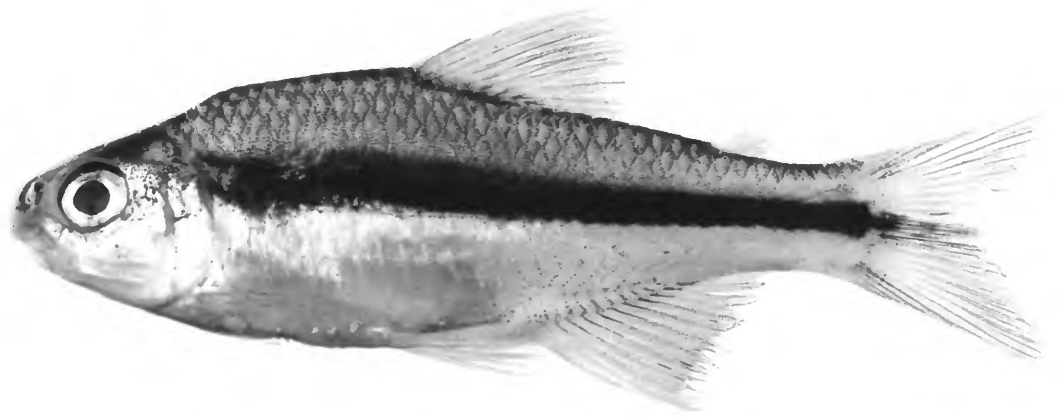

FIGURE 53.—*Creagrutus lepidus*, holotype, MHNLS 9659, 37.9 mm SL; Venezuela, Estado Yaracuy, Río Aroa basin, Quebrada El Charal, Finca El Jaguar, Sierra de Aroa (approximately 10°32'N, 68°32'W).

to, or slightly beyond, pelvic-fin insertion. Pelvic-fin rays i,7. Tip of pelvic fin usually extending posteriorly to beyond anal-fin origin; with distal portion turned medially, giving fin slightly cup-shaped appearance. Branched rays of pelvic fin in mature males with hooks present on all portions of fin rays with exception of smaller distal branches.

Gill rakers 6–7 + 9–10.

COLORATION IN LIFE (based on photographs of live aquarium specimens provided by H.G. Evers).—Overall coloration darker on dorsal portions of head and body. Dorsal portion of iris golden. Head and body flecked with golden spots. Golden coloration concentrated into patches on opercle and on ventrolateral portion of body above anal-fin base. Dark midlateral stripe obvious, continuing onto middle caudal-fin rays. Lateral ray of pelvic fin and distal portions of anterior rays of dorsal and anal fins white.

COLORATION IN ALCOHOL.—Head of specimens from the type locality in the Río Aroa basin with pattern of diffuse, dark chromatophores on dorsal surface, chromatophores most concentrated posteriorly and on snout and upper lip, with small crescent of dark pigmentation immediately anterior of nares; crescent particularly obvious in some overall darker specimens from Río Urama. Some specimens from the Río Urama with overall head pigmentation significantly darker than samples from the Río Aroa system, with chromatophores larger and more concentrated. Band of scattered, dark chromatophores extending from pigmentation on snout posteriorly to anteroventral margin of orbit, continuing around ventral and posterior margins of orbit; band developed to differing degrees along its length and between specimens. Lateral surface of head with numerous scattered, dark chromatophores overlying posterodorsal portions of infraorbital series and dorsal, and sometimes middle, regions of opercle. Pigmentation on middle region of opercle limited to scattered chromatophores other than in subset of specimens from Río Urama in which pigmentation more concentrated. Those specimens also have dark chromatophores on dorsal portion of opercle forming solid dark mark.

Dorsal portion of body with dark pigmentation concentrated on posterior exposed portion of scales, but with posterior margin of each scale unpigmented; overall pigmentation pattern reticulate. Reticulate pattern nearly completely masked by darker overall body pigmentation in some individuals from Río Urama basin. Distinct midlateral dark stripe extending posteriorly from pectoral girdle to slightly beyond bases of central caudal-fin rays. Stripe generally most sharply defined ventrally, extending below lateral line in region posterior of vertical through anal-fin origin, gradually merging dorsally into dark pigmentation on body, more so anteriorly. Limits of anterior portion of midlateral stripe somewhat variable, but always extending ventral of lateral line, perhaps representing imbedded humeral mark of many *Creagrutus* species. Stripe not quite as distinct in Río Urama sample, perhaps as a result of specimens having been kept as aquarium specimens. Two Río Urama specimens with stripe fainter than in Río Aroa samples, fading anteriorly. Other two Río Urama specimens with anterior and to a degree dorsal portions of stripe merging into overall dark body pigmentation.

Central caudal-fin rays with large dark chromatophores basally. Diffuse dark smaller chromatophores associated with remainder of central rays and extending across distal portion of ventral lobe of fin. Dark chromatophores also associated with five dorsalmost branched rays of upper lobe of caudal fin. Posterior dorsal and ventral procurrent rays darkly pigmented. Anal fin with dark pigmentation associated with anterior surface of basal portions of rays. Río Aroa population samples with scattered, darker, small chromatophores on distal portions

of fin membranes; pigmentation on this portion of anal-fin rays more pronounced in limited sample from the Río Urama, particularly in two specimens with distinctly darker overall pigmentation. Pectoral-fin rays outlined by small dark chromatophores. Pelvic fins hyaline in nearly all specimens, with scattered chromatophores in darker specimens from Río Urama.

ECOLOGY.—The type locality of *Creagrutus lepidus* is a relatively small stream with alternating pools (to 3 m depth) and regions of rapid current. The bottom is mostly sandy with numerous larger stones and lacks submerged vegetation. *Creagrutus lepidus* in more abundant in pools than in regions of rapid current flow, gathering in groups of 15 to 30 individuals typically distributed from the middle to the bottom of the water column (C.A. Lasso, pers. comm., 1992). Johannes (1996: 13–14) reported that in the Quebrada Aqua Clara, a tributary to the Río Urama, the species' habitat was a 50 cm deep stream with pools 2 m deep. The pH of the water at that locality was 8.0. Two specimens prepared for clearing and staining in this study and examined for gut contents, had only chopped seeds in their stomach and intestines.

DISTRIBUTION.—*Creagrutus lepidus* is only known from the Río Aroa and Río Urama, Caribbean Sea versant drainages of northern Venezuela (Figure 51, square; see also "Remarks," below).

COMPARISONS.—In addition to *Creagrutus lepidus,* only one other *Creagrutus* species, *C. lassoi,* is known from the Río Aroa basin. The two species can be readily distinguished by the presence of a distinct, vertically elongate humeral mark in *C. lassoi,* which is absent in *C. lepidus,* and by the continuous midlateral stripe in *C. lepidus,* which contrasts with a midlateral stripe limited to the posterior one-half to two-thirds of the body in *C. lassoi. Creagrutus lepidus* is the only member of the genus known from the Río Urama system.

REMARKS.—Subsequent to the description of *Creagrutus lepidus,* an aquarium specimen of the species was illustrated in color by Evers (1996, cover photo). That author (1996:7) cited the specimen as having originated in northern Venezuela. The exact collection locality (H.G. Evers, in litt.; Johannes, 1996:13) is the Quebrada Aqua Clara, a tributary of the Río Urama (the latter locality at 10°35′N, 69°16′W), an independent drainage in the northern portions of Carabobo State. This locality represents a more easterly record for the species relative to its only previous record, the Río Aroa basin. We know of no specimens of the species from the Río Yaracuy basin which lies between the Aroa and Urama drainage basins. Interestingly, Ceas and Page (1996:671) recently described *Chaetostoma yurubiense,* a species of loricariid catfish, only from the basins of the Ríos Aroa, Yaracuy, and Urama, distributional limits matching those of *Creagrutus lepidus.*

GEOGRAPHIC VARIATION.—As far as we are aware, the only population sample of *Creagrutus lepidus* captured subsequent to its original description (Vari et al., 1993) was a series of specimens collected by Thomas Johannes in the Río Urama, northern Venezuela (see Evers, 1966; Johannes, 1996). These specimens were kept alive in aquaria, and a subsample, which evidently died in that habitat, were subsequently deposited in the holdings of MTD and borrowed for examination. The four specimens are nearly all larger (38.1–47.1) than the more extensive samples from the Río Aroa basin (n=42, 24.2–42.4 mm SL in 36 specimens). The samples from the two river basins agree in examined meristics and morphometrics, with the only notable feature being that three specimens from the Río Urama have 11 branched anal-fin rays (fin damaged in fourth specimen), all at the lower end of the range for this feature within the Río Aroa samples (11 to 13 branched anal-fin rays). As noted above (see under "Coloration in Alcohol"), various details of head and body pigmentation in the Río Urama sample show a broader range of variation than found in the series of specimens that were the basis for the original species description. It is impossible to determine to what degree, if any, this variation is a consequence of the specimens having been maintained for a period of time in aquaria. The variation, furthermore, overlaps the conditions found in the original population samples from the Río Aroa system; therefore, we consider the populations from the Río Aroa to be conspecific with those from the Río Urama. Additional field-preserved samples from the Ríos Aroa and Urama and intervening streams will be necessary to determine the significance, if any, of the variation in the limited sample from the Río Urama relative to conditions in the type series.

MATERIAL EXAMINED.—51 specimens (46, 24.5–47.1).

VENEZUELA. *Yaracuy:* Sierra de Aroa, Río Aroa basin, Finca El Jaguar, Quebrada El Charal (approximately 10°32′N, 68°32′W), MHNLS 9659, 1 (37.9, holotype of *Creagrutus lepidus*); MHNLS 4144, 12 (27.8–39.2, paratypes of *Creagrutus lepidus*); MBUCV V-23560, 12 (24.5–37.8; paratypes of *Creagrutus lepidus*); USNM 325045, 10 (25.7–42.4; paratypes of *Creagrutus lepidus;* 2 specimens cleared and counterstained for cartilage and bone); CAS 79520, 7 (26.3–40.1; paratypes of *Creagrutus lepidus*); MHNLS 4715, 5 (paratypes of *Creagrutus lepidus*). *Carabobo:* Quebrada Aqua Clara, tributary of Rio Urama (latter locality at 10°35′N, 69°16′W), MTD F 17701–17704, 4 (38.1–47.1).

Creagrutus machadoi, new species

FIGURES 51, 54, TABLE 29

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 6, occasionally 5, teeth in the rimary series of each premaxilla, 2 to 4 maxillary teeth, 5 teeth on each dentary, 8 or 9 predorsal median scales, 38 or 39 lateral line scales without a lamellar process over each pore, 4 scale rows between the dorsal-fin origin and the lateral line, 3 scale rows between the anal-fin origin and the lateral line, 9 or 10 branched anal-fin

TABLE 29.—Morphometrics and meristics of *Creagrutus machadoi*, new species: (A) holotype of *C. machadoi*, MCNG 18852; and (B) paratypes of *C. machadoi* (n=11). Standard length is expressed in mm; measurements 1 to 14= percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	43.8	26.7–44.5
1. Snout to anal-fin origin	66.6	62.4–67.7
2. Snout to pelvic-fin insertion	49.4	46.9–52.1
3. Snout to pectoral-fin insertion	26.3	25.6–27.6
4. Snout to dorsal-fin origin	48.0	46.4–49.3
5. Dorsal-fin origin to hypural joint	55.2	51.8–55.9
6. Dorsal-fin origin to anal-fin origin	30.4	25.9–28.3
7. Dorsal-fin origin to pelvic-fin insertion	26.3	20.9–24.4
8. Dorsal-fin origin to pectoral-fin insertion	32.1	28.3–31.1
9. Caudal peduncle depth	11.1	9.9–11.2
10. Pectoral-fin length	21.7	18.1–21.7
11. Pelvic-fin length	15.6	14.2–16.4
12. Dorsal-fin length	23.0	20.4–24.0
13. Anal-fin length	19.1	17.5–19.6
14. Head length	28.1	26.2–29.8
15. Postorbital head length	43.8	38.4–43.4
16. Snout length	28.5	25.5–32.0
17. Bony orbital diameter	35.1	33.5–43.0
18. Interorbital width	27.8	26.1–30.1
	Meristics	
lateral line scales	39	38–39
Scale rows between dorsal-fin origin and lateral line	4	4
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	8	8–9
Branched dorsal-fin rays	8	8
Branched anal-fin rays	10	9–10
Branched pelvic-fin rays	5–6[1]	6–7[2]
Pectoral-fin rays	13	11–13
Vertebrae	37	36–38

[1]Five branched pelvic-fin rays with 1 unbranched medial ray present on left side and 6 branched and 1 unbranched medial ray present on right side of holotype.

[2]Medial pelvic-fin ray unbranched when 6 branched rays present; 7 branched rays present in only 1 specimen.

rays, 5 to 7 gill rakers on the upper limb and 10 or 11 gill rakers on the lower limb of the first gill arch, the distance from the snout to the dorsal-fin origin (46.4%–49.3% of SL), the distance from the dorsal-fin origin to the hypural joint (51.8%–55.9% of SL), the distance from the dorsal-fin origin to the anal-fin origin (25.9%–30.4% of SL), the distance from the dorsal-fin origin to the pelvic-fin insertion (20.9%–26.3% of SL), the postorbital head length (38.4%–43.8% of HL), the interorbital width (26.1%–30.1% of HL), the bony orbital diameter (33.5%–43.0% of HL), the gap between the ventral margin of the third infraorbital and the horizontal limb of the preopercle, the absence of a distinct spot of dark pigmentation at the base of the middle caudal-fin rays, the vertical humeral mark without a secondary, dorsal patch of pigmentation, the absence of a distinct patch of pigmentation on the dorsal fin, and the lack of a series of dark spots along the midlateral surface of the body distinguishes *Creagrutus machadoi* within the clade formed by *Creagrutus* and *Piabina*.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus machadoi* in Table 29. Body fusiform to slightly compressed. Greatest body depth 1 or 2 scale rows anterior of base of anteriormost dorsal-fin ray. Dorsal profile of head distinctly convex from margin of upper lip to vertical through anterior margin of orbit, straight from that point across dorsal surface of head to posterior tip of supraoccipital spine. Predorsal profile of body with distinct, but shallow, convexity from tip of supraoccipital to origin of first dorsal-fin ray. Dorsal profile of body straight to slightly concave from dorsal-fin origin to anterior procurrent caudal-fin ray. Ventral profile of lower jaw broadly rounded. Ventral profile of body slightly convex from isthmus to pelvic-fin insertion; straight to slightly convex from anterior anal-fin ray posteriorly to caudal peduncle.

Anterior profile of head forming broadly rounded angle ranging from as low as approximately 90 degrees to about 120 degrees, with its apex located on horizontal plane through ventral portion of orbit. Angle in profile on central portion of lower jaw not as highly accentuated as in many *Creagrutus* species. Upper jaw longer than, and overhanging, lower jaw, with up to three anterior premaxillary teeth projecting anterior of lower lip. Anterior portion of snout relatively soft and fleshy, with concentration of soft tissues. Minute papillae concentrated on snout and area between nostrils, upper lip, and continuing into mouth on fleshy flaps and plicae between outer and medial premaxillary teeth. Lower jaw distinctly fleshy anteriorly, with papillae concentrated on lip and extending ventrally in decreasing concentrations along surfaces of jaw. Inner surfaces of lower lip convolute and papillose, with fleshy flaps extending into mouth. Papillae apparently absent on isthmus and cheek.

Elements of infraorbital series moderately well developed, with gap separating posterior and posteroventral margins of infraorbitals from vertical limb of preopercle equally at most approximately one-half of width of third infraorbital bone. Shape of third infraorbital hemispherical, with greater curvature to posterior margin of infraorbital than that of orbit. Fourth infraorbital nearly rectangular.

Premaxillary teeth in three distinct series: primary series in form of arch, with 5 (3 of 14 specimens) or 6 unicuspidate to tricuspidate teeth, anteriormost 2 or 3 teeth series unicuspidate; medial, triangular cluster of three large tricuspidate teeth, posterior two largest and with most highly developed cusps; and single outer unicuspidate tooth located approximately lateral to, or slightly posterior of, fourth tooth in main row. Maxilla with 2 to 4 weakly tricuspidate flattened teeth. Dentary usually with 5 unicuspidate to weakly tricuspidate teeth. Two anterior dentary teeth largest with distinct, but small, lateral cusps; third tooth tricuspidate and slightly smaller than preceding teeth; remaining dentary teeth unicuspidate or tricuspidate with indistinct lateral cusps and distinctly smaller than anterior three teeth.

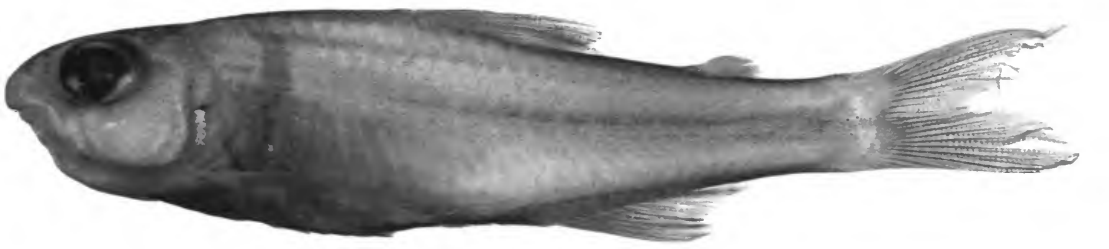

FIGURE 54.—*Creagrutus machadoi*, new species, holotype, MCNG 18852, 43.8 mm SL; Venezuela, Bolivar, upper Río Caura, Caño Yumucukena, within 4 km of its mouth.

Dorsal-fin rays ii,8 in all specimens. Dorsal-fin origin located slightly anterior to vertical through pelvic-fin origin. Distal margin of dorsal fin slightly concave, resulting from elongation of posterior unbranched and anterior 2 or 3 branched rays, and 2 posterior branched rays. Anal-fin rays ii,9–10 or iii,9 (latter in only one specimen). Anal fin with hooks, when present (one 26.5 mm SL specimen; MCNG 18917), singly on third and fourth segments of first branched ray. Distal margin of anal fin slightly sigmoidal, with second unbranched and first and second branched rays forming slightly elongate lobe. Posterior two anal-fin rays longer than immediately preceding rays. Pectoral-fin rays i,11 to 13, typically 12 to 13. Pectoral fin moderately long, extending posteriorly nearly to pelvic-fin origin. Pelvic-fin rays i,6,i or i,7 (only in one specimen) (holotype with i,6,i on one side and i,5,i on other). Hooks on pelvic-fin rays, when present, on medial surfaces of segmented and unsegmented portions of main shaft and medial secondary branches of all branched rays. Pelvic fin relatively long, in some specimens reaching posteriorly slightly beyond anterior anal-fin ray. Posterior margin of body scales smoothly rounded. Pelvic axillary process comprising a single, elongate scale.

Gill rakers 5–7+10–11.

COLORATION IN ALCOHOL.—Overall pigmentation very poorly developed. Ground coloration very pale straw, with observed dark chromatophores very small and punctate, ranging from dark brown to black in most portions of head and body. Dorsal surface of head with scattered, small, dark brown chromatophores, most concentrated over snout and central portion of upper lip, and extending onto plicate tissues of roof of mouth, dorsal surfaces of frontal and parietal portions of cranium, including frontal fontanel. Dark crescent-shaped batch of dark chromatophores located immediately anterior of anterior nares. Little or no dark pigmentation on lateral portions of upper lip and maxilla and interorbital area. Band of scattered, dark brown chromatophores extending from immediately lateral of nares posteroventrally and continuing around ventral and posterior margins of orbit. Dorsal one-half of gill cover in region posterior to orbit with numerous scattered, small, dark chromatophores; number of chromatophores decreasing from posterodorsal region of head ventrally onto upper portion of cheek and gill cover. Lower lip and fleshy portion of jaw speckled with small, black chromatophores; other ventral areas of head unpigmented.

Dark body pigmentation diffuse, mostly confined to region dorsal of lateral line. Pigmentation concentrated as vertical bands along anteriormost exposed portion of each scale on four dorsalmost, longitudinal rows of scales. Scattered chromatophores present in posterior fields of all scales dorsal of lateral line. Small area of middorsal region in area of two median scales with cluster of large dark chromatophores similar in size and color to those of humeral mark. Humeral mark usually in form of anteriorly concave vertical bar without region of particularly dense pigmentation and tapered ventrally to narrow band below lateral line. Flank unpigmented ventral of lateral line except for dark pigmentation associated with humeral bar and posterior portion of lateral stripe, and for very sparsely scattered, dark chromatophores delineating hypaxial myosepta immediately dorsal of anal-fin base. Midlateral stripe highly diffuse anteriorly, with anterior portion overlying first and second scale rows dorsal of lateral line, becoming more densely pigmented and somewhat wider posteriorly and extending ventral of lateral line on posterior portion of caudal peduncle.

All unbranched and anterior four branched dorsal-fin rays darkly pigmented, especially along distal one-fourth to one-half of their lengths. Smaller dark pigment cells associated with basal one-half of all dorsal-fin rays. Unbranched and anterior branched anal-fin rays hyaline; remainder of anal fin with small dark chromatophores located along anterior margin and adjacent membrane of each ray. Caudal-fin rays delineated mainly by dark brown pigmentation, with more lightly pigmented cells over central portion of fin. Caudal fin with distal one-half of dorsal lobe and distal one-fourth of ventral mostly unpigmented. Pelvic and pectoral fins hyaline except in larger (greater than 40 mm SL) specimens, which have dark line of pigmentation delineating lateral pectoral-fin ray and patch of more lightly pigmented chromatophores near tip of longest three or four branched rays.

ETYMOLOGY.—The specific name, *machadoi,* is in honor of our coauthor on other papers involving *Creagrutus,* Antonio Machado-Allison of the Universidad Central de Venezuela, in acknowledgment of his assistance to the authors in the laboratory and the field through the years, and in recognition his many contributions to our knowledge of Neotropical fishes.

ECOLOGY.—A specimen of *Creagrutus machadoi* prepared for clearing and staining in this study had insects in its stomach.

DISTRIBUTION.—*Creagrutus machadoi* is known only from Río Caura basin, a right bank tributary of the main Río Orinoco (Figure 51, star).

COMPARISONS.—In addition to *Creagrutus machadoi,* three other members of the genus occur in the Río Caura basin, *C. bolivari, C. phasma,* and *C. xiphos. Creagrutus machadoi* is readily distinguished from these other species by the features cited in "Key to the *Creagrutus* Species in the Río Orinoco Basin."

MATERIAL EXAMINED.—14 specimens (14, 26.5–44.5).

HOLOTYPE.—VENEZUELA. *Bolivar:* Departamento Cedeno, upper Río Caura, Caño Yumucukenã, within 4 km of its mouth, collected by B. Stergios et al., 15 May 1988, MCNG 18852, 1 (43.8).

PARATYPES.—11 specimens (11, 26.7–44.5).

VENEZUELA. *Bolivar:* Departamento Cedeno, upper Río Caura, Caño Yumucukenã, within 4 km its mouth, collected with holotype, MCNG 41717, 6 (28.1–44.5); USNM 359641, 2 (31.0–38.2). Departamento Cedeno, Río Caura, at the base of Raudal Sejiato (=Cietao; 5°34′N, 64°19′W), collected by B. Stergios, 22 May 1988, MCNG 18896, 3 (26.7–30.6).

NONTYPE SPECIMENS.—2 specimens (2, 26.5–27.7).

VENEZUELA. *Bolivar:* Departamento Cedeno, Río Caura, Isla Guanaguanadi, MCNG 18917, 2 (26.5–27.7).

Creagrutus magoi, new species

FIGURES 51, 55, TABLE 30

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 6 teeth in the primary series of each premaxilla, 2 or 3 maxillary teeth, 5 teeth on each dentary, 9 to 11 predorsal median scales, 37 to 41 lateral line scales without a lamellar process over each pore, 4, rarely 5, scale rows between the dorsal-fin origin and the lateral line, 3 scale rows between the anal-fin origin and the lateral line, 11 or 12 branched anal-fin rays, 9 to 11 gill rakers on the upper limb and 13 or 14 gill rakers on the lower limb of the first gill arch, the distance from the dorsal-fin origin to the anal-fin origin (29.2%–33.8% of SL), the distance from the dorsal-fin origin to the pelvic-fin insertion (24.8%–29.0% of SL), the postorbital head length (39.2%–46.2% of HL), the interorbital width (30.4%–34.3% of HL), the contact, or near contact, between the ventral margin of the third infraorbital and the horizontal limb of the preopercle, the lack of a distinct spot of dark pigmentation at the base of the middle caudal-fin rays, the vertically elongate humeral mark in the form of an inverted comma without a secondary, dorsal patch of pigmentation, the absence of a distinct patch of pigmentation on the dorsal fin, and the lack of a series of dark spots along the midlateral surface of the body distinguishes *Creagrutus magoi* within the clade formed by *Creagrutus* and *Piabina.*

TABLE 30.—Morphometrics and meristics of *Creagrutus magoi,* new species (A) holotype of *C. magoi,* UF 80477; and (B) paratypes of *C. magoi* (n=49). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	62.9	18.7–64.8
1. Snout to anal-fin origin	66.7	62.3–66.6
2. Snout to pelvic-fin insertion	49.7	46.3–49.6
3. Snout to pectoral-fin insertion	26.1	24.2–28.8
4. Snout to dorsal-fin origin	48.5	45.3–48.5
5. Dorsal-fin origin to hypural joint	54.8	53.7–58.4
6. Dorsal-fin origin to anal-fin origin	33.7	29.2–33.8
7. Dorsal-fin origin to pelvic-fin insertion	28.9	24.8–29.0
8. Dorsal-fin origin to pectoral-fin insertion	32.9	30.1–33.3
9. Caudal peduncle depth	11.8	10.1–12.2
10. Pectoral-fin length	18.6	18.6–21.5
11. Pelvic-fin length	15.5	14.8–16.6
12. Dorsal-fin length	19.4	19.3–23.4
13. Anal-fin length	15.6	15.0–18.1
14. Head length	27.0	24.9–28.8
15. Postorbital head length	42.4	39.2–46.2
16. Snout length	31.8	27.0–31.9
17. Bony orbital diameter	31.8	31.0–37.1
18. Interorbital width	34.2	30.4–34.3
	Meristics	
Lateral line scales	38	37–41
Scale rows between dorsal-fin origin and lateral line	5	4–5[1]
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	10	9–11
Branched dorsal-fin rays	8	7–8[2]
Branched anal-fin rays	12	11–12
Branched pelvic-fin rays	6	6
Pectoral-fin rays	13	12–14
Vertebrae	37	36–38

[1]Five scales between dorsal-fin origin and lateral line present in only 2 of 49 paratypes.

[2]Seven branched anal-fin rays present in only 1 of 49 paratypes.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus magoi* in Table 30. Head and body relatively robust, more so in anterior portion of body in larger specimens. Greatest body depth at, or sometimes slightly anterior of, dorsal-fin origin. Dorsal profile of head distinctly convex from margin of upper lip to vertical through posterior nostril, slightly convex from that point to above center of orbit and then straight to tip of supraoccipital spine. Interorbital region transversely rounded. Dorsal profile of body slightly convex from tip of supraoccipital spine to dorsal-fin origin, but without any distinct

change in alignment relative to dorsal profile of head; convexity more pronounced in larger specimens. Dorsal surface of body with obtuse middorsal ridge; ridge more obvious posteriorly. Ventral profile of head with obtuse angle at anteroventral corner of dentary, angle variably obvious, profile slightly convex from angle to isthmus. Prepelvic profile of body barely convex in smaller individuals, only somewhat more convex in certain larger specimens. Prepelvic region of body obtusely flattened transversely.

Head obtusely pointed in lateral view, more compressed in dorsal view. Upper jaw longer than, and overhanging, lower jaw. Anterior of snout, particularly anteromedial portion, with numerous papillae. Papillae more concentrated on fleshy upper lip, especially along ventral margin of lip and on folds and plicae extending between outer and medial premaxillary teeth. Lower lip with numerous papillae on dorsal surface and scattered papillae anteriorly.

Infraorbital series well developed in all specimens larger than 30 mm SL, with ventral margin of third infraorbital contacting, or nearly contacting, horizontal limb of preopercle. Posterior margins of third through fifth infraorbitals distinctly separated from vertical limb of preopercle in smaller specimens; gap decreasing proportionally, but still distinct, in larger specimens.

Premaxillary dentition in three series: primary series sigmoid, with 6 tricuspidate teeth, without pronounced gap between first and second tooth of series but with medial tooth separated from contralateral series by distinct gap; triangular cluster of 3 teeth, all larger to distinctly larger than those of primary series; and single tooth of form similar to that of primary series occurring lateral to fourth tooth of primary series. Maxilla with 2 or 3 tricuspidate teeth. Dentary with 5 tricuspidate teeth; second tooth more massive and about one-third longer than first tooth; second tooth more than twice as high as much smaller third tooth; third tooth two and one-half times as high as fourth tooth; fourth tooth slightly larger than fifth tooth.

Dorsal-fin rays typically ii,8, rarely ii,7. Dorsal-fin origin approximately at vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin slightly concave. Anal-fin rays iii,11–12. Profile of distal margin of anal fin concave, with moderate lobe anteriorly in larger individuals. Single mature male having anal-fin hooks on first and second branched rays. Pectoral-fin rays i,11–13. Tip of pectoral fin falling 1 or 2 scales short of pelvic-fin insertion. Pelvic-fin rays i,6,i. Tip of pelvic fin nearly contacting, or more typically falling 1 scale short of, anal-fin origin. Single mature male with pelvic-fin ray hooks limited to medial branch of all branched rays.

Gill rakers 9–11 (9 rare) + 13–14.

COLORATION IN ALCOHOL.—Ground coloration tan. Dorsal surface of head in smallest specimens with dense deep-lying pigmentation overlying brain and with scattered, dark chromatophores on dorsal surface of head and snout. Surface chromatophore field getting increasingly dense with larger size, with largest individuals having entire dorsal surface of head covered with dense field of small, dark chromatophores extending anteriorly to margin of upper lip and to distal margin of maxilla in larger specimens. Region anterior to nostrils with pigmentation more intense, forming distinct crescent-shaped patch present in specimens of all sizes. Smaller individuals with narrow band of dark pigmentation extending from anteroventral to nostrils to under orbit; band subsumed into overall darker pigmentation in that region in larger specimens. Region posterior to orbit and dorsal portion of opercle with scattered, dark chromatophores in smaller specimens, chromatophore field expanding ventrally in larger individuals. Largest specimens with patch of scattered chromatophores on posteroventral corner of cheek near angle of preopercle.

Scales of posterolateral surface of body in smaller specimens with patch of dark chromatophores on basal portion of exposed field. Medium-sized specimens with series of small chromatophores along posterior margin of scales; chromatophore field becoming progressively wider in larger individuals and forming reticulate pattern. Humeral mark obvious and vertically elongate in specimens of all sizes. Mark in form of inverted comma, with main body of mark dorsal to lateral line and with chromatophore field density highest in portion of mark within one and one-half to two scales of dorsal midline. Humeral mark in some individuals extending slightly ventral of lateral line as ventrally tapering patch of chromatophores. Midlateral stripe of deep-lying chromatophores limited to posterior two-thirds of body, more intense posteriorly; merging anteriorly into overall dark pigmentation on lateral surface of the body in larger individuals.

Dorsal fin with second unbranched ray and distal portions of first and second branched rays covered with dark stellate chromatophores. Membranes of all but posterior one or two branched dorsal-fin rays with dispersed dark, irregularly shaped chromatophores. Chromatophore field becoming progressive shorter on distal portions of successive fin membranes. First through third unbranched rays along with first and sometimes second branched anal-fin rays unpigmented; otherwise anal-fin rays outlined by small dark chromatophores, particularly basally, with scattered chromatophores on intervening portions of fin membranes. Rays of upper and lower margins of caudal fin along with middle caudal-fin rays outlined to varying degrees by small dark chromatophores; intervening rays hyaline. Large specimens with pronounced darkening of ventral caudal-fin rays with pigmentation almost appearing as dark stripe. Pectoral and pelvic fins hyaline, or with some scattered, small, dark chromatophores in larger specimens.

ETYMOLOGY.—The specific name, *magoi,* is in honor of Francisco Mago Leccia, formerly of the Universidad Central de Venezuela, in honor of his major contributions to our understanding of South American freshwater fishes and for all his assistance to the senior author through the years.

ECOLOGY.—A portion of the paratype series (ANSP 159834, USNM 353306) and the nontypes collected with them (ANSP

FIGURE 55.—*Creagrutus magoi,* new species, holotype, UF 80477, 62.9 mm SL; Venezuela, Bolivar, Río Chaviripa, where crossed by bridge on road from Caicara to San Fernando de Atabapo (approximately 7°11′N, 66°18′W).

177716) were collected in a caño of up to 1.5 m depth over a bottom of sand, bedrock, aquatic vegetation, and debris.

DISTRIBUTION.—*Creagrutus magoi* occurs in the Ríos Chaviripa and Parguaza, right bank tributaries to the Río Orinoco in Bolivar, Venezuela (Figure 51, triangles).

COMPARISONS.—Within the Río Orinoco basin *Creagrutus magoi* is most similar to *C. provenzanoi,* a species that occurs in the Río Cataniapo, a right bank tributary to the Río Orinoco upstream of the range of *C. provenzanoi.* The two species can be readily distinguished by differences in the number of gill rakers on the upper limb of the first gill arch (9 to 11, rarely 9, in *C. magoi* versus 7 or 8 in *C. provenzanoi*), and in the number of scales above the lateral line to the dorsal-fin origin (4, rarely 5, in *C. magoi* versus 5, very rarely 4, in *C. provenzanoi*). The two species also differ in the width of the interorbital region (30.4%–34.3% of HL in *C. magoi* versus 27.4%–30.1% of HL in *C. provenzanoi*).

Creagrutus magoi is rather similar in meristics and morphometrics to *C. ephippiatus* of the Río Siapa, an endemic to a tributary to the upper Río Negro. The species differ, however, in overall body form, which is best reflected in the relative distance from the dorsal-fin origin to the anal-fin origin (29.2%–33.8% of SL in *C. magoi* versus 27.8%–29.7% of SL in *C. ephippiatus*), and in details of pigmentation (form of humeral mark and pigmentation of middle caudal-fin rays). The species also have a pronounced modal shift in the number of total vertebrae (*C. magoi:* 36(6), 37(38), 38(2) versus *C. ephippiatus:* 38 (34), 39(10), 40(1)).

GEOGRAPHIC VARIATION.—Available specimens of *Creagrutus magoi* originated in two right bank tributaries of the Río Orinoco, the Río Chaviripa, and the Río Parguaza. The samples from these basins agree in morphometrics and meristics, but the population sample from the Río Parguaza has more intense development of body, head, and caudal-fin pigmentation.

MATERIAL EXAMINED.—203 specimens (50, 18.7–64.8).

HOLOTYPE.—VENEZUELA. *Bolivar.* Río Chaviripa, where crossed by bridge on road from Caicara to San Fernando de Atabapo (approximately 7°11′N, 66°18′W), collected by D.C. Taphorn et al., 14 Apr 1984, UF 80477, 1 (62.9).

PARATYPES.—49 (49, 18.7–64.8).

VENEZUELA. *Bolivar:* Río Chaviripa, where crossed by bridge on road from Caicara to San Fernando de Atabapo (approximately 7°11′N, 66°18′W), collected with holotype, UF 11079, 6 (30.2–55.9); USNM 353864, 2 (56.3–58.6; 1 specimen cleared and counterstained for cartilage and bone). Río Chaviripa, where crossed by bridge on road from Caicara to San Fernando de Atabapo (approximately 7°11′N, 66°18′W), collected by D.C. Taphorn et al., 6 Apr 1984, UF 80423, 5 (26.8–57.9); USNM 353863, 1 (42.2). Caño 15.1 km E of ferry crossing on Río Parguaza along road from Caicara to Puerto Ayacucho (approximately 6°26′28″N, 67°09′24″W), collected by B. Chernoff et al., Nov 1985, MBUCV V-17787, 8 (18.7–64.8); USNM 355118, 2 (30.9–48.2); ANSP 159834, 10 (32.7–56.9); USNM 353305, 2 (38.8–44.6). Caño 8 km N of Ciudad Bolivar to Caicara highway on Las Majadas Road, Río Chimaico crossing (7°32′30″N, 64°47′W), collected by W. Saul et al., ANSP 159835, 10 (27.5–49.7); USNM 353306, 2 (36.0–50.9). Rio Agua Blanca, from 100 to 600 m below bridge at crossing of Caicara-Ciudad Bolivar Highway (7°50′N, 63°51′18″W), collected by B. Chernoff et al., 21 Nov 1985, ANSP 161405, 1 (40.8).

NONTYPE SPECIMENS.—153 specimens.

VENEZUELA. *Bolivar:* Caño 15.1 km E of ferry crossing on Río Parguaza along road from Caicara to Puerto Ayacucho (approximately 6°26′28″N, 67°09′24″W), ANSP 177714, 118. Caño 8 km N of Ciudad Bolivar to Caicara highway on Las Majadas Road, Río Chimaico crossing (7°32′30″N, 64°47′W), ANSP 177715, 28. Río Agua Blanca, from 100 to 600 m below bridge at crossing of Caicara-Ciudad Bolivar Highway (7°50′N, 63°51′18″W), ANSP 177716, 7.

Creagrutus manu, new species

FIGURES 51, 56, TABLE 31

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 6, rarely 5, teeth in the primary series on the premaxilla, 2 or 3 teeth on the maxilla, 5 teeth on each dentary, 36 or 37 vertebrae, 13 to 15 branched anal-fin rays, 10 or 11 predorsal median scales, 5 scale rows between the lateral line and the dorsal-fin origin, 6 gill rakers on the upper limb and 12 gill rakers on the lower limb of the first gill arch, the distance from the dorsal-fin origin to the anal-fin origin (33.8%–37.5% of SL), the caudal-peduncle depth (11.9%–13.1% of SL), the postorbital head length (39.5%–46.3% of HL), the bony orbital diameter (31.1%–36.0% of SL), the lack of a series of dark midlateral spots on the body, the vertically elongate humeral mark, and the laterally compressed, relatively deep body distinguish *C. manu* from *Piabina argentea* and all congeners other than *C. barrigai* and *C. pearsoni*. *Creagrutus manu* can be separated from *C. barrigai* by the distance from the snout to the anal-fin origin (63.5%–66.4% of SL versus 58.5%–63.4% of SL, respectively), and the presence in *C. manu* of a dark midlateral stripe that is absent in *C. barrigai*. *Creagrutus manu* can, in turn, be discriminated from *C. pearsoni* by a distinct midlateral body stripe, which is absent in *C. pearsoni*, and by differences in the distance from the snout to the anal-fin origin (63.5%–66.4% of SL versus 59.0%–61.9% of SL, respectively), and the anal-fin length (20.4%–21.8% of SL versus 15.6%–17.4% of SL, respectively).

DESCRIPTION.—Morphometric and meristic data for *Creagrutus manu* in Table 31. Head and body moderately compressed laterally compared with most other *Creagrutus* species. Greatest body depth at or slightly anterior to dorsal-fin origin. Dorsal profile of head distinctly convex from margin of upper lip to vertical through posterior nostril, straight from that point to tip of supraoccipital spine. Interorbital region distinctly convex transversely. Predorsal profile of body smoothly slightly convex and without change in alignment relative to dorsal profile of head in smaller individuals. Convexity more pronounced, with distinct change in alignment of predorsal profile relative to that of head in larger specimens. Predorsal midline with obtuse median ridge. Ventral profile of head with obtuse angle at anteroventral angle of dentary, nearly straight from that point to isthmus. Ventral profile of body slightly convex from isthmus to anal fin, convexity more pronounced in larger individuals. Prepelvic region of body transversely rounded.

Head obtusely rounded in lateral view, somewhat compressed in dorsal view. Upper jaw longer than, and overhanging, lower jaw, somewhat less so in larger individuals. Snout fleshy anteromedially with scattered papillae in that region. Papillae also distributed on lateral surface of upper jaw, and on folds and plicae extending between outer and medial premaxillary teeth. Lower lip fleshy anteriorly, with numerous papillae along dorsal surface and scattered papillae on anteromedial portion.

TABLE 31.—Morphometrics and meristics of *Creagrutus manu*, new species: (A) holotype of *C. manu*, MUSM 8867; and (B) paratypes of *C. manu* (n=5). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	39.7	26.1–39.3
1. Snout to anal-fin origin	65.3	63.5–66.4
2. Snout to pelvic-fin insertion	47.1	46.0–47.6
3. Snout to pectoral-fin insertion	25.4	24.4–25.5
4. Snout to dorsal-fin origin	47.6	49.5–53.4
5. Dorsal-fin origin to hypural joint	54.4	52.4–55.8
6. Dorsal-fin origin to anal-fin origin	37.5	33.8–37.5
7. Dorsal-fin origin to pelvic-fin insertion	34.5	30.5–33.8
8. Dorsal-fin origin to pectoral-fin insertion	40.3	35.1–39.6
9. Caudal peduncle depth	13.1	11.9–13.1
10. Pectoral-fin length	18.4	19.0–20.7
11. Pelvic-fin length	17.4	15.6–17.3
12. Dorsal-fin length	22.6	23.0–26.2
13. Anal-fin length	21.4	20.4–21.8
14. Head length	27.2	25.6–28.0
15. Postorbital head length	46.3	39.5–46.2
16. Snout length	25.9	23.0–26.7
17. Bony orbital diameter	32.4	31.1–36.0
18. Interorbital width	28.8	28.0–32.6
	Meristics	
Lateral line scales	37	37–38
Scale rows between dorsal-fin origin and lateral line	5	5
Scale rows between anal-fin origin and lateral line	4	3–4
Predorsal median scales	11	10–11
Branched dorsal-fin rays	8	8
Branched anal-fin rays	15	13–15
Branched pelvic-fin rays	6	6
Pectoral-fin rays	12	12–13
Vertebrae	36	36[1]

[1]Thirty-seven vertebrae present in 2 of 11 nontype specimens (see also comments under "Remarks").

Infraorbital series moderately developed. Third infraorbital with posteroventral margin curved and central portion of ventral margin of third infraorbital most closely approaching but falling short of horizontal limb of preopercle. Posterior margins of third through fifth infraorbitals falling distinctly short of vertical limb of preopercle.

Premaxillary dentition in three series: primary row slightly sigmoid, consisting of 6, or more rarely 5, teeth, without pronounced gap between first and second tooth of series but with medial tooth separated from anterior tooth of contralateral series by distinct gap; triangular cluster of 3 larger teeth; and single tooth of form similar to that of primary series occurring lateral to fourth tooth of primary premaxillary tooth row, or lateral to area of contact of third and fourth teeth in that series. Maxilla with 2 or 3 tricuspidate teeth. Dentary with 5 teeth; anterior 4 teeth tricuspidate, fifth tooth unicuspidate. First and second

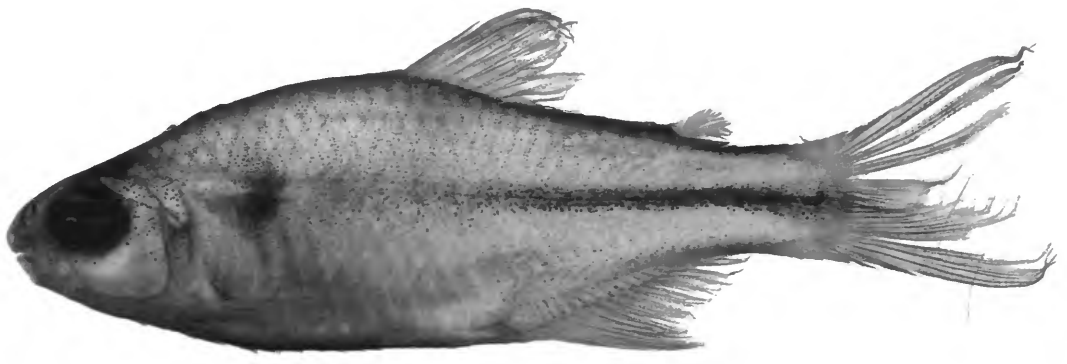

FIGURE 56.—*Creagrutus manu*, new species, holotype, MUSM 8867, 39.7 mm SL; Peru, Madre de Dios, Rio Manu basin, Parque Nacional Manu, Quebrada Agua Clara (approximately 11°57'S, 71°17'W).

teeth distinctly larger than others, subequal, approximately twice height of third tooth; fourth and fifth teeth distinctly smaller and compressed.

Dorsal-fin rays ii,8 in all specimens. Dorsal-fin origin somewhat posterior of vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin slightly concave. Anal-fin rays ii, or iii,13–15; first unbranched ray short in specimens with 3 unbranched rays. Profile of distal margin of anal fin slightly concave, somewhat more so in larger specimens. Hooks typically present on anal-fin rays in mature males of many *Creagrutus* species not present in examined specimens. Pectoral-fin rays i,11–12. Tip of pectoral fin extending posteriorly nearly to pelvic-fin insertion in smaller specimens, only approximately three-fourths of that distance in larger individuals. Pelvic-fin rays i,6,i in all specimens. Tip of pelvic fin extending posteriorly to, or slightly beyond, anus. Hooks typically present on pelvic-fin rays in mature males of many *Creagrutus* species not present in examined specimens.

Gill rakers 6 + 12.

COLORATION IN ALCOHOL.—Ground coloration tan. Dorsal surface of head with scattered moderate-sized chromatophores extending anteriorly onto snout. Deep-lying, dark chromatophores visible on membranes overlying brain. No obvious concentration of dark chromatophores anterior to nostrils contrary to situation in many congeners. Chromatophores anterior to nostril continuous with narrow band of dark chromatophores along ventral and, to varying degrees, posterior margins of orbit. Infraorbitals posterior to orbit along with dorsal portion of opercle covered with varying numbers of scattered chromatophores.

Scales of dorsal portion of body with patch of chromatophores on basal portion of exposed field of scale; chromatophore field delimited posteriorly by distinct margin. Few scattered, dark chromatophores along distal margins of scales. Humeral mark vertically elongate to rotund. All margins of humeral mark quite distinct in smaller specimens; chromatophores of dorsal portion of mark merging into field of dark background chromatophores in larger individuals. Distinct midlateral stripe formed by surface chromatophores present in all examined specimens. Stripe extending from region between vertical approximately through anterior of dorsal fin (larger individuals) or middle of fin (smaller specimens) posteriorly to rear of caudal peduncle. Stripe more intense overall in larger specimens; continuous posteriorly with horizontal stripe extending along middle caudal-fin rays.

Dorsal fin with chromatophores scattered over distal two-thirds of all but posterior rays in larger specimens, chromatophore field less extensive in smaller specimens. Anal fin with most rays variably outlined by small dark chromatophores and with chromatophores scattered over membranes of all but anteriormost and posteriormost rays; density of chromatophores and extent of chromatophore field greater in larger specimens. Caudal fin with dark horizontal stripe across middle rays. Stripe more intense anteriorly in specimens of all sizes and more obvious in larger individuals, particularly those with overall darker head and body pigmentation. Pectoral and pelvic fins hyaline or with few scattered, dark chromatophores in larger individuals.

ETYMOLOGY.—The specific name, *manu*, refers to the type region of the species, the upper portions of the Río Manu of southeastern Peru, and to the Parque Nacional de Manu in which all the examined specimens were collected.

ECOLOGY.—The type series of *Creagrutus manu* was collected in small forest streams with moderate water current over stone, pebble, and sand bottoms.

Stomach contents of the one specimen prepared for clearing and staining in this study consisted solely of chopped up seeds and plant matter.

DISTRIBUTION.—*Creagrutus manu* is known only from a limited region in the upper Río Manu system of southeastern Peru (Figure 51, diamond).

REMARKS.—In addition to the type series, a lot of 11 smaller individuals in somewhat poor condition (USNM 352953, MUSM 13933) also was collected at the type locality. The poor condition of these specimens prevented the taking of counts and measurements for most examined features. The only notable difference between these specimens and the type species is the slightly greater range of vertebrae in the nontypes (36 or 37, versus 36 in the holotype and paratypes).

MATERIAL EXAMINED.—17 specimens (6, 26.1–39.7).

HOLOTYPE.—PERU. *Madre de Dios:* Provincia Manu, Río Manu basin, Parque Nacional Manu, Quebrada Agua Clara, first major quebrada on trail 1 leading from Pakitza (approximately 11°57′S, 71°17′W), collected by H. Ortega et al., 13 Sep 1988, MUSM 8867, 1 (39.7).

PARATYPES.—5 specimens (5, 26.1–39.3).

PERU. *Madre de Dios:* Provincia Manu, Río Manu basin, Parque Nacional Manu, second major quebrada on trail 1 leading from Pakitza (approximately 11°57′S, 71°17′W), collected by H. Ortega et al., 17 Sep 1988, USNM 303067, 2 (27.5–28.5). Provincia Manu, Parque Nacional Manu, Pakitza and vicinity (approximately 11°57′S, 71°17′W), collected by H. Ortega, Oct 1987, MUSM 8868, 1 (26.1). Provincia Manu, Parque Nacional Manu, Pakitza, Quebrada Martín Pescador (approximately 11°57′S, 71°17′W), collected by H. Ortega, 28 Sep 1991, USNM 326903, 1 (39.3; specimen cleared and counterstained for cartilage and bone). Provincia Manu, Parque Nacional Manu, Pakitza and vicinity (approximately 11°57′S, 71°17′W), collected by H. Ortega, Oct 1987, USNM 313476, 1 (32.8).

NONTYPE SPECIMENS.—11 specimens.

PERU. *Madre de Dios:* Provincia Manu, Río Manu basin, Parque Nacional Manu, Pakitza, Quebrada Martin Pescador (approximately 11°57′S, 71°17′W), USNM 352953, 6; MUSM 13933, 5.

Creagrutus maxillaris (Myers, 1927)

FIGURES 57–59, TABLE 32

Creagrudite maxillaris Myers, 1927:118 [type locality: (Brazil, Amazonas), sandbank on the Colombian border Rio Negro, Cucuhy (=Cucuí); also from mouth of [Río] Curamuni (=Curamoni), Río Cassiquiare (=Casiquiare)].—Eigenmann and Myers, 1929:547 [based on Myers, 1927].—Fowler, 1948:82 [literature summary]; 1975:25 [literature summary; *Creagrutus melanzonus* Eigenmann incorrectly listed as junior synonym].—Böhlke, 1953:23 [holotype and paratype depositories].—Roberts, 1967:236 [replacement pattern of jaw teeth].—Myers and Roberts, 1967:248 [discussion of reported ontogenetic variation in premaxillary dentition in species].—Mago-Leccia, 1970:70 [Venezuela]; 1971:10 [Venezuela, (Amazonas), Río Casiquiare].—Böhlke and Saul, 1975:28 [transfer to *Creagrutus*].—Géry and Renno, 1989:3 [dentition noted].

Creagrutus maxillaris Böhlke and Saul, 1975:28 [transfer of species from *Creagrudite* to *Creagrutus*].—Taphorn et al., 1997:71 [cited for Venezuela].

TABLE 32.—Morphometrics and meristics of *Creagrutus maxillaris* (A) holotype of *C. maxillaris*, CAS 30419 (formerly IU 17682); and (B) all other specimens of *C. maxillaris* from which counts and measurements were taken (n= 20). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length. Dashes indicate measurements that could not be taken because of poor condition of holotype.

Characters	A	B
	Morphometrics	
Standard length	75.2	34.2–75.2
1. Snout to anal-fin origin	70.2	64.9–70.2
2. Snout to pelvic-fin insertion	51.2	47.0–51.2
3. Snout to pectoral-fin insertion	26.0	23.0–26.4
4. Snout to dorsal-fin origin	51.4	44.7–51.4
5. Dorsal-fin origin to hypural joint	51.9	50.6–56.3
6. Dorsal-fin origin to anal-fin origin	28.9	26.3–29.1
7. Dorsal-fin origin to pelvic-fin insertion	21.1	18.7–22.1
8. Dorsal-fin origin to pectoral-fin insertion	30.6	27.0–30.6
9. Caudal peduncle depth	9.1	8.8–10.0
10. Pectoral-fin length	18.2	15.1–18.1
11. Pelvic-fin length	13.3	12.5–14.6
12. Dorsal-fin length	–	17.4–20.2
13. Anal-fin length	–	13.8–15.1
14. Head length	28.7	25.1–28.8
15. Postorbital head length	46.8	40.0–46.6
16. Snout length	28.8	25.0–29.0
17. Bony orbital diameter	28.7	29.1–34.6
18. Interorbital width	22.7	21.7–26.8
	Meristics	
Lateral line scales	42	39–42
Scale rows between dorsal-fin origin and lateral line	4	4
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	11	9–11
Branched dorsal-fin rays	8	8
Branched anal-fin rays	10	8–10
Branched pelvic-fin rays	7	6–7
Pectoral-fin rays	13	13–15
Vertebrae	40	38–40

DIAGNOSIS.—The presence of two distinct rows of premaxillary teeth, the very elongate, moderately sloping maxilla compared to the condition in most congeners, and the presence of 5 median scales between the posterior margin of the anus and the anal-fin origin distinguish *Creagrutus maxillaris* from all congeners with the exception of *C. cracentis*, a species only known from the Rio Tapajós basin. These two species can be differentiated by the length of the postorbital portion of the head (40.0%–46.8% of HL in *C. maxillaris* versus 36.8%–38.0% of HL in *C. cracentis*), the bony orbital diameter (28.7%–34.6% of HL in *C. maxillaris* versus 37.0%–40.0% of HL in *C. cracentis*), and to a lesser degree on the pectoral-fin length (15.1%–18.2% of SL in *C. maxillaris* versus 17.9%–20.0% of SL in *C. cracentis*).

DESCRIPTION.—Morphometric and meristic data for *Creagrutus maxillaris* in Table 32. Overall appearance of head and body distinctly elongate compared to most congeners; elongation more obvious in smaller individuals. Body proportionally more elongate in specimens smaller than 25 mm SL in which greatest body occurring at vertical through dorsal-fin origin;

FIGURE 57.—*Creagrutus maxillaris,* holotype, CAS 30419 (formerly IU 17682), 75.2 mm SL; Brazil, Amazonas, Rio Negro at Cucuhy (=Cucuí), sandbank on Colombian border.

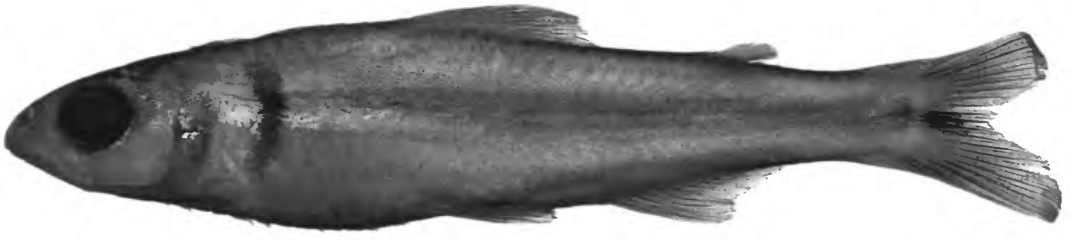

FIGURE 58.—*Creagrutus maxillaris,* ANSP 161235, 41.8 mm SL; Venezuela, Amazonas, Río Ventuari, above confluence with Río Orinoco.

position of greatest body depth shifting anteriorly approximately to vertical through tip of pectoral fin with increasing relative body depth in larger individuals. Dorsal profile of head smoothly rounded from margin of upper lip to region of vertical through posterior nostril at all body sizes; nearly straight from that point to rear of supraoccipital spine. Interorbital region slightly transversely convex in smaller individuals, flat in larger specimens. Dorsal profile of body slightly convex from tip of supraoccipital spine to dorsal-fin origin, barely angled at dorsal-fin base; straight from rear of dorsal-fin base to caudal peduncle in smaller individuals, slightly convex in that region in larger specimens. Ventral profile of head gently convex along anterior of dentary, nearly straight for much of length of dentary and then to isthmus. Distinct angle at anteroventral corner of dentary obvious in many congeners not apparent in *C. maxillaris.* Ventral profile of body from isthmus to anal fin nearly straight or very slightly convex in individuals of up to approximately 30 mm SL; convexity more notable, albeit not pronounced, in larger specimens.

Head pointed anteriorly in lateral view and more so in dorsal view. Upper jaw slightly longer than, and overhanging, lower jaw. Anterior portion of mouth nearly horizontal. Ventral margin of upper jaw gently curved with jaw relatively longer than in all other *Creagrutus* species with exception of *C. cracentis.* Anterior surface of snout not as fleshy as in congeners other than *C. cracentis;* with numerous minute papillae over anterior surface. Papillae also line ventral margin of upper lip, dorsal margin of lower lip, and anterior and anterolateral surfaces of lower jaw. Plicae and fleshy flaps extending between premaxillary teeth of most *Creagrutus* species absent. Lower lip not as fleshy anteriorly as in other *Creagrutus* species.

Infraorbital series well developed. Ventral margin of third infraorbital in contact, or nearly in contact, with horizontal limb of preopercle for much of its length. Posterior margins of third through fifth infraorbitals slightly separated from vertical limb of preopercle, separation between fifth infraorbital and preopercle very slight in larger specimens.

Premaxillary dentition unusual for *Creagrutus* species, with only two distinct rows of teeth. Outer row consisting of 3 teeth arranged in slightly irregular series. First and third teeth unicuspidate with medially recurved distal portions, middle tooth with very weak lateral cusps and slight medial curvature of central cusp. Inner tooth row consisting of 4 tricuspidate teeth, with middle cusp of each tooth distinctly stronger. Elongate maxilla with 10 to 12 tricuspidate teeth. Maxillary teeth with central cusp longer and typically somewhat posteroventrally recurved. Dentary teeth 10 to 12; anterior 3 teeth largest, teeth following those becoming progressively smaller. Dentary teeth

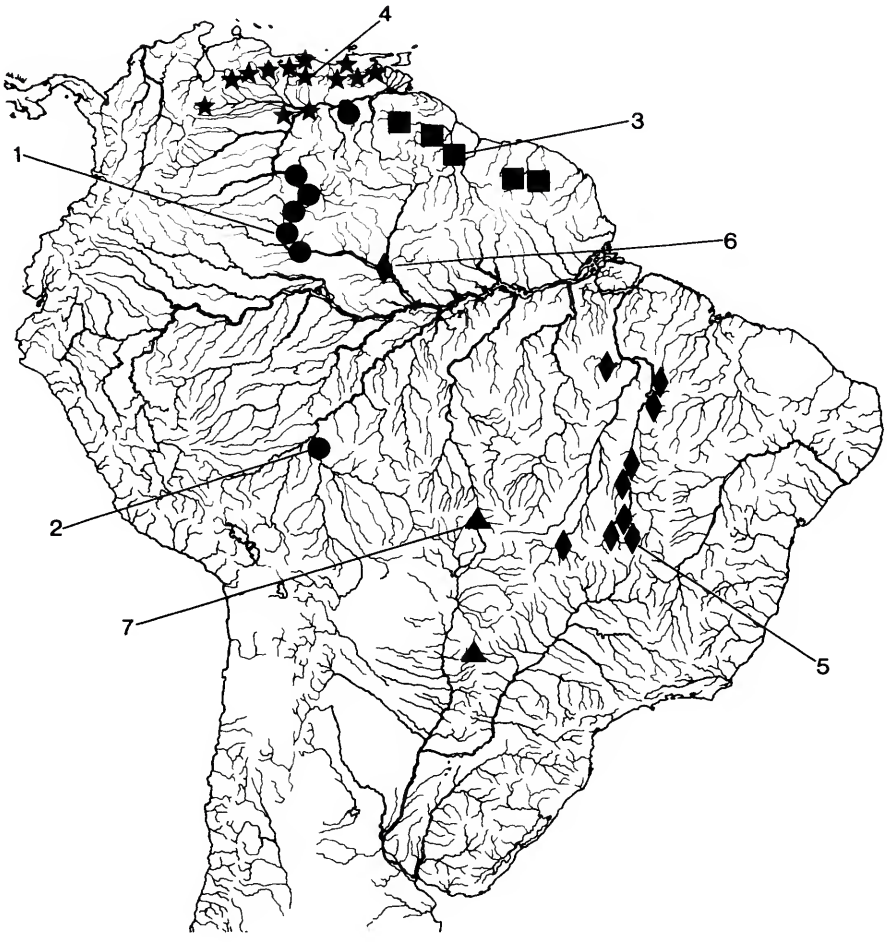

FIGURE 59.—Map of central and northern South America showing geographic distribution of *Creagrutus maxillaris* (dots, 1=type locality, 2=geographically disjunct population tentatively identified as *C. maxillaris*), *Creagrutus melanzonus* (squares, 3=type locality), *Creagrutus melasma* (stars, 4=type locality), *Creagrutus menezesi* (diamonds, 5=type locality, 6=geographically disjunct population tentatively identified as *C. menezesi*), and *Creagrutus meridionalis* (triangles, 7=type locality) (some symbols represent more than one locality or lot of specimens).

tricuspidate with central cusp stronger in smaller individuals, becoming progressively penticuspidate ontogenetically, with central cusp most developed in larger specimens.

Dorsal-fin rays ii,8. Dorsal-fin origin anterior to vertical through pelvic-fin insertion. Profile of distal margin of dorsal-fin slightly concave. Anal-fin rays ii,8–10. Profile of distal margin of anal fin concave. Hooks typically occurring on anal-fin rays in mature males of many *Creagrutus* species not present in examined specimens. Pectoral-fin rays i,12–14; fin extending posteriorly approximately one-half of distance to pelvic-fin insertion, fin proportionally somewhat shorter in larger individuals. Pelvic-fin rays i,6,i in smaller individuals, i,7 in larger specimens. Hooks typically occurring on pelvic-fin rays in mature males of many *Creagrutus* species not present in examined specimens. Tip of pelvic fin extending posteriorly approximately two-thirds of distance to anus.

Gill rakers 7 + 10–12.

COLORATION IN ALCOHOL.—Overall coloration light tan. Dorsal surface of head in smaller individuals covered with superficial small, dark chromatophores. Membranes overlying brain covered with larger, dark, stellate chromatophores in smaller specimens. Dark pigmentation overlying brain, if present, masked by thicker bones and intracranial adipose deposits in larger individuals. Snout and upper jaw with scattering of small dark chromatophores; these slightly more concentrated anterior to nares in smaller specimens. Larger individuals with additional scattered, dark chromatophores on lower jaw, and dorsal portions of opercle and infraorbital series. Distinct concentration of dark chromatophores present an-

terior to nares and along ventral and posterior margins of orbit in other *Creagrutus* species not apparent in *C. maxillaris*. Dorsolateral portion of body with scattered, dark chromatophores. Dorsal portion of body with small dark chromatophores concentrated along posterior portion of scales, forming irregular reticulate pattern. Faint band formed by small dark chromatophores on midlateral surface of body of smaller specimens. Distinction between midlateral band and dark dorsolateral pigmentation on body becoming increasingly obscure with increasing overall body size on anterior portion of body such that band only discrete on posterior one-third of body on specimens larger than approximately 35 mm SL. Presence or absence of distinct midlateral band on posterior portion of body cannot be evaluated in largest examined specimens as a consequence of guanine overlying this region. Humeral mark vertically elongate, typically with anterior margin concave; mark extending dorsally from slightly above horizontal through pectoral-fin insertion to approximately one scale width from dorsal midline. Pigmentation of humeral mark most intense in region centered along lateral line, variably less intense dorsal and ventral of that area.

Dorsal-fin ray margins and membranes with small dark chromatophores. Basal portions of anal-fin rays outlined by chromatophores. Caudal fin with dark stripe formed by superficial chromatophores extending over middle caudal-fin rays; stripe more intensely pigmented basally. Deep-lying dark spot apparent at base of middle caudal-fin rays in smaller specimens. Stripe on middle caudal-fin rays flanked dorsally and ventrally by 2 or 3 relatively unpigmented rays. Remaining caudal-fin rays and procurrent rays covered with scattered, dark chromatophores; chromatophores somewhat more concentrated along ray margins. Pectoral and pelvic fins with only few scattered, small chromatophores.

COMPARISONS.—The distinctive dentition pattern of *Creagrutus maxillaris* readily distinguishes it from all of its congeners other than *C. cracentis*. These two species can be discriminated by the features cited in the "Diagnosis," above.

DISTRIBUTION.—*Creagrutus maxillaris* is known to occur in the Río Orinoco basin rivers draining the Guyana shield, the upper Rio Negro in Brazil and Venezuela, and perhaps upper portions of the Rio Madeira system along Brazilian-Bolivian border (Figure 59, dots; see also "Remarks" immediately following with respect to some locality records).

