

ANTONY S. HAROLD and RICHARD P. VARI

SERIES PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

Emphasis upon publication as a means of "diffusing knowledge" was expressed by the first Secretary of the Smithsonian. In his formal plan for the Institution, Joseph Henry outlined a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge." This theme of basic research has been adhered to through the years by thousands of titles issued in series publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

Smithsonian Contributions to Anthropology
Smithsonian Contributions to Astrophysics
Smithsonian Contributions to Botany
Smithsonian Contributions to the Earth Sciences
Smithsonian Contributions to the Marine Sciences
Smithsonian Contributions to Paleobiology
Smithsonian Contributions to Zoology
Smithsonian Folklife Studies
Smithsonian Studies in Air and Space
Smithsonian Studies in History and Technology

In these series, the Institution publishes small papers and full-scale monographs that report the research and collections of its various museums and bureaux or of professional colleagues in the world of science and scholarship. The publications are distributed by mailing lists to libraries, universities, and similar institutions throughout the world.

Papers or monographs submitted for series publication are received by the Smithsonian Institution Press, subject to its own review for format and style, only through departments of the various Smithsonian museums or bureaux, where the manuscripts are given substantive review. Press requirements for manuscript and art preparation are outlined on the inside back cover.

Robert McC. Adams Secretary Smithsonian Institution

Systematics of the Trans-Andean Species of *Creagrutus* (Ostariophysi: Characiformes: Characidae)

Antony S. Harold and Richard P. Vari



SMITHSONIAN INSTITUTION PRESS

Washington, D.C.

ABSTRACT

Harold, Antony S., and Richard P. Vari. Systematics of the Trans-Andean Species of Creagrutus (Ostariophysi: Characiformes: Characidae). Smithsonian Contributions to Zoology. number 551, 31 pages, 14 figures, 8 tables, 1994.—The species of Creagrutus Günther occurring to the west and north of the Andean Cordilleras in Venezuela, Colombia, and Panama are revised. Eight species are recognized: Creagrutus affinis Steindachner (1880) distributed from the Río Magdalena west into central Panama and southwest to the Río San Juan of the Pacific slope of Colombia: Creagrutus brevipinnis Eigenmann (1913) and Creagrutus caucanus Eigenmann (1913) of the Río Cauca in northwestern Colombia; Creagrutus hildebrandi Schultz (1944b) of the Lago Maracaibo basin and coastal rivers draining into the southeastern portion of the Golfo de Venezuela; Creagrutus magdalenae Eigenmann (1913) of the Río Magdalena in northern Colombia; Creagrutus maracaiboensis (Schultz, 1944b) known from western and southern tributaries to Lago Maracaibo; Creagrutus nigrostigmatus Dahl (1960) known only from Caño Pechilín, a small drainage basin on the Caribbean coast of Colombia in the state of Sucre; and Creagrutus paralacus, new species, from southern tributaries to Lago Maracaibo.

Two specimens of an undescribed species (not formally treated in this paper) from the upper Río Magdalena that are very similar to Creagrutus paralacus are discussed.

Creagrutops Schultz (1944b) is considered a synonym of Creagrutus Günther. Four species are placed into the synonymy of Creagrutus affinis: Creagrutus leuciscus Regan (1913), Creagrutus londonoi Fowler (1945), Creagrutus notropoides Meek and Hildebrand (1912), and Creagrutus simus Meek and Hildebrand (1913).

Records of Creagrutus beni from the Lago Maracaibo system (Schultz, 1944b) and from the Río Magdalena (Dahl, 1971) and Creagrutus cf. caucanus from the Río Negro of the Amazon basin (Goulding et al., 1988) are erroneous. A key is provided to the Creagrutus species of trans-Andean South America. A neotype is designated for Creagrutus nigrostigmatus Dahl and lectotypes for Creagrutus affinis and Creagrutus leuciscus.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, Smithsonian Year. SERIES COVER DESIGN: The coral Montastrea cavernosa (Linnaeus).

Library of Congress Cataloging-in-Publication Data

Harold, Antony S

Systematics of the trans-Andean species of Creagratus (Ostariophysi: Characiformes: Characidae) / Antony S. Harold and Richard P. Vari.

p. cm. — (Smithsonian contributions to zoology; no. 551)

Includes bibliographic references (p.) and index.

1. Creagrutus—Andes Region—Classification. 2. Creagrutus—Venezuela—Classification. Creagrutus— Colombia—Classification. 4. Creagrutus—Panama—Classification. I. Vari, Richard P. II. Title. III. Series. QL1.S54 no. 551 [QL638.C5] 591 s-dc20 [597'.52] 93-48088

The paper used in this publication meets the minimum requirements of the American National Standard for Permanence of Paper for Printed Library Materials Z39.48—1984.

Contents

Pag	e
ntroduction	1
Acknowledgments	1
Methods and Materials	2
Institutional Abbreviations	
Genus Creagrutus Günther	3
Dentition in Trans-Andean Creagrutus Species	4
Key to the Trans-Andean Species of Creagrutus Günther	
Creagrutus caucanus Eigenmann	
Creagrutus nigrostigmatus Dahl	
Creagrutus maracaiboensis (Schultz), new combination	
Creagrutus paralacus, new species	
Creagrutus magdalenae Eigenmann	
Creagrutus brevipinnis Eigenmann	
Creagrutus hildebrandi Schultz	
Creagrutus affinis Steindachner	
Resumen	
Literature Cited	
ndex	

Systematics of the Trans-Andean Species of *Creagrutus* (Ostariophysi: Characiformes: Characidae)

Antony S. Harold and Richard P. Vari

Introduction

The species of Creagrutus Günther (1864) inhabit running waters across the expanse from Panama to the Río de La Plata basin in Paraguay. It is striking that 11 of the 28 nominal species of Creagrutus are based on specimens from the relatively small, northern portion of the range of the genus in eastern Panama, northern Colombia, and the Lago Maracaibo system of northwestern Venezuela; an area encompassing only a small portion of the total range of the genus. The descriptions of species of Creagrutus in this trans-Andean region began when Steindachner (1880) proposed C. affinis from the Río Cauca of northern Colombia. No other species of the genus were proposed from the region during the next two decades. The stasis in the number of recognized trans-Andean Creagrutus species was altered in quick succession when Meek and Hildebrand (1912, 1913) proposed C. notropoides and C. simus from Panama, Eigenmann (1913) described C. brevipinnis, C. caucanus, and C. magdalenae from various portions of the Río Magdalena basin, and Regan (1913) based C. leuciscus on specimens from the Río San Juan of Colombia, a small Pacific versant river. Schultz (1944b), the first to consider the members of the genus in the Lago Maracaibo basin, described two new species, C. hildebrandi and C. maracaiboensis (placed by him in the monotypic *Creagrutops*); he also reported *C. beni* from that basin, the first citation of the species in trans-Andean South America. Fowler (1945) added to the species from northern Colombia with his description of *C. londonoi* from the Río Magdalena, as did Dahl (1960) who described *C. nigrostigmatus* from a coastal basin to the west of the mouth of that river.

This diversity of nominal *Creagrutus* species makes the region from Lago Maracaibo to eastern Panama an appropriate focus for the first phase of our revision and phylogenetic analysis of all members of the genus and its near relatives. Also all members of *Creagrutus* from the trans-Andean basins are different species from those in rivers east of the Andean Cordilleras, a situation found in other groups of lowland fishes that have been critically examined (curimatids (Vari, 1988, 1992a); prochilodontids (Castro, 1990); ctenoluciids (Vari, in press), ageneiosids (Walsh, 1990), the anostomid genera *Abramites* (Vari and Williams, 1987) and *Schizodon* (Vari and Raredon, 1991), and various other taxa both in fishes (see references in Vari (1988:350)) and freshwater crabs (Rodríquez, 1992).

This paper has two primary aims: first, to determine the recognizable species of *Creagrutus* in the region from Lago Maracaibo through eastern Panama; and second, to determine the distribution of these species. Preliminary studies indicate that the trans-Andean assemblage of *Creagrutus* species is not monophyletic. The analysis of the phylogenetic relationships of those species will consequently be dealt with in a subsequent study treating the entire genus.

ACKNOWLEDGMENTS.—We are greatly indebted to the following individuals and institutions for the loan and exchange of specimens, information, hospitality during visits, and other types of assistance: Gareth J. Nelson, M. Norma Feinberg, and Carl J. Ferraris, Jr. (AMNH); Scott A. Schaefer

Antony S. Harold, Department of Ichthyology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118. Richard P. Vari, Division of Fishes, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Review Chairman: George R. Zug, National Museum of Natural History, Smithsonian Institution.

Reviewers: Mário C.C. de Pinna, Universidade de São Paulo; Scott A. Schaefer, Academy of Natural Sciences of Philadelphia; and William L. Fink, University of Michigan.

and William G. Saul (ANSP); Gordon J. Howes, Darrell J. Siebert, and Amanda Banner (BMNH); Tomio Iwamoto and David Catania (CAS); Barry Chernoff and Mary Anne Rogers (FMNH); Plutarco Cala (ICNMHN); Lawrence M. Page, Kevin S. Cummings, and Michael R. Retzer (INHS); Antonio Machado-Allison and Francisco Provenzano (MBUCV); Karsten E. Hartel (MCZ); Guy Duharnel and Martine Desoutter (MNHN); Hernán Ortega (MUSM); Naércio A. Menezes, Heraldo A. Britski, and José L. Figueiredo (MZUSP); Barbara Herzig (NMW); Sven O. Kullander and Erik Åhlander (NRM); George Burgess and John Matter (UF); and Douglas W. Nelson and William L. Fink (UMMZ).

The maps of South America are based on a map prepared by Marilyn Weitzman (NMNH). The photographs were prepared by T. Britt Griswold (NMNH). Technical support during this project at NMNH was provided by Jeffrey M. Clayton, William F. Hoffman, Thomas M. Orrell, Lisa F. Palmer, and in particular Sandra J. Raredon. The Spanish translation of the Resumen was provided by Hernán Ortega. Research, collecting efforts, and museum studies in South America associated with this paper were funded by the Neotropical Lowland Research Program of the International Environmental Sciences Program of the Smithsonian Institution. Personal support to the senior author was provided by a Natural Sciences and Engineering Research Council of Canada Postdoctoral Fellowship. This paper benefited from numerous very useful comments and suggestions from Stanley H. Weitzman, Wayne C. Starnes, and Greg J. Klassen and the very careful copy editing and composition of the final paper by Craig Warren, Smithsonian Institution Press.

METHODS AND MATERIALS.—Measurements were made with dial calipers and ocular micrometer and data recorded to tenths of a millimeter. Counts and measurements were made on the left side of specimens whenever possible. Measurements in this and following papers dealing with Creagrutus and its allies were taken as follows: Standard Length (SL): tip of snout to posterior margin of hypural plate; snout to dorsal-fin origin: tip of snout to base of first well developed (not obscured by basal scale sheath) dorsal-fin ray; snout to anal-fin origin: tip of snout to base of first well-developed anal-fin ray; snout to pectoral-fin origin: tip of snout to base of lateral pectoral-fin ray; snout to pelvic-fin origin: tip of snout to base of lateral pelvic-fin ray; dorsal to caudal: base of first well-developed dorsal-fin ray to posterior margin of hypural plate; dorsal-fin origin to anal-fin origin: anterior base of first well-developed dorsal-fin ray to base of first well-developed anal-fin ray; dorsal-fin origin to pectoral-fin origin: base of first welldeveloped dorsal-fin ray to base of lateral pectoral-fin ray; dorsal-fin origin to pelvic-fin origin: base of first welldeveloped dorsal-fin ray to base of lateral pelvic-fin ray; head length (HL): greatest distance from tip of snout to posterior bony margin of opercle; snout length: maximum distance from tip (anteriormost point) of snout to anterior bony orbital margin; bony orbital diameter: horizontal bony orbital diameter; postorbital head length: maximum distance from posterior bony orbital margin to posterior bony margin of opercle; interorbital width: minimum distance between orbits, taken across frontals; caudal peduncle depth: minimum depth of caudal peduncle; pectoral fin length: base of lateral pectoral-fin ray to tip of longest ray; pelvic-fin length: base of lateral pelvic-fin ray to tip of longest ray; dorsal-fin length: base of first well-developed dorsal-fin ray to tip of longest ray; anal fin length: base of first well-developed anal-fin ray to tip of longest fin ray; lateral-line scales: complete lateral line series including pored and unpored scales and those on basal portions of caudal fin; pored scales: number of pored scales in lateral line; scale rows between dorsal-fin origin and lateral line: number of scale rows between base of first well-developed dorsal-fin ray and lateral line, not including lateral-line scale or sheath scale(s); scale rows between anal-fin origin and lateral line: number of scale rows between base of first well-developed anal-fin ray and lateral line, not including lateral line scale or sheath scale(s); predorsal median scales: number of median scales between occipital spine and dorsal fin; dorsal-fin rays: number of unbranched + number of branched rays; anal-fin rays: number of unbranched + number of branched rays (when last ray is divided to its base ray is counted as one element); pelvic-fin rays: number of unbranched + number of branched rays, not including pelvic splint; pectoral-fin rays: total number of rays excluding lateral unbranched element; gill rakers: number of rakers on upper limb (epibranchial) + number on lower limb (ceratobranchial), with the raker at the "angle" added to count for lower limb; vertebrae: total number of vertebrae with fused PU1+U1 considered a single bone, and vertebrae incorporated into Weberian apparatus counted as four elements.

The "Material Examined" section for each species is arranged in the following sequence: number of specimens of the species examined, 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 less than the total number of specimens, and the standard lengths (in mm) of the individuals whose standard length could be accurately determined). As a consequence of limited samples and the poor condition of most available juveniles of most species presented morphometric ranges are based on adult specimens. Males were identified by the presence of hooks on the anal and sometimes pelvic fins, with sex confirmed in a subsample via examination of the gonads. The presence of such hooks may be seasonal.

Geographic descriptors are in the sequence of country (capitalized), state, province, department, or district (italicized), followed by specific locality data. The common names are from the literature. In the synonymies for each species, localities are presented as originally cited, followed by modern or corrected equivalents, in parentheses, if that differs. Generic genders are as cited by Eschmeyer (1990).

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. Osteological terminology follows that in Vari (1989).

INSTITUTIONAL ABBREVIATIONS.—Follow Leviton et al. (1985) and Leviton and Gibbs (1988).

Genus Creagrutus Günther

Creagrutus Günther, 1864:339 [type species Leporinus muelleri Günther, 1859:92, by monotypy. Gender masculine].

Creagrutops Schultz, 1944b:327 [type species Creagrutops maracaiboensis Schultz, 1944b:327, by original designation. Gender masculine].

REMARKS.—The taxonomic limits of Creagrutus have been debated (Böhlke and Saul, 1975; Mahnert and Géry, 1988) with Creagrudite Myers and Piabina Reinhardt proposed as synonyms. Those alternative taxonomic schemes were advanced on the basis of the external similarities of a few involved taxa without extensive surveys of all included species. A definitive resolution of the question of the monophyly of Creagrutus must, however, await future revisionary and phylogenetic studies of Creagrutus and its near relatives on a continent wide basis. Furthermore, Creagrudite and Piabina are limited to South American drainages east of the Andean Cordilleras and are not germane to the present study. A fourth genus, Creagrutops Schultz, occurs in the region of interest and is included in this study.

Schultz (1944b:327), in his description of the monotypic Creagrutops, briefly diagnosed it as "a Creagrutus without a complete lateral line," and subsequent authors added little data to clarify the status of the genus. Géry (1977:410) reiterated Schultz' (1944b) characterization and described the teeth as "atypically set." He also proposed that C. maracaiboensis may be most closely related to the sympatric Creagrutus hildebrandi. Géry and Renno (1989:4), who also recognized Creagrutops, tentatively related it to an assemblage of Creagrutus species confined to drainages east of the Andean Cordilleras.

Creagrutops maracaiboensis, known from 48 specimens with a maximum known standard length of 22 mm and reaching sexual maturity by this size, is one of the smallest species in the assemblage it forms with the species included in Creagrutus. In addition to fitting the length criterion for a miniature species utilized by Weitzman and Vari (1988:450), this species has many paedomorphic reductions (e.g., number of vertebrae, number of scales in longitudinal scales that includes lateral line, development of laterosensory canal system). Elsewhere among characiforms such reductions arise independently both at higher phylogenetic levels (see listing in Weitzman and Vari, 1988) and within smaller clades within some families (e.g., in the Curimatidae, Vari, 1989:61; 1992b:124–126). The high level of homoplasy typical of such

reductive features within characiformes makes it difficult to determine the appropriate phylogenetic level at which they should be applied. The limitation of pores to the anterior portion of the lateral line, in particular, is problematical as a basis for distinguishing taxa (see Weitzman and Fink (1983)). That reductive feature was, however, the primary character proposed by Schultz to distinguish *Creagrutops maracaiboensis* from the species of *Creagrutus*. Géry and Renno (1989) appear to have continued to recognize a separate *Creagrutops* not based on possible relationships of its single species but because of its apparent morphological divergence from *Creagrutus*. We reject the use of such information in classification and propose synonymy of *Creagrutops* to be consistent with phylogenetic data available to us at this time.

Above and beyond the question of the utility of reductive features in phylogenetic analyses, we find that in the assemblage formed by Creagrutops and Creagrutus, such characters are limited to the monotypic Creagrutops. Initial phylogenetic analysis indicates that the characters listed here, which are apparently unique to Creagrutops, are parsimoniously regarded as autapomorphies and not indicative of a basal position within the Creagrutus-Creagrutops clade. A clade containing all Creagrutus (including Piabina) can be diagnosed based on the presence of an anteriorly truncated lower jaw with a thick, fleshy anterior region and modified outer premaxillary teeth, which are rounded in cross-section and displaced laterally and medially, causing the inner and outer rows to interdigitate to varying degrees (see illustrations of premaxillary dentition of selected species; Eigenmann, 1927, pl. 35: figs. 3a, 4, 7, pl. 80: fig. 15). Within this clade is a monophyletic subgroup containing many Creagrutus, including C. maracaiboensis. The monophyly of the clade is supported by a further modification of the premaxillary teeth, as described and illustrated here for C. brevipinnis (see "Dentition in Trans-Andean Creagrutus Species" below). Recognizing Creagrutops, therefore, renders Creagrutus paraphyletic and we accordingly treat the former as a junior synonym of Creagrutus.

DISTRIBUTION OF TRANS-ANDEAN Creagrutus SPECIES.—Rivers tributary to Lago Maracaibo and southeastern portion of Golfo de Venezuela, Caribbean drainages of Colombia from Río Magdalena west to coastal basin of Chocó Department, Pacific slope rivers of Panama from Río Bayano to Río Tuira, Río Chagres of Caribbean slope of Panama, and Río Baudo and Río San Juan systems of Pacific slope of Colombia.

