JAW MORPHO-FUNCTIONAL DIVERSITY, TROPHIC ECOLOGY, AND HISTORICAL BIOGEOGRAPHY OF THE NEOTROPICAL SUCKERMOUTH ARMORED CATFISHES (SILURIFORMES, LORICARIIDAE)

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DISSERTATION ABSTRACT

JAW MORPHO-FUNCTIONAL DIVERSITY, TROPHIC ECOLOGY, AND HISTORICAL BIOGEOGRAPHY OF THE NEOTROPICAL SUCKERMOUTH ARMORED CATFISHES (SILURIFORMES, LORICARIIDAE)

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Tropical South America is renowned for its unparalleled biodiversity. Among vertebrates, fish diversity exceeds that of any other group. Estimates of total Neotropical fish richness range between 5000 and 8000 species, of which approximately 3600 (45–72%) are currently described; and of described species, nearly 20% (>700 spp.) are catfishes in the Neotropical-endemic family Loricariidae. Loricariid catfishes, popularly known as plecos in the aquarium trade, are distinguished by their armor plating, ventral oral disk, and highly derived jaw structure and function. Loricariids have likely existed in South American rivers in close to their modern form since at least the Late Cretaceous, and they are part of a superfamilial lineage (Loricarioidea) that is sister to all other catfishes, and has likely inhabited South American rivers since well into the Early Cretaceous. Today, loricariids have radiated to consume a variety of basal food resources including algae, detritus, seeds, sponges, insects, and even wood, the surface layers of which are gouged into by specialized taxa having hypertrophied jaw muscles and teeth shaped like adzes.

In this dissertation, I attempt to fill major gaps in the knowledge of loricariid taxonomy, jaw morphological and functional diversity, trophic ecological structure, and historical biogeography. My taxonomic research has resulted in the discovery and/or description of dozens of new loricariid species and at least three new genera. Published results of this work are summarized in Appendix I. In chapter two of this dissertation, I describe jaw morpho-functional diversity across a diverse assemblage of 25 species, 12 genera, five tribes, and two subfamilies of loricariids from the upper Amazon Basin in Northern Peru. In chapter three, I describe gross aspects of loricariid assemblage trophic structure as revealed by carbon and nitrogen isotope data from 19 loricariid assemblages ranging in species richness from two to 16 species, and geographically broadly distributed across northern South America. In chapter 4, I review the geological and hydrological history of the Guiana Shield, a highly biodiverse and geologically ancient region of northern South America which shelters a broad range of basal and derived loricariid lineages. From these studies, it is clear that tremendous loricariid diversity accumulated in the Neotropics gradually over tens of millions of years and across a broad geographic range, and that their novel oral morphology has likely been key to their diversification across a variety of basal resources consumed almost exclusively by invertebrate faunas at more temperate latitudes.

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Comparative investigations of loricariid ecology, jaw morphology and function face many hurdles. Beyond incomplete and rapidly changing taxonomies, weakly supported phylogenies, and paucity of museum specimens, are the financial, logistical and political challenges of reaching parts of South America where loricariid catfishes are most diverse. I surmounted none of these obstacles alone. Indeed, the research described in this dissertation would not have been possible without the generous assistance of many people, in matters academic, logistic and domestic. For ensuring that I remained clothed, sheltered, fed, and mentally and physically healthy while in the United States, I would like to gratefully acknowledge the indispensable support of my parents Jeanne and Leo Lujan, and sisters Tracy Lujan and Stephanie Rickerman. For enthusiastically funding my international travels, while maintaining near limitless patience with my frequently digressionary research, slow dissertation development, and half-cocked first drafts, I thank my advisor Jon Armbruster. For funding of research and domestic travel and for feeding my earliest flames of interest in tropical fishes, I thank Chris Beggin, owner of the Aquatic Critter in Nashville, TN. For their friendship and indefatigable assistance in the field and in the museum, I thank Mark Sabaj Pérez, Donald Taphorn and David Werneke. For being open to discussions of my research at a moment's notice, I thank my committee: Dennis Devries, Jack Feminella, Craig Guyer, and long-distance advisor Kirk Winemiller. For equally impromptu discussions of my hair-brained hypotheses and novel data applications, I thank my fellow graduate students Jeff Stratford, Richard Mitchell, Steve Herrington, Michael Lowe, Brian Helms; and my labmates Marcelo Melo, Keith Ray, Ricardo Betancur, Lesley deSouza, and Shobnom Ferdous. For the frequent loans of specimens and access to collections, I thank collection managers Mark Sabaj Pérez (ANSP), Sandra Raredon (NMNH), Karsten Hartel (MCZ), and Mary Anne Rogers (FMNH). Finally, I would like to thank those people who frequently went above and beyond their individual responsibilities to facilitate fieldwork in several South American countries. For field and museum work in Venezuela, I thank Oscar Leon Mata, Augusto Luna, Octaviano Santaella, Mariangeles Arce, Mayme Grant, Erin Richmond, Tim Wesley, David Brooks, Juan Valadez, Raphael Pajua, Luiz Camico, and Franci Britto. For field and museum work in Peru, I thank Hernan Ortega, Blanca Rengifo, Darwin Osorio, Max Hidalgo, and Vanessa Meza. For field and museum work in Brazil, I thank Osvaldo Oyakawa, Jose Birindelli, Leandro Sousa, and André Netto-Ferreira. For field and museum work in Guyana, I thank Calvin Bernard, Elford Livingston, and Stacy Lord. This research was funded by the Planetary Biodiversity Inventory: All Catfish Species (Siluriformes), a five year grant through the US National Science Foundation (NSF DEB-0315963) and NSF grant DEB-0107751 to Jonathan W. Armbruster.

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CHAPTER 1. INTRODUCTION

1.1 GENERAL INTRODUCTION

“The most curious fact is the perfect gradation in the size of the beaks in the different species of *Geospiza*, from one as large as that of a hawfinch to that of a chaffinch…”

[Darwin, 1845: 379]

“As might be expected in the greatest river in the world, there is a corresponding abundance and variety of fish. They supply the Indians with the greater part of their animal food, and are at all times more plentiful, and easier to be obtained, than birds or game from the forest. … From the number of new fishes constantly found in every locality and in every fisherman’s basket, we may estimate that at least five hundred species exist in the Rio Negro and its tributary streams. The number in the whole valley of the Amazon it is impossible to estimate with any approach to accuracy.”

[Wallace, 1889: 324-325]

Since variation in beak sizes across finches from the Galapagos Islands first piqued Darwin’s curiosity, ranges of trophic morphologies across closely related groups of organisms have intrigued evolutionary biologists and inspired myriad contributions to the fields of ecology, functional morphology, and ontogenetics. Darwin’s empirical observations of the birds that have come to bear his name began a research arc that continues to this day (e.g. Lack, 1947, Grant, 1999, Schluter, 2000, Abzhanov et al., 2006), and has been broadly successful in providing detailed explanations of major ecological, functional, and morphogenetic mechanisms driving diversification in at least the 14 species radiation of Geospizinae finches. My doctoral dissertation differs in taxonomic scope, focusing instead on a diverse family of catfishes (Loricariidae), but like Darwin's early observations of finches, provides empirical observations of biogeographical patterns and jaw morphological diversity that lay the foundation for more mechanistically detailed explanations of an incredible New World trophic radiation.

Like Darwin, Alfred Russell Wallace was inspired by the diversity he encountered in the Neotropics. He was especially taken with the diversity of fishes, over 200 species of which he illustrated with care and precision despite the near constant torment of biting insects (Wallace, 1889). Wallace's estimates of fish diversity in the Negro River were surprisingly accurate, coming close to the 450 species that have been described to date from the Negro's main channel (Goulding et al., 1988). And indeed, fish diversity across the Neotropics exceeds that of any other vertebrate group. Modern estimates of total Neotropical fish richness range between 5000 and 8000 species (Lundberg et al., 2000), of which approximately 3600 (45–72%) are currently described (Reis et al., 2003). Of described species, a disproportionate number (nearly 20%, or over 700 species) are catfishes in the Neotropical-endemic family Loricariidae, which is also one of the fastest growing of all fish families in terms of new species described, having increased by 35 species in 2008 alone.

Biogeographical patterns and taxonomic, morphological, and ecological diversity of this group have been the foci of my research for the last seven years, including eight expeditions to Brazil, Guyana, Peru, and Venezuela. My taxonomic research, frequently conducted in collaboration with others, has resulted in description of 15 new species and 3 new genera (see Appendix I). The remainder of my research into loricariid biogeography, and jaw morphological and trophic ecological diversity is the subject of my dissertation.

1.2 INTRODUCTION TO THE LORICARIIDAE

Popularly known as plecos in the aquarium trade, where some rare and boldly patterned species fetch upwards of several hundred dollars each, loricariid catfishes are externally distinguished by having a ventral oral disk with jaws that are ventrally rotated and highly modified to allow for efficient scraping of surfaces (Adriaens et al., 2009) and/or winnowing of loosely aggregated food particles. They are further distinguished by having bodies covered with ossified dermal plates and bristle-like odontodes histologically similar to teeth (Sire & Huysseune, 1996). These distinctive morphological characteristics earn loricariids the English common name of suckermouth armored catfishes or, in Latin America, ‘chupa piedras’ (rock suckers). Other regional names include cuchas (Colombia, Venezuela), corronchos (Colombia, Venezuela), carachamas (Ecuador, Perú), and cascudos (Brazil).

Loricariidae is further diagnosed by several internal characters of the jaw, including insertion of a novel division of the adductor mandibulae directly onto the premaxilla, and absence of 3 plesiomorphic jaw linkages: 1) the interoperculomandibular ligament, 2) the medial symphysis between left and right lower jaw rami, and 3) the tight ligamentous connection of premaxillae to the mesethmoid (Schaefer & Lauder, 1986). The biomechanical result of these decouplings is a highly dynamic upper jaw that can be adducted independently of left and right lower jaw rami, which are themselves bilaterally independent (Adriaens et al., 2009). Sequential evolutionary loss of these linkages has also been correlated with a trend toward increased minimum ranges of jaw morphological diversity within the superfamilial clade Loricarioidea, of which Loricariidae is the most derived family (Schaefer & Lauder, 1996). This correlation supports the proposition (termed the ‘decoupling hypothesis’, Schaefer & Lauder, 1986, 1996) that these linkages may function as evolutionary constraints in basal clades where they remain present, whereas loss or decoupling of these linkages in derived clades permits greater evolutionary freedom and, therefore, increased rates of morphological and functional diversification.

The relative contribution of intrinsic morphological innovations versus extrinsic ecological opportunity in shaping morphological and/or functional diversification is a fundamental question in loricariid evolution, as it is in organismal evolution as a whole (Lauder et al., 1980). Heterogeneity in rates of morphological change appears likely within Loricariidae, but no studies have addressed how changes in the rate or pattern of loricariid jaw morphological diversification might be correlated with extrinsic factors such as trophic ecology or biogeography. Previous research correlating rates of morphological diversification with losses of morphological constraints in Loricarioidea (Schaefer & Lauder, 1996) focused on interfamilial comparisons, and was unable to reveal intrafamilial patterns because of its inclusion of relatively few taxa (8 species) per family. More comprehensive taxon sampling has been needed to both reveal intrafamilial patterns and determine the validity of previous interfamilial generalizations based on small sample sizes. Correlation of intrafamilial patterns of jaw morphological diversity with ecological data would also provide support for alternative, albeit not necessarily mutually exclusive, hypotheses of extrinsic mechanisms for morphological change.

1.3 INTRODUCTION TO DISSERTATION RESEARCH

Evidence suggesting correlative form and trophic ecological function has been observed within a few sympatric, paraphyletic assemblages of loricariids (e.g. Delariva & Agostinho, 2001), but these studies have been universally qualitative and without standardized methods. This limitation has complicated broad synthesis and comparison across diverse regions and taxa. Most descriptions of morphological variation within Loricariidae are taxonomic or phylogenetic in focus. These studies provide an important indication of the range of variation, but they typically only examine external aspects of jaw morphology (e.g. tooth row angle and length, tooth number, size, and cusp shape). These commonly examined characters are among the most highly variable morphological traits below the rank of subfamily, which is where most variation in loricariid gross body morphology occurs. Externally visible variation in jaw morphology at the rank of genus and species has given these characters taxonomic significance as a means for diagnosing lower level taxa throughout the family (e.g. Lujan et al., 2007, Armbruster, 2008, Appendix I). Phylogenetic patterns of variation in just those characters examined for their taxonomic value reveals the frequent convergence and repeated evolution of both long, straight-jawed morphologies with many small teeth (e.g. Fig. 1A) and relatively short, more-highly angled jaws with fewer teeth (e.g. Fig. 1B). Two notable examples of the latter for which distinctive diets are documented are the wood-eating lineages *Panaque* and the *Hypostomus cochliodon*-group, which both have relatively large adz-shaped teeth set in short, highly angled tooth rows (Schaefer & Stewart, 1993, Armbruster, 2003). Such examples support an important role for trophic ecology in allowing the diversification of loricariid jaws and/or canalizing evolutionary outcomes of jaw decoupling.

Standardizing morphometric methods so that they quantify homologous axes of evolutionary divergence in shape is a central challenge to investigations of the considerable variation in jaw morphologies across Loricariidae. Loricariid jaw elements are highly 3-dimensional and curvilinear in outline, with few anatomically homologous landmarks by which measurements can be standardized. In dynamic, functional systems such as the loricariid jaw, defining landmarks or distances based on their functional role (e.g. fulcrum, lever arm) provides an alternative to strictly anatomical homology. Such functional homology has the potential advantage of directly linking quantification of variation in form with variation in function, but the reliability of such a link depends on accurate biomechanical models of system function. Recent investigations of loricariid ontogeny and anatomy have provided detailed descriptions of jaw osteology and myology of a few representative taxa (Geerinckx, 2006; Geerinckx et al., 2007), and a preliminary study of kinematics has revealed gross aspects of loricariid jaw function (Adriaens et al., 2009). The nomenclature of muscles involved with jaw function and the static relationships between jaw muscles and bones are well understood, but the dynamic motion and mechanics of loricariid jaws have yet to be described in precise detail.

Modeling of loricariid jaw mechanics is complicated by their high degree of kineticism and three-dimensional freedom of movement. In contrast to the extensively investigated planar 4-bar linkage by which the jaws of most teleosts function (Westneat, 2004), loricariid jaws are characterized by the absence of key linkages, allowing a degree of independent upper and lower jaw movement that is without precedent among fishes (Adriaens et al., 2009). Studies of fish jaw mechanics rely heavily upon 2-dimensional cineradiographic analyses, but these standard methods are insufficient for loricariids because of their poor ability to resolve motion in 3 dimensions, and because dermal armor on heads of most loricariids reduces the resolution of x-ray images of the jaws.