REMARKS.—The material of *Creagrutus maxillaris* examined in this study has a notably disjunct distribution relative to the more compact ranges of most members of the genus. Most population samples of *C. maxillaris* originated in the upper portions of Rio Negro in northern Brazil and southern Venezuela and in the upper Río Orinoco in southern Venezuela. Outside of this area, a single specimen originated in the Río Aro, a southern tributary of the Río Orinoco, and a single sample is from the upper portions of Rio Madeira basin along the Bolivian-Brazilian border (Figure 59, dot indicated by 2).

The single specimen from the lower portions of the Río Orinoco basin (MCNG 19270), although a major range extension to the northeast, relative to the other records of this species in Venezuela, nonetheless originated in a river draining the Guyana shield; a pattern common to the other samples of the species in that region. This specimen from the lower portions of the Orinoco basin cannot be discriminated from the population samples of *C. maxillaris* that originated in the upper Río Orinoco and Rio Negro.

The series of 15 specimens from the Rio Madeira system (AMNH 39855), herein identified as *Creagrutus maxillaris*, largely lack scales and are in relatively poor overall condition, precluding a definitive identification, but they are either that species or a very similar form. A determination of whether the Rio Madeira population is conspecific with the populations in the Ríos Orinoco and Negro must await the examination of other specimens in good condition from the Rio Madeira.

In his original description of *Creagrudite maxillaris* and in a subsequent publication, Myers (1927:117; 1958:29) proposed that the species underwent an ontogenetic shift from three rows of premaxillary teeth in juveniles, the condition typical for *Creagrutus*, to two rows in larger specimens, an unusual shift in characiforms (Note: the descriptive system for premaxillary dentition utilized by Myers (1927) differs from that used herein). Myers and Roberts (1967:248) corrected this observation and noted that the presumed change in the number of premaxillary tooth rows was rather a consequence of the complex nature of the type series of *Creagrudite maxillaris*. These authors reported that the smaller specimens with three rows of teeth cited by Myers (1927) as *Creagrudite maxillaris* were actually individuals of *Creagrutus melanzonus* Eigenmann. The results of this study indicate, however, that the material identified as the latter species from the upper Rio Negro, the type region of *Creagrudite maxillaris*, is actually *Creagrutus zephyrus*. The examination of a series of specimens of *C. maxillaris* of various body sizes does not reveal any ontogenetic differences in the number of tooth rows, only an ontogenetic increase in the number of cusps on the jaw teeth.

It is unclear whether Myers' association of *Creagrudite* with *Creagrutus* was a consequence of the admixture in the type series of *Creagrudite maxillaris* of specimens of *Creagrutus zephyrus* (see comments in previous paragraph). No other basis is apparent for his statement that *Creagrudite maxillaris* is a "specialized *Creagrutus*" (Myers, 1927:118). Böhlke and Saul (1975:27), in their description of *Creagrutus gephyrus*, synonymized *Creagrudite* into *Creagrutus* because, in their opinion, their new species bridged the morphological gap between the two nominal genera. The phylogenetic results of this study support the inclusion of *Creagrudite* in *Creagrutus*.

Fowler (1975:25) listed *Creagrutus melanzonus* Eigenmann as a junior synonym of *Creagrudite maxillaris* (=*Creagrutus maxillaris* of this study) but did not detail the basis for this synonymy. Although the two species have elongate heads and bodies, they differ in numerous features, most notably in their ar-

rangements of premaxillary teeth, and they and have totally allopatric distributions under the results of this study.

MATERIAL EXAMINED.—60 specimens (20, 34.2–75.2).

BRAZIL. *Amazonas:* Rio Negro, Cucuhy (=Cucuí), sandbank on the Colombian border (1°12′N, 66°50′W), CAS 30419, 1 (75.2, holotype of *Creagrudite maxillaris;* formerly IU 17682); MCZ 31572, 1 (71.5, paratype of *Creagrudite maxillaris*); CAS 157925, 1 (67.7). Rio Negro, Paraná do Jacare (0°30′S, 66°30′W), USNM 330354, 1.

VENEZUELA. *Amazonas:* Río Casiquiare, mouth of the Curamuni (?=Río Curamoní or Guramoni, 2°37′N, 66°12′W), CAS 30420, 2 (39.1–46.0, paratypes of *Creagrudite maxillaris;* formerly IU 17684); CAS 158030, 7 (formerly SU 58030); CAS 158988, 2. Playa and side channel of Río Ventuari, approximately 12 km above confluence with Río Orinoco (4°04′N, 66°56′W), ANSP 161230, 5. Río Ventuari, approximately 10–12 km above confluence with Río Orinoco (4°04′N, 66°56′W), ANSP 161235, 6 (34.5–41.8). Río Orinoco near mouth of Río Iguapo (3°07′N, 65°28′W), ANSP 161234, 1 (34.2). Río Casiquiare, near Solano (2°00′N, 66°57′W), USNM 340955, 1 (40.2). Mata de Palma (3°44′N, 67°00′W), CAS 151036, 1 (specimen cleared and stained for bone); CAS 157965, 5 (1, 36.3); CAS 158198, 3; CAS 160469, 7. Río Aro, Salto El Pajaro, on road to Borbón, near Peñas Negras (latter locality at 7°54′S, 64°18′W), MCNG 19270, 1 (56.0).

The following sample is tentatively identified as *Creagrutus maxillaris* (see comments under "Remarks," above, concerning this identification).

BOLIVIA. *El Beni:* Río Itenez, approximately 9 km SE of Costa Marquez, AMNH 39855, 15 (5, 34.3–43.2).

Creagrutus melanzonus Eigenmann, 1909

FIGURES 59–61, TABLE 33

Creagrutus melanzonus Eigenmann, 1909:30 [British Guiana (=Guyana), Crab Falls, Warraputa, Tumatumari]; 1910:435 [literature compilation]; 1912:347, pl. 45: fig. 1 [redescription based on type series]; 1927:418, pl. 34: fig. 2 [redescription based on type series].—Henn, 1928:63 [holotype in Carnegie Museum].—Myers and Roberts, 1967:248–249 [in part; citation of species from British Guiana (=Guyana); not cited presence of species in "upper Rio Negro-upper Orinoco" system; not cited specimens of *C. melanzonus*].—Böhlke and Saul, 1975:27, fig. 4b [form of upper jaw; not citation of species from upper Río Orinoco and upper Rio Negro].—Ibarra and Stewart, 1987:28 [holotype in FMNH].—Planquette et al., 1996:324, fig. [French Guiana, Crique Anne, Fleuve Sinnamary system and Gaa Kaba, Fleuve Maroni basin].—Machado-Allison et al., 2000:16 [Venezuela, Río Cuyuni basin].—Not Böhlke and Saul, 1975:28.—Not Mago-Leccia, 1970:70.

Creagrudite melanzonus.—Myers, 1927:119 [*Creagrutus melanzonus* suggested as juvenile form of *Creagrudite*].—Fowler, 1975:25 [citation].

Creagrudite melanzona.—Eigenmann and Myers, 1929:546 [*Creagrutus melanzonus* shifted to *Creagrudite* and described as based on juveniles].

Creagrudite maxillaris [not of Myers, 1927].—Fowler, 1975:25 [misidentification] [*Creagrutus melanzonus* incorrectly listed as synonym].

DIAGNOSIS.—The possession of premaxillary dentition with the three components generalized for the species of *Creagrutus*, but with a distinct gap between the first and second teeth of primary tooth row and a forward position of the triangular cluster of three posteromedial teeth distinguishes *C. melanzonus* from all members of the clade formed by *Creagrutus* and *Piabina* with the exception of *Creagrutus maracaiboensis, C. muelleri, C. nigrostigmatus, C. ouranonastes, C. peruanus, C. runa,* and *Piabina argentea. Creagrutus melanzonus* can be distinguished from these seven species by the combination of the possession of 5, occasionally 6, teeth in primary series of each premaxilla, 3 or 4 maxillary teeth, 8 to 10 predorsal median scales, 35 to 38 lateral line scales without a lamellar process over each pore, 9 to 11 branched anal-fin rays, 35 to 38 vertebrae, the relatively well developed third infraorbital whose ventral margin approaches, but does not contact, the horizontal limb of the preopercle, and the lack of a large spot of dark pigmentation at the base of the middle caudal-fin rays.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus melanzonus* in Table 33. Body relatively shallow and fusiform to slightly compressed transversely. Greatest body depth at, or slightly anterior of, dorsal-fin origin. Dorsal profile of head distinctly convex from margin of upper lip to vertical through anterior margin of orbit, straight to slightly convex from that point to posterior tip of supraoccipital spine. Dorsal profile of body ranging from straight to slightly and smoothly convex to dorsal-fin origin, straight to slightly concave from that point to anterior adipose-fin base, straight to slightly concave from that point to vertical through anterior procurrent caudal-fin rays. Ventral profile of head with obtuse angle (shallow convexity in some specimens) approximately midway between margin of lower lip and posterior of dentary, slightly convex from that point to isthmus. Ventral profile of body slightly convex from isthmus to anal-fin origin and slightly concave from that point to caudal peduncle.

Anterior profile of head forming broadly rounded obtuse angle. Upper jaw slightly longer than, and overhanging, lower jaw. Most external surfaces of head covered with minute papillae. Anterior portion of snout relatively firm and without concentration of soft tissues found in that region in many congeners, with minute papillae present on snout and upper lip. Papillae continuing into mouth on fleshy flaps and plicae between outer and medial premaxillary teeth. Lower jaw distinctly fleshy anteriorly, inner surfaces of lower lip convolute with papillose flaps.

Elements of infraorbital series moderately well developed, with ventral margin of third infraorbital approaching, or barely contacting, horizontal limb of preopercle. Posterior margin of third infraorbital distinctly separated from vertical limb of preopercle by gap ranging from one-third to one-half of width of fourth and fifth infraorbital bones. Posterior and ventral margins of third infraorbital broadly rounded and approximately concentric with orbit. Posterior margins of fourth and fifth infraorbitals distinctly separated from vertical limb of preopercle.

Premaxillary teeth in threeistinct groups: main row typically comprising 5, rarely 4 (1 specimen) or 6 (2 specimens), elongate, distally recurved unicuspidate to weakly tricuspidate teeth, anteriormost premaxillary tooth doften unicuspidate and

TABLE 33.—Morphometrics and meristics of *Creagrutus melanzonus:* (A) holotype of *C. melanzonus,* FMNH 52705; (B) other specimens of *C. melanzonus* from Guyana (n=14; vertebral counts taken from an additional 22 specimens); and (C) specimens of *C. melanzonus* from French Guiana (n=10). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length. Dashes indicate values that could not be determined because of damage to holotype.

Characters	A	B	C
		Morphometrics	
Standard length	35.2	22.8–32.0	32.4–36.1
1. Snout to anal-fin origin	65.1	61.6–68.4	60.5–65.5
2. Snout to pelvic-fin insertion	47.2	46.2–50.2	44.7–48.0
3. Snout to pectoral-fin insertion	24.1	23.3–27.0	22.2–26.0
4. Snout to dorsal-fin origin	48.0	45.7–52.5	44.8–49.2
5. Dorsal-fin origin to hypural joint	54.3	51.7–56.1	53.1–57.1
6. Dorsal-fin origin to anal-fin origin	27.3	23.8–27.4	25.5–27.8
7. Dorsal-fin origin to pelvic-fin insertion	21.9	18.3–22.9	20.2–23.6
8. Dorsal-fin origin to pectoral-fin insertion	30.7	27.9–32.9	27.7–30.8
9. Caudal peduncle depth	9.9	9.0–10.5	9.0–10.7
10. Pectoral-fin length	17.9	17.3–20.7	16.1–19.3
11. Pelvic-fin length	15.1	12.8–17.3	13.2–14.4
12. Dorsal-fin length	–	19.7–22.4	18.7–21.7
13. Anal-fin length	–	13.3–18.5	16.4–18.5
14. Head length	25.3	24.4–27.4	23.9–27.0
15. Postorbital head length	41.6	35.4–41.7	37.3–44.0
16. Snout length	29.2	23.9–33.3	25.6–31.9
17. Bony orbital diameter	37.1	34.8–42.9	34.8–41.2
18. Interorbital width	27.0	25.3–30.3	26.6–30.8
		Meristics	
Lateral line scales	37	35–38[1]	36–38
Scale rows between dorsal-fin origin and lateral line	4	4[1]	4
Scale rows between anal-fin origin and lateral line	3	2–3[1,2]	3
Predorsal median scales	9	8–10	8–9
Branched dorsal-fin rays	8	8	8
Branched anal-fin rays	10	9–11	10–11
Branched pelvic-fin rays	6[3]	6[3]	6–7[3]
Pectoral-fin rays	13	11–14	11–13
Vertebrae	37	35–38[4]	36–37

[1]Specimens mostly lacking scales and count estimated from scale pockets.
[2]Two scales between anal-fin origin and lateral line present in only 1 of 14 specimens.
[3]Medial pelvic-fin unbranched when 6 branched rays present.
[4]Thirty-eight vertebrae present in only 3 of 36 nontype specimens from Guyana.

always separated from second tooth in series by distinct gap; triangular cluster of three large tricuspidate teeth with anterior tooth occasionally unicuspidate and partially inserted into gap between first and second teeth of primary series; and single elongate, unicuspidate outer tooth positioned lateral to third or fourth tooth in main row. Maxilla with 3 or 4 tricuspidate teeth. Dentary with 6 or 7 tricuspidate teeth with third tooth slightly recurved; first two teeth largest, with second tooth slightly larger than first tooth, third tooth about two-thirds height of second tooth, remaining teeth in series distinctly smaller than anterior three teeth.

Dorsal-fin rays ii,8 in all specimens. Dorsal-fin origin located at, or slightly anterior to, vertical through pelvic-fin insertion. Distal margin of dorsal fin nearly straight, with very slight concavity as result of elongation of first 3 or 4 rays. Anal-fin rays ii,9–11 or iii,11 (in only 1 specimen). Anal fin with hooks, when present, limited to 1 hook per segment on segments of first, or first and second, branched ray (2 hooks observed on 1 segment in one specimen). Distal margin of anal fin slightly sigmoidal, with anterior rays forming relatively elongate lobe and outline of posterior 5 or 6 rays concave. Pectoral-fin rays i,11–14, typically 11 or 12. Pectoral fin short, tip of fin extending posteriorly maximally to within 2 or 3 scale rows of pelvic-fin insertion. Pelvic-fin rays i,6,i. Tip of pelvic fin approaching, or reaching, anal-fin origin; with hooks on medial surfaces of segmented and unsegmented portions of main shaft and medial secondary branches of all rays medial of the lateral unbranched element.

Posterior margin of body scales smoothly rounded to slightly undulate.

Gill rakers 4–7 + 10–12.

COLORATION IN ALCOHOL.—Overall ground coloration straw with dark pigmentation ranging from light brown to dark sepia. Dorsal surface of head with diffuse pattern of small, light

brown chromatophores on upper lip and over snout. Dorsal surfaces of frontal and parietal portions of cranium uniformly and densely invested with medium- to large-sized, dark brown, deep-lying chromatophores. Distinct small crescent-shaped patch of dark chromatophores located immediately in front of anterior nares. Band of scattered, dark chromatophores extending from immediately lateral of nares posteroventrally and continuing along ventral margin of orbit, but with unpigmented disjunction of band ventral of lens of eye. Lower lip and ventrolateral surface of head unpigmented with exception of three or four dark chromatophores that may occur over posterior one-half of lower jaw. Reflective guanine not observed in association with head or any other body components, although reported to be present in association with body stripe by Eigenmann (1909).

Body pigmentation most concentrated dorsally in association with dorsalmost lateral scale row and median scale row, these scales outlined by bands of scattered, dark chromatophores; darkest pigmentation flanking dorsal-fin base, with group of somewhat more concentrated, but still scattered, chromatophores immediately posterior of supraoccipital spine. Humeral mark usually in form of anteriorly concave crescent, with pigmentation most concentrated immediately dorsal of lateral line and terminating somewhat abruptly about 2 scale rows dorsal and ventral of lateral line. Dark flank pigmentation, other than humeral bar, in region anterior to vertical through anal-fin origin restricted to area dorsal of lateral line, except for scattered chromatophores associated with myosepta immediately dorsal of anal-fin base. Some specimens with such myoseptal pigmentation extending anteriorly to near vertical through pelvic-fin insertion. Dark midlateral body stripe extending to within 2 or 3 scale rows of humeral mark, becoming more densely pigmented and somewhat wider posteriorly on caudal peduncle.

Dorsal-fin membrane with dark chromatophores most concentrated on distal one-fourth to one-third of anterior 4 branched rays, unbranched rays darkly pigmented. Unbranched anal-fin rays unpigmented except for small number of basal dark chromatophores, proximal one-half of branched rays delineated by dark pigmentation along their anterior surfaces. Caudal fin with all fin rays delineated by dark pigmentation, pigmentation darkest on central and ventral rays. Dorsal-fin rays outlined by very small, less densely pigmented chromatophores, central rays generally darkest, and associated pigmentation usually appearing as small diffuse spot. Deep-lying dark pigmentation arranged in vertical line delineating posterior extremities of hypural plates. Pelvic fin hyaline. Pectoral fin either with scattered, dark chromatophores restricted to distal one-fourth of lateral 4 or 5 rays, or with several isolated chromatophores scattered over fin.

ECOLOGY.—Planquette et al. (1996:324) reported that *Creagrutus melanzonus* inhabits creeks with sand bottoms, sometimes with gravel and rocks in French Guiana. These authors also noted that the species is relatively rare and frequents the higher portions of rivers.

DISTRIBUTION.—*Creagrutus melanzonus* is known from scattered localities extending from the Río Cuyuni basin of eastern Venezuela to the Fleuve Sinnamary system of French Guiana (Figure 59, squares). The species is, however, unknown in the region between the Essequibo River in Guyana and the river basin along the Suriname-French Guiana border region (the Marowijne River or Fleuve Maroni, respectively; see also comments under "*Creagrutus* in Cis-Andean South America," above).

REMARKS.—Myers and Roberts (1967:248) identified specimens form the "Upper Orinoco-Upper Negro" as *Creagrutus melanzonus.* This identification has been followed by subsequent authors (Mago-Leccia, 1970; Böhlke and Saul, 1975; Géry and Renno, 1989), but analysis has shown that the population samples identified as *C. melanzonus,* which originated from that region, are instead representatives of a distinct species, *C. zephyrus.*

Myers (1927:117–119), in his original description of *Creagrudite maxillaris,* reported that the species underwent an ontogenetic shift from three to two rows of premaxillary dentition. Myers and Roberts (1967:248) noted that the original series of specimens on which Myers (1927) based his description of *C. maxillaris* was complex, and that the small specimens in the series were actually *Creagrutus melanzonus.* This problem also was commented on by Böhlke and Saul (1975). The specimens on which the original description of *Creagrudite maxillaris* were based all originated within the known range of *Creagrutus zephyrus* in the upper Rio Negro system, an area distant from the known range of *C. melanzonus.* These records are consequently considered to represent *C. zephyrus.*

Mago-Leccia (1970:70) reported *C. melanzonus* from Venezuela. This report presumably was based on Myers and Roberts (1967) who, in turn, had based their records on specimens from southern Venezuela. Although those populations are considered herein to be *C. zephyrus, C. melanzonus* is, nonetheless, present in eastern Venezuela in the Río Cuyuni basin, which forms the northwestern portion of the Essequibo River system.

Myers (1927:119) followed by Eigenmann and Myers (1929:546) proposed that *Creagrutus melanzonus* was most closely related to *Creagrudite maxillaris* and shifted the former species to *Creagrudite.* The available evidence does not support such an association (see "Intrageneric Relationships within *Creagrutus,*" above) and *Creagrudite* is furthermore herein considered a synonym of *Creagrutus* (see "Synonymy of *Creagrutus,*" above).

A possible misinterpretation of the shift of *Creagrutus melanzonus* to *Creagrudite* by Myers (1927:119) and Eigenmann and Myers (1929:546) may have led Fowler (1975:25) to place *Creagrutus melanzonus* as a synonym of *Creagrudite maxillaris.* The species differ in numerous features, in particular their dentition, so such a synonymy is unjustified.

MATERIAL EXAMINED.—81 specimens (46, 22.8–36.1).

VENEZUELA. *Bolivar:* "charco" 7 km west of Anacoco (latter locality at 6°43′N, 61°08′W), upper Río Cuyuni basin, MCNG 1031, 20 (28.5–30.9).

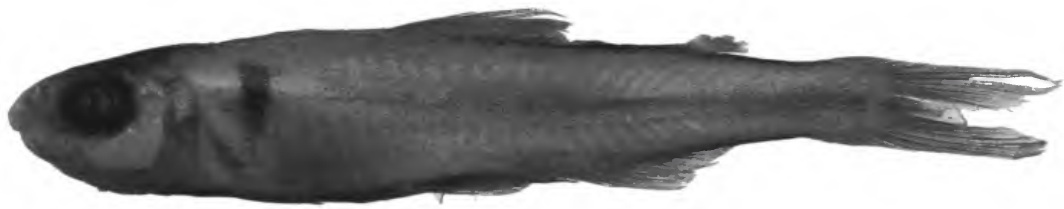

FIGURE 60.—*Creagrutus melanzonus,* ANSP 176596, 33.4 mm SL; Guyana, Essequibo River, extensive sandbar 500 m downstream from Paddle Rock campsite (4°44′N, 58°43′W).

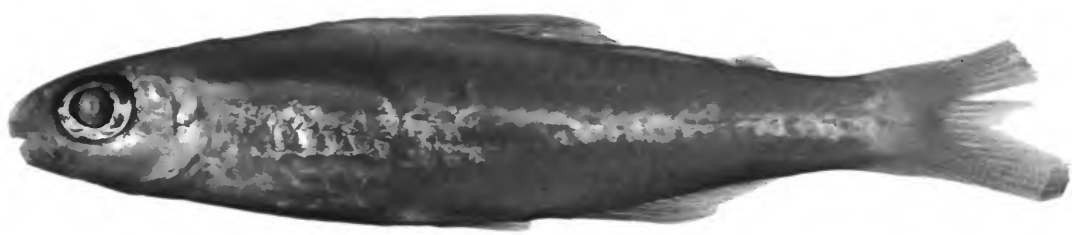

FIGURE 61.—*Creagrutus melanzonus,* MHNG 2183.45, 35.6 mm SL; French Guiana, Maroni, Gaa Kaba.

GUYANA. Crab Falls, Essequibo River (5°24′N, 58°51′W), FMNH 52705, 1 (35.2, holotype of *Creagrutus melanzonus;* formerly CM 1067). Essequibo River, Warraputa (=Warraputa (=Waraputa, 5°15′N, 58°50′W), FMNH 52706, 1 (paratype of *Creagrutus melanzonus;* formerly CM 1068); CAS 30421, 1 (paratype of *Creagrutus melanzonus;* formerly IU 11753). Lower Potaro River, Tumatumari (5°22′N, 59°00′W), FMNH 72707, 1 (32.0, paratype of *Creagrutus melanzonus;* formerly CM 1069); CAS 30422, 2 (paratypes of *Creagrutus melanzonus;* formerly IU 11754). Mazaruni-Potaro District: Little Takutu River, AMNH 72990, 9 (22.8–29.2). Mazaruni River, 5 km W of Issano (05°49′05″N, 59°28′09″W), ROM 70239, 4 (26.4–28.6). Isolated stagnant pool/pond about 40 m from main channel of Essequibo River (04°32′43″N, 58°35′02″W), ANSP 175688, 1. Essequibo River, sand bar (4°44′N, 58°43′W), ANSP 176597, 10 (of 72). Essequibo River, sand bar (4°44′22″N, 58°42′23″W), ANSP 176598, 3 (of 6). Essequibo River, extensive sandbar 500 m downstream from Paddle Rock campsite (4°44′N, 58°43′W), ANSP 176596, 10 (of 22).

SURINAME. *Marowijne District:* Oelemari River, 2 km N of Oelemari airstrip (latter locality at 3°06′N, 54°32′W), ZMA 107.557, 1 (27.2).

FRENCH GUIANA. Fleuve Maroni basin, Gaa Kaba (4°28′N, 54°24′W), MHNG 2183.45, 6 (32.4–35.6). Fleuve Sinnamary basin, Saut Takari Tanté (approximately 4°35′N, 52°56′W), ORSTOM 1015, 2 (32.5–36.1). Fleuve Sinnamary basin, Crique des Frères Anicet (approximately 4°09′N, 52°58′W), ORSTOM 6007, 2 (33.5–36.1). Fleuve Sinnamary basin, Crique Anne (approximately 4°33′N, 52°50′W), ORSTOM uncataloged, 7.

Creagrutus melasma Vari, Harold, and Taphorn, 1994

FIGURES 59, 62, TABLE 34

Creagrutus beni [not of Eigenmann 1911].—Eigenmann 1920:12 [misidentification] [Venezuela, Carabobo, Lago de Valencia and adjoining rivers; specimens from Maracay, IU 15133, and Isla del Buro (=Isla El Burro), IU 15134]; 1927:422 [in part; specimens from Venezuela, Carabobo, Maracay, IU 15133, and Isla del Buro (=Isla El Burro), IU 15134].—Pearse 1920:12, 24, 25, 43 [Venezuela, Carabobo, Lago de Valencia; food items and parasites; specimens served as basis for Eigenmann 1920 and 1927 citations].—Roman, 1992:169 [color photo; common name; cited distribution in (Río) Orinoco and Lago de Valencia; not cited occurrence in Amazon basin].—Baensch and Riehl, 1993:270, photo on page 271 [life coloration, breeding].

Creagrutus species.—Géry, 1977:392, 407 [color plate, in key].

Creagrutus sp.—Winemiller, 1989:239 [Venezuela: Río Apure, Caño Volcán; life history attributes]; 1990:364 [Venezuela: Río Apure basin, Caño Volcán].

Creagrutus n. sp.—Taphorn, 1992:173–175 [Venezuela, Río Apure basin; natural history; common name].

Creagrutus melasma Vari et al., 1994:90, fig. 1 [type locality: Venezuela, Guarico, Parque Nacional Guatopo, Río Orituco, first bridge along road from Santa Teresa to Altagracia].—Weitzman et al., 1996, fig. 1 [life coloration].—Sabaj et al., 1997:269 [paratype depository].—Lasso et al., 1997:42 [paratype depository].

Creagrutus melasmus.—Taphorn et al., 1997:71 [cited for Venezuela].

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the

TABLE 34.—Morphometrics and meristics of *Creagrutus melasma:* (A) holotype of *C. melasma,* MBUCV V-22918; and (B) paratypes of *C. melasma* from which counts and measurements were taken (n=15). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard Length	32.4	22.8–40.7
1. Snout to anal-fin origin	61.4	61.9–66.7
2. Snout to pelvic-fin insertion	47.7	46.8–51.2
3. Snout to pectoral-fin insertion	26.5	24.3–27.2
4. Snout to dorsal-fin origin	49.8	48.4–53.8
5. Dorsal-fin origin to hypural joint	56.9	53.3–57.7
6. Dorsal-fin origin to anal-fin origin	31.3	30.7–36.8
7. Dorsal-fin origin to pelvic-fin insertion	30.2	29.0–35.2
8. Dorsal-fin origin to pectoral-fin insertion	34.5	32.5–39.0
9. Caudal peduncle depth	11.9	11.5–13.1
10. Pectoral-fin length	21.3	18.7–21.5
11. Pelvic-fin length	15.9	14.8–16.7
12. Dorsal-fin length	25.7	21.4–28.5
13. Anal-fin length	21.3	18.6–21.6
14. Head length	26.4	24.5–26.9
15. Postorbital head length	43.8	42.4–47.8
16. Snout length	28.3	24.0–29.0
17. Bony orbital diameter	32.8	30.9–36.2
18. Interorbital width	31.9	29.3–34.7
	Meristics	
Lateral line scales	35	34–36
Scale rows between dorsal-fin origin and lateral line	5	5–6
Scale rows between anal-fin origin and lateral line	4	4–5
Predorsal median scales	10	10–11
Branched dorsal-fin rays	8	7–8
Branched anal-fin rays	11	0–12
Branched pelvic-fin rays	7	7
Pectoral-fin rays	11	11–13
Vertebrae	35	34–36

primary series, 2 or 3 teeth on the maxilla, 5 teeth in the primary tooth row of the premaxilla, 6 dentary teeth, 34 to 36 lateral line scales without a lamellar process over each pore, 10 or 11 predorsal median scales, 5 or 6 scale rows between the dorsal-fin origin and the lateral line, 34 to 36 vertebrae, 10 to 12 branched anal-fin rays, 10 to 12 gill rakers on the lower portion of the first gill arch, 2 post-anal median scales to the anal-fin origin, the snout length (24.0%–29.0% of HL), the poorly developed third infraorbital with the curvature of posteroventral margin of the bone roughly concentric with the orbital margin and with the ventral margin of the third infraorbital distinctly separated from the horizontal limb of the preopercle, the lack of a series of dark midlateral spots on the body, the vertically elongate humeral mark, and a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus melasma* within the clade composed of *Creagrutus* and *Piabina.*

DESCRIPTION.—Morphometric and meristic data for *Creagrutus melasma* in Table 34. Maximum body depth along vertical through pelvic-fin insertion. Anterior profile of snout and dorsal profile of head meeting in rounded obtuse angle near vertical immediately anterior to nares. Dorsal profile of head posterior to that line posterodorsally inclined and slightly convex. Predorsal profile of body slightly arched between supraoccipital spine and dorsal-fin origin. Dorsal profile of body straight to slightly concave between dorsal-fin origin and adipose fin and straight from adipose fin to dorsal procurrent rays. Ventral profile of head and body smoothly convex from margin of lower lip to pelvic-fin origin or with indistinct rounded obtuse angle delimiting anteroventral angle of dentary.

Upper jaw longer than, and overhanging, lower jaw. Anterior surface of snout fleshy, with minute papillae over surface. Greatest concentration of papillae on upper lip, margin of upper jaw, and in mouth on fleshy folds and plicae between inner and medial series of premaxillary teeth. Lower lip with thick, fleshy anterior region and with numerous papillae on dorsal surface of lip.

Infraorbital series poorly developed compared to many *Creagrutus* species, covering less than one-half of cheek. Ventral margin of third infraorbital distinctly separated from horizontal limb of preopercle. Posteroventral margins of infraorbitals 3 and 4 rounded, with indentation or concavity at their juncture. Curvature of posteroventral margin of third infraorbital approximately concentric with margin of orbit. Posterior margins of third through fifth infraorbitals broadly separated from vertical limb of preopercle.

Premaxillary dentition in three series: primary series undulating, with 5 rounded, unicuspidate to tricuspidate teeth, with anterior tooth slightly displaced anteromedially but without pronounced gap between first and second tooth of series; triangular cluster of 3 larger teeth, crowded together medially; and single tooth occurring lateral to third or fourth tooth of primary premaxillary row. Maxilla with 2 or 3, rarely 4, unicuspidate to tricuspidate teeth. Dentary teeth 6, anterior 3 teeth largest and tricuspidate, albeit with relatively small lateral cusps. Second dentary tooth slightly higher and wider than first tooth, more than twice as high and wide as third tooth. Fourth through sixth dentary teeth unicuspidate or with barely apparent lateral cusps; teeth becoming progressively shorter posteriorly.

Unpaired fins relatively large compared with most *Creagrutus* species. Dorsal-fin rays typically ii,7–8, ii,7 rare. Distal margin of dorsal fin nearly straight, with slight elongation of anterior rays. Dorsal-fin origin slightly posterior of vertical through pelvic-fin origin. Anal-fin rays ii,10–12 or iii,10–12. Distal margin of anal fin slightly concave, with anterior rays most elongate. Single, paired hooks present on 3 to 6 anterior branched anal-fin rays in mature males. Anal-fin hooks of mature males restricted to posterolateral surface of main shaft and posterior secondary branch of each ray. Pectoral-fin rays i,10–12. Tip of pectoral fin extending posteriorly almost to pelvic-fin base. Pelvic-fin rays i,7. Tip of pelvic fin approaching or, especially in well-developed mature males, extending posteriorly to anal-fin origin. Distal portion of pelvic fin turned medially in some individuals, giving fin slightly cupped form.

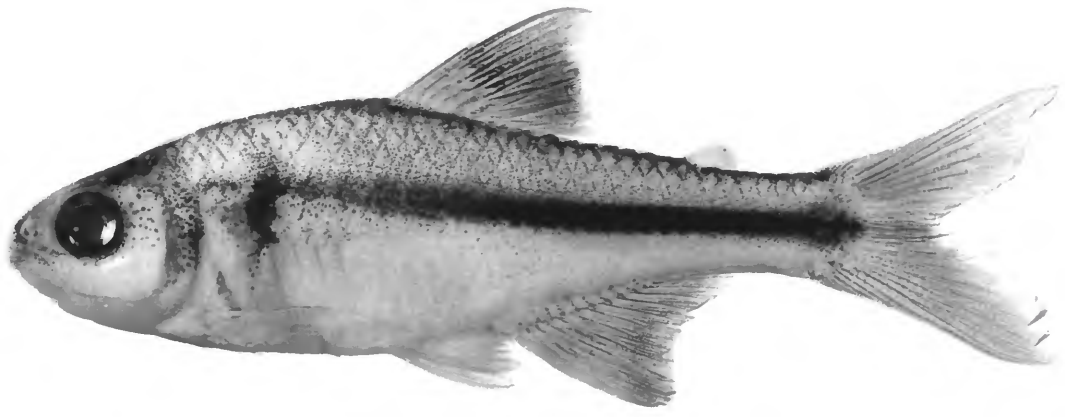

FIGURE 62.—*Creagrutus melasma*, holotype, MBUCV V-22198, 32.4 mm SL; Venezuela, Estado Guarico, Parque Nacional Guatopo, Río Orituco, first bridge along road from Santa Teresa to Altagracia.

Pelvic-fin hooks of mature males, when present, located on all but smallest, distal branches of all branched rays.

Gill rakers 3–6 + 8–10.

COLORATION IN LIFE.—Dorsal and anal fins with bright red markings anteriorly, and black centrally (see color plates in Roman, 1992:169, and Géry, 1977:393). Dorsal lobe of caudal fin red. Dorsal surface of eye with red patch overlying reflective guanine. Dark body pigmentation as in specimens preserved in alcohol other than for guanine partially masking anterior one-third of dark midlateral stripe (e.g., Weitzman et al., 1996, fig. 1).

COLORATION IN ALCOHOL.—Dorsal surface of head with dark, shallow and deep chromatophores. Large, stellate, deep-lying chromatophores lining exterior surface of frontal, except in region of anterior fontanel. Shallow, dark chromatophores present over most of dorsal surface of head; most concentrated on snout and on ventral portion of upper lip, but not forming distinct crescent-shaped mark present in many congeners. Three patches of dark chromatophores extending posteriorly from portion of main field immediately dorsal to anterior margin of orbit; one over each orbit and one along midline over fontanel. Band of scattered, dark chromatophores extending posteriorly from pigmentation on snout to anteroventral margin of orbit and then around ventral and posterior margins of orbit. Scattered, stellate, dark chromatophores overlying dorsal portions of infraorbitals and opercle.

Dorsal portion of body with small, dark chromatophores concentrated on and below posterior portion of scales; these chromatophores forming overall dark reticulate pattern. Anterior one-half of predorsal surface of body with longitudinal concentration of large, stellate, dark chromatophores. Small dark chromatophores along dorsal-fin base. Humeral mark darkest immediately dorsal to lateral line. Overall form of mark vertically elongate with orientation ranging from vertical to somewhat posterodorsally oblique. Dark midlateral body stripe extending from pectoral girdle posteriorly to caudal-fin base. Body stripe diffuse anteriorly, most sharply defined along ventral margin and on posterior portion of body. Stripe expanded posteriorly into diffuse triangle extending slightly ventral to lateral line on caudal peduncle. Region of body between midlateral stripe and anal-fin base unpigmented or with series of very small dark chromatophores delineating myosepta. Dorsally tapered concentrations of dark pigmentation located between bundles of fin-ray musculature at anal-fin base.

Small dark chromatophores on caudal-fin membranes; chromatophore concentration greatest along central and outer branched rays and dorsal and ventral procurrent rays. Small dark chromatophores on anal-fin membranes mainly restricted to narrow bands along fin-ray margins. Slightly larger, darker chromatophores forming diffuse longitudinal band on distal one-third of anal fin; some specimens with greatly enlarged, dark chromatophores, giving appearance of dark spot on fin anteriorly. Small dark chromatophores present across dorsal-fin membranes with large, very dark chromatophores concentrated in central portion of anterior one-half of fin, giving appearance of large dark spot (spot well-developed across observed size range; present in 14.8 mm SL juvenile, MBUCV V-21257). Pectoral fins with series of dark chromatophores associated with most rays; chromatophores most numerous laterally. Pelvic fins hyaline.

ECOLOGY.—*Creagrutus melasma* inhabits small, shallow, shady streams of the Andean piedmont where the water is usually clear and the substrate ranges from sand to gravel (Taphorn, 1992:174). Diet of adults consists of small seeds, ostracods, gastropods, and aquatic insects, especially chironomid larvae (Pearse, 1920:24, 25; Winemiller, pers. comm., 1997; in Taphorn, 1992:174). Spawning occurs for six to eight months, with individuals probably spawning two or more times per

spawning season (Winemiller, 1989:239; Winemiller, pers. comm., 1997). In Caño Volcán in the Río Apure system, three ripe females (23–26 mm SL) had 93–96 oocytes larger than 0.6 mm (Winemiller, pers. comm., 1997). The relatively low number of oocytes may be correlated with apparent insemination of the female and the laying of fertilized eggs as reported by Baensch and Riehl (1993:270).

COMMON NAME.—Venezuela, Río Orinoco basin: "Sardina" (Roman, 1992:169), "Dientefrio Pintada" (Taphorn, 1992:173).

DISTRIBUTION.—*Creagrutus melasma* occurs in the northern portions of Venezuela east of the Andes from the state of Táchira in the west to the state of Sucre in the east. The species also occurs in many upland tributaries of the Río Orinoco basin and in the Ríos Tuy and Neverí of the Caribbean versant (Figure 59, stars).

REMARKS.—Material herein referred to as *Creagrutus melasma* from Lago de Valencia and tributary rivers was identified as *C. beni* by Eigenmann (1920:12; 1927:422). This identification is puzzling in light of the distinctiveness of the new species relative to *C. beni* and given that Eigenmann (1911) described *C. beni* from a locality in the upper Rio Madeira basin in northeastern Bolivia, a considerable distance from Lago de Valencia of northern Venezuela. *Creagrutus melasma* and *C. beni* are readily distinguished by the number of vertebrae (typically 34 or 35, 1 specimen out of 60 had 36 vertebrae, in *C. melasma* versus 37 to 39 in *C. beni*) and by the relative size of the infraorbital bones (poorly developed, with posteroventral margin of the series distinctly separated from both the horizontal and the vertical limbs of the preopercle in *C. melasma* compared to the well-developed third infraorbital with its ventral margin approaching, or often contacting, the horizontal limb of the preopercle in *C. beni*).

MATERIAL EXAMINED.—1364 specimens (21, 22.8–40.7).

VENEZUELA. *Anzoátegui:* Quebrada Las Minas, tributary of Río Querecual (approximately 9°57′N, 64°35′W), MBUCV V-15444, 1. *Apure:* Caño Naporal, tributary of Río Portuguesa, MCNG 10302, 19. Río Capanaparo, approximately 5 km downstream from crossing of highway between San Fernando de Apure and Puerto Paez (7°02′N, 67°25′W), ANSP 165139, 1. *Aragua:* Río Tuy basin, mouth of Río Cagua, approximately 10 km from Guayas (approximately 10°16′N, 67°09′W), MBUCV V-21257, 56 (3, 34.2–40.7, paratypes of *Creagrutus melasma;* 2 specimens cleared and counterstained for cartilage and bone); CAS 79622, 10 (paratypes of *Creagrutus melasma*); USNM 326056, 10 (paratypes of *Creagrutus melasma;* 2 specimens cleared and counterstained for cartilage and bone). Río Bue, at Maracay (10°15′N, 67°36′W), CAS 69297 (formerly IU 15133), 75. Lago de Valencia basin, Río Limon, east of I.N.A. (Agricultural Research Institute), MBUCV V-3045, 6. Río Pao, near La Candelaria (approximately 10°07′N, 67°14′W), MCNG 14201, 3. *Bolivar:* Caicara, MHNLS 7240, 2. *Barinas:* Caño at entrance to Boconó dam, MCNG 5271, 402; MCNG 5401, 9. Río Boconó at dam site, MCNG 8877, 8. Río Tucupido at Las Cañoas, MCNG 5648, 12. Caño Musao, MCNG 6347, 2. Caño Las Maravillas, MCNG 11944, 4. Caño at Estero Chiguira, MCNG 6546, 2. *Carabobo:* Río Guacara basin, Río Vigirima, approximately 10 km NNW of Guacara (approximately 10°24′N 67°55′W), ANSP 134171, 48 (3, 33.5–34.2, paratypes of *Creagrutus melasma*). Río Las Penitas at Vigirima, MCNG 24647, 4. Lago de Valencia basin, Vigirima, Río Las Penitas (approximately 10°20′N 67°52′W), INHS 60021, 10 (3, 33.2–36.0, paratypes of *Creagrutus melasma*). Lago de Valencia, at Guataparo dike, W of Valencia, MHNLS 503, 6 (paratypes of *Creagrutus melasma*). Río Manuare, approximately 16 km along river from Manuare (09°59′N 67°45′10″W), MCNG 15354, 56 (paratypes of *Creagrutus melasma*). Caño La Camarca, N of San Diego (10°15′N, 67°57′W), MCNG 24622, 34 (paratypes of *Creagrutus melasma*). Lago de Valencia, Isla El Burro, CAS 69294 (formerly IU 15134), 266. Lago de Valencia, Muelle Nuevo, opposite Isla El Burro, MHNLS 5882, 1. Lago de Valencia basin, Caño la Cumara, 3 km N of San Diego (10°16′33″N 67°56′13″W), INHS 60446, 35 (5, 32.2–35.0). Lago de Valencia, MBUCV V-uncataloged, 6. Río Onoto, Puente Onoto, about 40 km from San Carlos (9°59′N, 68°22′W), MBUCV V-9919, 1. Río Chirigu, tributary of Río Pao, MCNG 15281, 5. Caño near Belen, MCNG 15295, 7. Caño Guamita, MCNG 15342, 60. *Cojedas:* Quebrada Camoruco, MCNG 6786, 2. Río Chorreron, 10 km from Apartaderos (approximately 9°41′N, 68°56′W), MCNG 13780, 6. Río Portuguesa basin, Río Onoto, 2 km E of Apartaderos (approximately 9°41′N, 68°54′W), MHNLS 502, 7. Quebrada Guabinas, at highway from San Carlos to Acarigua, MHNLS 2502, 1. Río Portuguesa basin, Río Manrique, 2 km upstream of Manrique (approximately 9°49′N, 68°32′W), MHNLS 499, 6. Río Portuguesa basin, Quebrada Tierra Caliente, 5 km W of Manrique, MHNLS 520, 10. *Guarico:* Parque Nacional Guatopo, Río Orituco, first bridge along road from Santa Teresa to Altagracia (approximately 9°59′N, 66°30′W), MBUCV V-22198, 1 (32.4, holotype of *Creagrutus melasma*); MBUCV V-24020, 2 (32.0–33.9, paratypes of *Creagrutus melasma*). *Miranda:* At bridge near Araguita (10°13′N, 66°27′W), MCNG 14296, 3. *Monagas:* Río Caripe, Sector Salle, on the Las Parcelas Road, 6 km from Carripito, MBUCV V-9753, 1. Río Cocoyal, MCNG 16977, 3. Quebrada N of San Francisco de Maturin, MHNLS 517, 2. Río Colorado at San Antonio de Maturin (10°07′N, 63°43′W), MHNLS 527, 9. Río Aragua, at road from Maturin to Quiriquire, approximately 10 km from Maturin (approximately 9°58′N, 63°25′W), MHNLS 8064, 1. Río Aragua, 10 km from Aragua de Maturin, at road from Maturin to Quiriquire (9°58′N, 63°49′W), MHNLS 8879, 1. Distrito Acosta, Río Caripe basin, Embalse El Guamo, MHNLS 9437, 16. *Portuguesa:* Caño La Lora, tributary of Río Tucupido, MCNG 122, 1. Tributary of Río Tucupido, MCNG 2443, 9. Río Tucupido at dam site, MCNG 8835, 3. Río Tucupido, Los Hierros (8°59′N, 69°53′W), MCNG 9215, 2. Río Tucupido, Los Hierros, 7 km N of Tucupido (8°59′N, 69°53′W), MHNLS 6361, 2. Caño N of Tucupido, 6 km along road to Los Hierros, MHNLS

2678, 6. Embalse Tucupido, MCNG 19638, 1; MCNG 19798, 6; MCNG 19303, 3. Caño, tributary of Río Boconó, near dam, MCNG 10666, 6. Tributary of Río Boconó, upstream from Puerto Paez, MCNG 703, 8. Caño at road from Chabasquen to Barquismeto, tributary of upper Río Guanare, MCNG 124, 1. Caño Buchi, between Acarigua and Guanare, MCNG 10858, 5. Río Las Marias, bridge on Highway #5, MCNG 11261, 1. Río Las Marias, MCNG 13314, 1; MCNG 19769, 1. Río Are, at bridge on Highway 5 between km 227 and 228, MCNG 11616, 5. Caño Bombicito, near Aparición (9°24'N, 69°23'W), MCNG 11842, 1. Caño Volcán, MCNG 15380, 14. Caño San Rafael, at km 247 on Highway 5, MCNG 16727, 1. Río Saguas, MCNG 18737, 5. *Sucre:* Río Neverí, at road to Turimiquire, near Cambural, MBUCV V-15419, 2. Río Neverí, at road to Turimiquire, near Paraparo, MBUCV V-15423, 3. Río Neverí, near Paraparo, MBUCV V-15428, 4. Río Neverí, Quebrada Carrasposo, MBUCV V-15405, 2. Río Neverí, Los Morochos, MBUCV V-15447, 2. Caño Cruz de Agua, MBUCV V-15451, 3. Caño Juan Antonio, MCNG 17051, 1. *Táchira:* Tributary of Río Quinimari, MCNG 6484, 4. Caño tributary to Río Chururu, MCNG 6626, 3. Caño Toronduy, at bridge on San Cristobal road, MCNG 11661, 21. Río San Agaton, MCNG 11790, 1. *Yaracuy:* Río Cojedas basin, Quebrada Grande, between Nirgua and Chivacoa, USNM 219615, 3 (22.8–36.3, paratypes of *Creagrutus melasma*); USNM 219616, 1 (31.8, paratype of *Creagrutus melasma*).

Creagrutus menezesi, new species

FIGURES 59, 63, 64, TABLE 35

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 3 or 4 teeth on the maxilla, 6, rarely 7, teeth in the primary tooth row of the premaxilla, 5 or 6, rarely 4, dentary teeth, 37 to 41 lateral line scales without a lamellar process over each pore, 8 to 11 predorsal median scales, 4 scale rows between the dorsal-fin origin and the lateral line, 36 to 38 vertebrae, 9 or 10 branched anal-fin rays, 2 post-anal median scales to the anal-fin origin, 6 gill rakers on the upper and 11 or 12 gill rakers on the lower limb of the first gill arch, the caudal peduncle depth (11.0%–12.9% of SL), the anal-fin length (17.7%–19.9% of SL), the postorbital head length (35.1%–45.1% of HL), the bony orbital diameter (36.8%–41.8% of HL), the interorbital width (27.4%–34.7% of HL), the relatively well-developed third infraorbital approaching, but not contacting, the horizontal limb of the preopercle, the lack of a series of dark midlateral spots on the body, the distinctly vertically elongate, ventrally tapering humeral mark extending ventral of the lateral line, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus menezesi* within the clade composed of *Creagrutus* and *Piabina*.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus menezesi* in Table 35. Head and body moderately robust. Greatest body depth at, to slightly anterior of, dorsal-fin origin. Dorsal profile of head convex from margin of upper lip to vertical through anterior margin of orbit, straight from that point to tip of supraoccipital spine in smaller specimens, slightly convex in that region in larger individuals. Interorbital region transversely convex. Predorsal profile of body slightly convex across size range of examined specimens, without change in alignment relative to dorsal profile of head. Dorsal surface of body with median ridge proximate to dorsal-fin origin, ridge more obvious in largest examined specimens. Ventral profile of head with obtuse angle at anteroventral corner of dentary, gently convex from that point to isthmus. Profile of prepelvic region of body slightly convex at all sizes. Prepelvic region of larger specimens obtusely flattened transversely.

Head obtusely pointed in lateral view and more laterally compressed and pointed in dorsal view. Upper jaw longer than, and distinctly overhanging, lower jaw. Snout slightly fleshy anteromedially, with few scattered papillae above margin of upper lip. Upper lip along with plicae and folds extending between outer and medial premaxillary teeth covered with concentrations of papillae. Lower lip fleshy anteriorly, with papillae concentrated on dorsal margin of lip and immediately proximate portions of anterior and lateral margins of lip.

Infraorbital series relatively well developed. Third infraorbital approaching but not contacting horizontal limb of preopercle. Posterior margins of third and fourth infraorbitals falling slightly short of vertical limb of preopercle.

Premaxillary dentition in three series: primary row curved overall, somewhat sigmoid in larger specimens, consisting of 6, rarely 7, teeth, without pronounced gap between first and second tooth of series but with medial tooth well separated from anterior tooth of contralateral series; triangular cluster of 3 larger teeth; and single tooth of form similar to that of primary series occurring lateral to fourth tooth of primary premaxillary row, or occasionally slightly more anterior of that position. Maxilla with 3 teeth in smaller specimens, with largest examined individuals having 3 or 4 teeth. Teeth shifting ontogenetically from unicuspidate in small specimens, to bicuspidate in medium-sized individuals, to tricuspidate in large specimens. Small specimens with 6 dentary teeth. First through third dentary teeth in juveniles distinctly larger, with first and second teeth subequal and approximately 1.5 times height of third tooth. First and second teeth tricuspidate with middle cusp well developed, second tooth bicuspidate with anterior cusp distinctly larger. Fourth through sixth teeth unicuspidate with posteriorly recurved tip. Larger specimens with 5, rarely 4, dentary teeth. Tricuspidate first and second dentary teeth of larger individuals distinctly larger than other teeth in series, with second tooth larger both vertically and especially horizontally than first tooth; tricuspidate third tooth approximately one-half height of fourth tooth; fourth and fifth teeth (when latter

TABLE 35.—Morphometrics and meristics of *Creagrutus menezesi*, new species: (A) holotype of *C. menezesi*, MZUSP 50544; (B) paratypes of *C. menezesi* (n=63), and (C) samples of *C. menezesi* from Rio Branco basin (n=13). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B	C
		Morphometrics	
Standard length	58.7	32.0–64.3	27.2–51.2
1. Snout to anal-fin origin	63.4	62.9–68.3	61.9–66.9
2. Snout to pelvic-fin insertion	47.7	44.2–49.3	45.5–50.9
3. Snout to pectoral-fin insertion	24.1	23.2–27.1	24.1–27.2
4. Snout to dorsal-fin origin	46.8	45.2–49.9	44.9–48.5
5. Dorsal-fin origin to hypural joint	57.9	54.8–59.7	53.6–57.7
6. Dorsal-fin origin to anal-fin origin	33.8	31.4–35.0	29.4–33.2
7. Dorsal-fin origin to pelvic-fin insertion	29.5	27.5–33.1	26.3–27.9
8. Dorsal-fin origin to pectoral-fin insertion	33.6	31.8–35.5	30.0–32.8
9. Caudal peduncle depth	12.6	11.5–12.9	11.0–12.1
10. Pectoral-fin length	19.8	18.7–21.3	18.6–21.6
11. Pelvic-fin length	15.3	14.8–17.8	14.0–17.1
12. Dorsal-fin length	21.8	20.2–23.0	20.1–25.0
13. Anal-fin length	18.7	17.7–19.9	17.7–19.5
14. Head length	26.0	25.2–27.9	25.2–28.4
15. Postorbital head length	44.9	39.1–45.1	35.1–42.6
16. Snout length	29.9	27.4–33.1	24.3–31.0
17. Bony orbital diameter	38.1	36.9–39.6	36.8–41.8
18. Interorbital width	32.6	29.4–34.7	27.4–30.5
		Meristics	
Lateral line scales	39	38–41	37–41[1]
Scale rows between dorsal-fin origin and lateral line	4	4	4
Scale rows between anal-fin origin and lateral line	3	3	3
Predorsal median scales	9	9–11	8–10
Branched dorsal-fin rays	8	8	8
Branched anal-fin rays	10	9–10	9–10
Branched pelvic-fin rays	7	6–7	6–7
Pectoral-fin rays	13	13–15	12–14
Vertebrae	37	36–38	37–38

[1]Forty-one lateral line scales present in only 1 of 13 specimens from Rio Branco.

present) distinctly smaller than third toothwith fourth tooth unicuspidate or weakly tricuspidate and fifth tooth unicuspidate.

Dorsal-fin rays ii,8 in all specimens. Dorsal-fin origin slightly anterior of vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin slightly concave. Anal-fin rays ii,9–10. Profile of distal margin of anal fin concave, more so in largest examined specimens in which anterior branched rays form moderate lobe. Mature males with hooks present on first and second branched anal-fin rays. Pectoral-fin rays i,11–14. Tip of pectoral fin extending posteriorly slightly less than two-thirds of distance to pelvic-fin insertion. Pelvic-fin rays typically i,6,i; sometimes i,7 in larger specimens. Tip of pelvic fin extending posteriorly to anus in smaller specimens, falling slightly short of that point in larger individuals. Mature males with hooks present on all branched anal-fin rays.

Gill rakers 6+11–12.

COLORATION IN ALCOHOL.—Overall coloration of majority of specimens ranging from quite pale to light tan. Dark pigmentation on specimens very subtle and often not readily apparent unless examined microscopically. Smaller specimens with dorsal surface of head lacking surface pigmentation, or with few scattered chromatophores in region posterior of snout. Dark, surface chromatophores on posterior portion of head more concentrated, but still relatively sparse, in larger individuals. Field of dark, relatively evenly spaced, deep-lying chromatophores located over surface of posterior portion of brain, with two longitudinally elongate contralateral patches of chromatophores positioned over anterior portion of brain; pigmentation quite dense in many larger specimens. Dark chromatophores scattered over snout. Region immediately anterior to nostrils typically with distinct crescent-shaped patch of chromatophores; patch not obvious in largest specimens examined. Region anteroventral of orbit with diffuse, dark chromatophores forming narrow, posteroventrally angled stripe; stripe not continuous anterodorsally with patch of pigmentation anterior to nostrils. Irregular series of chromatophores along posteroventral margin of orbit. Scattered chromatophores over dorsal portions of infraorbitals and opercle.

Scales of dorsal surface of body with scattered chromatophores along margins and diffuse patch of chromatophores

FIGURE 63.—*Creagrutus menezesi*, new species, holotype, MZUSP 50544, 58.7 mm SL; Brazil, Goiás, Rio Tocantins basin, Ribeirão Paranoa do Meio, at road crossing 11 air km NNE of Formosa (approximately 15°25′S, 47°18′W).

FIGURE 64.—*Creagrutus menezesi*, new species, nontype specimen, MZUSP 29892, 28.3 mm SL; Brazil, Roraima, Rio Branco, beach of Rio Xeriuini (approximately 1°0′S, 61°50′W).

over center of exposed portion of scale; pattern most distinct anteriorly on dorsolateral portion of body. Diffuse pattern of scattered chromatophores covering much of lateral surface of body in smaller specimens, these chromatophores slightly more concentrated midlaterally on caudal peduncle, but not forming discrete horizontal stripe. Diffuse lateral chromatophore field terminating anteriorly approximately two scales posterior of humeral mark resulting in intervening hyaline region. Region anterior to humeral mark in smaller specimens typically hyaline as a consequence of lack of dispersed chromatophores, but with some scattered chromatophores in that region in larger individuals. Humeral mark present, but relatively faint compared to condition in many congeners, albeit with pigmentation in mark more concentrated than scattered chromatophores present on lateral surface of body. Concentration of chromatophores more noticeable on dorsal portion of mark in some individuals. Mark vertically elongate, slightly ventrally tapering, and extending ventrally nearly to horizontal through pectoral-fin insertion. Orientation of mark somewhat variable around vertical line (Figures 63, 64). Smaller specimens with mark continuing dorsally to horizontal through dorsal margin of orbit; mark extending somewhat more dorsally in larger individuals. Dorsal portion of mark with slight anterior extension. Midlateral surface of body with very diffuse dusky band in specimens of most sizes; band anteriorly attenuate and less intense, not reaching to rear of humeral mark. Surface portion of band formed of dispersed, dark chromatophores that overlie narrower, deeper, and more intense region of pigmentation forming most of longitudinal band. Deep-lying, dark pigmentation irregularly dispersed in smaller specimens, with localized areas more intensely pigmented, particularly along myosepta.

Dorsal fin with distal portion of second unbranched ray covered with dark chromatophores. Distal portions of membranes of anterior 4 or 5 branched dorsal-fin rays with scattered chromatophores that form diffuse spot. Anal fin with scattered chromatophores along bases of anterior branched rays. Caudal-fin rays variably outlined by dark chromatophores, those along middle caudal-fin rays forming faint stripe in many specimens; chromatophores on middle caudal-fin rays more concentrated basally in some smaller individuals. Basal portions of rays of mid portions of upper and lower lobes of caudal fin variably

outlined by dark chromatophores. Pectoral and pelvic fins hyaline.

ETYMOLOGY.—The specific name, *menezesi,* is in honor of Naércio A. Menezes, Museu de Zoologia, Universidade de São Paulo, Brazil, in recognition of his myriad contributions to our knowledge of South American fishes and all his assistance to the senior author through the years.

ECOLOGY.—Stomach contents of two specimens prepared for clearing and counter staining consisted of chopped up seeds and insect parts.

Creagrutus menezesi has been captured within the upper Rio Tocantins basin sympatrically with *C. atrisignum* in the Rio Maranhão and with *C. saxatilis* and *C. figueiredoi* in residual pools in the channel of the Rio Tocantins formed during filling of the Serra da Mesa Reservoir. In the upper Rio Araguaia at Barra do Garças, Mato Grosso, Brazil, *C. menezesi* was collected jointly with *C. seductus* and *C. figueiredoi.*

DISTRIBUTION.—*Creagrutus menezesi* is widespread in the Rio Tocantins basin and is tentatively considered to occur in the Rio Branco basin and the Rio Negro near the mouth of the Rio Branco (Figure 59, diamonds; see "Remarks," below, with respect to localities outside the Rio Tocantins).

COMPARISONS.—*Creagrutus menezesi* can be readily distinguished from the other members of the genus known from the Rio Tocantins and Rio Negro basins by a combination of details of dentition and meristic characteristics (see keys to the species in each basin, above).

REMARKS.—The above description is based on the holotype and paratype series of *Creagrutus menezesi* that originated in the upper portions of the Rio Tocantins, a region from which an extensive series of specimens is available (see "Material Examined," below, and Figure 59). Although we have only two specimens of *Creagrutus menezesi* from the other major branch of the Rio Tocantins system, the Rio Araguaia (USNM 342234, USNM 342236), this population sample agrees with the upper Rio Tocantins samples in all examined features. Various lots of smaller specimens in poor condition, but apparently conspecific with *C. menezesi,* originated in the lower portions of the Rio Tocantins basin.

Several lots of *C. menezesi,* including lots of both small specimens and larger specimens in somewhat poor condition, from the Rio Branco and from portions of the Rio Negro adjoining the confluence of the Branco with the Negro (Figure 59, locality labeled 6) also are apparently conspecific with *C. menezesi.* This is surprising, given the usual limited geographic distribution of most *Creagrutus* species. The population samples originating in the Rio Tocantins and Rio Branco basins agree in meristic features (Table 35), although they have a modal shift in vertebral numbers. The Rio Tocantins population has 36 to 38 vertebrae with a strong mode of 37 (36, 27 specimens; 37, 119 specimens, 38, 19 specimens), whereas the Rio Branco and Rio Negro samples have equal numbers of specimens with 37 and 38 vertebrae (15 specimens apiece).

The ranges of several proportional values in the Rio Tocantins samples (dorsal-fin origin to pelvic-fin insertion, dorsal-fin origin to pectoral-fin insertion, and postorbital head length), although overlapping to a degree with those of specimens from the Rios Branco and Negro, are shifted modally compared with the samples from those basins (see Table 35). The samples from the Rio Branco and Rio Negro systems, however, have either significantly smaller body size than those from the Rio Tocantins or are of relatively comparable body size but are somewhat twisted, making comparisons difficult. The Rio Branco samples are, furthermore, not as well preserved as the bulk of the material from the upper Rio Tocantins, making direct comparisons problematic. Additional samples from the Rio Branco and Rio Negro basins are necessary to clarify the significance of these modal differences between populations, and until that time we tentatively assign the examined lots from those basins to *C. menezesi.*

MATERIAL EXAMINED.—634 specimens (64, 23.1–75.2).

HOLOTYPE.—BRAZIL. *Goiás:* Rio Tocantins basin, Ribeirão Paranoa do Meio, at road crossing 11 air km NNE of Formosa (approximately 15°25′S, 47°18′W), collected by W.C. Starnes et al., 13 Nov 1984, MZUSP 50544, 1 (58.7).

PARATYPES.—63 specimens (63, 32.0–75.2).

BRAZIL. *Goiás:* Rio Tocantins basin, Ribeirão Paranoa do Meio, at road crossing 11 air km NNE of Formosa (approximately 15°25′S, 47°18′W), collected with holotype, MZUSP 50545, 8 (36.5–46.5); USNM 292229, 11 (32.0–64.2; 2 specimens cleared and counterstained for cartilage and bone). Minaçu, Cavalcante, Rio Tocantins in Serra da Mesa (13°50′S, 48°19′W), collected by G.W. Nunan and D.F. Moraes, Jr., 20 Oct 1985, MNRJ 12614, 8 (36.1–55.9). Minaçu/Colinas do Sul, Rio Tocantins, in large pools below Usina Hidroelectrica Serra da Mesa during filling of reservoir, collected by D.F. Moraes et al., 28 Oct to 3 Nov 1996, MNRJ 17338, 11 (48.8–71.2); USNM 350456, 10 (56.0–75.2; formerly MNRJ 16566, in part); MNRJ 17333, 10 (55.3–69.3); USNM 350456, 5 (61.2–73.7; formerly MNRJ 16562, in part).

NONTYPE SPECIMENS.—570 specimens (18, 23.1–74.0).

BRAZIL. *Pará:* Rio Itacaiunas, Caldeirão (5°45′S, 50°30′W), MZUSP 30576, 25. *Maranhão:* Rio Tocantins, Estreito (approximately 6°32′S, 47°27′W), MZUSP 4970, 57 (5, 23.1–25.7; 2 specimens cleared and counterstained for cartilage and bone). Rio Tocantins at Carolina (7°20′S, 47°28′W), CAS 69243, 6. *Tocantins:* Rio Tocantins at Porto Nacional (10°42′S, 48°25′W), CAS 69258, 1. *Goiás:* small "brook" into Rio Maranhão at Mosondo, CAS 69262, 2. Ribeirão Tacaural, tributary of Rio dal Almas, CAS 69242, 10. Minaçu, Cavalcante, Rio Tocantins in Serra da Mesa (13°50′S, 48°19′W), MNRJ 13343, 5. Minaçu, Cavalcante, Rio Tocantins, MNRJ 13049, 39. Campinaçu, Niquelândia, Rio Maranhão, at Porto Alfredinho (14°04′S, 48°30′W), MNRJ 12558, 7. Campinaçu, Rio Boa Nova, left bank tributary of Rio Tocantins (13°52′S, 48°21′W), MNRJ 12576, 1. Niquelândia, Rio Maranhão, at Estreito, near mouth of Rio Bagagem (13°59′S, 48°22′W), MNRJ 12741, 7.