The report of the trans-Andean Creagrutus caucanus from the upper portions of the Rio Negro, Amazon basin (Goulding et al., 1988) is a misidentification (see "Remarks" under Creagrutus caucanus). Eigenmann (1910:435) considered Creagrutus affinis of western Colombia to be a synonym of Creagrutus muelleri (Günther) described on the basis of material from the eastern slopes of the Andes. Although Eigenmann (1913:7, 1927:418) later recognized the two species as distinct he (Eigenmann and Allen, 1942:227)

subsequently repeated the synonymy. The results of our study indicate that the two species are distinct. Eigenmann (1921:5) reported *Creagrutus* from the Guayaquil (= Río Guayas) basin of southwestern Ecuador, a record not repeated in his later publications on the genus, and an evident error.

Dentition in Trans-Andean Creagrutus Species

The form of the premaxillary dentition in *Creagrutus* has been a criterion for the recognition of the genus and for delimiting its subunits (e.g., Eigenmann, 1927) although the utility of such characters in differentiating species and genera has been widely discussed (e.g., Böhlke and Saul, 1975). For simplicity in this paper, the dentition in *Creagrutus brevipinnis*, a species with the condition typical for the members of the genus in trans-Andean South America, is illustrated (Figure 1) and described. Only differences relative to the condition in *Creagrutus brevipinnis* are discussed in the species accounts.

The premaxillary dentition in Creagrutus brevipinnis consists of three major components. A main row of six, occasionally five, transversely rounded tricuspid teeth lie in a shallow arch from the anterior of the symphysis to the posterolateral region of the premaxilla, with the anterior tooth missing in some individuals. A triangular cluster of three larger teeth with more prominent cusps is medial to the main row. A single tooth similar in morphology to those of the main row occurs lateral to the third or fourth tooth of the main row. The preceding morphology is unique among examined characiforms and is hypothesized to be a synapomorphy for Creagrutus or a major component of that genus. Evidently some individuals have regenerated the dentition on one side of the upper jaw because the teeth are arranged in roughly two parallel rows, a condition approximating that in outgroup characiforms. The dentition on the contralateral premaxilla in

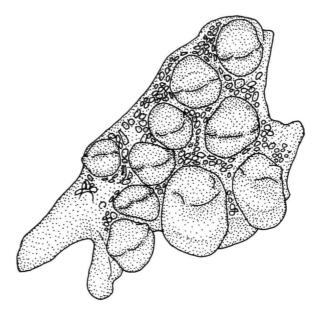


FIGURE 1.—Ventral view of right premaxilla of *Creagrutus brevipinnis*, USNM 120148, 44.7 mm SL; showing arrangement of teeth; anterior at top, medial to right.

such individuals and conspecifics reveals the typical Creagrutus arrangement of the teeth.

Dentition of the dentary is difficult to survey because examination either severely damages the lower jaw or requires extensive dissection. In all examined specimens, the dentary has either five or six teeth, with the anterior four teeth much larger than the others. Teeth on the dentary are typically tricuspid, occasionally unicuspid, with cusps reduced in some individuals. The maxilla has two to four tricuspid teeth.

Key to the Trans-Andean Species of Creagrutus Günther

1.	Lateral-line scales modified, with lateral lamellar process overlying pore [see Figure
	3]; lateral-line scales 39 to 42; anterior premaxillary tooth displaced anteriorly
	relative to rest of series
	(upper portions of Río Cauca basin
	Lateral-line scales unmodified, without lateral lamellar process overlying pore
	lateral-line scales fewer than 39; anterior premaxillary tooth usually in line with rest of premaxillary tooth series
2.	Lateral-line scales 29 to 32; vertebrae 32 or 33; miniature species, not known to exceed 27.0 mm SL
	Lateral-line scales 33 to 38; vertebrae 34 to 39; maximum body size at least 48.1 mm SL
3.	Lateral line completely pored; humeral mark distinct, dark, vertically elongate; scale rows between dorsal-fin origin and lateral line; 4 scale rows between anal-fin
	origin and lateral line
	(Caño Pechilín, Caribbean basir
	drainage in state of Sucre. Colombia

	Lateral line incomplete, anterior 8 to 10 scales pored; diffuse, barely visible, rounded humeral mark; 4 scale rows between dorsal-fin origin and lateral line; 3 scale rows
	between anal-fin origin and lateral line C. maracaiboensis, new combination
	(southwestern tributaries of Lago Maracaibo)
4.	Third infraorbital relatively small, with posterior margin concentric with posterior margin of orbit, large gap present between ventral margin of infraorbital and ventral limb of preopercle (see "Remarks" concerning cf. paralacus); dorsal fin
	originating slightly posterior to vertical through pelvic-fin origin; pelvic fins short (13.5%-16.8% SL)
	(upland southern tributaries to Lago Maracaibo)
	Third infraorbital well developed, with posteroventral margin angular, ventral
	margin approaching or contacting ventral limb of preopercle; dorsal fin originating at or anterior to vertical through pelvic-fin origin; pelvic fins relatively
_	long (15.5%–24.2% SL)
5.	Predorsal body profile distinctly convex, often not smoothly rounded, convexity most pronounced in anterior one-third; branched anal-fin rays 8 to 10, rarely 11 in
	magdalenae
	Predorsal body profile straight to slightly convex; branched anal-fin rays 10 to 13
6.	Body strongly compressed and deep posteriorly through region of anal fin, distance
87.0	between origins of dorsal and anal fins 35.0%-41.1% SL; caudal peduncle deep
	and compressed (caudal peduncle depth 13.5%-15.3% SL); longitudinal scale
	series 33 to 36
	(upper Río Magdalena)
	Body moderately compressed and not deep posteriorly, distance between origins of
	dorsal and anal fins 30.7%-36.0% SL; caudal peduncle relatively shallow
	appearing somewhat elongate (caudal peduncle depth 9.6%-12.4% SL);
	longitudinal scale series 36 to 38
	(upper Río Cauca)
7.	Central rays of caudal fin with heavy concentration of dark pigment basally,
	appearing as a caudal spot
	(tributaries to Lago Maracaibo and
	southwestern portions of Golfo de Venezuela)
	Central rays of caudal fin with series of dark chromatophores along margins, giving
	appearance of diffuse caudal stripe
	(Río Magdalena west to central
	Panama and south to Río San Juan)

Creagrutus caucanus Eigenmann

FIGURES 2-4; TABLE 1

Creagrutus caucanus Eigenmann, 1913:9 [type locality: Colombia: Paila; also specimens from (Río) Cauca at Cali, Cartago, Cali]; 1922:147 [Colombia: upper Río Cauca]; 1927:428, pl. 34: fig. 5 [Colombia: Paila, Cauca, Cartago].—Miles, 1943:55 [Colombia: Río Cauca basin; Creagrutus brevipinnis as a possible synonym].—Dahl, 1971:138 [Colombia: upper Río Cauca; distinctiveness from Creagrutus brevipinnis discussed; common name].—Fowler, 1975:26 [literature compilation].—Géry, 1977:410 [Colombia: Río Cauca].—Ibarra and Stewart, 1987:28 [location of holotype and part of paratypic series].—Román-Valencia, 1988:110 [Colombia: Río Cauca].—[Not Creagrutus cf. caucanus, Goulding et al., 1988:124, 156, 160].

DIAGNOSIS.—Creagrutus caucanus can be distinguished from all its congeners by its unique and evidently autapomor-

phic modification of the lateral-line scales. These scales have a lateral lamellar process resulting from the abrupt expansion of the posterior osteum of the lateral-line canal in each scale (Figure 3). Anterior displacement of the first premaxillary tooth is also a diagnostic, possibly autapomorphic, feature. Creagrutus caucanus has 39 to 42 lateral-line scales contrary to 29 to 38 in its congeners to the west of the Andes. Other characters which, in combination, serve to separate Creagrutus caucanus from its trans-Andean congeners are the completely pored lateral-line system on the body, the lack of discrete dark pigmentation on the central rays of the caudal fin forming either a stripe or basal spot, and the possession of 37 to 39 vertebrae (versus 32 to 38).

DESCRIPTION.—Body moderately deep and compressed. Greatest body depth ranging from slightly anterior of pelvic-fin

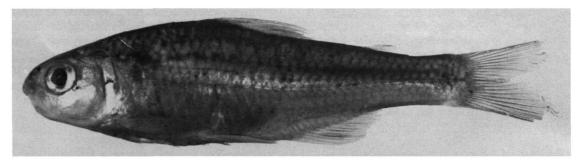


FIGURE 2.—Creagrutus caucanus, paratype, FMNH 56105, 79.9 mm SL; Colombia, Valle, Paila, Río Cauca basin.

origin anteriorly as far as half of distance to pectoral-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 rear of supraoccipital. Dorsal profile of body slightly convex to dorsal-fin origin, typically straight from that point to caudal peduncle, some specimens with slight concavity between origins of dorsal and adipose fins. Ventral profile of head with obtuse angle approximately midway between margin of lower lip and posterior of dentary, straight to slightly convex from that point to approximately to pelvic-fin origin; slightly concave from anal-fin origin to caudal peduncle.

Upper jaw longer than and overhanging lower jaw. Anterior portion of snout fleshy; with many minute papillae on anteromedian portion of snout, papillae continue ventrally onto upper lip and into mouth on fleshy flaps between premaxillary teeth. Lower jaw fleshy anteriorly, with papillae concentrated on lip and decreasing in number ventrally and laterally, extending ventrally and posteriorly in small numbers nearly to isthmus. Elements of infraorbital series well-developed, with ventral margin of third infraorbital approaching or contacting ventral limb of preopercle and posterior margin distinctly separated from vertical limb of preopercle by space of at most one-quarter width of orbit; posteroventral corner of third infraorbital rounded with rest of posterior and ventral margins of bone approximately at a perpendicular.

Dentition as in *Creagrutus brevipinnis* except that anterior tooth of main premaxillary row displaced somewhat anteriorly.

Dorsal fin with ii,8 rays. Dorsal-fin origin located at vertical through pelvic-fin origin. Distal margin of dorsal fin slightly concave and with noticeably elongate anterior lobe. Anal fin with ii or iii,10–13 rays. Anal fin of males with hooks on segments of first three to five branched rays. Distal margin of anal fin slightly sinusoidal. Pectoral fin approaching or reaching pelvic-fin origin. Pelvic fin with i,7 rays. Pelvic fin typically nearly reaching anal-fin origin; hooks on segmented and unsegmented portions of all branched rays in at least some males.

Gill rakers 6-8 + 10-12 (10 specimens).

COLOR IN ACOHOL.—Dorsal surface of head with uniform

diffuse pattern of dark chromatophores continuing anteriorly onto snout, with distinct small crescent 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. Lateral surface of head unpigmented. Body with pigmentation concentrated dorsally, particularly at base of dorsal fin and over center of exposed surface of scales. Humeral mark most concentrated immediately dorsal of lateral line, extending ventrally towards pectoral-fin base and dorsally to about one-half distance to middorsal line, either as vertical or slightly anterodorsally inclined bar. Flank pigment other than humeral bar restricted to area dorsal of lateral line in some

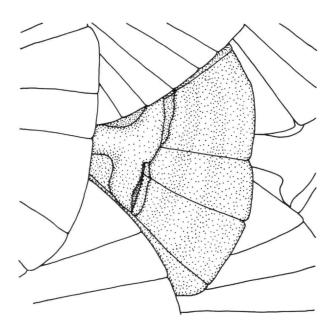


FIGURE 3.—Creagrutus caucanus, pored lateral-line scale showing lateral lamellar process, a posterior terminal broadening of the lateral surface of the tube in each lateral-line tube which overlies pore in scale; lateral view, posterior to right; neighboring scales not stippled.

TABLE 1.—Morphometrics and meristics of (A) holotype of *Creagrutus caucanus* (FMNH 56104); and (B) 22 other specimens of *Creagrutus caucanus* from which measurements and counts were taken. Standard length is expressed in mm; measurements 1 to 14 are percentages of standard length; 15 to 17 are percentages of head length.

	A	В	
	Morph	OMETRICS	
Standard Length	84.8	43.0-83.4	
1. Snout to anal-fin origin	66.5	59.5-65.9	
2. Snout to pelvic-fin origin	47.5	42.4-48.2	
3. Snout to pectoral-fin origin	25.5	23.3-26.5	
4. Snout to dorsal-fin origin	47.8	44.5-50.6	
5. Dorsal-fin origin to hypural joint	58.8	55.3-63.2	
6. Dorsal-fin origin to anal-fin origin	34.7	28.9-35.1	
7. Dorsal-fin origin to pelvic-fin origin	30.8	23.4-30.2	
8. Dorsal-fin origin to pectoral-fin origin	34.2	29.1-34.1	
9. Caudal peduncle depth	11.8	8.2-11.7	
10. Pectoral-fin length	20.2	16.9-21.8	
11. Pelvic-fin length	16.6	15.1-17.6	
12. Dorsal-fin length	23.3	20.4-24.9	
13. Anal-fin length	17.7	16.8-24.7	
14. Head length	26.7	24.2-27.1	
15. Postorbital head length	50.4	42.3-50.2	
16. Snout length	28.3	22.7-29.2	
17. Bony orbital diameter	28.8	28.9-35.5	
18. Interorbital width	37.2	29.7-35.9	
	MERISTICS		
Lateral-line scales	39	39-42	
Scale rows between dorsal-fin origin and lateral line	4	3–5	
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	12	10-13	
Branched pelvic-fin rays	7	7	
Pectoral-fin rays	13	11-13	
Vertebrae	38	37-39	

individuals, other specimens with pigmentation along posterior margins of scales that gradually decreases ventrally in that region. Midlateral stripe becoming denser and somewhat wider posteriorly on caudal peduncle.

Caudal fin with all fin rays delineated by dark pigment, pigmentation darkest on central rays of fin. Unbranched anal-fin rays unpigmented, branched rays delineated by dark pigment. Dorsal-fin membrane with dark chromatophores most concentrated on central portion of fin. Pectoral-fin rays delineated by dark chromatophores. Pelvic fin hyaline.

COMMON NAME.—Colombia: "sardina" (Dahl, 1971:138).

DISTRIBUTION.—Known only from the upper portions of the Río Cauca, northwestern Colombia (Figure 4). Creagrutus caucanus is sympatric with C. brevipinnis at least at several localities in that basin.

REMARKS.—The specimens of the type series are uniform in their morphology. We note, however, that the holotype of C.

caucanus has values for several morphometric features (Table 1) slightly outside the range for the paratypes. The holotype is the largest specimen examined and the observed minor morphometric discrepancies are explained by allometric effects.

As discussed under "Remarks" for Creagrutus brevipinnis, Miles (1943:55, 1947:159) considered C. brevipinnis as a synonym of C. caucanus, with the nominal forms representing the males and females of the latter species. The nominal forms actually differ in a variety of features (see "Key to the Species of Trans-Andean Creagrutus" and "Remarks" under C. brevipinnis below) and each is represented by both sexes. The species consequently are recognized as distinct.

Goulding et al. (1988:124, 156, 160) tentatively identified some *Creagrutus* samples from the Rio Negro system of the Amazon basin as C. cf. caucanus. Examination of a portion of those samples (MZUSP 29888) reveals that they are not caucanus.

MATERIAL EXAMINED.—56 specimens.

COLOMBIA. Upper Río Cauca and tributaries (no exact localities), USNM 120147, 3; MCZ 35887, 3 (46.7-48.4). Valle: Paila, FMNH 56104, 1 (84.8, holotype of Creagrutus caucanus; formerly CM 4895); FMNH 56105, 6 (63.2-72.7, paratypes of Creagrutus caucanus); USNM 79187, 3; CAS 69304, 8 (59.5-65.9, paratypes of Creagrutus caucanus). Río Cauca, at Cali, CAS 41373, 10 (3, 62.4-65.5, paratypes of Creagrutus caucanus; formerly IU 12736); FMNH 56106, 10 (paratypes of Creagrutus caucanus; formerly CM 4896, in part); FMNH 56108, 10 (paratypes of Creagrutus caucanus; formerly CM 4896, in part). Cartago, FMNH 56107, 1 (67.1, paratype of Creagrutus caucanus; formerly CM 4897); CAS 41374, 1 (51.0, paratype of Creagrutus caucanus; formerly IU 12737).

Creagrutus nigrostigmatus Dahl

FIGURES 4-5; TABLE 2

Creagrutus nigrostigmatus Dahl, 1960:353 [type locality: Colombia: Departamento Bolivar (that portion of the department now in Departamento Sucre), municipio de Tuloviejo, arroyo Pechilín (approx. 9°31'N, 75°35'W)]; 1971:139 [Colombia: Caños Pechilín and Zaragocilla].

DIAGNOSIS.—Creagrutus nigrostigmatus is distinguished from all congeners except C. maracaiboensis by a low number of lateral-line scales (30 to 32 in C. nigrostigmatus and 29 to 31 in C. maracaiboensis versus a range of 33 to 41 in other trans-Andean species) and reduced number of vertebrae (32 to 33 in both species versus 34 or more in other trans-Andean species). These low counts may represent one or more synapomorphies for this species pair. Creagrutus nigrostigmatus has a complete lateral line and distinct vertically elongate humeral mark contrary to the incompletely pored lateral line and barely apparent rounded humeral mark of C. maracaiboensis. The distinct patch of dark pigmentation on the basal

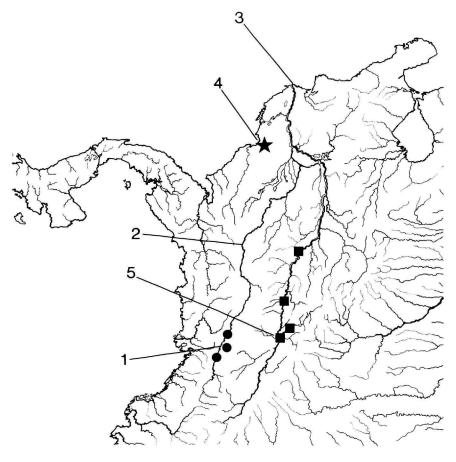


FIGURE 4.—Map of northwestern South America showing distribution of *Creagrutus caucanus* (filled in circle; 1 = type locality; 2 = Río Cauca; 3 = mouth of Río Magdalena), *Creagrutus nigrostigmatus* (star; 4 = type locality), and *Creagrutus magdalenae* (squares; 5 = type locality) (some symbols represent more than one locality or lot of specimens).

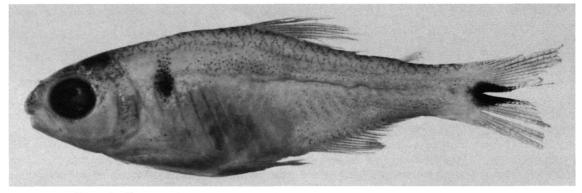


FIGURE 5.—Creagrutus nigrostigmatus, neotype, ICNMHN 989, 23.4 mm SL; Colombia, Sucre, Tuloviejo, Caño Pechilín (approx. 9°31′N, 75°35′W).

portions of the caudal fin also distinguishes nigrostigmatus from all trans-Andean Creagrutus species other than C. hildebrandi, which also has a basal caudal spot and C. affinis and C. maracaiboensis, which have very dark pigmentation variably developed on the central caudal rays.

DESCRIPTION.—Body moderately deep, particularly relative to congeners of comparable body size. Greatest body depth slightly anterior of dorsal-fin origin. Dorsal profile of head broadly convex from margin of upper lip to vertical through anterior margin of orbit. Dorsal surface of head and body slightly convex from that point to dorsal-fin origin, straight from there to caudal peduncle. Ventral profile of head with obtuse angle situated approximately at one-half of distance from tip of lower jaw. Ventral profile of head and body slightly convex from that point to pelvic-fin origin.