Precise descriptions of dietary variation present a second major challenge to investigations of correlated jaw and trophic ecological diversification in Loricariidae. Previous studies of fish community ecology in the Neotropics have revealed little trophic segregation among loricariids, generally classifying them, instead, as undifferentiated algivores and detritivores (see Table 1 for summary). Historically low-resolution descriptions of loricariid diets are at least partially attributable to frequently small sample sizes and a heavy dependence on gut content data, which are inherently low resolution due to the amorphous nature of partially digested algal and detrital food particles. Loricariid gut content data are further plagued by low accuracy caused by incredibly fast gut passage rates (as little as 40 minutes; Hood et al., 2005), and the fact that annual dry seasons, when most specimens are collected, are frequently times of suspended feeding (Lowe-McConnell, 1964). A broad spectrum of trophic resources, from seeds to sponge to wood and insects, have been hypothesized in loricariid taxonomic literature, sometimes accompanied by hypotheses of specialization on such resources, but these observations and conclusions are typically drawn from few, and sometimes single, specimens. More robust support for a nutrient axis on which loricariids might be segregating basal resources has recently been provided by Hood et al. (2005), who demonstrated that some loricariids appear to maintain a stoichiometrically balanced diet by selectively consuming the most phosphorus-rich fractions of the available epilithon. Indeed, fine-scale feeding selectivity is a capability that has been broadly demonstrated in both aquatic vertebrate (Bakare, 1970, Bowen, 1979, Ahlgren, 1996, Yossa & Araujo-Lima, 1998) and invertebrate detritivores (Newell, 1965, Bärlocher & Kendrick, 1973, Arsuffi & Suberkropp, 1985).

In this dissertation, I advance a research program intended to ultimately provide a mechanistically detailed explanation of jaw morphological and trophic ecological diversification in Loricariidae. I begin, in Chapter 2, by proposing several metrics by which jaw morphological variation may be quantified in both a functionally homologous and functionally informative manner across all Loricariidae and I use these metrics to quantify jaw morphological variation across 2 loricariid subfamilies, 4 tribes, and 25 species. In Chapter 3, I use stable isotope data to examine the trophic structure of 19 sympatric loricariid assemblages distributed across 4 countries and 3 major Neotropical river basins (Essequibo, Orinoco, Amazon). Here, I suggest that across this range, loricariid assemblages are trophically structured, and that structuring forces increase with species richness. Together, these chapters provide the first standardized comparison of trophic morphological and ecological variation across a broad taxonomic and/or geographic spectrum of loricariids. In Chapter 4, I discuss loricariid taxonomic diversification in light of the geologic and hydrologic history of northern South America.

Loricariid diversity is distributed heterogeneously across the Neotropics, and patterns within this diversity are likely to be closely linked to the geochemistry and geologic history of Neotropical rivers. Any comprehensive explanation of loricariid taxonomic and/or morphological diversification must take this landscape scale variation into account. Loricariids are basal consumers and their trophic diversity and abundance are likely at least partially linked to biogeochemistry, as illustrated by the Hood et al. (2005) study of phosphorus limitation in Loricariidae.

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Table 1. Summary of published descriptions of loricariid diets. Only dominant constituents are reported where gut contents were reported as extended lists of taxa. Species identity updated to reflect current taxonomy. References: 1=Alvim and Peret, 2004; 2=Armbruster, 2002; 3=Armbruster, 2003; 4=Armbruster, 2004; 5=Cardone et al., 2006; 6=DeLariva and Agostinho, 2001; 7=Ferreira, 2007; 8=Forsberg et al., 1993; 9=Fugi et al., 1996; 10=Hamilton et al., 1992; 11=Hood et al., 2005; 12=Jepsen and Winemiller, 2002; 13=Kramer and Bryant, 1995; 14=Melo et al., 2004; 15=Mérigoux and Ponton, 1998; 16=Mérona et al., 2008; 17=Nonogaki et al., 2007; 18=Peretti and Andrian, 2004; 19=Power, 1981, including several subsequent papers by this author; 20=Saul, 1975; 21=Schaefer and Stewart, 1993; 22=Vaz et al., 1999; 23=Winemiller, 1990; 24=Yossa and Araujo-Lima, 1998; 25=Zaret and Rand, 1971 (nr = not recorded).

Species (corrected)	**Reference**	**Drainage**	**Country**	**Method**	**n**	**Diet**
Hypoptopomatinae						
Hypoptopomatini						
Hypoptopoma sp.	14	Araguaia	Brazil	gut contents	3	detritus
Hypoptopoma sp.	23	Apure	Venezuela	gut contents	52	nr
Otocinclus cf. *mariae*	20	Napo	Ecuador	gut contents	2	detritus
Otocinclus sp.	23	Apure	Venezuela	gut contents	686	nr
Otothyrini						
Hisonotus sp.	7	Mogi-Guaçu	Brazil	gut contents	128	organic matter, vascular plants, algae
Parotocinclus sp.	14	Araguaia	Brazil	gut contents	117	detritus, other, filamentous algae
Hypostominae						
Ancistrini						
Ancistrus	12	Cinaruco	Venezuela	isotopes	nr	detritus
Ancistrus chagresi	13	Rio Frijoles	Panama	gut contents	10	detritus
Ancistrus chagresi	19	Rio Frijoles	Panama	behavior	nr	algae

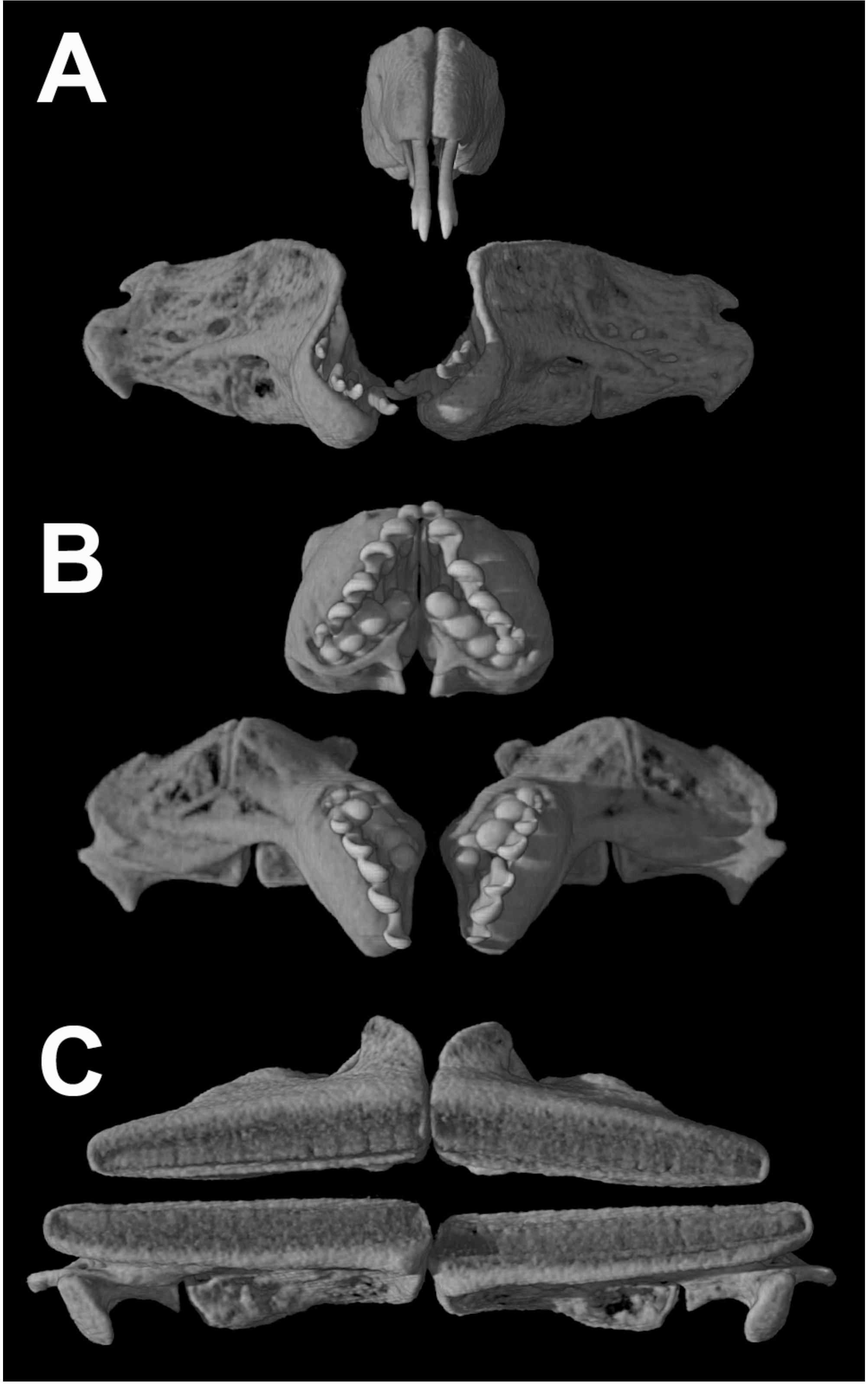
Ancistrus hoplogenys	15	Sinnamary	French Guiana	gut contents	24	vegetative detritus, substratum
Ancistrus hoplogenys	20	Napo	Ecuador	gut contents	4	sand; detritus of undetermined composition
Ancistrus sp.	23	Apure	Venezuela	gut contents	62	nr
Ancistrus triradiatus	11	Apure	Venezuela	gut contents	nr	algae
Chaetostoma dermorhynchum	20	Napo	Ecuador	gut contents	3	detritus
Chaetostoma fischeri	13	Rio Frijoles	Panama	gut contents	6	detritus
Chaetostoma milesi	11	Apure	Venezuela	gut contents	nr	algae
Dekeyseria scaphirhyncha	8	Amazon basin	Brazil	isotopes	1	phytoplankton
Dekeyseria scaphirhyncha	12	Cinaruco	Venezuela	isotopes	nr	detritus
Hypancistrus inspector	2	Casiquiare	Venezuela	gut contents	~1	detritus, algae, seeds
Lasiancistrus tentaculatus	12	Pasimoni	Venezuela	isotopes	nr	detritus
Lasiancistrus tentaculatus	12	Pasimoni	Venezuela	isotopes	5	algae, detritus, plants
Megalancistrus aculeatus	6	Parana River	Brazil	gut contents	10	60% sponge, 18% organic detritus, 11% sediment, 8% Bryozoa
Panaque albomaculatus	21	Marañon	Peru	gut contents	~1	wood
Panaque cf. *nigrolineatus*	17	Mogi-Guaçu	Brazil	otolith isotopes	22	wood
Panaque dentex	21	Marañon	Peru	gut contents	~1	wood
Panaque gnomus	21	Marañon	Peru	gut contents	~1	wood
Panaque maccus	21	Apure	Venezuela	gut contents	~1	wood
Panaque nigrolineatus	20	Napo	Ecuador	gut contents	1	plant debris
Panaque nigrolineatus	21	Apure	Venezuela	gut contents	~1	wood
Panaque nocturnus	21	Marañon	Peru	gut contents	~1	wood
Panaque purusiensis	21	Purus	Peru/Brazil	gut contents	~1	wood
Hypostomini						
Hemiancistrus aspidolepis	13	Rio Frijoles	Panama	gut contents	2	detritus
Hemiancistrus aspidolepis	19	Rio Frijoles	Panama	behavior	nr	algae
Hemiancistrus aspidolepis	25	Pedro Miguel	Panama	gut contents	1	algae
Hypostomus ancistroides	7	Mogi-Guaçu	Brazil	gut contents	13	organic matter, vascular plants, algae
Hypostomus argus	23	Apure	Venezuela	gut contents	379	algae, detritus, microscopic animals
Hypostomus cochliodon	3	Paraguay	Brazil/Paraguay	gut contents	~1	wood

Hypostomus emarginatus	14	Araguaia	Brazil	gut contents	3	detritus
Hypostomus ericae	14	Araguaia	Brazil	gut contents	2	other (wood?)
Hypostomus ericius	3	Marañon	Peru	gut contents	~1	wood
Hypostomus gymnorhynchus	16	Mahury R.	French Guiana	gut contents	14	100% detritus
Hypostomus hemicochliodon	3	Amazon basin	Peru/Ecuador/Brazil	gut contents	~1	wood, detritus
Hypostomus hondae	3	Maracaibo/Magdalena	Colombia/Venezuela	gut contents	~1	wood
Hypostomus levis	3	Beni	Bolivia	gut contents	~1	wood
Hypostomus margaritifer	6	Parana River	Brazil	gut contents	10	49% Bryophyta, 21% organic detritus, 18% sediment, 10% Rhodophyta
Hypostomus microstomus	6	Parana River	Brazil	gut contents	10	60% sponge, 16% sediment, 11% organic detritus, 3% plant detritus
Hypostomus oculeus	3	Upper Amazon	Peru/Ecuador	gut contents	~1	wood
Hypostomus pagei	3	Aroa/Yaracuy	Venezuela	gut contents	~1	wood
Hypostomus plecostomoides	3	Orinoco	Colombia/Venezuela	gut contents	~1	wood
Hypostomus plecostomoides	23	Apure	Venezuela	gut contents	6	nr
Hypostomus plecostomus	8	Amazon basin	Brazil	isotopes	1	detritus
Hypostomus plecostomus	10	Orinoco	Venezuela	isotopes	1-10	herbivore
Hypostomus plecostomus	20	Napo	Ecuador	gut contents	5	detritus, sphaerid clams
Hypostomus pyrineusi	3	Upper Amazon	Peru/Ecuador/Brazil	gut contents	~1	wood
Hypostomus regani	6	Parana River	Brazil	gut contents	10	71% detritus, 21% sediment, 7% plant detritus
Hypostomus regani	17	Mogi-Guaçu	Brazil	otolith isotopes	14	algae
Hypostomus sculpodon	3	Negro/Orinoco	Venezuela/Brazil	gut contents	~1	wood, detritus
Hypostomus sp. a1	1	São Francisco	Brazil	gut contents	nr	detritus
Hypostomus sp. a2	1	São Francisco	Brazil	gut contents	nr	detritus
Hypostomus sp. b1	14	Araguaia	Brazil	gut contents	33	detritus, filamentous algae, other
Hypostomus sp. b2	14	Araguaia	Brazil	gut contents	6	detritus
Hypostomus sp. b3	14	Araguaia	Brazil	gut contents	17	detritus
Hypostomus sp. b4	14	Araguaia	Brazil	gut contents	12	detritus
Hypostomus spp. (seven)	22	Parana River	Brazil	guts & isotopes	nr	detritus

Hypostomus strigaticeps	5	Curumbataí	Brazil	gut contents	938	diatoms, fungi hyphae, chlorophytes, cyanophytes
Hypostomus taphorni	3	Essequibo	Venezuela/Guyana	gut contents	~1	wood
Hypostomus ternetzi	6	Parana River	Brazil	gut contents	10	42% Bryozoa, 32% sediment, 23% organic detritus
Pterygoplichthini						
Pterygoplichthys multiradiatus	23	Apure	Venezuela	gut contents	479	nr
Pterygoplichthys pardalis	24	Amazon basin	Brazil	gut contents	29	detritus
Pterygoplichthys radiatus	8	Amazon basin	Brazil	isotopes	5	detritus
Rhinelepini						
Rhinelepis aspera	6	Parana River	Brazil	gut contents	10	96% detritus, 4% sediment
Loricariinae						
Farlowellini						
Farlowella kneri	20	Napo	Ecuador	gut contents	2	detritus
Farlowella sp.	14	Araguaia	Brazil	gut contents	20	detritus, filamentous algae, insects
Farlowella sp.	23	Apure	Venezuela	gut contents	1	nr
Harttiini						
Sturisoma nigrirostrum	14	Araguaia	Brazil	gut contents	8	detritus, other, leaves and flowers
Sturisoma sp.	23	Apure	Venezuela	gut contents	1	nr
Loricariini						
*Crossoloricaria*sp.	4	not cited	not cited	gut contents	~1	seeds
Loricaria cataphracta	16	Mahury R.	French Guiana	gut contents	21	45.7% aquatic inverts., 28.1% detritus, 21% higher plants, 13.3% terr. inverts., 12.9% plankton
Loricaria cataphracta	20	Napo	Ecuador	gut contents	1	detritus
Loricaria filamentosa	20	Napo	Ecuador	gut contents	3	detritus
Loricaria sp.	4	not cited	not cited	gut contents	~1	seeds
Loricaria sp.	14	Araguaia	Brazil	gut contents	35	fruits and seeds, detritus, other, leaves and flowers, aquatic insects
Loricariichthys platymetopon	8	Amazon basin	Brazil	isotopes	3	nr
Loricariichthys platymetopon	9	Parana River	Brazil	gut contents	116	organic detritus, chironomids