Niquelândia, Rio Maranhão, 20 km above confluence with Rio Bagagem, near mouth of Rio Arara (14°00′S, 48°26′W), MCP 15886, 12. Uruaçú, Rio Maranhão, along road between Niquelândia and Uruaçú (14°31′S, 49°03′W), MCP 15852, 11. Minaçu/Colinas do Sul, Rio Tocantins, in large pools below Usina Hidroelectrica Serra da Mesa during filling of reservoir, USNM 350451 (formerly MNRJ 16566, in part), 10; USNM 350454 (formerly MNRJ 16562, in part), 5; MNRJ 16567, 6; USNM 350455 (formerly MNRJ 16567, in part), 20. Minaçu/ Colinas do Sul, Rio Tocantins, in large pools formed by a riacho on left bank of Rio Tocantins during filling of Usina Hidroelectrica Serra da Mesa reservoir, MNRJ 16563, 9; MNRJ (ex 16564) 3; USNM 350453 (formerly MNRJ 16564, in part) 16. *Mato Grosso:* Upper Rio Araguaia basin, Município de Barra do Garças, Córrego Fundo (approximately 15°53′S, 52°15′W), USNM 342236, 1 (74.0, formerly ICLMA 190, in part); USNM 342234, 1 (formerly ICLMA uncataloged, in part).

The following specimens from the Rio Negro and Rio Branco basins are tentatively assigned to *Creagrutus menezesi:* BRAZIL. *Roraima:* Rio Branco, beach of Rio Xeriuini (approximately 1°0′S, 61°50′W), MZUSP 29892, 311 (10, 27.2–29.4). Rio Branco system, Rio Surumu (approximately 3°22′N, 60°19′W), MZUSP 16512, 2 (1, 51.2; other specimen twisted and only proportional head measurements and meristic data taken). Rio Branco, Boa Vista, MZUSP 17714, 1. *Amazonas:* W of Moura, near junction of Rio Negro and Rio Branco (1°30′S, 61°48′W), ANSP 135566, 1 (29.9); ANSP 146130, 1.

Creagrutus meridionalis, new species

FIGURES 59, 65, TABLE 36

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 2 or 3 teeth on the maxilla, 6, much less commonly 5, teeth in the primary tooth row of the premaxilla, 4 or 5 dentary teeth, 38 to 41 lateral line scales without a lamellar process over each pore, 9 to 11 predorsal median scales, 4 scale rows between the dorsal-fin origin and the lateral line, 37 to 39 vertebrae, 11 to 13 branched anal-fin rays, 2 post-anal median scales to the anal-fin origin, 6 to 8 gill rakers on the upper limb and 9 or 10 gill rakers on the lower limb of the first gill arch, the distance from the snout to the dorsal-fin origin (45.5%–49.8% of SL), the distance from the snout to the anal-fin origin (62.1%–66.4% of SL), the distance from the dorsal-fin origin to the pectoral-fin insertion (31.0%–34.8% of SL), the caudal-peduncle depth (10.5%–12.2% of SL), the dorsal-fin length (20.2%–24.0% of SL), the bony orbital diameter (32.0%–36.0% of HL), the postorbital head length (39.3% –44.5% of HL), the snout length (28.0%–31.1% of SL), the interorbital width (30.6%—34.4% of HL), the moderately developed third infraorbital with its ventral margin falling distinctly short of the horizontal limb of preopercle, the lack of a series of dark midlateral spots on the body, the vertically elongate, ventrally attenuating humeral mark, the absence of a spot of dark pigmentation on the basal portion of the middle caudal-fin rays, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus meridionalis* within the clade composed of *Creagrutus* and *Piabina.*

TABLE 36.—Morphometrics and meristics of *Creagrutus meridionalis,* new species: (A) holotype of *C. meridionalis,* new species, MZUSP 50546; and (B) paratypes of *C. meridionalis* (n=63). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	59.9	19.9–62.0
1. Snout to anal-fin origin	64.1	62.1–66.4
2. Snout to pelvic-fin insertion	47.7	46.4–50.5
3. Snout to pectoral-fin insertion	23.7	23.1–25.0
4. Snout to dorsal-fin origin	48.4	45.5–49.8
5. Dorsal-fin origin to hypural joint	56.4	55.8–59.8
6. Dorsal-fin origin to anal-fin origin	34.1	29.3–34.8
7. Dorsal-fin origin to pelvic-fin insertion	30.0	25.1–29.8
8. Dorsal-fin origin to pectoral-fin insertion	34.2	31.0–34.8
9. Caudal peduncle depth	12.0	10.5–12.2
10. Pectoral-fin length	20.0	18.0–20.7
11. Pelvic-fin length	15.4	14.5–17.4
12. Dorsal-fin length	21.7	20.2–24.0
13. Anal-fin length	17.4	16.6–18.9
14. Head length	25.7	24.7–26.8
15. Postorbital head length	44.2	39.3–44.5
16. Snout length	30.5	28.0–31.1
17. Bony orbital diameter	33.1	32.0–36.0
18. Interorbital width	33.1	30.6–34.4
	Meristics	
Lateral line scales	39	38–41
Scale rows between dorsal-fin origin and lateral line	4	4
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	10	9–11
Branched dorsal-fin rays	8	8
Branched anal-fin rays	12	11–13
Branched pelvic-fin rays	6	6
Pectoral-fin rays	14	12–14
Vertebrae	38	37–39

DESCRIPTION.—Morphometric and meristic data for *Creagrutus meridionalis* in Table 36. Examined juveniles (approximately 20–30 mm SL) relatively elongate; specimens larger than 40 mm SL becoming increasingly deep-bodied, with relative body depth greatest in larger specimens. Greatest body depth at vertical through dorsal-fin origin in smaller individuals; located at, or somewhat anterior of, that point in larger specimens. Dorsal profile of head distinctly convex from margin of upper lip to region of vertical through posterior margin of orbit, straight from that point to rear of supraoccipital spine. Dorsal surface of head medially flattened transversely, more so posterior to vertical through center of orbit. Predorsal profile of body smoothly continuous with that of head and very slightly convex in smaller specimens, with notable change in alignment

relative to profile of head and convexity distinctly more pronounced in larger specimens. Dorsal profile of body posteroventrally angled along dorsal-fin base; straight from that point to caudal peduncle in smaller specimens, somewhat convex in larger specimens. Ventral profile of head with rounded obtuse angle delimiting anteroventral angle of dentary, angle typically more obvious in larger specimens. Profile of head and body gently convex from anteroventral corner of dentary to anal-fin origin in smaller specimens; convexity more pronounced in larger individuals. Prepelvic region of body somewhat flattened transversely in larger specimens.

Head obtusely pointed in lateral view, more pointed in dorsal view. Upper jaw longer than, and overhanging, lower jaw. Anterior portion of snout fleshy, more so in larger individuals, with numerous papillae scattered over anterior surface, across upper lip, and on plicae and folds extending between outer and medial premaxillary teeth. Lower lip fleshy anteriorly, with numerous papillae over lip.

Infraorbital series moderately developed. Ventral margin of third infraorbital distinctly curved, with ventralmost portion falling somewhat short of horizontal limb of preopercle even in larger examined specimens. Posterior margins of third through fifth infraorbitals falling distinctly short of vertical limb of preopercle, gap gradually diminishing dorsally.

Premaxillary dentition in three series: primary row slightly curved, typically with 6 teeth, but with 5 teeth present on one or both premaxillae in a few specimens, without pronounced gap between first and second tooth of series but with medial teeth of contralateral series distinctly separated; triangular cluster of 3 larger teeth with posterolateral tooth of cluster largest; and single tooth of form similar to that of primary series lying lateral to region of contact of fourth or fifth teeth of primary premaxillary series. Maxilla with 2 or 3 triscupidate teeth. Dentary with 4 or 5 teeth. First and second teeth subequal or second slightly larger; both teeth tricuspidate with middle cusp largest. Third tooth approximately one-half size of preceding teeth, bicuspidate with first cusp distinctly larger. Fourth and fifth teeth (when latter present) compressed and tricuspidate.

Dorsal-fin rays ii,8. Dorsal-fin origin at, or slightly anterior of, vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin slightly concave. Anal-fin rays ii,11–13. Profile of distal margin of anal fin distinctly concave, with last unbranched and anterior two branched rays forming distinct lobe. Hooks typically present on anal-fin rays in mature males of many *Creagrutus* species not found in examined specimens. Pectoral-fin rays i,11–13. Tip of pectoral fin extending posteriorly two-thirds to three-fourths of distance to pelvic-fin insertion. Pelvic-fin rays i,6,i. Hooks typically present on pelvic-fin rays in mature males of many *Creagrutus* species not found in examined specimens. Tip of pelvic fin extending posteriorly to point somewhat short of anus.

Gill rakers 6–8 + 9–10.

COLORATION IN ALCOHOL.—Dorsal surface of head in smaller specimens with large, stellate, dark chromatophores on membranes overlying brain, and with scattered, dark, smaller surface chromatophores; deep-lying chromatophores in adults obscured by denser field of surface chromatophores, connective- tissue layers, and thick bones. Field of small, dark chromatophores on dorsal surface of head continuing anteriorly across snout to anterior of nares. Pigmentation anterior to nares more concentrated and forming dark crescent-shaped mark. Chromatophore field continuing in medium-sized individuals around ventral and posterior margins of orbit. Pigmentation at posterior margin of orbit continuous with broader pigmentation field on infraorbitals posterior to orbit and on dorsal one-half of opercle in larger specimens.

Scales of dorsal surface of body covered with scattered, dark, small chromatophores, these more concentrated along posterior portions of scales, forming faint reticulate pattern. Obscure midlateral band formed by deep-lying chromatophores; band overlain by guanine in available specimens. Humeral mark vertically elongate in specimens of all sizes, relatively more developed in larger specimens. Mark becoming attenuate ventrally, barely extending ventrally as far as lateral line in smaller specimens, extending approximately 1 scale ventral of lateral line in largest available individuals. Posterior margin of humeral mark typically nearly straight; anterior margin often with distinct concavity in its dorsal portion.

Dorsal fin with scattered, dark chromatophores, more so on distal portions of anterior fin membranes. Basal portions of anterior anal-fin rays outlined by dark chromatophores, with increased concentration of chromatophores on membranes of distal one-half of anterior lobe of fin. Caudal fin with scattered chromatophores on rays and membranes, but without distinct pigmentation pattern. Pectoral and pelvic fins ranging from unpigmented to pale with scattered, dark chromatophores on membranes.

ETYMOLOGY.—The specific name, *meridionalis*, from the Latin for southern, refers to the distribution of the species in the southern portions of the range of *Creagrutus*.

ECOLOGY.—The type locality of *Creagrutus meridionalis* is a small, clear stream. A single specimen prepared for clearing and staining in this study had stomach contents consisting of adult and larval insects.

DISTRIBUTION.—*Creagrutus meridionalis* is known from the upper portion of the Rio Paraguai basin, Mato Grosso, Brazil, and eastern tributaries to Río Paraguay in Paraguay (Figure 59, triangles).

COMPARISONS.—In addition to *Creagrutus meridionalis*, only one other *Creagrutus* species, *C. paraguayensis*, is known from the Río Paraguay basin. The two species differ in the number of branched anal-fin rays (11 to 13 in *C. meridionalis* versus 13 to 15 in *C. paraguayensis*) and in the number of scale rows between the lateral line and the dorsal-fin origin (4 versus 5, respectively).

REMARKS.—Mahnert and Géry (1988:8), in their paper describing *Creagrutus paraguayensis*, reported one specimen collected in Paraguay as *Creagrutus* sp. (aff. *paraguayensis*). They noted that the single specimen available to them, collected in the province of Cordillera, Paraguay, differed from *C. paraguayensis* in various meristic and morphometric details.

FIGURE 65.—*Creagrutus meridionalis,* new species, holotype, MZUSP 50546, 59.9 mm SL; Brazil, Mato Grosso, Município de Jangada, Ribeirão Chiqueirão (tributary of Rio Jangada that, in turn, drains into the Rio Cuiabá), approximately 21 km W of Jangada (Jangada is at 15°14′S, 56°29′W).

We have not examined this specimen, which was found within the geographic range of *C. paraguayensis* but outside the known distribution of *C. meridionalis.* The specimen of *Creagrutus* sp. (aff. *paraguayensis*) was reported by Mahnert and Géry to have 4 scales above the lateral line, a count that is found in *C. meridionalis* but that contrasts with the 5 scales above the lateral line in *C. paraguayensis,* the only other member of the genus known from the Río Paraguay basin. The relative length from the snout to the pelvic-fin insertion cited by Mahnert and Géry for their specimen (1.6 times in SL = 62.5% of SL) falls within the range for that value for *C. meridionalis* (62.1%–66.4% of SL) but falls outside that for *C. paraguayensis* (55.3%–61.0% of SL). Mahnert and Géry's specimen has, however, a somewhat different overall appearance (compare Mahnert and Géry, 1988, figs. 6, 7 with Figure 65 herein), particularly in the anterior portions of the head; thus, we only tentatively identify it as an individual of *C. meridionalis.* If additional specimens reveal this population to be conspecific with *C. meridionalis,* then the range of *C. meridionalis* extends approximately 200 km further south in the Río Paraguay basin and overlaps the known distribution of *C. paraguayensis,* contrary to the apparent allopatry of the two species based on specimens examined in this study.

MATERIAL EXAMINED.—143 specimens (73, 21.5–62.0).

HOLOTYPE.—BRAZIL. *Mato Grosso:* Ribeirão Chiqueirão (tributary of Rio Jangada that, in turn, drains into the Rio Cuiabá), approximately 21 km W of Jangada (latter locality at 15°14′S, 56°29′W) on road to Barra do Bugres, Município de Jangada; collected by R.E. Reis et al., 10 Aug 1991, MZUSP 50546, 1 (59.9).

PARATYPES.—71 specimens (63, 19.9–62.0).

BRAZIL. *Mato Grosso:* Ribeirão Chiqueirão (tributary of Rio Jangada, which, in turn, drains into the Rio Cuiabá), approximately 21 km W of Jangada (latter locality at 15°14′S, 56°29′W) on road to Barra do Bugres, Município de Jangada, collected with holotype, MZUSP 50547, 12 (23.1–62.0; 1 specimen cleared and counterstained for cartilage and bone); MCP 18738, 13 (21.5–61.9); USNM 341363, 12 (24.7–61.7; 2 specimens cleared and counterstained for cartilage and bone); FML 2527, 1 (52.0).

PARAGUAY. *Amambay.* Río Apa, 400 m below bridge to Bella Vista, Río Paraguay basin (22°07′15″S, 56°31′15″W), collected by A. Silfvergrip et al., 14 Jun 1994, NRM 22619, 20 (28.3–45.6); MNHNP 2999, 13 (5, 19.9–44.7).

NONTYPE SPECIMENS.—71 specimens (9, 43.2–54.5).

PARAGUAY. *Amambay:* Río Aquidaban in Parque Nacional Cerro Cora, approximately 32 km WSW of Pedro Juan Caballero, Río Paraguay drainage (22°38′12″S, 56°03′W), UMMZ 206757, 33. Arroyo Aquidaban-Niqui at monument site and slightly upstream in Parque Nacional Cerro Corá (22°38′S, 56°11′W), NRM 15966, 13 (2, 43.2–45.0). *Concepcion:* Arroyo Guaireno, at bridge on dirt highway, 33 km S of junction with highway 5, at Yby-Yau, tributary to Río Ypane of Río Paraguay drainage (23°15′18″S, 56°30′00″W), UMMZ 208001, 25 (7, 51.0–54.5).

Creagrutus molinus, new species

FIGURES 66, 67, TABLE 37

DIAGNOSIS.—The elongate form of the head and body and, in particular, the unusual premaxillary dentition with only two of the three principal components of the premaxillary dentition generalized for the species of *Creagrutus,* the primary tooth row without a pronounced gap between the first and second teeth, and the posteromedial triangular cluster of three teeth, combined with the absence of the third component, the separate tooth lateral to the fourth tooth in the primary premaxillary tooth row distinguishes *Creagrutus molinus* from all other species in the clade consisting of *Creagrutus* and *Piabina.* In addition, the combination of the contact of the first and second teeth of the primary premaxillary series, 3 teeth on the maxilla, 6 teeth in the primary tooth row of the premaxilla, 41 lateral

TABLE 37.—Morphometrics and meristics of holotype of *Creagrutus molinus*, new species, MZUSP 41461. Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	Morphometrics
Standard length	55.8
1. Snout to anal-fin origin	63.4
2. Snout to pelvic-fin insertion	44.8
3. Snout to pectoral-fin insertion	24.7
4. Snout to dorsal-fin origin	45.3
5. Dorsal-fin origin to hypural joint	53.8
6. Dorsal-fin origin to anal-fin origin	26.0
7. Dorsal-fin origin to pelvic-fin insertion	21.5
8. Dorsal-fin origin to pectoral-fin insertion	27.8
9. Caudal peduncle depth	11.3
10. Pectoral-fin length	18.6
11. Pelvic-fin length	13.1
12. Dorsal-fin length	19.7
13. Anal-fin length	18.6
14. Head length	25.1
15. Postorbital head length	39.3
16. Snout length	31.0
17. Bony orbital diameter	33.6
18. Interorbital width	30.7
	Meristics
Lateral line scales	41
Scale rows between dorsal-fin origin and lateral line	4
Scale rows between anal-fin origin and lateral line	3
Predorsal median scales	11
Branched dorsal-fin rays	8
Branched anal-fin rays	12
Branched pelvic-fin rays	6
Pectoral-fin rays	12
Vertebrae	38

line scales without a lamellar process over each pore, 11 predorsal median scales, 4 scale rows between the dorsal-fin origin and the lateral line, 38 vertebrae, 12 branched anal-fin rays, 2 post-anal median scales to the anal-fin origin, 11 gill rakers on the lower limb of the first gill arch, the distance from the snout to the pectoral-fin insertion (24.7% of SL), the distance from the dorsal-fin origin to the anal-fin origin (26.0% of SL), the distance from dorsal-fin origin to the pectoral-fin insertion (27.8% of SL), the snout length (31.0% of SL), the postorbital head length (39.3% of HL), the well-developed third infraorbital ventrally contacting the horizontal limb of the preopercle, the lack of a series of dark midlateral spots on the body, the rotund, albeit indistinct, humeral mark, the absence of chevron-shaped marks on the body, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus molinus* within the clade composed of *Creagrutus* and *Piabina*.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus molinus* in Table 37. Head and body elongate, much more so than in the majority of its congeners. Greatest body depth at dorsal-fin origin. Dorsal profile of head distinctly convex from margin of upper lip approximately to vertical through posterior nostril, nearly straight from that point to rear of supraoccipital spine. Predorsal profile of body slightly convex. Postdorsal profile of body nearly straight. Ventral profile of head and body gently convex from margin of upper lip to anal-fin origin. Obtuse angle at anteroventral corner of dentary obvious in most congeners not apparent in this species.

Head obtusely pointed in lateral and dorsal views. Upper jaw longer than, and overhanging, lower jaw. Anterior portion of snout fleshy, with numerous papillae over median region, upper lip, lateral surface of maxilla, and on plicae and folds extending between outer and medial premaxillary teeth. Lower lip thick and fleshy anteriorly, with numerous papillae along dorsal surface.

Infraorbital series moderately well developed. Ventral margin of third infraorbital contacting horizontal limb of preopercle. Posterior margins of third through fifth infraorbitals falling short of vertical limb of preopercle.

Premaxillary dentition of the holotype (the only known specimen) proportionally relatively massive on one side of head; premaxillary dentition in process of replacement on other side of head. Premaxilla with only two of three major components typically present in other *Creagrutus* species. Primary row of premaxillary dentition consisting of 6 distally rounded teeth, with brown-tipped central raised point, without pronounced gap between first and second tooth of series; 6 partially developed teeth in the process of replacement also apparent in main tooth row on right side. Single tooth, typically lateral to primary row of premaxillary teeth in *Creagrutus* species, absent, and no space apparent on premaxilla onto which tooth would have attached. No indication of single replacement tooth on side of premaxilla in which teeth are in process of replacement. Triangular cluster of median teeth formed by 3 massive rounded teeth with central raised point. Three worn maxillary teeth present. Dentary with 3 massive teeth anteriorly. Total number of dentary teeth indeterminable without forcing open lower jaw and potentially damaging the unique specimen.

Dorsal-fin rays ii,8. Dorsal fin located slightly anterior of vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin straight. Anal-fin rays ii,12. Profile of distal margin of anal fin distinctly concave. Mature male holotype with paired hooks present on all but distal segments of first branched pelvic-fin rays and some, but not most, of distal segments of second branched ray. Hooks limited to main shaft and posterior branches of these rays. Pectoral-fin rays i,11. Tip of pectoral fin extending posteriorly slightly more than three-fourths of distance to pelvic-fin insertion. Pelvic-fin rays i,6,i. Tip of pelvic fin extending posteriorly approximately three-fourths of distance to anal-fin origin. Mature males with hooks present on all branched anal-fin rays and on medial unbranched rays. Hooks distributed both on basal portion of ray and each segment, other than distalmost segment; limited to posterior margin of main shaft and posterior branch of branched rays except for medialmost ray having hooks on both branches.

Gill rakers 7+11.

FIGURE 66.—*Creagrutus molinus*, new species, holotype, MZUSP 41461, 55.8 mm SL; Brazil, Mato Grosso, Rio Araguaia basin, riacho (small stream) tributary to Ribeirão Lajeadinho, Município de Alto Araguaia (approximately 17°19′S, 53°12′W).

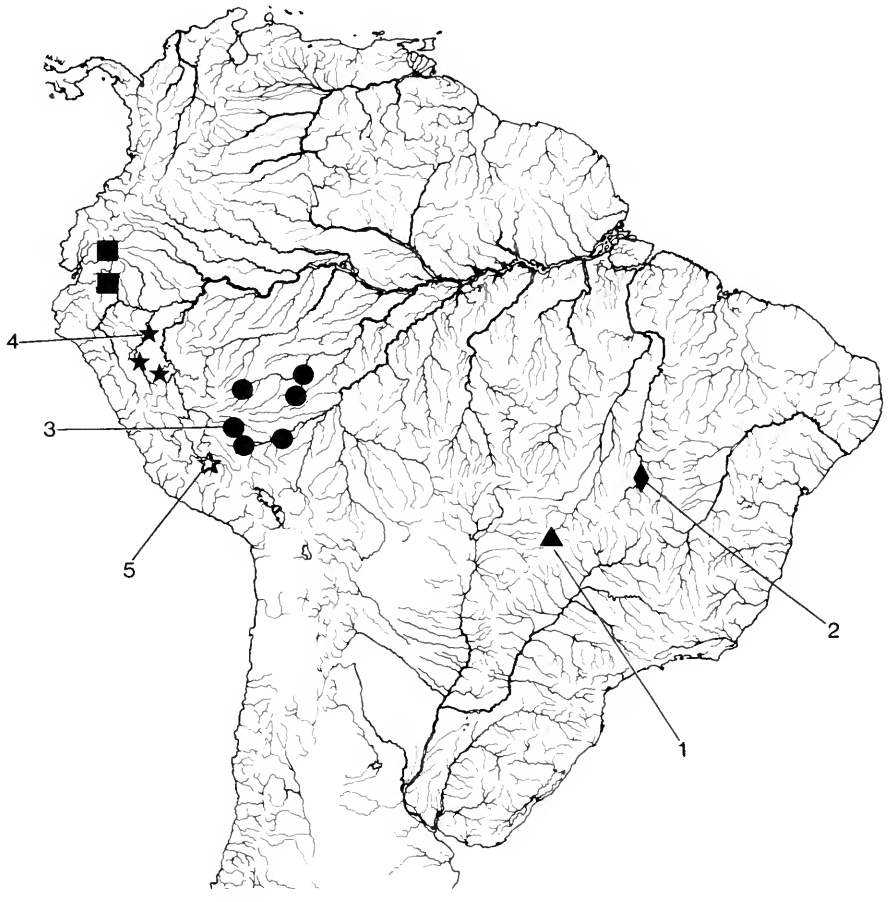

FIGURE 67.—Map of central and northern South America showing geographic distribution of *Creagrutus molinus* (triangle, 1=type locality), *Creagrutus mucipu* (diamond, 2=type locality), *Creagrutus muelleri* (squares; type locality inexact=Andes of Western Ecuador), *Creagrutus occidaneus* (dots, 3=type locality), *Creagrutus ortegai* (solid stars, 4=type locality), and *Creagrutus ouranonastes* (open star, 5=type locality) (some symbols represent more than one locality or lot of specimens).

COLORATION IN ALCOHOL.—Overall ground coloration yellowish, overlain midlaterally and on portions of head by guanine in single known specimen. Dorsal surface of head with field of small, dark chromatophores most concentrated over fontanelle. Chromatophore field denser over snout and upper lip. Region anterior to nares without dense concentration of chromatophores typical of many *Creagrutus* species. Region ventral of nares and along ventral margin of anterior portion of adipose eyelid with posteroventrally inclined band of small, dark chromatophores. Scattered, dark chromatophores over fourth and fifth infraorbitals and dorsal portion of opercle.

Body with scattered, dark chromatophores over dorsolateral and dorsal surface, more concentrated dorsally, with chromatophores denser along posterior region of scales in this region and forming dark, reticulate pattern. Humeral mark relatively faint, formed of small chromatophores arranged in irregularly rotund blotch; mark mostly located dorsal of lateral line. Faint midlateral stripe on posterior portion of caudal peduncle and on base of middle caudal-fin rays. Dorsal- and anal-fin rays outlined by scattered, small, dark chromatophores. Caudal-fin rays mostly delimited by small, dark, chromatophores, other than for basal portions of rays lying dorsal and ventral of middle rays of fin. Pectoral and pelvic fins mostly hyaline.

ETYMOLOGY.—The specific name, *molinus,* from the Latin for grinder, refers to the large teeth in the upper and lower jaws of this species.

DISTRIBUTION.—*Creagrutus molinus* is known only from the type locality in the upper Rio Araguaia basin (Figure 67, triangle).

COMPARISONS.—The distinctive premaxillary dentition characterized by large teeth limited to two of the three components typical for the species of *Creagrutus,* with a lack of the single tooth of form similar to that of primary series lateral to the primary tooth series, is unique to *C. molinus* in the genus. Within the greater Rio Tocantins drainage system, including the Rio Araguaia, *C. molinus* is distinguished from the other *Creagrutus* species of the basin by having 4 scales above the lateral line to the dorsal-fin origin (contrary to 5 in *C. atrisignum* and *C. britskii*), 12 branched anal-fin rays (contrary to 9 or 10 in *C. figueiredoi* and *C. menezesi*), 5 teeth in the primary premaxillary tooth row and 38 vertebrae (contrary to 6 teeth in the primary premaxillary tooth row and 35 or 36 vertebrae in *C. mucipu*), 9 to 11 gill rakers on the lower limb of the first arch and 41 lateral line scales (versus 13 or 14 rakers and 37 to 39 scales in *C. saxatilis*), and various proportional morphometric values (numbers 7, 8, 11 in *C. seductus,* compare Tables 37 and 53).

REMARKS.—*Creagrutus molinus* is known only from a single specimen, which unfortunately was in the process of replacing its dentition in both the right dentary and premaxilla. The distinctive dentition apparent on the left side of the jaws and its overall appearance readily distinguish *C. molinus* from other *Creagrutus* species, and we describe it herein to draw attention to this unusual form.

MATERIAL EXAMINED.—1 specimen (1, 55.8).

HOLOTYPE.—BRAZIL. *Mato Grosso:* Rio Araguaia basin, riacho (small stream) tributary to Ribeirão Lajeadinho, Município de Alto Araguaia (approximately 17°19′S, 53°12′W); collected by L.P.S. Portugal and F. Langeani, MZUSP 41461, 1 (55.8).

Creagrutus mucipu, new species

FIGURES 67, 68, TABLE 38

DIAGNOSIS.—The pattern of very dark, posteriorly directed, chevron-shaped pigmentation patches along the midlateral surface of the body is autapomorphic for *Creagrutus mucipu* among the species of *Creagrutus* and *Piabina. Creagrutus mucipu* also has the distal margin of the caudal fin outlined with a band of dusky pigmentation. This dark distal caudal-fin pigmentation is separated from more basal dusky pigmentation by a hyaline region, a pigmentation pattern not found elsewhere in *Creagrutus* and *Piabina.* In addition to these autapomorphic pigmentation features, the combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a pronounced gap between the first and second teeth of the primary series, 5 teeth in the primary series of each premaxilla, 3 maxillary teeth, 7 teeth on each dentary, 9 or 10 predorsal median scales, 2 post-anal median scales to the anal-fin origin, 36 to 39 lateral line scales without a lamellar process over each pore, 4 scale rows between the dorsal-fin origin and the lateral line, 11 branched anal-fin rays, 6 or 7 gill rakers on the upper limb and 9 to 11 gill rakers on the lower limb of the first arch, the distance from the snout to the dorsal-fin origin (45.0%–47.9% of SL), the distance from the dorsal-fin origin to the anal-fin insertion (32.4%–36.5% of SL), the caudal peduncle depth (12.5%–13.3% of SL), the head length (24.9%–27.5% of SL), the snout length (24.5%–29.0% of HL), the postorbital head length (40.6%–44.8% of HL), the interorbital width (29.7%–33.0% of HL), the well-developed third infraorbital whose straight ventral margin contacts the horizontal limb of the preopercle, the lack of a distinct spot of dark pigmentation at the base of the middle caudal-fin rays, the faint, vertically elongate, ventrally attenuating humeral mark with straight anterior and posterior margins and lacking a secondary, dorsal patch of pigmentation, the absence of a distinct patch of pigmentation on the dorsal fin, and the lack of a series of dark, round spots along the midlateral surface of the body distinguishes *Creagrutus mucipu* within the clade formed by *Creagrutus* and *Piabina.*

DESCRIPTION.—Morphometric and meristic data for *Creagrutus mucipu* in Table 38. Head and body moderately robust; body more robust in larger individuals. Greatest body depth proportionally greater in larger individuals; at, or slightly anterior to, vertical through dorsal-fin origin in smaller examined paratypes; at dorsal-fin origin in larger examined individuals. Dorsal profile of head convex from margin of upper lip to

TABLE 38.—Morphometrics and meristics of *Creagrutus mucipu*, new species: (A) holotype of *C. mucipu*, MCP 19511; and (B) paratypes of *C. mucipu* (n=8). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	50.1	37.6–56.1
1. Snout to anal-fin origin	65.3	62.0–66.0
2. Snout to pelvic-fin insertion	47.5	46.2–48.9
3. Snout to pectoral-fin insertion	26.7	24.3–26.4
4. Snout to dorsal-fin origin	46.1	45.0–47.9
5. Dorsal-fin origin to hypural joint	59.1	57.6–59.6
6. Dorsal-fin origin to anal-fin origin	35.7	32.4–36.5
7. Dorsal-fin origin to pelvic-fin insertion	30.1	28.5–32.6
8. Dorsal-fin origin to pectoral-fin insertion	34.1	32.1–36.2
9. Caudal peduncle depth	12.8	12.5–13.3
10. Pectoral-fin length	20.4	19.2–22.3
11. Pelvic-fin length	17.2	16.0–18.5
12. Dorsal-fin length	21.8	21.5–23.4
13. Anal-fin length	19.6	18.0–20.4
14. Head length	27.5	24.9–27.2
15. Postorbital head length	41.9	40.6–44.8
16. Snout length	24.5	24.6–29.0
17. Bony orbital diameter	32.2	32.4–36.4
18. Interorbital width	29.7	29.9–33.0
	Meristics	
Lateral line scales	39	36–39
Scale rows between dorsal-fin origin and lateral line	4	4
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	9	9–10
Branched dorsal-fin rays	8	8
Branched anal-fin rays	11	11
Branched pelvic-fin rays	7	5–7[1]
Pectoral-fin rays	13	12–14
Vertebrae	36	35–36

[1]Five branched anal-fin rays present on only on one pelvic fin of 1 of 8 paratypes; 7 branched anal-fin rays limited to larger specimens.

slightly posterior of vertical through posterior nostril, then nearly straight to tip of supraoccipital spine. Interorbital region transversely convex. Predorsal profile of body slightly convex, with moderate change in alignment relative to profile of posterior portion of head. Predorsal region of body with obtuse median ridge along posterior half of its length in larger specimens. Prepelvic profile of lower jaw with obtuse angle at anteroventral corner of dentary. Ventral profile of head posterior to obtuse angle on dentary slightly convex to isthmus. Ventral profile of body slightly convex overall and continuing profile of ventral profile of head. Prepelvic region of body obtusely flattened transversely.

Head obtusely rounded in lateral view, but more compressed transversely in dorsal view. Upper jaw slightly longer than, and overhanging, lower jaw. Snout fleshy anteriorly, with scattered papillae on anterior surface, papillae field continuing onto fleshy folds between premaxillary teeth. Lower lip fleshy anteriorly, with scattered papillae on upper and anterior portions.

Infraorbital series well developed. Ventral margin of third infraorbital straight and contacting horizontal limb of preopercle in specimens of all available sizes. Posterior margins of third through fifth infraorbitals approaching, but not contacting, vertical limb of preopercle; gap narrow in specimens of all available sizes.

Premaxillary dentition in three series: primary row arched, with 5 teeth, without pronounced gap between first and second tooth of series; triangular cluster of 3 larger teeth, without pronounced gap between first and second tooth of series but with medial teeth of contralateral clusters nearly in contact; and single tooth of form similar to that of primary series occurring lateral to third tooth of primary tooth row. Maxilla with 3 tricuspidate teeth. Dentary with 5 or 6 tricuspidate teeth. Second dentary tooth somewhat larger than first tooth and distinctly larger and about approximately one and one-half times vertical extent of third tooth; fourth tooth distinctly smaller than third tooth; fourth through last teeth in series progressively gradually decreasing in size.

Dorsal-fin rays ii,8 in all specimens. Distal margin of dorsal fin slightly concave. Anal-fin rays ii,11 in all specimens. Distal margin of anal fin concave. Anal-fin hooks present on first, first and second, or first through third rays of mature males. Pectoral-fin rays i,11–13. Tip of pectoral fin reaching posteriorly nearly to pelvic-fin insertion. Pelvic-fin rays i,5–7; 5 branched rays limited to pelvic fin on one side of one specimen; 7 branched rays occurring only in larger examined specimens. Tip of pelvic fin reaching posteriorly nearly to anal-fin origin. Pelvic-fin hooks present on 5 or 6 branched rays in mature males; medial branched ray lacking hooks when only 5 hook-bearing rays present.

Gill rakers 6–7 + 9–11.

COLORATION IN ALCOHOL.—Ground coloration of specimen very light tan to tan. Dorsal surface of head in smaller individuals with dense field of dark chromatophores on membranes overlying brain and with field of scattered, smaller, dark chromatophores on surface of head; chromatophore concentration distinctly less pronounced anteriorly. Surface chromatophore field gradually becoming more concentrated in larger specimens and forming field of dense pigmentation in larger specimens, albeit somewhat less concentrated on dorsal surface of snout. Region anterior to nostrils with only slightly more concentrated field of dark chromatophores in specimens of all sizes; these not forming distinct crescent-shaped patch in that region such as found in many congeners. Area anteroventral to orbit with diffuse field of small, dark chromatophores extending from ventral margin of nares to ventral margin of orbit. Dorsal portion of opercle and lateral surface of fourth though sixth infraorbitals with scattered, stellate, dark chromatophores in smaller individuals; chromatophore field extending somewhat more ventrally and to a degree under orbit in larger specimens.

Scales on dorsal portion of body with exposed margins outlined by small, dark chromatophores, giving region overall

FIGURE 68.—*Creagrutus mucipu,* new species, holotype, MCP 19511, 50.1 mm SL; Brazil, Goiás, Municipio de Minaçu, Rio Tocantins, at port of Rubao (13°44′31″S, 48°08′29″W).

dark, reticulate, pigmentation pattern. Midlateral region of body with series of dark, chevron-shaped marks formed by deep-lying chromatophores. Individual chevron-shaped marks with arms relatively straight, sometimes with secondary branches extending at angles from main body of mark. Chevron pattern most obvious in region ventral of dorsal fin, becoming less apparent on body posteriorly. Dorsal portions of chevrons more obvious than ventral portions in many individuals, particularly smaller specimens. Ventral portion more apparent in most larger individuals. Humeral mark formed of relatively faint to distinct, small, dark chromatophores. Overall form of humeral mark vertically elongate and ventrally attenuating, with anterior and posterior margins somewhat variable, ranging from relatively straight to having concave anterodorsal and posterodorsal margins, or convex anterodorsal margin. Humeral mark extending dorsally to one scale from middorsal line and ventrally to level approximately one scale dorsal of horizontal through dorsal limit of pectoral-fin insertion. Faint midlateral body stripe formed by small, dispersed, dark chromatophores extending from about 2 scales posterior of humeral mark posteriorly to rear of caudal peduncle. Stripe widest and overlying dark chevron-like marks anteriorly, gradually narrowing and only partially overlapping dark midlateral marks along posterior portion of body. Stripe merging into field of scattered, dark chromatophores on caudal peduncle.

Dorsal fin with small dark chromatophores on membranes and outlining many fin rays. Anal fin with scattered, dark chromatophores on distal two-thirds of membranes of branched rays. Pectoral fin with small chromatophores on membranes. Pelvic fin hyaline. Caudal fin with basal dusky pigmentation extending out along rays of each lobe. Distal margin of caudal fin outlined by band of diffuse dark pigmentation. Distal and basal regions of caudal pigmentation separated by hyaline region.

ETYMOLOGY.—The species name, mucipu, is an acronym derived from Museu de Ciências e Tecnologia, PUCRS (Pontificia Universidade Católica do Rio Grande do Sul) whose staff collected the holotype of the species and brought it to our attention, and who have provided valuable assistance to the authors in this and other projects. It is treated as a noun in apposition.

ECOLOGY.—The holotype and paratypes, the only know specimens of *Creagrutus mucipu,* were collected in residual ponds in the bed of the Rio Tocantins following the interruption of water flow through the channel as a result of the closure of a dam, the Repressa da Usina Hidroelectica de Serra da Mesa. The natural habitat of *C. mucipu* is, thus, unknown, but the river had clear water and a bottom of small stones and rocks prior to the dam closure (C. Lucena, pers. comm., 2000). The paratype series of *C. mucipu* was collected together with specimens of *C. menezesi* and *C. figueiredoi.* A female that was prepared for clearing and staining in this study (USNM 350449, 41.4 mm SL) had numerous well-developed eggs. It was collected in the late October to early November period of 1996.

SEXUAL DIMORPHISM.—The relatively small available sample of *Creagrutus mucipu* shows a definite difference in the relative size of the two sexes. Mature males, as indicated by the presence of body hooks on the anterior rays of the anal fin and on the branched rays of the pelvic fin range from 37.6 to 44.9 mm SL (n=3). Females lacking those modifications range from 40.8 to 56.1 mm SL (n=6).

DISTRIBUTION.—*Creagrutus mucipu* is known only from the type locality in the upper portions of the Rio Tocantins basin (Figure 67, diamond).

REMARKS.—Although *Creagrutus mucipu* is known only from a limited series of specimens, its distinctive features, in particular the pattern of dark chevron-shaped pigmentation patches along the midlateral surface of the body and the caudal-fin pigmentation, readily distinguish it from all congeners.

MATERIAL EXAMINED.—9 specimens (9, 37.6–56.1).

HOLOTYPE.—BRAZIL. *Goiás*: Município de Minaçu, Rio Tocantins, at port of Rubao (13°44′31″S, 48°08′29″W), col-

lected by C.A.S. Lucena and J.J.P. Silva, 7 Nov 1996; MCP 19511, 1 (50.1).

PARATYPES.—8 specimens (8, 37.6–56.1).

BRAZIL. *Goiás:* Município de Minaçu/Colinas do Sul. Rio Tocantins, in large pools below dam of Usina Hidroelectica de Serra da Mesa following closure of dam to fill reservoir (approximately 13°44′S, 48°08′W), collected by D.F. Moraes et al., 28 Oct to 3 Nov 1996, MNRJ 17337, 6 (37.6–56.1); USNM 350449, 2 (41.4–51.7).

Creagrutus muelleri (Günther, 1859)

FIGURES 67, 69, TABLE 39

Leporinus mülleri Günther, 1859:92 [type locality: Andes of Western Ecuador].

Creagrutus mülleri.—Günther, 1864:339 [redescription based on Günther (1859); designated as type species of *Creagrutus* Günther].—Steindachner, 1882b:20 [Ecuador (Pastaza) Canelos].—Eigenmann and Eigenmann, 1891:14 [listing].—Eigenmann, 1910:435 [in part, Ecuador; not synonymy of *Creagrutus affinis* Steindachner or reported occurrence of *C. mülleri* in [Río] Cauca [Colombia]]; 1927:420, pl. 35: figs. 6, 7 [based on Günther's 1864 account].—Eigenmann and Allen, 1942:227 [literature listing; not reported occurrence of species in [Río] Cauca [Colombia]].—Fowler, 1943b:1 [Ecuador, Tungurahua, Río Pastaza, Hacienda Las Mascota].—Barriga, 1991:17 [eastern Ecuador].—Not Böhlke, 1958:30.—Not Saul 1975:106.

Creagrutus muelleri.—Fowler, 1948:84 [literature compilation]; 1975:26 [literature compilation].—Géry, 1977:407 [in key].—Géry and Renno, 1989, fig. 4b [maxillary dentition].—Barriga, 1994:29 [Ecuador, Parque Nacional Yasuní].—Not Boulenger, 1887.

Creagrutus mulleri.—Ovchynnyk, 1968:246 [Ecuador, eastern slopes of Andes].

Creagrutus aff. *mulleri.*—Barriga, 1982:64 [Ecuador, Zamora-Chinchipe: Río Nangaritza, Río Samora, Quebrada Tunanza; life history; common name].

DIAGNOSIS.—The possession of premaxillary dentition with the three components generalized for the species of *Creagrutus,* but with a distinct gap between the first and second teeth of primary tooth row and a forward position of the triangular cluster of three posteromedial teeth distinguishes *C. muelleri* from all members of the clade formed by *Creagrutus* and *Piabina* with the exception of *Creagrutus maracaiboensis, C. melanzonus, C. nigrostigmatus, C. ouranonastes, C. peruanus, C. runa,* and *Piabina argentea. Creagrutus muelleri* can be distinguished from these seven species by the combination of the possession of 39 to 41 lateral line scales, 11 to 13 predorsal median scales, 10 to 12 branched anal-fin rays, 39 or 40 vertebrae, the relatively wide third infraorbital nearly contacting the horizontal and vertical limbs of the preopercle, the distance from the snout to the anal-fin origin (60.1%–65.6% of SL), the anal-fin length (15.3%–17.8% of SL), the caudal peduncle depth (11.7%–13.4% of SL), the bony orbital diameter (24.9%–29.7% of HL), and the absence of two small distinct spots of dark pigmentation on the basal portion of the caudal fin.

DESCRIPTION.—Morphometric andmeristic data for *Creagrutus muelleri* in Table 39. Overall body relatively robust, particularly anteriorly. Greatest body depth at vertical through dorsal-fin origin in specimens of approximately 30 mm SL,

TABLE 39.—Morphometrics and meristics of *Creagrutus muelleri:* (A) lectotype of *C. muelleri,* BMNH 1858.7.25:42; and (B) all other specimens of *C. muelleri* from which counts and measurements were taken (n=26). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	82.5	35.1–108.3
1. Snout to anal-fin origin	61.7	60.1–65.6
2. Snout to pelvic-fin insertion	44.7	43.0–48.3
3. Snout to pectoral-fin insertion	23.9	21.6–25.8
4. Snout to dorsal-fin origin	49.8	47.3–51.0
5. Dorsal-fin origin to hypural joint	56.1	53.7–58.9
6. Dorsal-fin origin to anal-fin origin	30.7	28.6–31.6
7. Dorsal-fin origin to pelvic-fin insertion	29.0	25.0–29.9
8. Dorsal-fin origin to pectoral-fin insertion	33.1	31.3–35.8
9. Caudal peduncle depth	12.7	11.7–13.4
10. Pectoral-fin length	20.0	19.0–20.9
11. Pelvic-fin length	14.5	14.4–15.7
12. Dorsal-fin length	18.2	17.8–22.4
13. Anal-fin length	16.2	15.3–17.8
14. Head length	25.8	23.7–26.5
15. Postorbital head length	54.0	47.3–54.1
16. Snout length	24.5	24.4–29.4
17. Bony orbital diameter	25.3	24.9–29.7
18. Interorbital width	34.2	30.0–34.8
	Meristics	
Lateral line scales	41	39–41
Scale rows between dorsal-fin origin and lateral line	4	4–5
Scale rows between anal-fin origin and lateral line	3	3–4
Predorsal median scales	13	11–13
Branched dorsal-fin rays	8	7–8[1]
Branched anal-fin rays	10	10–12[2]
Branched pelvic-fin rays	6	5–6[3]
Pectoral-fin rays	13	12–14
Vertebrae	40	39–40

[1]Seven branched dorsal-fin rays present in only 1 of 26 specimens.

[2]Ten and 11 branched anal-fin rays most common, 12 rays present in only 2 of 26 specimens.

[3]Five branched pelvic-fin rays present in only 1 of 26 specimens.

shifting somewhat anterior of that point in larger individuals, more notably in specimens with distended abdomens. Dorsal profile of head smoothly curved from margin of upper lip to vertical through posterior nostril, straight, or nearly so, from that point to rear of supraoccipital spine. Dorsal profile of body gently convex from rear of supraoccipital spine to dorsal-fin origin at all body sizes, convexity somewhat more pronounced in larger examined specimens. Profile posteroventrally angled along dorsal-fin base and nearly straight from posterior of dorsal-fin base to caudal peduncle in smaller specimens. Changes in profile at anterior and posterior insertions of dorsal fin less notable in larger specimens. Ventral profile of head convex, with barely apparent obtuse angle at anteroventral region of dentary. Ventral profile of body between isthmus and pelvic fin convex; convexity more pronounced in larger specimens.

Head obtusely pointed in lateral view and more obviously pointed in dorsal view. Upper jaw longer than, and slightly

overhanging, lower jaw. Anterior portion of snout fleshy, with scattered papillae that extend onto lips and on folds and plicae extending between outer and medial premaxillary teeth. Larger individuals with field of large papillae all over head.

Infraorbital series moderately well developed. Large portion of ventral margin of third infraorbital in contact with horizontal limb of preopercle. Posterior margins of third through fifth infraorbitals not contacting vertical limb of preopercle; gap between infraorbitals and vertical limb of preopercle decreasing slightly dorsally.

Premaxillary teeth in three series: primary row curved, consisting of 5 teeth, with distinct gap between first and second tooth and between medial teeth of contralateral series; triangular cluster of three teeth with anterior tooth approximately same size as teeth of primary row and slightly medial to pronounced gap between first and second teeth of primary row, two other teeth of medial cluster, particularly posteromedial tooth, larger than remaining teeth in jaw; and single tooth of form similar to that of primary series lying lateral to area of contact of third and fourth teeth of primary premaxillary row. Maxilla with 3 or 4 tricuspidate teeth. Dentary with 5 or 6 tricuspidate teeth. Three anterior dentary teeth distinctly larger than other teeth in series, with second tooth slightly larger than first tooth. Third tooth approximately two-thirds height of second tooth. Middle cusp on anterior 3 teeth particularly well developed. Last 2 or 3 teeth on dentary compressed, tricuspidate, and distinctly smaller than third tooth and becoming progressively smaller posteriorly.

Dorsal-fin rays typically ii,8; very rarely ii,7. Dorsal-fin origin at vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin slightly convex in smaller individuals, nearly straight in largest examined specimens. Anal-fin rays ii,10–12. Profile of distal margin of anal fin very slightly concave. Hooks typically present on anal-fin rays in mature males of many *Creagrutus* species not present in examined specimens. Pectoral-fin rays i,11–13. Tip of pectoral fin extending posteriorly nearly to pelvic-fin insertion in smaller specimens, only approximately two-thirds of distance in larger specimens. Pelvic-fin rays typically i,6,i, one specimen with i,5,i. Tip of pelvic fin extending posteriorly to anus. Hooks typically present on pelvic-fin rays in mature males of many *Creagrutus* species not present in examined specimens.

Gill rakers 7–8 + 10–11.

COLORATION IN ALCOHOL.—Ground coloration of specimens collected within the last two decades tan to light brown. Dorsal surface of head with scattered, small, dark chromatophores overlying deep-lying chromatophores over membranes of brain. Region anterior to nostrils somewhat more intensely pigmented, but without distinct crescent-shaped patch of dark pigmentation found in this region in some congeners. Lateral surface of head with scattered, dark chromatophores, chromatophores more concentrated on dorsal portions of opercle and infraorbitals. Body pigmentation darker dorsally, with distinctly darker pigmentation over center of scales dorsally and dorsolaterally. Margins of scales less intensely pigmented, with chromatophores forming dark, reticulate pattern on dorsolateral portions of body. Deep-lying obscure, dark band along midlateral surface of body. Humeral mark irregularly shaped, but vertically elongate overall. Mark ventrally attenuate with somewhat less intensely pigmented region extending up to one-half scale ventral of lateral line. Anterior margin of humeral mark slightly concave.

Margins of fin-rays of dorsal, anal, and caudal fins outlined with small, dark chromatophores, giving fins, particularly caudal fin, dusky overall appearance. Paired fins hyaline to slightly dusky.

ECOLOGY.—Barriga (1982:67) reported that in southeastern Ecuador this species (identified therein as *Creagrutus* aff. *mulleri*) inhabits large rivers with strong currents, turbid waters, and muddy bottoms, but within that region it was collected in regions of pebble beaches.

Creagrutus muelleri feeds most commonly on seeds, but some individuals also had fed on insect larvae and fish scales (Barriga, 1982:67). Stomach contents of specimens prepared for clearing and staining in this study consisted of parts of larvae and adult insects, and chopped-up seeds. A female collected in September has ovaries full of eggs.

COMMON NAME.—Southeastern Ecuador: "Blancos" (Barriga, 1982:64).

DISTRIBUTION.—*Creagrutus muelleri* occurs in the rivers draining the eastern slopes of the Andean piedmont in Ecuador (Figure 67, squares).

REMARKS.—There are five specimens presently identified as the syntypes of *Leporinus mülleri* (BMNH 1858.7.25:42-45), four of which were examined during this study. Two of those individuals, distinctly smaller than the other specimens in the type series, are individuals of *Ceratobranchia* Eigenmann, a characiform genus apparently not closely related to *Creagrutus* and whose characters, particularly dentition (see illustrations of teeth of *Ceratobranchia* in Chernoff and Machado-Allison, 1990), differ significantly from those of *Creagrutus* and *Piabina*.

Günther (1859) did not explicitly note how many specimens served as the basis for his original description of *Leporinus mülleri*. Nonetheless, the detailed information on the number of pyloric caeca and vertebrae in the original description of the species must have been based on a dissected specimen. One of the two examined *Creagrutus* specimens in the type series of *Leporinus mülleri*, an 82.5 mm SL individual, has been dissected in a manner as to provide the information cited by Günther. Given that this specimen is obviously the individual that served as the basis for much of the information in the original description of the species, it is herein designated as the lectotype of *Leporinus mülleri* (BMNH 1858.7.25:42). The other four syntypes, at least two of which are specimens of *Ceratobranchia*, become paralectotypes.

The original description of *Creagrutus muelleri* provided by Günther (1859) was relatively brief, and his description of its

FIGURE 69.—*Creagrutus muelleri,* USNM 340984, 72.5 mm SL; Ecuador, Pastaza, Río Pastaza, tributary stream 2 km downstream of Cumandá (1°27′S, 78°08′W).

dentition, particularly of the premaxillary teeth, was subject to alternate interpretations, a problem with many descriptions of the dentition in the genus. As a consequence several subsequent identifications of the species have proven to be erroneous. Böhlke (1958:30) reported *Creagrutus mülleri* from a number of localities in eastern Ecuador. In his description of *C. boehlkei,* Géry (1972:65) equated Böhlke's material with that species. A reappraisal has shown that Böhlke's specimens were mostly *C. amoenus* (a senior synonym of *C. boehlkei*) with some lots of *C. kunturus,* a species very similar in overall appearance to *C. amoenus,* which also occurs in eastern Ecuador.

Saul (1975:106) reported on the food and habitat preferences of material he identified as *Creagrutus muelleri.* These specimens have proved to be *C. amoenus.*

MATERIAL EXAMINED.—41 specimens (27, 35.1–108.3).

ECUADOR. "Andes of Western Ecuador," BMNH 1858.7.25:42, 1 (82.5, lectotype of *Leporinus mülleri*); BMNH 1858.7.25:43, 1 (78.3, paralectotype of *Leporinus mülleri*). *Tungarahua:* N shore of Río Pastaza below town of Río Negro (1°24′S, 78°13′W), KU 20003, 10 (35.1–74.2). Río Pastaza, Hacienda Las Mascota, ANSP 70154, 1 (88.0). *Pastaza:* Río Pastaza, tributary stream 2 km downstream of Cumandá (1°27′S, 78°08′W), USNM 340984, 10 (6, 38.9–72.5; 2 specimens cleared and counterstained for cartilage and bone). *Zamora Chincipe:* Río Zamora, near city of Zamora (4°04′S, 78°08′W), MEPN 4637, 1 (57.0); MEPN 4638, 1 (53.3). Río Nangaritza, near village of Guayzimi (4°02′S, 78°40′W), MEPN 4636, 2 (48.2–78.0). Río Nangaritza (3°45′S, 78°36′W), MEPN 6195, 10. Río Zamora above mouth of Río Jamboe (approximately 4°04′S, 78°56′W), USNM 340983, 4 (60.0–108.3; 1 specimen cleared and counterstained for cartilage and bone).

Creagrutus occidaneus, new species

FIGURES 67, 70, TABLE 40

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 3 or 4 teeth on the maxilla, 6, rarely 5, teeth in the primary tooth row of the premaxilla, 4 or 5 dentary teeth, 38 to 43 lateral line scales without a lamellar process over each pore, 9 or 10 predorsal median scales, 3 or 4 scale rows between the dorsal-fin origin and the lateral line, 37 to 39 vertebrae, 10 or 11 branched anal-fin rays, 2 post-anal median scales to the anal-fin origin, 6 to 8 gill rakers on the upper limb of the first gill arch, 11 to 13 gill rakers on the lower limb of the first gill arch, the bony orbital diameter (32.6%–37.9% of HL), the anal-fin length (15.9%–19.5% of SL), the distance from the dorsal-fin origin to the anal-fin origin (30.3%–36.0% of SL), the distance from the dorsal-fin origin to the pelvic-fin insertion (25.4%–30.8% of SL), the distance from the dorsal-fin origin to the pectoral-fin insertion (30.9%–35.8% of SL), the caudal peduncle depth (10.9%–12.8% of SL), the head length (24.1%–27.7% of SL), the postorbital length (41.0%–46.1% of HL), the interorbital width (29.9%–32.9% of HL), the well-developed third infraorbital approaching, or in some specimens contacting, the horizontal limb of the preopercle, the lack of a series of dark midlateral spots on the body, the vertically elongate, ventrally tapering humeral mark, the lack of a large spot of pigmentation on the basal portions of the middle caudal-fin rays, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus occidaneus* within the clade compose of *Creagrutus* and *Piabina.*

TABLE 40.—Morphometrics and meristics of *Creagrutus occidaneus*, new species: (A) holotype of *C. occidaneus*, MUSM 8869; and (B) paratypes of *C. occidaneus* (n=27). Standard length is expressed in mm; measurements 1 to 14= percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	60.4	26.8–65.9
1. Snout to anal-fin origin	62.9	61.8–69.2
2. Snout to pelvic-fin insertion	45.5	44.3–51.0
3. Snout to pectoral-fin insertion	24.2	23.0–26.8
4. Snout to dorsal-fin origin	44.2	44.1–49.5
5. Dorsal-fin origin to hypural joint	60.4	55.3–60.7
6. Dorsal-fin origin to anal-fin origin	32.3	30.3–36.0
7. Dorsal-fin origin to pelvic-fin insertion	27.6	25.4–30.8
8. Dorsal-fin origin to pectoral-fin insertion	31.3	30.9–35.8
9. Caudal peduncle depth	11.1	10.9–12.8
10. Pectoral-fin length	19.3	19.0–22.2
11. Pelvic-fin length	15.9	13.6–17.0
12. Dorsal-fin length	21.2	20.1–25.7
13. Anal-fin length	17.1	15.9–19.5
14. Head length	26.2	24.1–27.7
15. Postorbital head length	45.6	41.0–46.1
16. Snout length	26.6	25.5–30.9
17. Bony orbital diameter	33.4	32.6–37.9
18. Interorbital width	30.0	29.9–32.9
	Meristics	
Lateral line scales	42	38–43
Scale rows between dorsal-fin origin and lateral line	4	3–4[1]
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	10	9–10
Branched dorsal-fin rays	8	8
Branched anal-fin rays	11	10–11
Branched pelvic-fin rays	6	6
Pectoral-fin rays	13	12–13
Vertebrae	39	37–39

[1]Three scales between anal-fin origin and lateral line present in only 1 of 27 paratypes.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus occidaneus* in Table 40. Head moderately robust, body ranging from moderately elongate in some mature males to relatively robust in gravid females. Greatest body depth typically at dorsal-fin origin, but shifted anterior of that point in some gravid females. Dorsal profile of head gently convex from tip of snout to vertical through posterior nostril, straight from that point to tip of supraoccipital spine. Interorbital region slightly convex transversely. Predorsal profile straight and continuous with dorsal profile of body in smaller individuals, becoming slightly convex, with variably distinct change in alignment relative to profile of head in larger specimens. Dorsal surface of body with distinct median ridge extending anteriorly from dorsal-fin insertion approximately one-half of distance to tip of supraoccipital spine. Ventral profile of head with obvious obtuse angle at anteroventral corner of dentary, nearly straight from that angle to rear of isthmus. Ventral profile of body ranging from nearly straight in smaller specimens and mature males to distinctly convex in gravid females. Prepelvic region of body obtusely flattened transversely.

Head somewhat pointed in lateral view, more so in dorsal view. Upper jaw not very fleshy, longer than, and distinctly overhanging, lower jaw. Snout not very fleshy, with scattered papillae anteromedially; papillae concentrated along upper lip and on folds and plicae extending between outer and medial premaxillary teeth. Lower jaw fleshy, more so anteriorly, with numerous papillae on dorsal margin of lip and scattered papillae on anterior surface of jaw.

Infraorbital series moderately well developed. Anterior one-half of ventral margin of third infraorbital falling slightly short of or, more rarely, contacting horizontal limb of preopercle. Posterior margins of third through fifth infraorbitals falling distinctly short of vertical limb of preopercle.

Premaxillary dentition in three series: primary row typically consisting of 6, sometimes 5, teeth arranged in nearly straight to slightly sigmoid series without pronounced gap between first and second tooth of series; triangular cluster of slightly larger teeth with posterolateral tooth largest; and typically single tooth of form similar to that of primary series lying lateral to fourth tooth of primary premaxillary series, or lateral to area of contact of third and fourth teeth of primary series; few specimens with 2 teeth lying lateral to area of contact of fourth tooth with third and fifth teeth respectively. Maxilla with 3 or 4 tricuspidate teeth. Dentary with 4 or 5 tricuspidate teeth; first and second teeth distinctly larger than remaining teeth in series, with second tooth somewhat larger than first tooth; third tooth only approximately one-third vertical extent of second tooth, but about 3 times height of fourth tooth. Fifth tooth, when present, smaller than fourth tooth.

Dorsal-fin rays ii,8 in all examined specimens. Dorsal-fin origin at, or slightly anterior to, vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin slightly concave. Anal-fin rays ii,10–11. Profile of distal margin of anal fin nearly straight in smaller individuals, increasingly concave in larger specimens. Mature males with hooks occasionally present on last unbranched anal-fin ray and anterior 2 to 4 branched anal-fin rays. Pectoral-fin rays i,11–12. Tip of pectoral fin extending posteriorly slightly over three-fourths of distance to pelvic-fin insertion. Pelvic-fin rays i,6,i. Tip of pelvic fin extending posteriorly to, or falling slightly short of, anus. Hooks present on all branched pelvic-fin rays in mature males.

Gill rakers 6–8 + 11–13.

COLORATION IN ALCOHOL.—Ground color of specimens in alcohol tan. Dorsal surface of head with scattered field of small superficial dark chromatophores and obscure field of deep-lying, very dark chromatophores overlying membranes of brain. Chromatophore field more concentrated anteriorly on head, over snout, and on portions of upper lip. Region of snout anterior to nostrils with concentrated chromatophores forming dark, crescent-shaped patch continuous posteroventrally with narrow band of dark chromatophores extending along ventral and posterior margins of orbit. Dorsal portions of opercle and

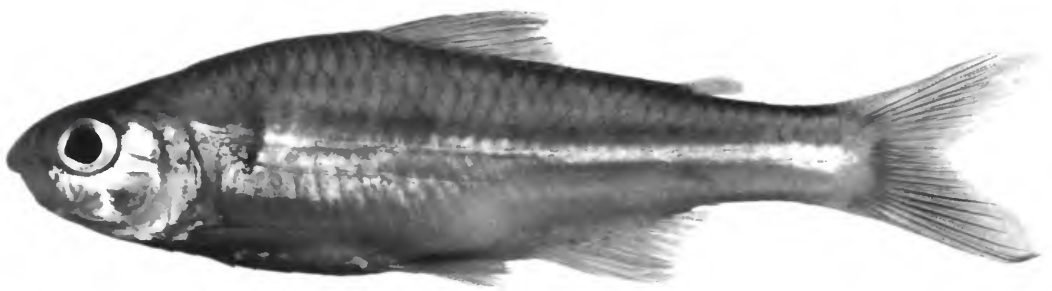

FIGURE 70.—*Creagrutus occidaneus,* new species, holotype, MUSM 8869, 60.4 mm SL; Peru, Madre de Dios, Provincia Manu, Parque Nacional Manu, Pakitza, beach along Río Manu close to mouth of Quebrada Pachija (approximately 11°57′S, 71°17′W).

all infraorbitals posterior to orbit with scattered, dark chromatophores. Dark pigmentation on head obscured by surface guanine layer in many specimens.

Scales of dorsal portion of body with diffuse chromatophore field on basal portions of exposed field and some scattered chromatophores along distal margin resulting in dark, reticulate pigmentation pattern on those portions of body. Humeral mark prominent, distinctly tapering ventrally, extending ventrally approximately one-half of scale below lateral line and dorsally about two scales above lateral line. Margins of humeral mark somewhat variable, but distinct dorsally. Diffuse midlateral band formed of small, dark chromatophores extending from slightly posterior of humeral mark to middle of caudal peduncle.

Dorsal fin with anterior margin of last unbranched ray and basal portions of branched fin rays outlined by dark chromatophores. Membranes of anterior rays with scattered, dark chromatophores, extent of chromatophore field more extensive anteriorly. Anal fin with scattered, dark chromatophores on membranes in some individuals. Caudal fin with scattered, light brown chromatophores over membranes and rays. Pectoral and pelvic fins hyaline.

ETYMOLOGY.—The specific name, *occidaneus,* from the Latin for western, refers to the distribution of the species along the western lowlands of the Amazon basin.

ECOLOGY.—The type locality was a white-water rainforest stream with a sandy bottom at an elevation of approximately 325 m. Other Peruvian localities for which habitat data is available had similar water conditions with substrates of mixed rubble, silt, sand, gravel, and clay. These localities ranged between 190 and 290 m elevation.

SEXUAL DIMORPHISM.—The examined samples of *Creagrutus occidaneus* apparently do not demonstrate the distinct size difference between mature males and females found in many members of the genus. Mature males, as shown by the presence of well-developed hooks on the anal and pelvic fins, ranged from 38.6 to 61.1 mm SL, whereas females measured up to only 65.9 mm SL.

DISTRIBUTION.—*Creagrutus occidaneus* is distributed across the foothills and lowlands of eastern Peru in the Río Manu basin of the Department of Madre de Dios and in the upper Rio Purus basin in the states of Acre and Amazonas, Brazil, and the Department of Ucayali, Peru (Figure 67, dots).

REMARKS.—The majority of the specimens of *Creagrutus occidaneus,* including all larger individuals, were collected in the upper portions of the Madre de Dios basin in southeastern Peru. Several lots of mostly juvenile specimens from the states of Acre and Amazonas, Brazil, and the Department of Ucayali in the western portions of the Río Purus basin in Peru (see "Nontype Specimens," below) were not found to differ from juveniles collected in Río Madre de Dios basin of Peru. Samples of adults from these Brazilian and eastern Peruvian rivers are necessary to confirm whether those populations and that in the Río Madre de Dios basin are indeed conspecific.

MATERIAL EXAMINED.—183 specimens (33, 26.8–65.9).