Head with orbit large relative to snout. Upper jaw longer than and overhanging lower. Anterior portion of snout quite fleshy, with papillae particularly apparent centrally and continuing along margin of upper lip and extending into mouth on fleshy flaps between premaxillary teeth. Lower jaw fleshy anteriorly, with papillae most concentrated along margin of lower lip with decreasing numbers posteriorly on ventral surface. Elements of infraorbital series moderately well developed, with ventral margin of third infraorbital approaching but not contacting ventral limb of preopercle and posterior margin separated from vertical limb of preopercle by space approximately one-quarter width of orbit; posterior and ventral margins of third infraorbital approximately at a perpendicular with posteroventral corner of bone broadly rounded.

Teeth arranged as in Creagrutus brevipinnis.

Dorsal fin with ii,8 rays. Dorsal-fin origin slightly posterior of vertical through pelvic-fin origin. Dorsal fin damaged in available specimens, shape unknown, but apparently with some of anterior branched rays slightly elongate. Anal fin with ii,11-12 rays. Anal-fin hooks not observed in small available sample including largest specimen which is, however, apparently a female with eggs showing through body wall. Anal fin damaged in available specimens, shape unknown. Pectoral fin moderately elongate, tip nearly reaching pelvic-fin origin; with i,13-14 rays. Pelvic fin nearly reaching anal-fin origin; with i,7 rays. Pelvic fin hooks not apparent in available specimens.

COLOR IN LIFE.—The following life coloration description is paraphrased from Dahl (1960:355). Dorsal surface of body grayish but not too dark with brilliant silvery stripe on side of body beginning at humeral mark and ventral surfaces of body white. Humeral mark is vertical, very dark, with nearly square borders other than for few scattered chromatophores, and crosses third and fourth scales of lateral line without indication of lunate form of mark very common in genus. Caudal band is more or less rectangular, beginning on last myomere of caudal peduncle and continuing nearly to end of central caudal fin rays. Fins are slightly yellowish with dorsal and anal fins bearing some scattered chromatophores.

TABLE 2.—Morphometrics and meristics of (A) neotype of *Creagrutus nigrostigmatus* (ICNMHN 989); and (B) 7 other specimens collected with neotype; all specimens topotypic to original type series. See also "Remarks" in species account concerning various meristic values reported in original description of species. Standard length is expressed in mm; measurements 1 to 14 are percentages of standard length; 15 to 17 are percentages of head length.

	A	В
	MORPH	OMETRICS
Standard Length	23.4	17.5-20.5
1. Snout to anal-fin origin	65.6	62.9-65.5
2. Snout to pelvic-fin origin	49.7	47.3-52.1
3. Snout to pectoral-fin origin	27.8	25.9-28.4
4. Snout to dorsal-fin origin	54.0	50.7-54.1
5. Dorsal-fin origin to hypural joint	49.5	49.1-52.2
6. Dorsal-fin origin to anal-fin origin	34.7	30.8-35.0
7. Dorsal-fin origin to pelvic-fin origin	32.5	29.1-34.6
8. Dorsal-fin origin to pectoral-fin origin	36.7	36.0-37.7
9. Caudal peduncle depth	12.8	11.7-13.2
10. Pectoral-fin length	21.8	17.8-22.4
11. Pelvic-fin length	18.2	15.3-18.4
12. Dorsal-fin length	25.6	26.7-27.0*
13. Anal-fin length	19.2	19.1-19.5*
14. Head length	28.6	26.9-28.6
15. Postorbital head length	41.5	39.0-42.0
16. Snout length	21.0	21.0-22.0
17. Bony orbital diameter	37.0	37.0-39.0
18. Interorbital width	34.0	34.0-36.0
	Ме	RISTICS
Lateral-line scales	31	30-32
Scale rows between dorsal-fin origin	5	5
and lateral line		
Scale rows between anal-fin origin and lateral line	4	4
Predorsal median scales	11	11
Branched dorsal-fin rays	8	8
Branched anal-fin rays	11	11-12
Branched pelvic-fin rays	7	7
Pectoral-fin rays	14	13–14
Vertebrae	33	32-33

^{*}Range of values based on only 3 specimens due to damaged fins in rest of sample.

COLOR IN ACOHOL.—Dorsal surface of head with numerous large, light brown chromatophores, except on fontanel and snout where they appear smaller and darker. Line of diffuse chromatophores extends from snout posteroventrally to margin of orbit, and continuing around ventral and posterior margins of orbit. Posterolateral surface of head posterior of orbit with 20 to 30 scattered large chromatophores. Scales of dorsal and dorsolateral surfaces of body with series of dark chromatophores along posterior margins, forming overall reticulate pattern. Middorsal scales with additional chromatophores on central exposed portion of scales, giving appearance of thin middorsal stripe. Lateral and ventrolateral surface of body above anal fin with scattered dark chromatophores; with some of chromatophores above anal fin arranged along myosepta.

Region anterior of humeral mark largely unpigmented. Humeral mark vertically elongate, subrectangular; largely confined to region dorsal of lateral line. Midlateral stripe formed by deep-lying, small, dark chromatophores; extending from vertical through dorsal-fin origin top basal portion of hypurals.

Caudal fin with darkest chromatophores of body associated with six central rays and their membranes; pigmentation most intense on basal two-thirds of these rays, tapering posteriorly with overall form of mark approximately teardrop-shaped. Branched rays of anal fin delineated by rows of dark chromatophores. Dark chromatophores delineating basal portions of dorsal-fin rays, with scattered darker chromatophores on membranes distally. Pectoral fin unpigmented. Pelvic fins with small number of scattered chromatophores.

ECOLOGY.—Dahl (1960:357) noted that Creagrutus nigrostigmatus usually occurs in the "quiet parts" [translated] of the stream in areas with large amounts of detritus. All of his specimens had "detritus" in the digestive tract. Although the largest available specimen is only 23.4 mm SL, it is apparently a mature female as indicated by the relatively large eggs visible through the body wall. Dahl (1960:354) noted that both males and females are fully mature with developed gonads at 18 to 20 mm SL.

DISTRIBUTION.—Examined specimens are from the type-locality, Caño Pechilín (Figure 4, locality 4). Dahl (1971:139) also reported the species from Caño Zaragocilla, a site apparently close to the type locality.

REMARKS.—Dahl (1960) described Creagrutus nigrostigmatus from Arroyo (= Caño) Pechilín, a small stream draining into the Caribbean Sea in the region west of the mouth of the Río Magdalena (Figure 4, locality 4). The types of the species are lost (Cala, 1981; Dr. Plutarco Cala, pers. comm.) and we designate a topotypic specimen made available through the generous assistance of Dr. Cala as the neotype of the species (ICNMHN 989, 23.4 mm SL).

Contrary to Dahl (1960), the purported distinguishing feature for *C. nigrostigmatus*, the presence of well-developed, dark pigmentation on the middle rays of the caudal fin, is not unknown in other *Creagrutus* species from the west of the Andes but also occurs in various configurations in *C. affinis*, *C. hildebrandi*, and *C. maracaiboensis*.

Dahl also reported that *C. nigrostigmatus* has 5 to 7 branched dorsal-fin rays, values that are striking both for the low counts and the range of variation, which is not encountered elsewhere in genus. The specimens of the species examined all have 8 branched dorsal-fin rays, a value typical for all trans-Andean *Creagrutus* species. We conclude, therefore that Dahl's counts are in error.

MATERIAL EXAMINED.—8 specimens.

COLOMBIA. Sucre: Tuloviejo, Caño Pechilín (approx. 9°31'N, 75°35'W), ICNMHN 989, (1, 23.4; designated herein as neotype of Creagrutus nigrostigmatus); ICNMHN ex. 989, 7 (17.5–20.5, collected with neotype).

Creagrutus maracaiboensis (Schultz), new combination

FIGURES 6-7: TABLE 3

Creagrutops maracaiboensis Schultz, 1944b:327, figs. 45, 46 [type locality: Venezuela: Lago Maracaibo basin, Río Negro below mouth of Río Yasa].—Mago-Leccia, 1970:23, 70 [Venezuela: Lago Maracaibo].—Vari and Howe, 1991:15 [location of type specimens].—Géry and Renno, 1989:4 [possible phylogenetic relationships].

DIAGNOSIS.—Creagrutus maracaiboensis is unique among Creagrutus and its close allies in having pores only on the anterior 8 to 10 scales of the lateral-line series, an evidently autapomorphic reductive feature. A second autapomorphy for C. maracaiboensis is the reduced laterosensory canal system on the head. Creagrutus maracaiboensis shares with C. nigrostigmatus a reduced number of vertebrae (32 to 33 versus 34 or more in other trans-Andean species) and a low number of lateral-line scales (29 to 31 in C. maracaiboensis and 30 to 32 in C. nigrostigmatus versus a range of 33 to 41 in other trans-Andean species). These low counts may represent synapomorphies for the species pair. The distinct stripe dark pigmentation on the basal portions of the caudal fin also serves to distinguish C. maracaiboensis from all trans-Andean Creagrutus species other than C. hildebrandi, which has a basal caudal spot and C. affinis and C. nigrostigmatus, which have dark pigmentation on the central caudal fin rays forming a horizontal stripe.

DESCRIPTION.—Head and body relatively stout for a trans-Andean species of Creagrutus, somewhat compressed, less so in smaller individuals. Greatest body depth in region from slightly anterior to pelvic fin to midway between pelvic and pectoral-fin origin, variation in position of greatest depth a function of degree of distension of abdomen. Dorsal profile of head distinctly convex from margin of upper jaw to approximately vertical through middle of eye, nearly straight from that point to supraoccipital. Dorsal profile of body nearly straight to slightly convex from supraoccipital to dorsal-fin origin; straight to slightly convex from insertion of dorsal fin to adipose fin. Ventral profile of head with obtuse angle approximately one-third of distance between margin of upper lip and posterior of dentary, straight to convex from that point to pelvic-fin origin, convex to slightly concave along base of anal fin.

Head with orbit relatively large compared to snout. Upper jaw length and degree of overhang variable; variation a function of fleshiness of lower jaw. Anterior of snout fleshy, but not greatly produced anteriorly, with papillae sparsely distributed on snout, more concentrated on upper lip and margin of upper jaw, continuing into mouth on fleshy flaps between premaxillary teeth. Lower jaw fleshy, with small numbers of papillae on lip, most concentrated on anterior surface of lower jaw, with decreasing numbers posteriorly on ventral surface. Elements of infraorbital series reduced in width relative to other trans-Andean *Creagrutus* species, with ventral and posterior margins of series distinctly separated from

preopercle, posteroventral margin of series rounded, concentric with posteroventral margin of orbit.

Teeth arranged as in *Creagrutus brevipinnis* except that premaxillary teeth apparently in process of regeneration in holotype at time of fixation, perhaps accounting for Géry's comment (1977:410) that the teeth in the species are "atypically set."

Dorsal fin with ii,8 rays. Dorsal-fin origin slightly posterior of vertical through pelvic-fin origin. Posterior unbranched and anterior two branched rays of dorsal fin longest, forming distinct anterior lobe. Anal fin with ii,11–12 rays. Anal fin in males with hooks on posterior surface of segmented portions of posterior branch and main shaft of first to sixth rays, number of involved rays and degree of development of hooks varies between specimens and individual fin rays. Distal margin of anal fin slightly concave with distinct anterior lobe. Pectoral fin reaching slightly posterior of pelvic-fin origin. Pelvic fin falling slightly short of anal-fin origin in many species, sometimes reaching fin; with i,7 rays. Pelvic fin in males with poorly developed hooks on segmented and unsegmented portions of all branched rays.

COLOR IN LIFE.—Schultz (1944b:329) noted that in life *Creagrutus maracaiboensis* "had a reddish coloration on the upper third of the eye. Peritoneum silvery, with a few scattered black pigment cells at sides dorsally."

COLOR IN ACOHOL.—Type material with body largely unpigmented perhaps because of poor preservation. Following description based on non-type specimens (UF 23808) from Santa Cruz de Zulia (Figure 7, locality 2). Dorsal surface of head with chromatophores concentrated on central and posterior regions. Entire surface of snout with concentration of smaller chromatophores. Line of diffuse chromatophores extending from snout posteroventrally to margin of orbit, and continuing around ventral and posterior margins of orbit. Body pigmentation very diffuse, heaviest concentration middorsally, particularly at base of dorsal fin and in scale pockets, giving

TABLE 3.—Morphometrics and meristics of (A) holotype of *Creagrutus maracaiboensis* (USNM 121531); and (B) 17 other specimens of *Creagrutus maracaiboensis* from which measurements and counts were taken. Standard length is expressed in mm; measurements 1 to 14 are percentages of standard length; 15 to 17 are percentages of head length.

	A	В
	MORPH	OMETRICS
Standard Length	21.0	15.9-22.0
1. Snout to anal-fin origin	63.8	62.0-65.5
2. Snout to pelvic-fin origin	48.6	45.1-51.5
3. Snout to pectoral-fin origin	27.6	26.8-27.8
4. Snout to dorsal-fin origin	53.3	50.3-54.8
5. Dorsal-fin origin to hypural joint	52.3	47.8-51.9
6. Dorsal-fin origin to anal-fin origin	32.9	31.2-33.1
7. Dorsal-fin origin to pelvic-fin origin	31.9	28.6-32.6
8. Dorsal-fin origin to pectoral-fin origin	35.2	32.6-37.0
9. Caudal peduncle depth	11.9	11.4-12.6
10. Pectoral-fin length	18.9	19.0-21.6
11. Pelvic-fin length	16.2	15.3-17.7
12. Dorsal-fin length	23.3	23.6-25.5
13. Anal-fin length	19.5	19.2-21.7
14. Head length	26.5	26.5-27.8
15. Postorbital head length	45.0	40.0-45.0
16. Snout length	18.0	18.0-23.0
17. Bony orbital diameter	37.0	35.0-40.0
18. Interorbital width	35.0	31.0-36.0
	ME	RISTICS
Lateral-line scales	30	29-31
Pored lateral-line scales	8	8-10
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	_	10-11
Branched dorsal-fin rays	8	8
Branched anal-fin rays	11	11-12
Branched pelvic-fin rays	7	7
Pectoral-fin rays	13	11-14
Vertebrae	33	32-33

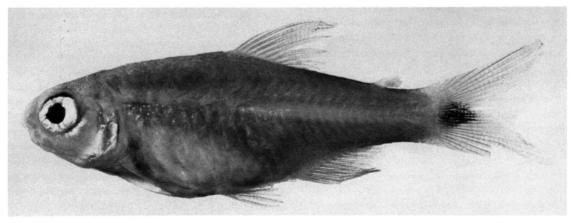


FIGURE 6.—Creagrutus maracaiboensis, paratype of Creagrutops maracaiboensis, USNM 121532, 20.5 mm SL; Venezuela, Zulia, Río Negro, below mouth of Río Yasa.

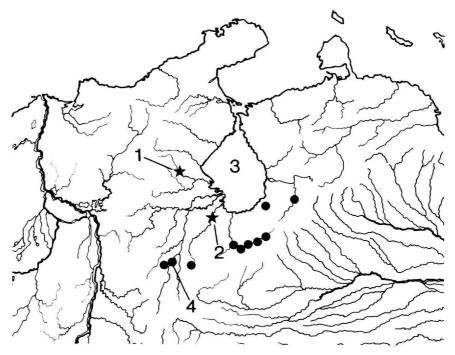


FIGURE 7.—Map of Lago Maracaibo basin and adjoining regions showing geographic distribution of *Creagrutus maracaiboensis* (stars; 1 = type locality of *Creagrutops maracaiboensis*; 2 = Santa Cruz de Zulia; 3 = Lago Maracaibo) and *Creagrutus paralacus* (filled in circles; 4 = type locality)(some symbols represent more than one locality or lot of specimens).

overall reticulate appearance. Humeral spot present, but small and highly diffuse, with chromatophores noticeably darker than in surrounded areas. Pigmentation along flank most concentrated posteriorly and in association with myosepta.

Caudal fin with approximately eight central rays with heavy concentration of chromatophores along basal one-half to two-thirds of rays, chromatophores overlying both rays and membranes. Distal portions of second unbranched and anterior two branched dorsal-fin rays sometimes with diffuse dark pigment. Anterior margin of branched anal-fin rays outlined by lines of small chromatophores. Paired fins apparently unpigmented.

ECOLOGY.—The type-locality was described by Schultz (1944a:177) as being a "river, 35 to 50 feet wide, with deep muddy holes and gravelly riffles."

DISTRIBUTION.—Known from only two localities in the rivers of western and southwestern portions of Lago Maracaibo basin (Figure 7). Creagrutus maracaiboensis is sympatric, at least at its type locality, with C. hildebrandi.

REMARKS.—Schultz (1944b:327) proposed the monotypic genus Creagrutops for a single Creagrutus-like species, maracaiboensis, which he distinguished from Creagrutus species on the basis of its truncated pored lateral line. As noted in "Remarks" in the generic account for Creagrutus, such

reduced poring of the lateral line, although unique to *C. maracaiboensis*, is probably a paedomorphic feature autapomorphic for the species.

The illustration of the holotype in the original description of maracaiboensis is somewhat misleading in several features. Although Schultz (1944b:329) specifically noted that the species lacked a humeral spot, the figure (1944b, fig. 45) shows a faint, but discrete, spot in the humeral region. Géry (1977:410) used this feature as the basis, in part, for his hypothesis of a close relationship between Creagrutops maracaiboensis and the sympatric species Creagrutus hildebrandi, which has distinct humeral pigmentation. The holotype has a slight concentration of dark chromatophores in the humeral region but lacks the discrete patch of pigmentation shown in the original figure. Based on the intensity of the other dark pigmentation on the specimen is it unlikely that the pigmentation originally formed a discrete spot. Rather the dark humeral spot in the original illustration probably represents the reduced musculature overlying the anterior chamber of the swimbladder. Schultz' figure also shows a discrete small dark spot at the base of the caudal fin rays continued posteriorly as a more diffuse region of dark pigmentation. Reference to the holotype and other specimens (Figure 6) demonstrates a larger region of basal pigmentation than illustrated by Schultz. That pigmentation is not divided into a discrete dark basal portion

and diffuse distal area but rather grades in intensity posteriorly (see "Color in Alcohol" above for more detailed description).

Although Schultz (1944b:327) described the premaxillary dentition of *Creagrutops maracaiboensis* as "practically the same as on *Creagrutus*," Géry (1977:410) remarked that "the upper teeth are atypically set." Géry's comments may have been based on an examination of the holotype in which the teeth were regenerating. It should also be noted that the illustration of the premaxillary teeth (Schultz, 1944b, fig. 46) are not based on the holotype.

Some of the features characteristic of *Creagrutus maracaiboensis* (incompletely pored lateral line, reduced degree of development of the laterosensory canal system on the head) are also juvenile conditions in many characiforms that achieve significantly larger maximum sizes than *C. maracaiboensis*. Several specimens of *C. maracaiboensis* of less than 22 mm SL are gravid females. This early maturity supports the hypothesis that the incompletely developed laterosensory canal systems on the head and body of the species are paedomorphic rather than juvenile characters.