Loricariichthys platymetopon	18	Parana River	Brazil	gut contents	49	detritus, sediment, organic detritus, diatoms
Loricariichthys typus	23	Apure	Venezuela	gut contents	501	large fractions of plant and animal material
Pseudohemiodon cf. *laticeps*	20	Napo	Ecuador	gut contents	2	insect debris, caddisfly larvae, snail
Pseudoloricaria sp.	14	Araguaia	Brazil	gut contents	47	filamentous algae, detritus, aquatic insects, leaves and flowers
Rineloricara lanceolata	20	Napo	Ecuador	gut contents	2	aquatic plants, detritus
Rineloricaria caracasensis	12	Aguaro, Apure	Venezuela	isotopes	nr	detritus
Rineloricaria caracasensis	12	Aguaro, Apure	Venezuela	isotopes	4	algae, detritus, plants
Rineloricaria caracasensis	12	Apure	Venezuela	isotopes	5	algae, detritus, plants
Rineloricaria caracasensis	23	Apure	Venezuela	gut contents	628	nr
Rineloricaria uracantha	13	Rio Frijoles	Panama	gut contents	8	detritus, aquatic invertebrates
Rineloricaria uracantha	19	Rio Frijoles	Panama	behavior	nr	algae
Spatuloricaria caquetae	20	Napo	Ecuador	gut contents	1	detritus
Spatuloricaria sp.	14	Araguaia	Brazil	gut contents	12	fruits and seeds, aquatic insects, detritus, arthropod, terrestrial insects

Figure 1. Representative diversity of loricariid upper and lower jaw morphologies: A. *Leporacanthicus* (carnivore), B. *Panaque* (wood-eater), C. *Chaetostoma* (periphytivore).



CHAPTER 2. METHODOLOGICAL APPROACHES TO THE QUANTIFICATION AND COMPARISON OF LOWER JAW MORPHO-FUNCTIONAL DIVERSITY AMONG SUCKERMOUTH ARMORED CATFISHES (SILURIFORMES, LORICARIIDAE)

2.1 ABSTRACT

I examined lower jaw morphological diversity across 25 species, 12 genera, 5 tribes, and 2 subfamilies of the Neotropical riverine catfish family Loricariidae (Siluriformes, Loricarioidea) and I interpreted this diversity in light of the unique form and function of the loricariid jaw. The loricariid jaw is highly derived and adapted to surface scraping: the upper jaw is kinetic but independent of the lower jaw, which is divided into bilaterally independent rami. Lower jaws are posteromedially deflected and rotate predominantly around their long axis, although axes of rotation are variable and not precisely determinable. Quantification, comparison, and functional interpretation of loricariid jaw morphological diversity is complicated by highly 3-dimensional variation in both shape and motion. Putatively functionally relevant morphological diversity across lower jaws of the sampled taxa was quantified by measuring the area of insertion of the combined adductor mandibulae muscle (AM_{area}), and 5 linear distances, 3 of which were analogous to traditional teleost in- and out-levers for jaw closure. Adductor mandibulae volume was also measured from a subset of sampled taxa and found to correlate with

AM_{area} ($p<0.001$), supporting treatment of AM_{area} as a proxy for force into the loricariid lower jaw. Principle component analysis of the morphometric dataset demonstrated a broad spectrum of jaw morphologies and patterns consistent with both taxon at the ranks of tribe, genus, and species, and broad dietary categories including lignivory, herbivory/periphytivory, and granivory/nsectivory. Loricariid jaws exhibit a broad range of mechanical advantages as traditionally defined, but inability to define axes of loricariid lower jaw rotation hinders the functional interpretation of traditional mechanical advantage metrics, and several additional aspects of function were considered. A key metric hypothesized to be a reliable means of predicting loricariid jaw function from morphology is the ratio AM_{area}/tooth row length (TRL), interpreted as a measure of force intensity, or the magnitude of force applied to substrate per unit of tooth row length. Hypotheses of correspondance between changes in jaw geometry and changes in jaw function were developed using a model of three-dimensional relationships between measured parameters, potential forces, axes of rotation, and the jaw ramus. This model, in conjunction with known kinematics of loricariid jaw function, illustrate theoretical problems with the application of traditional metrics of mechanical advantage to Loricariidae, and the need for novel metrics – several of which are proposed and discussed. Morphometric methods used in this study provide a standardized means of quantitative comparison of shape across lower jaws of all Loricariidae, and the hypothetical model of jaw mechanics developed herein generates specific predictions about how select combinations of the parameters measured herein are linked to jaw function.

2.2 INTRODUCTION

With approximately 30,000 species, ray-finned fishes (Actinopterygii) contribute just over half of all vertebrate taxa. An evolutionary progression can be observed across this radiation from strictly rigid lower jaw movement in basal lineages such as Polypteriformes and Lepisosteiformes, to various manifestations among more derived lineages of integrated upper and lower jaw articulation (Westneat, 2004). An early major step in this progression resulted in the maxilla being decoupled from the neurocranium, and ligamentously linked to the mandible – a character first observed in the Amiiformes but likely homologous with the character observed in most higher actinoptergians (Lauder, 1979, Westneat, 2004). In contrast to a hypothesized single origin of the maxillary-mandibular linkage, evolution of a kinetic premaxilla may have occurred up to five times in Siluriformes, Cypriniformes, Gadiformes, Stylephoriformes, and Zeiformes (Westneat, 2004, modified with findings of Miya et al., 2007). In the most derived of these lineages (Zeiformes, sister to Percomorpha), the premaxilla is linked to the maxilla, and movement of both remains linked to the lower jaw. Morphological and functional diversity and kinematics of the integrated mandible-maxilla-premaxilla mechanism have been described in detail for many members of the percomorph suborder Labroidea (e.g. Cichlidae: Bouton et al., 1998; Albertson et al., 2005; Hulsey et al., 2006; Labridae: Alfaro et al., 2004, 2005). Relatively little attention has been given to morphological variation across, and function within, Loricariidae, a highly diverse siluriform exception to this mechanism of upper and lower jaw movement.

Among catfishes (Siluriformes), the strictly Neotropical superfamily Loricarioidea exhibits an evolutionary progression from immobile premaxillae that are plesiomorphically fused to the mesethmoid, to highly mobile premaxillae loosely suspended from a ventrally directed mesethmoid condyle (Fig. 1), and linked neither to the maxilla nor to the mandible (Schaefer and Lauder, 1986). In the most derived loricarioid family, Loricariidae, the premaxillae are tightly ligamentously connected to each other along their anterior and mesial faces (Schaefer and Stewart, 1993; Geerinckx et al., 2007), and are adducted as a single unit via direct insertion of the retractor premaxillae muscle, a novel division of the adductor mandibulae (Geerinckx et al., 2007; Adriaens et al., 2009). This muscle extends dorsomedially over the dentary and inserts in a fossa along the posterior face of the premaxilla (retractor premaxilla fossa or rpf, Fig. 1B, C). In contrast to most other teleost groups with mobile premaxillae (e.g. Cichlidae, Cyprinidae), loricariid premaxillae have only a modest ascending process, or none at all (ap, Fig. 1A), and are largely reduced to hollow tooth cups. Emergent teeth are born in a single row along the anteroventral margin of the tooth cup, and batteries of unerupted teeth fill the cup's interior (Geerinckx et al., 2007). In some taxa (e.g. *Reganella*; Rapp Py-Daniel, 1997), the premaxilla may be highly reduced and poorly ossified with few to no teeth, and in others (e.g. *Chaetostoma*, Fig. 2A), the premaxilla may be broadly expanded laterally away from the mesethmoid condyle, and supports a single row of >100 emergent teeth.

Loricariid lower jaw rami, consisting of the fused dentary and anguloarticular, are morphologically and functionally more complex and interspecifically variable than the upper jaw, and are more consistently well-ossified across all taxa (Schaefer, 1987; Rapp Py-Daniel, 1997; Armbruster, 2004). Each lower jaw ramus in Loricariidae is functionally independent of the upper jaw and its opposite ramus – the medial mandibular symphysis being absent. The long axis of the loricariid lower jaw ramus is largely perpendicular to the longitudinal body axis and sagittal plane (Fig. 2A). Each ramus extends medially from a prominent, lateral, anguloarticular condyle and the lateral condyle articulates within a shallow fossa at the anteroventral corner of the quadrate (Fig. 2). As with the premaxilla, a single tooth row variable in numbers of teeth, length, and angle, emerges from the posteroventeral margin of the dentary tooth cup, and batteries of replacement teeth fill the cup's interior (Geerinckx et al., 2007). A cartilage plug extends rostrally from the hyoid arch, just behind the lower jaw, into the posteromedial gap between left and right dentaries (Schaefer and Lauder, 1986); and although this plug has no direct attachment to either jaw ramus, it has been hypothesized to provide medial support for the lower jaw during adduction (Geerinckx et al., 2007; Adriaens et al., 2009). The variable angle and length of the dentary tooth row typically matches that of the premaxilla (Fig. 2A, C), although divergent premaxillary and dentary tooth row morphologies are diagnostic of a few taxa (e.g. *Hypancistrus, Leporacanthicus, Spectracanthicus*; Fig. 2B). Morphology of the region between the dentary tooth cup and the anguloarticular condyle, where the main mass of the adductor mandibulae inserts dorsally, is also highly variable – ranging from a largely featureless column in some Loricariinae (e.g. *Reganella*, *Rineloricaria*; Fig. 3O; Rapp Py-Daniel, 1997), to a flattened, broadly expanded flange and/or coronoid arch in a few Loricariinae (e.g. *Lamontichthys*, *Spatuloricaria*; Fig. 3N, P) and most Hypostominae (e.g. *Panaque* n. sp. 'Marañon'; Fig. 3F). The predominant axis of lower jaw rotation likely passes through this region and the observed morphological variation would alter geometric relationships between the axis and regions of force-in and -out, thereby contributing to variation in the mechanical advantage produced during rotation of the jaw ramus.

Functional ramifications of the highly derived, deintegrated, and ventrally rotated jaw morphology described above include the capacity for up to 180º of jaw abduction, so that upper and lower tooth rows can be synchronously occluded by, and adducted across, flat surfaces proximal to the mouth (Figs. 1, 2; Adriaens et al., 2009). Premaxillae are adducted from anterior to posterior with rostrocaudal translation and rotation in the sagittal plane, whereas each lower jaw ramus is adducted anteromedially with rotation possible in at least the horizontal and sagittal planes (Adriaens et al., 2009). Loricariid jaws function within a fleshy, papillose labial disk (Fig. 4) that likely serves several functions, including chemosensory food detection (Ono, 1990), substrate attachment (Geerinckx et al., 2007a), dislodgement of food particles (Geerinckx et al., 2007b), and funneling of dislodged food particles into the buccal cavity (Arens, 1994). The maxillary barbel is integrated with the labial disk, and inserts on the maxilla, which can be adducted independently of all other jaw elements by direct insertion of the levator tentaculi muscle (another novel aspect of loricariid jaw anatomy; Geerinckx et al., 2007). Although anatomically independent of tooth-bearing jaw rami, adduction of the maxilla/maxillary barbel system may still interact with jaw function by enhancing the labial disk's capacity for surface attachment (Geerinckx et al., 2007). Surface attachment increases the normal force and, therefore, the frictional force of tooth rows against substrates during jaw adduction, likely similar to that of leeches, lampreys, larval anurans (Wassersug and Yamashita, 2001; Larson and Reilly, 2003), and several teleosts (e.g. Benjamin, 1986; Roberts, 1989). Complicated force and flow dynamics of the integrated oral disk system are poorly understood, but appear to allow simultaneous surface attachment, surface scraping, ingestion of food particles, and respiration (Geerinckx et al., 2007).

Loricariidae and 5 other strictly Neotropical catfish families comprise the Loricarioidea, a clade sister to all other catfishes (Sullivan et al., 2006). Loricariidae is the most derived of these families, and several evolutionary stages precursor to the highly derived loricariid jaw can be observed among loricarioid lineages. Sequential loss of ligamentous linkages between jaw elements is particularly apparent. In addition to an increased range of movement, sequential decoupling of jaw elements within the loricarioid lineage has been hypothesized to have contributed to a progressive increase in rates of functional and morphological diversification (Schaefer and Lauder, 1986). This decoupling hypothesis states that plesiomorphic linkages function as evolutionary constraints in basal clades where they remain present, and that greater evolutionary freedom is allowed by the absence of these linkages in derived clades (Vermeij, 1973, 1974; Schaefer and Lauder, 1986). Previous quantification of morphological diversity across small subsamples of the 4 most species-rich loricarioid lineages provides support for the decoupling hypothesis by demonstrating a trend toward increased morphological diversity correlated with extent of jaw decoupling (Schaefer and Lauder, 1996); however, it is likely that Schaefer and Lauder (1996) greatly underestimated intrafamilial diversity by examining only eight species from each of the four most species-rich loricarioid families. No other study has quantitatively examined jaw morphological diversity in the Loricarioidea.

The relative contribution of intrinsic morphological innovations, such as decoupling, versus extrinsic ecological opportunity in controlling morphological and/or functional diversification is a fundamental question in studies of both loricariid evolution and organismal evolution as a whole (Lauder et al., 1980; Hughes and Eastwood, 2006). As the most highly decoupled and derived of the loricarioid families, Loricariidae would be predicted to have jaws that are the most plastic in their response to natural selection and, therefore, most highly adaptive in their correlation of form with function. The loricariid jaw has diversified across a species-rich radiation whose members are ubiquitous in tropical Central and South American rivers and streams. Over 700 species are currently described, and many species remain undescribed. Fine-scale patterns of ecological and jaw morphological diversity across this radiation remain largely undescribed. External features of loricariid trophic morphology (e.g. tooth row angle and length, and tooth number, size, and cusp shape) have been associated with trophic ecology, but only among small, paraphyletic groups, and only in a qualitative or non-standardized manner (e.g. Delariva and Agostinho, 2001; Fugi et al., 2001; Mérona et al., 2008). Most descriptions of morphological variation within Loricariidae have had only taxonomic or phylogenetic foci; and although taxonomically significant external jaw characters provide an indication of the wide potential range of jaw variation, these studies have thus far ignored the considerable internal morphological variation described herein (Fig. 3). In addition to holistic quantification of jaw morphological variation, there is a need for biomechanical hypotheses linking morphological variation with variation in jaw function and trophic ecology.