HOLOTYPE.—PERU. *Madre de Dios:* Provincia Manu, Parque Nacional Manu, Pakitza, beach along Río Manu close to mouth of Quebrada Pachija (approximately 11°57′S, 71°17′W), collected by H. Ortega and F. Pinares, 9 Oct 1991, MUSM 8869, 1 (60.4).

PARATYPES.—27 specimens (27, 26.8–65.9).

PERU. *Madre de Dios:* Provincia Manu, Parque Nacional Manu, Pakitza, beach along Río Manu close to mouth of Quebrada Pachija (approximately 11°57′S, 71°17′W), collected with holotype, MUSM 8870, 4 (26.8–63.9); USNM 326920, 7 (38.3–65.9; 2 specimens cleared and counterstained for cartilage and bone). Provincia Manu, mouth of Rio Pinquen, near Boca Manu (12°10′S, 71°01′W), collected by R. Horwitz, 4 Aug 1977, ANSP 143765, 1 (61.3). Provincia Manu, Río Manu, approximately 2 hours by boat upstream from Boca Manu, collected by H. Ortega et al., 7 Sep 1988, USNM 303065, 1 (50.7). Provincia Manu, Parque Nacional Manu, Pa-

kitza and vicinity (approximately 11°57′S, 71°17′W), collected by H. Ortega, Oct 1987, USNM 295621, 9 (49.0–61.8); MUSM 8871, 5 (29.9–56.1).

NONTYPE SPECIMENS.—155 specimens (5, 46.8–60.5).

PERU. *Madre de Dios:* Provincia Manu, Parque Nacional Manu, Pakitza and vicinity (approximately 11°57′S, 71°17′W), USNM 295571, 5 (46.8–60.5). Provincia Manu, Parque Nacional Manu, Río Manu, near mouth of Quebrada Fortaleza, USNM 319661, 1. Provincia Manu, Parque Nacional Manu, Pakitza, Quebrada Fortaleza, USNM 326875, 2. Provincia Manu, Parque Nacional Manu, Río Manu, Quebrada Fortaleza, 15 m above mouth, USNM 319657, 1. Provincia Manu, Parque Nacional Manu, Río Manu at Pakitza, USNM 302789, 3; USNM 302787, 4. Provincia Manu, Parque Nacional Manu, Pakitza, Quebrada Pachija (approximately 11°57′, 71°17′W), USNM 326818, 5. Provincia Manu, Río Manu, approximately 2 hours by boat upstream from Boca Manu, USNM 303064, 2. Provincia Manu, Boca Panahua, where Quebrada Panahua enters Río Manu, USNM 302790, 1. Provincia Manu, Río Manu, approximately 3 hours upriver by boat from Romero, USNM 302784, 3. Provincia Manu, cocha off Río Alto Madre de Dios, 2 km below Erika (latter locality at approximately 12°53′S, 71°12′W), USNM 302786, 2. Provincia Manu, Río Alto Madre de Dios, 15 km upstream from Boca Manu (12°19′30″S, 70°58′W), ANSP 143768, 1. *Ucayali:* Provincia Purus, Río Curanja basin, Caserío Grau (9°58′S, 71°02′W), MUSM 9986, 2. Provincia Purus, Río Purus (9°50′S, 70°55′W), MUSM 10440, 6. Provincia Purus, Esperanza, Quebrada Esperancillo (9°42′S, 70°40′W), MUSM 10032, 15. Atalaya, Sepahua, Quebrada Shamboyacu, USNM 358016, 13. Atalaya, Sepahua, Nuevo Horizonte, Río Bajo Urubamba, USNM 358017, 21.

BRAZIL. *Acre:* Rio Acre between Seringal Paraiso and Lago Amapá, MZUSP 49760, 2. Município de Rio Branco, Rio Acre, Coloação do Chalé, 6 hours below Rio Branco (latter locality at 9°58′S, 67°48′W), MZUSP 49625, 5. *Amazonas:* Rio Acre, Seringal Floresta, 10 minutes above Boca do Acre (latter locality at 8°45′S, 67°23′W), MZUSP 49600, 44. Rio Purus, at mouth of Rio Acre (8°45′S, 67°23′W), MZUSP 49708, 10. Município de Porto Acre, Rio Acre, Seringal Bom Destino, 1 hour above Porto Acre (latter locality at 9°34′S, 67°31′W), MZUSP 49688, 7.

Creagrutus ortegai, new species

FIGURES 67, 71, TABLE 41

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 3 or 4 teeth on the maxilla, 6, less commonly 5, teeth in the primary tooth row of the premaxilla, 6 dentary teeth, 37 to 39 lateral line scales without a lamellar process over each pore, 11 or 12 predorsal median scales, 4 or 5 scale rows between the dorsal-fin origin and the lateral line, 36 to 38 vertebrae, 9 to 12 branched anal-fin rays, 2 post-anal median scales to the anal-fin origin, 9 to 11 gill rakers on the lower limb of the first gill arch, the postorbital head length (44.4%–48.8% of HL), the snout length (24.2%–29.1% of HL), the bony orbital diameter (28.8%–33.3% of HL), the interorbital width (28.3%–31.6% of HL), the moderately developed third infraorbital with its ventral margin approaching or contacting the horizontal limb of the preopercle, the lack of a series of dark midlateral spots on the body, the presence of a rhomboidal humeral mark centered above the lateral line without an associated, slightly more dorsally located, secondary pigment mark, the lack of a distinct spot of pigmentation on the basal portions of the middle caudal-fin rays, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus ortegai* within the clade composed of *Creagrutus* and *Piabina*.

TABLE 41.—Morphometrics and meristics of *Creagrutus ortegai*, new species; (A) holotype of *C. ortegai*, MUSM 7498; and (B) paratypes of *C. ortegai* (n= 39). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	66.5	28.0–71.1
1. Snout to anal-fin origin	63.2	61.0–65.1
2. Snout to pelvic-fin insertion	47.6	44.4–48.5
3. Snout to pectoral-fin insertion	24.5	22.0–25.1
4. Snout to dorsal-fin origin	48.1	46.4–49.7
5. Dorsal-fin origin to hypural joint	55.6	54.7–59.4
6. Dorsal-fin origin to anal-fin origin	32.0	29.4–34.7
7. Dorsal-fin origin to pelvic-fin insertion	28.4	25.1–28.0
8. Dorsal-fin origin to pectoral-fin insertion	33.9	31.7–33.8
9. Caudal peduncle depth	13.2	11.5–13.7
10. Pectoral-fin length	20.5	19.1–20.7
11. Pelvic-fin length	15.8	14.9–17.9
12. Dorsal-fin length	22.0	21.7–24.8
13. Anal-fin length	19.0	17.9–19.1
14. Head length	26.0	24.1–27.3
15. Postorbital head length	47.9	44.4–48.8
16. Snout length	28.9	24.2–29.1
17. Bony orbital diameter	30.6	28.8–33.3
18. Interorbital width	30.6	28.3–31.6
	Meristics	
Lateral line scales	38	37–39
Scale rows between dorsal-fin origin and lateral line	4	4–5
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	11	11–12
Branched dorsal-fin rays	8	7–8[1]
Branched anal-fin rays	10	9–12
Branched pelvic-fin rays	6	5–6[2]
Pectoral-fin rays	13	12–14
Vertebrae	38	36–38

[1]Seven branched dorsal-fin rays present in only 1 of 39 paratypes.
[2]Five branched pelvic-fin rays present in only 1 of 39 paratypes.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus ortegai* in Table 41. Head and body relatively robust, more so in specimens larger than 30 mm SL. Greatest body

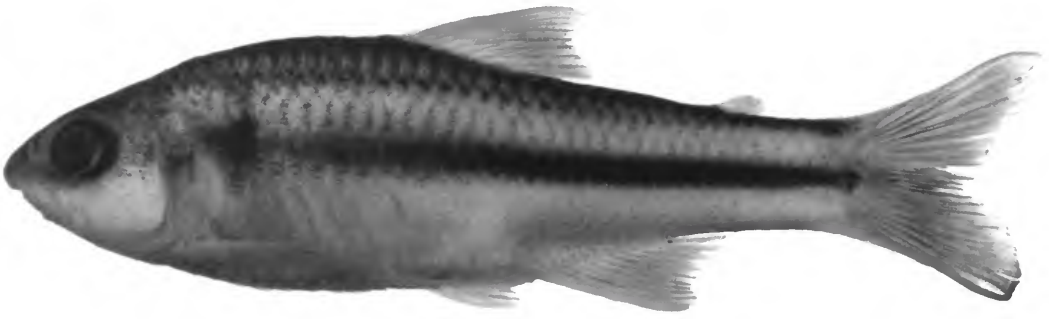

FIGURE 71.—*Creagrutus ortegai*, new species, holotype, MUSM 7498, 66.5 mm SL; Peru, San Martin, Provincia San Martin, Banda de Shilcayo, upper portions of Quebrada Choclin, tributary to Río Huallaga, near Shapaja (latter locality is at 6°36′S, 76°16′W).

depth at dorsal-fin origin in specimens of approximately 30 mm SL, located at that point or shifted variably anteriorly in larger individuals, and lying approximately midway between dorsal-fin origin and tip of supraoccipital spine in some of largest examined specimens. Dorsal profile of head distinctly convex from margin of upper lip to vertical through posterior nostril in all specimens larger than 30 mm SL, straight from that point to rear of supraoccipital spine in smaller individuals, slightly convex in that region in larger specimens. Dorsal profile of body convex from rear of supraoccipital spine to dorsal-fin origin, convexity more pronounced in larger specimens; profile angled at dorsal-fin base. Ventral profile of head and body typically smoothly rounded from tip of lower jaw to pelvic-fin insertion. Obtuse angle at anteroventral corner of dentary found in many *Creagrutus* species either absent, or barely evident. Prepelvic region of body broadly rounded transversely.

Head obtusely rounded in lateral view and more compressed in dorsal view. Upper jaw distinctly longer than, and overhanging, lower jaw. Anterior portion of snout fleshy, with scattered papillae; papillae more concentrated on fleshy upper lip, albeit with papillae less well developed than in many congeners. Lower lip fleshy anteriorly, with numerous papillae on dorsal margin and anterior surface.

Infraorbital series moderately developed, ventral margin of third infraorbital approaching horizontal limb of preopercle in smaller specimens, ventrally in contact with preopercle in larger individuals. Posterior margins of third through fifth infraorbitals distinctly separated from vertical limb of preopercle.

Premaxillary dentition in three series: primary row slightly curved, typically consisting of 6 teeth, although only 5 teeth present in about 5% of examined specimens, without pronounced gap between first and second tooth of series; triangular cluster of 3 larger teeth; and single tooth of form similar to that of primary series located lateral to fourth tooth of primary premaxillary series, or sometimes lateral to area of contact of third and fourth teeth of primary series. Maxilla with 3, or rarely 4, tricuspidate teeth. Dentary with 6 tricuspidate teeth; first and second teeth distinctly larger than other teeth, subequal, approximately 1.7 times height of third tooth; fourth through sixth teeth much smaller and compressed.

Dorsal-fin rays typically ii,8, iii,8 in one specimen, ii,7 in one specimen. Dorsal-fin origin located approximately at vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin slightly concave in all specimens larger than 30 mm SL. Anal-fin rays ii,9–12, both 9 and 12 branched rays rare. Hooks typically present on anal-fin rays in mature males of many *Creagrutus* species not present in examined specimens. Profile of distal margin of anal fin with slight anterior lobe and distinctly concave distal margin. Pectoral-fin rays i,11–13. Tip of pectoral fin extending posteriorly approximately three-fourths of distance to pelvic-fin insertion. Pelvic-fin rays typically i,6,i, i,5,i in one specimen. Tip of pelvic fin extending posteriorly to anal-fin origin. Hooks typically present on pelvic-fin rays in mature males of many *Creagrutus* species not present in examined specimens.

Gill rakers 6–7 + 9–11.

COLORATION IN ALCOHOL.—More recently collected specimens retaining guanine on scales and head with silvery head and body. Guanine on body somewhat masking dark midlateral body stripe and humeral mark. Ground coloration yellow in relatively recently collected specimens not retaining guanine on body. Specimens preserved in alcohol for longer periods light brown. Dorsal surface of head with dense field of dark chromatophores; chromatophore field not as pronounced on dorsal surface of snout, particularly in smaller individuals, and fading out along anterior margin of upper lip. Denser crescent-shaped patch of dark pigmentation present immediately anterior to nares. Curved band of dark pigmentation extending from posteroventral portion of pigmented region anterior to nares to around ventral and posterior margins of orbit, band widest an-

teroventral to orbit. Region of head posterior to orbit with scattered, dark chromatophores on infraorbitals and opercle; pigmentation somewhat more concentrated on opercle in many specimens.

Scales of dorsal portion of body with dark chromatophores concentrated over center of exposed portion and along posterior margin of scales; these more highly pigmented regions on each scale separated by hyaline arch. Pigmentation on scales less prominent on dorsolateral portion of body. Dark humeral mark apparent in all examined specimens. Mark with densely pigmented middle region centered above lateral line at all available body sizes. Less heavily pigmented, variably shaped extensions continue dorsally and ventrally from main body of mark. Midlateral body stripe consisting of deep-lying and dark surface pigmentation. Stripe relatively darkest posteriorly and becoming more diffuse anteriorly. Stripe not obvious anterior to vertical through dorsal-fin origin in specimens less than 40 mm SL, denser and more elongate horizontally in larger individuals with stripe extending anteriorly to posterior margin of humeral mark.

Dorsal fin with membranes and fin-ray margins covered with small dark chromatophores, particularly on distal two-thirds of rays; intensity of pigmentation increasing ontogenetically, with number of rays bearing such pigmentation also increasing with body size, albeit not forming black spot even in largest specimens. Central portions of anal-fin rays overlain with dark chromatophores, forming faint longitudinal stripe along fin. Caudal fin with midlateral stripe along body extending very slightly onto extreme basal portion of middle caudal-fin rays. Caudal-fin rays and membranes overlain by dark chromatophores. Pectoral and pelvic fins hyaline.

ETYMOLOGY.—The specific name, *ortegai,* in honor of our colleague and co-author in other papers, Hernán Ortega of the Museu de Historia Natural, Lima Peru, who collected nearly all known specimens of the species and in recognition of his many contributions to our knowledge of Peruvian freshwater fishes.

ECOLOGY.—At the end of the dry season, the type locality of *Creagrutus ortegai* is a clear water, moderately swiftly flowing stream about 3 m wide and 40–60 cm deep, with a substrate of stones, pebbles, sand, and debris, with dense vegetation along its banks, and a water temperature of approximately 20-22°C (H. Ortega, pers. comm., 1996). During the rainy season the water volume and flow increase significantly with increased sediment load, making it a white-water stream. The Quebrada Ahuashiyacu, from which some paratypes originated, is slightly larger than, but otherwise similar to, the holotype locality. The Río Cumbaza, another site of origin for some of the paratype series, is significantly larger than the other type localities, being approximately 25 to 30 m wide during the dry season, but with conditions otherwise comparable to the holotype locality.

Stomach contents of two specimens of *Creagrutus ortegai* prepared for clearing and staining in this study consisted mostly of insect parts and occasional small intact and chopped-up seeds.

DISTRIBUTION.—*Creagrutus ortegai* is known primarily from the rivers near Tarapoto, Department of San Martin, Peru (Figure 67, filled stars), but the species also occurs further upstream in the Río Huallaga basin and in the headwaters of the Río Aguaytia (see comments under "Remarks," below).

REMARKS.—*Creagrutus ortegai* is the only member of the genus know from the Río Huallaga valley. Nearly all specimens of *C. ortegai* were collected in the region of Tarapoto, a city in the central portion of that river basin, which is one of the few regions in the Río Huallaga basin that has been the subject of intense ichthyological sampling efforts. As a consequence, samples are not available to determine the actual range of the species with any certainty. Three lots of the species came from distinctly further upstream within the Huallaga basin in the region of Tingo Maria (ANSP 136832, 136912, 136914). In addition to the samples from the Río Huallaga basin, three lots (MUSM 2949, 5675, 6572) originated outside of that river system in the upper reaches of the Río Aguaytia, a left bank tributary of the Río Ucayali in the western portions of the Department of Ucayali. Headwaters of the Río Aguaytia approach some of the right bank tributaries of the central portions of the Río Huallaga (see Isbrücker and Nijssen, 1983, fig. 5). One of these lots (MUSM 6572) originated in the Boquerón del Padre Abad, the gap between the Río Huallaga and Río Aguaytia basins. The other two lots (MUSM 2949, 5675) were collected in the same general area in the Río Huacamayo, a right-bank tributary of the upper Río Aguaytia.

MATERIAL EXAMINED.—107 specimens (44, 28.0–71.1).

HOLOTYPE.—PERU. *San Martin:* Provincia San Martin, Banda de Shilcayo, upper portions of Quebrada Choclin, tributary to Río Huallaga, near town of Shapaja (latter locality at 6°36′S, 76°16′W), collected by H. Ortega, 15 Nov 1991, MUSM 7498, 1 (66.5).

PARATYPES.—39 specimens (39, 28.0–71.1).

PERU. *San Martin:* Provincia San Martin, Banda de Shilcayo, upper portions of Quebrada Choclin, tributary to Río Huallaga, near town of Shapaja (latter locality at 6°36′S, 76°16′W), collected with holotype, MUSM 7499, 2 (42.0–49.8); USNM 340969, 2 (44.3–49.3). Provincia San Martin, Tarapoto, Quebrada Ahuashiyacu (approximately 6°30′S, 76°25′W), collected by H. Ortega, 13 Nov 1991, MUSM 7538, 2 (28.9–52.8). Provincia San Martin, Tarapoto, Morales, Río Cumbaza (6°28′S, 76°28′W), collected by H. Ortega, 14 Nov 1991, MUSM 7539, 3 (35.4–55.3); MUSM 2948, 1 (45.5). Provincia San Martin, Tarapoto, Río Shilcayo (approximately 6°30′S, 76°25′W), collected by H. Ortega, 15 Nov 1991, USNM 340970, 3 (42.5–54.0). Provincia San Martin, Tarapoto, stream tributary to Río Shilcayo (approximately 6°30′S, 76°25′W), collected by H. Ortega, 15 Nov 1991, MUSM 5678, 4 (37.9–64.0); USNM 340971, 4 (35.4–67.0). Provincia San Martin, km 6 along road to Juanjui, Quebrada Pucayacu, collected by H. Ortega and C. Cañas, 18 Dec 1994,

MUSM 6571, 2 (39.2–47.5). Provincia San Martin, km 30 along road to Yurimaguas, Río Cainarachi, collected by H. Ortega and C. Cañas, MUSM 6552, 8 (28.0–71.1); USNM 340972, 8 (29.0–55.0; 2 specimens cleared and counterstained for cartilage and bone).

NONTYPE SPECIMENS.—67 specimens (4, 42.5–49.8).

PERU. *San Martin:* Provincia San Martin, Río Ahuashiyacu (6°30′S, 76°25′W), MUSM 1626, 4; MUSM 5676, 4 (2, 49.0–49.8); USNM 340968, 2 (42.5–49.7). Provincia San Martin, Tarapoto, Río Shilcayo, MUSM 5677, 4. Provincia Lamas, stream tributary to Río Cainarachi, km 33 on road from Tarapoto to Yurimaguas, MUSM 7540, 3. Provincia Moyobamba, Puerto Juan Antonio, upper Río Mayo, MUSM 1631, 6. *Huanuco:* Provincia Leoncio Prado, vicinity of Tingo Maria, Cueva de Pavos near Puente Perez, approximately 0.15 km above Río Huallaga (town at 9°19′S, 75°56′W), ANSP 136832, 1; ANSP 136912, 16. Vicinity of Tingo Maria, Río Monzón basin, Río Rondos (=Río Patay Rondos; mouth approximately 9°15′S, 76°05′W), ANSP 136914, 1. *Pucallpa:* Provincia Padre Abad, Río Aguaytia, Boguerón del Padre Abad, Velo de Novia, MUSM 6572, 3. Provincia Padre Abad, Aguaytia, Río Huacamayo, MUSM 2949, 3. Río Chio, 80 km from Pucallpa on road to Tingo Maria, MUSM 5675, 20.

Creagrutus ouranonastes, new species

FIGURES 67, 72, TABLE 42

DIAGNOSIS.—The possession of premaxillary dentition with the three components generalized for the species of *Creagrutus*, but with a distinct gap between the first and second teeth of primary tooth row and a forward position of the triangular cluster of three posteromedial teeth distinguishes *C. ouranonastes* from all members of the clade formed by *Creagrutus* and *Piabina* with the exception of *Creagrutus maracaiboensis, C. melanzonus, C. muelleri, C. nigrostigmatus, C. peruanus, C. runa,* and *Piabina argentea. Creagrutus ouranonastes* can be distinguished from these seven species by the combination of 7 dentary teeth, 41 to 45 lateral line scales, 13 to 15 predorsal median scales, 6 scale rows between the dorsal-fin origin and the lateral line, 4 scale rows between the anal-fin origin and the lateral line, 40 to 43 vertebrae, 10 or 11 branched anal-fin rays, the distance from the snout to the anal-fin origin (62.7%–65.6% of SL), the caudal peduncle depth (12.4%–14.1% of SL), the bony orbital diameter (25.7%–29.4% of HL), and the possession of two small, discrete spots of dark pigmentation on the basal portions of the middle caudal-fin rays, a pigmentation pattern that is an autapomorphy for the species.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus ouranonastes* in Table 42. Head and body quite robust, increasingly so in larger specimens. Greatest body depth at vertical through dorsal-fin origin in smaller specimens, shifting distinctly anterior of that point in larger, more robust individuals (e.g., holotype, Figure 72). Dorsal profile of head distinctly convex from margin of upper lip to vertical through posterior margin of posterior nares, nearly straight from that point to rear of head in specimens of all sizes. Dorsal profile of body smoothly continuous with profile of head in smaller individuals, more convex with distinct change in slope relative to alignment of dorsal profile of head in larger specimens; nearly straight from dorsal-fin origin to caudal peduncle in specimens of all sizes. Ventral profile of head somewhat more convex at anteroventral corner of dentary or somewhat posterior of that point, nearly straight from convex region to rear of isthmus. Ventral profile of body gently convex in smaller individuals, convexity more pronounced in larger specimens.

Head obtusely pointed in both lateral and dorsal views. Upper jaw slightly longer than, and overhanging, lower jaw. Anterior of snout only slightly fleshy compared to many congeners, with papillae only obvious along anteromedial portion of snout, along margin of upper lip and on folds and plicae extending between outer and medial premaxillary teeth. Lower lip relatively fleshy anteriorly, with numerous papillae on dorsal surface of lip.

Infraorbital series moderately developed, without notable variation in degree of development across available body size range. Ventral margin of third infraorbital falling distinctly

TABLE 42.—Morphometrics and meristics of *Creagrutus ouranonastes*, new species: (A) holotype of *C. ouranonastes*, MUSM 8872; and (B) paratypes of *C. ouranonastes* (n=24). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	100.1	38.2–91.2
1. Snout to anal-fin origin	62.4	62.7–65.6
2. Snout to pelvic-fin insertion	46.2	45.4–49.6
3. Snout to pectoral-fin insertion	22.2	21.5–25.3
4. Snout to dorsal-fin origin	48.7	46.4–51.4
5. Dorsal-fin origin to hypural joint	56.0	52.1–57.9
6. Dorsal-fin origin to anal-fin origin	31.7	27.4–32.3
7. Dorsal-fin origin to pelvic-fin insertion	28.2	25.6–30.0
8. Dorsal-fin origin to pectoral-fin insertion	36.0	33.3–37.2
9. Caudal peduncle depth	13.4	12.4–14.1
10. Pectoral-fin length	20.5	20.0–21.0
11. Pelvic-fin length	15.3	14.9–16.7
12. Dorsal-fin length	21.3	20.6–23.6
13. Anal-fin length	18.6	15.7–18.7
14. Head length	23.8	22.7–25.9
15. Postorbital head length	52.1	46.7–54.5
16. Snout length	28.2	24.0–29.0
17. Bony orbital diameter	27.3	25.7–29.4
18. Interorbital width	34.8	30.0–35.7
	Meristics	
Lateral line scales	45	41–45
Scale rows between dorsal-fin origin and lateral line	6	6
Scale rows between anal-fin origin and lateral line	4	4
Predorsal median scales	14	13–15
Branched dorsal-fin rays	8	8
Branched anal-fin rays	10	10–11
Branched pelvic-fin rays	7	6–7
Pectoral-fin rays	12	13–14
Vertebrae	42	40–43

FIGURE 72.—*Creagrutus ouranonastes*, new species, holotype, MUSM 8872, 100.1 mm SL; Peru, Apurimac, Aymaraes, Río Chalhuanca (approximately 14°01'S, 73°11'W).

short of horizontal limb of preopercle. Posterior margins of third through fifth infraorbitals falling distinctly short of vertical limb of preopercle.

Premaxillary dentition in three series: primary row curved, consisting of 6, rarely 5, teeth, with distinct gap between first and second tooth in row, and between medial teeth of contralateral series; triangular cluster of three teeth with anterior tooth approximately same size as teeth of primary row and slightly medial to pronounced gap between first and second teeth of primary row, two other teeth of triangular cluster, particularly posteromedial tooth larger than remaining teeth in jaw; and single tooth of form similar to that of primary series lying lateral to fourth tooth of primary premaxillary tooth row. Maxilla with 3 or 4 tricuspidate teeth. Dentary with 7 teeth; first and second teeth distinctly larger than others, subequal and tricuspidate; third tooth tricuspidate, about two-thirds height of second tooth; fourth through seventh teeth unicuspidate, distinctly smaller than third tooth, and gradually decreasing in size posteriorly.

Dorsal-fin rays ii,8. Dorsal-fin origin slightly behind vertical though pelvic-fin insertion. Profile of distal margin of dorsal fin slightly concave. Anal-fin rays ii,10–11. Profile of distal margin of anal fin distinctively concave. Hooks typically present on anal-fin rays in mature males of many *Creagrutus* species not present in examined specimens. Pectoral-fin rays i,11–13. Tip of pectoral fin extending posteriorly slightly more than three-fourths of distance to vertical through pelvic-fin insertion. Pelvic-fin rays i,6,i in smaller examined specimens, i,7 in larger individuals. Hooks typically present on pelvic-fin rays in mature males of many *Creagrutus* species not found in examined specimens. Tip of pelvic fin falling distinctly short of anal-fin origin.

Gill rakers 7–8 + 10–11.

COLORATION IN ALCOHOL.—Overall coloration of head and body relatively dark other than in specimens less than 30 mm SL. Dorsal surface of head with dense field of small, dark, stellate chromatophores. Chromatophore field extending over snout, upper lip, and continuing posteriorly under and posterior to orbit. No intense patch of crescent-shaped pigmentation anterior to nares as present in many other *Creagrutus* species. Pigmentation ventral and posterior of orbit not forming discrete band present in many congeners. Pigmented regions on head becoming progressively more intense in larger specimens. Pigmentation on infraorbitals posterior of orbit concentrated into dark irregular spots in some individuals. Deep-lying patch of dark pigmentation located medial to posterior portion of fifth infraorbital and central portion of opercle; pigmentation in latter region more intense in larger specimens and forming distinct patch of dark coloration on opercle.

Dorsolateral surface of body with scale margins marked by bands of dark pigmentation forming overall reticulate pattern. Humeral mark vertically elongate, overall form that of inverted comma; particularly dark portion of humeral mark located immediately dorsal of lateral line, and less intensely pigmented curved portion of mark extending anterodorsally from that region for distance of about two scales. Midlateral dark pigmentation on body composed of two components: deep-lying band of chromatophores extending somewhat obliquely from behind humeral mark to center of caudal peduncle and narrower, irregular band of darker surface pigmentation.

Dorsal fin with small dark chromatophores on rays and membranes, particularly on anterior rays and distal portions of middle dorsal-fin rays. Anal fin with scattered, dark chromatophores on rays and membranes. Caudal fin with dark chromatophores outlining rays. Basal portion of middle rays of caudal fin flanked by two discrete, horizontally elongate patches of particularly dark pigmentation. Pectoral and pelvic fins with scattered, dark chromatophores on membranes.

ETYMOLOGY.—The specific name, *ouranonastes*, from the Greek, ouranos, heaven or sky, and nastes, inhabitant, refers to the relatively high elevation localities where the species has been collected.

ECOLOGY.—Nothing is known about the life history of *Creagrutus ouranonastes,* but it is found at a notable elevation for a *Creagrutus* species. Some of the localities at which specimens were collected are at approximately 1900 m altitude, the greatest elevation recorded for any member of the genus.

Stomach contents of the single specimen prepared for clearing and counter staining consisted of parts of larval insects.

DISTRIBUTION.—*Creagrutus ouranonastes* is known only from the uplands of the Río Apurimac basin in the southern highlands of Peru (Figure 67, open star) where it is the only member of the genus collected to date.

MATERIAL EXAMINED.—25 specimens (25, 38.2–100.1).

HOLOTYPE.—PERU. *Apurimac:* Provincia Aymaraes, Río Chalhuanca (approximately 14°01′S, 73°11′W), collected by E. Estacio, 25 Dec 1989, MUSM 8872, 1 (100.1).

PARATYPES.—24 specimens (24, 38.2–91.2).

PERU. *Apurimac:* Provincia Aymaraes, Río Chalhuanca (approximately 14°01′S, 73°11′W), collected with holotype, USNM 340989, 1 (91.2). Provincia Abancay, Hacienda Matara, Quebrada Matara, Río Matara system (mouth of river at 13°44′S, 72°55′W), 6200 ft (=1890 m) elevation, collected by C. Sanborn, Dec 1941, FMNH 41801, 14 (38.2–86.1). *Cusco:* Provincia Anta, Río Apurimac, Conocc (13°33′S, 72°37′W), collected by E. Estacio, 9 Nov 1992, MUSM 6574, 5 (41.8–82.0); USNM 340988, 4 (57.2–84.6; 1 specimen cleared and counterstained for cartilage and bone).

Creagrutus paraguayensis Mahnert and Géry, 1988

FIGURES 73, 74, TABLE 43

Creagrutus paraguayensis Mahnert and Géry, 1988:5, figs. 4, 5, pl. 3 [type locality: Río Azotey à Cororo près de l'embouche du Río Ypane, prov. Concepcion, Paraguay (=Paraguay, Concepcion Province, Río Azotey at Cororo, near mouth of Río Ypane)].

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 2 or 3 teeth on the maxilla, 6, less commonly 5, teeth in the primary tooth row of the premaxilla, 5 or 6 dentary teeth, 37 to 41 lateral line scales without a lamellar process over each pore, 11 to 13 predorsal median scales, 5 scale rows between the dorsal-fin origin and the lateral line, 37 to 39 vertebrae, 13 to 15 branched anal-fin rays, 2 post-anal median scales to the anal-fin origin, the distance from the snout to the anal-fin origin (55.3%–61.0% of SL), the distance from the snout to the dorsal-fin origin (47.2%–51.8% of SL), the distance from the dorsal-fin origin to the anal-fin origin (28.2%–33.8% of SL), the distance from the dorsal-fin origin to the hypural joint (52.5%–57.8% of SL), the distance from the dorsal-fin origin to the pectoral-fin insertion (32.8%–38.3% of SL), the anal-fin length (17.6%–20.7% of SL), the interorbital width (32.0%–38.8% of HL), the lack of a series of dark midlateral spots on the body, the moderately developed third infraorbital with its ventral margin falling distinctly short of the horizontal limb of the preopercle, the vertically elongate humeral mark, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus paraguayensis* within the clade composed of *Creagrutus* and *Piabina.*

TABLE 43.—Morphometrics and meristics of *Creagrutus paraguayensis:* (A) holotype of *C. paraguayensis,* MHNG 2386.1; and (B) all other specimens of *C. paraguayensis* from which counts and measurements were taken (n=29). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	32.9	30.1–57.5
1. Snout to anal-fin origin	58.7	55.3–61.0
2. Snout to pelvic-fin insertion	43.5	42.6–46.8
3. Snout to pectoral-fin insertion	23.7	22.8–25.1
4. Snout to dorsal-fin origin	49.0	47.2–51.8
5. Dorsal-fin origin to hypural joint	53.8	52.5–57.8
6. Dorsal-fin origin to anal-fin origin	28.7	28.2–33.8
7. Dorsal-fin origin to pelvic-fin insertion	26.5	26.4–31.7
8. Dorsal-fin origin to pectoral-fin insertion	33.4	32.8–38.3
9. Caudal peduncle depth	12.2	10.5–12.5
10. Pectoral-fin length	20.7	19.5–22.3
11. Pelvic-fin length	15.2	15.0–17.7
12. Dorsal-fin length	24.0	21.9–24.8
13. Anal-fin length	20.4	17.6–20.7
14. Head length	24.6	23.0–26.7
15. Postorbital head length	45.2	37.3–45.7
16. Snout length	30.0	26.3–30.1
17. Bony orbital diameter	35.8	31.5–37.6
18. Interorbital width	34.6	32.0–38.8
	Meristics	
Lateral line scales	38	37–41
Scale rows between dorsal-fin origin and lateral line	5	5
Scale rows between anal-fin origin and lateral line	4	3–4
Predorsal median scales	13	11–13
Branched dorsal-fin rays	8	8
Branched anal-fin rays	15	13–15
Branched pelvic-fin rays	6	6–7
Pectoral-fin rays	12	11–13
Vertebrae	39	37–39

DESCRIPTION.—Morphometric and meristic data for *Creagrutus paraguayensis* in Table 43. Overall form of head and body moderately elongate in smaller individuals up to approximately 35 mm SL, becoming relatively deeper ontogenetically, with larger examined individuals having proportionately deeper bodies than majority of congeners. Greatest body depth at dorsal-fin origin in smaller individuals and at, or slightly anterior to, that point in larger specimens. Dorsal profile of head distinctly convex anteriorly from margin of upper lip posteriorly to approximately vertical through anterior margin of anterior nares; straight to slightly convex from that point to rear of supraoccipital spine. Predorsal profile of body slightly convex and smoothly continuous with that of head in smaller specimens, somewhat more convex, with associated change in alignment of dorsal profile of body relative to that of rear of head in

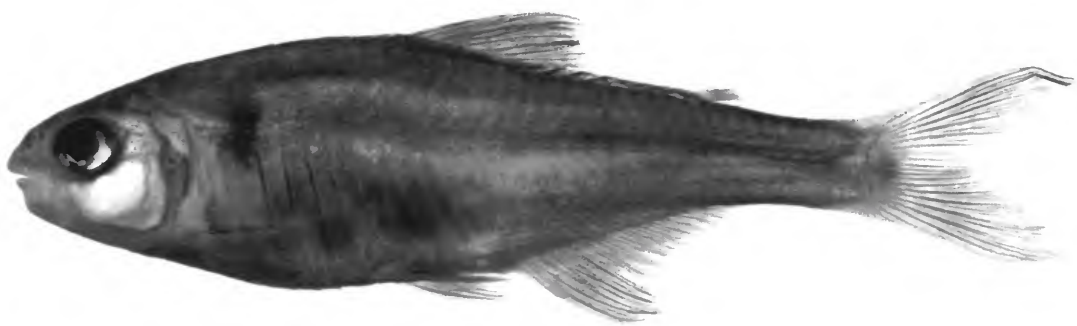

FIGURE 73.—*Creagrutus paraguayensis*. UMMZ 206266, 57.2 mm SL; Paraguay, Caaguazú, Arroyo Tapiracuaí (tributary to Arroyo Tabatiry, Río Manduvira basin) at boundary between Departamento Caaguazú and Departamento San Pedro, 17.7 km ENE of Mbutuy (23°53′24″S, 56°09′00″W).

larger individuals. Dorsal profile of portion of body posterior of dorsal fin relatively straight at all sizes. Ventral profile of head with distinct change in angle at anteroventral corner of dentary; nearly straight from that point to isthmus. Ventral profile of body gently curved, convexity more pronounced in larger specimens. Prepelvic region of body somewhat flattened transversely, with obtuse lateral angles.

Head obtusely pointed in both lateral and dorsal views. Upper jaw longer than, and overhanging, lower jaw. Anterior portion of snout somewhat fleshy, albeit less so than in some congeners. Scattered papillae over anterior portion of snout and upper jaw; papillae more concentrated along margin of upper and lower jaws. Lower lip fleshy anteriorly, with scattered papillae on dorsal surface.

Infraorbital series only moderately developed. Third infraorbital with rounded margin, its ventral margin falling distinctly short of horizontal limb of preopercle. Posterior margins of third to fifth infraorbitals falling distinctly short of vertical limb of preopercle at all body sizes.

Premaxillary dentition in three series: primary row of 6, less commonly 5, teeth arranged in slightly curved row without pronounced gap between first and second tooth of series; single tooth of form similar to that of primary series lying lateral to fourth tooth of primary premaxillary series; and triangular cluster of 3 teeth, larger than those of the primary row and with median tooth of cluster contacting its contralateral partner. Maxilla with 2 or 3 tricuspidate teeth. Dentary with 5 or 6 teeth; first and second teeth tricuspidate, distinctly larger than other teeth, with second tooth larger than first tooth; third tooth approximately one-third height of second tooth. Fourth through sixth teeth distinctly smaller than anterior teeth with fourth and sometimes fifth teeth tricuspidate and sixth and sometimes fifth teeth conical.

Dorsal-fin rays ii,8. Dorsal-fin origin slightly posterior of vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin straight. Anal-fin rays iii,13–15. Profile of distal margin of anal fin distinctly concave. Anal fin in mature males with bony hooks on anterior 5 or 6 branched anal-fin rays; hooks restricted to posterolateral surface of main shaft of ray. Pectoral-fin rays i,10–12. Tip of pectoral fin extending posteriorly to point somewhat short of vertical through pelvic-fin insertion. Pelvic-fin rays typically i,6,i, occasionally i,7. Pelvic fin in mature males with hooks on second through fourth, or more rarely fifth, branched rays. Tip of pelvic fin extending posteriorly to, or slightly beyond, anal-fin origin.

Gill rakers 5–7 + 9–10.

COLORATION IN LIFE.—Field notes associated with some of the nontype specimens (UMMZ 206477) indicate that in life *Creagrutus paraguayensis* has pale orange fins with a white leading edge to the anal fin. A photo of the live specimen (Axelrod, 1993:111) shows that the species (identified therein as *C. beni*) has a reddish region above the iris, a pinkish cast to the anal and dorsal fin, and a white stripe along the distal two-thirds of the last unbranched anal-fin ray and distal portion of the following membrane. Guanine mostly masks the dark midlateral body pigmentation and to a degree masks the humeral mark.

COLORATION IN ALCOHOL.—Overall coloration yellowish to tan, without any prominent dark pigmentation pattern on head or body. Dorsal surface of head with scattered, small, dark chromatophores. Chromatophore field somewhat more concentrated anterior to nares, but not forming prominent dark crescent-shaped mark as in many congeners. Faint, but discrete, narrow band of dark chromatophores extending posteriorly from region anterior to nares along ventral and posterior margins of orbit. Fourth and fifth infraorbitals and dorsal portion of opercle with scattered, dark chromatophores. Dorsal and dorsolateral surface of body with field of scattered, dark chromatophores. Chromatophores slightly more concentrated along margins of scales in this area, giving hint of dark reticulate pattern, as pattern not readily visible. Humeral mark mostly located dorsal of lateral line, formed by somewhat larger dark chromatophores that those of surrounding areas of body. Overall form of humeral mark vertically elongate; humeral mark expanding dorsally and merging in that region into slightly darker pigmentation of dorsolateral portion of body.

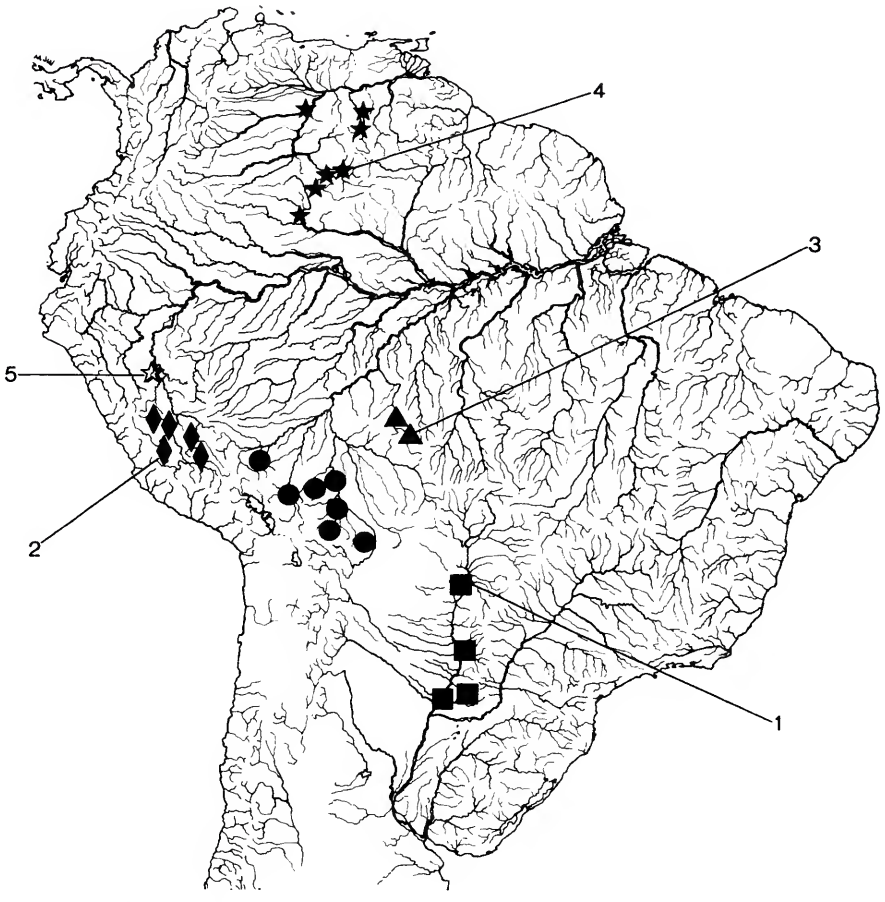

FIGURE 74.—Map of central and northern South America showing geographic distribution of *Creagrutus paraguayensis* (squares, 1=type locality), *Creagrutus pearsoni* (dots, type locality inexact=Popoi River), *Creagrutus peruanus* (diamonds, 2=type locality), *Creagrutus petilus* (triangles, 3=type locality), *Creagrutus phasma* (solid stars, 4=type locality), and *Creagrutus pila* (open star, 5=type locality) (some symbols represent more than one locality or lot of specimens).

Dorsal, caudal, and anal fins with scattered, dark chromatophores over rays and membranes; chromatophores typically more concentrated along fin-ray margins in larger specimens. Pectoral and pelvic fins hyaline.

ECOLOGY.—Some of the nontype specimens of *Creagrutus paraguayensis* (UMMZ 206266, UMMZ 206277, UMMZ 206385) were collected in 8 to 15 m wide streams of up to 2 m depth. The water in two of localities was reported to be "fairly clear" and that of the third site was red-brown during the flood season. The substrate consisted mostly of sand and mud.

DISTRIBUTION.—*Creagrutus paraguayensis* is known primarily from tributaries of the Río Paraguay in central and northern Paraguay. One lot (NRM 22490) is cited as originating in the headwaters of one unnamed right bank tributary to the Río Paraná (Figure 74, squares). We are, however, unable to confirm that the stream in question actually drains into the Río Paraná because it occurs in a region where the headwaters of rivers draining to Río Paraguay and Río Paraná interdigitate.

COMPARISONS.—Only one *Creagrutus* species, *C. meridionalis,* in addition to *Creagrutus paraguayensis,* is known to occur in the Río Paraguay basin. The two species differ in the number of branched anal-fin rays (13 to 15 in *C. paraguayensis* versus 11 to 13 in *C. meridionalis*) and in the number of scales rows between the lateral line and the dorsal-fin origin (5 versus 4, respectively).

REMARKS.—In their paper describing *Creagrutus paraguayensis,* Mahnert and Géry (1988:8) reported one specimen as *Creagrutus* sp. (aff. *paraguayensis*). The specimen, collected in the province of Cordillera, Paraguay, differed from *C. paraguayensis* in various meristic and morphometric details. As discussed in the "Remarks" section under *Creagrutus meridionalis,* this specimen is apparently an individual of the latter species rather than *C. paraguayensis.*

MATERIAL EXAMINED.—288 specimens (30, 30.1–57.5).

PARAGUAY. *Concepcion:* Río Azotey at Cororo, near the mouth of Río Ypane, MHNG 2386.1, 1 (32.9, holotype of *Cre-*

agrutus paraguayensis); MHNG 2386.2, 1 (33.8, paratype of *Creagrutus paraguayensis*). *Canendiyu:* Arroyo Carimbatay (tributary of Río Jejuí-Guazú, Río Paraguai basin), approximately 15 km WSW by dirt road of Curuguaty (24°31′06″S, 56°43′30″W), UMMZ 206277, 27. Arroyo Curuguaty (tributary of Río Jejuí-Guazú, Río Paraguai basin), 5.1 km N of Curuguaty (24°25′24″S, 55°38′24″W), UMMZ 206385, 36 (12, 30.1–51.5). Small stream approximately 12 km on road from Curuguaty to Mbutuy, Río Paraguay basin (24°29′47″S, 55°47′8″W), NRM 22446, 70; MNHNP 1249, 10. Stream near road approximately 3 km before Curuguaty, Río Paraguay basin (24°29′28″S, 55°39′13″W), NRM 22540, 44. Río Jejuí-Guazú, 76 km on road to Curuguaty, Río Paraguay basin (24°19′34″S, 55°5′15″W), NRM 22674, 44; MNHNP 465, 11. Río Paraná basin (see also comments under "Distribution," above), stream along roadside, 71 km on road leading to Curuguaty (24°18′54″S, 55°4′44″W), NRM 22490, 4. Stream along roadside, approximately 3 km before road leading to Curuguaty (24°29′28″S, 55°39′13″W), MNHNP 1538, 13. *Caaguazú:* Arroyo Tapiracuaí (tributary to Arroyo Tabatiry, Río Manduvira basin) at boundary between Departamento Caaguazú and Departamento San Pedro, 17.7 km ENE of Mbutuy (23°53′24″S, 56°09′00″W), UMMZ 206266, 20 (11, 33.0–57.5). *Alto Paraguay:* Estancia Doña Julia, 5 km N of Bahia Negra, Río Paraguay system (approximately 20°10′S, 58°12′W), USNM 340958, 7 (5, 37.5–52.5; 2 specimens cleared and counterstained for cartilage and bone).

Creagrutus pearsoni Mahnert and Géry, 1988

FIGURES 74–76, TABLE 44

Piabina beni Pearson, 1924:45, pl. X: fig. 5 [type locality: Bolivia (Cochabamba) Popoi River (=Río Popoi), upper Beni (=Río Beni)].—Eigenmann and Myers, 1929:431, pl. 59: fig. 5 [repetition of original description; illustrated specimen incorrectly cited as originating in Argentina].—Pearson, 1937b:108 [occurrence in Río Beni].—Fowler, 1940:70, 90 [Bolivia: Department of Cochabamba, Río Chapare, Todos Santos, 1000 ft [=305 m] altitude; Boca Chapare, Río Chimore]; 1943c:3 [Bolivia, Río Mamoré, Todos Santos]; 1948:162 [literature compilation].—Terrazas-Urquidi, 1970:25 [listing].—Mahnert and Géry, 1988:5 [species transferred to *Creagrutus; pearsoni* proposed as replacement name for *beni* preoccupied in *Creagrutus* by *C. beni* Eigenmann, 1911].

Creagrutus pearsoni Mahnert and Géry, 1988:5 [replacement name for *Piabina beni* Pearson, 1924, which became a secondary junior homonym of *Creagrutus beni* Eigenmann, 1911, when included in *Creagrutus* by Mahnert and Géry (1988)].

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 2 or 3 teeth on the maxilla, 5 teeth on each dentary, 36 to 38 vertebrae, 15 to 18 branched anal-fin rays, 10 to 12 predorsal median scales, 5 or 6 scale rows between the lateral line and the dorsal-fin origin, the lack of a series of dark midlateral spots on the body, the vertically elongate humeral mark, and a laterally compressed, relatively deep body distinguish *Creagrutus pearsoni* from all members of the clade consisting of *Creagrutus* and *Piabina* with the exception of *C. barrigai* and *C. manu. Creagrutus pearsoni* can be discriminated from *C. barrigai* by differences in the distance from the snout to the dorsal-fin origin (49.4%–52.9% of SL versus 45.4%–49.2% of SL, respectively), the anal-fin length (15.6%–17.4% of SL versus 18.0%–20.7% of SL, respectively), the postorbital head length (41.0%–45.1% of HL versus 34.2%–41.9% of HL, respectively), and the number of scale rows between the lateral line and the dorsal-fin origin (5 or 6 versus 4, respectively). *Creagrutus pearsoni* differs, in turn, from *C. manu* by the absence of the distinct midlateral stripe on the posterior one-half to two-thirds of the body that characterizes the latter species, and by differences in the distance from the snout to the anal-fin origin (59.0%–61.9% of SL in *C. pearsoni* versus 63.5%–66.4% of SL in *C. manu*), and the anal-fin length (15.6%–17.4% of SL versus 20.4%–21.8% of SL, respectively).

TABLE 44.—Morphometrics and meristics of *Creagrutus pearsoni:* (A) lectotype of *Piabina beni* and *Creagrutus pearsoni,* CAS 62272 (formerly IU 19317, in part); and (B) all other specimens of *Creagrutus pearsoni* from which counts and measurements were taken (n=26). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length. Dash indicates measurement that could not be taken because of damage to specimen.

Characters	A	B
	Morphometrics	
Standard length	30.7	22.4–36.1
1. Snout to anal-fin origin	60.3	59.0–61.9
2. Snout to pelvic-fin insertion	44.6	41.6–47.2
3. Snout to pectoral-fin insertion	24.8	21.8–24.9
4. Snout to dorsal-fin origin	51.8	49.4–52.9
5. Dorsal-fin origin to hypural joint	54.4	52.4–57.1
6. Dorsal-fin origin to anal-fin origin	33.9	30.9–35.9
7. Dorsal-fin origin to pelvic-fin insertion	33.9	30.1–34.9
8. Dorsal-fin origin to pectoral-fin insertion	36.8	35.6–38.4
9. Caudal peduncle depth	11.7	11.0–12.6
10. Pectoral-fin length	17.9	17.1–20.9
11. Pelvic-fin length	17.3	14.4–17.5
12. Dorsal-fin length	24.4	23.9–27.3
13. Anal-fin length	–	15.6–17.4
14. Head length	24.4	23.5–26.2
15. Postorbital head length	41.3	41.0–45.1
16. Snout length	26.7	23.4–27.0
17. Bony orbital diameter	37.3	34.8–39.1
18. Interorbital width	34.7	32.8–37.7
	Meristics	
Lateral line scales	38	36–38
Scale rows between dorsal-fin origin and lateral line	6	5–6
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	11	10–12
Branched dorsal-fin rays	8	8
Branched anal-fin rays	15	15–18
Branched pelvic-fin rays	6	6
Pectoral-fin rays	12	12–14
Vertebrae	37	36–38

DESCRIPTION.—Morphometric and meristic data for *Creagrutus pearsoni* in Table 44. Head and particularly body more laterally compressed than typical for species of *Creagrutus*.

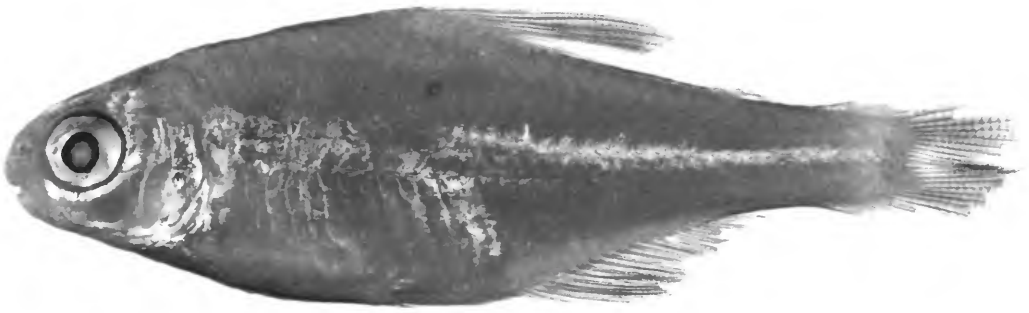

FIGURE 75.—*Creagrutus pearsoni,* CAS 62272 (formerly IU 19317, in part), lectotype of *Piabina beni* and *Creagrutus pearsoni,* 30.7 mm SL; Bolivia, Cochabamba, Rio Popoi (=Popoy) (approximately 15°37'S, 67°18'W), upper Río Beni basin.

FIGURE 76.—*Creagrutus pearsoni,* USNM 302288, 30.1 mm SL; Bolivia, El Beni, Estacion Biologica Beni, Río Trapiche.

Greatest body depth at dorsal-fin origin for all examined body sizes. Dorsal profile of head distinctly convex from margin of upper lip to vertical through anterior margin of eye; straight or very slightly convex from that point to tip of supraoccipital spine. Interorbital region of head distinctly convex transversely. Predorsal region of body ranging from straight in some smaller specimens to slightly convex in larger individuals, but without any distinct change in alignment relative to profile of head. Ventral profile of head either smoothly rounded or more commonly with barely distinct angle at anteroventral corner of dentary. Ventral profile of body convex to anal-fin origin, convexity more pronounced in larger individuals. Ventral body profile slightly concave posterior to anal-fin origin.

Head obtusely rounded in lateral profile, with snout relatively short; head laterally compressed in dorsal view. Upper jaw slightly longer than, and overhanging, lower jaw. Snout slightly fleshy anteromedially, with only few scattered papillae anteriorly. Papillae more numerous, but not dense, along margin of upper jaw and on plicae and folds extending between outer and medial premaxillary teeth. Lower lip fleshy anteriorly, with papillae along dorsal surface and limited number of papillae scattered on anteromedial surface.

Infraorbital series moderately developed. Ventral margin of third infraorbital falling distinctly short of horizontal limb of preopercle in specimens of all sizes. Posterior margins of third to fifth infraorbitals falling distinctly short of vertical limb of preopercle, gap decreasing slightly dorsally.

Premaxillary dentition in three series: primary row somewhat sigmoid, formed by 5 or 6 teeth, when 6 teeth present then primary tooth row continuous, but when primary tooth row with only 5 teeth, then gap sometimes present between third and fourth teeth, but without pronounced gap between first and second tooth of series in any specimens; triangular cluster of 3 larger teeth; and single tooth of form similar to that of primary

series occurring lateral to fourth tooth of primary series (when 6 teeth present in primary series) or lateral to area of contact of third and fourth tooth (when 5 teeth present in primary series). Maxilla with 2 or 3 tricuspidate teeth. Dentary with 5 teeth, first through third teeth distinctly larger than other teeth in series, with first and second teeth subequal and about twice vertical extent of third tooth. Fourth tooth tricuspidate, approximately twice height of unicuspidate fifth tooth.

Dorsal-fin rays ii,8 in all examined specimens. Dorsal-fin origin distinctly posterior to vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin distinctly concave. Anal-fin rays typically ii,15–18, rarely either ii,15 or iii,16–18, first unbranched ray very short when 3 unbranched rays present. Profile of distal margin of anal fin distinctly concave. Scattered, poorly developed hooks present on anterior 3 or 4 branched rays in 2 examined mature males. Pectoral-fin rays i,11–12. Tip of pectoral fin extending posteriorly approximately three-fourths of distance to pelvic-fin insertion. Pelvic-fin rays i,6,i in all specimens. Tip of pelvic fin extending posteriorly approximately to anus. Pelvic-fin hooks present on all branched rays in two examined mature males.

Gill rakers 5–6 + 7–9.

COLORATION IN ALCOHOL.—Ground coloration of more recently collected specimens (CBF 1008) yellowish with silvery sheen where guanine still present. Dorsal surface of head with scattered, large, dark chromatophores that overlie deep-lying, dark chromatophores on membranes over surface of brain. Field of dark, surface chromatophores extending anteriorly onto snout. Region immediately anterior to nostrils with chromatophores more concentrated and forming distinct, dark, crescent-shaped mark. This region of darker pigmentation not continuous with narrow band of chromatophores extending along ventral and posterior margins of orbit, contrary to condition in many *Creagrutus* species. Scattered, dark chromatophores over infraorbitals in region posterior of orbit.

Scales of dorsal portion of body with narrow field of dark chromatophores arranged in crescent pattern located approximately one-third of distance from margin of scale; chromatophores forming faint, dark, reticulate pattern on dorsolateral portion of body in some individuals. Lateral surface of body lacking midlateral stripe, but with diffuse pattern of dispersed, small, dark chromatophores starting about 2 scales posterior of humeral mark and extending to caudal peduncle. Myosepta above anal fin outlined by small dark chromatophores in some individuals. That region of body also with field of small, dark, dispersed chromatophores. Overall form of humeral mark vertically elongate but with variable degree of distinctiveness of humeral mark. Form of anterior and posterior margins of humeral mark variable, ranging from nearly straight to highly irregular. Pigmentation of humeral mark ranging from uniform in some specimens, to more intense in lower one-half of mark in other individuals.

Dorsal fin with scattered, dark chromatophores on membranes, less so on posterior rays. Membranes of branched anal-fin rays with scattered, dark chromatophores, more so along central portions of rays in some specimens and somewhat less developed posteriorly. Caudal fin with fin rays in some specimens outlined by small, dark chromatophores. Pectoral and pelvic fins hyaline or with few scattered, dark chromatophores.

ECOLOGY.—No ecological information is available for the collecting sites of the Bolivian samples of *Creagrutus pearsoni,* which comprise the majority of the material examined during this study. Two lots collected in the department of Madre de Dios, southeastern Peru (USNM 263951, 263953), originated in small rainforest streams over mud and rocky substrates with significant amounts of detritus. Current in the streams ranged from moderate to swift, and the water was moderately to distinctly turbid.

Stomach contents of specimens prepared for clearing and staining in this study consisted of detritus and insect parts.

DISTRIBUTION.—*Creagrutus pearsoni* is limited to various rivers in northeastern Bolivia and southeastern Peru that lie within the Rio Madeira basin (Figure 74, dots).

REMARKS.—Mahnert and Géry (1988:5) synonymized *Piabina* Reinhardt (1867) into *Creagrutus* Günther (1864), an action that made *Piabina beni* Pearson (1924) a secondary homonym of *Creagrutus beni* Eigenmann (1911). As a consequence, Mahnert and Géry (1988:5) replaced *Piabina beni* Pearson with *Creagrutus pearsoni.*

Pearson (1924:45) described *Piabina beni* on the basis of 11 "cotype" (=syntype) specimens (IU 19317). A 30.7 mm SL specimen, which is in the best condition of the known extant syntypes (CAS 62272, formerly IU 19317, in part), is designated as the lectotype. The remaining syntypes originally in IU 19317 (CAS 87389, 6 specimens; UMMZ 66495, 3 specimens) become paralectotypes. One of the syntypes originally cited by Pearson (1924:45) has not been located.

Fowler (1940:70) reported 36 specimens of *Piabina beni* from Todos Santos, Bolivia, collected 8 August 1937, and that author subsequently (1943c:3) cited an additional 18 specimens collected at the same locality on the same day. The two samples may now be intermingled in ANSP 84161, which now consists of 55 specimens.

MATERIAL EXAMINED.—101 specimens (26, 22.4–36.1).

BOLIVIA. *Cochabamba:* Río Popoi (=Popoy) (approximately 15°37′S, 67°18′W), upper Río Beni basin, CAS 62272, 1 (30.7, lectotype of *Piabina beni* and *Creagrutus pearsoni;* formerly IU 19317, in part); CAS 87389, 6 (5, 24.9–34.0, paralectotypes of *Piabina beni;* formerly IU 19317, in part); UMMZ 66495, 3 (28.2–34.0, paralectotypes of *Piabina beni;* formerly IU 19317, in part). Río Chapare, Todos Santos (16°49′S, 65°08′W), ANSP 84161, 55. Boca Chapare, at mouth of Río Chapare (15°56′S, 64°41′W), ANSP 84164, 9. Río Isiboro, Laguna Motacusal (15°40′S, 65°00′W), USNM 278594, 1 (24.6). *Santa Cruz:* Río Jorge, 12 km W of Warnes, Río Piray basin (17°31′S, 63°15′W), UF 82332, 2. *El Beni:* Estacion Biologica Beni, Río Trapiche, USNM 302288, 2 (26.3–30.1); USNM 302274, 2 (29.0–29.1). Mojos, unnamed arroyo 1 km S of Oromomo, Territori Indígena Parque Nacional Isiboro-Sécure (ap-

proximately 15°10′S, 65°00′W), CBF 1008, 10 (22.4–36.1). *Pando:* Provincia Madre de Dios, San Miguel, Río Madre de Dios basin, unnamed arroyo, CBF 848, 4.

PERU. *Madre de Dios:* Reserva Natural de Tambopata, Río Tambopata system, stream near Laguna Chica (12°50′30″S, 69°17′30″W), USNM 263951, 5 (2, 26.4–30.1; 2 specimens cleared and counterstained for cartilage and bone). Right bank tributary to Río Tambopata, approximately 200 m above mouth of Río La Torre (12°50′S, 69°18′W), USNM 263953, 1.

Creagrutus peruanus (Steindachner, 1875)

FIGURES 74, 77, TABLE 45

Piabina peruana Steindachner, 1875:596 [type locality: Peru (Ayacucho) Monterico (=Montericco); on page 46 of separate].

Creagrutus nasutus Günther, 1876:400 [type locality: Peru (Ayacucho) Monterico (=Montericco)].—Steindachner, 1878:384 [placed as a synonym of *Piabina peruana* Steindachner, 1875].—Eigenmann and Eigenmann, 1891:56 [listing].

Creagrutus peruanus.—Steindachner, 1878:384 [transfer to *Creagrutus; Creagrutus nasutus* Günther, 1876, placed as a synonym].—Eigenmann, 1910: 435 [literature compilation]; 1927:420, pl. 35: fig. 4 [Peru: (Ayacucho) Monterico (=Montericco), Santa Ana, Río Comberciato; description based on Günther, 1876].—Eigenmann and Allen, 1942:226 [Peru: (Cuzco) Río Urubamba, Santa Ana, Río Comberciato; Río Chanchomayo at La Merced].—Fowler, 1945a:148 [literature compilation]; 1948:84 [literature compilation]; 1975:27 [literature compilation].—Ortega and Vari, 1986:8 [Amazonian Peru, common name].—Ortega, 1992:43 [above 1000 m elevation in Peru].—Not Barriga, 1991:18 [eastern Ecuador].

Creagrutus peruana.—Eigenmann and Eigenmann, 1891:56 [listing; as senior synonym of *C. nasutus* Günther].

DIAGNOSIS.—The possession of premaxillary dentition with three components generalized for the species of *Creagrutus* and *Piabina,* but with a distinct gap between the first and second teeth of primary tooth row and a forward position of the triangular cluster of three posteromedial teeth distinguishes *C. peruanus* from all members of the clade formed by *Creagrutus* and *Piabina* with the exception of *Creagrutus maracaiboensis, C. melanzonus, C. muelleri, C. nigrostigmatus, C. ouranonastes, C. runa,* and *Piabina argentea. Creagrutus peruanus* can be distinguished from these seven species by its possession of 9 to 11 branched anal-fin rays, 38 to 40 vertebrae, 10 to 12 predorsal median scales, a narrow third infraorbital falling distinctly short ventrally and posteriorly of the preopercle, the length of the anal fin (18.4%–20.0% of SL), the depth of the caudal peduncle (11.5%–14.0% of SL), and the distance from the dorsal-fin origin to the hypural joint (55.7%–59.0% of SL).

DESCRIPTION.—Morphometric and meristic data for *Creagrutus peruanus* in Table 45. Overall form of head and body relatively robust, more so in larger examined individuals. Greatest body depth typically at dorsal-fin origin, shifted somewhat anterior of that point in larger individuals with distended abdomens; relative greatest body depth somewhat greater in larger specimens. Dorsal profile of head distinctly convex anteriorly from margin of upper lip to vertical through posterior nostril, straight from that line to rear of supraoccipital spine. Predorsal profile of body slightly convex and continuing profile of posterior portion of head in small- and medium-sized specimens, somewhat more convex in larger individuals, with associated change in alignment at rear of supraoccipital spine between profile of head and that of body. Profile of portion of body posterior to dorsal fin relatively straight at all body sizes. Ventral profile of head slightly convex, but not demonstrating distinct change in angle at anteroventral corner of dentary typical of most *Creagrutus* species. Prepelvic region of body convex, more so in larger individuals.