MATERIAL EXAMINED.—48 specimens.

VENEZUELA. Zulia: Río Negro, below mouth of Río Yasa, USNM 121531, 1 (21.0, holotype of *Creagrutops maracaiboensis*); USNM 121532, 42 (15, 17.9-22.0, paratypes of *Creagrutops maracaiboensis*). Municipio Santa Cruz de Zulia, 4 km from El Moralito, Hacienda Chiquiquira, UF 23808, 5 (2, 15.9-17.5).

Creagrutus paralacus, new species

FIGURES 7-8; TABLE 4

Creagrutus beni.—Schultz, 1944b:336 [Venezuela: Lago Maracaibo basin: Río Cobre, Río Gonzáles, Río Chama, Río Motatán, Río Táchira, Río Barregas (= Albarregas); not specimens from Río Orinoco basin].—Mago-Leccia, 1970:70 [Venezuela: in part, Lago Maracaibo].

DIAGNOSIS.—The relatively narrow infraorbital series, the posterior position of the dorsal fin relative to the pelvic-fin origin, the nearly straight distal margins of the dorsal and anal fins, and the presence of hooks on the lateral surface of the pelvic rays of males are possible autapomorphies for Creagrutus paralacus. A final evaluation must await thorough studies of congeners to the east of the Andes. The combination of unmodified lateral-line scales, a completely pored lateral line, and a relatively small third infraorbital distinguishes Creagrutus paralacus from its trans-Andean congeners. Creagrutus paralacus can be additionally distinguished from all trans-Andean congeners by its limited pigmentation on the basal portions of the middle caudal fin rays (versus a distinct spot or horizontal bar on those rays in nigrostigmatus, maracaiboensis, hildebrandi, and affinis), its relatively rotund, not deep body (versus the highly compressed and very deep body of magdalenae), and number of lateral-line scales (36 to 38 versus 39 to 42 in caucanus, 29 to 31 in maracaiboensis, and 30 to 32 in nigrostigmatus).

DESCRIPTION.—Body moderately elongate, only slightly compressed relative to other trans-Andean Creagrutus species. Greatest body depth approximately midway between vertical lines through origins of pectoral and pelvic fins. Dorsal profile of head distinctly convex from margin of upper lip to region between vertical through posterior nares and vertical through anterior margin of orbit; approximately straight from that area to posterior end of supraoccipital. Dorsal profile of body with notable change in alignment relative to that of head, convex from posterior portion of supraoccipital to dorsal-fin origin; convexity asymmetrical, most pronounced in anterior one-third of predorsal profile. Dorsal profile nearly straight from dorsal-fin origin to caudal peduncle. Ventral profile of head with barely obvious angle approximately midway between margin of upper lip and posterior of dentary; some non-type specimens with angle more pronounced. Ventral profile of remainder of head and body posteriorly to anal fin slightly convex.

Head large with small orbit. Upper jaw distinctly longer than and overhanging lower jaw. Anterior portion of snout quite fleshy, with minute papillae distributed over anterior portion of snout and with numerous papillae continuing onto upper lip, margin of upper jaw, and into mouth on fleshy flaps between premaxillary teeth. Lower jaw fleshy, with numerous papillae on lip and gradually decreasing numbers of papillae continuing onto ventral portion of head as far as isthmus. Elements of infraorbital series reduced in width relative to other trans-Andean *Creagrutus* species other than *C. maracaiboensis*; ventral and posterior margins of series distinctly separated from preopercle, posteroventral margin of series rounded, and concentric with posteroventral margin of orbit.

Teeth arranged as in Creagrutus brevipinnis.

Dorsal fin with ii,8 rays. Dorsal fin origin slightly posterior to vertical through pelvic-fin origin. Distal margin of dorsal fin slightly concave centrally with anterior rays longest. Anal fin with ii,10-12 rays. Anal fin of males with hooks on anterior one to four, typically three, branched rays; males with hooks usually on posterior branch but occasionally also on main anterior branch. Distal margin of anal fin nearly straight, with anterior rays slightly elongate in some specimens. Pectoral-fin length variable; reaching well posterior to pelvic-fin origin in some individuals. Pelvic fin with i,7, rarely 8, rays. Pelvic fin proportionally short relative to other species; relative length variable, occasionally reaching posteriorly beyond anal-fin origin; males with hooks on rays on all branched rays, males with hooks usually on both main branches of three or four medial rays, and medial ray with a medial and a lateral hook on most hooked segments.

Gill rakers 5-7 + 8-10 (14 specimens).

COLOR IN LIFE.—Schultz (1944b:337) reported the following life coloration for *Creagrutus paralacus* (identified by him as *C. beni*): "Specimen from the Río Chama at Estanques: Pelvic, pectoral, and adipose fins yellowish orange; front of anal fin orange; dorsal surface of eye red; area in front of eye

yellow; central area of upper and lower caudal lobes bright red; back yellowish orange; lateral band and lower sides silvery, the lateral band is dark grayish or plumbeous in color on caudal peduncle; no caudal spot." Schultz noted that a specimen from the Río Motatán, 4 km above Motatán, had "dorsal surface of eye orange; back yellowish; pelvics yellowish orange as is front of anal fin; central area of caudal lobes bright red, with yellowish color basally; lateral band grayish; dorsal and anal fins grayish distally; no caudal spot."

COLOR IN ACOHOL.—Head with pattern of diffuse dark chromatophores on dorsal surface, most concentrated over fontanel and snout, with distinct but small crescent of dark pigmentation immediately in front of anterior nares. Continuous band of dark chromatophores extending posteroventrally from just anterior of nares posteriorly to anteroventral margin of orbit, becoming restricted to margin of orbit posteriorly and merging with diffuse pigmentation of dorsolateral surface of head. Second band of dark chromatophores extending laterally from snout across dorsal surface of premaxilla, maxilla, and portion of infraorbital series proximal to orbit. Dorsum of body with scattered small chromatophores more concentrated over centers of exposed portions of scales. Scales of dorsolateral surface of body with dark chromatophores concentrated along posterior margins, forming overall reticulate pattern. Region anterior of humeral mark diffusely pigmented. Humeral mark vertically elongate and tapering ventrally; chromatophores most concentrated dorsal of lateral line. Midlateral stripe formed largely by deep-lying, dark chromatophores, somewhat more diffuse ventral to dorsal fin, and partially masked by guanine in available specimens.

Caudal fin diffusely pigmented with some concentration of chromatophores on basal half of membranes of approximately central four rays. Central portion of branched anal-fin membranes darkly pigmented. Dorsal fin with dark chromatophores associated with unbranched rays. Dorsal fin membranes with dark chromatophores on all but basal one-quarter of membrane, forming an overall posteriorly tapering band.

Lateral rays of pectoral fin with scattered dark chromatophores delimiting rays. Pelvic fins hyaline.

ETYMOLOGY.—The species name paralacus, from the Greek "para," beside or near and the Latin "lacus," meaning lake, referring to the distribution of the species in the rivers near Lago Maracaibo.

ECOLOGY.—All specimens with exact locality data were collected in high gradient streams in the mountains to the south and southeast of Lago Maracaibo. Schultz (1944a:178) described the type locality as "width of river bed up to 200 feet, but only a small flow of water among rubble bottom; current rapid; depth in a pool up to 2 feet." The collecting site for samples of *C. paralacus* from the Río Cobre (USNM 121501) were described as "bottom large rubble to sand; current torrential," comparable to the conditions described by Schultz (1944a) for the Río Gonzáles (USNM 121506), Río Chama (USNM 121503, 121506), Río Barregas (= Albarregas) (USNM 121499), and Río Motatán (USNM 121502).

DISTRIBUTION.—Southern and southeastern tributaries to Lago Maracaibo (Figure 7). Creagrutus paralacus was collected with C. hildebrandi at least in some localities in the Río Motatán system in the southeastern portion of the basin (compare Figures 7 and 13).

REMARKS.—Schultz (1944b:337) reported this species as Creagrutus beni, a species described by Eigenmann (1911:172) based on a specimen from the Río Beni basin in Bolivia approximately 2600 kms to the south of Lago Maracaibo. Schultz did not explain his identification of his Lago Maracaibo basin samples as C. beni but indicated (1944b:337) he thought it likely that the Lago Maracaibo specimens would be shown to be "subspecifically distinct" from what he considered to be C. beni from the Río Orinoco system, once additional specimens from the latter basin became available.

Although samples of *Creagrutus* from a broad region of South America on both sides of the Andean Cordilleras have been identified as *C. beni*, these identifications have been made without critical discussion. Resolution of the question of the

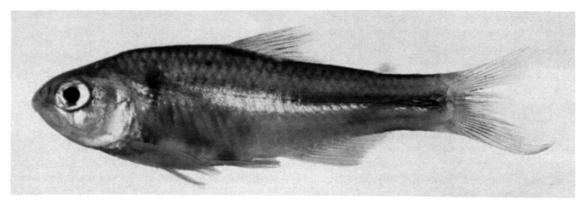


FIGURE 8.—Creagrutus paralacus new species, holotype, USNM 121504, 44.4 mm SL; Venezuela, Zulia, Río Catatumbo basin, Río Táchira, N of San Antonio.

TABLE 4.—Morphometrics and meristics of (A) holotype of *Creagrutus paralacus*, new species, (USNM 121504); (B) 25 paratype specimens of *Creagrutus paralacus*, from which measurements and counts were taken; and (C) *Creagrutus* cf. paralacus, (USNM 100738, see under "Remarks" concerning this sample). Standard length is expressed in mm; measurements 1 to 14 are percentages of standard length; 15 to 17 are percentages of head length.

	A	В	С
		MORPHOMETRICS	
Standard Length	44.4	32.3-66.6	71.2
1. Snout to anal-fin origin	61.3	56.4-64.6	65.0
2. Snout to pelvic-fin origin	45.3	40.7-47.8	49.6
3. Snout to pectoral-fin origin	26.4	21.4-27.5	26.4
4. Snout to dorsal-fin origin	49.1	45.9-51.7	50.1
5. Dorsal-fin origin to hypural joint	57.0	52.2-60.7	54.9
6. Dorsal-fin origin to anal-fin origin	30.6	26.8-33.8	29.8
7. Dorsal-fin origin to pelvic-fin origin	26.3	25.3-31.8	26.0
8. Dorsal-fin origin to pectoral-fin origin	33.3	31.2-37.8	33.3
9. Caudal peduncle depth	13.5	11.1-14.2	11.4
10. Pectoral-fin length	23.6	18.5-22.9	18.0
11. Pelvic-fin length	18.0	13.5-16.8	13.2
12. Dorsal-fin length	24.1	18.4-24.7	18.1
13. Anal-fin length	20.3	15.0-20.6	17.1
14. Head length	27.3	24.1-28.2	27.2
15. Postorbital head length	49.6	45.2-56.5	54.1
16. Snout length	24.8	22.6-31.4	30.9
17. Bony orbital diameter	32.2	24.9-34.0	23.7
18. Interorbital width	32.2	29.0-36.5	31.4
		MERISTICS	
Lateral-line scales	36	36-38	~37
Scale rows between dorsal-fin origin and lateral line	4	4-5	44
Scale rows between anal-fin origin and lateral line	3	2-4	34
Predorsal median scales	11	10-13	13
Branched dorsal-fin rays	8	8	8.
Branched anal-fin rays	10	10-12	10°
Branched pelvic-fin rays	7	7-8	7*
Pectoral-fin rays	12	11-13	116
Vertebrae	36	35-37	37*

^{*}Cited meristic value same in damaged specimen.

identity of C. beni and the determination of the actual distribution of that nominal form must await future studies of the Creagrutus species east of the Andean Cordilleras. The Lago Maracaibo populations identified by Schultz as C. beni (C. paralacus of this study) differ from the holotype of C. beni in the number of vertebrae (35 to 37, typically 36, in C. paralacus versus 38 in holotype of C. beni), form of the humeral mark (elongate inverted teardrop versus vertical bar respectively (see Eigenmann, 1927, pl. 58 for photograph of holotype of C. beni)), and degree of development of infraorbital series (moderately developed and falling distinctly short of preopercle ventrally and posteriorly in C. paralacus versus welldeveloped and contacting preopercle ventrally and posteriorly in C. beni). Comparisons to all other nominal Creagrutus species have not revealed any that are conspecific with what Schultz (1944b) termed C. beni from the Lago Maracaibo basin. The populations from the tributaries to Lago Maracaibo originally identified as *C. beni* by Schultz and subsequent researchers are consequently recognized herein as a new species, *Creagrutus paralacus*.

Two specimens of Creagrutus (here referred to C. cf. paralacus) from the upper portions of the Río Magdalena basin, at Sasaima, southeast of Honda (USNM 100738), match Creagrutus paralacus in the majority of features. They differ, however, slightly in relative length of snout to anal-fin origin, snout to pelvic-fin origin, pectoral-fin length, pelvic-fin length, dorsal-fin length, and bony orbital diameter (see Table 4). These specimens have the dark pigmentation on the head and body more pronounced and widely distributed. In particular, the pigmentation on the infraorbitals is more intense than in C. paralacus and extends further posteriorly up to the preopercle. In addition, the infraorbital series in the two specimens from the Río Magdalena are relatively much broader than in C. paralacus with the posterior and ventral margins of the third

^bPectoral-fin rays 12 in damaged specimen.

infraorbital closer to a right angle and describing a broad arch rather than being concentric with the orbital margin. Given that we have available only two specimens of the form from the Río Magdalena, each of which is somewhat damaged and one of which has its snout flattened, we prefer not to describe this sample as a new species. This Río Magdalena form, if distinct, may prove to be closely related to *C. paralacus* given some of the exceptional features they have in common (short paired fins, high number of predorsal median scales, cheeks darkly pigmented). If these populations are conspecific *C. paralacus* is the only *Creagrutus* species known to be common to the Río Magdalena and Lago Maracaibo basins. Dahl's (1971:136) citation of *Creagrutus beni* from the Río Magdalena basin may be based on specimens of this form.

TYPE MATERIAL EXAMINED.—26 specimens.

HOLOTYPE.—VENEZUELA. *Tachira:* Río Catatumbo basin, Río Táchira, 7 km N of San Antonio, USNM 121504 (44.4).

PARATYPES.—VENEZUELA. *Tachira*: Río Catatumbo basin, Río Táchira, 7 km N of San Antonio, USNM 324379, 3 (32.3-53.6); MBUCV V-23300, 2 (39.8-44.0). *Merida*: Río Chama system, Río Albarregas (cited by Schultz, 1944b:336 as Río Barregas), just below Egido, USNM 121499, 10 (46.2-66.6); MBUCV V-23301, 10 (41.8-66.6).

NON-TYPE SPECIMENS EXAMINED.—861 specimens.

VENEZUELA. Tachira: Río Catatumbo basin, Río Cobre above its mouth in Río Quinta, tributary of Río La Grita, USNM 121501, 50. Río Catatumbo basin, Río Táchira, N of San Antonio, USNM 324380, 1 (juvenile collected with holotype). Río Motatán, 4 km above Motatán, USNM 121502, 25. Río Motatán, at bridge in Agua Viva, UF 25456, 5. Mérida: Río Chama basin, Río Gonzáles at La Gonzáles, USNM 121505, 356. Río Chama, 10 km below Lagunillas, USNM 121506, 4. Rio Chama at Estanques, USNM 121503, 28. Río Chama system, Río Barregas, just below Egido, USNM 324378, 358 (formerly USNM 121499, in part). Río Chama, near Mérida, UMMZ 145388, 24. Río Albirregas, near Mérida, CAS 69289, 2. Mérida, BMNH 1902.7.29:94-96, 3. Río

Muyapas, Río Torondoy basin, 4.5 km S of Nueva Bolivia along Highway 1, INHS 60342, 4.

COLOMBIA. Norte de Santandar: Cucuta, La Silla, small brook, NRM 16855, 1.

The following lot was discussed above under "Remarks": Creagrutus cf. paralacus, COLOMBIA. Cundinamarca: Sasaima, SE of Honda (4°58'N, 74°26'W), USNM 100738, 2 (1, 71.2).

Creagrutus magdalenae Eigenmann

FIGURES 4, 9; TABLE 5

Creagrutus magdalenae Eigenmann, 1913:8 [type-locality: Colombia: Girardot; also specimens from Honda, Peñas Blancas]; 1920a:18 [Colombia: Río Magdalena basin]; 1922:146 [Colombia: upper and lower Río Magdalena basin]; 1927:424, pl. 34: fig. 5, pl. 80: figs. 12-16 [Colombia: Girardot, Honda, Peñas Blancas].—Fowler, 1945:3 [Colombia: Honda].—Miles, 1947:158 [Colombia: Río Magdalena, lower Río Cauca].—Dahl, 1971:137, fig. [Colombia: lower portions of Río Magdalena; common name].—Fowler, 1975:26 [literature compilation].—Ibarra and Stewart, 1987:28 [location of holotype and part of paratypic series].—[Not C. magdalenae var.?, Eigenmann, 1913:9; 1927:425].

DIAGNOSIS.—The highly compressed body that is very deep posteriorly through the region of the anal fin is unique to *C. magdalenae* among trans-Andean *Creagrutus* species. This distinctive body form may represent a complex autapomorphy for the species. The combination of unmodified lateral-line scales, a completely pored laterosensory canal system on the body, a relatively broad third infraorbital, an asymmetrical convex predorsal profile, and the lack of a distinct pattern of dark pigmentation on the middle rays of the caudal fin further distinguishes *Creagrutus magdalenae* from its trans-Andean congeners.

DESCRIPTION.—Body in adults deep and highly compressed, notably deep as far posteriorly as caudal fin base. Greatest body depth at dorsal-fin origin. Dorsal profile of head distinctly convex from margin of upper lip posteriorly nearly to vertical through anterior nares, nearly straight from that point to rear of

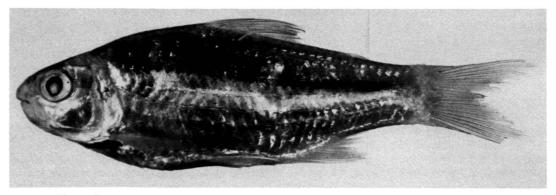


FIGURE 9.—Creagrutus magdalenae, paratype, FMNH 56089, formerly CM 4881, 63.4 mm SL; Colombia, Cundinamarca, Girardot.

head. Dorsal profile of body with notable change in alignment relative to that of head, degree of change variably developed, convex from anterior portion of supraoccipital to dorsal-fin origin; convexity ranging from nearly smooth (Figure 9) to distinctly asymmetrical and most pronounced in anterior one-third of predorsal profile. Dorsal profile of body nearly straight from dorsal-fin origin to caudal peduncle. Ventral profile of head with rounded angle approximately midway between margin of upper lip and posterior of dentary, slightly convex from that point to anal-fin origin.

Upper jaw distinctly longer than and overhanging lower. Anterior portion of snout fleshy, with minute papillae widely distributed; papillae most concentrated on upper and lower lips and fleshy flaps extending into mouth between premaxillary teeth. Lower jaw distinctly fleshy, with papillae most concentrated on lip, becoming sparse on anterior surface of lower jaw. Elements of infraorbital series well developed, with ventral margin of third infraorbital extending to ventral limb of preopercle and posterior margin approaching vertical limb of preopercle; posterior and ventral margins of third infraorbital approximately perpendicular with posteroventral corner broadly rounded.