Defining homology across a wide range of taxa and highly variable morphologies presents a central challenge to the standardized quantification of jaw morphological variation in Loricariidae. Loricariid jaw elements are highly variable, 3-dimensional, and curvilinear in outline, with few discrete, anatomically homologous landmarks by which measurements can be standardized (e.g., Type l landmarks, or discrete juxtapositions of tissues; sensu Bookstein, 1991). In dynamic systems such as the loricariid jaw, the functional role of a given landmark or dimension (e.g., fulcrum, lever arm) can also be used to standardize measurements. Such an approach has the added advantage of directly linking variation in form with variation in function, thereby facilitating ecological interpretations of morphological diversity. Tools for ecological inference from loricariid jaw morphology would be particularly valuable given the scarcity of such data; however, the reliability of any ecomorphological inference depends on accurate biomechanical models of system function, which are also lacking for the loricariid jaw. Recent investigations of loricariid ontogeny and anatomy have provided detailed descriptions of jaw osteology and myology for only a few representative taxa (Geerinckx, 2006; Geerinckx et al., 2007) and a preliminary study of kinematics has described gross aspects of loricariid jaw motion (Adriaens et al., 2009). Dynamic function of the loricariid jaw has yet to be described in detail, but it seems that the absence of key linkages allows 3-dimensional freedom of independent upper and lower jaw movement that is unique among fishes (Adriaens et al., 2009).

In most gnathostomes, the lower jaw is a single, rigid unit, allowing all parts of the jaw to be modeled as if they exist within the same 2-dimensional plane of rotation, and allowing jaw morphology to be matched to jaw function along a single gradient of mechanical optimization, either for speed (short input lever/long output lever) or force (long input lever/short output lever). The unique structure and function of the loricariid jaw challenges this traditional approach to jaw function, and invites consideration of several additional aspects of function. A central challenge to modeling loricariid lower jaw function in a manner consistent with traditional investigations is the inability to define a dominant axis of rotation and measure its distance from regions where force is either entering or leaving the jaw – the definition of respective input and output lever arms. Adriaens et al. (2009) demonstrated quantitatively what can also be easily observed qualitatively by watching a loricariid scrape the inside glass walls of an aquarium: rotation of the lower jaws is predominantly in the sagittal plane, but also in the horizontal plane, sweeping anteriorly around the anguloarticular-quadrate joint. My goals in this study are (1) to provide empirical, quantitative data describing variation in several aspects of loricariid jaw morphology, and (2) to make explicit predictions about how variation in these dimensions contribute to variation in function.

2.3 METHODS

2.3.1 Specimen collection, preparation, and imaging

I examined 25 species and 379 individuals from 5 tribes and 2 subfamilies within Loricariidae (two to 83 individuals per species; Table 1). All specimens were collected by seining and electroshocking middle reaches of the Marañon River, a tributary of the upper Amazon Basin in northern Peru in August 2006. New Genus 3 refers to an undescribed genus and species of Ancistrini (Hypostominae) whose phylogenetic relationships to other loricariid genera are discussed by Armbruster (2008). All dissections were made from voucher specimens cataloged at the Auburn University Museum Fish Collection.

Quantitative morphological comparison of the upper jaw across Loricariidae is complicated by extreme diminution of the premaxilla in some taxa (e.g. *Reganella, Pseudohemiodon*; Rapp Py-Daniel, 1997) and by a scarcity of landmarks on the premaxilla that might be considered homologous across all taxa. Additionally, premaxilla morphological variation is difficult to relate to function using only disarticulated osteal elements because a highly variable (Armbruster, 2004) cartilage meniscus separates the premaxilla from its rotational axis in the mesethmoid condyle. Therefore, I restricted this study to the right lower jaw ramus (fused dentary, mentomeckelium, and anguloarticular; Geerinckx et al., 2007), which I dissected from each specimen, then cleared and stained individually (Fig. 3). Loricariid lower jaw elements are small, ranging in this study from three to 15 mm in greatest linear dimension. To facilitate manipulation and imaging, I removed all soft tissue following clearing and staining and allowed the osteal elements to air dry. I then photographed each lower jaw element in at least 2 of the 3 perspectives illustrated in Fig. 5 using a Nikon Coolpix 990 digital camera mounted to a Leica MZ6 stereomicroscope.

Interspecific torsional variation in the relative position and orientation of distal versus proximal jaw regions eliminates the possibility of any one perspective being homologous relative to all jaw regions across all loricariid taxa. Therefore, I arbitrarily standardized jaw orientations by ensuring that the broad anguloarticular-dentary coronoid flange was orthogonal (parallel or perpendicular) to the field of view in each image. Horizontal orientations in ventral (Fig. 5A, D) and dorsal (Fig. 5C, F) perspectives were defined as having the flange parallel with the stage; vertical orientations (Fig. 5B, E) were defined as having the flange perpendicular to the stage. These positions were advantageous by being stable resting positions for many specimens, and by presenting at least one, but usually two, parameters both parallel with and proximal to the stage, further standardizing measurements. I used a small piece of wire mesh as a support should a jaw element not rest naturally in the defined orientations.

2.3.2 Morphometrics

I measured 5 linear distances and 1 area (hereafter referred to as parameters) from digital images of each lower jaw ramus (Fig. 5). Parameters were selected based on the criteria that they quantify distinct components of interspecific morphological variation observable in gross visual surveys of loricariid lower jaw rami (e.g., Fig. 3), and that they be measurable in a standardized manner across all Loricariidae. All parameters were measured from digital images using tpsDIG2 software (Rohlf, 2008, v. 2.12), and were individually standardized to a millimeter scale attached to the microscope stage and visible in each frame. Three linear distance parameters were anatomically analogous with lever arms for lower jaw closure in the majority of actinopterygians (e.g. Westneat, 2004) and were named accordingly. Two of these linear distances were measured from a midpoint along the surface of the anguloarticular condyle (AAC) to respective distalmost (distal out-lever, $\mathrm{Out}_{\mathrm{dist}}$; Fig. 5B, E) and proximalmost (proximal out-lever, $\mathrm{Out}_{\mathrm{prox}}$; Fig. 5B, D) tooth insertions, and the third was measured from a midpoint along the surface of the AAC to the center of the adductor mandibulae (AM) area of insertion (in-lever, In; Fig. 5C, F). To accommodate jaw samples that lost teeth during clearing, staining, and soft tissue removal, and to standardize morphometric methods across loricariid taxa with a broad diversity of dentition, I defined tooth landmarks as the tooth insertion rather than the tooth cusp. I also measured the following 3 parameters (2 linear distances, 1 area) not typically examined in previous investigations of fish jaw morphology and function: (1) linear distance from proximalmost to distalmost tooth insertions (tooth row length, TRL; Fig. 5A, D), (2) area across which the combined adductor mandibulae (AM; A1-OST and A3' divisions; Geerinckx, 2006) muscle inserts (AM_{area}; Fig. 5C, F), and (3) the linear distance perpendicular to Out_{dist}, from Out_{dist} to the maximum excursion of the coronoid arch (H1; Fig. 6). I examined the cumulative extent to which measured parameters differentiated loricariid lower jaw morphologies at various taxonomic ranks by conducting a principle component analysis in JMP statistical software (SAS Institute, v. 5.0.1a).

2.3.3 Jaw mechanics

Little is known about loricariid lower-jaw mechanics. I synthesized traditional studies of fish jaw levers (e.g. Westneat, 2004) with the single published study of loricariid jaw kinematics (Adriaens et al., 2009), personal qualitative observations of loricariid jaw function in the field and in aquaria, and detailed studies of loricariid jaw anatomy (e.g. Geerinckx et al., 2007) to develop several hypotheses of how interspecific variation in the above morphometric parameters might relate to interspecific variation in loricariid lower jaw function. Aspects of the putative functional variation predicted by these hypotheses are presented as a series of 6 ratios and 1 angle (hereafter referred to as metrics). Ratios and angles serve the dual purposes of adding functional significance (e.g., lever-arm ratios) and compensating for allometric variation. The first ratio is a novel metric hypothesized to predict force intensity and will be discussed separately from the remaining 5 ratios (2 traditional, 3 novel) and the angle, which describe aspects of force geometry (i.e. spatial relationships between areas of force-in, force-out, and axes of rotation).

2.3.4 Jaw mechanics: force intensity

The combined adductor mandibulae (AM) of loricariids is approximately columnar is gross dimensions and inserts broadly on the dorsal surface of the anguloarticular-dentary coronoid flange (Fig. 5), which is hypertrophied in loricariids known to be durophages (e.g., Fig. 3F). Given this morphology, I hypothesized that AM insertion area (AM_{area}) correlates with AM volume (AM_{vol}) and variation in anguloarticular-dentary coronoid flange area might thereby provide an indicator of interspecific variation in magnitude of force into the lower jaw system. I examined the relationship between AM_{area} and AM_{vol} after all jaw osteological data had been collected by selecting a subset of approximately six specimens from each of 12 species (Table 1) spanning subfamilies Hypostominae and Loricariinae, and dissecting the AM from the left side of each specimen. Muscle volume was measured to the nearest 0.01 mL via displacement of water in a 5 mL graduated cylinder. In order to examine whether interspecific variation in AM_{area} is correlated with variation in AM_{vol} after collecting these data from separate specimens, I standardized AM_{vol} and AM_{area} to standard body lengths (SL) of the respective specimens from which they were dissected, and regressed mean values of AM_{vol}/SL for each species against mean values of AM_{area}/SL for each species (Fig. 7).

Loricariids exhibit considerable variation in tooth number, shaft morphology, length, rigidity, and cusp dimensions (e.g. Fig. 4; Delariva and Agostinho, 2001; Muller and Weber, 1992; Geerinckx et al., 2007), but all loricariids have the ability to synchronously apply their entire dentary tooth row to substrates, and most loricariids have teeth and tooth cusps distributed in a single contiguous row from proximalmost to distalmost tooth. As a single standardized measure of variation in dentition, I measured tooth row length (TRL; distance from proximalmost to distalmost tooth) and hypothesized that interspecific variation in TRL correlates with interspecific variation in the area across which force through the lower jaw is distributed. I related TRL to AM_{area} in the metric AM_{area}/TRL, which I hypothesize predicts interspecific variation in the magnitude of force applied to substrates per unit of tooth row length, assuming no variation in mechanical advantage.

2.3.5 Jaw mechanics: force geometry

Mechanical advantage is the factor by which a rotating system, or lever, multiplies force; it can be predicted by dividing the system's in-lever (distance from region of force-in to axis of rotation) by its out-lever (distance from axis of rotation to region of force out), with high values indicating optimization for force and low values indicating optimization for speed. In-levers for fish jaw closure are commonly defined as distances from anguloarticular condyle (AAC) to area of adductor mandibulae (AM) insertion, and out-levers as distances from AAC to tooth cusps (e.g. Westneat, 2004). I calculated 2 mechanical advantage metrics using similar parameters (In/Out_{dist} and

In/Out$_{prox}$), but relevance of these metrics to Loricariidae is reduced by the highly derived structure and function of loricariid jaws.

In contrast to most fish mandibles, which close by rotating around the AAC-quadrate joint in a manner similar to flexion of human forearms around the ulna-humerus joint, the loricariid lower jaw rotates around its long axis, in a manner more similar to human forearm torsion, or rotation of the radius around the ulna. Although Adriaens et al. (2009) described gross jaw kinematics in the single loricariid species *Pterygoplichthys disjunctivus* (Hypostominae, Pterygoplichthyini), intra- and interspecific variation in loricariid lower jaw kinematics are poorly understood. Given the high degree of freedom of loricariid lower jaws, it seems likely that loricariid lower jaw kinematics are inherently highly variable and largely dependent on variation in substrate friction coefficients. To compensate for the absence of kinematic data specific to loricariid species in this study and the kinematic flexibility likely inherent to the loricariid jaw system, I related 1-dimensional parameters measured herein to each other, to potential axes of rotation, and back to the loricariid lower jaw with a 3-dimensional rotating cone model of loricariid lower jaw function (Fig. 8). This jaw model, in conjunction with the gross kinematic observations of Adriaens et al. (2009), provided a means for interpreting the probable effects of interspecific jaw morphological variation on variation in jaw function, and provided the foundation upon which the following 4 novel metrics (3 ratios and 1 angle) are discussed:

H1/TRL: treated as a combined measure of force intensity and novel calculation of mechanical advantage.

$Out_{dist}/H1$: treated as a measure of the predominant plane of torque through the jaw ramus.

TR_{angle} (calculated trigonometrically by treating Out_{dist}, Out_{prox}, and TRL as three sides of a scalene triangle): treated as a measure of torque differential across the tooth row, correlated with $Out_{dist}-Out_{prox}/In$.

$Out_{dist}-Out_{prox}/In$: treated as a measure of torque differential across the tooth row.

A central component of the rotating cone model is the output plane, defined by a triangle with sides formed by Out_{prox}, Out_{dist}, and TRL (shaded gray, Fig. 8). The posterolateralmost vertex of the triangle is the anguloarticular condyle and the other vertices are the distalmost and proximalmost teeth (Fig. 8). Extending dorsomedially away from the anguloarticular condyle, oblique with respect to the output plane, is the in-lever arm (In, Fig. 8). Rotation around the long axis of the jaw (Axis 1) is illustrated as a rotating cone with the anguloarticular condyle at its apex, and excursion of the distalmost tooth tracing an arc around the base of the cone. A portion of the morphological variation observed across loricariid jaws is represented by cones of 2 different dimensions: a relatively long cone with a small angle between in-lever and output plane and a relatively shorter arc describing excursion of the distalmost tooth (Cone 1, e.g. *Chaetostoma* cf. *milesi*, Fig. 8), and a shorter cone with a greater angle between in-lever and output plane and a longer arc describing excursion of the distalmost tooth (Cone 2, e.g. *Panaque nigrolineatus*, Fig. 8).

Variation in TRL and TR_{angle} (∂, Fig. 8) within the output plane are also illustrated, with Cone 1 having a relatively long TRL and a low TR_{angle}, and Cone 2 having a shorter TRL and a greater TR_{angle}. Angle between left and right dentary tooth-rows is a variable and important taxonomic character diagnostic for several genera and species. The genera *Peckoltia* and *Hemiancistrus*, for example, are currently differentiated based solely on whether angle between left and right dentary tooth-rows is <90º (*Peckoltia*) or >100º (*Hemiancistrus*; Armbruster, 2008); however, angle between left and right dentary tooth-rows is variable within an individual because of the independent articulation of left and right lower jaw rami, and is difficult to quantify without reference to a point or line that is fixed relative to the tooth-row. I calculated angle of the tooth-row (TR_{angle}, ∂ in Fig. 8) with respect to the distal out-lever arm trigonometrically, by treating Out_{dist}, Out_{prox}, and TRL as 3 sides of a scalene triangle (shaded gray in Fig. 8).