Head obtusely pointed in lateral view and more so in dorsal view. Upper jaw longer than, and overhanging, lower jaw. Anterior portion of snout and lateral surface of upper jaw fleshy and covered with numerous papillae; field of papillae continuing from snout and lip onto folds and plicae extending between outer and medial premaxillary teeth. Lower lip fleshy anteriorly, with scattered papillae on anterior and ventral surfaces.

Infraorbital series poorly developed. Ventral margin of third infraorbital falling distinctly short of horizontal limb of preopercle in specimens of all sizes. Distal margin of third infraorbital approximately concentric with orbital rim. Posterior margin of third to fifth infraorbitals falling distinctly short of vertical limb of preopercle even in largest individuals examined.

Premaxillary dentition in three series: primary row curved, with 5 teeth and distinct gap between first and second teeth of series, first tooth separated from anterior tooth of contralateral series by distinct gap, but separation less pronounced than in most congeners; triangular cluster of three teeth, larger than those of primary series, with posterolateral tooth of cluster distinctly largest, anterior tooth of cluster partially in pronounced gap between first and second tooth of primary series, two posterior teeth not in as close contact as in most congeners, posteromedial tooth of triangular cluster very closely applied to matching tooth of contralateral cluster; and single tooth of form similar to that of primary series lying lateral to area of contact of third and fourth teeth of primary row. Maxilla with 3 or 4 tricuspidate teeth. Dentary with 5 or 6 teeth, anterior 5 teeth tricuspidate, these sometimes followed by 1 unicuspidate tooth. Anterior 3 dentary teeth larger than remaining teeth in series, with first and second teeth subequal and twice height of third tooth. Fourth through sixth teeth compressed and gradually decreasing in size posteriorly.

Dorsal-fin rays ii,8–9. Dorsal-fin origin at vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin slightly concave. Anal-fin rays ii,9–11. Profile of distal margin of anal fin slightly concave. Hooks typically present on anal-fin rays in mature males of many *Creagrutus* species not present in examined specimens. Pectoral-fin rays i,11–13. Tip of pectoral fin extending posteriorly nearly to pelvic-fin insertion in smaller individuals, falling somewhat short of that point in larger specimens. Pelvic-fin rays i,6,i in smaller individuals, more typically i,7 in larger specimens. Tip of pelvic fin reaching posteriorly to anal-fin insertion. Hooks typically present on pelvic-fin rays in mature males of many *Creagrutus* species not present in examined specimens.

TABLE 45.—Morphometrics and meristics of *Creagrutus peruanus:* (A) lectotype of *Piabina peruana,* NMW 19852; (B) lectotype of *Creagrutus nasutus,* BMNH 1875.10.12:26; and (C) all other specimens of *C. peruanus* from which counts and measurements were taken (n=37). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B	C
		Morphometrics	
Standard length	87.0	78.9	37.2–84.8
1. Snout to anal-fin origin	62.2	62.5	58.7–63.6
2. Snout to pelvic-fin insertion	45.5	44.4	42.4–46.9
3. Snout to pectoral-fin insertion	24.5	22.8	21.9–25.2
4. Snout to dorsal-fin origin	48.1	46.9	44.8–48.3
5. Dorsal-fin origin to hypural joint	55.9	58.0	55.7–59.0
6. Dorsal-fin origin to anal-fin origin	34.5	34.0	30.0–34.6
7. Dorsal-fin origin to pelvic-fin insertion	32.5	31.8	26.6–32.5
8. Dorsal-fin origin to pectoral-fin insertion	34.9	34.6	30.2–35.2
9. Caudal peduncle depth	13.9	13.3	11.5–14.0
10. Pectoral-fin length	20.4	21.9	19.6–22.3
11. Pelvic-fin length	15.9	16.2	15.3–17.4
12. Dorsal-fin length	22.1	22.4	21.0–24.7
13. Anal-fin length	18.8	19.7	18.4–20.0
14. Head length	26.0	25.3	23.9–26.6
15. Postorbital head length	49.2	49.2	46.4–51.9
16. Snout length	28.2	28.1	23.6–29.1
17. Bony orbital diameter	26.1	26.6	25.7–30.6
18. Interorbital width	31.6	34.2	30.4–35.3
		Meristics	
Lateral line scales	38	38	36–40
Scale rows between dorsal-fin origin and lateral line	4	4	4–5[1]
Scale rows between anal-fin origin and lateral line	3	3	3
Predorsal median scales	11	11	10–12
Branched dorsal-fin rays	8	8	8–9[2]
Branched anal-fin rays	10	10	9–11
Branched pelvic-fin rays	6	6	6–7
Pectoral-fin rays	13	13	12–14
Vertebrae	38	39	38–40

[1]Five scales between dorsal-fin origin and lateral line present in only 3 of 39 specimens.
[2]Nine branched dorsal-fin rays present in only 2 of 39 specimens.

Gill rakers 6–7+8–10.

COLORATION IN ALCOHOL.—Overall ground coloration of relatively recently collected specimens light tan. Dorsal surface of head with scattered, dark chromatophores, region dorsal to brain relatively darker in small individuals. Chromatophore field extending onto snout, with dark chromatophores more concentrated anterior to nares, forming discrete, dark, crescent-shaped patch. Discrete band of chromatophores extending posteriorly from crescent-shaped patch anterior to nares along ventral and posterior margins of orbit. Scattered, dark chromatophores overlying fourth and fifth infraorbitals and dorsal portion of opercle. This region with denser and more intense pigmentation in larger specimens. Dorsal and dorsolateral surfaces of body with scattered chromatophores, chromatophore field denser over center of scales, particularly on dorsal portion of body. Humeral mark vertically elongate and with irregular margins. Pigmentation most intense over center of spot and fading in dorsal and ventral portions of mark. Deep-lying band of midlateral pigmentation extending along body, band beginning 3 to 6 scales posterior of humeral mark and extending posteriorly to caudal peduncle. Deep-lying midlateral band overlain by diffuse surface band formed by field of scattered chromatophores extending from slightly posterior of humeral mark onto caudal peduncle. Band of surface chromatophores somewhat denser and wider proximate to base of caudal-fin rays. Dorsal-fin pigmentation ranging from all rays evenly delimited by dark chromatophores to only anterior rays and central portions of other rays distinctly outlined by dark chromatophores, thus forming indistinct stripe across fin. Anal-fin rays outlined with dark chromatophores; chromatophores sometimes more concentrated along middle portions of rays and forming indistinct band across center of fin. Pectoral and pelvic fins with scattered, dark chromatophores on rays and membranes.

ECOLOGY.—Exact ecological information on the collecting localities of examined specimens is unavailable. All localities are in regions of distinct gradient ranging from more than 500 m to approximately 900 m altitude.

Stomach contents of specimens of *Creagrutus peruanus* prepared for clearing and staining in this study consisted of ap-

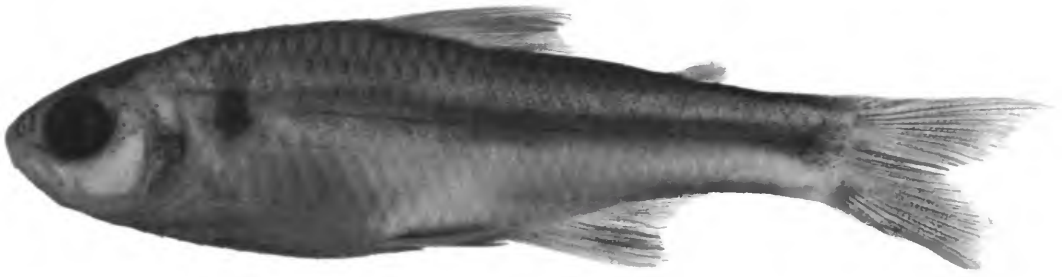

FIGURE 77.—*Creagrutus peruanus,* USNM 340979, 46.0 mm SL; Peru, Junin, Distrito Chanchamayo, Río Mijandari, along road from La Merced to Villa Rica in Department of Pasco.

proximately equal amounts of chopped larger seeds, whole smaller seeds, and parts of adult and larval insects. At one locality in the Río Chanchamayo, Department of Junin, Peru, *C. peruanus* was collected along with *C. changae.*

DISTRIBUTION.—*Creagrutus peruanus* occurs in portions of the Río Apurimac and Río Urubamba basins in eastern Peru (Figure 74, diamonds).

COMMON NAME.—Peru: "Majorita" (Ortega and Vari, 1986:8).

REMARKS.—The specimens on which Steindachner (1875: 46) based *Piabina peruana* were collected at "Monterico," Peru, by Taczanowski. Soon after Steindachner's publication, Günther (1876:400) described *Creagrutus nasutus* from a series of specimens collected at the same locality by the same collector, perhaps at the same time. Steindachner (1878:384) synonymized *C. nasutus* into his *Piabina peruana,* at the same time transferring the latter species from *Piabina* to *Creagrutus.* This synonymy was accepted by all subsequent authors who utilized the name *Creagrutus peruanus* for the species (see synonymy for the species, above). A comparison of the type series of the two nominal species failed to reveal any differences in examined meristic and morphometric features (Table 45) or other characters. *Creagrutus nasutus* Günther is, therefore, considered a junior synonym of *Piabina peruana* (=*Creagrutus peruanus*), an action first proposed by Steindachner (1878).

According to Stephens and Traylor (1983:137), the exact site of the locality reported by Taczanowski (1884:73) as "Monterico" has been the subject of differing opinions. Those authors suggest that the type locality is probably Monterrico (approximately 12°28′S, 73°54′W) in the Department of Ayacucho, Peru.

Steindachner (1875:46) based his description of *Piabina peruana* on a series of specimens; we have examined approximately one-half of them (NMW 19852-54, NMW 19867-71). A 87.0 mm SL specimen that is in the best condition of the examined syntypes is herein designated as the lectotype (NMW 19852), and the remaining syntypes thus become paralectotypes.

Günther (1876:400) based his description of *Creagrutus nasutus* on "several" specimens, and seven syntypes are known to be extant (BMNH 1875.10.12:26–33). Eigenmann (1927:420) in his account of *C. peruanus* noted that he examined a type in the "Brit. mus" (=British Museum (Natural History), now the Natural History Museum). No formal designation of a lectotype for *C. nasutus* was made by Eigenmann (1927), however, and that author did not provide any data in his account that allows for the identification of the "type." In order to resolve this question, a 78.9 mm SL syntype (BMNH 1875.10.14:26), which also is in the best condition of the examined portion of the series, is designated as the lectotype, and the remaining syntypes thus become paralectotypes.

Barriga (1991:18) reported *Creagrutus peruanus* from eastern Ecuador, a region far from the known distribution of the species but which is inhabited by some externally similar species. That record is presumed to refer to one of those other *Creagrutus* species that are known to occur in that region, although we cannot determine which species is involved.

MATERIAL EXAMINED.—141 specimens (39, 37.2–87.0).

PERU. *Ayacucho:* Monterico (=? Monterrico, approximately 12°28′S, 73°54′W), NMW 19852, 1 (87.0, lectotype of *Piabina peruana*); NMW 19853–54 and NMW 19867–71, 7 (45.9–87.0, paralectotypes of *Piabina peruana*); BMNH 1875.10.12:26, 1 (78.9, lectotype of *Creagrutus nasutus*); BMNH 1875.10.14:27–33, 6 (61.5–78.2, paralectotypes of *Creagrutus nasutus*). *Cusco:* Río Comberciato (Río Compursiato), small tributary of middle Río Urubamba, 30 km above Pongo de Mainique (latter locality at approximately 11°56′S, 72°52′W), at 1800 ft (=555 m) elevation, MCZ 30994, 15; CAS 69314 (formerly IU 13759), 9 (3, 55.8–65.8); FMNH 58066, 4. Middle Río Urubamaba, Santa Ana (12°52′S, 72°43′W), at approximately 3000–3400 ft (=914–1040 m) elevation, CAS 69313 (formerly IU 16050), 2; MCZ 30993, 1. *Junin:* Provincia Chanchamayo, Río Chanchamayo, Mijandari, highway from La Merced to Villa Rica (11°04′S, 75°20′W), MUSM 1074, 15; USNM 340979, 8 (2, 46.0–50.1; 2 specimens cleared and counterstained for cartilage and bone). Provincia Chanchamayo, Río Colorado, La Merced (11°03′S,

75°19′W), MUSM 5914, 6; USNM 340980, 4 (37.2–46.8); MUSM 8873, 8; USNM 340982, 2. Provincia Chanchamayo, Río Blanco, La Merced, MUSM 5918, 1. Provincia Chanchamayo, La Merced, Río Minjandara (approximately 11°03′S, 75°18′W), MUSM 2974, 12; USNM 340981, 7 (4, 39.8–44.2; 2 specimens cleared and counterstained for cartilage and bone). Provincia Chanchamayo, Río Chanchamayo, La Merced, 9 km from Oroya, approximately 2500 ft (=762 m) elevation, CAS 69135, 19 (5, 67.0–72.4). Provincia Chanchamayo, San Ramón, Quebrada Inia, MUSM 5915, 4 (1, 43.3), MUSM 5916, 1. Provincia Chanchamayo, Santa Ana, Río Santa Ana, MUSM 5917, 2. Provincia Satipo, Mazamari, Río Mazamari, on highway to San Martin de Pongao (11°21′S, 74°34′W), MUSM 5241, 6 (5, 55.0–74.3).

Creagrutus petilus, new species

FIGURES 74, 78, TABLE 46

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 2 or 3 teeth on the maxilla, 6 teeth in the primary tooth row of the premaxilla, 5 dentary teeth, 37 to 39 lateral line scales without a lamellar process over each pore, 9 or 10 predorsal median scales, 4 scale rows between the dorsal-fin origin and the lateral line, 36 to 39 vertebrae, 10 or 11 branched anal-fin rays, 2 post-anal median scales to the anal-fin origin, 5 or 6 gill rakers on the upper limb of the first gill arch and 9 to 11 gill rakers on the lower limb of the first gill arch, the distance from the snout to the anal-fin origin (61.5%–65.6% of SL), the distance from the snout to the pelvic-fin insertion (46.5%–50.0% of SL), the distance from the snout to the pectoral-fin insertion (24.5%–27.5% of SL), the distance from the dorsal-fin origin to the anal-fin origin (26.5%–29.6% of SL), the distance from the dorsal-fin origin to the pelvic-fin insertion (22.1%–26.1% of SL), the distance from the dorsal-fin origin to the pectoral-fin insertion (28.5%–31.9% of SL), the caudal peduncle depth (9.4%–10.8% of SL), the head length (26.6%–27.7% of SL), the postorbital head length (40.7%–45.3% of HL), the bony orbital diameter (34.0%–40.1% of HL), the snout length (27.0%–31.4% of HL), the interorbital width (26.0%–30.5% of HL), the moderately developed third infraorbital, which does not contact the horizontal limb of the preopercle, the lack of a series of dark midlateral spots on the body, the vertically elongate humeral mark with variable anterior and posterior margins, the lack of a distinct spot of pigmentation on the basal portions of the middle caudal-fin rays, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus petilus* within the clade composed of *Creagrutus* and *Piabina*.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus petilus* in Table 46. Head relatively robust, body relatively slender but transversely robust, more so in larger individuals. Greatest body depth at vertical through dorsal-fin origin in smaller individuals, shifted somewhat anterior of that point in larger examined specimens, particularly individuals with distended abdomens. Dorsal profile of head distinctly convex from margin of upper lip to vertical through anterior margin of orbit, nearly straight from that point to tip of supraoccipital spine in smaller specimens, slightly convex in larger individuals. Predorsal profile of body straight to slightly convex, but without distinct change in alignment relative to profile of head common to many congeners. Predorsal portion of body without median ridge. Ventral profile of head convex anteriorly, with variably developed, but obvious, obtuse angle at anteroventral corner of dentary, approximately straight from that angle to isthmus. Prepelvic profile of body slightly convex, more so in larger specimens, particularly those with distended abdomens. Prepelvic region of body obtusely flattened transversely.

Head obtusely flattened in both lateral and dorsal views. Upper jaw distinctly longer than, and overhanging, lower jaw. Snout slightly fleshy anteromedially, with numerous papillae anteriorly and on plicae and folds extending between outer and medial premaxillary teeth. Scattered papillae present on lateral surface of anterior portion of maxilla. Lower lip fleshy, particu-

TABLE 46.—Morphometrics and meristics of *Creagrutus petilus*, new species: (A) holotype of *C. petilus*, MNRJ 14807; and (B) paratypes of *C. petilus* (n=21). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	42.9	29.8–48.8
1. Snout to anal-fin origin	65.3	61.5–65.6
2. Snout to pelvic-fin insertion	49.2	46.5–50.0
3. Snout to pectoral-fin insertion	27.0	24.5–27.5
4. Snout to dorsal-fin origin	46.2	45.3–49.3
5. Dorsal-fin origin to hypural joint	53.2	53.0–56.9
6. Dorsal-fin origin to anal-fin origin	29.6	26.5–29.5
7. Dorsal-fin origin to pelvic-fin insertion	23.1	22.1–26.1
8. Dorsal-fin origin to pectoral-fin insertion	30.5	28.5–31.9
9. Caudal peduncle depth	10.5	9.4–10.8
10. Pectoral-fin length	18.2	18.0–21.1
11. Pelvic-fin length	14.9	13.4–16.4
12. Dorsal-fin length	20.3	20.2–25.1
13. Anal-fin length	17.7	17.3–19.0
14. Head length	26.6	26.7–27.7
15. Postorbital head length	43.0	40.7–45.3
16. Snout length	30.7	27.0–31.4
17. Bony orbital diameter	35.1	34.0–40.1
18. Interorbital width	26.3	26.0–30.5
	Meristics	
Lateral line scales	39	37–39
Scale rows between dorsal-fin origin and lateral line	4	4
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	10	9–10
Branched dorsal-fin rays	8	8
Branched anal-fin rays	11	10–11
Branched pelvic-fin rays	6	6
Pectoral-fin rays	12	11–12
Vertebrae	37	36–39

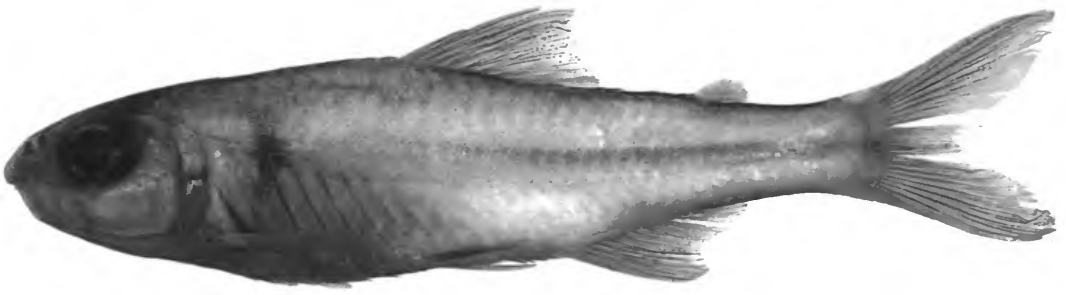

FIGURE 78.—*Creagrutus petilus*, new species, holotype, MNRJ 14807, 42.9 mm SL; Brazil, Rondônia, Rio Marco Rondon, Pimenta Bueno (approximately 11°29′S, 61°12′W).

larly anteriorly, with numerous papillae along dorsal margin and few scattered papillae anteromedially.

Infraorbital series moderately developed. Third infraorbital horizontally elongate, ventral margin of infraorbital ranging from falling distinctly short of horizontal limb of preopercle to approaching, but not contacting, that bone. Posterior margins of third through fifth infraorbitals falling distinctly short of vertical limb of preopercle.

Premaxillary dentition in three series: primary row distinctly sigmoid, consisting of 6 teeth without pronounced gap between first and second tooth of series but with medial tooth widely separated from its contralateral partner by gap filled by fleshy folds; triangular cluster of 3 larger teeth; and single tooth of form similar to that of primary series lying lateral to fourth tooth of primary premaxillary series. Maxilla with 2 or 3 tricuspidate teeth. Dentary with 5 tricuspidate teeth; first and second dentary teeth distinctly larger than other teeth, second tooth slightly larger than first tooth and about 1.5 times height of third tooth; fourth and fifth teeth distinctly smaller than third tooth and compressed.

Dorsal-fin rays ii,8 in all specimens. Dorsal-fin origin approximately at, or slightly anterior to, vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin ranging from straight to slightly concave. Anal-fin rays ii,10–11. Profile of distal margin of anal fin slightly concave. Hooks present on first, or first and second, branched anal-fin rays in mature males. Pectoral-fin rays i,10–11. Tip of pectoral fin extending posteriorly to pelvic-fin insertion in some individuals, falling slightly short of that point in other, typically larger, specimens. Pelvic-fin rays i,6,i in all specimens. Tip of pelvic fin extending posteriorly to, or nearly to, anus in smaller individuals, fin typically shorter in larger specimens. Hooks present on all branched pelvic-fin rays of mature males.

Gill rakers 5–6 + 9–11.

COLORATION IN ALCOHOL.—Ground coloration of specimens tan. Dorsal surface of head with few scattered, dark, surface chromatophores anteriorly, over snout, and on anterior portion of upper jaw. Chromatophore field somewhat more concentrated in larger individuals. Dorsal surface of head otherwise without surface pigmentation. Series of very dark, stellate chromatophores on membranes overlying posterior portion of brain. Anterior portion of brain overlain by contralateral, horizontally elongate patches of dark chromatophores. Region anterior to nostrils with indistinct, crescent-shaped patch of dark chromatophores; patch more obvious in smaller individuals that have little other dark pigmentation on snout. Region anteroventral to orbit, with scattered, dark chromatophores; chromatophores not concentrated into distinct stripe as in some congeners. No distinct band of dark chromatophores along ventral and posterior margins of orbit. Dorsal portion of infraorbital series and proximate portion of opercle with scattered, dark chromatophores.

Scales of anterodorsal portion of body with crescent-shaped patch of dark chromatophores over center of exposed field and with irregular series of chromatophores along distal margin of scale. Two regions of chromatophores on each scale separated by hyaline area. Humeral mark prominent, more obvious in larger specimens. Mark vertically elongate, proportionally more so in larger individuals, extending ventrally approximately one-half scale beyond lateral line. Anterior and posterior margins of humeral mark variable in form, mark generally wider midway along its vertical extent. Larger specimens often with anterodorsally arched region of less intense chromatophores extending from dorsal portion of primary body of mark. Diffuse midlateral stripe formed of deep-lying, dark chromatophores and extending varying distances along body. Stripe in smaller individuals barely apparent, beginning under dorsal fin and extending posteriorly onto base of caudal fin. Stripe becoming more prominent, longer, and wider with increasing body size. Largest examined specimens with midlateral stripe extending from region anterior to humeral mark, through mark, and posteriorly to caudal-fin base. Body stripe continuous posteriorly with horizontal stripe on middle caudal-fin rays.

Dorsal fin with basal portions of fin rays outlined by dark chromatophores in medium-sized and larger examined specimens. Anterior margin of second unbranched dorsal-fin ray often outlined by dark chromatophores with distal membranes of branched rays having scattered chromatophores, particularly in

larger specimens. Anal fin with basal portions of rays, particularly anterior and middle rays, outlined by chromatophores, chromatophore field extending varying degrees distally on some anterior branched rays. Caudal fin in smaller individuals with few scattered, dark chromatophores on basal portions of middle rays. Chromatophore field on caudal fin expanding progressively with increasing body size. Dark chromatophores forming distinct horizontal stripe over middle rays of caudal-fin, stripe most intense basally, giving appearance of basal spot in some individuals. Rays of dorsal and ventral portions of fin variably outlined by dark chromatophores, giving those portions of fin dusky appearance. Pectoral and pelvic fins hyaline or with few scattered, dark chromatophores.

ETYMOLOGY.—The specific name, *petilus,* from the Latin for thin or slender, refers to the relatively elongate body form of this species.

ECOLOGY.—It appears that the largest mature males (33.2–37.2 mm SL) (maturity indicated by the presence of hooks on the anal and pelvic fins) in the single available large population sample of *Creagrutus petilus* (MNRJ 13370, MNRJ 14807, USNM 340957) are consistently smaller than the largest females (36.7–48.8 mm SL).

Stomach contents of two specimens cleared and counterstained for this study consisted mostly of chopped seeds with occasional insect parts. One of the cleared and stained specimens, collected in late July, had ovaries with well-developed eggs.

DISTRIBUTION.—*Creagrutus petilus* is only known from the upper portion of the Rio Machado, a right bank tributary of the Rio Madeira in Rondônia, Brazil (Figure 74, triangles).

COMPARISONS.—In addition to *C. petilus,* only one *Creagrutus* species, *C. anary,* is known from the central portions of the Rio Madeira basin. The two species are readily distinguishable in overall appearance, numbers of lateral line scales, and in their relative head lengths, snout lengths, and interorbital widths (Tables 5, 46).

MATERIAL EXAMINED.—25 specimens (22, 29.8–48.8).

HOLOTYPE.—BRAZIL. *Rondônia:* Rio Marco Rondon, Pimenta Bueno (approximately 11°29′S, 61°12′W), collected by G.W. Nunan and W.D. Bandeira, 17 Jul 1986, MNRJ 14807, 1 (42.9).

PARATYPES.—21 specimens (21, 29.8–48.8).

BRAZIL. *Rondônia:* Rio Marco Rondon, Pimenta Bueno (approximately 11°29′S, 61°12′W), collected with holotype, MNRJ 13370, 12 (31.5–45.5); USNM 340957, 8 (29.8–44.5; 2 specimens cleared and counterstained for cartilage and bone). Rio Mariape, Ouro Preto do Oeste (approximately 10°40′S, 62°18′W), collected by G.W. Nunan and W.D. Bandeira, 15 Jul 1986, MNRJ 13368, 1 (48.8).

NONTYPE SPECIMENS.—3 specimens.

BRAZIL. *Rondônia:* Igarapé at Riozinho (approximately 11°30′S, 61°18′W), MNRJ 13369, 1. Rio Boa Vista, Ouro Preto do Oeste, along highway BR 364 to Nova União (approximately 10°40′S, 62°18′W), MNRJ 13371, 2.

Creagrutus phasma Myers, 1927

FIGURES 74, 79, TABLE 47

Creagrutus phasma Myers, 1927:117 [Venezuela, mouth of Curamuni (=Río Curamoni Rio Cassiquiare (=Río Casiquiare); see "Remarks," below)].—Eigenmann and Myers, 1929:548 [based on Myers, 1927].—Mago-Leccia, 1971:9 [Venezuela, Río Casiquiare].—Fowler, 1975:27 [literature compilation].—Géry and Renno, 1989:3 [as possible senior synonym of *Creagrutus bolivari*].—Taphorn and Garcia Tenia, 1991:5 [Venezuela: Río Caroni].—Jepsen, 1997:454 [Venezuela, Río Cinaruco].

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 5 teeth in the primary series of each premaxilla, 4 to 6 maxillary teeth, 6 or 7 teeth on each dentary, 8 or 9 predorsal median scales, 38 to 43 lateral line scales without a lamellar process over each pore, 2 post-anal median scales to the anal-fin origin, 4 scale rows between the dorsal-fin origin and the lateral line, 9 or 10 branched anal-fin rays, 5 to 8 gill rakers on the upper limb of the first gill arch and 9 to 12 gill rakers on the lower limb of the first gill arch, the distance from the dorsal-fin origin to the hypural joint (55.1%–60.3% of SL), the distance from the dorsal-fin origin to the anal-fin origin (27.4%–32.1% of SL), the distance from the dorsal-fin origin to the pelvic-fin insertion (20.0%–25.1% of SL), the caudal peduncle depth (9.0%–10.4% of SL), the dorsal-fin length (17.3%–22.1% of SL), the anal-fin length (13.7%–17.3% of SL), the snout length (25.3%–31.7% of HL), the near contact of the ventral margin of the third infraorbital and the horizontal limb of the preopercle, the presence of a distinct spot of dark pigmentation at the base of the middle caudal-fin rays, the prominent, anteriorly concave, crescent-shaped humeral mark without a secondary, dorsal patch of pigmentation, the absence of a distinct patch of pigmentation on the dorsal fin, and the lack of a series of dark spots along the midlateral surface of the body distinguishes *Creagrutus phasma* within the clade formed by *Creagrutus* and *Piabina.*

DESCRIPTION.—Morphometric and meristic data for *Creagrutus phasma* in Table 47. Body fusiform and slightly compressed laterally, compression accentuated in specimens less than approximately 50 mm SL. Greatest body depth at base of anteriormost ray of dorsal-fin. Dorsal profile of head distinctly convex from margin of upper lip to vertical through posterior margin of posterior nares, straight from that point to posterior tip of supraoccipital spine. Dorsal profile of body slightly convex from supraoccipital spine to origin of dorsal fin, straight from that point to anterior procurrent caudal-fin ray. Ventral profile of head variably developed, with obtuse angle approximately midway between margin of lower lip and posterior extremity of dentary, straight to slightly convex from that point to isthmus. Ventral profile of body slightly convex from isthmus to pelvic-fin insertion; straight from that point to anal-fin origin; straight to slightly concave from that point to caudal peduncle.

TABLE 47.—Morphometrics and meristics of *Creagrutus phasma:* (A) lectotype of *C. phasma,* CAS 44210; (B) paralectotype of *C. phasma,* CAS 209191; and (C) other specimens of *C. phasma* from which counts and measurements were taken (n=18). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B	C
		Morphometrics	
Standard length	50.2	47.2	42.2–68.4
1. Snout to anal-fin origin	66.2	65.9	62.9–68.6
2. Snout to pelvic-fin insertion	46.5	46.6	45.2–49.4
3. Snout to pectoral-fin insertion	24.4	23.3	21.3–26.0
4. Snout to dorsal-fin origin	48.6	46.6	43.6–47.9
5. Dorsal-fin origin to hypural joint	55.3	56.2	55.1–60.3
6. Dorsal-fin origin to anal-fin origin	29.8	29.6	27.4–32.1
7. Dorsal-fin origin to pelvic-fin insertion	22.5	22.6	20.0–25.1
8. Dorsal-fin origin to pectoral-fin insertion	30.6	30.8	28.4–32.4
9. Caudal peduncle depth	9.6	9.7	9.0–10.4
10. Pectoral-fin length	16.9	17.9	16.1–19.5
11. Pelvic-fin length	15.9	14.6	12.4–15.8
12. Dorsal-fin length	18.0	20.2	17.3–22.1
13. Anal-fin length	16.2	16.0	13.7–17.3
14. Head length	25.4	24.8	22.5–26.8
15. Postorbital head length	42.6	44.3	38.4–45.2
16. Snout length	28.6	27.4	25.3–31.7
17. Bony orbital diameter	34.6	36.1	30.0–39.5
18. Interorbital width	28.3	27.9	26.1–31.8
		Meristics	
Lateral line scales	42	40	38–43
Scale rows between dorsal-fin origin and lateral line	4	4	4
Scale rows between anal-fin origin and lateral line	3	3	3–4[1]
Predorsal median scales	9	9	8–9
Branched dorsal-fin rays	8	8	8
Branched anal-fin rays	9	10	9–10
Branched pelvic-fin rays	7	7	6–8
Pectoral-fin rays	12	11	11–13
Vertebrae	39	40	37–40

[1]Four scale rows between anal-fin origin and lateral line present in only 1 of 19 specimens.

Anterior profile of head broadly rounded in lateral view. Upper jaw slightly longer than, and overhanging, lower jaw. Most external surfaces of ventral and ventrolateral portions of head covered with scattered, minute papillae. Anterior portion of snout relatively soft and fleshy, with concentration of soft tissues; minute papillae highly concentrated on snout and upper lip, continuing into mouth on fleshy flaps and plicae between outer and medial premaxillary teeth. Lower jaw distinctly fleshy anteriorly, with concentrated papillae, inner surfaces of lower lip convolute and papillose, with fleshy flaps extending into mouth.

Infraorbital series moderately well developed, with ventral margin of third infraorbital separated from ventral limb of preopercle by narrow gap in some specimens and with bones nearly in contact in other individuals. Posterior and ventral margins of third infraorbital usually forming broadly rounded obtuse angle, occasionally describing an arc and nearly concentric with orbit. Fourth infraorbital small and triangular, with its base at margin of orbit and apex directed posteriorly. Posterior margins of third through fifth infraorbitals narrowly separated from vertical limb of preopercle.

Premaxillary teeth in three distinct groups: primary row with 5 unicuspidate to tricuspidate teeth, anteriormost 3 premaxillary teeth often unicuspidate, without pronounced gap between first and second tooth of series; a medial, triangular cluster of 3 large tricuspidate teeth; and a single outer unicuspidate tooth positioned lateral to third or fourth tooth of primary tooth row. Maxilla with 4 to 6 tricuspidate teeth. Dentary usually with 6 or 7 usually tricuspidate teeth; first 2 teeth in dentary occasionally pentacuspidate, with minute outer pair of cusps. Two anteriormost dentary teeth largest and subequal, third tooth slightly smaller than second; remaining teeth in series distinctly smaller than 3 anterior teeth; third through sixth teeth slightly recurved.

Dorsal-fin rays ii,8 in all specimens. Dorsal-fin origin located slightly anterior to vertical through origin of pelvic fin. Distal margin of dorsal fin nearly straight or with very slight concavity as a result of elongation of second unbranched and anterior 2 or 3 branched rays. Anal-fin rays ii–iii,9–10. Mature males with anal-fin hooks, when present, on segments of first branched ray. Distal margin of anal fin slightly sigmoidal, with second unbranched and anterior 3 branched rays forming slightly elongate lobe, outline of posterior 5 or 6 rays concave.

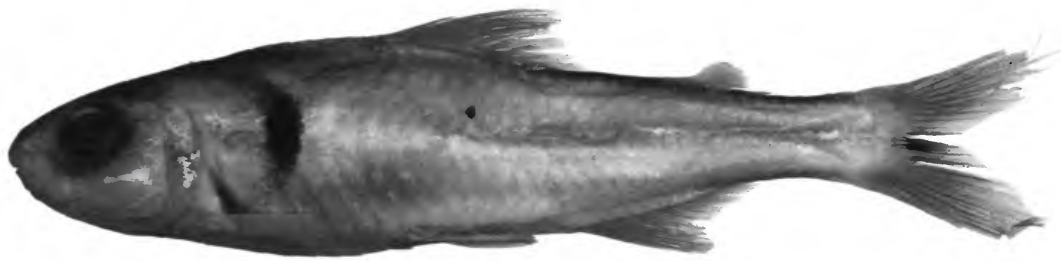

FIGURE 79.—*Creagrutus phasma*, MCNG 21491, 61.3 mm SL; Venezuela, Bolivar, pools and beaches below Salto de Icutu, Río Caura basin.

Pectoral-fin rays i,11–13 (i,11 in only 1 specimen). Pectoral fin short; tip reaching posteriorly, at most, to within 2 or 3 scale rows of pelvic-fin origin. Pelvic-fin rays i,7–8 or i,6,i; typically i,7. Mature males, with pelvic-fin hooks, when present, on medial surfaces of segmented and unsegmented portions of main shaft and on medial, occasionally also on lateral, secondary branches of all rays medial of the lateral unbranched element. Tip of pelvic fin falling 2 or 3 scales short of anal-fin origin.

Posterior margin of body scales smoothly rounded to slightly undulate, latter condition especially developed ventrally and ventrolaterally.

Gill rakers 5–8 + 9–12.

COLORATION IN ALCOHOL.—Overall ground color straw to light brown, with pigment cells ranging from dark brown to sepia in most areas to nearly black in areas of concentrated pigmentation. Dorsal surface of head with diffuse pattern of small, light brown chromatophores; chromatophores most highly concentrated on median portion of upper lip and over snout. Dorsal surfaces of frontal and parietal portions of cranium densely pigmented with small, highly concentrated dark chromatophores over fontanelle, with larger, more scattered chromatophores present over other areas. Band of scattered, dark chromatophores extending from immediately lateral of nares posteroventrally and then continuing along ventral margin of orbit no further than midpoint of orbit. Infraorbitals posterior of orbit and dorsal one-half of opercle covered with numerous, scattered, small to large, dark chromatophores. Lower lip and ventrolateral surface of head unpigmented.

Body pigmentation diffuse, most concentrated dorsal of lateral line and in association with posteriormost exposed portions of scales. Scattered, dark chromatophores concentrated on dorsal portion of body between head and anterior of dorsal-fin base. Humeral mark usually in form of anteriorly concave crescent with dark pigmentation highly concentrated immediately dorsal of lateral line where more darkly pigmented area forms vertically elongate, rotund blotch within humeral mark. Humeral mark continuing dorsally from dark central portion of mark to within about 1 scale row of midline, with intensity of pigmentation decreasing dorsally. Humeral mark extending ventrally from central dark portion as less intensely pigmented, albeit continuous, field followed ventrally by scattered stellate chromatophores continuing to within about 1 scale row of medial pectoral-fin ray. Dark pigmentation of lateral surface of body ventral to lateral line, other than that associated with humeral bar, restricted to scattered, dark chromatophores outlining hypaxial myosepta immediately dorsal of anal-fin base and extending anteriorly to near pelvic-fin base. Faint midlateral body stripe associated with first and second scale rows dorsal of lateral line in some specimens, becoming denser and somewhat wider posteriorly and extending well ventral of lateral line on caudal peduncle.

Dorsal-fin membranes with dark chromatophores most concentrated on distal one-fourth to one-third of anterior 4 to 6 branched rays, unbranched rays distally pigmented; basal portions of shafts of all, or nearly all, fin rays with dark pigment. Anal fin mostly unpigmented; anterior surfaces of basal one-half of rays with dark pigment; several dark chromatophores scattered over rays and membranes of central portion of fin. Caudal fin with all fin rays delineated by dark pigment, pigmentation darkest on middle fin rays and giving appearance of elongate black spot. Pelvic fin hyaline. Pectoral fin unpigmented except for several isolated dark chromatophores associated with membrane of medial fin rays.

DISTRIBUTION.—*Creagrutus phasma* ranges from the upper portion of the Rio Negro in Brazil, north to various localities in the Río Orinoco basin in both Venezuela and Colombia (Figure 74, filled stars).

REMARKS.—In his original description of *Creagrutus phasma*, Myers (1927:116) cited two specimens as "types," thereby making them syntypes. The syntype in better overall condition (CAS 44210, 50.2 mm SL) is designated herein as the lectotype of the species, and the second syntype (CAS 209191, 47.2 mm SL) thus becomes a paralectotype.

Myers (1927:116) cited the collecting information for the syntypes of *Creagrutus phasma* as "Venezuela, mouth of the Curamuni, Rio Cassiquiare. 7 March 1925. Carl Ternetz." According to an unpublished itinerary of the collecting site for Ternetz compiled by G.S. Myers, this locality is located in up-

per Río Casiquiare in the region between Curare, where Ternetz collected on 2 March 1925, and the bifurcation of the Río Orinoco, which he reached on 10 March. This information indicates that the material was likely collected at the mouth of the Río Curamoni, a drainage cited by Ternetz as "the Curamuni."

Géry and Renno (1989:3) cited *Creagrutus phasma* as a possible senior synonym of *Creagrutus bolivari.* The results of this study indicate that the species are distinct.

Taphorn and Garcia Tenía (1991, fig. 5) cited *Creagrutus phasma* from the Río Caroni basin. That region is outside the known range of the species, which is based on the material that we have examined in this study. The record, nonetheless, is not unexpected because it agrees with the ranges of other fish species within the region.

MATERIAL EXAMINED.—67 specimens (20, 42.2–68.4).

VENEZUELA. *Amazonas:* Río Casiquiare, mouth of Curamuni (=Río Curamoni, approximately 2°37′N, 66°12′W; see "Remarks" under species account), CAS 44210, 1 (50.2, lectotype of *Creagrutus phasma;* formerly IU 17681, in part); CAS 209191, 1 (47.2, paralectotype of *Creagrutus phasma;* formerly IU 17681, in part). Río Orinoco at playa approximately 0.5 km above La Esmeralda (3°09′N, 65°32′W), ANSP 161241, 7. Playa and backwater of Río Casiquiare, approximately 2.0 km downstream from mouth of Río Pamoni (2°48′N, 65°57′W), ANSP 161243, 6 (1, 43.9). Río Mavaca, beaches above base camp, Tapirapeco Expedition, MBUCV V-17823, 2. Caño entering into a laguna of Río Mavaca (2°17′22″N, 65°06′28″W), MCNG 28855, 1 (68.4). *Apure:* Río Cinaruco, near mouth (approximately 6°39′N, 67°07′W), MCNG 17961, 24 (7, 42.2–51.1). *Bolivar:* Sand bar along Río Mato (7°02′N, 65°13′W), ANSP 139598, 11. Pools and beaches in front of Salto de Icutu, Río Nichare system, Río Caura basin (5°53′00″N, 64°51′00″W), MCNG 21491, 10 (9, 42.6–63.4). Río Caura basin, island slightly below mouth of Río Nichare (6°30′N, 64°39′30″W), MCNG 21936, 1.

BRAZIL. *Amazonas:* Rio Negro, rapids at São Gabriel (0°08′S, 67°05′W), ANSP 150050, 1.

COLOMBIA. *Meta:*.Río Yucao River, 13.5 km SW of Puerto Gaitan (latter locality at 4°19′N, 72°04′W), UF 33527, 2.

Creagrutus pila, new species

FIGURES 74, 80, TABLE 48

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 3 or 4 teeth on the maxilla, 6 teeth in the primary tooth row of the premaxilla, 5 dentary teeth, 36 to 38 lateral line scales without a lamellar process over each pore, 9 to 11 predorsal median scales, 4 or 5 scale rows between the dorsal-fin origin and the lateral line, 3 or 4 scale rows between the lateral line and the anal-fin origin, 35 to 37 vertebrae, 9 to 11 branched anal-fin rays, 2 post-anal median scales to the anal-fin origin, 6 or 7 gill rakers on the upper limb of the first gill arch and 8 to 10 gill rakers on the lower limb of the first gill arch, the length from the snout to the pectoral-fin insertion (25.7%–28.5% of SL), the length from the snout to the dorsal-fin insertion (47.6%–52.0% of SL), the distance from the dorsal-fin origin to the pelvic-fin insertion (29.3%–32.9% of SL), the pelvic-fin length (16.4%–19.6% of SL), the caudal peduncle depth (11.9%–13.4% of SL), the anal-fin length (19.3%–22.7% of SL), the bony orbital diameter (28.4%–33.5% of SL), the moderately developed third infraorbital that does not contact the horizontal limb of the preopercle, the lack of a series of dark midlateral spots on the body, the vertically elongate, ventrally tapering humeral mark, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus pila* within the clade composed of *Creagrutus* and *Piabina.*

TABLE 48.—Morphometrics and meristics of *Creagrutus pila,* new species: (A) holotype of *C. pila,* MUSM 8874; and (B) paratypes of *C. pila* (n=32). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	58.3	41.3–70.5
1. Snout to anal-fin origin	64.5	60.8–68.9
2. Snout to pelvic-fin insertion	48.9	46.2–51.2
3. Snout to pectoral-fin insertion	26.0	25.7–28.5
4. Snout to dorsal-fin origin	50.6	47.6–52.0
5. Dorsal-fin origin to hypural joint	54.0	53.3–58.1
6. Dorsal-fin origin to anal-fin origin	31.7	31.6–36.1
7. Dorsal-fin origin to pelvic-fin insertion	30.0	29.3–32.9
8. Dorsal-fin origin to pectoral-fin insertion	35.5	33.1–36.5
9. Caudal peduncle depth	12.5	11.9–13.4
10. Pectoral-fin length	21.4	19.4–22.8
11. Pelvic-fin length	16.8	16.4–19.6
12. Dorsal-fin length	23.7	21.1–25.7
13. Anal-fin length	20.6	19.3–22.7
14. Head length	28.3	25.4–29.2
15. Postorbital head length	45.5	43.6–50.3
16. Snout length	26.7	24.1–29.9
17. Bony orbital diameter	30.3	28.4–33.5
18. Interorbital width	30.3	28.4–32.8
	Meristics	
Lateral line scales	37	36–38
Scale rows between dorsal-fin origin and lateral line	4	4–5
Scale rows between anal-fin origin and lateral line	3	3–4
Predorsal median scales	10	9–11
Branched dorsal-fin rays	8	8
Branched anal-fin rays	10	9–11
Branched pelvic-fin rays	6	6
Pectoral-fin rays	14	13–14
Vertebrae	36	35–37

DESCRIPTION.—Morphometric and meristic data for *Creagrutus pila* in Table 48. Head and body robust, body becoming progressively more robust in larger specimens. Greatest body depth at dorsal-fin origin in smaller specimens, shifted anteriorly in larger specimens, particularly those with distended abdomens. Dorsal profile of head smoothly convex from margin

of upper lip to vertical through posterior nostril in all examined specimens, straight to very slightly convex from that point to rear of supraoccipital spine. Dorsal profile of body slightly convex and without pronounced break in alignment relative to head profile in smaller individuals, progressively more convex in larger individuals, with variably evident change in alignment relative to that of head. Ventral profile of head with variably obvious obtuse angle at anteroventral corner of dentary, nearly straight from that point to isthmus. Ventral profile of body variably convex from isthmus to anal-fin origin; convexity more pronounced in some larger specimens.

Head obtusely pointed in lateral view, moderately compressed in dorsal view. Upper jaw distinctly longer than, and overhanging, lower jaw. Snout moderately fleshy, with scattered papillae anteriorly; papillae more concentrated on ventral margin of upper lip and on numerous folds and plicae extending between outer and medial premaxillary teeth. Lower lip very fleshy, particularly anteriorly, with numerous papillae on dorsal surface and fewer on anterior and ventral surfaces.

Infraorbital series moderately developed. Third infraorbital relatively compact, with proportionally high vertical extent but with ventral margin of third infraorbital falling well short of horizontal limb of preopercle along its particularly posterior portion. Posteroventral margin of third infraorbital distinctly rounded. Posterior margins of third through fifth infraorbitals falling distinctly short of vertical limb of preopercle.

Premaxillary dentition in three series: primary row slightly sigmoid, typically with 6 teeth (5 teeth present on 1 premaxilla in 1 specimen), without pronounced gap between first and second tooth of series but with medial tooth separated from anterior tooth of contralateral series by distinct gap; triangular cluster of 3 larger teeth, with posteromedial tooth largest; and a single tooth of form similar to that of primary series occurring lateral to fourth tooth of premaxillary series. Maxilla with 3 or 4 tricuspidate teeth. Dentary with 5 teeth; 3 anteriormost teeth distinctly larger than other teeth in series and tricuspidate. First and second teeth distinctly larger than third tooth, with second tooth somewhat larger than first tooth. Fourth tooth tricuspidate, about twice as large as triscupidate or conical fifth tooth.

Dorsal-fin rays ii,8. Dorsal-fin origin approximately at vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin slightly concave in all specimens, with slightly developed lobe anteriorly. Anal-fin rays ii,9–11. Profile of distal margin of anal fin concave. Hooks in mature males, when present, located on anterior 3 to 5 branched anal-fin rays and sometimes also on last unbranched fin ray. Pectoral-fin rays i,12–13. Tip of pectoral fin extending posteriorly nearly to pelvic-fin insertion. Pelvic-fin rays i,6,i in all specimens. Tip of pelvic fin extending posteriorly to anus or slightly beyond anal-fin origin. Hooks in mature males, when present, on all branched pelvic-fin rays and occasionally on medial unbranched ray.

Gill rakers 6–7 +8–10.

COLORATION IN ALCOHOL.—Overall ground coloration ranging from light tan to light brown. Dorsal surface of head with relatively dense field of dark chromatophores. Pigmentation denser in larger individuals with chromatophore field continuing onto upper lip and across snout; pigmentation noticeably more concentrated anterior to nostrils and forming distinct crescent-shaped mark in many specimens. Region ventral and posterior to eye lacking discrete curved band of dark chromatophores found in some congeners, but covered by diffuse field of small dark chromatophores. Region posterior to orbit and across dorsal portion of opercle with scattered, small, dark chromatophores; chromatophore field in some larger specimens extending more ventrally both on opercle and posterior portion of cheek.

Scales of dorsal and dorsolateral surface of body with center of exposed section of scale covered with field of small dark chromatophores and with band of chromatophores along distal margin of scales. Two pigmented regions on each scale separated by hyaline crescent of variable extent. In some specimens hyaline region on scales relatively wider and distal chromatophore field poorly developed giving appearance of clear scale margin. In specimens with overall darker coloration, hyaline region narrower and pigmentation along scale margin more developed but hyaline region, nonetheless, still obvious and forming pattern of lightly pigmented reticulation again darker background. Smallest examined individuals (24.7–29.2; nontypes, MZUSP 26073) with humeral mark vertically rotund; mark becoming progressively more elongate in specimens of approximately 30–34 mm SL, and fully developed vertically by 37 mm SL. Humeral mark in medium- to large-sized specimens pronounced, in form of ventrally tapering, vertically elongate bar. Bar terminating dorsally approximately one and one-half scales ventral of dorsal midline, usually with dorsal margin of bar quite distinct and horizontal or nearly horizontal. Anterior and posterior margins of humeral bar somewhat variable but approximately straight. Diffuse midlateral body stripe consisting of dark, deep-lying and surface chromatophores extending from under, or slightly anterior of, dorsal fin posteriorly onto caudal peduncle; stripe not continuing onto basal portions of middle caudal-fin rays. Midlateral stripe less obvious and slightly wider on caudal peduncle.

Dorsal fin with anterior rays overlain by small dark chromatophores. Margins of remaining dorsal-fin rays, particularly posterior margins, outlined with small chromatophores; fin membranes with scattered, dark chromatophores on distal portions, more so on anterior branched rays. Anal fin with margins of branched rays, particularly second through fifth rays, outlined by small dark chromatophores; chromatophore series extending along two-thirds of fin-ray length anteriorly, limited to basal one-fourth of fin rays posteriorly. Caudal-fin rays outlined by small dark chromatophores, basal portions of rays with pigmentation more intense. Pectoral and pelvic fins hyaline or with few scattered, dark chromatophores.

ETYMOLOGY.—The specific name, *pila,* from the Latin for javelin, refers to the vertically elongate, ventrally tapering humeral mark on the side of the body in this species.

FIGURE 80.—*Creagrutus pila,* new species, holotype, MUSM 8874, 58.3 mm SL; Peru, Ucayali, Provincia Padre Abad, Río Huacamayo, km 155 on road from Pucallpa to Tingo Maria.

ECOLOGY.—The Río Huacamyao, the type locality for *Creagrutus pila,* is a clear water stream with highly transparent water, a sand and pebble bottom, and thick vegetation along its bank (see Isbrücker et al. (1983, fig. 1) for photograph of river in region of type locality).

Mature males of *C. pila,* as indicated by anal- and pelvic-fin hooks, are all less than 54 mm SL and were collected in the months of September through November. *Creagrutus pila* was captured with *C. cochui* (MUSM 5240 and 8887; MUSM 8876 and 8885, respectively) within the Río Neshuya, a tributary of the Río Aguaytia the southern limit of the range of the latter species.

DISTRIBUTION.—The distribution of *Creagrutus pila* is very restricted, with all specimens originating in smaller rivers draining into the Río Aguaytia, a left bank tributary of the Río Ucayali in the Department of Ucayali, Peru (Figure 74, open star).

COMPARISONS.—Only two other *Creagrutus* species, *C. ortegai* and *C. cochui,* are known to occur sympatrically with *C. pila.* Neither of those species has the vertically elongate humeral mark of *C. pila,* and each differs from that species in various meristic and morphometric features (see "Key to the Species of *Creagrutus* in the Amazon Basin").

MATERIAL EXAMINED.—47 specimens (36, 38.0–70.5).

HOLOTYPE.—PERU. *Ucayali:* Provincia Padre Abad, Río Huacamayo, km 155 on Highway (Carratera Federico Basadre) from Pucallpa to Tingo Maria, collected by H. Ortega, 24 Sep 1983, MUSM 8874, 1 (58.3).

PARATYPES.—32 specimens (32, 41.3–70.5).

PERU. *Ucayali:* Provincia Padre Abad, Río Huacamayo, km 155 on Highway (Carratera Federico Basadre) from Pucallpa to Tingo Maria, collected with holotype, MUSM 8875, 6 (41.7–59.6); USNM 341365, 5 (41.3–54.4). Provincia Padre Abad, Río Huacamayo, Aguaytia, collected by H. Ortega and J. Cánepa, 24 Nov 1983, MUSM 2956, 3 (50.0–61.5); USNM 341366, 3 (48.5–70.5). Provincia Padre Abad, Río Aguaytia basin, Río Neshuya (mouth of river at 8°17′S, 75°03′W), collected by C. Contreras, 20 Aug 1981, MUSM 8876, 1 (59.5). Provincia Padre Abad, Río Tahuayo, km 72 on road from Pucallpa to Tingo Mario, collected by H. Ortega and J. Cánepa, 9 Nov 1993, MUSM 5240, 3 (49.5–54.0); USNM 341364, 3 (47.8–60.2). Provincia Padre Abad, Río Tahuayo, km 72 on road from Pucallpa to Tingo Mario, collected by H. Ortega and J. Cánepa, 19 Nov 1983, MUSM 8877, 4 (41.8–52.5); USNM 341367, 4 (44.5–55.5; 2 specimens cleared and counterstained for cartilage and bone).

NONTYPE SPECIMENS.—14 specimens (3, 38.0–47.6).

PERU. *Ucayali:* Provincia Padre Abad, Río Huacamayo, road from Pucallpa to Huánuco, MZUSP 26073, 8 (3, 38.0–47.6). Provincia Padre Abad, Río Neshuya, on road from Pucallpa to Huánuco, MZUSP 26476, 6.

Creagrutus planquettei Géry and Renno, 1989

FIGURES 81–83, TABLE 49

Creagrutus planquettei Géry and Renno, 1989:1, figs. 1–3, 5 [type locality: crique Japigmy, Arataye, affluent de l'Approuage en monte de Pierrette, Guyane (=French Guiana (Guyane), Crique Japigny, Arataye, tributary of Fleuve Approuague, upriver of Pierette].—Boujard et al., 1990:178 [French Guiana, Fleuve Arataye].—Géry et al., 1991:45, pl. 14: fig. 2 [based on Géry and Renno, 1989].—Planquette et al., 1996:326 [unnumbered figure on page 327; brief redescription, biology, and distribution].—Boujard et al., 1997:86, pl. 9 [French Guiana, Fleuve Approuague].

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 6 teeth in the primary series of the premaxilla, 3 maxillary teeth, 5 teeth on the dentary, 9 or 10 predorsal median scales, 38 to 40 lateral line scales without a lamellar process over each pore, 4 scale rows between the dorsal-fin origin and the lateral line, 10 or 11 branched anal-fin rays, 6 gill rakers on the lower limb and 12 or 13 gill rakers on the upper limb of the first gill arch, the distance from the snout to the anal-fin origin (65.0%–68.3% of SL), the head length (27.2%–29.3% of

TABLE 49.—Morphometrics and meristics of *Creagrutus planquettei:* (A) holotype of *C. planquettei*, MNHN 1989-31 and (B) other specimens of *C. planquettei* from which counts and measurements were taken (n=7). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	66.6	33.0–65.5
1. Snout to anal-fin origin	68.0	65.0–68.3
2. Snout to pelvic-fin insertion	51.1	46.9–51.0
3. Snout to pectoral-fin insertion	28.1	25.7–28.5
4. Snout to dorsal-fin origin	46.8	46.7–48.8
5. Dorsal-fin origin to hypural joint	54.8	56.2–61.6
6. Dorsal-fin origin to anal-fin origin	33.6	28.5–32.9
7. Dorsal-fin origin to pelvic-fin insertion	26.4	25.1–28.8
8. Dorsal-fin origin to pectoral-fin insertion	31.5	29.1–32.2
9. Caudal peduncle depth	10.7	10.5–11.4
10. Pectoral-fin length	19.4	19.2–20.7
11. Pelvic-fin length	17.6	14.4–17.5
12. Dorsal-fin length	21.0	20.4–22.5
13. Anal-fin length	17.3	15.8–20.2
14. Head length	29.3	27.2–29.1
15. Postorbital head length	49.7	41.3–48.0
16. Snout length	28.6	26.0–30.3
17. Bony orbital diameter	29.2	30.5–36.7
18. Interorbital width	25.1	25.0–28.9
	Meristics	
lateral line scales	39	38–40
Scale rows between dorsal-fin origin and lateral line	4	4l
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	9	9–10
Branched dorsal-fin rays	8	8
Branched anal-fin rays	10	10–11[1]
Branched pelvic-fin rays	6	5–6
Pectoral-fin rays	12	12–14
Vertebrae	38	38–39

[1]Nine branched anal-fin rays reported as occurring in 1 specimen by Géry and Renno (1989:2).

SL), the postorbital head length (41.3–49.7% of HL), the interorbital width (25.0%–28.9% of HL), the moderately developed third infraorbital approaching but not contacting the horizontal limb of the preopercle, the absence of a distinct spot of dark pigmentation at the base of the middle caudal-fin rays, the horizontally elongate humeral mark without a secondary, dorsal patch of pigmentation, the distinct patch of dark pigmentation on the distal portion of the unbranched and first through third or fourth branched dorsal-fin rays, and the lack of a series of dark spots along the midlateral surface of the body distinguishes *Creagrutus planquettei* within the clade formed by *Creagrutus* and *Piabina.*

DESCRIPTION.—Morphometric and meristic data for *Creagrutus planquettei* in Table 49. Head and body relatively robust in specimens of all available sizes. Greatest body depth at dorsal-fin origin. Dorsal profile of head distinctly convex from margin of upper lip to vertical through posterior nostril, straight from that point to tip of supraoccipital spine in specimens of all sizes. Interorbital region nearly flat transversely. Dorsal profile of body straight from tip of supraoccipital spine to dorsal-fin origin in smaller individuals, straight to slightly convex with slight change in angle relative to dorsal profile of head in some larger specimens. Dorsal surface of body with predorsal median ridge; ridge extending anteriorly approximately one-half of distance to tip of supraoccipital in some smaller individuals, reaching that bone in larger specimens. Ventral profile of head with distinct obtuse angle at anteroventral corner of dentary, straight to slightly convex from that point to isthmus (illustrated specimens with hyoid apparatus depressed changing ventral profile of head). Prepelvic profile of body slightly convex in smaller individuals, convexity somewhat more pronounced in larger specimens.

Head obtusely pointed in lateral view, more compressed laterally from dorsal view. Upper jaw distinctly longer than, and overhanging, lower jaw. Anterodorsal median portion of snout with scattered papillae. Papillae more concentrated on anterior surface of snout and particularly on fleshy upper lip and on folds and plicae extending between outer and medial premaxillary teeth. Lower jaw very fleshy with numerous papillae over dorsal surface and scattered papillae on anteroventral surface.

Infraorbital series moderately developed. Ventral margin of third infraorbital rounded, margin approaching, but not contacting, horizontal limb of preopercle even in largest examined specimens. Posterior margins of third through fifth infraorbitals falling distinctly short of vertical limb of preopercle.

Premaxillary dentition in three series: primary series slightly sigmoid, with 6 tricuspidate teeth and without pronounced gap between first and second tooth of series but with medial tooth of series distinctly separated from medial tooth of contralateral series; triangular cluster of 3 teeth, all larger than teeth of primary series; and single tooth of form similar to that of primary series occurring lateral to fourth tooth of primary series. Maxilla with 3 teeth, gradually decreasing in size posteriorly, with indistinct cusps in smaller specimens and three distinct cusps in larger individuals. Dentary with 5 tricuspdate teeth, cusps barely apparent on fifth tooth; second tooth only slightly larger than first tooth, but about twice as high as third tooth; fourth tooth distinctly smaller than third tooth, and fifth tooth smaller than fourth tooth.

Dorsal-fin rays ii,8 in all specimens. Dorsal-fin origin slightly anterior to vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin slightly concave. Anal-fin rays iii,10–11 in examined specimens (iii,9 reported for one specimen by Géry and Renno (1989:2)). Bony hooks present on first four branched anal-fin rays of males (Planquette et al., 1996: 326). Distal margin of anal fin distinctly concave. Few hooks present on first and second branched anal-fin rays in single examined male, as shown by presence of anal-fin ray hooks. Pectoral-fin rays i,11–13. Tip of pectoral fin extending posteriorly nearly to pelvic-fin insertion in smaller individuals, falling about 2 scales short of that point in larger specimens. Pelvic-fin rays i,5,i or i,6, or i,6,i. Tip of pelvic fin falling slightly short of

FIGURE 81.—*Creagrutus planquettei,* holotype, MNHN 1989-31, 66.6 mm SL; French Guiana, Crique Japigny, Fleuve Arataye system, Fleuve Approuague basin, above Pierrette.

FIGURE 82.—*Creagrutus planquettei,* MHNG 2522.75, 39.7 mm SL; French Guiana, Fleuve Arataye system, Fleuve Approuague basin.

anal-fin origin. Mature males with hooks on all branched pelvic-fin rays.

Gill rakers 6 + 12–13.

COLORATION IN LIFE.—In the original description of *Creagrutus planquettei,* Géry and Renno (1989, fig. 1) provided a photo of an apparently recently preserved specimen (photo reproduced in Géry et al. (1991, pl. 4: fig. 2) and Planquette et al. (1996:327)). Specimen with guanine covering upper lip, lower jaw, region anteroventral and ventral to orbit, infraorbitals, and opercle. Darker region apparent on ventral portion of opercle. Dorsal portion of iris above pupil with crescent of reddish pigmentation. Midlateral and central portions of body covered with guanine, more so anteriorly. Prominent humeral spot obvious midlaterally, with field of diffuse dark chromatophores extending anterodorsally from that mark. Anterodorsal portion of dorsal fin dark. Middle, dorsalmost, and ventralmost caudal-fin rays apparently dark.

COLORATION IN ALCOHOL.—Ground coloration tan. Dorsal surface of head with scattered, dark, small chromatophores on surface of head and overlying dorsal surface of brain. Concentration of dark chromatophores greater on snout and upper lip. Region anterior and anteroventral to nostrils with crescent-shaped field of dense dark chromatophores. Region anteroventral to nostrils with field of denser dark chromatophores in larger specimens. Some larger specimens with distinct narrow band of dark chromatophores posteroventral to orbit, but not forming discrete band of pigmentation continuing around ventral and posterior margins of orbit present in many congeners. Some larger individuals with diffuse field of chromatophores extending around ventral border of orbit and overlapping darker narrow posteroventral band. Dorsal portion of opercle and infraorbital series with field of small, dark chromatophores; chromatophores in field more concentrated in larger specimens, particularly in region posterior of infraorbitals and on anterodorsal portion of opercle.