Teeth arranged as in Creagrutus brevipinnis.

Dorsal fin with ii,8 rays. Dorsal-fin origin slightly anterior to vertical through pelvic-fin origin. Distal margin of dorsal fin nearly straight, but with anterior rays slightly elongate. Anal fin with ii,9-11 rays. Some males with hooks on posterior branches of first two or three branched anal-fin rays, hooks less developed when present on third ray. Distal margin of anal fin concave, with anterior lobe relatively elongate. Pectoral-fin length variable, reaching posteriorly just beyond three-quarters of distance to pelvic-fin origin. Pelvic fin with i,7 rays. Pelvic fin reaching posteriorly to anal-fin origin, males with hooks, when present, on all branched rays.

Gill rakers 8-10 + 11-12 (8 specimens).

COLOR IN LIFE.—Unknown.

COLOR IN ACOHOL.—Available material with pigmentation poorly preserved. Numerous small, dark chromatophores on dorsal surface of head, densest around anterior portion of fontanel, anterolateral surface of head, and in region from just anterior of nares anteriorly onto snout. Dark crescent of pigmentation immediately in front of anterior nares. Stripe of scattered dark chromatophores extending from middle of snout posteriorly to anteroventral margin of orbit, narrowing and dissipating as it continues around margin of eye to join with scattered chromatophores on dorsolateral surface of head.

Dorsum scales with scattered small chromatophores more concentrated over centers of exposed portion of scales, with larger and darker chromatophores delimiting posterior margin of dorsal and dorsolateral scales. Few scattered chromatophores on lateral surface of body other than for distinct humeral mark. Humeral mark darkest region of pigmentation on body, entirely dorsal of lateral line in most specimens, tapering and

TABLE 5.—Morphometrics and meristics of (A) holotype of *Creagrutus magdalenae* (FMNH 56088); and (B) 38 other specimens of *Creagrutus magdalenae* from which measurements and counts were taken. Standard length is expressed in mm; measurements 1 to 14 are percentages of standard length; 15 to 17 are percentages of head length.

	A	В	
	MORPHOMETRICS		
Standard Length	60.0	35.5-56.3	
1. Snout to anal-fin origin	66.3	65.6-71.3	
2. Snout to pelvic-fin origin	48.2	46.8-52.9	
3. Snout to pectoral-fin origin	24.2	24.1-29.0	
4. Snout to dorsal-fin origin	46.8	46.7-51.2	
5. Dorsal-fin origin to hypural joint	57.3	52.3-59.6	
6. Dorsal-fin origin to anal-fin origin	37.0	35.0-41.1	
7. Dorsal-fin origin to pelvic-fin origin	30.3	29.1-33.9	
8. Dorsal-fin origin to pectoral-fin origin	35.0	33.3-37.6	
9. Caudal peduncle depth	13.8	13.5-15.3	
10. Pectoral-fin length	20.8	19.8-26.1	
11. Pelvic-fin length	18.0	16.6-19.4	
12. Dorsal-fin length	23.0	21.6-30.6	
13. Anal-fin length	19.2	16.8-22.4	
14. Head length	24.9	25.3-29.4	
15. Postorbital head length	44.3	40.4-48.2	
16. Snout length	29.5	22.8-29.7	
17. Bony orbital diameter	26.8	26.8-35.3	
18. Interorbital width	34.9	30.7-37.5	
	Ме	RISTICS	
Lateral-line scales	34	33-36	
Scale rows between dorsal-fin origin and lateral line	4	4	
Scale rows between anal-fin origin	3	3	
and lateral line	_		
Predorsal median scales	10	9-10	
Branched dorsal-fin rays	8	8	
Branched anal-fin rays	9	9-11	
Branched pelvic-fin rays	7	7	
Pectoral-fin rays	12	12-14	
Vertebrae	35	34-36	

becoming diffuse anterodorsally. Very diffuse midlateral stripe largely masked by guanine.

Caudal fin with scattered chromatophores on rays and membranes, chromatophores slightly concentrated towards distal portion of central rays and on ventral lobe of fin. Anal-fin membranes hyaline, rows of dark chromatophores along anterior surfaces of basal portions of branched rays. Dorsal fin with dark pigment overlying unbranched rays, membranes of branched rays with numerous dark chromatophores most concentrated distally. Pectoral fin with membranes hyaline, rows of small chromatophores delimiting outer three rays, chromatophores most concentrated distally. Pelvic-fin membranes hyaline.

COMMON NAME.—Colombia: "sardinita," "tota" (Dahl, 1971:137).

DISTRIBUTION.—Río Magdalena basin of northwestern Colombia (Figure 4).

REMARKS.—Eigenmann (1913:9, 1927:425) identified Creagrutus samples from the lower and upper portions of the Río Magdalena basin as "Creagrutus magdalenae var.?," noting, however, that the specimens "have the number of anal rays of affinis and the shape of magdalenae." As discussed below under "Remarks" for Creagrutus affinis, these samples fall within the range of affinis for examined features but differ from magdalenae in various characters and are consequently considered to be members of the former species.

MATERIAL EXAMINED.—145 specimens.

COLOMBIA. Cundinamarca: Girardot, FMNH 56088 1 (60.0, holotype of Creagrutus magdalenae; formerly CM 4880); FMNH 56089, 20 (7, 43.0-56.3, paratypes of Creagrutus magdalenae; formerly CM 4881a-o); FMNH 69730, 72 (10, 37.7-48.9, paratypes of Creagrutus magdalenae). Apulo, CAS 69305, 25 (11, 40.1-58.0; formerly IU 12724, in part). Tolima: Honda, FMNH 56072, 7 (paratypes of Creagrutus magdalenae; formerly CM 4884a-g); ANSP 84389, 2 (44.6-53.0). Antioquia: Penas Blancas, FMNH 56093, 9 (4, 36.8-40.0, paratypes of Creagrutus magdalenae; formerly CM 4885a-i); CAS 60057, 9 (4, 36.8-40.0, paratypes of Creagrutus magdalenae; formerly IU 12726).

Creagrutus brevipinnis Eigenmann

FIGURES 1, 10-11; TABLE 6

Creagrutus brevipinnis Eigenmann, 1913:10 [type-locality: Colombia: Piedra Moler; also specimens from Paila, Cartago]; 1920a:18 [Colombia: Río Magdalena basin]; 1920b:17 [Colombia: upper Río Cauca basin]; 1922:146 [Colombia: upper Río Cauca basin]; 1927:423, pl. 34: fig. 1 [Colombia: upper Río Cauca, Piedra Moler, Paila, Cartago].—Miles, 1943:55 [Colombia: Río Cauca; distinctiveness from Creagrutus caucanus questioned; differences between nominal species suggested to represent sexual dimorphism]; 1947:159 [as Miles, 1943].—Dahl, 1971:137, fig. [Colombia: upper Río Cauca; distinctiveness from Creagrutus caucanus discussed].—Miles, 1973:50 [as Miles, 1943].—Géry, 1977:410 [Colombia: upper Río Cauca].—Fowler, 1975:26 [literature compilation].—Ibarra and Stewart, 1987:28 [location of holotype and portion of paratypic series].—Román-Valencia, 1988:110 [Colombia: upper Río Cauca].—Vari and Howe, 1991:15 [location of portion of paratype series].

DIAGNOSIS.—The combination of unmodified lateral-line scales, a completely pored laterosensory canal system on the body, a broad third infraorbital, a convex asymmetrical predorsal profile, lack of a distinct pattern of dark pigmentation on the middle rays of the caudal fin, an apparently elongate caudal peduncle with a depth 9.6%–12.4% of SL, and 36 to 38 lateral-line scales distinguishes *Creagrutus brevipinnis* from its trans-Andean congeners.

DESCRIPTION.—Body moderately elongate and somewhat compressed in adults, less so in smaller individuals. Greatest body depth at, to somewhat anterior of, dorsal-fin origin. Dorsal profile of head distinctly convex from margin of upper lip to vertical through posterior nares, nearly straight from that point to supraoccipital. Dorsal profile of body with notable change in alignment relative to that of head, convex from anterior portion of supraoccipital to dorsal-fin origin; convexity asymmetrical, most pronounced in anterior one-third of predorsal profile. Dorsal profile slightly concave from dorsal-fin origin to adipose fin. Ventral profile of head with obtuse angle approximately midway between margin of upper lip and posterior of dentary, slightly convex from that point to anal-fin origin.

Head relatively depressed, particularly apparent in larger specimens. Upper jaw distinctly longer than and overhanging lower. Anterior portion of snout fleshy. Minute papillae widely distributed over anterior portion of snout, upper lip, and margin of upper jaw, continuing into mouth on fleshy flaps between premaxillary teeth. Lower jaw fleshy, with papillae most concentrated on lip and with progressively decreasing concentrations on jaw posteriorly as far as isthmus. Elements of infraorbital series well developed, with ventral margin of third infraorbital extending to ventral limb of preopercle; posterior margin closely approaching vertical limb of preopercle; posterior and ventral margins of third infraorbital approximately at perpendicular with posteroventral corner of bone broadly rounded.

Teeth arranged as described under "Dentition in Trans-Andean Creagrutus Species."

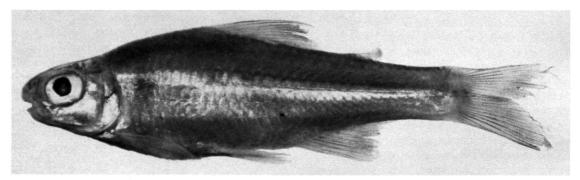


FIGURE 10.—Creagrutus brevipinnis, holotype, FMNH 56095, formerly CM 4887a, 49.4 mm SL; Colombia, Valle, Piedra Moler.

Dorsal fin with ii,8 rays. Dorsal-fin origin at vertical through pelvic-fin origin. Distal margin of dorsal fin with anterior lobe formed by second unbranched and first two branched rays, overall border slightly concave. Anal fin ii or iii,8-10 rays; when three unbranched rays present first very small. Anal fin of males with series of hooks on first branched ray and sometimes one or two hooks on second branched ray. Most specimens with one hook per ray segment, but some individuals with two hooks on some segments, and one specimen with mostly two hooks per segment. Distal margin of anal fin slightly concave with distinct anterior lobe. Pectoral fin reaching posteriorly slightly over three-quarters distance to pelvic-fin origin. Pelvic fin with 1 unbranched ray followed by typically 7, sometimes 8, branched rays. Pelvic fin reaching posteriorly to slightly anterior of pelvic-fin origin; males with hooks on segmented and unsegmented portions of all branched rays.

Gill rakers 16-19 (based on 8 specimens).

COLOR IN LIFE.—Unknown.

COLOR IN ACOHOL.—Head with distinct pattern of diffuse dark chromatophores on dorsal surface and small crescent of dark pigmentation immediately anterior of nares. Band of scattered dark chromatophores extending from middle of snout posteriorly to anteroventral margin of orbit, narrowing and continuing around ventral and posterior margins of orbit to merge dorsally into diffuse pigmentation on lateral and dorsolateral surface of head. Dorsal portion of body with scattered small chromatophores more concentrated over centers of exposed portions of scales. Region anterior of humeral bar unpigmented. Humeral bar vertical, chromatophores most concentrated dorsal of lateral line. Midlateral stripe masked by guanine in available specimens, diffuse anteriorly.

Caudal fin with series of dark chromatophores along margins of four central rays, most concentrated basally and with appearance of diffuse spot. Dorsal and ventral procurrent rays with concentration of dark chromatophores. Distal pigmentation present on all of ventral caudal rays and those of dorsal lobe above approximately seventh ray. Anal fin with membrane between last unbranched and first branched rays hyaline; posteriorly, membranes with dark pigmentation most concentrated distally on middle rays, associated rays with scattered chromatophores. Narrow band of dark chromatophores across bases of branched anal-fin rays. Dorsal fin with last unbranched and anterior branched ray with dark chromatophores that continue posteriorly across distal portion of remaining branched rays, field of chromatophores becoming gradually narrower posteriorly. Dorsal-fin rays with dark chromatophores forming a basal band. Pectoral and pelvic fins hyaline.

DISTRIBUTION.—Known only from a limited region in the upper portion of the Río Cauca, northwestern Colombia (Figure 11); perhaps as a consequence of limited collecting in that region. *Creagrutus brevipinnis* is sympatric with *C. caucanus* at least at several localities in the basin.

REMARKS.—Miles (1943:55, 1947:159) noted that Creagrutus brevipinnis differed from C. caucanus in having fewer

TABLE 6.—Morphometrics and meristics of (A) holotype of *Creagrutus* brevipinnis (FMNH 56095); and (B) 37 other specimens of *Creagrutus* brevipinnis from which measurements and counts were taken. Standard length is expressed in mm; measurements 1 to 14 are percentages of standard length; 15 to 17 are percentages of head length.

	A	В
	MORPH	OMETRICS
Standard Length	49.4	33.2-48.1
1. Snout to anal-fin origin	64.0	62.2-69.6
2. Snout to pelvic-fin origin	46.6	44.7-52.2
3. Snout to pectoral-fin origin	24.9	23.9-27.2
4. Snout to dorsal-fin origin	45.3	45.8-51.3
5. Dorsal-fin origin to hypural joint	57.5	53.9-60.2
6. Dorsal-fin origin to anal-fin origin	34.0	30.7-36.0
7. Dorsal-fin origin to pelvic-fin origin	29.1	27.2-32.5
8. Dorsal-fin origin to pectoral-fin origin	32.6	30.3-36.3
9. Caudal peduncle depth	12.3	9.6-12.4
10. Pectoral-fin length	21.1	18.4-22.4
11. Pelvic-fin length	17.2	15.5-18.7
12. Dorsal-fin length	25.1	19.1-28.8
13. Anal-fin length	20.0	19.8-28.3
14. Head length	24.9	25.2-28.2
15. Postorbital head length	40.7	36.4-46.2
16. Snout length	28.5	20.7-28.0
17. Bony orbital diameter	36.6	33.3-40.2
18. Interorbital width	32.5	28.0-31.8
	Ме	USTICS
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	10	9-11
Branched dorsal-fin rays	8	8
Branched anal-fin rays	9	8-10
Branched pelvic-fin rays	1 7	7–8
Pectoral-fin rays	12	11-13
Vertebrae	36	36-38

anal-fin rays and that *C. caucanus* was characterized by distinctive modifications of the pored lateral-line scales (see Figure 3). He, nonetheless, proposed that these samples represented the males (caucanus) and females (brevipinnis) of a single species, which he recognized as *C. caucanus*. Dahl (1971:137) in his discussion of *C. brevipinnis* labeled Miles' idea as "absurd" without, however, explicitly detailing his own reasons for recognizing the nominal forms as distinct, other than incidently in his "key" to the northern Colombian members of the genus. Our results indicate that the two species are indeed different, differing in lateral-line scale morphology and number (39 to 42 in caucanus versus 36 to 38 in brevipinnis), anal-fin ray counts (10 to 13 versus 8 to 10 respectively), and modal vertebral counts (38, range 37 to 39 versus 37, range 36 to 38 respectively).

MATERIAL EXAMINED.—82 specimens.

COLOMBIA. "Upper Río Cauca and tributaries," USNM

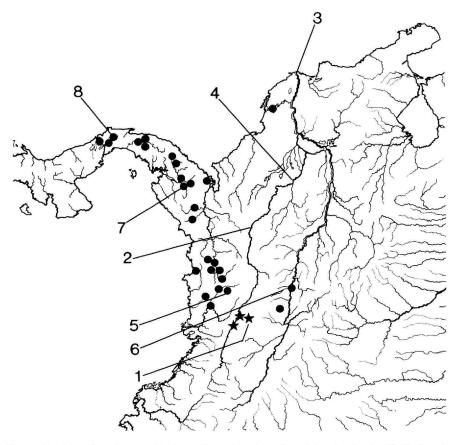


FIGURE 11.—Map of northwestern South America and southern Central America showing distribution of Creagrutus brevipinnis (stars; 1 = type locality; 2 = Río Cauca; 3 = mouth of Río Magdalena) and Creagrutus affinis (filled in circles; 4 = lower Río Cauca, type drainage of Creagrutus affinis; 5 = type locality of Creagrutus leuciscus; 6 = type locality of Creagrutus londonoi; 7 = type locality of Creagrutus simus, and 8 = type locality of Creagrutus notropoides) (some symbols represent more than one locality or lot of specimens).

120148, 3 (42.7-46.3); MCZ 35884, 3 (2, 47.8-48.1). Valle: Piedra Moler, FMNH 56095, 1 (49.4, holotype of Creagrutus brevipinnis; formerly CM 4887a); FMNH 56096, 10 (paratypes of Creagrutus brevipinnis; formerly CM 4887b-i); FMNH 75172, 34 (15, 34.3-47.4, paratypes of Creagrutus brevipinnis; formerly CM 4887b-i); CAS 41341, 11 (5, 35.5-43.0, paratypes of Creagrutus brevipinnis; formerly IU 12728, in part; 1 specimen of Creagrutus magdalenae in lot); USNM 79188, 4 (3, 33.5-43.0, paratypes of Creagrutus brevipinnis; formerly CM 4887b-i, in part). Paila, FMNH 56098, 10 (4, 36.7-45.2, paratypes of Creagrutus brevipinnis; formerly CM 4889a-h). Cartago, FMNH 56097, 5 (33.2-37.7, paratypes of Creagrutus brevipinnis; formerly CM 4888a-e).

Creagrutus hildebrandi Schultz

FIGURES 12, 13; TABLE 7

Creagrutus hildebrandi Schultz, 1944b:330, figs. 47-49 [type locality: Venezuela: Lago Maracaibo basin, Río Catatumbo system, Río Táchira, 7

km N of San Antonio; also Río Motatán, Río Jimelles, Río Palmar, Río San Juan, Río San Pedro, Río Machango, Río Negro, Río Apon, Río Socuy].—Fernández-Yépez and Martin, 1953:228 [Lago Maracaibo basin, Río Negro, Tokio, 16 km W of Machiques].—Géry, 1977:407 [as a possible synonym of *Creagrutus anary* Fowler, 1913].—Mago-Leccia, 1970:23, 70 [Venezuela: Lago Maracaibo].—Vari and Howe, 1991:15 [location of type series].—[Not Cala, 1990:92].

DIAGNOSIS.—The combination of unmodified pores on the lateral-line scales, a completely pored laterosensory canal system on the body, a relatively broad third infraorbital, a straight to slightly convex predorsal profile, 10 to 12 anal-fin rays, and the distinct pattern of dark pigmentation on the middle rays of the caudal fin appearing as a basal caudal spot distinguishes *Creagrutus hildebrandi* from its trans-Andean congeners.