Interpretation and discussion of the jaw model and novel metrics are largely contingent upon four assumptions: (1) that rotation is predominantly in the sagittal plane (around Axis 1; Fig. 8), (2) that rotation in the horizontal plane (around Axis 2; Fig. 8) is secondary, and (3) that rotation in the transverse plane (Axis 3; Fig. 8) is negligible. All of these assumptions are supported by kinematic data from the loricariid species *Pterygoplichthys disjunctivus* (Adriaens et al., 2009). The final assumption is (4) that the predominant rotational axis (Axis 1) crosses through a midpoint along the long axis of the ramus, approximately equidistant from the input lever arm and the output plane. The importance of this assumption is discussed further under *Results and Discussion: Force Geometry-Novel Metrics*.

2.4 RESULTS AND DISCUSSION

2.4.1 Gross morphological differentiation

Principle component (PC) analysis of the loricariid jaw parameters measured in this study (Figs. 9, 10) revealed morphological segregation of the jaws of most taxa at the ranks of genus and species, and jaw morphological segregation corresponding with the following three broad trophic guilds: lignivores (wood-eating), periphytivores/detritivores, and insectivores/granivores. The subfamilies Hypostominae (Ancistrini, Hypostomini; Fig. 9A, B) and Loricariinae (Loricariini, Farlowellini, Harttiini; Fig. 9A, B) broadly overlap in jaw morphologies, but jaw morphologies become differentiable at the rank of tribe. Loricariini are largely differentiable from Harttiini along PC2 (Fig. 9A) and are differentiable from all other tribes along PC3 and PC4 (Fig. 9B), which also allow differentiate Harttiini from Farlowellini. Ancistrini exhibits the broadest range in jaw morphologies across all PCs, but is also the tribe with the greatest taxonomic diversity and largest sample sizes represented in the dataset.

Jaw morphological diversity and differentiation is greatest among genera (Fig. 9C, D), which is likely at least partially attributable to the frequent reliance upon jaw characters for the diagnosis of loricariid genera. Jaw morphologies of most of the 6 Ancistrini genera in the dataset can be distinguished along PC2, although *Peckoltia* occurs within the distribution of *Panaque*, and *Lasiancistrus* is overlapped slightly by both *Panaque* and *Ancistrus*. All Ancistrini genera exhibit broad overlap along PC3 and PC4 (not shown).

Jaw morphological patterns at the rank of species vary among genera. Of the three genera with the greatest number of species in the dataset, *Chaetostoma* exhibits broad overlap among several species (Fig. 10A), whereas most *Panaque* species have distinctive jaw morphologies described by PC3 and PC4 (Fig. 10B) and most

Hypostomus species have distinctive jaw morphologies described by PC2 (Fig. 10C). Within *Chaetostoma*, jaw morphologies of *C. microps*, *C.* cf. *milesi*, and *Chaetostoma* sp. 1, are largely differentiable from each other along PC2, as is *Chaetostoma* sp. 4 from *Chaetostoma* sp. 1 (Fig. 10C). Jaw morphologies of *Chaetostoma* sp. 2 and *Chaetostoma* sp. 3 broadly overlap both each other and the other *Chaetostoma* species along PC2, and jaw morphologies of *Chaetostoma* sp. 4 broadly overlap those of both *C. microps* and *C.* cf. *milesi* (Fig. 10C). Jaw morphologies of all *Chaetostoma* exhibit broad overlap along PC3 and PC4 (not shown).

Distributions of jaw morphologies across species in the genera *Panaque* and *Hypostomus* deserve special attention because of the specialization within some species in these genera on diets consisting largely of wood (Schaefer and Stewart, 1993; Nelson et al., 1999; Armbruster, 2003; Nonogaki et al., 2007; German, 2008). Submerged, solid wood in the form of tree boles and branches (coarse woody debris or CWD) is a food resource consumed by few other aquatic metazoans. Besides loricariids, only the caddisfly *Heteroplectron californicum* (Calamoceratidae, Anderson et al., 1978), the beetle *Lara avara* (Elmidae, Anderson et al., 1978), and the beaver (Mammalia, *Castor* spp.) are known to be specialist consumers of CWD in stream systems, and all of these are restricted to temperate latitudes. Recent studies of the nutritional physiology of lignivorous loricariids indicate that these trophic specialists have an unspecialized alimentary canal and that, like many aquatic insect detritivores (Cummins, 1973), the energy and nutritive value of the wood they consume is largely derived from associated fungi and free monosaccharides and amino acids released during fungal predigestion of the wood (German, 2008).

Loricariid specializations for consumption of wood, therefore, appear to be restricted to the jaw system and, indeed, all lignivorous loricariids have specialized spoon-shaped teeth (Fig. 3D, E, F, G, K; Armbruster, 2003), and occupy a region of jaw morphospace along the PC2 axis also occupied by only one other non-lignivorous species (*Peckoltia bachi*; Figs 9C, 10C). *Peckoltia bachi*, which is phylogenetically close to *Panaque* (Armbruster, 2008), lacks the spoon-shaped teeth of other lignivores, but overlaps *Panaque* along PC2 (Fig. 9C), PC3, and PC4 (not shown). Diet of *Peckoltia bachi* has not been described. Within *Hypostomus*, only the single lignivorous species *H. pyrineusi* (Fig. 10C) has a jaw morphology overlapping that of the largely lignivorous genus *Panaque* along PC2 (cf. Fig. 9C). *Hypostomus pyrineusi* is a member of the largely wood-eating *Hypostomus cochliodon*-group defined by Armbruster (2003). Segregation of *Panaque* species along PC3 and PC4 (Fig. 10B) suggests the possibility that loricariids are further partitioning trophic resources within the highly specialized lignivorous niche. Additional support for trophic segregation within sympatric assemblages of lignivorous *Panaque* species is provided by partially differentiable patterns of carbon and nitrogen consumer stable isotope data (Appendix II). The most distinctive of the *Panaque* species jaw morphologies is that of *Panaque* n. sp. 'Marañon', which is segregated along PC3 from most other taxa in the dataset, including all other *Panaque* species.

2.4.2 Jaw mechanics: force intensity

Differentiation of *Panaque* n. sp. 'Marañon' along the PC3 axis is derived mostly from its increased area of adductor mandibulae (AM) insertion (Fig. 10B), which correlates with AM hypertrophy (Fig. 7), and is consistent with its membership of the durophagous lignivorous guild. Additional differentiation of lignivorous taxa along PC2 is driven mostly by their relatively short tooth row lengths (TRL; Figs. 9C, 10C), which can be interpreted functionally as a means of concentrating jaw forces onto smaller areas of substrate. As a group, lignivorous taxa have jaw morphologies consistent with increases in force generation, and decreases in force distribution – aspects of loricariid jaw function that are related in the single metric AM_{area}/TRL. The aspect of jaw function that this metric is hypothesized to predict can be referred to as force intensity, or the degree of force per unit of tooth row length. This metric ranges from high values indicative of forces being concentrated, as with wood-gouging lignivorous taxa, to low values indicative of forces being distributed, as with the periphytivorous genus *Chaetostoma* and the detritivorous/insectivorous species *Rineloricaria lanceolata* (Fig. 11).

Relative distribution or concentration of jaw force per unit of substrate area is an aspect of jaw function not typically examined in teleosts, but one which is important for both aquatic and terrestrial herbivores that use teeth for both food gathering and for the grinding or trituration of plant cell walls necessary to enhance digestion of these low quality (i.e. N-poor, C-rich) foods. Most loricariids are described as detritivores or herbivores based on gut contents (Melo et al., 2004) and stable isotope analyses (Jepsen and Winemiller, 2002). Unlike detritivorous/herbivorous fishes in the Perciformes, Characiformes, and Cypriniformes, which typically have well-developed pharyngeal jaws, a highly muscular stomach, and/or highly acidic stomachs for the trituration of cell walls (Bowen, 1976, 1981, 1983), loricariids have relatively unspecialized pharyngeal jaws (Armbruster, 2004), a thin-walled anterior alimentary canal (Delariva and

Agostinho, 2001), and intestinal pHs near neutral (German, 2008). Loricariid herbivores may, therefore, benefit from the grinding of food particles against solid substrates during jaw adduction and prior to ingestion.

Alternatively, nutritive deficiencies of low quality foods can be compensated for by increasing consumption rate and food volume (Horn and Messer, 1992). This appears to be the case in at least the species *Ancistrus triradiatus* and *Panaque nigrolineatus*, which have gut passage times measured at 40 minutes (Hood et al., 2005) and four hours (German, 2008), respectively. Given that loricariids have intestinal physiologies optimized for the rapid assimilation of free monosaccharides and amino acids associated with microbial degradation of detritus (German, 2008), it is likely that they ingest as much food as they are able, given the need to first separate it from substrates. For generalist consumers of flocculent detritus or loosely attached periphyton, low values of the metric AM_{area}/TRL indicative of force distribution would be expected. Indeed, species of *Chaetostoma* have some of the lowest AM_{area}/TRL values (Fig. 11) and some of the longest/ broadest tooth rows of any loricariid (Fig. 3C), and gut content studies have revelaed them to be detritivores in piedmont streams of Ecuador (Saul, 1975), Venezuela (Hood et al., 2005), and Panama (Kramer and Bryant, 1995).

Broad, truncate tooth rows, or their invertebrate equivalent, are characteristic of a wide variety of herbivorous/detritivorous grazers outside of Loricariidae. Caddisfly larvae (Trichoptera), which are among the most ubiquitous metazoan grazers in temperate streams, also frequently have a broad, bristly labrum with which they scrape algae and gather detritus from stream surfaces (Fig. 12A; see also Arens, 1989, 1990, 1994). Sereno et al. (2007) described a Cretaceous sauropod with an extremely broad muzzle

(*Nigersaurus taqueti*, Fig. 12B), and used the orientation of its otic canals and aspects of its cervical vertebrae to support the hypothesis that it was specialized for a low, grazing head posture, and the cropping of vegetation close to the ground. Solounias and Moelleken (1993) examined the jaws and feces of a wide range of modern and extinct ruminant mammals and were able to classify them into one of three feeding modes (browsers, mixed feeders, and grazers) based solely on premaxilla width (narrowest to widest, Fig. 12D; see also Janis and Erhardt, 1988). In Asian tropical streams, the Gastromyzontinae (Cypriniformes) exhibit a range of jaw widths (Fig. 12C) that Roberts (1989) associates with a diet spectrum from carnivory (narrow) to herbivory (wide). And in the tropical rivers of Africa, the surface-scraping catfish tribe Atopochilini (Mochokidae; Vigliotta, 2008) is remarkably convergent on members of the Loricariidae: all atopochilins have very wide jaws that function within a fleshy labial disk and the tribe is at least partially diagnosed by having a ventral mesethmoid condyle for articulation with premaxillae, although neither atopochilin jaw function nor trophic ecology has been described in detail.

In marine systems, Blenniidae (Springer, 1988) and the squamipinnes group (an assemblage of nine morphologically and taxonomically diverse fish families including the surgeonfishes, Acanthuridae, and the butterflyfishes, Chaetodontidae; Konow et al., 2008) are abundant on reefs and include many surface-scraping species with relatively broad, truncate muzzles. The squamipinnes group is also notable for having evolved a novel intramandibular joint at least three and possibly five times, in each case associated with a shift from suspended to surface-attached prey items (Konow et al., 2008). The increased jaw flexion allowed by this joint, in all cases between the dentary and the anguloarticular, appears to be an adaptation for surface scraping by allowing the tooth row to remain in more continuous contact with surfaces during adduction. Similar articulations between the dentary and the articular have been described in surface-scraping parrotfishes (Scaridae; Bellwood and Choate, 1990). Likewise, Yamaoka (1982) observed a weakening of the intramandibular symphysis between left and right mandibular rami in the *Petrochromis* genus (Cichlidae) of surface-scraping, epilithic algivores. Together, these comparative examples support the hypothesis that decoupling of linkages as observed in the lineage leading to Loricariidae may have at least partially been an adaptive response to a surface-scraping feeding mode, and the associated need to independently accommodate tooth rows to surface irregularities during jaw adduction.

Surface scraping in Loricarioidea is likely to have evolved in close association with surface attachment in high gradient hillstream habitats. Schaefer and Provenzano (2008) describe several features of the pelvic girdle in members of the Lithogeninae that they hypothesize are adaptations for surface attachment and, in conjunction with the labial disk, locomotion via surface attachment (i.e. climbing, even up vertical surfaces above the water line; Johnson, 1912). Lithogeninae is sister to either the Loricariidae (Schaefer, 2003) or Astroblepidae (Armbruster, 2004; Hardman, 2005); and the Astroblepidae, which are sister to the Loricariidae (Sullivan et al., 2006), are restricted to high-elevation Andean hillstream habitats (Armbruster, 2004). Likewise, the basal loricariid subfamily Delturinae is restricted to high gradient headwaters (Reis et al., 2006). These morphological features, and the high gradient habitats characteristic of the basal lineages Lithogeninae and Astroblepidae support the hypothesis that Loricariidae evolved in hillstream habitats. Convergent modifications of the pelvic fin and oral disk are common among several lineages of hillstream ichthyofaunas in tropical Asia and Africa (Hora, 1922, Annandale and Hora, 1922, Hora, 1930, Saxena and Chandy, 1966, Singh and Agarwal, 1993); in several of these lineages, jaw modifications for surface scraping modes of feeding have evolved in association with development of labial disks (Roberts and Stewart, 1976, Benjamen, 1986, Roberts, 1989).

2.4.3 Jaw mechanics: force geometry-traditional metrics

Relative distances between areas of force-in or force-out and axes of rotation determine a rotating system's mechanical advantage, or the degree to which the system is optimized for force or speed. Previous investigations of teleost jaw function have revealed a wide range of mechanical advantage ratios, calculated by dividing in-lever distance by out-lever distance. In general, piscivorous fishes feeding on elusive prey items have jaws with long out-levers, short in-levers, and mechanical advantages for jaw closure as low as 0.04 (e.g. needlefishes, Belonidae; Westneat, 2004), indicating optimization for speed. Conversely, fishes that feed on sessile, slow-moving, and/or hard prey items have jaws with short out-levers, long in-levers, and mechanical advantages for jaw closure as high as 0.68 (e.g. coralivorous parrotfishes, Scaridae; Westneat, 2004), indicating optimization for force. Loricariid diets are entirely benthic, non-living (detritus, wood), sessile (algae, diatoms, sponge), or slow-moving (e.g. aquatic Trichoptera and Lepidoptera larvae, snails). Loricariids might, therefore, be predicted to have relatively slow, force-optimized jaws; however, calculations of jaw closing mechanical advantage using traditionally defined parameters (Fig. 5) describe a wide range of mechanical advantages, from 0.24 at the distalmost tooth of the insectivorous species *Rineloricaria lanceolata*, to 1.26 at the proximalmost tooth of the detritivorous species *Chaetostoma* sp. 2 (Fig. 13).

If only the distalmost tooth is considered (as in most investigations of teleost jaw closure), the wood-eating species *Panaque* n. sp. 'Marañon' is the most force-optimized, with a mean mechanical advantage of 0.41 (Fig. 13). Given the ability of loricariids to synchronously apply distalmost and proximalmost teeth to substrates, mechanical advantage at the proximalmost tooth may be equally functionally relevant; and *Panaque* n. sp. 'Marañon' has a proximalmost mechanical advantage of 0.57, also among the highest of the sampled taxa (Fig. 13). Several species of algivorous/detritivorous taxa have proximalmost tooth values much greater than *Panaque* n. sp. 'Marañon', including all members of the algivorous/detritivorous genera *Ancistrus* and *Chaetostoma* (Fig. 13). In consideration of the functional relevance of these major mechanical advantage gradients between distalmost and proximalmost teeth, the force distributed per unit of tooth row length, as predicted by AM_{area}/TRL, should be factored into analyses of mechanical advantage (Figs. 11, 13).