Scales of dorsolateral portion of body with basal portion of exposed field covered with small dark chromatophores and distal portion of exposed region with pattern of larger, darker chromatophores. Region between those fields hyaline, becoming increasingly narrow with increased body size. Pigmentation pattern forming dark, reticulate pattern that becomes increasingly obvious in larger specimens, particularly in individuals with overall darker head and body pigmentation (compare Figures 81 and 82). Humeral spot very obvious and distinctly darker than midlateral stripe on body in smaller examined specimens. Main body of spot in smaller specimens variably

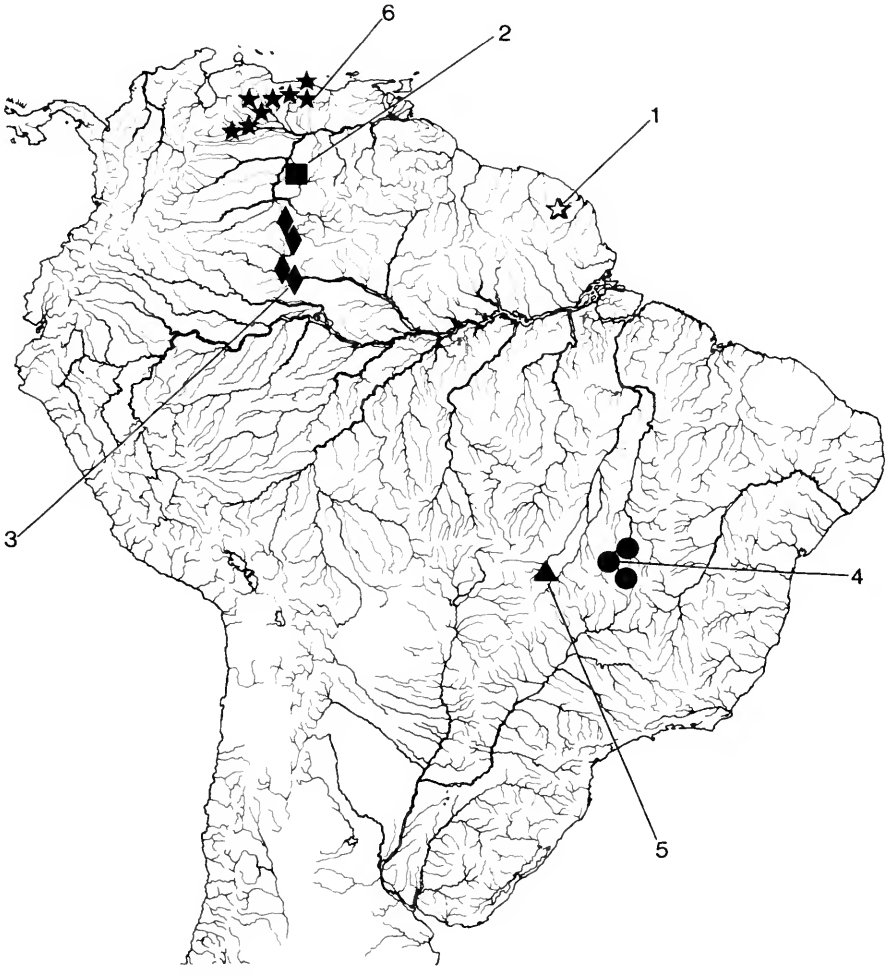

FIGURE 83.—Map of central and northern South America showing geographic distribution of *Creagrutus planquettei* (open star, 1=type locality), *Creagrutus provenzanoi* (square, 2=type locality), *Creagrutus runa* (diamonds, 3=type locality), *Creagrutus saxatilis* (dots, 4=type locality), *Creagrutus seductus* (triangle, 5=type locality), and *Creagrutus taphorni* (solid stars, 6=type locality) (some symbols represent more than one locality or lot of specimens).

shaped, usually horizontally elongate, with variably developed dorsal and ventral extensions. Ventral extension of humeral mark sometimes in shape of anteriorly concave comma that trails off into scattered, small chromatophores. Some individuals with field of less concentrated dark chromatophores extending dorsally about 1 scale from upper margin of spot. Humeral mark in larger specimens less distinct relative to overall darker midlateral stripe and horizontally elongate, with diffuse dorsal and ventral extensions. Midlateral stripe formed by surface and deep-lying dark chromatophores, extending from rear of pectoral girdle, through humeral spot, to base of middle caudal-fin rays across entire size range of examined specimens.

Dorsal fin with dark chromatophores overlying first unbranched ray and distal portions of second unbranched through third or fourth branched rays and intervening membranes; dark pigmentation forming diffuse distal patch apparent in specimens of all sizes. Anal-fin membranes with dispersed small dark chromatophores; chromatophores most concentrated on membranes of distal portions of anterior branched rays. Caudal fin with diffuse spot of chromatophores on middle rays. Pectoral and pelvic fins hyaline or with few scattered, small, dark chromatophores.

ECOLOGY.—Planquette et al. (1996:326) reported that *Creagrutus planquettei* is apparently rare within its known range.

DISTRIBUTION.—*Creagrutus planquettei* is known only from the middle and upper portions of the Fleuve Approuague basin in eastern French Guiana (Figure 83, open star).

REMARKS.—As a consequence of the restricted available

sample of *Creagrutus planquettei,* we were unable to clear and stain any specimens of the species in order to confirm its possession of all the characters diagnostic for the genus or determine its relationships within that taxon. Nonetheless, as noted under "Phylogenetic Position of *C. molinus, C. planquettei, C. veruina,* and *C. xiphos,*" above, the evidence from external body systems supports the assignment of *C. planquettei* to *Creagrutus* and indicates that its relationships lie with the species group characterized by the derived premaxillary dentition in which no gap occurs between the first and second teeth of the primary tooth series on the premaxilla.

MATERIAL EXAMINED.—8 specimens (8, 33.0–66.6).

FRENCH GUIANA. Crique Japigny, Fleuve Arataye system, Fleuve Approuague basin, above Pierrette, MNHN 1989-31, 1 (66.6, holotype of *Creagrutus planquettei*); MNHN 1989-36, 4 (34.7–65.5, paratypes of *Creagrutus planquettei*). Fleuve Arataye system, Fleuve Approuague basin, MHNG 2522.75, 3 (33.0–39.7).

Creagrutus provenzanoi, new species

FIGURES 83, 84, TABLE 50

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina,* without a distinctly larger gap between the first and second teeth of the primary series, 6, occasionally 5, teeth in the primary series of each premaxilla, 3 or 4 maxillary teeth, 6, less commonly 7, teeth on each dentary, 9 to 11 predorsal median scales, 38 to 42 lateral line scales without a lamellar process over each pore, 4 or 5, usually 5, scale rows between the dorsal-fin origin and the lateral line, 11 or 12 branched anal-fin rays, 37 to 39 vertebrae, 7 or 8 gill rakers on the upper limb of the first gill arch, 12 or 13 gill rakers on the lower limb of the first gill arch, the distance from the snout to the pectoral-fin insertion (24.4%–27.3% of SL), the distance from the dorsal-fin origin to the anal-fin origin (28.8%–32.6% of SL), the distance from the dorsal-fin origin to the pelvic-fin insertion (23.8%–28.0% of SL), the distance from the dorsal-fin origin to the pectoral-fin insertion (29.4%–33.0% of SL), the caudal peduncle depth (9.9%–11.4% of SL), the bony orbital diameter (33.2%–39.0% of SL), the interorbital width (27.4%–30.1% of SL), the close approach or contact between the ventral margin of the third infraorbital and the horizontal limb of the preopercle, the presence of a distinct, but narrow, dark midlateral stripe on the posterior two-thirds of the body, the lack of a distinct spot of dark pigmentation at the base of the middle caudal-fin rays, the rotund, but vertically elongate humeral markwithout a secondary, dorsal patch of pigmentation, the absence of a distinct patch of pigmentation on the dorsal fin, and the lack of a series of dark spots along the midlateral surface of the body distinguishes *Creagrutus provenzanoi* within the clade formed by *Creagrutus* and *Piabina.*

TABLE 50.—Morphometrics and meristics of *Creagrutus provenzanoi,* new species: (A) holotype of *C. provenzanoi,* MBUCV V-14392, and (B) paratypes of *C. provenzanoi* (n=29). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	44.2	40.9–57.6
1. Snout to anal-fin origin	62.0	60.3–65.7
2. Snout to pelvic-fin insertion	46.3	46.1–48.7
3. Snout to pectoral-fin insertion	25.1	24.4–27.3
4. Snout to dorsal-fin origin	46.4	45.3–48.9
5. Dorsal-fin origin to hypural joint	56.7	55.3–59.0
6. Dorsal-fin origin to anal-fin origin	31.0	28.8–32.6
7. Dorsal-fin origin to pelvic-fin insertion	25.8	23.8–28.0
8. Dorsal-fin origin to pectoral-fin insertion	29.4	29.4–33.0
9. Caudal peduncle depth	11.2	9.9–11.4
10. Pectoral-fin length	20.5	18.7–21.6
11. Pelvic-fin length	16.7	14.6–17.2
12. Dorsal-fin length	23.1	19.3–23.3
13. Anal-fin length	18.4	16.2–18.6
14. Head length	27.3	24.9–28.2
15. Postorbital head length	40.7	40.4–45.3
16. Snout length	29.8	27.4–30.9
17. Bony orbital diameter	38.2	33.2–39.0
18. Interorbital width	29.0	27.4–30.1
	Meristics	
Lateral line scales	39	38–42
Scale rows between dorsal-fin origin and lateral line	5	4–5[1]
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	9	9–11
Branched dorsal-fin rays	8	8
Branched anal-fin rays	11	11–12
Branched pelvic-fin rays	6	6–7[2]
Pectoral-fin rays	13	12–14
Vertebrae	37	37–39[3]

[1]Four scale rows between dorsal-fin origin and lateral line present in only 3 of 39 paratypes.

[2]Seven branched pelvic-fin rays present in only 3 of 39 paratypes.

[3]Thirty-nine vertebrae present in only 1 of 39 paratype.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus provenzanoi* in Table 50. Head and body moderately robust, more so in anterior portion of body in larger specimens. Greatest body depth at, to slightly anterior of, dorsal-fin origin. Dorsal profile of head distinctly convex from margin of upper lip to vertical through posterior nostril, slightly convex from that point to tip of supraoccipital spine; convexity in this region less pronounced in larger individuals. Interorbital region transversely rounded. Dorsal profile of body slightly convex from tip of supraoccipital spine to dorsal-fin origin, but without any distinct change in alignment relative to dorsal profile of head. Predorsal surface of body with obtuse middorsal ridge, ridge more obvious posteriorly. Ventral profile of head with obtuse angle at anteroventral corner of dentary, angle variably obvious; profile slightly convex from angle to isthmus. Prepelvic profile of body slightly convex in smaller individuals, more convex in certain larger specimens. Prepelvic region of body transversely rounded.

Head obtusely pointed in lateral view, somewhat more compressed in dorsal view. Upper jaw somewhat longer than, and overhanging, lower jaw. Anterior of snout, particularly anteromedial portion, with numerous papillae. Papillae more concentrated on fleshy upper lip, especially along ventral lip margin and on folds and plicae extending between outer and medial premaxillary teeth. Lower lip with numerous papillae along dorsal surface and scattered papillae anteriorly.

Infraorbital series well developed in all specimens larger than 30 mm SL, with ventral margin of third infraorbital falling slightly short of preopercle in smaller specimens, but contacting horizontal limb of preopercle in larger individuals. Posterior margins of third through fifth infraorbitals distinctly separated from vertical limb of preopercle in larger specimens; gap decreasing proportionally ontogenetically, but still distinct in larger specimens.

Premaxillary dentition in three series: primary series sigmoid, with 6, occasionally 5, tricuspidate teeth, without pronounced gap between first and second teeth in series, but with medial tooth separated from matching tooth of contralateral series by distinct gap; triangular cluster of 3 teeth, all larger than those of primary series; and single tooth of form similar to that of primary series occurring lateral to fourth tooth or in region slightly anterolateral to area of contact of third and fourth teeth of primary premaxillary row. Maxilla with 3 or 4 tricuspidate teeth, 3 teeth typically present in smaller individuals. Dentary with 6, less commonly 7, tricuspidate teeth, with cusps barely apparent on seventh tooth, when present; second tooth more massive than, and about one-fourth longer than, first tooth; about 1.5 times as high as third tooth; third tooth twice as high as fourth tooth; fourth through sixth or seventh teeth gradually becoming smaller.

Dorsal-fin rays ii,8 in all specimens. Dorsal-fin origin approximately at vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin slightly concave. Anal-fin rays iii,10–11 or ii,10. Profile of distal margin of anal fin concave. Mature males with hooks on distal margins of first 3 to 5 branched anal-fin rays, and occasionally on last unbranched ray; number of hooks decreasing posteriorly and becoming progressively limited to increasingly more distal portions of fin ray. Pectoral-fin rays i,11–13, typically i,11. Tip of pectoral fin falling 1 or 2 scales short of pelvic-fin insertion. Pelvic-fin rays i,6,i, or i,7, with i,7 limited to some larger specimens. Tip of pelvic fin falling 1 or 2 scales short of anal-fin origin. Mature males with hooks on all branched pelvic-fin rays, including medial ray when branched and sometimes on medial ray when it is unbranched; if hooks present on medial ray, then hooks usually less dense than those on branched rays.

Gill rakers 7–8 (typically 8) + 12–13.

COLORATION IN ALCOHOL.—Ground coloration tan. Dorsal surface of head in smallest specimens with dense dark pigmentation on membranes overlying brain and scattered, dark chromatophores on snout. Specimens greater than 30 mm SL with entire dorsal surface of head covered with dense field of small, dark chromatophores extending anterior to margin of upper lip and posterior to anterior margin of orbit. Density of field somewhat less on upper lip in some individuals. Region anterior of nostrils with pigmentation somewhat more intense, forming distinct crescent-shaped patch present in smaller specimens, but pigmentation patch not obvious and subsumed into darker overall pigmentation in that region in medium-sized to larger individuals. Smaller individuals with narrow band of dark pigmentation extending from anteroventral of nostrils to under orbit; band subsumed into overall darker pigmentation in that region in larger specimens. Region posterior to orbit and on dorsal portion of opercle with scattered, relatively large, dark chromatophores in smaller specimens, chromatophore field expanding further ventrally and becoming somewhat more dense, especially along posterior margin of orbit, in larger individuals.

Scales of dorsolateral surface of body with series of dark chromatophores along posterior margin in smaller individuals; chromatophore field becoming progressively wider in larger specimens but with basal portions of scales lacking chromatophores and forming regular pattern of lighter colored reticulation against darker background. Humeral mark very obvious and vertically elongate in specimens of all sizes. Mark comma-shaped and limited to lateral portion of body in smaller individuals; smaller specimens with main body of mark darkest and centered midlaterally, with anterior arching patch of more diffuse dark chromatophores extending dorsally from intensely pigmented region. Main portion of mark becoming more intensely pigmented and vertically elongate with increasing body size. Mark in larger individuals extending ventrally by more diffuse, usually ventrally tapering patch of chromatophores, continuing in largest specimens to about 1 scale dorsal of horizontal through pectoral-fin insertion. Humeral mark in larger specimens extending dorsally from main midlateral portion to dorsal midline as less densely pigmented anterodorsally angled patch. Contralateral humeral marks in largest specimens meeting middorsally and forming horizontally elongate dark stripe that extends about 3 scales along predorsal region; middorsal mark extending about 1 scale posteriorly from main body of humeral mark. Middorsal scales posterior to humeral mark with patches of dark pigmentation in larger specimens. Midlateral body stripe limited to posterior two-thirds of body, distinctly more intense posteriorly. Stripe distinct anteriorly in smaller specimens but merging anteriorly into overall dark pigmentation on lateral surface of the body in larger individuals.

Dorsal fin with first unbranched, and distal portions of second unbranched rays, covered with dark stellate chromatophores. Membranes of all but posterior 1 or 2 branched dorsal-fin rays with dispersed dark, irregularly shaped, chromatophores. Chromatophore field becoming progressive shorter on distal portions of successive fin membranes. Distal portion of second and third unbranched and first, and sometimes second, branched anal-fin rays unpigmented; otherwise fin rays outlined by small dark chromatophores, with scattered, dark chromatophores on intervening portions of fin membranes. Middle

FIGURE 84.—*Creagrutus provenzanoi,* new species, holotype, MBUCV V-14392, 44.2 mm SL; Venezuela, Amazonas, Río Cataniapo, small caño above Saramä Sota.

rays of caudal fin more intensely pigmented than rest of fin, with remaining fin rays outlined to varying degrees by small dark chromatophores. Pectoral and pelvic fins hyaline, or with some scattered, small, dark chromatophores in larger specimens.

ETYMOLOGY.—The specific name, *provenzanoi,* is in honor of our colleague, Francisco Provenzano, Universidad Central de Venezuela, for his contributions to our understanding of Venezuelan fishes, and for his assistance to the authors over many years.

ECOLOGY.—Some paratypes of *Creagrutus provenzanoi* (USNM 270229) were collected along the margin of the Río Cataniapo over sand and rocks in moderately to swiftly flowing, slightly turbid water. One paratype (ANSP 165530) was captured in a moderate to swift current over submerged vegetation. One specimen of *C. provenzanoi* (MBUCV V-29074) was captured with the type series of *C. veruina.*

DISTRIBUTION.—*Creagrutus provenzanoi* is only known from the Río Cataniapo, a right bank tributary of the Río Orinoco in Amazonas, Venezuela (Figure 83, square).

COMPARISONS.—*Creagrutus provenzanoi* is very similar to *C. ephippiatus* of the Río Siapa, a tributary of the Río Casiquiare, in the upper Río Negro basin. The two species can be distinguished on the basis of the more arcuate dorsal portion of the humeral mark, which extends further dorsally in *C. ephippiatus* compared to the mark in *C. provenzanoi,* the numbers of rows of scales above the lateral line (5, rarely 4, in *C. provenzanoi* versus 4, rarely 5, in *C. ephippiatus*), and less discretely in the relative distance from the snout to the pectoral-fin insertion (24.4%–27.3% of SL versus 22.8%–24.7% of SL, respectively).

Within the Río Orinoco basin, *C. provenzanoi* is most similar to *C. magoi,* a species that occurs in right bank tributaries to the Río Orinoco downstream of the range of *C. provenzanoi.* The two species can be readily distinguished by differences in the number of gill rakers on the upper limb of the first gill arch (7 or 8 in *C. provenzanoi* versus 9 to 11, rarely 9, in *C. magoi*) and in the number of scales above the lateral line to the dorsal-fin origin (5, very rarely 4, in *C. provenzanoi* versus 4, rarely 5, in *C. magoi*). The two species also differ in the relative width of the interorbital region (27.4%–30.1% of HL in *C. provenzanoi* versus 30.4%–34.3% of HL in *C. magoi*). The only other species of *Creagrutus* known from the Río Cataniapo basin is *C. veruina. Creagrutus provenzanoi* can be distinguished from *C. veruina* by the form of the humeral mark (expanded and rounded immediately above the lateral line in *C. provenzanoi* versus bar-like in *C. veruina*), the number of scales below the lateral line to the anal-fin origin (3 versus 2, respectively), and by various proportional morphometric features (compare Tables 50 and 56).

MATERIAL EXAMINED.—119 specimens (29, 40.9–57.6).

HOLOTYPE.—VENEZUELA. *Amazonas:* Upper Río Cataniapo basin, small caño above Saramä Sota, R. Royero et al., 18 Aug 1984, MBUCV V-14392, 1 (44.2).

PARATYPES.—29 specimens (29, 40.9–57.6).

VENEZUELA. *Amazonas:* Upper Río Cataniapo basin, small caño above Saramä Sota, collected with holotype, MBUCV V-29070, 5 (40.9–51.7); USNM 355117, 2 (45.0–53.4). Departamento Ature, Río Cataniapo where crossed by road from Puerto Ayacucho to Samariapo, R.P. Vari et al., 2 Dec 1984, USNM 207229, 3 (46.0–57.6). Río Cataniapo, approximately 30 km S of Puerto Ayacucho, F. Provenzano, 10 Nov 1989, MBUCV V-21657, 1 (49.9). Upper Río Cataniapo, caño approximately 2 km before Salto Nieve, MBUCV V-29071, 12 (42.4–52.1); USNM 355119, 5 (42.0–49.9; 2 specimens cleared and counterstained). Río Cataniapo, approximately 3.0 km S of Puerto Ayacucho (5°35′N, 67°35′W), S. Schaefer et al., 10 Nov 1989, ANSP 165530, 1 (50.2).

NONTYPE SPECIMENS.—89 specimens.

VENEZUELA. *Amazonas:* Río Cataniapo basin, Caño

Blanco, approximately 3 km by river above San Pedro, MBUCV V-14527, 16. Río Cataniapo, Saramä Sato, MBUCV V-14421, 38. Upper Río Cataniapo, caño approximately 2 km before Salto Nieve, MBUCV V-14547, 10. Río Cataniapo, Salto Nieve, MBUCV V-14450, 24. Río Cataniapo, 200 m above Las Pavas, MBUCV V-29074, 1.

Creagrutus runa, new species

FIGURES 83, 85, TABLE 51

Creagrutus cf. *caucanus*.—Goulding et al., 1988:156, 160 [Brazil, Amazonas, Rio Negro; diet].

DIAGNOSIS.—The possession of premaxillary dentition with the three components generalized for the species of *Creagrutus* and *Piabina*, but with a distinct gap between the first and second teeth of primary tooth row and a forward position of the triangular cluster of three posteromedial teeth distinguishes *C. runa* from all members of the clade formed by *Creagrutus* and *Piabina* with the exception of *Creagrutus maracaiboensis, C. melanzonus, C. muelleri, C. nigrostigmatus, C. ouranonastes, C. peruanus*, and *Piabina argentea*. *Creagrutus runa* can be distinguished from these seven species by the combination of the possession of 4 teeth in primary series on the premaxilla, 4 to 6 maxillary teeth, 6 to 8 dentary teeth, 8 or 9 predorsal median scales, 39 or 40 lateral line scales without a lamellar process over each pore, 4 scale rows between the dorsal-fin origin and the lateral line, 9 or 10 branched anal-fin rays, 37 to 39 vertebrae, 5 to 7 gill rakers on the upper limb of the first gill arch, 9 to12 gill rakers on the lower limb of the first gill arch, the distance from the snout to the anal-fin origin (63.6%–68.8% of SL), the distance from the snout to the pectoral-fin insertion (24.3%–27.2% of SL), the distance from the dorsal-fin origin to the pelvic-fin insertion (18.7%–24.5% of SL), the caudal peduncle depth (8.8%–10.5% of SL), the postorbital head length (36.4%–45.3% of HL), the bony orbital diameter (31.8%–41.8% of HL), the near approach of the ventral margin of the third infraorbital to the horizontal limb of the preopercle, the lack of a distinct spot of dark pigmentation at the base of the middle caudal-fin rays, the vertically elongate humeral mark without a secondary, dorsal patch of pigmentation, the absence of a distinct patch of pigmentation on the dorsal fin, and the lack of a series of dark spots along the midlateral surface of the body.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus runa* in Table 51. Head and body elongate. Body fusiform to slightly compressed. Greatest body depth slightly anterior of base of anteriormost dorsal-fin ray. Dorsal profile of head distinctly convex from margin of upper lip to vertical through posterior margin of posterior nares, straight from that point to tip of supraoccipital spine in specimens up to about 45 mm SL. Larger individuals with dorsal profile of head straight as far as posterior tip of supraoccipital spine and slightly convex from that point to tip of supraoccipital spine. Predorsal profile of body straight in specimens up to approximately 45 mm SL, slightly convex in larger individuals. Dorsal profile of body straight from dorsal-fin origin to anterior procurrent caudal-fin ray, with slight dorsal inflection at adipose-fin base. Ventral profile of head with broadly rounded angle approximately midway between margin of lower lip and posterior extremity of dentary, profile slightly convex from angle to isthmus. Ventral profile of body slightly convex to pelvic-fin insertion, straight along anal-fin base, and with slight concavity between base of posteriormost anal-fin ray and anterior ventral procurrent caudal-fin ray.

Anterior profile of head forming broadly rounded obtuse angle of about 120 degrees, with apex of angle located on horizontal plane through ventral portion of orbit; angle of lower jaw not highly accentuated. Upper jaw slightly longer than, and overhanging, lower jaw. Anterior portion of snout relatively soft and fleshy, with concentration of soft tissues; minute papillae concentrated on snout and upper lip, continuing into mouth on fleshy flaps between outer and medial premaxillary teeth.

TABLE 51.—Morphometrics and meristics of *Creagrutus runa*, new species: (A) holotype of *C. runa*, new species, MZUSP 29888; and (B) paratypes of *C. runa* (n=21). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	40.9	31.8–46.2
1. Snout to anal-fin origin	63.6	64.4–68.8
2. Snout to pelvic-fin insertion	46.1	45.3–50.0
3. Snout to pectoral-fin insertion	24.3	26.8–27.2
4. Snout to dorsal-fin origin	46.3	44.7–50.0
5. Dorsal-fin origin to hypural joint	56.3	53.5–58.2
6. Dorsal-fin origin to anal-fin origin	27.5	27.0–31.0
7. Dorsal-fin origin to pelvic-fin insertion	18.7	20.0–24.5
8. Dorsal-fin origin to pectoral-fin insertion	27.9	28.7–32.9
9. Caudal peduncle depth	8.8	9.1–10.5
10. Pectoral-fin length	17.5	16.1–19.1
11. Pelvic-fin length	14.8	12.9–15.4
12. Dorsal-fin length	19.6	18.1–21.6
13. Anal-fin length	15.9	14.1–16.2
14. Head length	24.4	24.2–27.5
15. Postorbital head length	39.8	36.4–45.3
16. Snout length	26.0	27.1–32.1
17. Bony orbital diameter	39.2	31.8–41.8
18. Interorbital width	30.1	25.7–30.2
	Meristics	
Lateral line scales	41	39–40
Scale rows between dorsal-fin origin and lateral line	4	4
Scale rows between anal-fin origin and lateral line	3	2–3[1]
Predorsal median scales	8	8–9
Branched dorsal-fin rays	8	8
Branched anal-fin rays	9	9–10
Branched pelvic-fin rays	7	7
Pectoral-fin rays	11	11–13[2]
Vertebrae	37	37–39

[1]Three scale rows between anal-fin origin and lateral line present in 3 of 17 paratypes from which count could be taken.

[2]One nontype specimen with 10 pectoral-fin rays present on one side of body and 11 rays on other side.

FIGURE 85.—*Creagrutus runa*, new species, holotype, MZUSP 29888, 40.9 mm SL; Brazil, Amazonas, Rio Negro, Paraná do Jacaré.

Lower jaw distinctly fleshy anteriorly, with concentrated papillae. Inner surfaces of lower lip convoluted and papillose, with fleshy flaps extending into mouth.

Elements of infraorbital series moderately well developed, with ventral margin of third infraorbital separated from ventral limb of preopercle by narrow gap. Posterior margins of third through fifth infraorbitals separated from vertical limb of preopercle by narrow gap; width of gap equal to, at most, about one-fourth of width of fourth infraorbital, gap practically absent in some specimens. Posterior and ventral margins of third infraorbital usually forming broadly rounded obtuse angle; fourth infraorbital nearly rectangular.

Premaxillary teeth in three distinct groups: primary series consisting of 4 unicuspidate to tricuspidate teeth, 2 anteriormost teeth unicuspidate and separated by distinct gap approximately width of one tooth; medial, triangular cluster of 3 large tricuspidate teeth with anterior tooth partially positioned in pronounced gap between first and second teeth of primary series, posterior 2 teeth largest and with most highly developed cusps; and single outer unicuspidate tooth positioned approximately lateral to second tooth in primary series. Maxilla with 4 to 6 tricuspidate teeth. Dentary with 6 to 8 typically tricuspidate teeth; second tooth slightly higher, but distinctly wider than first tooth and much larger than third tooth, remaining teeth in series distinctly smaller than anterior three teeth; third through sixth teeth slightly recurved.

Dorsal-fin rays ii,8 in all specimens. Dorsal-fin origin located anterior to vertical through pelvic-fin origin; base of second or third ray usually located at vertical through pelvic-fin insertion. Distal margin of dorsal fin slightly concave as consequence of relative elongation of second unbranched, anterior 2 or 3 branched rays, and posterior 2 branched rays. Anal-fin rays ii–iii,9–10. Mature males with 1 or 2 hooks, when present, on segments of first branched anal-fin ray. Distal margin of anal fin slightly sigmoidal, with second unbranched and first through third branched rays forming slightly elongate lobe, outline of posterior 5 or 6 rays concave. Pectoral-fin rays i, 10–12. Pectoral fin short; tip reaching to within 2 to 4 scale rows of pelvic-fin origin. Pelvic-fin rays i,7,i or i,7. Mature males with pelvic-fin hooks, when present, on medial surfaces of segmented and unsegmented portions of main shaft and medial secondary branches of all rays medial of lateral unbranched element. Tip of pelvic fin falling 2 or 3 scales short of anal-fin origin. Posterior margin of body scales smoothly rounded to slightly undulate. Pelvic axillary process well developed.

Gill rakers 5–7 + 9–12.

COLORATION IN ALCOHOL.—Overall pigmentation very poorly developed; ground color very pale straw to light brown, with dark chromatophores ranging from light to dark brown or sepia on most portions of head and body. Dorsal surface of head with scattered, small, light brown chromatophores; chromatophores most concentrated over snout but mostly absent from upper lip. Dorsal surfaces of frontal and parietal portions of cranium pigmented with small, concentrated, stellate, dark chromatophores over frontal fontanel. Largest, darkest chromatophores associated with supraorbital canal and frontal commissure. Poorly developed crescent-shaped patch of dark chromatophores immediately anterior of anterior nares. Band of scattered, light brown chromatophores extending from immediately lateral of nares posteroventrally and continuing along ventral margin of orbit no further than under middle of eye. Region posterior to orbit and dorsal portion of opercle with scattered, small to large chromatophores; chromatophores numerous in some specimens. Lower lip and ventrolateral surface of head unpigmented.

Body pigmentation diffuse, most concentrated dorsal of lateral line. Two dorsalmost rows of scales with vertical bands of very small chromatophores on anteriormost exposed portion of each scale and series of more scattered chromatophores on posterior field of each scale. Middorsal region without any notable concentration of dark chromatophores. Humeral mark usually in form of anteriorly concave, slightly crescent-shaped vertical bar. Pigmentation in bar most concentrated on first scale row immediately dorsal of lateral line. Bar gradually fading dorsally and terminating within about 1 scale row of midline. Lateral surface of body mostly unpigmented ventral to lateral line, other than for chromatophores associated with humeral bar.

Some specimens with scattered chromatophores immediately dorsal of anal-fin base and along midventral region between pelvic and anal fins. Larger specimens, more than 50 mm SL, with diffuse midlateral stripe consisting of dispersed, small, dark chromatophores along first and second scale rows dorsal of lateral line. Stripe becoming denser and somewhat wider posteriorly, extending well ventral of lateral line on caudal peduncle.

Dorsal-fin membranes with small number of moderately dark chromatophores associated with distal one-fourth of second unbranched and first 2 or 3 branched rays; basal portions of shafts of all, or nearly all, rays with scattered, dark chromatophores. Anal fin mostly unpigmented other than for dark chromatophores located at base of all rays immediately adjacent to point of insertion. Caudal fin with outer 2 or 3 branched and first unbranched fin rays delineated by brown pigment, with darkest pigmentation confined to basal portions of central 4 branched rays; pigmentation appearing as faint spot under magnification, especially in specimens smaller than approximately 45 mm SL. Pelvic and pectoral fins hyaline.

ECOLOGY.—Goulding et al. (1988:156, 160) reported that *Creagrutus runa* (identified therein as *Creagrutus* cf. *caucanus*) fed on terrestrial insects and terrestrial seeds. Nontype specimens from the upper reaches of the Río Negro in Venezuela (USNM 270228) were collected in black water along the margin of the main river channel along a sand bar over a sandy and rocky bottom.

COMPARISONS.—*Creagrutus runa* is most similar to *C. veruina,* an endemic of Río Cataniapo, a tributary of the Río Orinoco, which shares similar dentition and overall body form. The two species can be distinguished by differences in the number of branched anal-fin rays (9 or 10 in *C. runa* versus 11 in *C. veruina*), differences in the form of the humeral mark (compare Figures 85 and 91), and relative distance from the snout to the anal-fin origin and the snout to the pectoral-fin insertion (see Tables 51 and 56).

ETYMOLOGY.—The species name, *runa,* from the Latin for javelin or spear, refers to the elongate body form of the species.

DISTRIBUTION.—*Creagrutus runa* is limited to the upper portions of the Rio Negro basin in northern Brazil and southern Venezuela (Figure 83, diamonds).

REMARKS.—Goulding et al. (1988:156, 160) cited *Creagrutus* cf. *caucanus* from the upper Rio Negro. Examination of a portion of that material (MZUSP 29888 and MZUSP 55473 removed from it) has proved it to be *C. runa.*

MATERIAL EXAMINED.—57 specimens (26, 31.8–62.7).

HOLOTYPE.—BRAZIL. *Amazonas:* Rio Negro, Paraná do Jacaré (approximately 0°30′S, 66°30′W), collected by M. Goulding, 7 Oct 1979, MZUSP 29888, 1 (40.9).

PARATYPES.—37 specimens (21, 31.8–46.2).

BRAZIL. *Amazonas:* Rio Negro, Paraná do Jacaré, collected with holotype, MZUSP 55473, 30 (14, 31.8–39.1); USNM 359622, 5 (32.3–45.2). Rio Negro basin, Rio Daraá, Cachoeira do Aracu (approximately 0°30′S, 64°40′W), USNM 270228, 2 (40.4–46.2).

NONTYPE SPECIMENS.—19 specimens (4, 52.5–62.7).

VENEZUELA. *Amazonas:* Departamento Río Negro, Río Negro, approximately one-half hour upriver of San Carlos de Río Negro (01°58′N, 67°04′W), USNM 270228, 2. Río Guainia, at beach in Maroa (2°43′N, 67°33′W), MCNG 23311, 4 (52.5–62.7; 1 specimen cleared and counterstained for cartilage and bone).

BRAZIL. Amazonas: Rio Negro, Cachoeira de São Gabriel (4°19′N, 72°04′W), MZUSP 29890, 13.

Creagrutus saxatilis, new species

FIGURES 83, 86, TABLE 52

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 2 or 3 teeth on the maxilla, 6, rarely 5, teeth in the primary tooth row of the premaxilla, 5 dentary teeth, 37 to 39 lateral line scales without a lamellar process over each pore, 9 to 11 predorsal median scales, 4 scale rows between the dorsal-fin origin and the lateral line, 3 scale rows between the anal-fin origin and the lateral line, 2 post-anal median scales to the anal-fin origin, 36 to 38 vertebrae, 11 or 12 branched anal-fin rays, 8 to 10 gill rakers on the upper limb of the first gill arch, 11 to 13 gill rakers on the lower limb of the first gill arch, the distance from the snout to the anal-fin origin (60.2%–65.8% of SL), the distance from the dorsal-fin origin to the anal-fin origin (28.3%–34.9% of SL), the distance from the dorsal-fin origin to the pelvic-fin insertion (25.3%–30.6% of SL), the caudal peduncle depth (11.3%–12.2% of SL), the anal-fin length (14.9%–18.1% of SL), the dorsal-fin length (18.5%–22.7% of SL), the snout length (26.6%–31.7% of HL), the interorbital width (31.6%–36.4% of HL), the moderately developed third infraorbital with its anteroventral portion contacting the horizontal limb of the preopercle, the lack of a series of dark midlateral spots on the body, the vertically elongate humeral mark, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus saxatilis* within the clade composed of *Creagrutus* and *Piabina.*

DESCRIPTION.—Morphometric and meristic data for *Creagrutus saxatilis* in Table 52. Head and anterior portion of body moderately robust in smaller specimens, distinctly robust in largest specimens examined. Greatest body depth at vertical through pelvic-fin insertion in smaller specimens, at that point or shifted slightly anteriorly in larger individuals. Dorsal profile of head distinctly convex from margin of upper lip to vertical through posterior nostril, straight to slightly convex from that point to tip of supraoccipital spine. Interorbital region distinctly convex transversely. Dorsal profile of body gently convex from tip of supraoccipital spine to dorsal-fin origin, with slight change in alignment relative to profile of head in larger specimens. Predorsal surface of body somewhat flattened transversely anteriorly in larger specimens, with middorsal

TABLE 52.—Morphometrics and meristics of *Creagrutus saxatilis*, new species: (A) holotype of *C. saxatilis*, MNRJ 14544; and (B) paratypes of *C. saxatilis* (n=17). Standard length is expressed in mm; measurements 1 to 14= percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	80.5	38.1–62.3
1. Snout to anal-fin origin	65.7	60.2–65.8
2. Snout to pelvic-fin insertion	48.1	43.1–49.0
3. Snout to pectoral-fin insertion	25.0	22.9–26.6
4. Snout to dorsal-fin origin	47.0	44.4–49.0
5. Dorsal-fin origin to hypural joint	59.5	54.2–59.0
6. Dorsal-fin origin to anal-fin origin	34.9	28.8–34.5
7. Dorsal-fin origin to pelvic-fin insertion	30.3	25.3–30.6
8. Dorsal-fin origin to pectoral-fin insertion	34.5	29.8–35.4
9. Caudal peduncle depth	11.8	11.3–12.2
10. Pectoral-fin length	20.1	15.4–22.0
11. Pelvic-fin length	15.7	14.1–17.4
12. Dorsal-fin length	19.4	18.5–22.7
13. Anal-fin length	16.4	14.9–18.1
14. Head length	26.1	24.7–26.9
15. Postorbital head length	46.7	41.6–47.7
16. Snout length	30.5	26.6–31.7
17. Bony orbital diameter	32.4	31.6–36.0
18. Interorbital width	34.2	31.6–36.4
	Meristics	
Lateral line scales	39	37–39
Scale rows between dorsal-fin origin and lateral line	4	4
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	10	9–11
Branched dorsal-fin rays	8	8
Branched anal-fin rays	11	11–12
Branched pelvic-fin rays	6	6–7
Pectoral-fin rays	12	11–13
Vertebrae	37	36–38

ridge proximate to dorsal-fin insertion. Ventral profile of head with distinct obtuse angle at anteroventral cornerof dentary, nearly straight from that point to isthmus in smaller specimens, gently convex in that region in larger individuals. Prepelvic region of body nearly straight in smaller specimens of both sexes, becoming increasingly convex in larger individuals. Prepelvic region obtusely flattened transversely in smaller specimens, distinctly rounded transversely in larger females.

Head obtusely pointed in lateral view, more compressed in dorsal view. Upper jaw longer than, and overhanging, lower jaw. Snout slightly fleshy anteromedially and above upper lip, fleshiness less apparent in larger specimens, which have scattered papillae anteromedially and along lateral surface of lip. Papillae more concentrated on ventral margin of lip and on folds and plicae extending between outer and medial premaxillary teeth. Lower lip moderately fleshy, less so in largest specimens, with papillae mostly limited to dorsal margin.

Infraorbital series moderately developed. Anterior portion of ventral margin of third infraorbital barely approaching horizontal limb of preopercle in smaller specimens, in contact with preopercle along approximately one-third of its horizontal length in largest individuals examined. Posterior margins of third through fifth infraorbitals falling distinctly short of vertical limb of preopercle posteriorly. Gap between posterior margins of infraorbitals and vertical limb of preopercle narrowing dorsally.

Premaxillary dentition in three series: primary row curved, typically with 6 teeth, few specimens with only 5 teeth, without pronounced gap between first and second tooth of series but with medial tooth separated from anterior tooth of contralateral series; triangular cluster of 3 larger teeth; and single tooth of form similar to that of primary series occurring slightly anterolateral of fourth tooth of main premaxillary tooth row. Maxilla with 2 or 3 tricuspidate teeth. Dentary with 5 tricuspidate teeth, cusps on last tooth barely apparent; first and second teeth distinctly larger than other teeth in series, second tooth slightly larger than first tooth and approximately twice height of third tooth; fourth and fifth teeth graded in size, distinctly smaller than third tooth and compressed.

Dorsal-fin rays ii,8 in all specimens. Dorsal-fin origin at vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin slightly concave. Anal-fin rays ii,11–12. Profile of distal margin of anal fin concave in all specimens, more so in largest examined individuals. Mature males with hooks present on first and second branched anal-fin rays. Pectoral-fin rays i,10–12. Tip of pectoral fin extending posteriorly approximately to 1 or 2 scales from pelvic-fin insertion. Pelvic-fin rays i,6,i in most specimens, i,7 in two largest, apparently female, individuals. Tip of pelvic fin extending posteriorly to anus or to region between anus and anal-fin origin. Mature males with hooks on all branched pelvic-fin rays.

Gill rakers 8–10 + 13–14.

COLORATION IN ALCOHOL.—Overall coloration yellow to tan. Dorsal surface of head with numerous chromatophores, particularly overlying fontanelles and adjoining regions. Series of deep-lying, dark chromatophores on membranes overlying brain, with notable variation in concentration between comparable-sized specimens collected at same time. Deep-lying chromatophores overlying brain masked by bones of skull and intracranial adipose deposits in larger individuals. Chromatophore field more concentrated on snout and anteromedial portions of upper lip. Region anterior to nostrils with dark chromatophores somewhat more concentrated than in relatively dark proximate regions, but resultant crescent-shaped field not as apparent as in some congeners. Region ventral of nostrils and anteroventral to orbit with broad streak of dark chromatophores that terminate ventral of eye. Band of chromatophores ventral and posterior to orbit often present in many congeners absent. Dorsal portions of infraorbitals and opercle with scattered, dark chromatophores.

Scales of dorsolateral portion of body with relatively large, dark chromatophores arranged in irregular pattern along posterior scale margin and more concentrated on basal portion of exposed portion of scale. Chromatophore fields most concentrated and nearly continuous middorsally. Overall form of humeral mark variable, but vertically elongate overall, often with dorsal portion anteriorly inclined. Intensity of pigmentation typically greatest in lower two-thirds of humeral mark,

FIGURE 86.—*Creagrutus saxatilis,* new species, holotype, MNRJ 14544, 80.5 mm SL; Brazil, Goiás, Niquelândia, Rio Indaial, left bank tributary of Rio Maranhão, upper Rio Tocantins basin (14°12′S, 48°37′W).

with overall relative intensity more pronounced in smaller examined specimens. Diffuse midlateral body stripe formed by small, dark, surface chromatophores. Stripe more distinct in smaller specimens and extending posteriorly from humeral mark to rear of caudal peduncle. Stripe blending into background coloration in larger individuals and not, or barely, apparent in region anterior to vertical through dorsal-fin origin. Stripe vertically expanded posteriorly in some specimens.

Dorsal fin with scattered, dark chromatophores along distal two-thirds of anterior fin membranes. Anal fin with basal one-half to two-thirds of rays outlined by narrow lines of dark pigmentation. Caudal-fin rays irregularly outlined by dark chromatophores. Concentration of chromatophores over basal portion of middle caudal-fin rays forming diffuse spot in smaller specimens, spot continuous anteriorly with midlateral stripe on body. Caudal spot not obvious in all larger individuals examined. Pectoral and pelvic fins hyaline or with scattered, dark chromatophores on rays and membranes.

ETYMOLOGY.—The species name, *saxatilis,* from the Latin for among rocks, refer to the rocky substrate of the type locality of this species.

ECOLOGY.—The collecting locality for a portion of the paratype series (USNM 341480) is an upland river, approximately 30 m wide with a fast to moderate flow of moderately turbid water over a rocky and sandy bottom. *Creagrutus saxatilis* was collected sympatrically with *C. menezesi* at one locality in pools within the exposed riverbed below the dam of the Serra da Mesa Reservoir during the filling of the lake.

Stomach contents of the one specimen prepared for clearing and staining in this study consisted exclusively of chopped-up seeds.

DISTRIBUTION.—*Creagrutus saxatilis* is known only from the upper portions of the Rio Tocantins system in Goiás and Distrito Federal, Brazil (Figure 83, dots).

MATERIAL EXAMINED.—31 specimens (23, 38.1–81.7).

HOLOTYPE.—BRAZIL. *Goiás:* Niquelândia, Rio Indaial, left bank tributary of Rio Maranhão, upper Rio Tocantins basin (14°12′S, 48°37′W), collected by G.W. Nunan and D.F. Moraes, Jr., 9 Oct 1985, MNRJ 14544, 1 (80.5).

PARATYPES.—17 specimens (17, 38.1–62.3).

BRAZIL. *Distrito Federal:* Rio Maranhão, upper Rio Tocantins basin, approximately 35 air km N of Brasilia (approximately 15°32′S, 47°49′W), collected by W.C. Starnes et al., 14 Nov 1984, USNM 341480, 6 (39.9–48.4; one specimen cleared and counterstained for cartilage and bone). *Goiás:* Uruaçu, Córrego Novo, left bank tributary of Rio Palmeira, left bank tributary of Rio Maranhão, upper Rio Tocantins basin (14°30′S, 48°47′30″W), collected by G.W. Nunan and D.F. Moraes, Jr., 17 Oct 1985, MNRJ 12590, 3 (38.1–41.3). Niquelandia, Rio Indaial, left bank tributary of Rio Maranhão, upper Rio Tocantins basin (14°12′S, 48°37′W), collected with holotype, MNRJ 12641, 3 (60.1–62.3). Niquelândia, Arroio Arara, approximately 500 m from mouth of Rio Maranhão, in Rosariana (14°01′S, 48°25′W), MCP 15977, 2 (39.9–58.6). Minaçu-Colinas do Sul, Rio Tocantins, in pools formed by left bank riacho during filling of Serra da Mesa Reservoir (approximately 13°50′S, 48°19′W), collected by D.F. Moraes et al., 28 Oct to 3 Nov 1996, MNRJ 17335, 3 (39.3–46.1).

NONTYPE SPECIMENS.—13 specimens (5, 60.8–81.7).

BRAZIL. *Goiás:* Rio Maranhão into Rio Tocantins, CAS 69254, 5 (60.8–81.7). Minaçu-Colinas do Sul, Rio Tocantins, in pools formed by left bank riacho during filling of Serra da Mesa Reservoir (approximately 13°50′S, 48°19′W), MNRJ 17336, 4; USNM 350450, 4.

Creagrutus seductus, new species

FIGURES 83, 87, TABLE 53

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized

TABLE 53.—Morphometrics and meristics of *Creagrutus seductus*, new species: (A) holotype of *C. seductus*, MZUSP 51026; and (B) paratypes of *C. seductus* (n=26). Standard length is expressed in mm; measurements 1 to 14= percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	63.6	32.5–70.3
1. Snout to anal-fin origin	63.2	59.7–65.9
2. Snout to pelvic-fin insertion	48.0	45.4–48.5
3. Snout to pectoral-fin insertion	25.1	23.0–26.4
4. Snout to dorsal-fin origin	48.9	46.0–50.4
5. Dorsal-fin origin to hypural joint	54.9	51.6–58.4
6. Dorsal-fin origin to anal-fin origin	29.2	25.5–32.0
7. Dorsal-fin origin to pelvic-fin insertion	25.2	23.1–29.1
8. Dorsal-fin origin to pectoral-fin insertion	32.4	29.6–33.8
9. Caudal peduncle depth	10.8	10.6–11.2
10. Pectoral-fin length	18.1	17.2–20.5
11. Pelvic-fin length	14.5	14.0–15.8
12. Dorsal-fin length	19.8	19.3–23.4
13. Anal-fin length	17.6	16.7–19.1
14. Head length	27.0	24.7–28.0
15. Postorbital head length	44.8	40.0–46.8
16. Snout length	29.7	26.7–32.0
17. Bony orbital diameter	32.6	29.9–35.4
18. Interorbital width	29.1	28.4–31.9
	Meristics	
Lateral line scales	40	39–41
Scale rows between dorsal-fin origin and lateral line	4	4
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	9	9–10
Branched dorsal-fin rays	8	8
Branched anal-fin rays	13	11–13
Branched pelvic-fin rays	7	6–7
Pectoral-fin rays	12	11–13
Vertebrae	38	38–39

for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 2 or 3 teeth on the maxilla, 6, very rarely 7, teeth in the primary tooth row of the premaxilla, 6 dentary teeth, 39 to 41 lateral line scales without a lamellar process over each pore, 9 or 10 predorsal median scales, 4 scale rows between the dorsal-fin origin and the lateral line, 38 or 39 vertebrae, 11 to 13 branched anal-fin rays, 2 post-anal median scales to the anal-fin origin, 7 or 8 gill rakers on the upper limb of the first gill arch, 11 to 13 gill rakers on the lower limb of the first gill arch, the distance from the snout to the dorsal-fin origin (46.0%–50.4% of SL), the distance from the dorsal-fin origin to the anal-fin origin (25.5%–32.0% of SL), the distance from the dorsal-fin origin to the pelvic-fin insertion (23.1%–29.1% of SL), the distance from the dorsal-fin origin to the pectoral-fin insertion (29.6%–33.8% of SL), the caudal peduncle depth (10.6%–11.2% of SL), the head length (24.7%–28.0% of SL), the postorbital head length (40.0%– 46.8% of HL), the snout length (26.7%–32.0% of HL), the bony orbital diameter (29.9%–35.4% of HL), the interorbital width (28.4%–31.9% of HL), the moderately developed third infraorbital contacting the horizontal limb of the preopercle in larger specimens, the lack of a series of dark midlateral spots on the body, the moderately vertically elongate humeral mark with concave anterior and convex posterior borders, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus seductus* within the clade composed of *Creagrutus* and *Piabina*.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus seductus* in Table 53. Head and body relatively elongate in smaller specimens, larger individuals with anterior portion of body relatively deeper and more robust. Greatest body depth typically at dorsal-fin origin; shifted somewhat anterior of that point in ripe females. Dorsal profile of head slightly convex from margin of upper lip to vertical through anterior nostril, straight or very slightly convex from that point to tip of supraoccipital spine. Interorbital region convex. Predorsal profile of body very slightly convex across size range of examined specimens, without change in alignment relative to dorsal profile of head. Predorsal surface of body transversely flattened anteriorly in some specimens, with middorsal ridge proximate to dorsal-fin origin. Ventral profile of head with obtuse angle at anteroventral corner of dentary, straight or very slightly convex from that point to isthmus. Profile of prepelvic region of body nearly straight in smaller specimens, slightly convex in most larger individuals, convexity most pronounced in ripe females.

Head obtusely pointed in lateral view, more pointed in dorsal view. Upper jaw slightly longer than, and overhanging, lower jaw. Snout slightly fleshy anteromedially with few scattered papillae above margin of upper lip. Papillae more concentrated along ventral surface of upper lip and on folds and plicae extending between outer and medial premaxillary teeth. Lower jaw fleshy anteriorly, with scattered papillae along anteroventral margin and numerous papillae along dorsal margin.

Infraorbital series moderately developed. Ventral margin of third infraorbital typically convex, with central portion of ventral margin of infraorbital approaching (smaller specimens) or contacting (larger specimens) horizontal limb of preopercle. Posterior margins of third through fifth infraorbitals falling distinctly short of vertical limb of preopercle.

Premaxillary dentition in three series: primary row slightly sigmoid, typically consisting of 6 teeth (7 teeth present on one side of head in one specimen) without pronounced gap between first and second tooth of series but with medial tooth separated from anterior tooth of contralateral series by distinct gap; triangular cluster of 3 larger teeth; and single tooth of form similar to that of primary series lying lateral to fourth tooth of primary premaxillary series. Maxilla with 2 or 3 weakly tricuspidate teeth. Dentary with 5 or 6 teeth; anterior 4 dentary teeth tricuspidate with fifth and sixth teeth tricuspidate or distally truncate. Second tooth about one-fourth higher and wider than first tooth and more than twice as high and wide as third tooth. Fourth, fifth, and, when present, sixth teeth distinctly smaller than third tooth and becoming progressively shorter posteriorly. Symphyseal teeth distinctly separated.

FIGURE 87.—*Creagrutus seductus*, new species, holotype, MZUSP 51026, 63.6 mm SL; Brazil, Mato Grosso, Município de Barra do Garças, Córrego Fundo (approximately 15°53′S, 52°15′W).

Dorsal-fin rays ii,8 in all specimens. Dorsal-fin origin at, to anterior to, vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin straight, or nearly so, in smaller specimens, slightly convex in larger individuals. Anal-fin rays ii,11–13. Profile of distal margin of anal fin distinctly concave, with last unbranched ray and first and second branched rays forming discrete anterior lobe. Single examined male with hooks on first and second branched anal-fin rays. Pectoral-fin rays i,10–12. Tip of pectoral fin extending posteriorly at least three-fourths of distance to pelvic-fin insertion. Pelvic-fin rays i,6,i in smaller specimens, i,7 in most of larger individuals. Tip of pelvic fin extending posteriorly to anus. Single examined mature male with hooks on all six branched anal-fin rays.

Gill rakers 7–8 + 11–13.

COLORATION IN ALCOHOL.—Overall ground coloration of relatively freshly collected specimens light tan. Dorsal surface of head in smaller specimens with concentrated stellate chromatophores overlying fontanelles and immediately adjoining regions. Field of dark surface chromatophores in larger specimens more extensive, but still most concentrated medially. Membranes overlying brain covered with field of dense dark chromatophores. Chromatophore field on dorsal surface of anterior portion of head, on snout, and on medial portions of upper lip dense at all examined sizes. Region anterior to nostrils with chromatophore field continuous with, and sometimes slightly more intense than, that on snout; chromatophores forming crescent-shaped patch in individuals with more concentrated pigmentation in that region. Region ventral of nostrils and anteroventral of orbit with broad posteroventrally aligned patch of chromatophores continuous posteriorly with curved band of chromatophores continuing around ventral and posterior margins of orbit. Dorsal portions of infraorbital series and opercle with scattered, dark chromatophores.

Scales of dorsolateral portion of body with crescent-shaped pattern of dark chromatophores along margin of scales and wider basal patch of chromatophores. Two chromatophore fields on scales separated by hyaline region in smaller specimens, merging, particularly on dorsalmost scales, in larger specimens. Humeral mark somewhat elongate vertically, with anterior margin typically concave anteriorly and with posterior margin convex. Dark pigmentation most intense in portion of mark immediately dorsal of lateral line, with intensity of pigmentation progressively decreasing dorsally. Some specimens with scattered, dark chromatophores continuing ventral of lateral line to form ventrally tapering extension of main portion of humeral mark. Region immediately anterior to humeral mark hyaline. Area posterior to humeral mark hyaline for distance of approximately one and one-half scales and followed by midlateral body stripe formed by dark surface chromatophores. Density of chromatophores in midlateral stripe increasing in larger specimens. Midlateral stripe continuing posteriorly to rear of caudal peduncle.

Dorsal fin with anterior margin of unbranched rays and margins of distal portions of branched rays outlined by dark pigmentation. Basal two-thirds or less of anterior branched anal-fin rays outlined by dark pigmentation. Caudal fin with pigmentation along margins of dorsal and ventral rays, and along middle rays; central rays of each lobe hyaline or nearly so. Pigmentation on middle caudal-fin rays more concentrated basally, forming indistinct spot; spot more obvious in larger individuals.

ETYMOLOGY.—The species name, *seductus,* from the Latin for remote or apart, refers to the isolated location of the type locality relative to other sites from which *Creagrutus* species are known to occur.

ECOLOGY.—Stomach contents of a single specimen prepared for cleared and staining consisted solely of chopped-up seeds.

DISTRIBUTION.—*Creagrutus seductus* is known only from the upper portions of the Rio Araguaia basin (Figure 83, triangle). As discussed under "*Creagrutus* and *Piabina* in Cis-Andean South America," above, one *Creagrutus* specimen (ANSP 164289) purportedly collected at Russas, Ceará, in the Rio Jag-

uaribe, an isolated basin in northeastern Brazil, may be an individual of *C. seductus* with erroneous locality information.

COMPARISONS.—The *Creagrutus* species known from the Rio Araguaia basin, in addition to *C. seductus*, are *C. figueiredoi*, *C. menezesi*, *C. molinus*, and *C. mucipu*. *Creagrutus seductus* is readily separable from those species by details of dentition and meristics (see "Key to the Species of *Creagrutus* in the Rio Tocantins Basin").

REMARKS.—*Creagrutus seductus* (USNM 342231, USNM 342232) has been collected twice with *C. menezesi* (USNM 342234, USNM 342236) at the type locality, the only site from which *C. seductus* is known and has been captured at the same site on one occasion with *C. figueiredoi* (USNM 342235).

MATERIAL EXAMINED.—27 specimens (27, 32.5–70.3).

HOLOTYPE.—BRAZIL. *Mato Grosso:* Upper Rio Araguaia basin, Córrego Fundo, Município de Barra do Garças (approximately 15°53′S, 52°15′W), 19 Sep 1993, C.E. Melo et al., MZUSP 51026, 1 (63.6; formerly ICLMA 229, in part).

PARATYPES.—26 specimens (26, 32.5–70.3).

BRAZIL. *Mato Grosso:* Upper Rio Araguaia basin, Córrego Fundo, Município de Barra do Garças (approximately 15°53′S, 52°15′W), collected with holotype, MZUSP 51027, 1 (59.9; formerly ICLMA 229, in part); USNM 342233, 1 (66.8; formerly ICLMA 229, in part). Upper Rio Araguaia basin, Córrego Fundo, Município de Barra do Garças (approximately 15°53′S, 52°15′W), 15 Nov 1993, C.E. Melo et al., MZUSP 51028, 3 (39.5–66.5; formerly ICLMA 190, in part); USNM 342232, 3 (41.0–62.7; formerly ICLMA 190, in part). Upper Rio Araguaia basin, Córrego Fundo, Município de Barra do Garças (approximately 15°53′S, 52°15′W), 12 Nov 1993, P.C. Venere et al., MZUSP 51029, 9 (32.5–70.3); USNM 342231, 9 (44.9–66.8; 1 specimen cleared and counterstained for cartilage and bone).

TABLE 54.—Morphometrics and meristics of *Creagrutus taphorni*, new species: (A) holotype of *C. taphorni*, MBUCV V-29288; and (B) paratypes of *C. taphorni* (n=23). Standard length is expressed in mm; measurements 1 to 14= percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	52.5	45.6–74.1
1. Snout to anal-fin origin	61.5	61.5–65.1
2. Snout to pelvic-fin origin	44.8	44.2–47.4
3. Snout to pectoral-fin origin	25.1	24.2–26.7
4. Snout to dorsal-fin origin	49.3	47.8–51.4
5. Dorsal-fin origin to hypural joint	56.0	53.6–58.2
6. Dorsal-fin origin to anal-fin origin	33.0	29.2–33.3
7. Dorsal-fin origin to pelvic-fin insertion	30.5	28.3–32.1
8. Dorsal-fin origin to pectoral-fin insertion	35.4	33.5–38.2
9. Caudal peduncle depth	13.1	11.8–13.7
10. Pectoral-fin length	20.8	17.5–22.1
11. Pelvic-fin length	15.4	14.5–16.8
12. Dorsal-fin length	24.6	19.8–23.9
13. Anal-fin length	18.5	14.8–20.1
14. Head length	25.0	25.3–28.1
15. Postorbital head length	49.6	45.2–51.9
16. Snout length	26.7	25.0–34.0
17. Bony orbital diameter	30.5	26.4–32.8
18. Interorbital width	32.1	28.6–35.4
	Meristics	
Lateral line scales	37	36–38
Scale rows between dorsal-fin origin and lateral line	4	4–5
Scale rows between anal-fin origin and lateral line	3	3–4
Predorsal median scales	10	9–13
Branched dorsal-fin rays	8	8
Branched anal-fin rays	10	10–12
Branched pelvic-fin rays	7	6–7
Pectoral fin rays	13	11–13
Vertebrae	36	36–37

Creagrutus taphorni, new species

FIGURES 83, 88, TABLE 54

Creagrutus beni [not of Eigenmann, 1911].—Eigenmann, 1920:12 [misidentification] [Venezuela: only Rio Guaire record, IU 15124 (=CAS 69290)]; 1927:422 [as in Eigenmann, 1920; not citations from other portions of South America].—Schultz, 1944:336 [in part, Eigenmann, 1920a in synonymy; not Pearse, 1920 or Fowler, 1931, references; Rio Tuy system near Caracas, USNM 121500].—Beebe, 1948:149 [in part, not Eigenmann, 1911, and Schultz, 1944, references; Venezuela, Aragua, Rancho Grande].—Luengo, 1963:326 [in part, Eigenmann, 1920, in synonymy, Beebe, 1948].—Mago-Leccia, 1967:233 [in part, Eigenmann, 1920, in synonymy].—Géry and Renno, 1989:5 [comments on differences between material from Lago Valencia cited by Luengo, 1963, as *C. beni* and specimens of that species from type region].—Marrero and Machado-Allison, 1990:66 [in part, Eigenmann, 1920, in synonymy of *C. beni*].—Ortaz, 1992:552 [Venezuela: Parque Nacional Henri Pittier, Río Limon; food habits].

Creagrutus cf. *beni*.—Taphorn, 1992:167 [in part, upper Rio Apure drainage only].

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 3 to 5 teeth on the maxilla, 6 teeth in the primary tooth row of the premaxilla, 5 dentary teeth, 36 to 38 lateral line scales without a lamellar process over each pore, 9 to 13 predorsal median scales, 4 or 5 scale rows between the dorsal-fin origin and the lateral line, 36 or 37 vertebrae, 10 to 12 branched anal-fin rays, 2 post-anal median scales to the anal-fin origin, 13 or 14 gill rakers on the lower limb of the first gill-arch, the distance from the dorsal-fin origin to the anal-fin origin (29.2%–33.3% of SL), the distance from the dorsal-fin origin to the pelvic-fin insertion (28.3%–32.1% of SL), the postorbital head length (42.5%–51.9% of HL), the bony orbital diameter (26.4%–32.8% of HL), the interorbital width (28.6%–35.4% of HL), the moderately developed third infraorbital with its ventral margin approaching or contacting the horizontal limb of the preopercle, the lack of a series of dark midlateral spots on the body, a vertical or slightly anterodorsally inclined humeral mark, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus taphorni* within the clade composed of *Creagrutus* and *Piabina*.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus taphorni* in Table 54. Body moderately deep and transversely compressed. Greatest body depth ranging from slightly anterior of pelvic-fin insertion to anteriorly as far as one-half of distance to vertical through pectoral-fin insertion. Dorsal profile of head distinctly convex from margin of upper lip to vertical through posterior margin of posterior nares, straight from that point to rear of supraoccipital spine. Predorsal profile slightly convex to dorsal-fin origin. Body profile typically straight from posterior of dorsal-fin base to caudal peduncle, some specimens with slight concavity between bases of dorsal and adipose fins. Ventral profile of head with variably obvious obtuse angle approximately midway between margin of lower lip and posterior of dentary, straight to slightly convex from that point approximately to pelvic-fin insertion; slightly concave from anal-fin origin to caudal peduncle.

Upper jaw longer than, and overhanging, lower jaw. Anterior portion of snout quite fleshy, with many minute papillae on anteromedial portion of snout, papillae continuing ventrally onto upper lip and into mouth on fleshy flaps between premaxillary teeth. Lower lip distinctly fleshy anteriorly, with papillae concentrated on dorsal surface of lip. Papillae decreasing in number ventrally and laterally, extending ventrally and posteriorly in small numbers nearly to isthmus.

Infraorbital series moderately developed, occupying approximately two-thirds of cheek. Ventral margin of third infraorbital approaching or contacting ventral limb of preopercle. Posterior margin of third infraorbital distinctly separated from vertical limb of preopercle by space of at most one-fourth width of orbit. Posteroventral corner of bone broadly rounded, with posterior and ventral margins of third infraorbital approximately perpendicular to each other.

Premaxillary dentition in three series: primary row typically consisting of 6 teeth, 5 teeth present on 1 premaxilla of 1 specimen, teeth of primary series arranged in sigmoid pattern without pronounced gap between first and second tooth of series; cluster of 3 larger teeth lying medial to primary series with 2 posterior teeth larger; and single tooth of form similar to that of primary series lying lateral to fourth tooth of primary series. Maxilla usually with 3 or 4, occasionally 5, tricuspidate teeth. Dentary with 5 tricuspidate teeth, or with final tooth in series with only central cusp distinct. First and second dentary teeth distinctly larger than rest of series, with second tooth somewhat larger than first tooth and twice height of, and much larger overall than, third tooth. Remaining dentary teeth progressively decreasing in size posteriorly.

Dorsal-fin rays ii,8. Dorsal-fin origin located at vertical through pelvic-fin insertion. Distal margin of dorsal fin slightly concave, with noticeably elongate anterior lobe. Anal-fin rays ii,10–12 or iii,10–12. Mature males with anal-fin hooks on segments of first 3 to 5 branched rays. Distal margin of anal fin slightly sinusoidal. Pectoral-fin rays i,10–12; Tip of pectoral fin approaching, or reaching to, pelvic-fin insertion. Pelvic-fin rays i,6, less commonly i,7 (note: i,8 found on one pelvic fin in one specimen from Estado de Miranda, Río Guiare, MBUCV V-21244, which may represent a developmental abnormality). Tip of pelvic fin typically extending posteriorly nearly to anal-fin origin. Mature males with pelvic-fin hooks on medial surface of segmented and unsegmented portions of basal shaft and medial branches of all seven branched rays.

Gill rakers 6–8 + 9–11.

COLORATION IN LIFE.—(The following observations are based on the examination of specimens (MCNG 28752) from the Río Bocanó, Portuguesa, Venezuela, made less than 24 hours after their capture and fixation in formalin). All unbranched and anterior 1 or 2 branched rays of dorsal, anal, and pelvic fins pale yellow basally, fading nearly to white distally. Dorsal, anal, and pelvic fins with striking, nearly white, leading edge. Caudal-fin rays pale yellow with yellow color most intense on ventral lobe, becoming orange in distal one-fourth of fin. Distal margin of caudal fin with narrow black band. Pale orange middorsal stripe present, coloration most intense in region between rear of head and area lateral to dorsal-fin base. Anterodorsal surface of eye orange-red, overlying reflective guanine pigment.

Beebe's description (1948:149) of life coloration of specimens from Rancho Grande, Aragua state (identified by that author as *C. beni*), agreed with the above description, although that author noted that in life the species has the "distal portion [of the caudal fin], especially under lobe, pink, varying to scarlet in some individuals" and has the "distal parts of pelvic and anal rays yellow."