DESCRIPTION.—Body moderately elongate and somewhat to highly compressed in adults, typically less compressed in smaller individuals. Greatest body depth at dorsal-fin origin (Figure 12). Dorsal profile of head distinctly convex from

margin of upper lip to vertical through posterior nares, nearly straight from that point to dorsal-fin origin, or with slight convexity between supraoccipital and dorsal-fin origin. Dorsal profile of body straight from dorsal-fin origin to adipose fin. Ventral profile of head with rounded obtuse angle midway between margin of upper lip and posterior of dentary, typically gently rounded from that point to pelvic-fin origin, slightly convex from that point posteriorly to caudal peduncle.

Upper jaw distinctly longer than and overhanging lower. Anterior portion of snout fleshy, with scattered minute papillae. Concentration of papillae on upper lip and margin of upper jaw continuing into mouth on fleshy flaps between premaxillary teeth. Lower jaw distinctly fleshy, with papillae concentrated on lip and scattered across lower jaw. Elements of infraorbital series well developed but with ventral margin of third infraorbital falling short of ventral limb of preopercle and posterior margin falling short of vertical limb of preopercle; posterior and ventral of margin of infraorbital series rounded, concentric relative to posteroventral margin of orbit.

Teeth arranged as in Creagrutus brevipinnis.

Dorsal fin with ii,8 rays. Dorsal-fin origin situated slightly anterior to vertical through pelvic-fin origin. Distal margin of dorsal fin concave with anterior rays elongate. Anal fin with ii,10–12 rays. Anal fin of males with hooks on posterior branches of first and sometimes second branched fin rays. Distal margin of anal fin concave with anterior rays somewhat elongate, forming distinct lobe in some individuals. Pectoral-fin length variable, ranging from approximately three-quarters distance to pelvic-fin origin to somewhat beyond that point. Pelvic fin with i,7 rays. Pelvic-fin length variable, reaching posteriorly to anal-fin origin in majority of specimens; males with hooks, when present, on all branched rays.

COLOR IN LIFE.—Schultz (1944b:333) commented that in life *Creagrutus hildebrandi* has the "dorsal fin pinkish, back yellowish; adipose fin orange-yellow; dorsal part of eye bright red; upper and lower lobes of caudal fin yellowish; anal fin pinkish anteriorly; pectorals pale orange-yellow; lateral band

TABLE 7.—Morphometrics and meristics of (A) holotype of *Creagrutus hildebrandi* (USNM 121482); and (B) 43 other specimens of *Creagrutus hildebrandi* from which measurements and counts were taken. Standard length is expressed in mm; measurements 1 to 14 are percentages of standard length; 15 to 17 are percentages of head length.

			
	A	В	
	MORPHOMETRICS		
Standard Length	50.3	32.5-63.3	
1. Snout to anal-fin origin	62.6	61.4-67.3	
2. Snout to pelvic-fin origin	44.7	44.3-52.1	
3. Snout to pectoral-fin origin	24.9	44.3-52.1	
4. Snout to dorsal-fin origin	45.3	45.2-49.4	
5. Dorsal-fin origin to hypural joint	55.7	52.4-58.9	
6. Dorsal-fin origin to anal-fin origin	32.4	30.4-35.4	
7. Dorsal-fin origin to pelvic-fin origin	27.6	25.6-31.9	
8. Dorsal-fin origin to pectoral-fin origin	31.0	30.5-35.3	
9. Caudal peduncle depth	12.5	11.1-13.0	
10. Pectoral-fin length	21.5	19.8-22.9	
11. Pelvic-fin length	15.9	16.0-17.9	
12. Dorsal-fin length	24.9	23.1-28.0	
13. Anal-fin length	19.1	19.0-23.4	
14. Head length	25.4	25.3-29.1	
15. Postorbital head length	41.4	39.0-46.3	
16. Snout length	29.0	24.6-29.5	
17. Bony orbital diameter	33.6	29.7-35.3	
18. Interorbital width	33.6	29.7-35.3	
	Мея	USTICS	
Lateral-line scales	27	34-37	
Scale rows between dorsal-fin origin and lateral line	4	4	
Scale rows between anal-fin origin	3	3	
and lateral line			
Predorsal median scales	10	9–11	
Branched dorsal-fin rays	8	8	
Branched anal-fin rays	12	10-12	
Branched pelvic-fin rays	7	7	
Pectoral-fin rays	13	12-14	
Vertebrae	35	35-37	

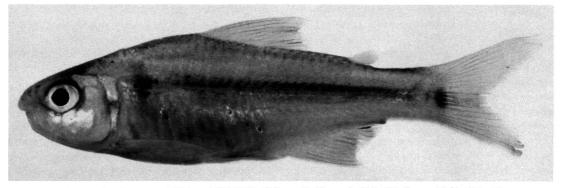


FIGURE 12.—Creagrutus hildebrandi, UF 30751, 58.5 mm SL; Venezuela, Zulia, Río Orope, at bridge between La Fria and La Honda.

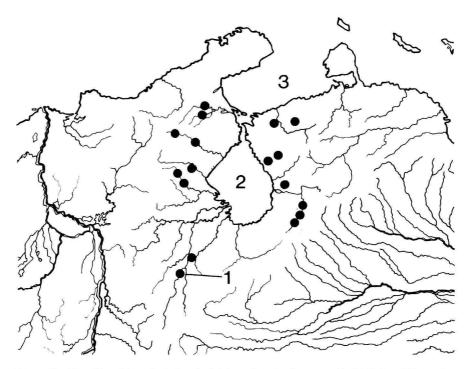


FIGURE 13.—Map of Lago Maracaibo basin and adjoining regions showing geographic distribution of *Creagrutus hildebrandi* (filled in circles; 1 = type locality, 2 = Lago Maracaibo, 3 = Golfo de Venezuela)(some symbols represent more than one locality or lot of specimens).

plumbeous, ending in a black spot at midbase of caudal fin; humeral bar black; sides silvery."

COLOR IN ACOHOL.—Head with pattern of diffuse dark chromatophores on dorsal surface, most concentrated over fontanel and on snout, with distinct small crescent of dark pigmentation immediately in front of anterior nares. Continuous band of dark chromatophores extending posteroventrally from just anterior of nares to anteroventral margin of orbit, continuing beneath orbit, narrowing, and progressively more diffuse around posterior margin of orbit. Dorsum of body with scattered small chromatophores more concentrated over centers of exposed portions of scales. Scales of dorsolateral and lateral surfaces of body with dark chromatophores concentrated along posterior margins. Series of small chromatophores delineating myosepta above anal fin. Region anterior of humeral mark largely unpigmented. Humeral mark margin anteriorly concave, chromatophores darker and most concentrated dorsal of lateral line. Midlateral stripe formed by deep-lying, dark chromatophores, more diffuse anterior to vertical through dorsal-fin origin.

Caudal fin with distinct basal caudal spot, and dark chromatophores overlying rays, particularly on ventral lobe. Unbranched and first branched rays of anal fin usually without associated dark pigmentation; dark pigmentation associated with anterior surfaces of proximal half of other branched rays. Dorsal fin with dark chromatophores associated with unbranched rays and basal portions of branched rays. Dorsal-fin membranes with dark chromatophores, gradually becoming diffuse posteriorly. Pectoral and pelvic fins hyaline.

Ecology.—Schultz (1944a:178) described the type-locality as "Width of river bed up to 200 feet, but only a small flow of water among rubble bottom; current rapid; depth in pool up to 2 feet." Most of the localities cited for paratypes were similar habitats, although in a few cases the bottoms were cited as muddy.

DISTRIBUTION.—Rivers draining into Lago Maracaibo and independent rivers draining into southeastern portions of Golfo de Venezuela (Figure 13). Creagrutus hildebrandi is the only member of the genus known from those latter drainages. Within the tributaries to Lago Maracaibo, C. hildebrandi was captured at the same locality as C. maracaiboensis at the type locality of that species and with C. paralacus in the Río Motatán basin in the southeastern portions of the basin (compare Figures 7 and 13).

REMARKS.—Géry (1977:407), in his key to the species of *Creagrutus*, questionably listed *C. hildebrandi* as a synonym of *C. anary*, described by Fowler (1913:552) from the middle portions of the Rio Madeira system in the southwestern portion of the Amazon basin. Although the holotype of *C. anary* is missing (Böhlke, 1984:42) and the single paratype has been partially cleared and stained, the illustration of the holotype (Fowler, 1913, fig. 16) shows that *anary* has a rounded humeral

spot and small spot of dark pigmentation at the base of the middle caudal fin rays, conditions that differ from the vertical elongate humeral mark and relatively large caudal spot of hildebrandi. The two nominal forms also differ in overall head and body form (compare Figure 12 of this paper with fig. 13 in Fowler (1913)).

MATERIAL EXAMINED.—2014 specimens.

VENEZUELA. Tachira: Río Catatumbo basin, Río Táchira, 7 km N of San Antonio, USNM 121482, 1 (50.3, holotype of Creagrutus hildebrandi); USNM 121491, 9 (8, 47.5-63.3, paratypes of Creagrutus hildebrandi). Zulia: Caño in Río Zulia system, 12 km S of intersection of Highways 6 and 2, INHS 60271, 27 (5, 40.4-54.4). Río Cachiri, near Embalse de Cachiri, MBUCV V-18269. Río Orope, at bridge between La Fria and La Honda, UF 30751, 23 (5, 38.3-45.2). Río Apón, ~35 km S of Rosario, USNM 121486, 314 (paratypes of Creagrutus hildebrandi). Río Palmar near Totuma, ~100 km SW of Maracaibo, USNM 121487, 219 (paratypes of Creagrutus hildebrandi). Río Palmar, at bridge, 70 km NW of Maracaibo, USNM 121495, 16 (paratypes of Creagrutus hildebrandi). Río Palmar, Hacienda El Milagro, NW of Villa del Rosario, at base of Sierra de Perija, MBUCV V-18283, 40. Río Negro, below mouth of Río Yasa, USNM 121488, 159 (paratypes of Creagrutus hildebrandi). Río Negro, 12 km S of Marchiques on road to Tucuco, INHS 59940, 19 (9, 32.5-44.5). Río Socuy, 3 km above its mouth, USNM 121483, 154 (paratypes of Creagrutus hildebrandi). Río Machango at bridge S of Lagunillas, USNM 121492, 66 (paratypes of Creagrutus hildebrandi). Río Machango, 20 km above bridge, S of Lagunillas, USNM 121493, 11 (paratypes of Creagrutus hildebrandi). Municipio Ricuarte, Río Cachiri, MBUCV V-9224, 4. Trujillo: Río Motatán, 8 km below Motatán, USNM 121490, 148 (paratypes of Creagrutus hildebrandi). Río Motatán, at bridge, 22 km N of Motatán, USNM 121494, 261 (paratypes of Creagrutus hildebrandi). Río Motatán, 4 km above Motatán, USNM 121496, 403 (paratypes of Creagrutus hildebrandi). Río San Pedro, at bridge, Río Motatán system, USNM 121483, 1 (paratype of Creagrutus hildebrandi). Río San Juan near bridge, Río Motatán system, USNM 121484, 20 (paratypes of Creagrutus hildebrandi). Río Jimelles, 12 km E of Motatán, USNM 121485, 97 (10, 49.0-55.3, paratypes of Creagrutus hildebrandi). Falcon: Río Cocuiza, near Mene de Mauroa, at highway 3 bridge, INHS 59927, 5 (2, 33.3-35.6). Río Mojino, Río Maticora basin, near Las Palmas, INHS 60360, 9 (2, 39.8-46.2). Río Ricieto, Río Maticora basin, at town of Goajira, IHNS 60025, 7 (2, 36.3-43.5).

Creagrutus affinis Steindachner

FIGURES 11, 14; TABLE 8

Creagrutus affinis Steindachner, 1880:79 [type-locality: Colombia: Río Cauca].—Eigenmann and Eigenmann, 1891:56 [Cauca].—Eigenmann, 1913:7 [Colombia: Puerto Negria, "half-way" between Puerto Negria and Istmina, Istmina, Boca de Raspadura; Panama: Río Chagres; Creagrutus notropoides Meek and Hildebrand, 1912, placed as a synonym]; 1920a:18

[Colombia: Rio Magdalena, Río Atrato, Río San Juan systems; Panama: Rio Tuyra (= Tuira) basin]; 1920b:11 [Colombia: Río Atrato, Río San Juan]; 1922:146 [Colombia: lower Río Cauca, Río San Juan, Río Atrato; Panama: Río Tuyra (= Tuira). Creagrutus simus Meek and Hildebrand and Creagrutus leuciscus Regan placed into synonymy]; 1927:425, pl. 34: fig. 3, pl. 97: fig. 13 [Colombia: Río San Juan, Río Cauca, Río Atrato; Panama: Río Tuyra (= Tuira)].—Breder, 1927:124 [Panama: Río Chucunaque below Yavisa and below Río Sucubit, Río Chico, Río Tuquesa, Río Metiti, Río Membrillo].—Fowler, 1944:230 [northwestern Colombia: Rio Jurubidá].—Miles, 1947:158 [Colombia: lower Río Cauca, lower Río Magdalena, Río Atrato, Río San Juan; Panama: Río Chagres].—Dahl, 1971:138 [Colombia: lower portions of Río Magdalena; common name].—Fowler, 1975:25 [literature compilation].

Creagrutus notropoides Meek and Hildebrand, 1912:68 [type-locality: Panama: Río Indio (upper Río Chagres basin)]; 1916:289 [Panama: Río Chagres basin].—Eigenmann, 1920a:18 [Panama: Río Chagres basin]; 1922:146 [Panama: upper Río Chagres].—Hildebrand, 1938:271 [Panama: upper Río Chagres basin].—Géry, 1964:59 [comments on distinctiveness].—Fowler, 1975:26 [literature compilation].—Ibarra and Stewart, 1987:28 [location of holotype and part of paratypic series]. [New synonymy.]

Creagrutus simus Meek and Hildebrand, 1913:85 [type-locality: Panama: Tuyra River (= Río Tuira) basin]; 1916:290 [Panama: Río Tuyra (= Tuira) basin; type-locality refined to Panama, Cituro, Río Cupe, tributary of Río Tuyra (= Tuira); similarity to C. affinis noted].—Eigenmann, 1922:146 [placed as synonym of Creagrutus affinis]; 1927:427 [Panama: Río Tuyra (= Tuira)].—Hildebrand, 1938:271 [as a synonym of Creagrutus affinis].—Géry, 1964:59 [comments on distinctiveness].—Fowler, 1975:26 [literature compilation].—Ibarra and Stewart, 1987:28 [location of holotype and part of paratypic series].—Vari and Howe, 1991:15 [location of portion of paratype series].

Creagrutus leuciscus Regan, 1913:463 [type-locality: Colombia: Río San Juan basin, Río Lisa and Río Condoto]; 1914:32 [comments on identification by Eigenmann (1913) of Creagrutus populations in Río San Juan as C. affinis; distinctiveness of leuciscus supported].—Eigenmann, 1920a:18 [type locality of Creagrutus leuciscus included within range of C. affinis]; 1920b:11 [as in Eigenmann, 1920a]; 1922:146 [as synonym of Creagrutus affinis]; 1927:425 [as in Eigenmann, 1922].

Creagrutus magdalenae var. ?.—Eigenmann, 1913:9 [Colombia: Bernal Creek near Honda, Soplaviento; questionably equated with C. magdalenae Eigenmann; noted to "have the number of anal rays of affinis and the shape of magdalenae]; 1927:425 [same as Eigenmann, 1913].

Creagrutus londonoi Fowler, 1945:3, figs. 1-3 [type locality: Colombia: Honda, Río Magdalena basin]; 1975:26 [literature compilation].—Böhlke, 1984:50 [location of type specimens]. [New synonymy.]

Creagrutus londoni.—Géry, 1977:403, 406 [dentition, distribution; species name misspelled].

DIAGNOSIS.—The combination of unmodified pores in the lateral-line scales, a completely pored laterosensory canal system on the body, a relatively broad third infraorbital, a straight to slightly convex predorsal profile, 10 to 13 anal-fin rays, and dark pigmentation extending along the middle rays of the caudal fin forming a caudal stripe distinguishes *Creagrutus affinis* from its trans-Andean congeners.

DESCRIPTION.—Body moderately elongate and somewhat compressed in adults, less compressed in smaller individuals. Greatest body depth at or slightly anterior of dorsal-fin origin (Figure 14). Dorsal profile of head distinctly convex from margin of upper lip to vertical through anterior margin of orbit, nearly straight to slightly convex from that point to dorsal-fin origin, without distinct change in profile in supraoccipital region. Dorsal profile of body nearly straight from dorsal-fin

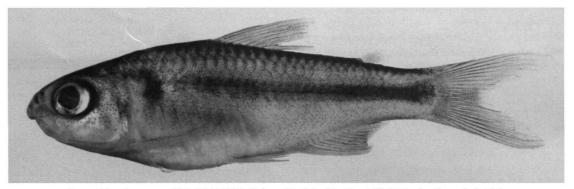


FIGURE 14.—Creagrutus affinis, NRM 16845, 45.9 mm SL; Colombia, Chocó, Río Ichó at San Fernando de Ichó, Río Atrato basin.

origin to caudal peduncle. Ventral profile of head with obtuse angle approximately midway between margin of lower lip and posterior of dentary, ranging from straight to convex from that point to pelvic fin, straight to slightly convex from pelvic-fin origin to caudal peduncle.

Head relatively large. Upper jaw distinctly longer than and overhanging lower. Anterior portion of snout fleshy, with minute papillae distributed over anterior portion of snout and continuing onto upper lip and into mouth on fleshy flaps between premaxillary teeth. Lower jaw fleshy anteriorly, with heaviest concentration of papillae along margin of lip and scattered papillae on anteroventral surface of jaw. Elements of infraorbital series well developed, with ventral margin of third infraorbital extending to ventral limb of preopercle; posterior margin closely approaching vertical limb of preopercle; posterior and ventral margins of third infraorbital approximately perpendicular with posteroventral corner of bone broadly rounded.

Teeth arranged as in *Creagrutus brevipinnis*. Many specimens with anterior premaxillary tooth missing on both sides. Main row of premaxillary teeth somewhat irregular in some specimens.

Dorsal fin with ii,8 rays. Dorsal-fin origin approximately at vertical line through pelvic-fin origin. Distal margin of dorsal fin very slightly concave. Anal fin with ii or iii,10–13 rays; when three unbranched rays present, first very short. Anal fin of males with hooks present on first two or three branched rays. Distal margin of anal fin slightly concave with distinct anterior lobe. Pectoral fin reaching posteriorly to or near to pelvic-fin origin. Pelvic fin with i,6–7, typically 7, rays. Pelvic fin reaching posteriorly to anal fin origin; males with hooks present on segmented and unsegmented portions of all branched rays.

Gill rakers 5-7 + 10-13 (27 specimens).

COLOR IN LIFE.—Unknown.

COLOR IN ACOHOL.—Head with pattern of diffuse dark chromatophores on dorsal surface of head and distinct small crescent of dark pigmentation immediately anterior to nares. Band of scattered dark chromatophores extending from middle of snout posteriorly to anteroventral margin of orbit, narrowing and continuing around ventral and posterior margins of orbit dorsally to merge into diffuse pigmentation on lateral and dorsolateral surface of head. Body with pigmentation most concentrated dorsally, overlying center of exposed surface of scales with narrow unpigmented region along posterior margin of each scale. Pattern becoming indistinct on lateral surface of body, with ventrolateral and ventral region of body unpigmented anterior to anal-fin origin. Humeral bar vertically elongate with pigmentation most concentrated immediately dorsal of lateral line, broadest and densest dorsal of lateral line and arching anterodorsally in some specimens, often appearing as rounded spot in individuals with dorsal and ventral portions of bar not readily apparent. Region anterior of humeral spot largely unpigmented. Broad midlateral stripe most concentrated posteriorly and expanding slightly on caudal peduncle. Stripe separated anteriorly from humeral bar by region lacking dark pigmentation.