Some taxa like *Panaque* n. sp. 'Marañon' have morphologies consistent with both force concentration (Y-axis, Fig. 13) and force optimization at distalmost and proximalmost teeth (X-axes, Fig. 13). Other taxa (e.g. *Rineloricaria lanceolata*, *Hypostomus unicolor*) have morphologies consistent with force distribution and speed optimization at distalmost and proximalmost teeth. Novel force intensity and traditional force geometry metrics for these taxa converge upon descriptions of morphologies at opposite ends of both functional spectra. In contrast, taxa such as *Ancistrus* and *Chaetostoma*, are predicted to be force-distributers, and have a range of mechanical advantage values from relatively speed optimized distalmost teeth, to force optimized proximalmost teeth (e.g. *Ancistrus* sp. 'longjaw'; Fig. 13). This wide range of mechanical advantage values across the tooth row challenges both the functional comparison of taxa within Loricariidae, and the comparison of loricariid jaw mechanical advantage with that of other teleosts. Indeed, several aspects of the relatively novel form and function of loricariid jaws provide caveats to uncorrected interpretations of mechanical advantage metrics computed using traditional anatomical definitions of in-levers and out-levers.

2.4.4 Jaw mechanics: force geometry-novel metrics

Variation in mechanical advantage is likely an important consequence of jaw morphological variation across the Loricariidae; however, accurate prediction of mechanical advantage is dependent upon precisely locating predominant axes of rotation. The high degree of freedom of loricariid lower jaw rotation makes it unlikely that a single, fixed axis of rotation exists, and the three-dimensional range across which the rotational axis might shift is likely subject to interspecific variation. Detailed kinematic data is generally lacking for Loricariidae, but the single cineradiographic study of *Pterygoplichthys gibbiceps* (Hypostominae) by Adriaens et al. (2009) observed rotation predominantly within the sagittal plane, represented by Axis 1 in Fig. 8. Viewed in this light, relevance of the in-lever and out-lever parameters to predictions of mechanical advantage is reduced by the nearly perpendicular orientation of these parameters with respect to the sagittal plane (Fig. 8). Dimensions of shape variation most relevant to loricariid jaw mechanical advantage are illustrated in the rotating cone model as radius 1 (r_1; Fig. 8), the distance perpendicular to the predominant axis of rotation, from the axis to the region of force-in, and radius 2 (r_2; Fig. 8), the distance perpendicular to the predominant axis of rotation, from the axis to the region of force-out. These are sagittal components of the respective in-lever and distalmost out-lever, and should, therefore, provide more accurate predictions of mechanical advantage generated during sagittal rotation than measured distances from the AAC to respective regions of force-in and force-out.

Direct measurement of r_1 and r_2 is not possible because of the inability to precisely locate a dominant rotational axis in three dimensions. Instead, the parameter H1 (Fig. 6) was measured and treated as a correlate of combined variation in r_1 and r_2. H1 increases relative to each of the unmeasurable r_1 and r_2 parameters. Absent the ability to compute ratios of r_1 to r_2, I hypothesize that major morphological trends observed among the lower jaws of loricariid lignivores toward a shortened long axis, toward hypertrophy of the coronoid arch, and toward increased distance between the coronoid arch and the tooth row (Fig. 3), are functionally correlated, and independently contribute to more forceful jaw geometries. Longer jaws with low or absent coronoid arches, and tooth rows closer to the jaw's long axis are hypothesized to be optimized for speed. Representing near opposite ends of these extremes are the jaws of *Chaetostoma* cf. *milesi* (Cone 1, Fig. 8), and *Panaque nigrolineatus* (Cone 2, Fig. 8). By measuring relative height of the coronoid arch, and its distance from the tooth row in the sagittal plane, H1 is hypothesized to be a direct indicator of mechanical advantage, with high values indicating optimization for force, and low values indicating optimization for speed.

Two metrics were calculated with the novel H1 parameter: H1/TRL and Out_{dist}/H1 (Fig. 14). The spectrum of H1/TRL values is hypothesized to provide a combined measure of force optimization and force concentration, versus combined speed optimization and force distribution. High values are observed among the wood-eating taxa *Panaque* spp., and *Hypostomus pyrineusi*, and low values are observed among both the algivorous long-tooth-row genus *Chaetostoma* and the short-tooth-row insectivorous or detritivorous genera *Loricaria* and *Rineloricaria* (Fig. 14). In these latter taxa, speed optimization may be adaptive for either the rapid consumption of large volumes of low quality food, or for the capture of prey items that are mobile. Zuanon (1999) examined the diet of *Ancistrus ranunculus*, which was not examined herein, but which has very elongate jaw rami and relatively short tooth rows convergent upon jaw morphologies of some Loricariini (per. obs.), and hypothesized that it is a filter-feeder. Likewise, K. O. Winemiller (pers. comm.) has hypothesized that many loricariines may feed by winnowing loosely aggregated benthic food items in a manner similar to that of sturgeon (Carroll and Wainwright, 2003). Fast adduction of speed-optimized jaws that are relatively long and gracile with low coronoid arches may serve a hydrodynamic function in filter-feeders and substrate winnowers by enhancing current flows into the buccal chamber.

Length to height ratios of loricariid jaws are described by the metric $\text{Out}_{\text{dist}}/\text{H1}$, with high values describing relatively long and gracile jaws (e.g. Loricariini), and intermediate values describing moderately long and moderately tall jaws (e.g. *Chaetostoma*, Fig. 14; Cone 1, Fig. 8). Low values of $\text{Out}_{\text{dist}}/\text{H1}$ describe relatively narrow and tall jaws (e.g. most Hypostominae, Fig. 14; Cone 2, Fig. 8). By describing gross dimensions, this metric is also hypothesized to predict the potential for torque magnification through the jaw ramus in sagittal (low values of $\text{Out}_{\text{dist}}/\text{H1}$) versus horizontal (high value of $Out_{dist}/H1$) planes. Relatively long and low jaws (e.g. *Loricaria, Rineloricaria*) would be expected to be subject to greater torque along the horizontal or transverse planes (Axis 2 and 3, Fig. 8), but given the correspondingly low AM_{area}/TRL and H1/TRL values for these taxa, they are likely subject to lower overall torsional forces. On the other hand, relatively narrow and tall jaws (e.g. *Panaque* spp., *Hypostomus pyrineusi*; Cone 2, Fig. 8) with low $Out_{dist}/H1$ values concentrate their mass more within the sagittal plane, and would be predicted to be subject to more intense torsional forces by their higher AM_{area}/TRL values.

The final two metrics TR_{angle} and Out_{dist}-Out_{prox}/In are correlated descriptors of the length and orientation of the tooth row, and are hypothesized to predict torque differentials across loricariid tooth rows during jaw adduction. Rotating systems that, like loricariid lower jaws, distribute forces across an extended surface with variable resistance are likely subject to torque differentials, or ranges of torque values from regions of force-out closest to the axis of rotation to regions of force-out furthest from the axis of rotation. One way to reduce such torque differentials is to reduce the area across which force is distributed (lower TRL). A second way is to change the orientation, or angle, of the area across which force is distributed. Increasing the angle of the loricariid dentary tooth row with respect to the distalmost out-lever arm, for example, shifts the relative positions of distalmost and proximalmost teeth so that the difference between their distances to the anguloarticular condyle is reduced. This result of increased tooth row angles is summarized by the metric Out_{dist}-Out_{prox}/In (i.e., the difference between out-lever arms standardized to the in-lever arm). Taxa with high TR_{angle} values (Fig. 15) are hypothesized to have a relatively low torque differential as predicted by the correlated metric Out_{dist}-Out_{prox}/In (Fig. 16). Selection for reduction of the torque differential via increased TR_{angle} is likely to be greatest among those taxa with jaws subject to more intense torsional forces as predicted by AM_{area}/TRL (e.g. *Panaque, Hypostomus pyrineusi*; Fig. 11). Relatively weak-jawed taxa in the Loricariinae also exhibit high TR_{angle} values; however, these morphologies may result not from selection for decreased torque differential but for increased tooth row protrusion associated with browsing or selective feeding – similar to increases in acuteness of premaxillary tooth row angles that can be observed in the muzzles of selectively browsing ruminants (Fig. 12).

2.5 CONCLUSIONS

I proposed methods by which morphological diversity across lower jaws of the Loricariidae may be quantified and compared in a homologous and functionally informative manner. These methods were used to describe jaw morpho-functional diversity across an assemblage of loricariids in the upper Amazon Basin of Northern Peru consisting of 5 tribes, 12 genera, and 25 species. Five of these species, comprised of species of two different lineages, have been previously described as specialized wood-eaters based on gut-content data; all had distinctive jaw morphologies consistent with convergence upon a durophagous jaw morphology and within this guild at least four species were distinguishable from each other by their distinctive jaw morpho-functional attributes alone. In addition to describing taxonomic patterns of jaw morphological diversity, several explicit hypotheses for how jaw morphometric parameters might be used to predict function were proposed. Loricariidae has been hypothesized to have higher rates of jaw morphological and functional diversification than loricarioid clades with plesiomorphic jaw linkages, or constraints, missing in Loricariidae (Schaefer and Lauder, 1986). Methods proposed herein provide several means by which jaw diversity in Loricariidae may be described and correlated with extrinsic ecological and biogeographical factors. They also provide several discrete, functionally related morphometrics that, in conjunction with morphology-independent phylogenies, can be used to investigate rates and patterns of loricariid jaw morphological, functional, and ecological diversification. Given the intrinsic capacity for morphological and functional diversification putatively enhanced by decoupling in the Loricarioidea, and the trophic ecological diversity available to loricariids as basal consumers in the world's largest tropical freshwater systems, there is great potential for considerable undescribed trophic and ecological diversity in Loricariidae. Highly derived structure and function of loricariid jaws confound attempts to place their morphological and functional radiation in the context of previous investigation of jaw functional diversity in the Actinopterygii. Indeed, the structure and function of loricariid jaws are perhaps best compared to other surface-attaching, surface-scraping feeders from tropical rivers in Asia and Africa (e.g. Cyprinidae, Balitoridae, and Gyrinocheilidae (Cypriniformes), and Mochokidae and Sisoridae (Siluriformes)) – all of which are still awaiting detailed investigations of jaw morphological and functional diversity.

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Table 1. Taxa and sample sizes examined in respective jaw and muscle parts of this study. All specimens collected from middle reaches of the Marañon River, a tributary of the upper Amazon in northern Peru.

Species	**N jaw**	**N muscle**
SUBFAMILY: Hypostominae		
TRIBE: Ancistrini		
Ancistrus sp. 'longjaw'	5	
Ancistrus sp. 'shortjaw'	3	
Ancistrus sp. 'wormline'	2	
Chaetostoma cf. *milesi*	4	
Chaetostoma microps	27	6
Chaetostoma sp. 1	27	
Chaetostoma sp. 2	16	6
Chaetostoma sp. 3	33	6
Chaetostoma sp. 4	15	
Lasiancistrus schomburgkii	22	6
New genus 3	18	6
Panaque albomaculatus	13	4
Panaque gnomus	30	6
Panaque n. sp. 'Marañon'	13	5
Panaque nocturnus	83	6
Peckoltia bachi	2	
TRIBE: Hypostomini		
Hypostomus emarginatus	3	
Hypostomus niceforoi	4	
Hypostomus pyrineusi	19	6
Hypostomus unicolor	4	
SUBFAMILY: Loricariinae		
TRIBE: Farlowellini		
Farlowella amazonum	3	
TRIBE: Harttiini		
Lamontichthys filamentosus	18	6
TRIBE: Loricariini		
Loricaria clavipinna	3	
Rineloricaria lanceolata	3	
Spatuloricaria puganensis	9	4

Figure 1. Medial, sagittal sections through the snout and jaws of (A) *Chaetostoma* cf. *milesi*, (B) *Leporacanthicus joselimai,* and (C) *Panaque nigrolineatus.* Labels: ap = ascending process of the premaxilla, dn = dentary, me = mesethmoid, mec = mesethmoid condyle, pm = premaxilla, rpf = retractor premaxillae fossa. CT (computer aided tomography) reconstructions courtesy of the Digimorph lab.

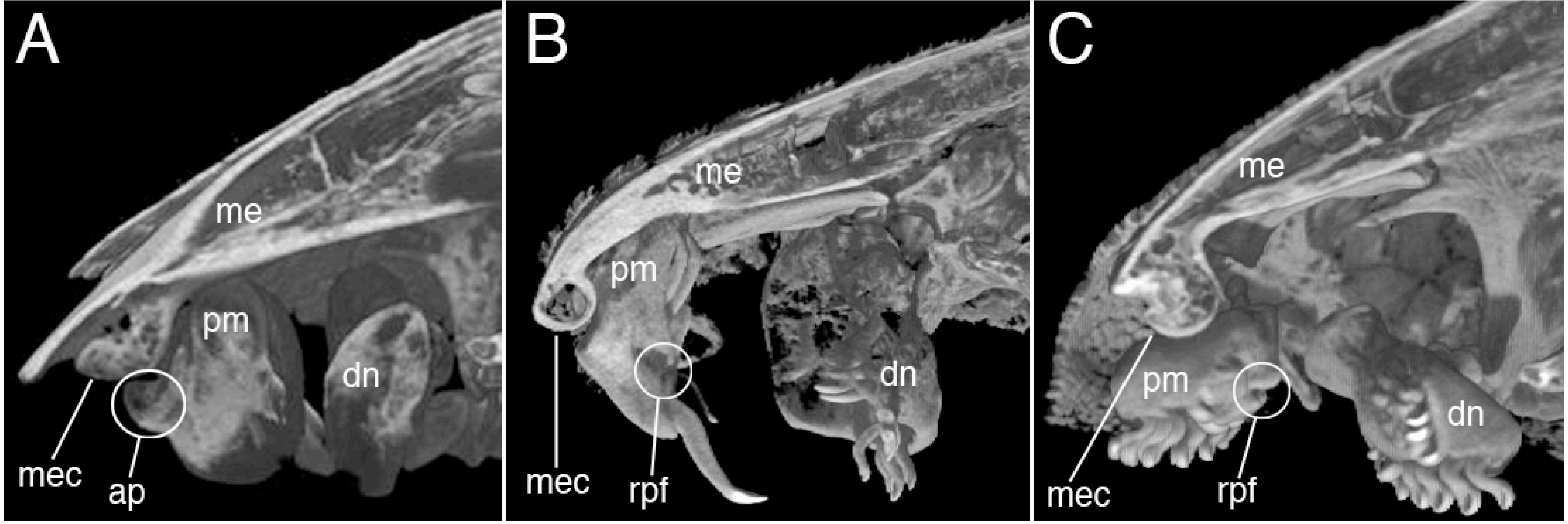


Figure 2. Ventral views of the snout and jaws of (A) *Chaetostoma* cf. *milesi*, (B) *Leporacanthicus joselimai*, and (C) *Panaque nigrolineatus*. Labels: dn = dentary, pm = premaxillae, aac = anguloarticular condyle. CT (computer aided tomography) reconstructions courtesy of the Digimorph lab.