COLORATION IN ALCOHOL.—Dorsal surface of head with uniform diffuse pattern of dark chromatophores continuing anteriorly onto snout, with distinct small crescent-shaped patch of dark chromatophores immediately in front of anterior nares. Band of scattered, dark chromatophores extending from diffuse pigmentation on dorsal surface of snout posteroventrally to anteroventral margin of orbit, narrowing and continuing around posterior margin of orbit. Infraorbitals posterior of orbit and dorsal portion of opercle with scattered, large, dark chromatophores, more so in larger individuals.

Body with dark pigmentation most concentrated dorsally, particularly at dorsal-fin base and over center of exposed surface of scales. Many specimens with dark pigmentation along posterior margins of scales on dorsal portion of body, with darker pigmentation forming irregular reticulate pattern most obvious in larger, more darkly pigmented specimens. Narrow dark middorsal stripe present, most intense anterior of dorsal fin. Humeral mark with dark pigmentation most concentrated in region immediately dorsal of lateral line. Less concentrated field of chromatophores extending from intensely pigmented region towards pectoral-fin origin as ventrally attenuating patch of variably sized chromatophores. Humeral mark extending dorsally from central region as less intensely pigmented patch to approximately one-half of distance to middorsal line. Overall form of bar variable, ranging from slightly anterodorsally to slightly posterodorsally inclined bar. Dark pigmenta-

FIGURE 88.—*Creagrutus taphorni,* new species, holotype, MBUCV V-29288, 52.5 mm SL; Venezuela, Guarico, Río Orituco, Parque Nacional Guatopo, first bridge along road from Santa Teresa to Altagracia.

tion on lateral surface of body, other than humeral bar, restricted to area dorsal of lateral line in some individuals. Midlateral dark stripe beginning several scales posterior of humeral mark, becoming denser and somewhat wider posteriorly on caudal peduncle.

Dorsal-fin membrane with dark chromatophores most concentrated on central portion of fin. Unbranched anal-fin rays unpigmented, branched anal-fin rays delineated by series of small, dark chromatophores. Caudal fin with all fin rays delineated by dark pigment, pigmentation darkest on central rays of fin, particularly basally. Pectoral-fin rays delineated by dark chromatophores. Pelvic fin hyaline.

ETYMOLOGY.—The species name, *taphorni,* is in acknowledgment of Donald C. Taphorn, Museu de Ciencias Naturales, Guanare, Venezuela, who collected much of the material of the species and in recognition of his contributions to our knowledge of the fishes of the Llanos of the Orinoco basin and his assistance to the authors in this and other projects.

ECOLOGY.—According to Beebe (1948:149), *C. taphorni* (identified by that author as *C. beni*) was collected in streams in montane cloud forest. *Creagrutus taphorni* was collected with *C. melasma* on several occasions in the Río Cojedas basin of the western portion of its geographic range and in the Río Orituco in the east.

Stomach contents of two specimens of *Creagrutus taphorni* examined by Beebe (1948; identified by that author as *C. beni*) consisted of firefly larvae, caterpillars, beetles, and undetermined adult and larval insects. Ortaz (1992:552) reported *C. beni* from the Río Limon, Parque Nacional Henri Pittier in northern Venezuela; however, that species is endemic to the upper Rio Madeira system in Bolivia, which is far distant from the Río Limon. Two *Creagrutus* species are known from the Río Limon basin, *C. melasma* and *C. taphorni.* The maximum size of the specimens examined by Ortaz (1992:552) was 80.05 mm SL, a length significantly larger than that for any examined specimen of *C. melasma,* but falling within the range of examined material of *C. taphorni.* Ortaz' record is thus considered to refer to *C. taphorni.* Ortaz (1992:552–553) reported that the species feeds mostly on various aquatic insects, with a number of families of dipterans represented in the diets. Various seeds and parts of flowers also were represented in the stomach contents of his sample.

COMMON NAME.—Venezuela: "Dientefrio," "buck-toothed tetra" (Taphorn, 1992:167).

DISTRIBUTION.—*Creagrutus taphorni* is known from piedmont streams of north central Venezuela, east of the Andean Cordilleras, mostly in the Río Orinoco basin and the Río Tuy basin of the Caribbean versant (Figure 83, filled stars). The pattern of distribution is approximately congruent with the western portion of the range of *C. melasma,* which occurs from Estado Tachira in the southwest to Yaracuy in the northeast and eastward to the Río Orituco, Estado Guarico (Figure 59, stars).

GEOGRAPHIC VARIATION.—Double-hooked pelvic rays and crenate scale margins occur in a sample from the Río Valle, Distrito Federal, Venezuela (see *Creagrutus* cf. *taphorni,* USNM 121500 under "Material Examined"). These characters were otherwise observed only in *C. lassoi,* a species endemic to the Río Aroa, and in *C. crenatus,* which is known only from the Río Tocuyo system. Both of these drainages are within the Caribbean Sea versant of northern Venezuela. All the other features of this sample (USNM 121500) are otherwise in agreement with those of samples ascribed herein to *C. taphorni,* and for that reason the Río Valle samples are equated with that species.

REMARKS.—A series of authors beginning with Eigenmann (1920) have cited samples of *Creagrutus* from Venezuela as *C. beni.* Our examination of the holotype of *Creagrutus beni* Eigenmann, 1911 (see "Remarks" under that species), reveals that the species has a much more restricted distribution than previously reported, being limited to the upper Rio Madeira ba-

sin in Bolivia. Material collected in Venezuela and ascribed to that nominal species in previous studies (e.g., Eigenmann, 1927; Schultz, 1944) represents a series of undescribed species, including *C. taphorni* (see synonymy above and discussions of *C. paralacus* in Harold and Vari (1994) and *C. hysginus* in Harold et al. (1994)). *Creagrutus taphorni* differs from *C. beni* in its relatively broad humeral mark (vertically elongate in *C. beni*), lower vertebral counts (36 or 37 in *C. taphorni* versus 37 to 39 in *C. beni*), lower numbers of lateral line scales (36 to 38 in *C. taphorni* versus 38 to 42 in *C. beni*), and only moderately developed infraorbitals (versus well developed and contacting the preopercle ventrally in *C. beni*).

Literature references to *Creagrutus beni* from many localities in central and northern Venezuela, especially from Lago de Valencia and adjoining regions, are probably based on specimens of *C. taphorni* and/or *C. melasma.* Eigenmann (1920:12) remarked that individuals of what he identified as *C. beni* of 30 to 40 mm in length had a dark spot on the dorsal fin (a feature of *C. melasma*), but the feature was absent in adult specimens (likely *C. taphorni,* which lacks such a dorsal-fin spot). Information in the publications cited in the above synonymy or examination of the specimens that served as the basis for those records has allowed us to equate those citations with *C. taphorni.* Other published references to *C. beni* occurring in northern Venezuela may be based, depending upon the specific region, on *C. taphorni* or on the various similar Cis-Andean *Creagrutus* species (*C. crenatus, C. lassoi,* or *C. hysginus*), which occur sympatrically with *C. taphorni,* or in some instances combinations of these species as was the case with Eigenmann's (1920) record of *C. beni.* In many instances no voucher material associated with the citations was available, or we were unable to examine those samples when extant, making it impossible to determine the identity of the cited specimens.

Géry and Renno (1989:5) noted that samples originating in northern Venezuela, which were identified by Fernández-Yépez (1972) as *Creagrutus beni,* differed from specimens of *C. beni* from its type region both in details of dorsal-fin pigmentation and in the number of transverse scale rows. Although those authors were correct in their assessment of the differences between *C. beni* and Venezuelan *Creagrutus* samples, the "forme vénézuélienne," cited by Géry and Renno, included two species: *C. taphorni* (the Lago de Valencia populations cited by those authors) and *C. lassoi* (the Río Yaracuy population).

Specimens in a population sample from near Rubío, in the uplands of Tachira state, Venezuela, in the western portions of the Río Orinoco basin (MBUCV V-9395) are similar to *Creagrutus taphorni* in general appearance and meristic characters. These specimens, however, demonstrate slight shifts in the ranges of values for several morphometric characters relative to samples of *C. taphorni* from the central portion of the Orinoco basin. The features of note are the distance from the snout to the anal-fin origin (60.4%–65.1% of SL in central Orinoco basin samples versus 57.1%–62.1% of SL in Tachira sample), the distance from the snout to the pelvic-fin origin (44.2%–47.4% of SL versus 42.2%–45.6% of SL, respectively), the bony orbital diameter (26.4%–32.8% of HL versus 25.3%–28.1% of HL, respectively), and the pelvic-fin length (14.5%–16.8% of SL versus 13.0%–14.7% of SL, respectively). Further samples from intervening areas are necessary to determine if these differences are significant or if they represent intraspecific geographic variation.

MATERIAL EXAMINED.—1015 specimens (32, 40.7–74.1).

HOLOTYPE.—VENEZUELA. *Guarico:* Río Orituco, Parque Nacional Guatopo, first bridge along road from Santa Teresa to Altagracia, collected by H. Moreno and A. Machado-Allison, 20 May 1992, MBUCV V-29288 (52.5).

PARATYPES.—81 specimens (23, 45.6–74.1).

VENEZUELA. *Aragua:* Quebrada Agua Fria, Río Tuy system, approximately 1 km from its mouth in Río Tuy, collected by R. Royero et al., 6 Apr 1991, MBUCV V-21032, 10 (2, 45.6–51.6). *Guarico:* Río Orituco, Parque Nacional Guatopo, first bridge along road from Santa Teresa to Altagracia, collected with holotype, MBUCV V-29289, 5 (46.3–63.6). *Miranda:* El Amoladero, Río Guiare, R. Royero et al., 1 Jun 1991, MBUCV V-21244, 18 (8, 46.5–67.9); USNM 357730, 2 (50.7–51.1; specimens cleared and counterstained for cartilage and bone). Río Araira, upper portion, near Quebrada Las Pailes (approximately 10°37′N, 66°59′W), USNM 357784, 6 (55.2–74.1). *Portuguesa:* Distrito Guanare, Río Boconó, caño below entrance to Boconó Dam (8°1′50″N, 70°52′34″W), collected by D.C. Taphorn et al., 31 Jul 1993, MCNG 28752, 4. Distrito Sucre, Río Saguas, at the bridge parking along Paraiso Highway from Biscucuy to Chabasquen (approximately 9°24′N, 70°02′W), collected by A. Flecker et al., 5 Jan 1988, MCNG 18736, 36.

NONTYPE SPECIMENS.—933 specimens (8, 40.7–63.5).

VENEZUELA. *Apure:* Caño Blanquita, 9.1 km S of La Cciba, MCNG 11905, 4. *Aragua:* Río Limon system, tributary 12 km NW of Maracay on highway to Ocumare de la Costa, Parque Nacional Henri Pittier, UMMZ 209405, 6. Río Tuy system, mouth of Cagua, approximately 10 km from Guayas (latter locality at 10°16′N, 67°09′W), MBUCV V-21024, 5. Quebrada La Mesa, NE of Maracay, MBUCV V-3012, 4. Río Pao, near La Candelaria (approximately 10°07′N, 67°14′W), MCNG 14102, 12. Lago de Valencia basin, tributary of Río Castaño, N of Las Delicias, MBUCV V-3036, 13. Parque Nacional Aragua, Rancho Grande, Río Guamitas (approximately 10°21′N, 67°41′W), USNM 132592, 3. *Barinas:* Caño emptying into Represa Boconó, MCNG 5270, 90. Caño Avaro, MCNG 5333, 1. Río Masparro (approximately 8°04′N, 69°26′W), MCNG 5380, 39. Caño in Estero Chiguira, MCNG 6547, 2. Caño along Río Paguey (8°01′N, 69°38′W), MCNG 7285, 6. Caño 17.5 km NW Río Paguey, MCNG 7333, 7. Caño Grande on Finca Caño Grande, MCNG 7924, 8. Caño Manamo near Coporito, MCNG 10530, 14. Upper Río Caparo, MCNG 10543, 2. Río Las Palmas, USNM 194122, 1. *Carabobo:* Las Dos Bocas (town on river draining into SE portion of Lago de Valencia, 9°55′N, 67°58′W), MHNLS 1095, 11. Río Agua Caliente, N of

El Cambur, MCNG 13980, 3. Río Chirgua, tributary of Río Pao (approximately 9°54′N, 68°09′W), MCNG 15282, 41; MCNG 18050, 170. Río Manuare (approximately 9°49′N, 67°41′W), MCNG 15355, 39. *Cojedes:* Río Chirgua, MCNG 14264, 14. *Distrito Federal:* Río Valle, S of Caracas, USNM 121500, 5. *Miranda:* Río Chuspita, in Chuspita de Lima, along highway from Araira to Salmeron (approximately 10°34′N, 66°19′W), MBUCV V-22531, 5. Río Iscaragua, at Club Iscaragua along highway from Caracas to Guarenas, MBUCV V-24001, 57. Río de Ulua, along border of Río Panaquire, MHNLS 3349, 1. Distrito Sucre, Quebrada Galinda, entrance to Parque Nacional El Avila, MHNLS 9627, 24. Río Tuy basin, Quebrada Ojo de Agua, Baruta (10°26′N, 66°53′W), MHNLS 521, 17; MHNLS 523, 10. San Antonio de Los Altos (10°22′N, 66°56′W), MHNLS 535, 2. Santa Teresa del Tuy, MHNLS 3183, 2. Quebrada Mesia, La Democracia (10°01′N, 66°45′W), MHNLS 2455, 10. Río Tuy basin, Río Las Minas, 7 km E of Santa Teresa del Tuy, MHNLS 524, 11; MHNLS 531, 3. Distrito Sucre, Río Tocome, approximately 200 m from border of Parque Nacional "El Avila" (approximately 10°28′N, 66°49′W), MHNLS 9448, 10. Río Grande, 200 m before the mouth of Río Santa Cruz into Río Grande, Parque Nacional Guatopo, MBUCV V-12519, 6. Río Guare de Tacata, MCNG 14090, 32. Unnamed caño 18 km SW of Tacata (latter locality at 10°12′N, 67°00′W), MCNG 14150, 2. Bridge near Araguita, MCNG 14297, 2. Caño El Lindero, MCNG 17166, 6. Río Mucarao, 8 mi (=12.8 km) W of Caracas, elevation 900 m, AMNH 14268, 13. Río Guiare, near Caracas, USNM 357729, 3 (40.7–62.7; cleared and counterstained for cartilage and bone). *Portuguesa:* Río Guanare in La Raya, MCNG 120, 8. Río Guanare, near Chabasquen (9°26′N, 69°57′W), MCNG 132, 6. Río Saguaz, along road to Chabasquen, MCNG 134, 5. Río Las Marias, MCNG 3419, 1. Río Tucupido, at dam site, MCNG 5288, 19. Caño emptying into Represa Boconó, MCNG 5399, 3. Pools in Río Boconó MCNG 5451, 28. Río Tucupido in Las Canoas (8°55′N, 69°44′W), MCNG 5649, 13. Río Tucupido at dam site, MCNG 8838, 2. Caño, at bridge km 30 on road from Biscucy, MCNG 9808, 36. Río Guanare, between Guanare and Biscucy, MCNG 10050, 1. Río Las Marias on route to San Juan, MCNG 10910, 3. Río La Estacion, MCNG 11608, 19. Río Moroturo, near Aparicion (approximately 9°24′N, 69°23′W), MCNG 11815, 22. Caño Bombicito, near Aparicion (approximately 9°24′N, 69°23′W), MCNG 11841, 13. Caño La Laja, Río Guarguero, MCNG 12484, 10. Puente Nuevo, 11 km E of Ospino (latter locality at 9°18′N, 69°27′W), MCNG 12748, 2. Caño N of Las Majaguas, Paso Cojedes, MCNG 12806, 2. *Yaracuy:* Quebrada Grande, Río Cojedas basin, near bridge between Nirgua and Chivacoa, USNM 357783, 4.

The following lot is tentatively identified as *Creagrutus taphorni* (see under "Remarks," above): VENEZUELA. *Tachira.* Quebrada La Lejia Bramoncito, near small village of Lejia, along highway from Rubio to La Petrolera, approximately 3 km from Rubio (latter locality at 7°43′N, 72°22′W), MBUCV V-9395, 20 (5, 51.6–63.5).

Creagrutus ungulus, new species

FIGURES 89, 90, TABLE 55

Creagrutus anary [not of Fowler, 1913].—Ortega, 1996:465 [misidentification] [Peru, Departamento de Madre de Dios, Parque Nacional Manu, Quebrada Soga, Río Salvación].

DIAGNOSIS.—The presence of four median scales between the posterior margin of the anus and the anal-fin origin distinguishes *Creagrutus ungulus* from all congeners. The only other members of the genus with more than 2 scales in that series (with three scales as a occasional variant) are *C. cracentis* and *C. maxillaris,* which have 5 post-anal median scales to the anus. Those species are readily distinguished from *C. ungulus* in having only two rows of premaxillary teeth contrary to the typical *Creagrutus* dentition with three major components found in *C. ungulus,* higher numbers of maxillary and dentary teeth, and in having the third infraorbital well developed contrary to the distinctly reduced third infraorbital of *C. ungulus.*

In addition to this post-anal scale character, the combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 4 or 5 teeth on the maxilla, 6 teeth in the primary tooth row of the premaxilla, 5 or 6 dentary teeth, 37 to 41 lateral line scales without a lamellar process over each pore, 9 to 12 predorsal median scales, 4 or 5 scale rows between the dorsal-fin origin and the lateral line, 3 scale rows between the anal-fin origin and the lateral line, 37 to 40 vertebrae, 9 or 10 branched anal-fin rays, 4 post-anal median scales to the anal-fin origin, the distance from the snout to the anal-fin origin (58.4%–63.4% of SL), the distance from the dorsal-fin origin to the pelvic-fin insertion (25.7%–30.7% of SL), the caudal peduncle depth (11.6%–13.0% of SL), the head length (26.8%–29.1% of SL), the postorbital head length (45.2%–51.0% of HL), the snout length (24.2%–27.9% of HL), the bony orbital diameter (27.7%–32.2% of HL), the highly reduced third infraorbital with its posteroventral margin concentric with the orbital rim, the lack of a series of dark midlateral spots on the body, the vertically elongate, ventrally attenuating humeral mark, and the absence of a discrete patch of dark pigmentation on the middle portion of the anterior dorsal-fin rays distinguishes *Creagrutus ungulus* within the clade composed of *Creagrutus* and *Piabina.*

DESCRIPTION.—Morphometric and meristic data for *Creagrutus ungulus* in Table 55. Head relatively large, more so in larger individuals; body robust anterior to dorsal-fin origin, less so posteriorly at all sizes. Greatest body depth at dorsal-fin origin in smaller specimens, distinctly shifted anterior of that point in larger individuals. Dorsal profile of head smoothly rounded from margin of upper lip to vertical through posterior nostril, slightly convex from that point to tip of supraoccipital spine in small specimens, nearly straight in that region in larger examined individuals. Dorsal profile of body convex from tip of supraoccipital spine to dorsal-fin origin at all body sizes, but

TABLE 55.—Morphometrics and meristics of *Creagrutus ungulus*, new species: (A) holotype of *C. ungulus*, MUSM 8878; (B) paratypes of *C. ungulus* (n=30); and (C) all specimens of *C. ungulus* from which counts and measurements were taken (n=42). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B	C
		Morphometrics	
Standard length	66.8	25.0–73.9	25.0–74.9
1. Snout to anal-fin origin	61.5	58.4–62.1	58.4–63.4
2. Snout to pelvic-fin insertion	45.2	44.7–47.7	44.6–48.2
3. Snout to pectoral-fin insertion	26.4	24.9–26.6	24.7–26.7
4. Snout to dorsal-fin origin	48.4	47.5–49.5	46.4–50.4
5. Dorsal-fin origin to hypural joint	58.8	54.7–58.8	54.0–59.9
6. Dorsal-fin origin to anal-fin origin	31.0	28.3–32.1	28.3–33.1
7. Dorsal-fin origin to pelvic-fin insertion	30.4	25.7–30.5	25.7–30.7
8. Dorsal-fin origin to pectoral-fin insertion	32.2	31.9–34.3	31.9–35.2
9. Caudal peduncle depth	12.4	11.9–13.0	11.6–13.0
10. Pectoral-fin length	21.0	19.5–23.1	19.5–23.4
11. Pelvic-fin length	15.9	15.0–16.7	14.7–17.1
12. Dorsal-fin length	21.3	20.5–22.9	20.5–24.0
13. Anal-fin length	18.4	17.1–20.9	17.1–21.8
14. Head length	28.2	27.1–28.4	26.8–29.1
15. Postorbital head length	50.3	45.8–51.0	45.2–51.0
16. Snout length	26.4	24.5–27.3	24.2–27.9
17. Bony orbital diameter	28.5	28.3–32.0	27.7–32.2
18. Interorbital width	31.7	27.9–32.0	27.9–32.6
		Meristics	
Lateral line scales	38	37–41	37–41
Scale rows between dorsal-fin origin and lateral line	4	4–5	4–5
Scale rows between anal-fin origin and lateral line	3	3	3
Predorsal median scales	10	9–11	9–12
Branched dorsal-fin rays	8	8	8–9[1]
Branched anal-fin rays	9	9–10	9–10
Branched pelvic-fin rays	6	5–6[b]	5–6[2]
Pectoral-fin rays	13	13–15	13–15
Vertebrae	39	37–40	37–40

[1]Nine branched dorsal-fin rays present in only 2 nontype specimens.
[2]Five branched pelvic-fin rays present in only 1 paratype.

with overall convexity of profile of posterior portion of head and predorsal region of body more pronounced in larger specimens. Dorsal profile of body posteroventrally angled along dorsal-fin base and nearly straight from rear of dorsal-fin base to caudal peduncle. Ventral profile of head with slight change in angle at anteroventral corner of dentary. Head and body profile gently convex from that point to anal-fin origin, convexity more pronounced in larger specimens.

Head obtusely pointed in both lateral and dorsal views. Upper jaw somewhat longer than, and overhanging, lower jaw. Snout slightly fleshy anteromedially, with scattered papillae anteriorly; papillae continue onto fleshy upper lip and onto folds and plicae extending between outer and medial premaxillary teeth. Lower lip fleshy, particularly anteriorly, with few scattered papillae.

Infraorbital series poorly developed. Ventral margin of third infraorbital falling distinctly short of horizontal limb of preopercle, more so posteriorly. Posterior margins of third through fifth infraorbitals distinctly separated from vertical limb of preopercle. Distal margins of third and fourth infraorbitals roughly concentric with margin of orbit.

Premaxillary dentition in three series: primary row consisting of 6 teeth arranged in slightly curved series without pronounced gap between first and second tooth of series but with anterior tooth distinctly separated from first tooth of contralateral row; cluster of three teeth with posterolateral tooth distinctly larger; and single tooth of form comparable to those of primary row, lateral to fourth tooth of that series. Maxilla with 4 or 5 tricuspidate teeth. Dentary with 5 or 6 teeth, all teeth tricuspidate when 5 teeth present, sixth tooth, when present, conical or sometimes with only slight indication of side cusps. First through third teeth largest, with first and second teeth subequal or second tooth somewhat larger than first tooth. Both first and second dentary teeth much larger than third tooth. Fourth through last tooth of series progressively decreasing in size.

Dorsal-fin rays typically ii,8, rarely ii,9. Dorsal-fin origin at vertical through pelvic-fin insertion. Profile of distal margin

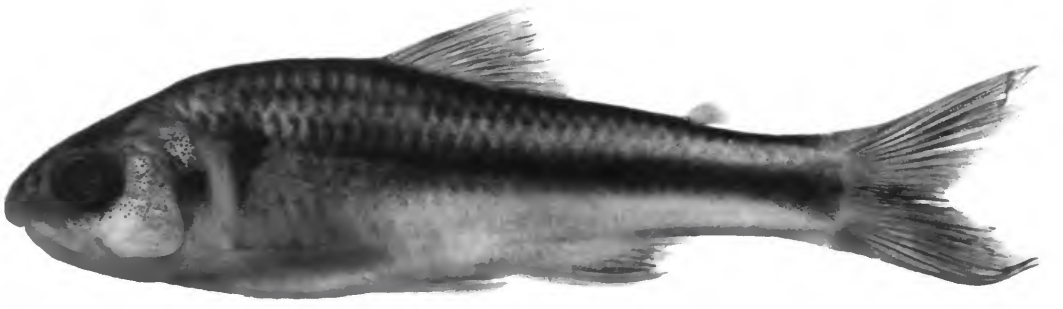

FIGURE 89.—*Creagrutus ungulus*, new species, holotype, MUSM 8878, 66.8 mm SL; Peru, Madre de Dios, Provincia Manu, stream tributary to Río Alto Madre de Dios, 1 km upstream from Erika, opposite Salvacion (latter locality at approximately 12°53'S, 71°12'W).

of dorsal fin straight to slightly convex. Anal-fin rays ii,9–10. Distal margin of anal fin distinctly convex, with anterior rays slightly longer but not forming distinct lobe. Anal-fin hooks present on only few examined mature males, located along posterior margin of first through fourth branched rays. Pectoral-fin rays i,12–14. Tip of pectoral fin extending posteriorly from slightly before, to slightly beyond, pelvic-fin insertion. Pelvic-fin rays typically i,6,i, with i,5,i in only 2 examined specimens. Tip of pelvic fin extending posteriorly slightly beyond anal-fin origin. Pelvic-fin hooks present in only few mature males, limited to medial margins of all branched pelvic-fin rays.

Gill rakers 5–7+9–11.

COLORATION IN LIFE.—No information available on coloration of live or recently collected specimens. Specimens fixed in formalin and preserved in alcohol examined approximately one month following their capture (MUSM 10362) with yellowish tint on dorsal fin and with yellow pigmentation most intense on basal one-half of branched and anterior unbranched dorsal-fin rays and membranes. Caudal fin with hemicircular patterns of yellow pigmentation on dorsalmost and ventralmost rays and intervening membranes. Caudal fin mostly yellow, pigmentation field most elongate dorsally and ventrally, and gradually shortening towards middle rays of fin, which lack yellow coloration. Middle portions of unbranched and anterior one or two branched anal-fin rays and membranes yellow. Middle portions of the lateral unbranched and first branched pelvic-fin rays with distinct patch of yellow pigmentation. No yellow coloration apparent on pectoral fins. Dark pigmentation as described under "Coloration in Alcohol," below.

COLORATION IN ALCOHOL.—Overall ground coloration tan to light brown. Dorsal surface of head with field of scattered, dark chromatophores in juveniles; field coalesced into continuous patch of dark pigmentation in larger individuals. Snout and lateral surface of upper jaw with scattered, dark chromatophores. Region in front of anterior nostril with chromatophores more concentrated, but not forming distinct crescent-shaped patch present in many *Creagrutus* species. Distinct band of dark chromatophores along ventral and posterior margins of orbit in smaller specimens, these subsumed into broader, more diffuse band in larger specimens. Dorsal portion of opercle and region posterior of orbit with scattered, dark chromatophores; chromatophore field in larger specimens extending further ventrally, particularly on posterior portion of check and on opercle. Variably developed dark spot on midlateral surface of opercle; spot typically less developed in smaller specimens. Lateral and dorsolateral surface of body with scattered, dark chromatophores; more concentrated in crescent-shaped patches over center of scales. Chromatophore field denser midlaterally, forming dark midlateral body stripe. Midlateral body stripe beginning about two scales posterior of humeral mark, somewhat diffuse anteriorly and most intense on posterior portion of body and along caudal peduncle. Humeral mark vertically elongate in all examined specimens, with deep-lying, more intensely pigmented dark central region. Humeral mark with less intensely pigmented areas extending dorsally and ventrally from dark central portion resulting in overall ventrally attenuating form, particularly in larger individuals. Dorsal portion of humeral mark merging into overall dark pigmentation of dorsal portion of body in larger specimens.

Dorsal-fin rays outlined with small dark chromatophores, with additional chromatophores scattered over membranes, giving fin dusky appearance, particularly in larger specimens. Anal fin with dark chromatophores along branched rays and intervening membranes, particularly anteriorly; pigmentation more pronounced in larger individuals. Caudal-fin rays delimited by dark chromatophores in smaller specimens, and with chromatophores scattered over membranes, increasingly so in larger specimens. Pectoral- and pelvic-fin rays slightly outlined with dark chromatophores, more so in case of pectoral fins. Pectoral fin in larger specimens with faint indication of dark transverse band.

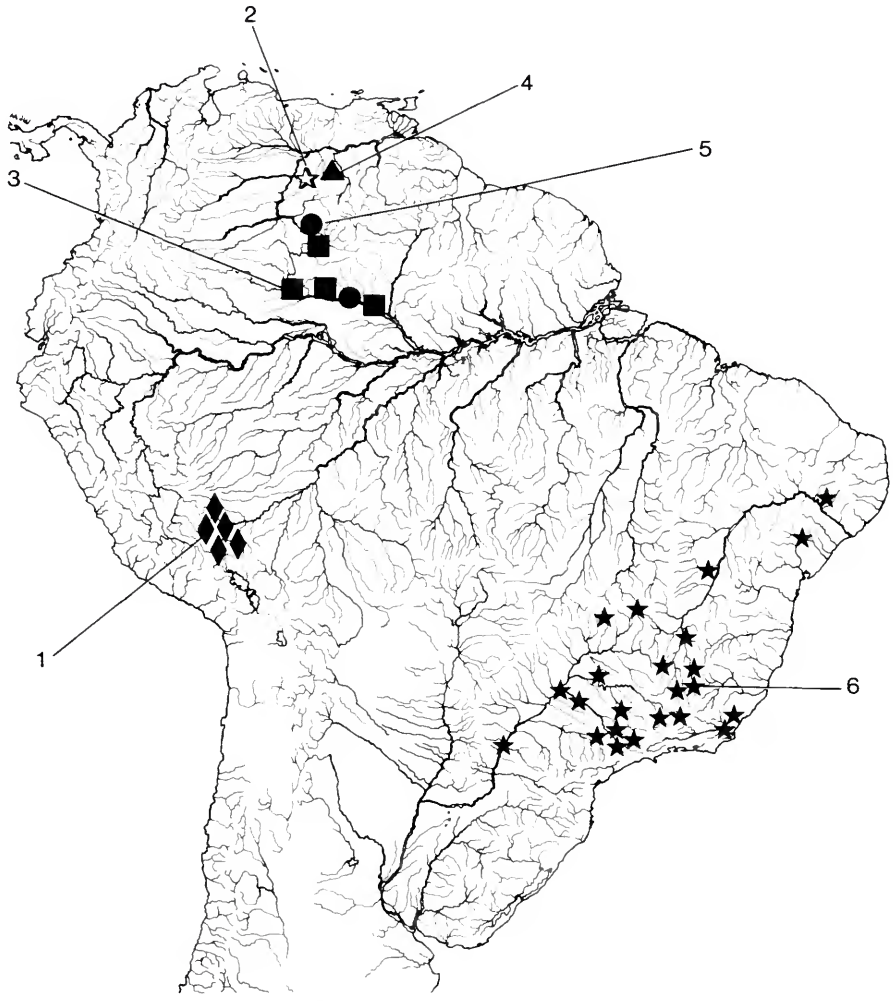

FIGURE 90.—Map of central and northern South America showing geographic distribution of *Creagrutus ungulus* (diamonds, 1=type locality), *Creagrutus veruina* (open star, 2=type locality), *Creagrutus vexillapinnus* (squares, 3=type locality), *Creagrutus xiphos* (triangle, 4=type locality), *Creagrutus zephyrus* (dots, 5=type locality), and *Piabina argentea* (solid stars, 6=approximate type locality) (some symbols represent more than one locality or lot of specimens).

ETYMOLOGY.—The specific name, *ungulus,* from the Latin for ring, refers to the narrow ring of infraorbitals bordering the ventral and posterior margins of the orbit.

ECOLOGY.—The type locality for the species, Quebrada Soga, is a small, rocky, rainforest stream approximately 5 m wide and 0.6 deep with clear water and rapid water flow over a substrate of rocks, sand, and detritus (Ortega, 1996:461). Most other specimens of *Creagrutus ungulus* captured near the type locality, and for which habitat information is available, came from comparable habitats, although some specimens were captured at the mouth of an stream tributary to the Alto Río Madre de Dios, a habitat with less gradient and slower water flow over a mud and cobble bottom.

DISTRIBUTION.—*Creagrutus ungulus* is known only from the Río Madre de Dios basin of southeastern Peru (Figure 90, diamonds).

COMPARISONS.—The only other species of *Creagrutus* known to occur within the range of *C. ungulus* are *C. manu* and *C. occidaneus.* Neither of those species has the narrow infraorbitals of *C. ungulus,* and both have only 2 median scales between the anus and the anal-fin origin contrary to the 4 postanal scales in *C. ungulus.* These species also differ from *C. ungulus* in various meristic and morphometric features.

MATERIAL EXAMINED.—185 specimens (42, 25.0–74.9).

HOLOTYPE.—PERU. *Madre de Dios:* Provincia Manu, Quebrada Soga, tributary of Río Alto Madre de Dios, 1 km upstream from Erika (opposite Salvacion; approximately

12°53′S, 71°12′W), collected by M. Rauchenberger et al., 5 Sep 1988, MUSM 8878, 1 (66.8).

PARATYPES.—30 specimens (30, 25.0–73.9).

PERU. *Madre de Dios:* Provincia Manu, Quebrada Soga, tributary of Río Alto Madre de Dios, 1 km upstream from Erika (opposite Salvacion; approximately 12°53′S, 71°12′W), collected with holotype, MUSM 8879, 7 (36.4–66.0); USNM 303066, 10 (47.5–73.9; 3 specimens cleared and counterstained for cartilage and bone). Provincia Manu, stream tributary to Río Alto Madre de Dios, at Erika (opposite Salvacion; approximately 12°53′S, 71°12′W; locality = Quebrada Soga according to Ortega, 1996:465), collected by M. Rauchenberger et al., 5 Sep 1988, MUSM 8880, 4 (47.8–52.8); USNM 302788, 3 (42.2–56.1). Provincia Manu, stream tributary to Río Alto Madre de Dios, approximately 1.5 km upstream from Erika (latter locality at approximately 12°53′S, 71°12′W), between Salvacion and Atalaya, collected by H. Ortega et al., 6 Sep 1988, MNRJ 14481, 6 (25.0–47.2).

NONTYPE SPECIMENS.—154 specimens (11, 41.8–74.9).

PERU. *Madre de Dios:* Provincia Manu, stream tributary to Río Alto Madre de Dios, approximately 1.5 km upstream from Erika (latter locality at approximately 12°53′S, 71°12′W), between Salvacion and Atalaya, USNM 302792, 36. Provincia Manu, Río Manu basin, Quebrada Pachija, at and above its mouth (approximately 11°57′S, 71°17′W), USNM 302785, 2. Provincia Manu, Quebrada Culli, left bank tributary of Río Alto Madre de Dios, 1.5 km upriver from Erika (latter locality at approximately 12°53′S, 71°12′W), USNM 317781, 6. Provincia Manu, Río Alto Madre de Dios, 15 km upstream from Boca Manu (12°19′30″S, 70°58′W), ANSP 143755, 7. Carabaya, Río Inambari, BMNH 1902.11.28:24, 1 (74.9). *Cusco:* Provincia Quispicanchis, Valley of Río Marcapata, BMNH 1902.5.29:208–209, 2 (60.5–73.8). Provincia Paucartambo, Río Tono, at Hacienda San Jorge, 4 km W on road from Patria (12°53′S, 71°27′W), ANSP 143762, 2 (44.0–56.8); ANSP 151518, 2. Provincia Paucartambo, Río Pilcopata, 3 km above Pilcopata (12°56′30″S, 71°24′W), ANSP 143752, 1 (65.5). Provincia Paucartambo, Pilcopata, Río Hospital, MUSM 10757, 1. *Puno:* Provincia Sandia, Río Inambari, Muspaypampa, MUSM 5673, 12 (5, 41.8–72.3). Provincia Sandia, Santa Elena, Huinchusmayo, MUSM 5674, 15; USNM 340954, 5. Provincia Sandia, Zona Reservada Tambopata Candamo, quebrada tributary to Río Candamo (13°25′S, 70°01′W), MUSM 12931, 14. Provincia Sandia, Zona Reservada Tambopata Candamo, quebrada tributary to Río Candamo (13°24′S, 70°01′W), MUSM 10362, 15; USNM 344537, 5. Provincia Sandia, Zona Reservada Tambopata Candamo, Río Beshuajali (approximately 13°25′S, 70°01′W), MUSM 10341, 23; USNM 344536, 5.

Creagrutus veruina, new species

FIGURES 90, 91, TABLE 56

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 5 teeth in the primary series of each premaxilla, 2 or 3 maxillary teeth, 4 teeth on each dentary, 9 predorsal median scales, 39 lateral line scales without a lamellar process over each pore, 4 scale rows between the dorsal-fin origin and the lateral line, 2 scale rows between the anal-fin origin and the lateral line, 11 branched anal-fin rays, 5 or 6 gill rakers on the upper limb of the first gill arch and 10 or 11 gill rakers on the lower limb of the first gill arch, 37 or 38 vertebrae, the distance from the dorsal-fin origin to the anal-fin origin (24.6%–25.3% of SL), the distance from the dorsal-fin origin to the pelvic-fin insertion (18.7%–20.2% of SL), the distance from the dorsal-fin origin to the pectoral-fin insertion (28.9%–30.2% of SL), the caudal peduncle depth (9.2%–9.4% of SL), the pectoral-fin length (16.9%–17.5% of SL), the pelvic-fin length (12.8%–13.5% of SL), the dorsal-fin length (17.2%–18.0% of SL), the anal-fin length (12.8%–14.6% of SL), the postorbital head length (38.6%–41.9% of HL), the snout length (30.8%–32.1% of HL), the interorbital width (24.8%–26.8% of HL), the near contact of the ventral margin of the third infraorbital with the horizontal limb of the preopercle in larger specimens, the absence of a distinct spot of dark pigmentation at the base of the middle caudal-fin rays, the vertically elongate humeral mark without a secondary, dorsal patch of pigmentation, the absence of a distinct patch of pigmentation on the dorsal fin, and the absence of a series of dark spots along the midlateral surface of the body distinguishes *Creagrutus veruina* within the clade formed by *Creagrutus* and *Piabina.*

DESCRIPTION.—Morphometric and meristic data for *Creagrutus veruina* in Table 56. Head and body relatively elongate, more so in smaller individuals. Greatest body depth at dorsal-fin origin in most individuals of all sizes, shifted anteriorly in one specimen with distended abdomen. Dorsal profile of head convex from margin of upper lip to vertical through anterior margin of eye, convexity slightly more pronounced in smaller individuals; convex from vertical through anterior margin of eye to tip of supraoccipital spine in smaller specimens, barely convex or straight in that region in larger individuals. Interorbital region transversely convex; convexity more pronounced in smaller specimens. Dorsal profile of body nearly straight from tip of supraoccipital spine to dorsal-fin origin, without change in alignment relative to dorsal profile of head. Dorsal surface of body with obtuse median keel proximate to dorsal-fin origin. Ventral profile of head with obtuse angle at anteroventral corner of dentary; straight or slightly convex from that point to isthmus Profile of prepelvic portion of body typically straight, convex in specimen with distended abdomen.

TABLE 56.—Morphometrics and meristics of *Creagrutus veruina*, new species: (A) holotype of *C. veruina*, new species, MBUCV V-29072; and (B) paratypes of *C. veruina* (n=4). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	44.7	26.9–41.1
1. Snout to anal-fin origin	62.1	61.6–62.0
2. Snout to pelvic-fin insertion	45.9	45.7–47.0
3. Snout to pectoral-fin insertion	22.6	23.0–24.1
4. Snout to dorsal-fin origin	44.7	45.0–47.0
5. Dorsal-fin origin to hypural joint	55.3	56.1–57.9
6. Dorsal-fin origin to anal-fin origin	24.8	24.6–25.3
7. Dorsal-fin origin to pelvic-fin insertion	19.0	18.7–20.2
8. Dorsal-fin origin to pectoral-fin insertion	30.2	28.9–30.1
9. Caudal peduncle depth	9.4	9.2–9.4
10. Pectoral-fin length	17.5	16.9–17.5
11. Pelvic-fin length	13.0	12.8–13.5
12. Dorsal-fin length	17.2	17.4–18.0
13. Anal-fin length	12.8	13.2–14.6
14. Head length	26.2	26.0–26.5
15. Postorbital head length	41.9	38.6–40.9
16. Snout length	30.8	31.2–32.1
17. Bony orbital diameter	35.9	34.9–36.1
18. Interorbital width	24.8	25.0–26.8
	Meristics	
Lateral line scales	39	39[a,b]
Scale rows between dorsal-fin origin and lateral line	4	4[a,c]
Scale rows between anal-fin origin and lateral line	2	2[c]
Predorsal median scales	9	9[c]
Branched dorsal-fin rays	8	8[c]
Branched anal-fin rays	11	11[c]
Branched pelvic-fin rays	7	6–7[c]
Pectoral-fin rays	13	13[c]
Vertebrae	38	37–38[d]

Prepelvic region of body obtusely flattened transversely in larger individuals.

Head obtusely pointed in both lateral and dorsal views. Upper jaw longer than, and overhanging, lower jaw. Papillae present on anteromedial portions of snout, but more concentrated on upper lip and on folds and plicae extending between outer and medial premaxillary teeth; papillae well developed on anteroventral portion of lower jaw, more concentrated on margin of lower lip. Orbit ovoid and slightly longer along its anteroposterior axis.

Infraorbital series moderately developed. Third infraorbital with posteroventral margin rounded; ventral margin distinctly separated from horizontal limb of preopercle in smaller specimens, anteroventral margin of bone approaching horizontal limb of preopercle in larger specimens. Posterior margin of third through fifth infraorbitals falling short of vertical limb of preopercle; gap progressively decreasing dorsally.

Premaxillary dentition in three series: primary series with 5 teeth arranged in slightly sigmoid pattern, teeth without pronounced gap between first and second tooth of series but with medial tooth separated from contralateral series by distinct gap, 3 anterior teeth unicuspidate with tips posteriorly recurved and fourth and fifth teeth with poorly developed lateral cusps; triangular cluster of 3 larger teeth with anterior tooth unicuspidate with slight lateral expansions in positions typically occupied by lateral cusps, and two posterior teeth with weak lateral cusps; and single unicuspidate tooth occurring lateral to third tooth of primary premaxillary row. Maxilla with 2 or 3 tricuspidate teeth. Dentary teeth difficult to examine because of lack of cleared and stained specimens; apparently 4 dentary teeth with first three teeth distinctly larger than fourth tooth; second tooth somewhat higher and wider than first tooth and distinctly larger than third tooth.

Dorsal-fin rays ii,8 in all examined specimens. Dorsal-fin origin slightly posterior to vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin slightly concave. Anal-fin rays ii,11 in all specimens. Profile of distal margin of anal fin concave. Anal-fin hooks present in mature males of many *Creagrutus* species not apparent in limited available population sample. Pectoral-fin rays i,12. Tip of pectoral fin reaching posteriorly approximately three-fourths of distance to pelvic-fin insertion. Pelvic-fin rays i,6 or 7 in holotype and paratypes; count cannot be determined in nontypes. Tip of pelvic fin reaching posteriorly to within 2 scales of anal-fin insertion. Anal-fin hooks present in mature males of many *Creagrutus* species not apparent in examined material.

Gill rakers 5–6+0–11.

COLORATION IN ALCOHOL.—Ground coloration light tan. Dorsal surface of head with stellate, dark chromatophores overlying brain in smaller specimens, chromatophores relatively smaller and partially obscured by intracranial adipose deposits in larger individuals. Surface of head with scattered chromatophores in larger individuals. Chromatophores somewhat more concentrated anterior to nares, but not forming dark, crescent-shaped patch of pigmentation present in that area in many congeners. Region anteroventral to nares with few chromatophores, but these not forming distinct stripe present in that region in many *Creagrutus* species. Dorsal portions of both infraorbital series and opercle with scattered chromatophores in smaller individuals, chromatophore field more concentrated in larger specimens.

Dorsalmost series of body scales in larger specimens outlined with dark chromatophores. Smaller individuals (18.6–21.4 mm SL) with a few scattered chromatophores in region of humeral mark; large individuals with vertically elongate humeral mark. Humeral mark ventrally attenuate and most intensely pigmented immediately dorsal to lateral line, somewhat expanded and anteriorly arching dorsally. Larger specimens with diffuse, dark pigmentation along midlateral portion of body. Caudal-fin base with diffuse vertical line of deep-lying pigmentation in smaller individuals, pigmentation masked in larger specimens. Distal portions of dorsal and anal fins with scattered chromatophores in larger specimens. Rays of dorsal and ventral portions of caudal fin outlined with small, dark chromatophores in larger specimens that also have dusky middle caudal-fin rays. Pectoral and pelvic fins hyaline.

FIGURE 91.—*Creagrutus veruina,* new species, holotype, MBUCV V-29072, 44.7 mm SL; Venezuela, Amazonas, Río Cataniapo, 200 m above Las Pavas.

COMPARISONS.—*Creagrutus veruina* shares similar dentition and overall body form with *C. runa,* which is endemic to the upper Rio Negro of the Amazon basin. The two species can be distinguished by differences in the number of branched anal-fin rays (11 in *C. veruina* versus 9 or 10 in *C. runa*), differences in the form of the humeral mark (compare Figures 85 and 91), the distance from the snout to the anal-fin origin (61.6%–62.1% of SL in *C. veruina* versus 64.4%–68.8% of SL in *C. runa*), and the distance from the snout to the pectoral-fin insertion (22.6%–24.1% of SL in *C. veruina* versus 24.3%–27.2% of SL in *C. runa*).

The only other species of *Creagrutus* known from the Río Cataniapo basin is *C. provenzanoi,* which was collected at various localities in that basin. The species are apparently syntopic, at least to a degree, because a paratype of *C. provenzanoi* was captured along with the type series of *C. veruina. Creagrutus veruina* can be distinguished from *C. provenzanoi* by the form of the humeral mark (bar-like in *C. veruina* versus expanded and rounded immediately above lateral line in *C. provenzanoi*), the number of scales below the lateral line to the anal-fin origin (2 versus 3, respectively), and various morphometric features (compare Tables 51 and 56).

ETYMOLOGY.—The species name, *veruina,* from the Latin for small javelin, refers to the elongate overall form of the species.

ECOLOGY.—One of the nontype species of *Creagrutus veruina* was captured in moderate to swift current over a rock and mud bottom with submerged vegetation.

DISTRIBUTION.—*Creagrutus veruina* is known only from the Río Cataniapo, an east bank tributary of the middle Río Orinoco is southern Venezuela (Figure 90, open star).

REMARKS.—In addition to the type series, three lots (MCNG 7613; ANSP 159829; ANSP 165531) of smaller specimens originated within the Río Cataniapo basin and were examined during this study. The specimens in these three lots mostly lack scales, and some are in poor overall condition, making a definitive identification problematic. The specimens, however, agree with *Creagrutus veruina* in vertebral counts and the other meristic features that can be unambiguously counted, and the four largest specimens (ANSP 159829; ANSP 165531) also demonstrate the vertical humeral bar present in the type series of *C. veruina.* Furthermore, these samples are quite distinct from *C. provenzanoi,* the second member of the genus present in the Río Cataniapo basin. Consequently they are tentatively identified as *C. veruina.*

MATERIAL EXAMINED.—25 specimens (5, 26.8–44.7; only meristics taken on some of the nontype specimens as a consequence of their condition; see under "Remarks," above).

HOLOTYPE.—VENEZUELA. *Amazonas:* Río Cataniapo, 200 m above Las Pavas, collected by R. Royero et al., 24 Dec 1983, MBUCV V-29072, 1 (44.7).

PARATYPES.—4 specimens (4, 26.8–41.1).

VENEZUELA. *Amazonas:* Río Cataniapo, 200 m above Las Pavas, collected with holotype, MBUCV V-14638, 2 (2, 26.9–41.1); USNM 355120, 2 (26.8–30.8).

NONTYPE SPECIMENS.—20 specimens.

VENEZUELA. *Amazonas:* Río Cataniapo, Caño Carinagua, MCNG 7613, 16. Río Cataniapo, approximately 3.0 km S of Puerto Ayacucho (5°35′N, 67°35′W), ANSP 165531, 1. Río Cataniapo, at bridge on Puerto Ayacucho-Samariapo highway, approximately 3.0 km S of Puerto Ayacucho (5°32′N, 67°31′W), ANSP 159829, 3.

Creagrutus vexillapinnus, new species

FIGURES 90, 92, TABLE 57

DIAGNOSIS.—The distinct patch of black pigmentation on the central portions of the posterior unbranched and anterior branched dorsal-fin rays autapomorphically distinguishes *Creagrutus vexillapinnus* from its congeners. In addition to this unique pigmentation pattern, the combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 2 or 3 teeth on the maxilla, 6 teeth in the primary tooth row of the premaxilla, 6 dentary teeth, 39 to 41 lateral line scales without a lamellar process over each pore, 8 or 9 predorsal median scales 4 scale rows between the dorsal-fin origin and the lateral line, 37 to 39 vertebrae, 12 to 14 branched anal-fin rays, 2 post-anal median scales to the

TABLE 57.—Morphometrics and meristics of *Creagrutus vexillapinnus*, new species: (A) holotype of *C. vexillapinnus*, MZUSP 29894; (B) paratypes of *C. vexillapinnus* (n=5); and (C) nontype specimens of *C. vexillapinnus* from Rio Orinoco basin (n=17; meristics and morphometrics from all nontype specimens, morphometrics solely from MCNG 27888, n=11). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B	C
		Morphometrics	
Standard length	50.4	33.3–42.0	28.1–43.6
1. Snout to anal-fin origin	59.9	60.4–62.4	59.8–62.5
2. Snout to pelvic-fin insertion	45.6	46.1–47.2	45.3–48.6
3. Snout to pectoral-fin insertion	24.6	24.6–25.8	24.9–27.5
4. Snout to dorsal-fin origin	46.6	46.1–47.7	46.3–48.6
5. Dorsal-fin origin to hypural joint	57.9	55.7–58.0	54.1–57.8
6. Dorsal-fin origin to anal-fin origin	34.7	32.1–34.5	29.3–33.3
7. Dorsal-fin origin to pelvic-fin insertion	30.9	27.4–29.0	25.7–30.0
8. Dorsal-fin origin to pectoral-fin insertion	33.5	31.8–32.9	30.2–33.5
9. Caudal peduncle depth	11.9	10.7–11.2	10.2–11.7
10. Pectoral-fin length	19.2	18.6–19.2	18.0–20.7
11. Pelvic-fin length	15.7	13.6–15.0	14.2–15.8
12. Dorsal-fin length	17.3	18.0–22.2	21.6–23.5
13. Anal-fin length	20.8	17.3–21.8	16.9–19.6
14. Head length	25.2	26.0–27.8	24.9–27.8
15. Postorbital head length	42.5	39.1–41.9	36.0–40.6
16. Snout length	29.1	26.8–29.0	26.0–29.2
17. Bony orbital diameter	37.1	37.6–39.1	35.7–42.5
18. Interorbital width	30.7	28.7–29.5	29.4–32.7
		Meristics	
Lateral line scales	40	38–40	39–41
Scale rows between dorsal-fin origin and lateral line	4	4	4
Scale rows between anal-fin origin and lateral line	3	3	3
Predorsal median scales	9	9	8–9[1]
Branched dorsal-fin rays	8	8	8
Branched anal-fin rays	12	12	12–14
Branched pelvic-fin rays	6	6	6
Pectoral-fin rays	13	13	12–14
Vertebrae	39	38–39	37–38

[1]One specimen with median scale series shifted out of alignment and not symmetrical about sagittal plane having 7 predorsal median scales.

anal-fin origin, 6 to 8 gill rakers on the upper limb of the first gill arch, the distance from the dorsal-fin origin to the pelvic-fin origin (25.7%–30.9% of SL), the distance from the dorsal-fin origin to the anal-fin origin (29.3%–34.7% of SL), the distance from the snout to the pectoral-fin insertion (24.6%–27.5% of SL), the distance from the dorsal-fin origin to the pectoral-fin insertion (30.2%–33.5% of SL), the dorsal-fin length (17.3%–23.5% of SL), the postorbital head length (36.0%–42.5% of HL), the bony orbital diameter (35.7%–42.5% of HL), the well-developed third infraorbital with its ventral margin approaching, or contacting, the horizontal limb of the preopercle, the lack of a series of dark midlateral spots on the body, and the vertically elongate, slightly ventrally attenuating humeral mark with straight anterior and posterior margins distinguishes *Creagrutus vexillapinnus* within the clade composed of *Creagrutus* and *Piabina*.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus vexillapinnus* in Table 57. Body relatively deep compared with many congeners, becoming proportionally deeper ontogenetically. Greatest body depth at dorsal-fin origin. Dorsal profile of head smoothly convex from margin of upper lip approximately to vertical through posterior nostril; degrec of convexity greater in larger specimens. Head profile nearly straight from above posterior nostril to tip of supraoccipital spine. Interorbital region gently convex transversely. Predorsal profile of body of smaller individuals nearly straight and smoothly continuing profile of posterior portion of head; profile in larger individuals distinctly convex, with notable change in alignment relative to dorsal profile of head. Postdorsal profile of body nearly straight in specimens of all sizes. Ventral profile of head with rounded obtuse angle delimiting anteroventral angle of dentary and nearly straight from that angle to isthmus. Prepelvic profile convex; convexity more pronounced in larger individuals.

Head obtusely pointed in both lateral and dorsal views. Upper jaw longer than, and overhanging, lower jaw. Anterior portion of snout fleshy, more so in larger individuals, with field of scattered papillae anteromedially. Papillae more concentrated

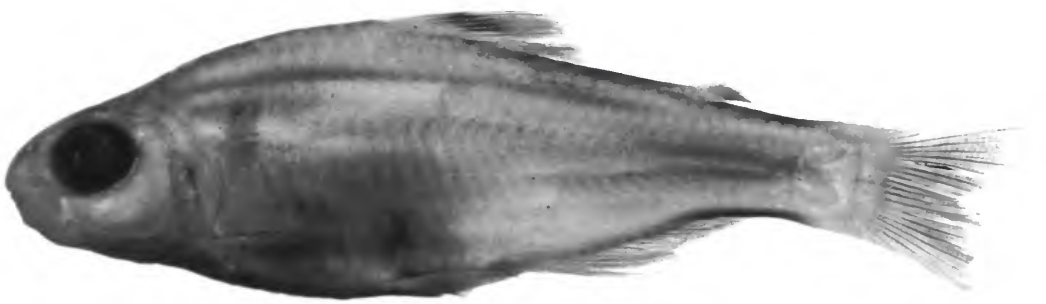

FIGURE 92.—*Creagrutus vexillapinnus*, new species, holotype, MZUSP 29894, 50.4 mm SL; Brazil, Amazonas, Rio Negro, Cachoeira de São Gabriel (0°08'S, 67°05'W).

along upper and lower lips and on folds and plicae extending between outer and medial premaxillary teeth. Lower lip very fleshy, particularly anteriorly, with scattered papillae anteromedially.

Infraorbital series moderately well developed. Ventral margin of third infraorbital ranging from falling slightly short of, to being in contact with, horizontal limb of preopercle. Posterior margins of third through fifth infraorbitals falling short of vertical limb of preopercle; extent of gap between infraorbitals and preopercle decreasing progressively dorsally.

Premaxillary dentition in three series: primary row consisting of 6 teeth arranged in slight curve without pronounced gap between first and second teeth of series; cluster of 3 larger teeth with posterolateral tooth largest; and single tooth of form similar to that of primary series, lateral to fourth tooth of primary series. Maxilla with 2 or 3 tricuspidate teeth. Dentary with 6 teeth; anterior 3 teeth tricuspidate and distinctly larger than remaining teeth; first and second teeth distinctly larger than third tooth, with second tooth somewhat larger than first tooth. Fourth through sixth teeth graded in size; fourth and fifth teeth tricuspidate and sixth tooth conical.

Dorsal-fin rays ii,8. Dorsal-fin origin approximately at vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin slightly concave in smaller individuals, concavity more pronounced in larger specimens. Anal-fin rays ii,12–14 or iii,13–14. Profile of distal anal-fin margin distinctly concave, with last unbranched and anterior 2 or 3 branched rays forming distinct lobe. Anterior 1 to 3 branched anal-fin rays in mature males with 1 or 2 bilaterally paired hooks. Hooks restricted to posterolateral surface of main shaft of ray. Pectoral-fin rays i,11–13. Tip of pectoral fin extending posteriorly nearly to pelvic-fin insertion in smaller specimens, falling distinctly short of that point in larger specimens. Pelvic-fin rays i,6,i in all specimens. Tip of pelvic fin extending posteriorly to anus in smaller specimens; falling somewhat short of that point in larger specimens. Mature males with pelvic-fin hooks, when present, located on both segmented and unsegmented portions of all branched rays; limited to medial branches of rays, with 1 or 2 hooks per segment.

Gill rakers 6–8 + 11–13.

COLORATION IN ALCOHOL.—Overall ground coloration light tan. Dorsal surface of head with scattered, small, dark, superficial chromatophores. Membranes overlying dorsal surface of brain covered by somewhat larger chromatophores in smaller specimens, these masked by thickened bones and connective tissue in adults. Concentration of dark surface chromatophores on dorsal surface of head greater anteriorly, but overall intensity of pigmentation not as pronounced as in many congeners. Chromatophores more concentrated anterior to nares, but not forming obvious crescent-shaped patch of dark pigmentation present in many *Creagrutus* species. Some irregularly situated dark chromatophores immediately ventral and posterior to orbit, but these, again, not forming distinct curved band present in many congeners. Fifth infraorbital and dorsal portion of opercle covered with scattered, dark chromatophores.

Dorsal and dorsolateral portions of body with field of scattered, dark chromatophores; posterior margin of scales in these areas with slightly denser series of chromatophores forming very faint reticulate pattern. Humeral mark faint, vertically elongate and variably attenuate ventrally. Humeral mark extending approximately 2 scales dorsal of lateral line and up to 1 scale ventral of lateral line.

Dorsal fin with distinct black patch extending across central portions of fin from membrane between first and second unbranched dorsal-fin rays posteriorly to membrane between fifth and sixth branched rays; dark pigmentation most intense on membranes but with portions of rays incorporated into patch partially overlain by dark chromatophores. Remaining portions of dorsal fin either hyaline or with scattered, dark chromatophores. Caudal fin with scattered chromatophores, some specimens with slightly greater concentration of dark chromatophores on basal portions of middle caudal-fin rays. Anal fin

hyaline or with scattered, small, dark, chromatophores. Pectoral and pelvic fins hyaline.

ETYMOLOGY.—The specific name, *vexillapinnus,* from the Latin, vexillum, for flag, and pinna, fin, is in reference to the prominent black spot on the dorsal fin.

DISTRIBUTION.—*Creagrutus vexillapinnus* is known from the upper portions of the Rio Negro in Brazil and Venezuela and the upper portions of the Río Orinoco in Venezuela (Figure 90, squares; see also comments under "Geographic Variation" following).

GEOGRAPHIC VARIATION.—The type series of *Creagrutus vexillapinnus* was collected at various localities along the upper Rio Negro within Brazil. In addition, two lots from the Río Orinoco basin (ANSP 162052, 6 specimens; MCNG 27888, 11 specimens), both consisting of specimens all smaller in body size than the type series, are apparently conspecific with *C. vexillapinnus.* Despite the small sample sizes, it is noteworthy that the Río Orinoco specimens tend to have modally fewer vertebrae (37, n=6; 38, n=11) than found in the samples of *C. vexillapinnus* from the Rio Negro (38, n=2; 39, n=4). The condition and relatively small body sizes of the specimens from the Río Orinoco makes it impossible, however, to take most counts and measurements with an accuracy comparable to those for the Rio Negro samples. The comparisons between the Río Orinoco sample and the Rio Negro specimens, nonetheless, show shifted, albeit overlapping, values in the relative length of the dorsal fin and the relative postorbital length (Table 57). Additional samples from intervening areas are necessary to determine whether these differences between the samples from the Rio Negro and Río Orinoco represent clinal variation or perhaps the existence of two species.

MATERIAL EXAMINED.—23 specimens (18, 28.1–50.4).

HOLOTYPE.—BRAZIL. *Amazonas:* Rio Negro, Cachoeira de São Gabriel (0°08′S, 67°05′W), collected by M. Goulding, 20 May 1979, MZUSP 29894, 1 (50.4).

PARATYPES.—5 specimens (5, 33.3–42.0).

BRAZIL. *Amazonas:* Rio Negro basin, Rio Marauiá, Cachoeira do Bicho-Açú (approximately 0°20′S, 65°20′W), collected by M. Goulding, 12 Dec 1979, MZUSP 29896, 1 (38.6); USNM 341360, 1 (33.6). Rio Negro basin, Rio Marauiá, Cachoeira do Bicho-Açú (approximately 0°20′S, 65°20′W), collected by M. Goulding, Oct 1979, MZUSP 31220, 1 (33.3). Rio Negro, praia de Urumari, above Barcelos (0°30′S, 63°30′W), collected by M. Goulding, 6 Dec 1979, MZUSP 29893, 1 (39.6); USNM 341361, 1 (42.0; specimen cleared and counterstained for cartilage and bone).

NONTYPE SPECIMENS.—17 specimens (12, 28.1–43.6).

VENEZUELA. *Amazonas:* main channel of Río Casiquiare, approximately 1.5 hr from its confluence with the Río Orinoco (3°05′N, 65°55′W), ANSP 162052, 6 (1, 29.0). Río Mavaca, Caño Huayapiwei (02°11′30″N, 65°06′W), MCNG 27888, 11 (28.1–43.6).

Creagrutus xiphos, new species

FIGURES 90, 93, TABLE 58

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 6 teeth in the primary series of each premaxilla, 3 maxillary teeth, 5 teeth on each dentary, 9 predorsal median scales, 36 or 37 lateral line scales without a lamellar process over each pore, 4 scale rows between the dorsal-fin origin and the lateral line, 3 scale rows between the anal-fin origin and the lateral line, 9 or 10 branched anal-fin rays, 6 gill rakers on the upper limb of the first gill arch, 10 or 11 gill rakers on the lower limb of the first gill arch, the distance from the dorsal-fin origin to the anal-fin origin (28.6%–29.5% of SL), the distance from the dorsal-fin origin to the pelvic-fin insertion (25.6%–28.0% of SL), the distance from the dorsal-fin origin to the pectoral-fin insertion (30.9%–32.1% of SL), the caudal peduncle depth (10.8%–11.7% of SL), the anal-fin length

TABLE 58.—Morphometrics and meristics of *Creagrutus xiphos,* new species: (A) holotype of *C. xiphos,* ANSP 165815; and (B) paratypes of *C. xiphos* (n=3). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	27.7	18.9–26.5
1. Snout to anal-fin origin	64.0	63.9–65.5
2. Snout to pelvic-fin insertion	48.1	48.0–50.9
3. Snout to pectoral-fin insertion	26.9	26.2–27.8
4. Snout to dorsal-fin origin	48.7	48.0–50.3
5. Dorsal-fin origin to hypural joint	53.1	53.0–54.3
6. Dorsal-fin origin to anal-fin origin	28.7	28.6–29.5
7. Dorsal-fin origin to pelvic-fin insertion	27.6	25.6–28.0
8. Dorsal-fin origin to pectoral-fin insertion	31.0	30.9–32.1
9. Caudal peduncle depth	11.2	10.8–11.7
10. Pectoral-fin length	18.7	18.5–19.3
11. Pelvic-fin length	15.2	15.0–16.5
12. Dorsal-fin length	22.8	21.8–23.1
13. Anal-fin length	14.5	15.0–17.9
14. Head length	27.6	27.1–28.0
15. Postorbital head length	39.8	37.9–39.7
16. Snout length	28.3	28.6–29.0
17. Bony orbital diameter	38.1	37.7–38.9
18. Interorbital width	29.5	30.1–32.0
	Meristics	
Lateral line scales	37	36–37
Scale rows between dorsal-fin origin and lateral line	4	4
Scale rows between anal-fin origin and lateral line	3	3
Predorsal median scales	9	9
Branched dorsal-fin rays	8	8
Branched anal-fin rays	9	9–10
Branched pelvic-fin rays	6	5–6
Pectoral-fin rays	12	12–13
Vertebrae	37	36–37

FIGURE 93.—*Creagrutus xiphos*, new species, holotype, ANSP 165815, 27.7 mm SL; Venezuela, Bolivar, sand bank along Río Mato (7°02'N, 65°13'W).