Caudal fin with series of dark chromatophores along margins of four central rays, forming a horizontal stripe, appearing as continuation of midlateral body stripe. Stripe variably distinct. Distal portions of fin anterior to first branched ray unpigmented. Anal-fin membranes darkly pigmented, particularly on middle rays. Dorsal fin dusky overall, slightly darker distally. Pectoral-fin rays outlined by series of dark chromatophores. Pelvic fin unpigmented.

GEOGRAPHIC VARIATION.—Creagrutus affinis, as recognized in this study, is highly variable in some proportional values. A critical evaluation of the significance of this variation is hampered by poor samples of specimens in good condition from the Río Magdalena basin (see Figure 11). One collection from that basin, the holotype and paratypes of Creagrutus londonoi (Figure 11, locality 6), tend towards the upper range for various counts and proportional values (see Table 8), but with overlap with the ranges found in samples of affinis from other portions of the species range. The lot from Bernal Creek

TABLE 8.—Morphometrics and meristics of (A) lectotype of Creagrutus affinis (NMW 67120.1); (B) lectotype of Creagrutus leuciscus (BMNH 1913.10.1:6); (C) holotype of Creagrutus londonoi (ANSP 71610); (D) holotype of Creagrutus notropoides (FMNH 7574); (E) holotype of Creagrutus simus (FMNH 7591); and (F) 55 other specimens of Creagrutus affinis from which measurements and counts were taken. Standard length is expressed in mm; measurements 1 to 14 are percentages of standard length; 15 to 17 are percentages of head length.

	A	В	С	D	E	F	
		MORPHOMETRICS					
Standard Length	34.1	-69.6	47.8	53.6	44.5	27.7-78.0	
1. Snout to anal-fin origin	63.9	65.8	68.0	63.8	67.0	61.1-69.1	
2. Snout to pelvic-fin origin	48.4	48.6	50.6	47.0	49.0	46.1-51.5	
3. Snout to pectoral-fin origin	25.2	25.1	26.6	25.2	26.5	24.4-28.5	
4. Snout to dorsal-fin origin	48.1	48.0	51.7	47.4	49.9	46.7-52.3	
5. Dorsal-fin origin to hypural joint	58.4	~58.8	53.6	59.3	53.3	53.0-62.2	
6. Dorsal-fin origin to anal-fin origin	33.1	36.5	34.3	31.5	33.2	29.5-36.5	
7. Dorsal-fin origin to pelvic-fin origin	28.2	32.8	31.8	27.1	30.3	24.6-33.7	
8. Dorsal-fin origin to pectoral-fin origin	31.4	34.5	37.0	31.5	35.1	30.4-37.7	
9. Caudal peduncle depth	11.7	13.6	12.1	11.9	12.6	10.5-14.0	
10. Pectoral-fin length	20.8	21.6	22.4	22.9	21.6	19.8-24.0	
11. Pelvic-fin length	16.4	16.7	17.2	18.5	16.6	15.5-24.2	
12. Dorsal-fin length	26.7	25.9	25.3	_	24.3	21.3-28.0	
13. Anal-fin length	21.4	19.0	21.1	22.2	21.6	18.6-23.0	
14. Head length	26.1	26.4	27.6	27.6	27.4	24.9-29.8	
15. Postorbital head length	38.2	45.7	45.5	39.2	40.2	36.1-47.6	
16. Snout length	27.0	22.3	27.3	27.0	24.6	20.0-30.4	
17. Bony orbital diameter	42.7	34.2	34.1	33.8	34.4	30.6-42.9	
18. Interorbital width	30.3	33.2	28.8	33.1	32.0	28.2-35.7	
			MERISTIC	CS			
Lateral-line scales	~35	36	36	34	-	34-37	
Scale rows between dorsal-fin origin and lateral line	5	4	5	5	5	4–5	
Scale rows between anal-fin origin and lateral line	3	3	3	3	3	3–4	
Predorsal median scales	-9	10	11	9	10	9-11	
Branched dorsal-fin rays	8	8	8	8	8	8	
Branched anal-fin rays	11	12	11	12	11	10-13	
Branched pelvic-fin rays	7	7	8	7	7	6-7	
Pectoral-fin rays	12	12	12	14	13	11-14	
Vertebrae	35	36	35	35	35	34-36	

tentatively identified as *Creagrutus magdalenae* by Eigenmann (1913:9) also falls within the range of *affinis*.

COMMON NAME.—Colombia: "sardinita," "sardina" (Dahl, 1971:138)

ECOLOGY.—Meek and Hildebrand (1916:291) noted that populations of the species (their *Creagrutus simus*) in the Río Tuira system of Panama inhabit swift currents in upland streams. Recent collections in eastern Panama found that *C. affinis* inhabits areas of moderate current in areas adjacent to and below riffles in clear water streams (W.C. Starnes, pers. comm.).

DISTRIBUTION.—Caribbean drainages of Colombia from Río Magdalena basin west to coastal basins of Chocó Department, Pacific slope rivers of Panama from Río Bayano to Rio Tuira, Río Chagres system of Atlantic slope of Panama, and Río Baudo and Río San Juan of Pacific slopes of Colombia (Figure 11). Creagrutus affinis is the only species of the genus known

from Panama and the Río Atrato, Río Baudo, and Río San Juan basins of western Colombia.

REMARKS.—Steindachner (1880:79) described *Creagrutus affinis* based on four specimens from the Río Cauca, northern Colombia (now NMW 67120). The two examined syntypes are relatively small and apparently juveniles. The largest of these (34.1 mm SL), is in the best overall condition (NMW 67120.1), and is designated as the lectotype. The other specimens (NMW 67120.2-5) thus become paralectotypes. Although Steindachner (1880:80) mentioned four small specimens in the description of *Creagrutus affinis*, five specimens are now in the syntypic lot (B. Herzig, in litt.). The smallest of these is in poor condition and may not have been utilized by Steindachner. Interestingly the type-series is the only material of the species known from the lower portions of the Río Cauca (Figure 11, locality 4). This situation reflects the poor samples of fishes from the region available for this study.

Creagrutus affinis, as defined herein, has four synonyms, C. notropoides and C. simus described by Meek and Hildebrand (1912, 1913) from the Pacific and Atlantic slopes of Panama, C. leuciscus proposed by Regan (1913) from the Río San Juan of the Pacific slope of Colombia, and C. londonoi proposed by Fowler (1945) for specimens from the Río Magdalena. It is difficult in some cases to determine why the authors proposed their species. The original description of Creagrutus affinis was, however, based on juveniles, thus poorly reflecting the relative morphometric values in adults. Furthermore, the variation of C. affinis across its range might not have been apparent to previous authors handicapped by limited comparative samples from Colombia and Panama.

Meek and Hildebrand (1912:68) did not compare their Creagrutus notropoides, of the Atlantic versant of Panama (Figure 11, locality 8), with congeners. Their brief description (1913:85) of Creagrutus simus from the Pacific slope Río Tuira (Figure 11, locality 7) noted that it differed from "C. notropoides in being less robust, more compressed, and having a slightly larger eye." Those differences were not quantified and the relative eye sizes cited in these descriptions ("21/2 in head" for C. notropoides and "2.5 to 2.6 in head" for C. simus) are identical. Subsequently Meek and Hildebrand (1916:289) contrasted the species based on entirely different features (body depth, degree of projection of upper jaw, degree of exposure of outer row of premaxillary teeth when the mouth is closed; and number of gill-rakers on the lower limb of first arch). Eigenmann soon thereafter (1922:146) placed C. simus as a synonym of C. affinis without comment, but included in a footnote contradictory comments by Hildebrand that C. simus differed from C. affinis in the number of transverse scale rows on the body. In the same paper Eigenmann (1922) recognized a distinct C. notropoides, evidently based on characters in his "Key to the Species of Creagrutus." The putative distinguishing features in that key overlapped in the two cases where comparable information was provided for C. affinis and C. notropoides. In later reversal, Eigenmann (1927:425, 428) synonymized C. notropoides into C. affinis and recognized C. simus as distinct, although all the features in his key (1927:418) completely or significantly overlap between C. affinis and C. simus. Finally, Hildebrand (1938:271) accepted Eigenmann's synonymy of C. simus into C. affinis, but continued to recognize C. notropoides as distinct. Thus no consensus existed as to which, if either, of the Panamanian species was distinct.

Examination of the types and extensive non-type series from the region from the Río Magdalena west to central Panama revealed no differences between the Panamanian populations identified at times as C. simus and C. notropoides and populations of C. affinis (Table 8). Creagrutus simus and C. notropoides are consequently considered synonyms of C. affinis.

In nearly simultaneous publications Eigenmann (1913) and Regan (1913) reported on *Creagrutus* samples from the Río San Juan of the Pacific versant of Colombia (Figure 11, locality

5). Eigenmann identified his material as *C. affinis* whereas Regan described his specimens as *C. leuciscus*. Regan later (1914:32) noted the incongruity between his conclusion and that of Eigenmann, but preferred to recognize *C. leuciscus* until critical comparisons were undertaken. Eigenmann (1922:146, 1927:425) formally synonymized *C. leuciscus* into *C. affinis*, an action not discussed subsequently. Although the lectotype of *Creagrutus leuciscus* is at the upper end of the range among *C. affinis* populations for relative dorsal-fin origin to anal-fin origin length (Table 8), the value in that specimen is approximated in *C. affinis* specimens from elsewhere in its range. Our studies found no differences to justify the recognition of *C. leuciscus* as distinct from *C. affinis* (Table 8) and, consistent with Eigenmann, the two are considered synonyms.

Creagrutus leuciscus (Regan, 1913:463) was based on three specimens from the Ríos Lisa and Condoto of the Río San Juan basin, southwestern Colombia (BMNH 1913.10.1:6-7 and evidently BMNH 1910.7.11:170; the latter not identified as a syntype in the BMNH ledgers (D. Siebert, in litt.), but agreeing with data in the original description). An ~69.6 mm SL syntype (BMNH 1913.10.1:6) from the Río Condoto is designated as the lectotype and the other syntypes (BMNH 1913.10.1:7, BMNH 1910.1.11:170) become paralectotypes.

Fowler (1945:5), in describing Creagrutus londonoi from the upper Río Magdalena (Figure 11, locality 6), focused his comparative comments on C. notropoides of Panama, although noting that "the dark median caudal rays appear to distinguish it from the other Colombian species. It differs further in having but 3 scales between the lateral line and the ventral origin." The diffuse dark pigmentation on the middle caudal-fin rays in C. londonoi is, however, common to varying degrees in the material herein considered C. affinis from across its range. The number of scales below the lateral line cited by Fowler and confirmed herein is, in turn, typical for the majority of C. affinis specimens (Table 8). Although the C. londonoi types fall towards the extreme of the range for some features in C. affinis (Table 8), no discrete differences exist between that sample and other material of C. affinis. Thus Creagrutus londonoi is considered a synonym of C. affinis. The noted extreme values in the type series of C. londonoi may reflect both its origin from near the known limit of the species range (Figure 11) and the limited samples of C. affinis from the Río Magdalena system.

Eigenmann (1913:9, 1927:425) identified *Creagrutus* samples from the lower and upper portions of the Río Magdalena basin as *Creagrutus magdalenae*. He noted that the specimens "have the number of anal rays of *affinis* and the shape of *magdalenae*." Analysis shows that these samples fall within the range of *affinis* for examined features, but differ from *magdalenae* in various characters (number of scales above the lateral line (5 versus 4 respectively), and number of anal-fin rays (11 or 12 versus 9 to 11, rarely 11 respectively)). Some individuals from these collections are deeper bodied than is typical of *C. affinis*. The body shape in this sample has

apparently been affected by poor preservation and dehydration. There is, therefore, no indication that the material is not conspecific with C. affinis.

MATERIAL EXAMINED.—815 specimens.

COLOMBIA. [Río] Cauca, NMW 67120.1 (34.1, lectotype of Creagrutus affinis); NMW 67120.2-5 (1, 27.2, paralectotypes of Creagrutus affinis; see also under "Remarks" above concerning number of paralectotypes). Chocó: Río Condoto (Río San Juan system), BMNH 1913.10.1:6, 1 (~69.6, lectotype of Creagrutus leuciscus); BMNH 1913.10.1:7, 1 (~47.0, paralectotype of Creagrutus leuciscus); BMNH 1914.5.18:17-19, 3 (2, 39.7-78.0). Río San Juan, BMNH 1910.7.11:183-184, 4. Río Ucati at Acandi, USNM 310460, 24 (5, 44.3-49.4). Río Lisa (Río San Juan system; exact locality not determined), BMNH 1910.7.11:170, 1 (evident paralectotype of Creagrutus leuciscus). Puerto Negría, FMNH 56099, 4 (1, 62.3, formerly CM 4890). Upper Río San Juan at Istmina, USNM 76948, 15; USNM 79186, 4 (2, 47.0-54.3); FMNH 56101, 12 (2, 57.0-65.3; formerly CM 4892); CAS 69279, 37 (formerly IU 12733, in part); BMNH 1920.12.20: 30-31, 2. Río Salado, -4 km upstream from confluence with Río Truando, USNM 310461, 3. Río Salado, near Teresita, USNM 310415, 1. Río Salado, ~6.4 km upstream from confluence with Río Truando (7°08'N, 77°27'W), USNM 310413, 11. Río Pavarando, tributary to Río Salaqui, Río Atrato basin, USNM 310456, 14. Quebrada Barrial, tributary to Río Nercua, Río Atrato basin, USNM 310458, 1. Tributary of Río Nercua, Río Atrato basin, USNM 310454, 12. Raspadura, FMNH 56626, 6 (formerly CM 5443); USNM 76947, 12. Certequi, Río Quito basin of upper Río Atrato system, CAS 69280, 29 (formerly IU 13128); MCZ 30957, 14 (5, 29.2-38.3); AMNH 5363, 10. Quibdo, FMNH 56103, 10 (formerly CM 4894). Tambo, Río Atrato basin, FMNH 56623, 4 (formerly CM 5440). Río Ichó at San Fernando de Ichó, Río Atrato basin, NRM 16845, 91. Quebrada Taridó, where crossing Carretera Panamericana, NRM 16854, 6. Río Jurubida, Nuquí (5°43'N, 77°16'W), ANSP 93234, 3. Pie de Pepé, Río Pepé, Río Baudo basin (5°07'N, 76°50'W), NRM 16853, 1. Tolima: Honda, Río Magdalena basin, ANSP 71610, 1 (47.8, holotype of Creagrutus londonoi); ANSP 71611, 9 (2, 66.1-69.1, paratypes of Creagrutus londonoi); ANSP 71620, 1 (paratype of Creagrutus londonoi). Bernal Creek, near Honda, CAS 69307, 50 (formerly IU 12723, in part); USNM 79189, 4. San Felipe, Río Magdalena basin, USNM 120216, 3 (38.1-48.6). Bolivar: Soplaviento, CAS 69306, 23 (formerly IU 12727).

PANAMA. Darien: Río Aruza, Aruza, FMNH 12604, 13 (paratypes of Creagrutus simus); FMNH 12605, 18 (paratypes of Creagrutus simus). Río Capeti, FMNH 12607, 18 (paratypes of Creagrutus simus). Río Cupe, Cituro, FMNH 7591, 1 (44.5, holotype of Creagrutus simus); USNM 78570, 41 (5, 28.0-50.3, possible paratypes of Creagrutus simus). Río Tuyra (= Tuira), Boca de Cupe, FMNH 12606, 12 (paratypes of Creagrutus simus). Río Morti at Hydro Station (8°54'N, 77°53'W), USNM 310414, 31. Río Pucuro, just above confluence with Río Tuira, USNM 293249, 121 (5, 39.1-52.4). Río Chico at Avelinos, AMNH 11289, 6. Río Sucubti, AMNH 11469, 16. Panama: Río Paja, at InterAmerican Highway, about 17 km W of Bayano Bridge, ANSP 151034, 4. River 156.5 km E of Bayano Bridge, ANSP 151060, 10 (5, 36.3-46.8). Río Bayano basin, probably Río Canita, W of Bayano Bridge on Carratera Panamericana, MCZ 56722, 1 (41.1). Río Parti, off Carretera Panamerican, about 30 km E of Bayano Bridge, MCZ 57892, 3. Río Boqueron, USNM 78562, 37 (5, 29.3-57.0); FMNH 12539, 39 (2, 45.7-47.5, paratypes of Creagrutus notropoides). Río Indio, FMNH 7574, 1 (53.6, holotype of Creagrutus notropoides); FMNH 32021-32022, 2 (paratypes of Creagrutus notropoides; lots combined). Río Pequeni, FMNH 12555, 5 (4, 62.0-66.1, paratypes of Creagrutus notropoides). Río Chagres, Alhajuela, FMNH 12556, 4 (paratypes of Creagrutus notropoides).

RESUMEN

Se revisan las especies de Creagrutus que se distribuyen hacia el norte y oeste de la Cordillera de Los Andes en Colombia, Venezuela y Panamá. Se reconocen ocho especies: Creagrutus affinis Steindachner (1879) distribuído desde el oeste del Río Magdalena a la parte central de Panamá y al suroeste del Río San Juan en la vertiente del Pacífico de Colombia; Creagrutus brevipinnis Eigenmann (1913) y Creagrutus caucanus Eigenmann (1913) del Río Cauca en el noroeste colombiano; Creagrutus hildebrandi Schultz (1944b) de la cuenca del Lago Maracaibo y de los ríos costeros que drenan en la porción suroriente del Golfo de Venezuela; Creagrutus magdalenae Eigenmann (1913) del Río Magdalena en el norte de Colombia; Creagrutus maracaiboensis (Schultz, 1944b) conocido de los tributarios occidentales y sureños del Lago Maracaibo; Creagrutus nigrostigmatus Dahl (1960) solamente conocido del Caño Pechilín, una pequeña cuenca en la costa caribeña de Colombia en el Estado de Sucre; y Creagrutus paralacus, nueva especie, procedente de los tributarios sureños del Lago Maracaibo.

Dos ejemplares de una especie aún no descrita (no tratada formalmente en esta publicación) provenientes del alto Río Magdalena que son muy similares a *Creagrutus paralacus* son discutidos.

Creagrutops Schultz (1944b) es considerado un sinónimo de Creagrutus Günther. Cuatro especies son colocadas dentro de los sinónimos de Creagrutus affinis: Creagrutus leuciscus Regan (1913), Creagrutus londonoi Fowler (1945), Creagrutus notropoides Meek and Hildebrand (1912), y Creagrutus simus Meek and Hildebrand (1913).