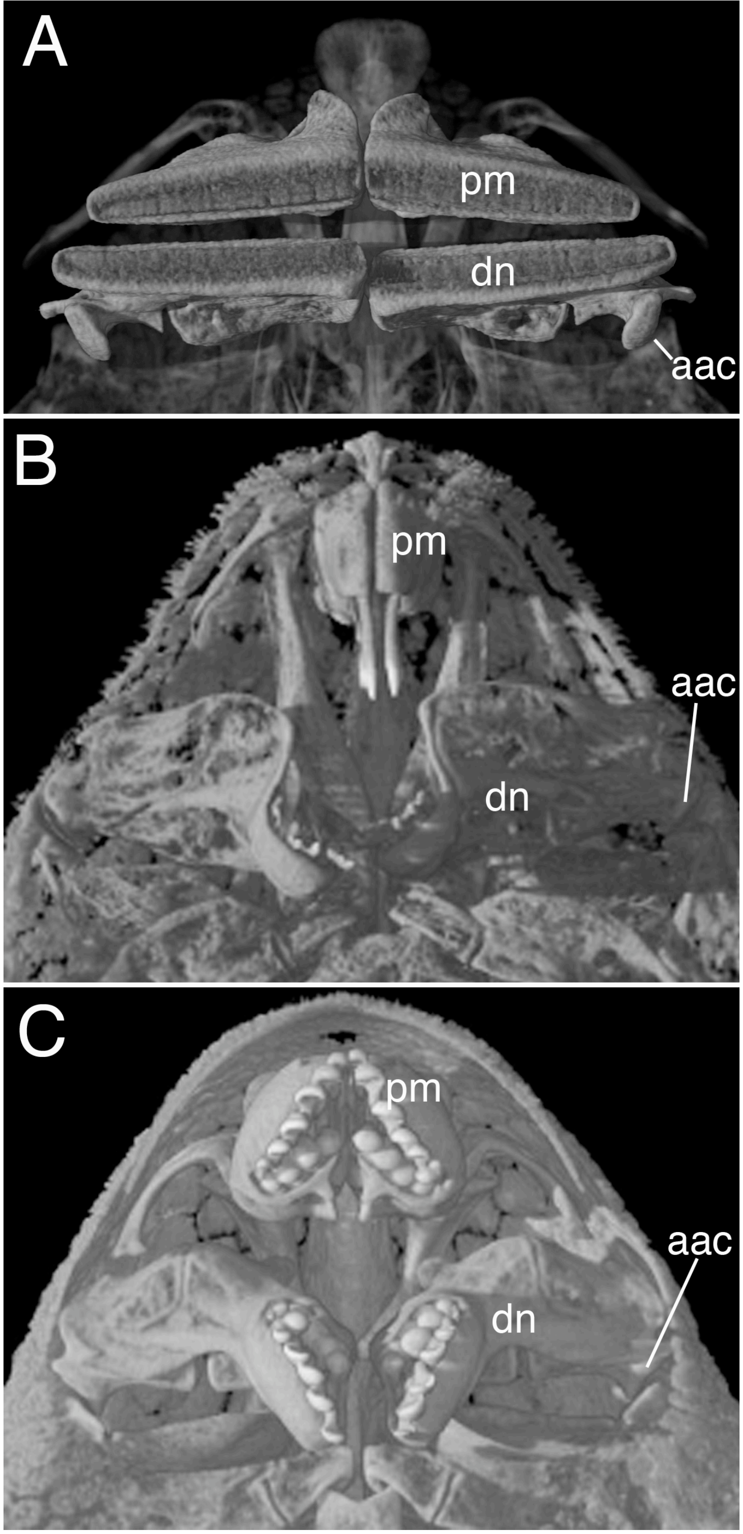


Figure 3. Representative sample of lower jaws from upper Amazon Loricariidae examined in this study: HYPOSTOMINAE: ANCISTRINI: (A) *Ancistrus* sp. 'longjaw', (B) *Ancistrus* sp. 'shortjaw', (C) *Chaetostoma* sp. 1, (D) *Panaque albomaculatus*, (E) *Panaque gnomus*, (F) *Panaque* n. sp. 'Marañon', (G) *Panaque nocturnus*, (H) *Peckoltia bachi*; HYPOSTOMINAE: HYPOSTOMINI: (I) *Hypostomus emarginatus*, (J) *Hypostomus niceforoi*, (K) *Hypostomus pyrineusi* in the *H. cochliodon*-group, (L) *Hypostomus unicolor*; LORICARIINAE: HARTTIINI: (M) *Farlowella amazona*, (N) *Lamontichthys filamentosus*, (O) *Rineloricaria lanceolata*; LORICARIINAE: LORICARIINI: (P) *Spatuloricaria puganensis*.

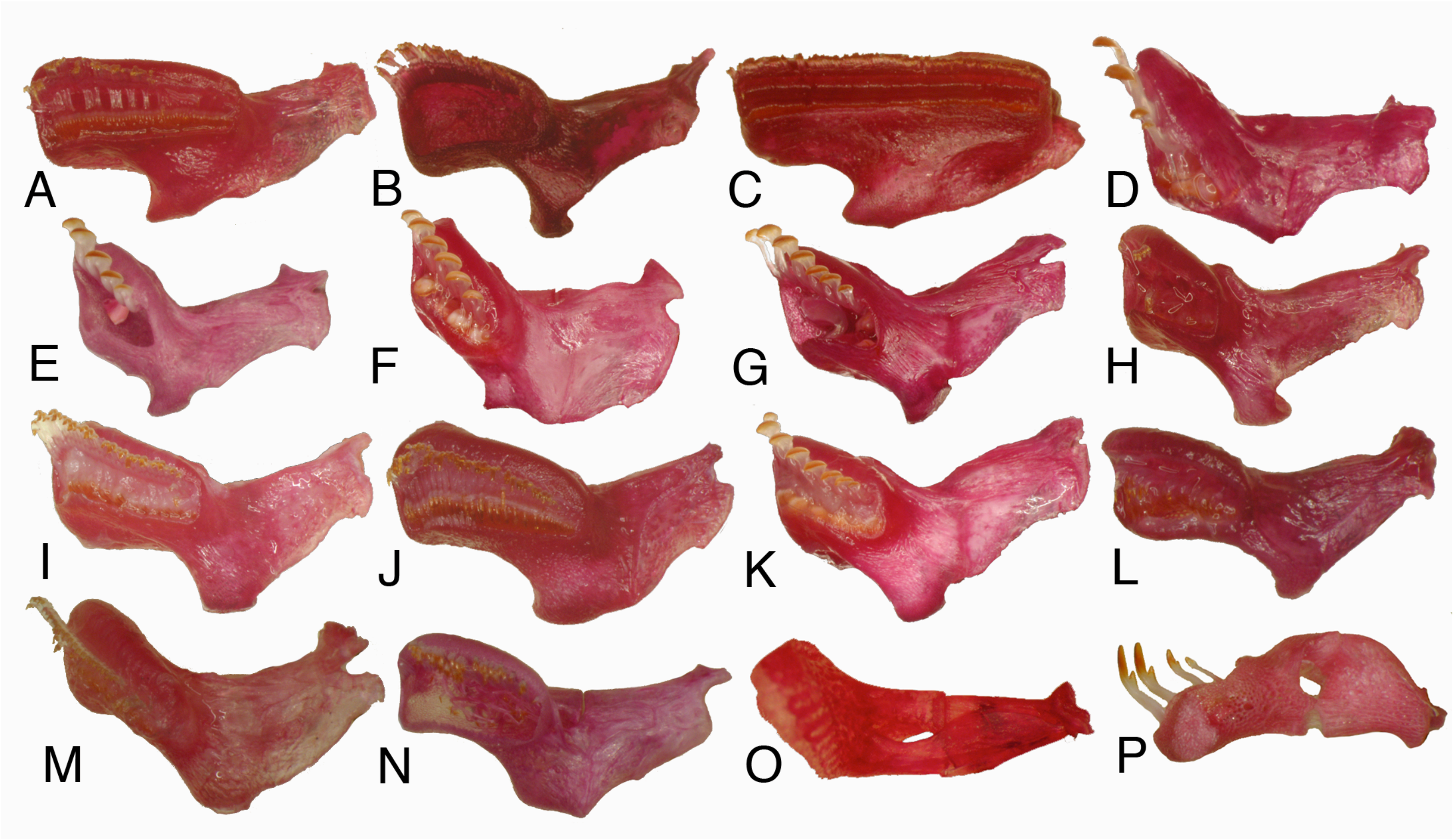


Figure 4. Examples of loricariid oral disks: (A) *Scobinancistrus* sp. and (B) *Leporacanthicus* cf. *galaxias*. Photos by M. Sabaj Pérez.

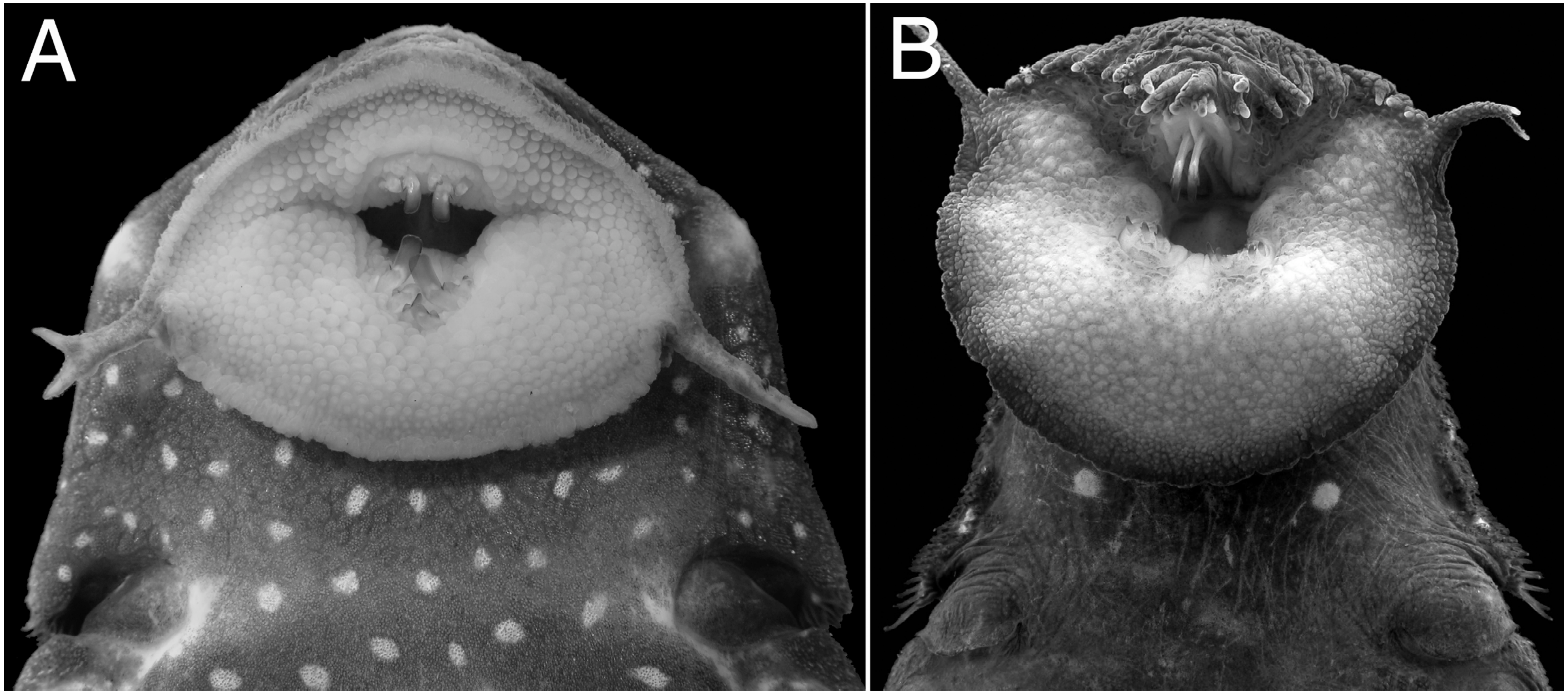


Figure 5. The lower jaw ramus of *Chaetostoma* cf. *milesi* (A, B, C) and *Panaque nigrolineatus* (D, E, F) in positions illustrating the horizontal orientation, ventral perspective (A, D), vertical orientation (B, E), and horizontal orientation, dorsal perspective (C, F). Functional parameters are labled on each perspective and view from which they were measured: AM_{area} = adductor mandibulae insertion area, In = in-lever from center of adductor mandibulae area of insertion to anguloarticular condyle, Out_{dist} = out-lever from anguloarticular condyle to distalmost tooth, Out_{prox} = out-lever from angularticular condyle to proximalmost tooth, TRL = tooth row length. CT (computer aided tomography) reconstructions courtesy of the Digimorph lab and Kyle Luckinbill, ANSP.

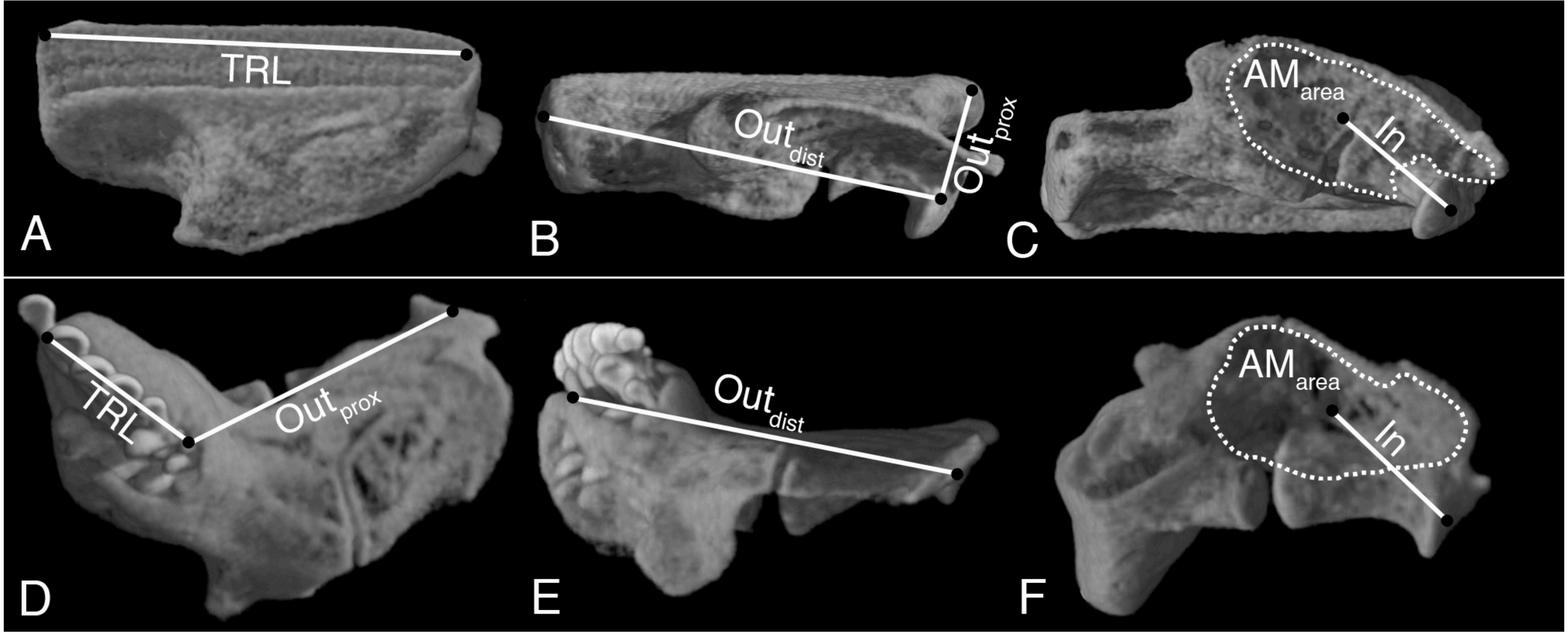


Figure 6. The lower jaw ramus of (A) *Chaetostoma* cf. *milesi* and (B) *Panaque nigrolineatus* in horizontal orientation, dorsal perspective, illustrating distances measured as the distalmost out-lever (Out_{dist}) and coronoid height (H1) parameters. CT (computer aided tomography) reconstructions courtesy of the Digimorph lab and Kyle Luckinbill, ANSP.