(15.0%–17.9% of SL), the postorbital head length (37.9%–39.8% of HL), the bony orbital diameter (37.7%–38.9% of HL), the proximity but lack of contact between the ventral margin of the third infraorbital and the horizontal limb of the preopercle, the absence of a distinct spot of dark pigmentation at the base of the middle caudal-fin rays, the vertically elongate humeral mark without a secondary, dorsal patch of pigmentation, the absence of a distinct patch of pigmentation on the dorsal fin, and the lack of a series of dark spots along the midlateral surface of the body distinguishes *Creagrutus xiphos* within the clade formed by *Creagrutus* and *Piabina*.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus xiphos* in Table 58. Head and body moderately elongate, more so in smaller specimens. Greatest body depth at dorsal-fin origin in paratypes, located anterior of that point in holotype with expanded abdomen. Dorsal profile of head distinctly convex from margin of upper lip to vertical through anterior nostril, slightly convex from that point to rear of supraoccipital. Interorbital region slightly convex. Dorsal profile of body very slightly convex from supraoccipital to dorsal-fin origin, without pronounced change in alignment relative to dorsal profile of head. Predorsal surface of body with obtuse median keel in larger examined specimens. Ventral profile of head with distinct obtuse angle at anteroventral corner of dentary, straight to very slightly convex from that point to isthmus. Prepelvic profile slightly convex in paratypes, distinctly convex in holotype, which has expanded abdominal region. Prepelvic region flattened to distinctly convex transversely depending on degree of distension of abdomen.

Head obtusely pointed in lateral view, somewhat more compressed transversely in dorsal view. Upper jaw longer than, and overhanging, lower jaw. Snout papillae broadly distributed over anterior portion of snout, increasingly so medially. Numerous papillae present on ventral margin of upper lip and on fleshy folds and plicae extending between outer and medial premaxillary teeth. Anteromedial portion of lower jaw with scattered papillae, and dorsal margin of lower lip with more concentrated papillae.

Infraorbital series moderately developed. Third infraorbital horizontally elongate with ventral and posterior margins approximately matching curvature of corresponding margin of orbital rim. Ventral and posterior margins of third infraorbital approaching, but not contacting, horizontal and vertical limbs of preopercle, respectively; gap between margin of infraorbital and preopercle somewhat greater posteriorly. Posterior margins of fourth and fifth infraorbitals separated from vertical limb of preopercle. No notable variation in degree of development of infraorbital series apparent across size range of available specimens.

Premaxillary dentition in three series: primary series curved and without pronounced gap between first and second teeth of series, with 6 tricuspidate teeth and medial tooth separated from contralateral series by distinct gap; triangular cluster of 3 teeth, larger than those of primary series; and single tooth of form similar to that of primary series occurring lateral to fourth tooth of primary premaxillary row. Maxilla with 3 tricuspidate teeth. Dentary apparently with five tricuspidate teeth (exact count of dentary teeth and determination of form of posterior dentary teeth hampered by lack of specimens for clearing and staining). First tooth about three-fourths height of second tooth, second tooth approximately twice as high, and much more massive than, third tooth.

Dorsal-fin rays ii,8 in all specimens. Dorsal-fin origin approximately at vertical through pelvic-fin insertion. Profile of distal margin of dorsal fin straight or very slightly concave. Anal-fin rays ii,9–10. Profile of distal margin of anal fin slightly concave. Single mature male paratype with hooks on first branched anal-fin ray. Pectoral-fin rays i,11–12. Tip of pectoral fin reaching posteriorly to point about 2 scales anterior of pelvic-fin insertion. Pelvic-fin rays i,5,i or i,6,i. Tip of pelvic fin reaching posteriorly to, or falling slightly short of, anal-fin origin. Single mature male with hooks on all branched pelvic-fin rays.

Gill rakers 6 + 10–11.

COLORATION IN ALCOHOL.—Ground coloration light tan. Dorsal surface of head in smallest specimens with patches of

relatively large dark chromatophores on membranes overlying brain. Chromatophore field becoming more intense over posterior portion of brain in larger individuals. Snout and upper lip with scattered, dark chromatophores in small specimens; chromatophore field somewhat more concentrated in larger specimens and forming moderately developed crescent-shaped, dark mark along base of anterior nostril. Irregular stripe of dark chromatophores extending from under nostrils to anteroventral margin of orbit in larger specimens. Remainder of head either lacking dark chromatophores, or with few scattered chromatophores in region posterior of orbit.

Scale margins along dorsal portions of body in larger specimens outlined with small, dark scales, but not forming well-developed reticulate pattern present in many congeners. Dark pigmentation most developed proximate to middorsal region anterior to dorsal fin and particularly along dorsal-fin base. Scale margins on lateral surface of body with scattered, dark chromatophores in smaller available specimens, with increased numbers of chromatophores present on posterior two-thirds of lateral surface of body in larger specimens. Humeral mark in form of a vertically elongate ovoid in smallest examined paratype, in form of vertically elongate bar in other paratypes and holotype. Bar vertically aligned with nearly straight anterior and posterior margins. Region between humeral mark and posterior margin of pectoral girdle hyaline. Lateral surface of body between rear of mark and vertical approximately three scales posterior of rear margin of humeral mark also lacking dark chromatophores. Chromatophore field slightly more concentrated along posterior two-thirds of midlateral surface of body, but not forming distinct, dark, midlateral stripe within size range of available specimens.

Dorsal fin with scattered, dark chromatophores along last unbranched and first branched rays and on distal portions of second through fourth rays. Anal fin with basal portions of anal-fin rays outlined with dark chromatophores. Caudal fin with faint dark chromatophores outlining rays of lower lobe of fin; extent of pigmentation difficult to determine as a consequence of damage to fins in all available specimens. Pectoral and pelvic fins hyaline in all specimens.

ECOLOGY.—The type locality was along a sand bar over a substrate of sand and logs in water ranging from 10 to 45 cm deep. One congener, *Creagrutus phasma* (ANSP 139598), was collected with the type series of *C. xiphos*.

ETYMOLOGY.—The species name, *xiphos*, from the Greek for sword or saber, refers to the elongate head and body of the species.

DISTRIBUTION.—*Creagrutus xiphos* is known only from the type locality in the Río Mato in the Río Caura system, a southern tributary of the main Río Orinoco (Figure 90, triangle).

COMPARISONS.—*Creagrutus xiphos* is most similar to *C. zephyrus* of the Rio Negro basin in Venezuela and Brazil. The species differ in the number of vertebrae (36 or 37 in *C. xiphos* versus 38 or 39 in *C. zephyrus*), the distance from the dorsal-fin origin to the anal-fin origin (28.6%–29.5% of SL in *C. xiphos* versus 26.1%–27.9% of SL in *C. zephyrus*), the distance from the dorsal-fin origin to the pelvic-fin insertion (25.6%–28.0% of SL in *C. xiphos* versus 21.4%–25.4% of SL in *C. zephyrus*), and the caudal peduncle depth (10.8%–11.7% of SL in *C. xiphos* versus 9.7%–10.9% of SL in *C. zephyrus*).

Only two species of *Creagrutus* are known from the Río Mato basin, *C. xiphos* and *C. phasma*, which were collected together at the type locality of the former species. Two other species, *C. machadoi* and *C. bolivari* are found in other portions of the Río Caura system. *Creagrutus xiphos* can be distinguished from all of those species by the features cited in "Key to the *Creagrutus* Species of the Río Orinoco Basin."

MATERIAL EXAMINED.—4 specimens (4, 18.9–27.7).

HOLOTYPE.—VENEZUELA. *Bolivar:* Sand bank along Río Mato (7°02'N, 65°13'W), collected by J.E. Böhlke et al., 1 Feb 1977, ANSP 165815, 1 (27.7).

PARATYPES.—3 specimens (3, 18.9–27.7).

VENEZUELA. *Bolivar:* Sand bank along Río Mato (7°02'N, 65°13'W), collected with holotype, ANSP 177717, 3 (18.9–26.5).

Creagrutus zephyrus, new species

FIGURES 90, 94, TABLE 59

Creagrudite maxillaris [not of Myers, 1927].—Myers, 1927:118 [misidentification] [not type series of C. maxillaris, only small specimens from Brazil, Rio Negro].

Creagrutus melanzonus [not of Eigenmann, 1909].—Myers and Roberts, 1967:248 [misidentification] [only smaller specimens in type series of *Creagrudite maxillaris*].—Mago-Leccia, 1970:70 [Venezuela].—Böhlke and Saul, 1975:27 [based on Myers and Roberts, 1967:248].—Géry and Renno, 1989:4 [in part, citation of species from Rio Negro].

DIAGNOSIS.—The combination of the possession of premaxillary dentition arranged in the three components generalized for most of the species of *Creagrutus* and *Piabina* without a distinctly larger gap between the first and second teeth of the primary series, 6 teeth in the primary series of each premaxilla, 3 to 5 maxillary teeth, 5 teeth on each dentary, 8 or 9 predorsal median scales, 40 or 41 lateral line scales without a lamellar process over each pore, 4 scale rows between the dorsal-fin origin and the lateral line, 2 or 3 scale rows between the anal-fin origin and the lateral line, 10 to 12 branched anal-fin rays, 5 to 9 gill rakers on the upper limb of the first gill arch, 11 to 13 gill rakers on the lower limb of the first gill arch, the distance from the snout to the pectoral-fin insertion (24.6%–26.4% of SL), the distance from the dorsal-fin origin to the anal-fin origin (26.1%–27.9% of SL), the distance from the dorsal-fin origin to the pelvic-fin insertion (21.4%–25.4% of SL), the caudal peduncle depth (9.7%–10.9% of SL), the postorbital head length (35.1%–41.0% of HL), the snout length (22.9%–28.6% of HL), the bony orbital diameter (36.9%–40.3% of HL), the proximity of, but lack of contact between, the ventral margin of the third infraorbital and the horizontal limb of the preopercle, the presence of a distinct spot of dark pigmentation at the base of the middle caudal-fin rays, the vertically oriented, elongate bar-

Table 59.—Morphometrics and meristics of *Creagrutus zephyrus*, new species: (A) holotype of *C. zephyrus*, ANSP 161238; and (B) paratypes of *C. zephyrus* (n=16) from which counts and measurements were taken. Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length.

Characters	A	B
	Morphometrics	
Standard length	38.5	25.4–39.8
1. Snout to anal-fin origin	61.8	62.1–63.6
2. Snout to pelvic-fin insertion	47.2	46.2–48.9
3. Snout to pectoral-fin insertion	25.3	24.6–26.4
4. Snout to dorsal-fin origin	45.7	45.4–48.9
5. Dorsal-fin origin to hypural joint	56.8	54.1–56.7
6. Dorsal-fin origin to anal-fin origin	27.9	26.1–27.2
7. Dorsal-fin origin to pelvic-fin insertion	24.0	21.4–25.4
8. Dorsal-fin origin to pectoral-fin insertion	29.8	28.6–31.9
9. Caudal peduncle depth	10.9	9.7–10.9
10. Pectoral-fin length	18.3	15.7–18.8
11. Pelvic-fin length	15.0	14.3–15.8
12. Dorsal-fin length	22.6	20.6–22.4
13. Anal-fin length	16.7	16.7–22.4
14. Head length	25.7	25.8–27.9
15. Postorbital head length	40.6	35.1–41.0
16. Snout length	26.9	22.9–28.6
17. Bony orbital diameter	37.7	36.9–40.3
18. Interorbital width	28.7	27.4–31.4
	Meristics	
Lateral line scales	40	40–41[1]
Scale rows between dorsal-fin origin and lateral line	4	4
Scale rows between anal-fin origin and lateral line	3	2–3
Predorsal median scales	8	8–9
Branched dorsal-fin rays	8	8
Branched anal-fin rays	12	10–11
Branched pelvic-fin rays	7	6–7
Pectoral-fin rays	12	13–15
Vertebrae	39	38–39

[1]Scales mostly missing in many paratypes so count estimated from scale pockets.

like humeral mark without a secondary, dorsal patch of pigmentation, the absence of a distinct patch of pigmentation on the dorsal fin, and the lack of a series of dark spots along the midlateral surface of the body distinguishes *Creagrutus zephyrus* within the clade formed by *Creagrutus* and *Piabina*.

DESCRIPTION.—Morphometric and meristic data for *Creagrutus zephyrus* in Table 59. Body moderately deep, more so in larger specimens, and somewhat compressed laterally in all available specimens. Greatest body depth at, or slightly anterior of, dorsal-fin origin. Dorsal profile of head distinctly convex from margin of upper lip to vertical through posterior margin of posterior nares, slightly convex from that point to tip of supraoccipital spine. Predorsal profile slightly convex to anterior of dorsal-fin base, straight to slightly concave from rear of dorsal-fin base to anterior of adipose-fin base, straight to slightly concave from rear of adipose fin to vertical through anterior procurrent caudal-fin rays. Ventral profile of head with distinct obtuse angle of about 120 degrees approximately midway between margin of lower lip and posterior of dentary, slightly convex from that point to isthmus. Ventral profile of body slightly convex from isthmus approximately to anal-fin origin; slightly concave from that point to caudal peduncle.

Snout in the form of broadly rounded obtuse angle with its apex located at dorsalmost point on premaxilla. Upper jaw slightly longer than, and overhanging, lower jaw, with anterior premaxillary teeth anterior to lower lip. Most external surfaces of head covered with minute papillae; papillae most concentrated on lips. Anterior portion of snout relatively firm and without concentration of soft tissues, with minute papillae present on snout and upper lip, papillae continuing into mouth on fleshy flaps between outer and medial premaxillary teeth. Lower jaw distinctly fleshy anteriorly, inner surfaces of lower lip convolute, with papillose flaps as present on upper lip.

Infraorbital series moderately well developed, with ventral margin of third infraorbital separated from ventral limb of preopercle by distinct but narrow gap. Posterior margin of third infraorbital distinctly separated from vertical limb of preopercle by space equal to about one-fourth of the width of fourth and fifth infraorbital bones; posterior and ventral margins of third infraorbital broadly rounded, describing arc of curvature greater than that of orbit. Fourth and fifth infraorbitals narrowly separated from vertical limb of preopercle.

Premaxillary teeth in three distinct groups: primary series consisting of 6, rarely 5, tricuspidate teeth in continuous row without pronounced gap between first and second tooth of series; triangular cluster of 3 large tricuspidate teeth; and single outer tooth positioned lateral to fourth tooth of primary series. Maxilla with 3 to 5 tricuspidate teeth. Dentary with 5 or 6 teeth. Dentary teeth either all tricuspidate (when 5 teeth present) or last tooth unicuspidate (when 6 teeth present). First and second dentary teeth largest and subequal, third tooth about one-half height of second tooth, and remaining teeth in series distinctly smaller than three anterior teeth.

Dorsal-fin rays ii,8 in all examined specimens. Dorsal-fin origin located slightly anterior to vertical through pelvic-fin origin. Distal margin of dorsal fin nearly straight, with very slight concavity as result of elongation of first 3 or 4 rays. Anal-fin rays ii,10–12 or iii,10–12. Anal-fin ray hooks present in mature males of many congeners not observed in examined specimens. Distal margin of anal fin slightly sigmoid, with posterior unbranched and anterior 3 or 4 branched rays forming relatively elongate lobe, fin margin along posterior 5 or 6 rays approximately straight. Pectoral-fin rays i,11–14. Pectoral fin short, tip reaching to within 2 or 3 scale rows of pelvic-fin origin. Pelvic-fin rays i,6,i or i,7. Juveniles with tip of pelvic fin falling short of anal-fin origin by 1 or 2 scales; tip of pelvic fin approaching, or reaching, anal-fin origin in larger specimens. Pelvic-fin hooks present in mature males of many congeners not observed in examined specimens.

Gill rakers 5–9+11–13.

COLORATION IN ALCOHOL.—Overall ground color straw, with dark pigment cells ranging from light brown to dark sepia. Dorsal surface of head with diffuse pattern of small, light

brown chromatophores on upper lip and over snout. Distinct, small, crescent-shaped patch of dark chromatophores present immediately in front of anterior nares. Dorsal surfaces of much of frontal and parietal portions of cranium uniformly and densely invested with medium to large, dark brown, deep-lying chromatophores. Frontal portion of dorsal surface of head nearly unpigmented in area directly above anterior one-half of eye. Band of scattered, dark chromatophores extending posteroventrally from immediately lateral of nares and continuing along ventral margin of orbit. Infraorbitals posterior to orbit and dorsal portion of opercle with scattered, large, dark chromatophores. Lower lip and ventrolateral surface of head unpigmented; reflective guanine not observed in association with head or any other body components.

Dark body pigmentation most concentrated dorsally, delineating or forming central, hemispherical patch on scales of 2 dorsalmost scale rows and middorsal scale row; dark pigmentation also present in form of series of crescent-shaped marks on scales flanking dorsal-fin base. Humeral mark usually in form of anteriorly slightly concave, narrow crescent. Pigmentation of mark most concentrated immediately dorsal of lateral line; extending as less intensely pigmented field about 2 scale rows dorsal from central portion of mark, and continuing ventrally as field of increasingly dispersed dark chromatophores to near pectoral-fin base. Region above anal fin with myosepta outlined by widely spaced dark chromatophores. Largest specimens examined (ANSP 161236) exhibit some very fine lines of dark pigmentation along posterior margins of flank scales ventral of lateral line and along either side of lateral line tube. Dark midlateral stripe on body very diffuse anteriorly, becoming denser and somewhat wider posteriorly, but still not very obvious, on caudal peduncle.

Dorsal-fin membranes with dark chromatophores most concentrated on distal one-fourth to one-third of 4 anterior branched rays; unbranched rays darkly pigmented. Unbranched anal-fin rays unpigmented except for small number of dark chromatophores at base of rays and with proximal one-half of branched rays delineated by dark pigmentation along their anterior surfaces. Caudal fin with all fin rays delineated by dark pigmentation, pigmentation darkest on central and ventral rays. Dorsalmost caudal-fin rays with very small, lighter chromatophores, central rays of fin generally darkest, with pigmentation usually forming rotund basal spot. Dark, deep-lying pigmentation forming variably visible, vertical line delineating posterior extremities of hypural plates. Pelvic fin hyaline. Pectoral fin hyaline except for several isolated dark chromatophores on membrane of medial rays.

ETYMOLOGY.—The specific name *zephyrus,* from the Latin for west wind, refers to the distribution of the species in the western portion of the range of three very similar species (*C. melanzonus, C. xiphos,* and *C. zephyrus*), two of which (*C. melanzonus* and *C. zephyrus*) have been considered conspecific by some previous authors.

ECOLOGY.—Specimens of *Creagrutus zephyrus* from several localities in the Río Casiquiare were collected in slightly turbid, sometimes green, waters with slow to moderate current over substrates of sand, mud, leaves, and sticks. Filamentous algae was present at one locality.

Two specimens prepared for clearing and staining in this study (ANSP 161236) had aquatic insect larvae in their stomachs.

DISTRIBUTION.—*Creagrutus zephyrus* is known from portions of the central and upper portions of the upper Rio Negro in Brazil and Venezuela (Figure 90, dots).

COMPARISONS.—*Creagrutus zephyrus* is most similar to *C. xiphos* of the Río Caura in the Río Orinoco basin. The two species differ in the number of vertebrae (38 or 39 in *C. zephyrus* versus 36 or 37 in *C. xiphos*), the distance from the dorsal-fin origin to the anal-fin insertion (26.1%–27.9% of SL in *C. zephyrus* versus 28.6%–29.7% of SL in *C. xiphos*), the distance from the dorsal-fin origin to the pelvic-fin insertion (21.4%–25.4% of SL in *C. zephyrus* versus 25.6%–28.0% of SL in *C. xiphos*), and the caudal-peduncle depth (9.7%–10.9% of SL in *C. zephyrus* versus 10.8%–11.7% of SL in *C. xiphos*).

REMARKS.—In his original description of *Creagrudite maxillaris,* Myers (1927:118) reported that some small specimens that he considered to be that species differed from adults in having a higher number of tooth rows, an unusual ontogenetic shift in dentition among characiforms. Myers and Roberts (1967:248) reported that the smaller specimens were rather a species distinct from *C. maxillaris* and noted that the latter species did not undergo the ontogenetic shift in the number of tooth rows as reported by Myers (1927). The small individuals identified as juveniles of *C. maxillaris* by Myers (1927) were reidentified by Myers and Roberts (1967) as *Creagrutus melanzonus.* The specimens in question originated, however, in the upper Rio Negro. This is within the known range of *C. zephyrus* but is far from the known distribution of *C. melanzonus,* which is apparently endemic to the coastal drainages of eastern Venezuela and the Guianas. Given the external similarities between *C. zephyrus* and *C. melanzonus,* it is likely that the specimens reported on by Myers and Roberts (1967:248) are actually *C. zephyrus.*

Samples from the Rio Negro cited by previous authors as *Creagrutus melanzonus,* the *C. zephyrus* of the present study, have been reported as occurring in the "Upper Orinoco-Upper Negro" region (Myers and Roberts, 1967:248), perhaps because some authors considered the Río Casiquiare to be a portion of the Orinoco basin. All the specimens of *C. zephyrus* we examined came from the Rio Negro and its tributary, the Río Casiquiare; however, some of the specimens that originated in the Río Casiquiare came from localities very close to where the Río Casiquiare forks from the Río Orinoco. The common occurrence of other *Creagrutus* species in the upper portions of the Río Negro and the upper reaches of the Río Orinoco implies that it is likely that *C. zephyrus* also occurs in at least the upper portions of the Río Orinoco basin. We consequently in-

FIGURE 94.—*Creagrutus zephyrus*, new species, holotype, ANSP 161238, 38.5 mm SL; Venezuela, Amazonas, playa and backwater of Río Casiquiare, approximately 2.0 km downstream from mouth of Río Pamoni (2°48′N, 65°57′W).

clude *C. zephyrus* in the identification in "Key to the *Creagrutus* Species of the Río Orinoco Basin."

Mago-Leccia (1970:70) reported *Creagrutus melanzonus* from Venezuela, presumably following Myers and Roberts (1967) whose record of that species in that country was based on specimens originating in the Río Casiquiare in southern Venezuela. The samples from that area previously identified as *C. melanzonus* are considered herein to be *C. zephyrus*. *Creagrutus melanzonus* is, however, present in the Río Cuyuni basin of eastern Venezuela (see account for that species).

MATERIAL EXAMINED.—19 specimens (17, 25.7–39.8).

HOLOTYPE.—VENEZUELA. *Amazonas:* Río Casiquiare, playa and backwater about 2 km downstream from mouth of Río Pamoni (2°48′N, 65°57′W), collected by B. Chernoff et al., 21 Mar 1987, ANSP 161238, 1 (38.5).

PARATYPES.—18 specimens (16, 25.4–39.8).

VENEZUELA. *Amazonas:* Río Casiquiare from mouth of Río Pamoni to 4 km below mouth (02°48′N, 65°57′W), collected by B. Chernoff et al., 17 Mar 1987, ANSP 161236, 10 (25.4–39.8). Río Orinoco at sand playa just upstream from Quiratare (02°59′N, 66°04′W), collected by B. Chernoff et al., 10 Mar 1987, ANSP 161237, 6 (25.7–32.5). Río Casiquiare main channel, near Río Orinoco confluence, ANSP 177829, 2.

Genus *Piabina* Reinhardt, 1867

Piabina Reinhardt, 1867:49 [type species *Piabina argentea* Reinhardt, 1867:50, by monotypy. Gender feminine; volume dated 1866 but actual date of publication was 1867 according to Nielsen, 1974:45, 112].—Eigenmann and Eigenmann, 1891:56 [*Piabina* placed as a synonym of *Creagrutus* Günther].—Eigenmann, 1910:435 [*Piabina* resurrected from synonymy of *Creagrutus*].—Mahnert and Géry, 1988:7 [*Piabina* returned to the synonymy of *Creagrutus*].

DIAGNOSIS.—*Piabina* is phylogenetically diagnosed by the possession of the synapomorphies listed under "Monophyly of *Piabina*," above. *Piabina* is externally distinguished within the clade formed by *Piabina* and *Creagrutus* by the posteriorly attenuating, triangular fourth infraorbital, which is excluded in larger specimens of the genus from the posterior margin of the infraorbital series as a consequence of the contact of the proximate posterior portions of the third and fifth infraorbitals.

REMARKS.—Reinhardt's description of *Piabina* (1867:49) followed soon after Günther's (1864:339) paper proposing *Creagrutus*. Reinhardt (1867) did not cite Günther's genus, *Creagrutus*, and in light of the relatively brief interval between the publication of the two papers, Reinhardt may have been unaware of Günther's paper. Alternately, the relatively brief, and somewhat confusing, description of the premaxillary dentition in *Creagrutus* provided by Günther may have made it difficult for Reinhardt to recognize the similarity between the two nominal genera. Regardless of the cause, the original description of *Piabina* did not distinguish that genus from *Creagrutus*, nor did Lütken (1875:224) address that question in his subsequent publication dealing with *Piabina*.

Eigenmann and Eigenmann (1891:56) first noted the similarity of the two genera by placing *Piabina* into the synonymy of *Creagrutus*, albeit without commenting on the basis for their action. Eigenmann (1910:435) resurrected *Piabina* from the synonymy of *Creagrutus*, but neither commented on this reversal of the previous synonymy of these genera by Eigenmann and Eigenmann (1891) nor identified the features that he considered served to distinguish the two genera. In their description of *Piabina analis*, a species subsequently transferred to *Piabarchus* (Myers, 1928:90), Eigenmann et al. (1914:8) noted that the species had a "mouth as in *Creagrutus*" and that the species had the "anal long" presumably identifying the difference in the length of the anal fin (= number of anal-fin rays) as distinguishing *Piabina* from *Creagrutus*. Although not commenting on the diagnostic features for *Piabina*, Pearson (1924:45) described a second species, *P. beni* (=*Creagrutus pearsoni* of this paper), which also was characterized by a relatively high number of anal-fin rays in comparison to most members of the *Creagrutus-Piabina* clade. The number of anal-fin rays was explicitly put forward by Eigenmann (1927:429) as diagnostic for *Piabina* versus *Creagrutus*.

In their description of *Creagrutus paraguayensis* Mahnert and Géry (1988:7) noted that the number of anal-fin rays in the

two nominal genera failed to separate *Piabina* from *Creagrutus* when all species in the two genera were considered. Those authors consequently returned *Piabina* to the synonymy of *Creagrutus*. Those authors did not explore the phylogenetic relationships of *Piabina* within such a more inclusive *Creagrutus*.

Our analysis of information from a series of body systems has shown that *Piabina argentea*, the type species of that genus, forms the sister group to *Creagrutus* rather than constituting a clade within the latter genus, or even being closely related phylogenetically to the species of *Creagrutus* (in the sense of this study), which also have relatively high anal-fin ray counts. *Creagrutus*, in turn, is defined by a large series of derived features unique in some cases to that genus among characiforms. We recognize *Piabina* as distinct from *Creagrutus* to highlight the differences between the clades, and we use the generic-level taxonomy as a vehicle to reflect the sister-group relationship between these taxa.

As noted above, Eigenmann et al. (1914:8) added a second species to *Piabina* with their description of *P. analis*, a species subsequently transferred to *Piabarchus* (Myers, 1928:90). Although the phylogenetic relationships of *Piabarchus* remain unresolved, the genus lacks the synapomorphies for *Piabina* and for the clade formed by *Piabina* plus *Creagrutus*. *Piabina analis* of Eigenmann et al. (1914:8) is consequently not included in this study.

The third nominal species originally described in *Piabina* is *P. beni* (the *Creagrutus pearsoni* of this paper), which was described by Pearson (1924:45). The available evidence indicates that this is a member of the *Creagrutus* clade as defined by a series of derived features rather than being closely aligned phylogenetically with *Piabina*.

Piabina argentea Reinhardt, 1867

FIGURES 90, 95–97, TABLE 60

Piabina argentea Reinhardt, 1867:50, pl. 1: figs. 1, 2 [Brazil (Minas Gerais), Lagoa Santa].—Lütken, 1874:141 [Brazil (Minas Gerais), Rio das Velhas]; 1875:226, fig. [Brazil (Minas Gerais), Rio das Velhas].—Eigenmann, 1910:434 [Brazil (Minas Gerais), Rio das Velhas basin].—Eigenmann and Myers, 1929:430, pl. 35: figs. 3–3a; pl. 97: fig. 9 [Brazil (Bahia), Rio San (= São) Francisco, Rio Itapicuru, upper (Rio) Paraná].—Amaral-Campos, 1945:433, fig. 2 [Brazil, São Paulo, Rio Mogi-Guaçu].—Fowler, 1948:162 [literature summary].—Gomes and Monteiro, 1955:105–106 [Brazil, São Paulo, Pirassununga].—Travassos, 1960:27 [Brazil, Rio São Francisco; common name].—Gomes and Azevedo, 1960:136 [Brazil, São Paulo, Rio Camanducáia, Monte Algre do Sul].—Britski, 1972:87 [Brazil, São Paulo, upper Rio Paraná].—Nielsen, 1974:45 [depository of syntypes].—de Godoy, 1975:122 [Brazil, São Paulo: Rio Mogi Guassu, Cachoeira de Emas; life history].—Ringuelet, 1975:58 [Rio Paraná basin].—Britski et al., 1984:44, 109, fig. 30 [Brazil, Minas Gerais, São Francisco basin, Três Marias].—Britski et al., 1986:20, 44, 96, fig. 30 [Brazil, Minas Gerais, São Francisco basin, Três Marias].—Mahnert and Géry, 1988:5 [synonymy of *Piabina* (including *P. argentea*) into *Creagrutus*].—Barrella and Petrere, 1994:164 (Brazil, São Paulo, Rio Tietê basin, Rio Jacaré Pepira].—Araújo, 1996:16 [Brazil, Rio de Janeiro, Rio Paraíba do Sul].—Evers, 1997:11, unnumbered fig. on p. 8 [Brazil, Minas Gerais].—Agostinho et al., 1997:184 [Brazil, upper Rio Paraná basin].—Alves and Vono, 1999:36 [Brazil, Minas Gerais, Rio Parapeba].

Creagrutus argentea.—Eigenmann and Eigenmann, 1891:56 [Brazil, Minas Gerais, Rio das Velhas; species shifted from *Piabina* to *Creagrutus*].—Mahnert and Géry, 1988:5 [synonymy of *Piabina*, including *P. argentea*, into *Creagrutus*].

Piabina piquira.—Eigenmann, 1910:434 [Brazil (São Paulo), Piracicaba; nomen nudum in listing of species].—Eigenmann and Myers 1929:430 [listed as synonym of *Piabina argentea*].—de Godoy, 1975:122 [in synonymy of *Piabina argentea*].

DIAGNOSIS.—*Piabina argentea* is unique within the *Creagrutus-Piabina* clade in the possession of a posteriorly tapering fourth infraorbital, which in adults is excluded posteriorly from the posterior margin of the infraorbital ring by the contact of the proximate posterior portions of the third and fifth infraorbitals. In addition to that autapomorphic feature, the possession of the form of premaxillary dentition with the three components generalized for the species of *Creagrutus* and *Piabina*, but with a distinct gap between the first and second teeth of the primary tooth row and a forward position of the triangular cluster of three posteromedial teeth distinguishes *Piabina argentea* from all members of the clade formed by *Creagrutus* and *Piabina* with the exception of *Creagrutus maracaiboensis, C. melanzonus, C. muelleri, C. nigrostigmatus, C. ouranonastes, C. peruanus*, and *C. runa*. *Piabina argentea* can be distinguished from these seven *Creagrutus* species by the combination of its possession of 4 or 5 rows of scales between the lateral line and the dorsal-fin origin, 15 to 18 branched anal-fin rays, 36 to 39 vertebrae, the caudal-peduncle depth (9.0%–10.9% of SL), and the distance from the dorsal-fin origin to the hypural joint (48.5%–52.7% of SL).

DESCRIPTION.—Morphometric and meristic data for the populations of *Piabina argentea* in Table 60. Greatest body depth in region between vertical through pelvic-fin insertion and vertical through dorsal-fin origin, typically located more anteriorly in ripe females and in both sexes in populations with proportionally deeper bodies. Anterior profile of snout distinctly rounded. Dorsal profile of head somewhat variable. At one extreme profiles of snout and remainder of head meeting in obtuse angle near vertical immediately anterior to nares, whereas at other extreme specimens with smoothly continuous profile between upper lip and tip of supraoccipital spine. Dorsal profile of head posterior of vertical through nares and predorsal region of body ranging from nearly straight to noticeably convex. Dorsal profile of body nearly straight between dorsal-fin origin and adipose fin in all populations and not demonstrating change in alignment relative to head profile. Ventral profile of head with distinct, but rounded, obtuse angle delimiting anteroventral of dentary. Ventral profile of head posterior of that angle and profile of anterior portion of body smoothly convex to pelvic-fin insertion; convexity more pronounced in some relatively deep-bodied populations, typically those from lacustrine habitats.

Upper jaw longer than, and overhanging, lower jaw. Anterior surface of snout fleshy, particularly anteroventrally, and covered with minute papillae. Papillae most concentrated on upper lip, margin of upper and lower jaws, and in mouth on fleshy,

TABLE 60.—Morphometrics and meristics of *Piabina argentea:* (A) lectotype of *P. argentea,* ZMUC 253; and (B) all specimens of *P. argentea* from which counts and measurements were taken (n=69). Standard length is expressed in mm; measurements 1 to 14=percentages of standard length; 15 to 18=percentages of head length. Dash indicates value for the damaged lectotype that could not be accurately measured.

Characters	A	B
	Morphometrics	
Standard length	59.2	27.4–68.0
1. Snout to anal-fin origin	63.1	59.0–63.7
2. Snout to pelvic-fin insertion	46.9	44.6–47.3
3. Snout to pectoral-fin insertion	24.8	22.5–27.0
4. Snout to dorsal-fin origin	51.5	48.5–52.7
5. Dorsal-fin origin to hypural joint	52.9	48.5–52.7
6. Dorsal-fin origin to anal-fin origin	29.4	25.8–30.7
7. Dorsal-fin origin to pelvic-fin insertion	27.0	23.4–30.0
8. Dorsal-fin origin to pectoral-fin insertion	35.1	32.5–38.3
9. Caudal peduncle depth	9.4	9.0–10.9
10. Pectoral-fin length	19.4	18.6–21.0
11. Pelvic-fin length	14.4	14.2–15.9
12. Dorsal-fin length	22.8	21.4–25.4
13. Anal-fin length	16.7	15.6–18.8
14. Head length	26.4	24.5–28.3
15. Postorbital head length	47.1	39.0–47.5
16. Snout length	27.3	26.8–31.2
17. Bony orbital diameter	32.7	29.4–36.2
18. Interorbital width	28.2	27.3–33.3
	Meristics	
Lateral line scales	40	39–42[1]
Scale rows between dorsal-fin origin and lateral line	5	4–5
Scale rows between anal-fin origin and lateral line	4	4
Predorsal median scales	12	11–13
Branched dorsal-fin rays	8	8
Branched anal-fin rays	18	15–18
Branched pelvic-fin rays	6	6
Pectoral-fin rays	–	12–13
Vertebrae	38	36–39

[1]Forty-two lateral line scales present in only 1 specimen.

plicate folds between premaxillary teeth. Lower lip very fleshy, particularly anteriorly.

Infraorbital series well developed. Ventral margin of third infraorbital approaching horizontal limb of preopercle; anteroventral portion of bone sometimes contacting horizontal limb of preopercle in larger specimens. Posterior portion of fourth infraorbital attenuated, barely reaching posterior margin of infraorbital ring in smaller individuals, excluded from the posterior margin of infraorbital series as consequence of contact of proximate posterior portions of the third and fifth infraorbitals. Posterior margins of third and fifth infraorbitals slightly separated from vertical limb of preopercle even in larger specimens.

Premaxillary dentition in three series: primary series sigmoid with 5 teeth; contralateral medial teeth distinctly separated from each other and somewhat less separated from second tooth of each series, but nonetheless with distinct gap between those teeth; triangular cluster of 3 larger teeth with medial teeth in contact and anterior tooth of triangular cluster partially occupying pronounced gap between first and second teeth of main series; and single tooth of form similar to that of primary series lying lateral to fourth tooth of primary series. Maxilla with 2, rarely 3, tricuspidate teeth. Dentary with 6 or 7 teeth; 3 anterior teeth tricuspidate and distinctly larger than other teeth in the series, with first and second teeth subequal in size and larger than third tooth. Remaining dentary teeth gradually decreasing in size posteriorly; either all tricuspidate (when 6 teeth present) or last tooth nearly conical (when 7 teeth present).

Dorsal-fin rays ii,8. Dorsal-fin origin located slightly posterior to vertical through pelvic-fin insertion. Distal margin of dorsal fin nearly straight. Anal-fin rays iii,15–18. Distal margin of anal fin distinctly concave, with last unbranched and anterior branched rays longest. Single hooks present on last unbranched and anterior 4 to 7 branched anal-fin rays of mature males; hooks restricted to posterolateral surface of main shaft of unbranched ray and posterior secondary branch of branched rays. Pectoral-fin rays i,11–12. Tip of pectoral fin extending posteriorly nearly to pelvic-fin insertion in smaller specimens, falling distinctly short of that point in larger individuals. Pelvic-fin rays i,6,i. Tip of pelvic fin extending posteriorly approximately to anus. Mature males with hooks on all branched pelvic-fin rays; hooks extending from basal unsegmented portion of ray distally onto all but distal portions of rays. Two lateralmost, branched rays with hooks only on medial margin of medial portion of ray, whereas other branched rays with hooks along medial margin of all major branches.

Gill rakers 6–7+9–11.

COLORATION IN LIFE (based on a transparency of a live specimen from the Rio Vermelho, Minas Gerais, Brazil, provided by Hans-Georg Evers and published in Evers, 1997).—Overall coloration of head and body silvery. Midlateral portion of body, fin rays, and basal portions of each caudal-fin lobe iridescent. Posterolateral portion of head iridescent dorsally. Eye along with lateral and ventral portions of head silvery. Humeral mark and reticulate pattern on body, particularly on dorsal portion of body, quite obvious. Dark midlateral stripe somewhat masked by overlying guanine deposits. Abdominal region silvery. Otherwise dark pigmentation as in preserved specimens (see "Coloration in Alcohol," following).

COLORATION IN ALCOHOL.—Dorsal surface of head with both shallow and deep-lying dark chromatophores. Large stellate chromatophores on membranes of brain obvious in smaller individuals, but masked by pigmentation on surface of head in larger specimens. Variably dense field of dark chromatophores over dorsal surface of head, snout, and upper lip. Chromatophores more concentrated in irregular band running from anterior of nares posterodorsally along ventral margin of adipose eyelid to near anteroventral margin of eye. Band continued as narrow series of chromatophores around ventral and posterior border of orbit. Dorsal portions of opercle and infraorbitals posterior to orbit with scattered, large chromatophores.

Dorsal portion of body with small dark chromatophores concentrated on posterior portion of scales, forming overall reticu-

late pattern. Form of humeral mark somewhat variable both ontogenetically and among similar-sized specimens within many population samples. Specimens of approximately 20 mm SL with mark formed by rotund patch of large, dark chromatophores entirely dorsal of lateral line. Individuals of approximately 40 mm retaining central patch of dense chromatophores, but often with sparse fields of dark chromatophores extending dorsal and ventral of main pigmentation patch and giving humeral mark overall vertically elongate appearance. Degree of vertical elongation variable, with some individuals having only slightly vertically elongate rotund mark and others with humeral mark approaching form of vertical bar. Specimens with distinctly vertically elongate mark, usually with portion of chromatophore field dorsal of main body of mark better developed than ventral of main portion of mark. Some individuals with ventral portion of mark forming ventrally attenuating bar.

Dark midlateral body stripe diffuse anteriorly at all sizes but with distinct dorsal and ventral margins. Stripe limited to caudal peduncle and posterior portion of body in specimens of approximately 20 mm SL, stripe extending progressively further anteriorly with increasing body size, and nearly extending to posterior margin of humeral mark in largest examined individuals.

Dorsal fin with series of small dark chromatophores along margins of distal one-half of anterior rays. Caudal and anal fins with small, dark chromatophores scattered over membranes and delimiting fin-ray margins. Pectoral and pelvic fins either hyaline or with scattered, dark chromatophores.

ECOLOGY.—de Godoy (1975:125–126) reported that in the upper Río Paraná basin *Piabina argentea* matures sexually beginning in late September. In the same region, that author reports that this species feeds primarily on phytoplankton and various life stages of diverse groups of aquatic insects (Chironomidae, Ephemeroptera, Odonata, Simulidae, and Trichoptera). Examination of a series of stomach contents during this study revealed primarily insect remains, small intact seeds, chopped-up seeds, and lesser amounts of phytoplankton.

COMMON NAME.—Brazil, Rio São Francisco: "Piaba" (Travassos, 1960:27); upper Rio Paraná: "Piquira" (de Godoy, 1975:122).

DISTRIBUTION.—*Piabina argentea* occurs in the upper Río Paraná basin in northeastern Paraguay and southern Brazil above the Salto de Guaira and in the Rio São Francisco, Rio Itapicuru, Rio Paraíba, and Rio Itapemirim basins of eastern Brazil (Figure 90, stars).

COMPARISONS.—*Piabina argentea* is allopatric to the *Creagrutus* clade and is readily distinguished from all *Creagrutus* species by its posteriorly attenuating, triangular fourth infraorbital, which is excluded from the posterior infraorbital margin in larger specimens by the contact of the proximate posterior portions of the third and fifth infraorbitals.

GEOGRAPHIC VARIATION.—*Piabina argentea* has a unusually broad distribution compared with the members of it sister clade, the species of *Creagrutus,* ranging from the central portions the Río Paraná basin to the area slightly north of the lower portions of the main channel of the Rio São Francisco. Although different population samples demonstrate modally differing variation in some features, there is, nonetheless, broad overlap between samples of different populations that have similar overall appearance (Figures 96, 97). In light of the degree of this overlap, we consider these populations to be conspecific. The most notable feature that varies geographically between the Rio Paraná populations and samples from the more northerly portions of the species' range is the number of vertebrae, although this feature has broad overlap between these major river basins. Populations samples from the Rio Paraná basin have 36 to 39 vertebrae, with a mean of 37.65 (n= 26), whereas those from the São Francisco basin have 37 to 39 vertebrae with a mean of 38.11 (n=53).

REMARKS.—*Piabina argentea* was described by Reinhardt (1867:49), who based the description on specimens collected in Lagoa Santa in the upper Rio São Francisco basin of the state of Minas Gerais, Brazil. Two syntypes are known to be extant (Nielsen, 1974: 45). Although the single syntype examined in the course of this study (Figure 95) is in somewhat poor condition, it demonstrates the form of the posterior infraorbitals synapomorphic for the genus along with the other features that in combination discriminate *Piabina* from *Creagrutus.* This syntype (ZMUC 253) is designated as the lectotype, and the other syntype (ZMUC 254, not examined in this study) consequently becomes a paralectotype.

In his listing of the then-known freshwater fishes of South America, Eigenmann (1910:434) listed *Piabina piquira* with a stated locality of Piracicaba, in the upper Rio Paraná basin of the state of São Paulo, Brazil. That species was not, however, ever formally described, and Eigenmann and Myers (1929:430) listed it in the synonymy of *Piabina argentea.*

MATERIAL EXAMINED.—1462 specimens (69, 27.4–68.0).

BRAZIL. *Bahia:* Queimadas, Rio Itapicuru basin (10°58′S, 39°38′W), CAS 70952 (formerly IU 13370), 5. Rio Itapicuru, FMNH 54322 (formerly CM 54322), 6. Rio Verde Pequeno, tributary to Rio Verde Grande, on road between Urandi and Espinosa (14°50′44″S, 42°45′36″W), ANSP 171966, 8. *Distrito Federal:* Ribeirão Santana, at road crossing approximately 30 air km S of Barragem do Paranoa (Rio Bartolomeu of Río Paraná basin; 15°55′S, 47°46′W), USNM 292220, 76 (10, 33.8–65.5; 1 specimen cleared and counterstained). Ribeirão Santana (Rio Paraná basin, 16°01′S, 47°49′W), UF 78195, 67 (10, 44.8–61.5). Rio Piripau, near Planaltina (approximately 15°37′S, 47°40′W), MZUSP 28040, 20 (5, 53.2–58.3); MZUSP 48361, 1. *Espírito Santo:* Rio de Frade e da Freira, Cachoeiro de Itapemirim (20°51′S, 41°06′W), MZUSP 17058, 1. *Goiás:* Goiâna, Rio Meia Ponte basin, Ribeirão João Leite (16°39′S, 49°16′W), MZUSP 47750, 1. *Minas Gerais:* Lagoa Santa (19°38′S, 43°53′W), ZMUC 253, 1 (59.2, lectotype of *Piabina argentea*). Córrego do Jacque, Campinho, near Lagoa Santa, MZUSP 18922, 5. Rio das Velhas, FMNH 54579, 6 (for-

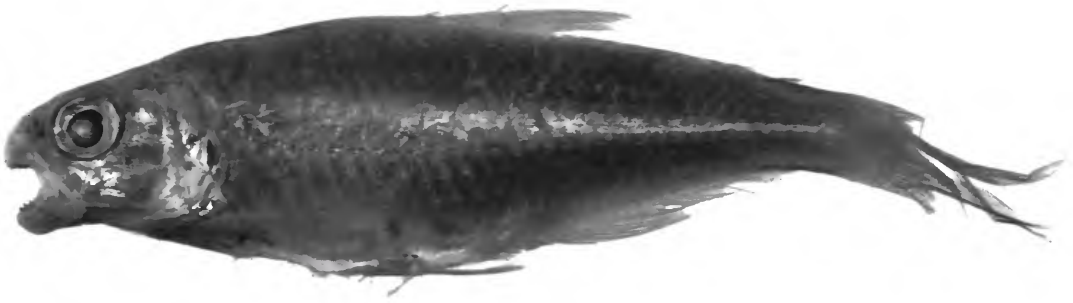

FIGURE 95.—*Piabina argentea*, lectotype, ZMUC 253, 59.2 mm SL; Brazil, Minas Gerais, Lagoa Santa (19°38′S, 43°53′W).

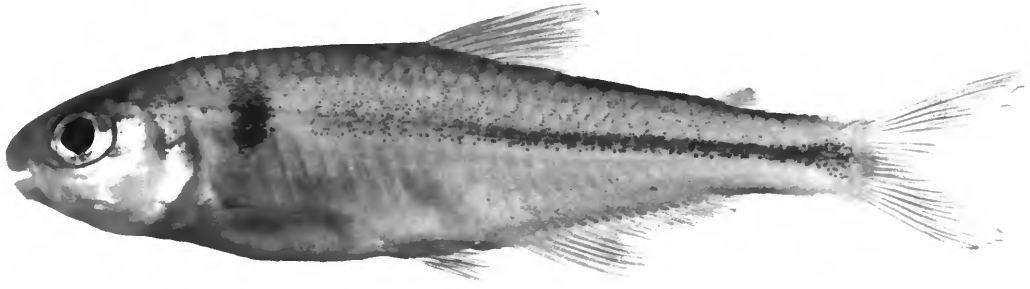

FIGURE 96.—*Piabina argentea*, MZUSP 38001, 57.4 mm SL; Brazil, Minas Gerais, Rio das Velhas basin, Ribeirão Jaboticatubas (19°26′S, 43°55′W).

FIGURE 97.—*Piabina argentea*, UF 78195, 61.0 mm SL; Brazil, Distrito Federal, Ribeirão Santana (Rio Paraná basin, 16°01′S, 47°49′W).

merly CM 4765). Córrego Chumbo, Rio Abaeté basin (approximately 18°37′S, 46°12′W), MZUSP 39650, 14. Major Porto, Rio Abaeté, Córrego Agua Limpa, MZUSP 39595, 54 (20, 27.4–39.8). Major Porto, Rio Abaeté, Córrego Capivara, MZUSP 39625, 21. Córrego Espraiado, Rio Abaeté, MZUSP 39681, 7. Rio São Francisco, Piraporinha (Buriti), opposite Pirapora (17°21′S, 44°56′W), USNM 100955, 3. Piraporinha, corrego tributary to Rio São Francisco, UMMZ 216283, 12. Córrego de Julião, along road to Tabuticatubas and Jabuticatuba, N of Lagoa Santa, USNM 311172, 10 (5, 35.6–52.0; 1

specimen cleared and counterstained for cartilage and bone). Rio das Velhas basin, Ribeirão Jaboticatubas (19°26′S, 43°55′W), MZUSP 38001, 66 (10, 44.3–56.3); MZUSP 37944, 23. Tributary to Rio Grande, 1.5 km W of Possos on highway between Possos and Itau de Minas, USNM 342929, 10. Córrego do Juliáo, along road to Jabuticatuhas (19°23′S, 49°01′W), MZUSP 18925, 22. São João del Rei, Rio das Mortes, upper Rio Paraná basin (21°09′S, 44°16′W), CAS 70953, 3 (formerly IU 13299, in part); USNM 167822, 1 (formerly IU 13299, in part); FMNH 54582, 10 (formerly CM 3767). Riacho dos Poções, tributary of Rio Coxá-Rio Carinhanha, approximately 11 km S of Montalvânia (14°31′S, 44°24′W), ANSP 171965, 60. Rio Meleno at Cachoeira de Meleno, approximately 23 km SE of Felixlandia, Rio Paraopeba drainage (18°51′43″S, 44°45′14″W), ANSP 171963, 14. Rio Pandeiras at the Rio Pandeiras campground, 48 km WSW of Januaria (15°30′43″S, 44°45′12″W), ANSP 171964, 1. Rio Grande basin, Repressa de Camargo, MZUSP 18578, 11. Rio Grande, Repressa de Furnas, Boa Esperança, MZUSP 18598, 3. Rio Grande, Repressa de Furnas, Alfonas, MZUSP 18575, 131. Rio Jequitai basin, along BR-135 between Buenópolis and Engenheiro Dolabela, MZUSP 47318, 1. Fortaleza de Minas, Riacho tributary to Rio São João, MZUSP 35394, 23. Fortaleza de Minas, along road from Fortaleza de Minas to Jacuí, MZUSP 35384, 28. Ribeirão da Prata, along road from São João del Rei to Itutinga, MZUSP 17835, 5. Ribeirão tributary to Rio Paraopeba, Município de Moeda, MZUSP 37153, 100. Córrego Jenipapo, Rio São Francisco basin, MZUSP 39538, 1. Três Lagoas, Ilha de Mandioca, Rio Sucuriú, MZUSP 16976, 3. Rio São Francisco, Três Marias, MZUSP 17091, 64. Rio São Francisco, mouth of Rio Formosa (approximately 17°25′S, 44°58′W), MZUSP 39455, 6. Rio São Francisco basin, Rio Formoso, MZUSP 39359, 1. Ribeirão do Gado, tributary of Rio São Francisco, MZUSP 39174, 44. Córrego Braço Grande, tributary of Rio São Francisco, MZUSP 39227, 1. *Pernambuco:* 350 km W of Recife, ZMH 5717, 4. *São Paulo:* Rio Pardo, Barragem de Itaipava, near Santa Rosa de Viterbo (21°25′S, 47°20′W), USNM 302510, 4. Ribeirão da Boiada, Fazenda Santa Carlota, Município de Cajuru (21°27′S, 47°14′W), USNM 322478, 15 (5, 52.7–68.0). Piracicaba, CAS 70951, 2 (formerly IU 11630); FMNH 54584, 1 (formerly CM 3215a). Upper Rio Piracicaba basin, near Jaguariuna, USNM 342928, 10. Rio Corumbatai, Município de Corumbatai (22°14′S, 47°38′W), USNM 322095, 10; MZUSP 16756, 66 (3, 49.3–54.2); MZUSP 10745, 50; MZUSP 17034, 2. Córrego de Pinheiro, Corumbatai, MZUSP 16913, 1. São Paulo, Ipiranga, Rio Tamanduatei, MZUSP 17091, 64. Rio Mogi-Guaçu, Emas (21°56′S, 47°22′W), MZUSP 16835, 1; MZUSP 16852, 12; MZUSP 16727, 1; MZUSP 16698, 2. Córrego de Abrigo, Barragem de Jupiá (approximately 20°47′S, 51°37′W), MZUSP 17245, 50; MZUSP 17234, 93. Rio Santo Inácio, Pardinho (23°06′S, 48°23′W), MZUSP 35190, 2. Rio Tietê, Itu, Fazenda Pau D'Alho (approximately 23°16′S, 47°19′W), MZUSP 17313, 1; MZUSP 16775, 5. Rio Tietê basin, Penápolis (21°24′S, 50°04′W), MZUSP 35712, 2. Rio Tietê basin, Município de José Bonifácio (21°03′S, 49°41′W), MZUSP 18457, 26. Campinas, Rio Atibaia, on road from Fortuna near Highway Dom Pedro I, MZUSP 45514, 10; MZUSP 45497, 5; MZUSP 49870, 4. Rio Jaguari, Pereira (22°43′S, 46°55′W), MZUSP 18794, 28. Rio Caligari, Botucatu, MZUSP 39874, 1. Pirassununga, MZUSP 16678, 8. Río Paraná, Ilha Psaltery, MZUSP 17161, 20. *Rio de Janeiro:* São Fidelis, Córrego Pedra D'Aqua (approximately 21°39′S, 41°44′W), MZUSP 17054, 2. Rio Paraíba, São Fidelis, MZUSP 17109, 8.

PARAGUAY. *Canendiyu:* Río Paraná basin, Río Piratiy, at Balneario Municipal, 1 km S of bridge on road just W of Salto Del Guaira (24°03′S, 54°18′W), UMMZ 206400, 1. Río Paraná basin, Río Piratiy just below bridge on road just W of Salto Del Guaira (24°03′48″S, 54°19′12″W), UMMZ 206437, 1.

Phylogenetic Biogeography of *Creagrutus* and *Piabina*

The lack of resolution across much of the phylogeny for the *Creagrutus-Piabina* clade severely limits the historical biogeographic information available for this group. The well-supported clades, nonetheless, do demonstrate some informative patterns.

The basal phylogenetic subdivision between *Creagrutus* and *Piabina* matches the noteworthy complete allopatry between the two genera (Figure 18), but with pronounced differences in the extent of areas of distribution of most species within the two clades. The known range for the single known species of *Piabina* (*P. argentea;* Figure 90) is much more extensive than that for most *Creagrutus* species (see distribution maps for various species). Within *Creagrutus* a basal dichotomy exists between two lowland Trans-Andean species (*C. nigrostigmatus* of the Caños Pechilín and Zaragocilla, two small coastal rivers to the west of the mouth of the Río Magdalena, and *C. maracaiboensis,* a species endemic to Lago Maracaibo; Figure 17, Clade D) and the remaining species of the genus (Figure 17, Clade E), most of which occur in Cis-Andean South America. The distribution of the species in this basal dichotomy is congruent with a hypothesis of the existence of *Creagrutus* prior to the uplift of at least the northern portions of the Andean Cordilleras. The Lago Maracaibo basin was mostly marine during the Late Tertiary up to approximately 10 million years before the present, but there was a progressive reduction of marine influences in the next two million years (Lundberg et al., 1998), a period during which the major drainage systems on the continent began to approximate their present forms. Thus, it seems likely that the division between the trans-Andean species pair (*C. nigrostigmatus* and *C. maracaiboensis*) and the remainder of the genus dates back to at least eight million years before present. Evidence from the phylogeny indicates, however, that this is likely an underestimate. Although the lack of resolution in major portions of the phylogeny for *Creagrutus* precludes a definitive statement, it is noteworthy that the remainder of the Trans-Andean species occur at higher-nodes within the tree

(Figure 17: *Creagrutus affinis,* Clade M; and various species in "remaining species"). Thus, the eight million year estimate for the minimum age for the *Piabina-Creagrutus* lineage actually applies to nodes higher in the phylogeny thereby extending the basal division between the clade consisting of *C. nigrostigmatus* and *C. maracaiboensis* and the remainder of the genus further back in time.

The basal multitomy within Clade E (Figure 17) involves three western Amazonian upland species (*C. muelleri, C. ouranonastes,* and *C. peruanus*), one of which, *C. ouranonastes,* occurs at the highest known elevation for any member of the genus. Regardless of the relationships between these three species, there appears to have been a speciation event between a western Amazonian component of *Creagrutus* and the remainder of the genus, with secondary sympatry at a later date given that both *C. muelleri* and *C. peruanus* occur sympatrically with congenerics within the *Creagrutus* species in Clade F (Figure 17).

Four of the six clades within the assemblage delimited by Clade F (Figure 17) are based on characters with low retention indices and are poor bases for biogeographic hypotheses (see comments under "Intrageneric Relationships within *Creagrutus*"). The two other clades within this multitomy are better supported and share an interesting pattern with distinct altitudinal difference between the sister groups within the clade. *Creagrutus kunturus,* although occurring in many of the same rivers as its sister species, *C. amoenus,* inhabits higher portions of those western Amazonian systems. Although *C. gephyrus* is geographically separated from the known range of the species pair (*C. cracentis* and *C. maxillaris*), it also occurs at higher elevations than do those two species.

Comments on *Creagrutus nigrostigmatus*

Creagrutus nigrostigmatus was described by Dahl (1960:353) on the basis of a series of specimens collected in Arroyo Pechilín, a small stream draining into the Caribbean Sea west of the mouth of the Río Magdalena. Cala (1981; pers. comm., 1992) reported that the types of the species were lost and have not been located subsequently (Román-Valencia and Cala, 1996:145). Harold and Vari (1994:10) consequently designated a neotype for the species. Subsequent to that publication a series of two specimens of *C. nigrostigmatus* was discovered in the holdings of the California Academy of Sciences (CAS 149491; formerly SU 49491). Although not specifically noted as paratypes of *C. nigrostigmatus,* the evidently original label associated with the specimens contains the following information: "*Creagrutus nigrostigmatus* n. sp., Pechelin, July 14th 1955, Dahl." This information on the label matches the type locality for the species, and the date falls within the range of dates for the collection of the paratype series (1955–1957) cited by Dahl (1960:354). Dahl sent paratypes of various species that he described to G.S. Myers, then at Stanford University (S.H. Weitzman, pers. comm., 1999), and these two specimens may, thus, represent the only portion of the type series known to be extant.

RESUMO

Creagrutus Günther (1864) e *Piabina* Reinhardt (1867) são diagnosticados como um grupo monofilético com base em uma série de sinapomorfias de caracteres osteológicos e de anatomia de sistemas não ósseos. Subconjuntos destas sinapomorfias diagnosticam cada gênero e resolvem parcialmente a filogenia intragenérica dentro de *Creagrutus*. *Piabina*, como previamente constituído, não é monofilético, sendo restrito aqui para a espécie-tipo *P. argentea*. *Creagrudite* Myers (1927) e *Creagrutops* Schultz (1944) compartilham os caracteres diagnósticos de *Creagrutus* e são considerados sinônimos juniores deste gênero, a fim de tornar *Creagrutus* monofilético. *Piabarchus* Myers (1928), proposto com base em uma espécie descrita originalmente em *Piabina*, não possui os caracteres derivados da linhagem *Creagrutus-Piabina*.

Um total de 64 espécies são reconhecidas em *Creagrutus*, 56 das quais ocorrem a leste das Cordilheiras dos Andes. As espécies cisandinas e suas distribuições são: *C. amoenus* Fowler (1943a), Amazonas oeste; *C. anary* Fowler (1913), Rio Madeira; *C. atratus*, espécie nova, bacia do Río Meta; *C. atrisignum* Myers (1927), bacia do Rio Tocantins; *C. barrigai*, espécie nova, leste do Equador e Peru; *C. beni* Eigenmann (1911), bacia do alto Rio Madeira; *C. bolivari* Schultz (1944), Río Orinoco; *C. britskii*, espécie nova, alto Rio Tocantins; *C. calai*, espécie nova, Río Meta; *C. changae*, espécie nova, leste do Peru; *C. cochui* Géry (1964), Amazonas oeste; *C. cracentis*, espécie nova, baixo Rio Tapajós; *C. crenatus*, espécie nova, Río Tocuyo, vertente do Caribe na Venezuela; *C. ephippiatus*, espécie nova, Río Siapa, bacia do alto Río Negro, Venezuela; *C. figueiredoi*, espécie nova, alto Rio Tocantins e Rio Araguaia; *C. flavescens*, espécie nova, leste do Equador; *C. gephyrus* Böhlke e Saul (1975), Amazonas oeste; *C. gracilis*, espécie nova, nordeste do Peru e leste do Equador; *C. gyrospilus*, espécie nova, oeste da bacia do Orinoco; *C. holmi*, espécie nova, nordeste do Peru; *C. hysginus* Harold et al. (1994), nordeste da Venezuela; *C. ignotus*, espécie nova, alto Rio Tapajós; *C. kunturus* Vari et al. (1995), Oeste da Amazônia; *C. lassoi*, espécie nova, vertente do Caribe na Venezuela; *C. lepidus* Vari et al. (1993), Ríos Aroa e Urama, vertente do Caribe na Venezuela; *C. machadoi*, espécie nova, Río Caura, Venezuela; *C. magoi*, espécie nova, bacia do Río Orinoco; *C. manu*, espécie nova, Río Madre de Dios, Peru; *C. maxillaris* (Myers, 1927), alto Río Orinoco, alto Rio Negro, e alto Rio Madeira; *C. melanzonus* Eigenmann (1909), Río Cuyuni, leste da Venezuela até Fleuve Sinnamary, French Guiana; *C. melasma* Vari et al. (1994), bacia do Río Orinoco; *C. menezesi*, espécie nova, Rio Tocantins e tentativamente a bacia do Rio Negro; *C. meridionalis*, espécie nova, Río Paraguay; *C. molinus*, espécie nova, alto Rio Araguaia; *C. mucipu*, espécie nova, Rio Tocantins; *C. muelleri* (Günther, 1859), região amazônica do Equador; *C. occidaneus*, espécie nova, Amazonas oeste; *C. ortegai*, espécie nova, leste do Peru; *C. ouranonastes*, espécie nova, terras altas no Peru; *C. paraguayensis* Mahnert e Géry (1988), Río Paraguay; *C. pearsoni* Mahnert e Géry (1988), bacia do alto Rio Madeira; *C. peruanus* (Steindachner, 1875), bacia do Río Ucayali; *C. petilus*, espécie nova, tributários a leste do Rio Madeira; *C. phasma* Myers (1927), alto Rio Negro e porção sul do Río Orinoco; *C. pila*, espécie nova, Río Aguaytia, leste do Peru; *C. planquettei* Géry e Renno (1989), Fleuve Approuague, French Guiana; *C. provenzanoi*, espécie nova, Río Cataniapo, Venezuela; *C. runa*, espécie nova, alto Río Negro; *C. saxatilis*, espécie nova, bacia do Rio Tocantins; *C. seductus*, espécie nova, alto Rio Araguaia; *C. taphorni*, espécie nova, Río Orinoco e vertente do Caribe do Río Tuy; *C. ungulus*, espécie nova, Río Manu, sudeste do Peru; *C. veruina*, espécie nova, Río Cataniapo, Venezuela; *C. vexillapinnus*, espécie nova, alto Rio Negro e Río Orinoco; *C. xiphos*, espécie nova, bacia do Río Caura, Venezuela; e *C. zephyrus*, espécie nova, alto Río Negro no Brasil e Venezuela e alto Río Orinoco. O número de espécies de *Creagrutus* reconhecidas aqui representa 337% do número de espécies consideradas válidas anteriormente a Harold e Vari (1994).

Ao contrário da prática taxonômica recente, *Piabina* é reconhecido como um gênero distinto, mas limitado a uma única espécie, *P. argentea* (Reinhardt, 1867), distribuída em vários rios do leste do Brasil.

Chaves são fornecidas para as espécies de *Creagrutus* e *Piabina* nas maiores bacias hidrográficas da área de distribuição destes gêneros.

Creagrutus nasutus Günther (1876) é considerado sinônimo de *C. peruanus*. *Creagrutus boehlkei* Géry (1972) é colocado na sinonímia de *Creagrutus amoenus*. *Creagrutus pellegrini* Puyo (1943) é assinalada para o gênero *Chalceus* em Characidae.

Lectótipos são designados para *Piabina argentea* Reinhardt, Leporinus *muelleri* Günther, *Creagrutus nasutus* Günther, *Creagrutus pearsoni* Mahnert e Géry, *Piabina peruana* Steindachner, e *Creagrutus phasma* Myers.

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(Pages of principle discussions in italics)

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