Registros de Creagrutus beni procedentes del Sistema del Lago Maracaibo (Schultz, 1944b) y del Río Magdalena (Dahl, 1971) y Creagrutus cf. caucanus provenientes del Río Negro de la Cuenca del Amazonas (Goulding et al., 1988) son considerados eqivocados. Se provee una clave para las especies de Creagrutus de Sudamérica transandina. Son designados lectotipos para Creagrutus affinis y Creagrutus leuciscus y un neotipo por Creagrutus nigrostigmatus.

Literature Cited

Böhlke, E.B.

1984. Catalog of Type Specimens in the Ichthyological Collection of the Academy of Natural Sciences of Philadelphia. Special Publications, Academy of Natural Sciences of Philadelphia, 14:1-246.

Böhlke, J.E., and W.G. Saul

1975. The Characid Fish Genus Creagrudite Myers a Synonym of Creagrutus Günther, with the Description of a New Species from Amazonian Ecuador. Proceedings of the Academy of Natural Sciences of Philadelphia, 127:25-28.

Breder, C.M.

The Fishes of the Rio Chuncunaque Drainage, Eastern Panama.
 Bulletin of the American Museum of Natural History, 57:91–176.

Cala, P.

1981. Catalogo de los ejemplares tipo en la coleccion de peces del Instituto de Ciencias Naturales-Museo de Historia Natural de la Universidad Nacional de Colombia. Lozania (Acta Zoologica Colombiana), 34:1-8.

1990. Nuevos registros de peces para la Orinoquia Colombiana, I: Los Rajiformes, Cluppeiformes, Characiformes, y Gynotiformes. Revista Unellez de Ciencia y Tecnologia, 4(1-2)(for 1986):89-99.

Castro, R.M.C.

1990. Reviso taxonômica da família Prochilodontidae (Ostariophysi: Characiformes). 293 pages. Unpublished Doctoral dissertation, Universidade de São Paulo, São Paulo, Brazil.

Dahl, G.

1960. Una especie nueva del genero Creagrutus Guenther del Norte de Colombia. Caldesia, 8(38):353-358.

1971. Los peces del Norte de Colombia. 391 pages. Bogota: INDERENA. Eigenmann, C.H.

1910. Catalogue of the Freshwater Fishes of Tropical and South Temperate America. Report of the Princeton University Expedition to Patagonia, 1896-1899, 3(4):375-511.

 New Characins in the Collection of the Carnegie Museum. Annals of the Carnegie Museum, 8(1):164-181

1913. Some Results of an Ichthyological Reconnaissance of Colombia, South America. *Indiana University Studies*, 10(8):1-27.

1920a. South America West of the Maracaibo, Orinoco, Amazon, and Titicaca Basins and the Horizontal Distribution of its Fresh-water Fishes. Indiana University Studies, 7(45):1-24.

1920b. The Fishes of the Rivers Draining the Western Slope of the Cordillera Occidental of Colombia, Rios Atrato, San Juan, Dagua, and Patia. Indiana University Studies, 7(46):1-19

1921. The Origin and Distribution of the Genera of the Fishes of South America West of the Maracaibo, Orinoco, Amazon, and Titicaca Basins. Proceedings of the American Philosophical Society, 60(1): 1-6.

1922. The Fishes of Western South America, Part 1: The Fresh-water Fishes of Northwestern South America, Including Colombia, Panama, and the Pacific Slopes of Ecuador and Peru, Together with an Appendix upon the Fishes of the Rio Meta in Colombia. Memoirs of the Carnegie Museum 9:1-346.

 The American Characidae. Memoirs of the Museum of Comparative Zoology, 43(4):311-428.

Eigenmann, C.H., and W.R. Allen

1942. Fishes of Western South America, I: The Intercordilleran and Amazonian Lowlands of Peru; II: The High Pampas, Bolivia, and Northern Chile; With a Revision of the Peruvian Gymnotidae, and of the Genus Orestias. 494 pages. Lexington, Kentucky: University of Kentucky. Eigenmann, C.H., and R.S. Eigenmann

 A Catalogue of the Fresh-water Fishes of South America. Proceedings of the United States National Museum, 14:1-81.

Eschmeyer, W.N.

1990. Catalog of the Genera of Recent Fishes. 697 pages. San Francisco: California Academy of Sciences.

Fernández-Yépez, A., and F. Martin

1953. Apuntes sobre la ictiologia de Perija. Memoria de la Sociedad de Ciencias Naturales, LaSalle, 13(35):227-243.

Fowler, H.W.

1913. Fishes from the Madeira River, Brazil. Proceedings of the Academy of Natural Sciences of Philadelphia, 65:517-579.

1944. Fresh-water Fishes from Northwestern Colombia. Proceedings of the Academy of Natural Sciences of Philadelphia, 96:227-248.

1945. Descriptions of Two New Fresh-water Fishes from Colombia. Notulae Naturae, 158:1-11.

 A Catalogue of World Fishes (XXIII). Quarterly Journal of the Taiwan Museum, 48(1-2):1-124.

Géry, J.

 Upper Amazonian Characoid Fishes Collected by Mr. Jack Roberts. Tropical Fish Hobbyist. 13(4):21–32, 53–68.

1977. Characoids of the World. 672 pages. Neptune City, New Jersey: TFH Publications.

Géry, J., and J.-F. Renno

1989. Un nouveau poisson characiforme (Ostariophysaires) de la Guyane: Creagrutus planquettei sp. n. Revue française de Aquariologie, 16:1-5.

Goulding, M., M. Leal Carvalho, and E.G. Ferreira

1988. Rio Negro, Rich Life in Poor Water: Amazonian Diversity and Foodchain Ecology as Seen Through Fish Communities. 200 pages. The Hague: SPB Academic Publishing.

Günther, A.

1859. List of Cold-blooded Vertebrata Collected by Mr. Fraser in the Andes of Western Ecuador. Proceedings of the Zoological Society of London. 89-93.

1864. Catalogue of the Fishes in the Collection of the British Museum. Volume 5, xii + 455 pages. London.

Hildebrand, S.F.

1938. A New Catalogue of the Fresh-water Fishes of Panama. Field Museum of Natural History, Zoological Series, 12(4):219-359.

Ibarra, M., and D.J. Stewart

1987. Catalogue of Type Specimens of Recent Fishes in the Field Museum of Natural History. Fieldiana, Zoology, new series, 35:iii + 112.

Leviton, A.E., R.H. Gibbs, Jr., E. Heal, and C.E. Dawson

1985. Standards in Herpetology and Ichthyology, Part I: Standard Symbolic Codes for Institutional Resource Collections in Herpetology and Ichthyology. Copeia, 1985(3):802-832.

Leviton, A.E., and R.H. Gibbs, Jr.

1988. Standards in Herpetology and Ichthyology. Standard Symbolic Codes for Institutional Resource Collections in Herpetology and Ichthyology. Supplement No. 1: Additions and Corrections. Copeia, 1988(1):280-282.

Mago-Leccia, F.

1970. Lista de los peces de Venezuela. 241 pages. Caracas: Ministerio de Agricultura y Cria.

Mahnert, V., and J. Géry

1988. Les genres Piabarchus Myers et Creagrutus Günther du Paraguay, avec la description de deux nouvelles espèces (Pisces, Ostariophysi, Characidae). Revue Française d'Aquariologie, 15(1):1-8.

- Meek, S., and S.F. Hildebrand
 - Description of New Fishes from Panama. Field Museum of Natural History, Zoological Series, 10(6):67-68.
 - New Species of Fishes from Panama. Field Museum of Natural History, Zoological Series, 10(8):77-90.
 - The Fishes of the Freshwaters of Panama. Field Museum of Natural History, Zoological Series, 10(15):217-374.

Miles, C.W.

- 1943. Estudio economico y ecologico de los peces de agua dulce del valle del Cauca. 97 pages. Cali: Secretaría de Agricultura y Fomento.
- 1947. Los peces del río Magdalena. 214 + xviii pages. Bogata: Ministerio de la Economia Nacional.
- 1973. Estudio economico y ecologico de los Peces de agua dulce del valle del Cauca. Cespedesia, 22(5):9-64.

Regan, C.T.

- 1913. The Fishes of the San Juan River, Colombia. Annals and Magazine of Natural History. series 8, 7:462-473.
- 1914. Fishes from the Condoto River Colombia, Collected by Dr. H.G.F. Spurrell. Annals and Magazine of Natural History, series 8, 9:31-33.

Rodrígues, G.

1992. The Freshwater Crabs of America: Family Trichodactylidae and Supplement to the Family Pseudothelphusidae. Faune Tropicale (ORSTOM), 33:1-189.

Román Valencia, C.

1988. Clave taxonomica para la determinacion de peces nativos del Departamento de Quindio, subsistema alta río Cauca, Colombia. Actualidades Biológicas. 17(64):107-114.

Schultz, L.P.

- 1944a. The Catfishes of Venezuela, with Descriptions of Thirty-eight New Forms. Proceedings of the United States National Museum, 94(3172):173-388.
- 1944b. The Fishes of the Family Characinidae from Venezuela, with Descriptions of Seventeen New Forms. Proceedings of the United States National Museum. 95:235-367.

Steindachner, F.

1880. Zur Fisch-Fauna des Cauca und der Flüsse bei Guayaquil. Denkschriften der Akademie der Wissenschaften, Wien, 42:55-101.

Taylor, W.R., and G.C. Van Dyke

1985. Revised Procedures for Staining and Clearing Small Fishes and Other Vertebrates for Bone and Cartilage. Cybium, 9(2):107-119.

Vari, R.P.

1988. The Curimatidae, a Lowland Neotropical Family (Pisces: Characi-

- formes); Distribution, Endemism, and Phylogenetic Biogeography. In P.E. Vanzolini and W. Ronald Heyer, editors, Neotropical Distribution Patterns: Proceedings of a Workshop, pages 343-377. Rio de Janeiro: Academia Brasiliera de Ciências.
- 1989. A Phylogenetic Study of the Neotropical Characiform Family Curimatidae (Pisces: Ostariophysi). Smithsonian Contributions to Zoology, 471:1-71.
- 1992a. Systematics of the Neotropical Curimatid Genus Curimatella Eigenmann and Eigenmann (Pisces: Ostariophysi), with Summary Comments on the Curimatidae. Smithsonian Contributions to Zoology, 533:1-48, 37 figures.
- 1992b. Systematics of the Neotropical Curimatid Genus Cyphocharax Fowler (Pisces: Ostariophysi). Smithsonian Contributions to Zoology, 529:1-137.
- In press. Phylogenetic and Revisionary Studies of the Neotropical Characiform Fish Family Ctenoluciidae (Teleostei: Ostariophysi). Smithsonian Contributions to Zoology.

Vari, R.P., and J.C. Howe

1991. Catalogue of Type-Specimens of Recent Fishes in the National Museum of Natural History, Smithsonian Institution, 1: Characiformes (Teleostei: Ostariophysi). Smithsonian Contributions to Zoology, 517:1-52.

Vari, R.P., and S.J. Raredon

1991. The Genus Schizodon (Teleostei, Ostariophysi, Anostomidae) in Venezuela: A Reappraisal. Proceedings of the Biological Society of Washington, 104(1):12-22, 3 figs.

Vari, R.P., and A.M. Williams

1987. Headstanders of the Neotropical Anostomid Genus Abramites (Pisces, Characiformes). Proceedings of the Biological Society of Washington, 100(1):89-104, figs. 1-7.

Walsh, S.

1990. A Systematic Revision of the Neotropical Catfish Family Ageneiosidae (Teleostei: Ostariophysi: Siluriformes). 363 pages. Unpublished Doctoral dissertation, University of Florida, Gainesville.

Weitzman, S.H., and W.L. Fink

1983. Relationships of the Neon Tetras, a Group of South American Freshwater Fishes (Teleostei, Characidae), with Comments on the Phylogeny of New World Characiforms. Bulletin of the Museum of Comparative Zoology, 150(6):339-395.

Weitzman, S.H., and R.P. Vari

1988. Miniaturization in South American Freshwater Fishes: An Overview and Discussion. Proceedings of the Biological Society of Washington, 101(2):444-465.

Index

(Page numbers of principal accounts in italics)

Abramites, 1 affinis, Creagrutus, 1, 3, 5, 10, 20, 23–27 anary, Creagrutus, 20, 22 beni, Creagrutus, 1, 13, 14, 15 brevipinnis, Creagrutus, 1, 5, 7, 18–20 caucanus, Creagrutus, 1, 3, 4, 5–7, 8, 18, 19 Creagrutus, 5, 7 Creagrutie, 3 Creagrutops, 1, 3 Creagrutops maracaiboensis, 1, 3 Creagrutus affinis, 1, 3, 5, 10, 20, 23–27 anary, 20, 22 beni, 1, 13, 14, 15 brevipinnis, 1, 5, 7, 18–20 caucanus, 1, 3, 4, 5–7, 8, 18, 19

cf. caucanus, 5, 7
hildebrandi, 1, 3, 5, 10, 12, 14, 20-23
leuciscus, 1, 20, 23, 25
londoni, 23
londonoi, 1, 20, 23, 24, 25
magdalenae, 1, 5, 8, 16-18, 24, 25
magdalenae var.?, 23
maracaiboensis, 1, 5, 10-13, 22
muelleri, 3
nigrostigmatus, 1, 4, 7-10
notropoides, 1, 20, 23, 25
paralacus, 5, 13-16, 22
simus, 1, 20, 23, 24, 25
hildebrandi, Creagrutus, 1, 3, 5, 10, 12, 14, 20-23
Leporinus muelleri, 3

leuciscus, Creagrutus, 1, 20, 23, 25 londoni, Creagrutus, 23 londonoi, Creagrutus, 1, 20, 23, 24, 25 magdalenae, Creagrutus, 1, 5, 8, 16–18, 24, 25 magdalenae var.?, Creagrutus, 23 maracaiboensis, Creagrutus, 1, 3 Creagrutus, 1, 5, 10–13, 22 muelleri, Creagrutus, 3 Leporinus, 3 Ieporinus, 3 nigrostigmatus, Creagrutus, 1, 4, 7–10 notropoides, Creagrutus, 1, 20, 23, 25 paralacus, Creagrutus, 5, 13–16, 22 Piabina, 3 Schizodon, 1 simus, Creagrutus, 1, 20, 23, 24, 25

REQUIREMENTS FOR SMITHSONIAN SERIES PUBLICATION

Manuscripts intended for series publication receive substantive review (conducted by their originating Smithsonian museums or offices) and are submitted to the Smithsonian Institution Press with Form SI-36, which must show the approval of the appropriate authority designated by the sponsoring organizational unit. Requests for special treatment—use of color, foldouts, case-bound covers, etc.—require, on the same form, the added approval of the sponsoring authority.

Review of manuscripts and art by the Press for requirements of series format and style, completeness and clarity of copy, and arrangement of all material, as outlined below, will govern, within the judgment of the Press, acceptance or rejection of manuscripts and art.

Copy must be prepared on typewriter or word processor, double-spaced, on one side of standard white bond paper (not erasable), with 11/4" margins, submitted as ribbon copy (not carbon or xerox), in loose sheets (not stapled or bound), and accompanied by original art. Minimum acceptable length is 30 pages.

Front matter (preceding the text) should include: title page with only title and author and no other information; abstract page with author, title, series, etc., following the established format; table of contents with indents reflecting the hierarchy of heads in the paper; also, foreword and/or preface, if appropriate.

First page of text should carry the title and author at the top of the page; second page should have only the author's name and professional mailing address, to be used as an unnumbered footnote on the first page of printed text.

Center heads of whatever level should be typed with initial caps of major words, with extra space above and below the head, but no other preparation (such as all caps or underline, except for the underline necessary for generic and specific epithets). Run-in paragraph heads should use period/dashes or colons as necessary.

Tabulations within text (lists of data, oftèn in parallel columns) can be typed on the text page where they occur, but they should not contain rules or numbered table captions.

Formal tables (numbered, with captions, boxheads, stubs, rules) should be submitted as carefully typed, double-spaced copy separate from the text; they will be typeset unless otherwise requested. If camera-copy use is anticipated, do not draw rules on manuscript copy.

Taxonomic keys in natural history papers should use the aligned-couplet form for zoology and may use the multi-level indent form for botany. If cross referencing is required between key and text, do not include page references within the key, but number the keyed-out taxa, using the same numbers with their corresponding heads in the text.

Synonymy in zoology must use the short form (taxon, author, year:page), with full reference at the end of the paper under "Literature Cited." For botany, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in "Literature Cited") is optional.

Text-reference system (author, year:page used within the text, with full citation in "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all Contributions Series and is strongly recommended in the Studies Series: "(Jones, 1910:122)" or "...Jones (1910:122)." If bibliographic footnotes are

required, use the short form (author, brief title, page) with the full citation in the bibliography.

Footnotes, when few in number, whether annotative or bibliographic, should be typed on separate sheets and inserted immediately after the text pages on which the references occur. Extensive notes must be gathered together and placed at the end of the text in a notes section.

Bibliography, depending upon use, is termed "Literature Cited," "References," or "Bibliography." Spell out titles of books, articles, journals, and monographic series. For book and article titles use sentence-style capitalization according to the rules of the language employed (exception: capitalize all major words in English). For journal and series titles, capitalize the initial word and all subsequent words except articles, conjunctions, and prepositions. Transliterate languages that use a non-Roman alphabet according to the Library of Congress system. Underline (for italics) titles of journals and series and titles of books that are not part of a series. Use the parentheses/colon system for volume (number):pagination: "10(2):5-9." For alignment and arrangement of elements, follow the format of recent publications in the series for which the manuscript is intended. Guidelines for preparing bibliography may be secured from Series Section, SI Press.

Legends for illustrations must be submitted at the end of the manuscript, with as many legends typed, double-spaced, to a page as convenient.

Illustrations must be submitted as original art (not copies) accompanying, but separate from, the manuscript. Guidelines for preparing art may be secured from the Series Section, SI Press. All types of illustrations (photographs, line drawings, maps, etc.) may be intermixed throughout the printed text. They should be termed Figures and should be numbered consecutively as they will appear in the monograph. If several illustrations are treated as components of a single composite figure, they should be designated by lowercase italic letters on the illustration; also, in the legend and in text references the italic letters (underlined in copy) should be used: "Figure 9b." Illustrations that are intended to follow the printed text may be termed Plates, and any components should be similarly lettered and referenced: "Plate 9b." Keys to any symbols within an illustration should appear on the art rather than in the legend.

Some points of style: Do not use periods after such abbreviations as "mm, ft, USNM, NNE." Spell out numbers "one" through "nine" in expository text, but use digits in all other cases if possible. Use of the metric system of measurement is preferable; where use of the English system is unavoidable, supply metric equivalents in parentheses. Use the decimal system for precise measurements and relationships, common fractions for approximations. Use day/month/year sequence for dates: "9 April 1976." For months in tabular listings or data sections, use three-letter abbreviations with no periods: "Jan, Mar, Jun," etc. Omit space between initials of a personal name: "J.B. Jones."

Arrange and paginate sequentially every sheet of manuscript in the following order: (1) title page, (2) abstract, (3) contents, (4) foreword and/or preface, (5) text, (6) appendices, (7) notes section, (8) glossary, (9) bibliography, (10) legends, (11) tables. Index copy may be submitted at page proof stage, but plans for an index should be indicated when the manuscript is submitted.