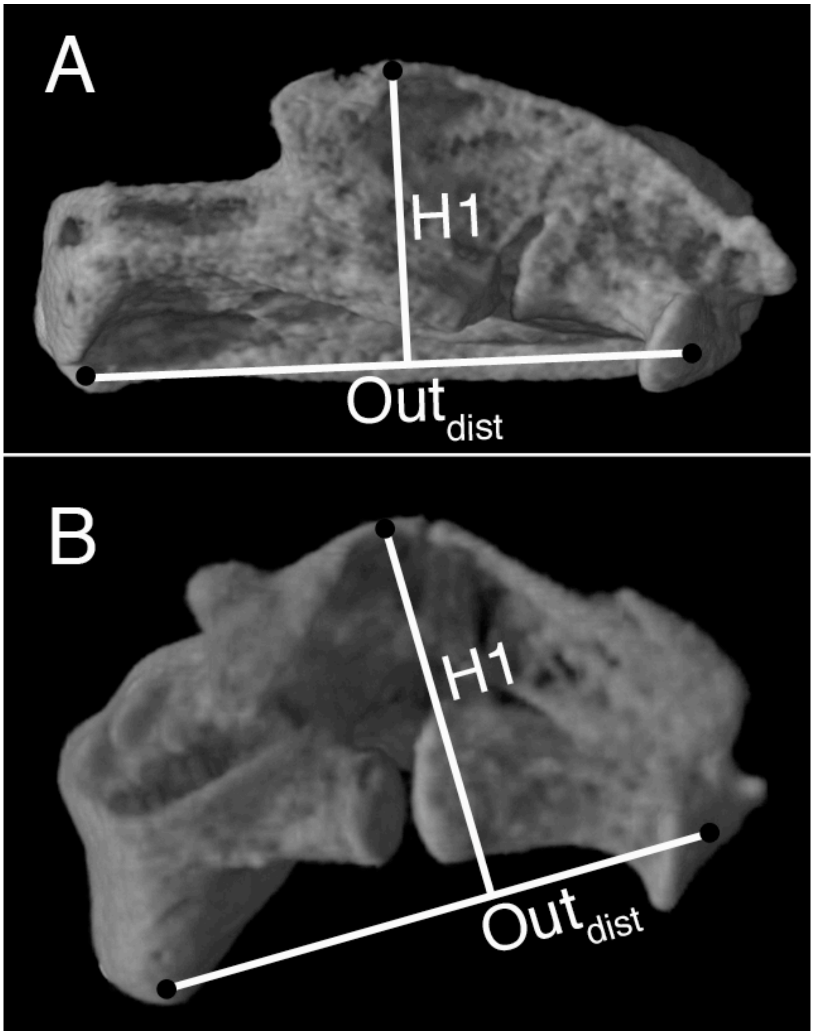


Figure 7. Relationship between combined adductor mandibulae area of insertion (AM_{area}) scaled to standard length (SL), and adductor mandibulae volume (AM_{vol}) scaled to standard length. Area of adductor mandibulae insertion and volume of adductor mandibulae were measured from separate subsets of specimens, so the correlation is of means of each scaled separately to standard length. Plotted values are means ± standard deviation. See Table 1 for species sample sizes.

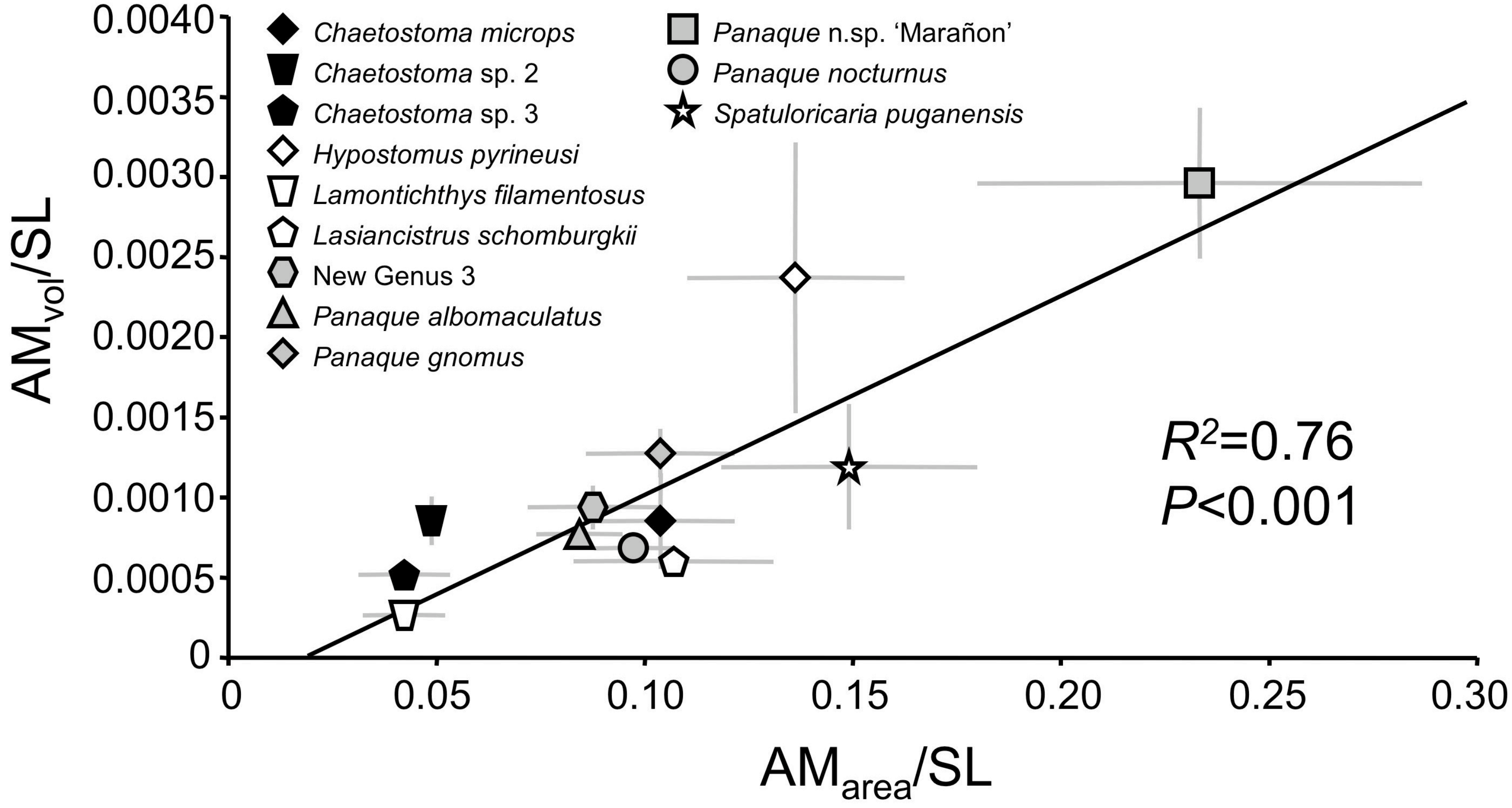


Figure 8. Three-dimensional rotating cone model linking loricariid lower jaw morphology and function. Cones modeled after the right lower jaw ramus of *Chaetostoma* cf. *milesi* (Cone 1) and *Panaque nigrolineatus* (Cone 2) illustrate near opposite ends of a spectrum of both measured and qualitatively described jaw morphology discussed in this study. Perspective is from the posterior. Red lines are potential axes of rotation, with Axis 1 representing rotation in the sagittal plane, Axis 2 representing rotation in the horizontal plane, and Axis 3 representing rotation in the transverse plane. Capitalized parameters and parameters represented by solid green, black, and gray lines were measured or quantified by proxy in this study (Fig. 5). See text for discussion of output plane represented by gray triangle. Tooth row angle (TR_{angle}) represented by ∂.

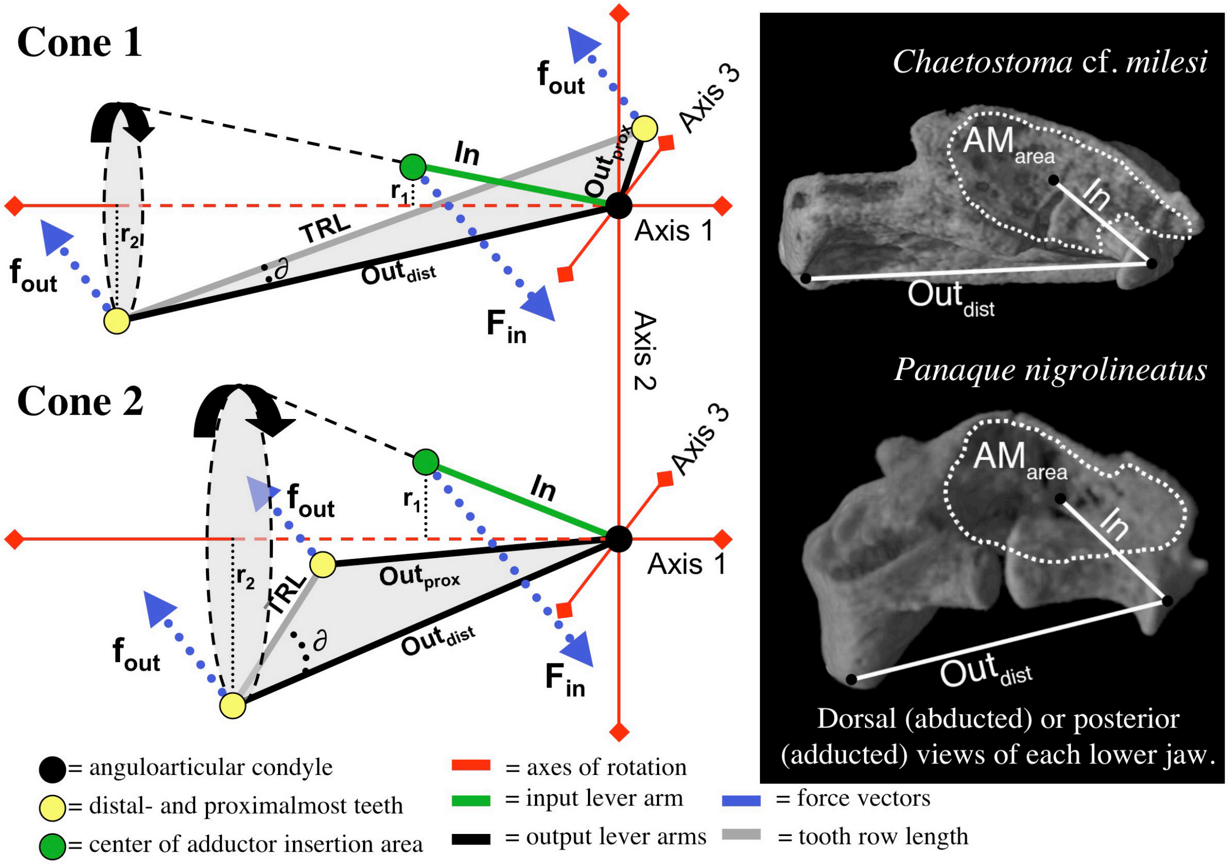


Figure 9. Principle component (PC) analysis of six parameters hypothesized to be functionally relevant to the loricariid lower jaw (see Figs. 5, 6). Data from 379 individuals and 25 species of Loricariidae collected from the upper Amazon in northern Peru (see Table 1). Parameters listed along each PC axis from left to right or from bottom to top in order of eigenvector magnitude. PCs one through four describe 85.7%, 11.9%, 2.0%, and 0.3% of variation in the dataset, respectively.

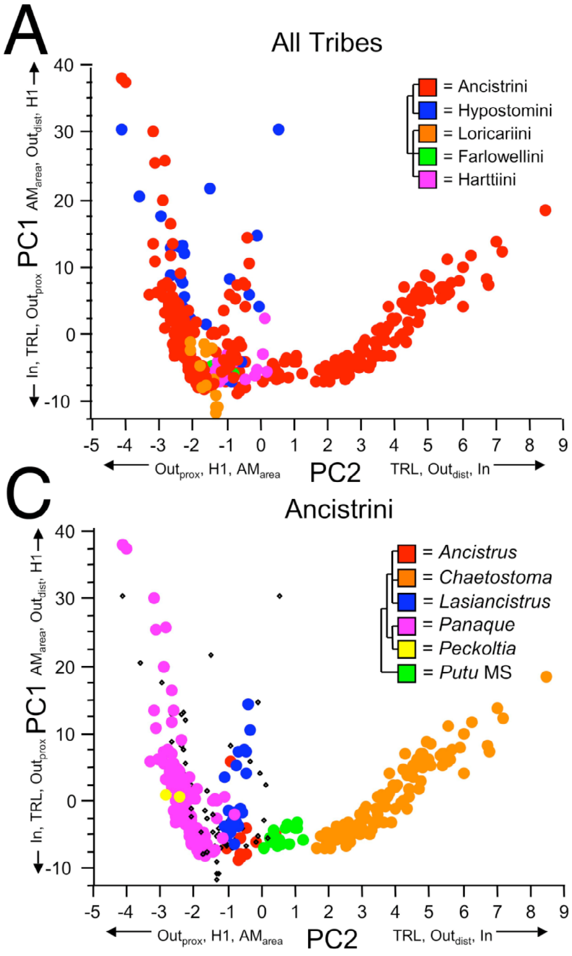


Figure 10. Principle component (PC) analysis of six parameters hypothesized to be functionally relevant to the loricariid lower jaw (see Figs. 5, 6). Data from 379 individuals and 25 species of Loricariidae collected from the upper Amazon in northern Peru (see Table 1). Parameters listed along each PC axis from left to right or from bottom to top in order of eigenvector magnitude. PCs one through four describe 85.7%, 11.9%, 2.0%, and 0.3% of variation in the dataset, respectively.

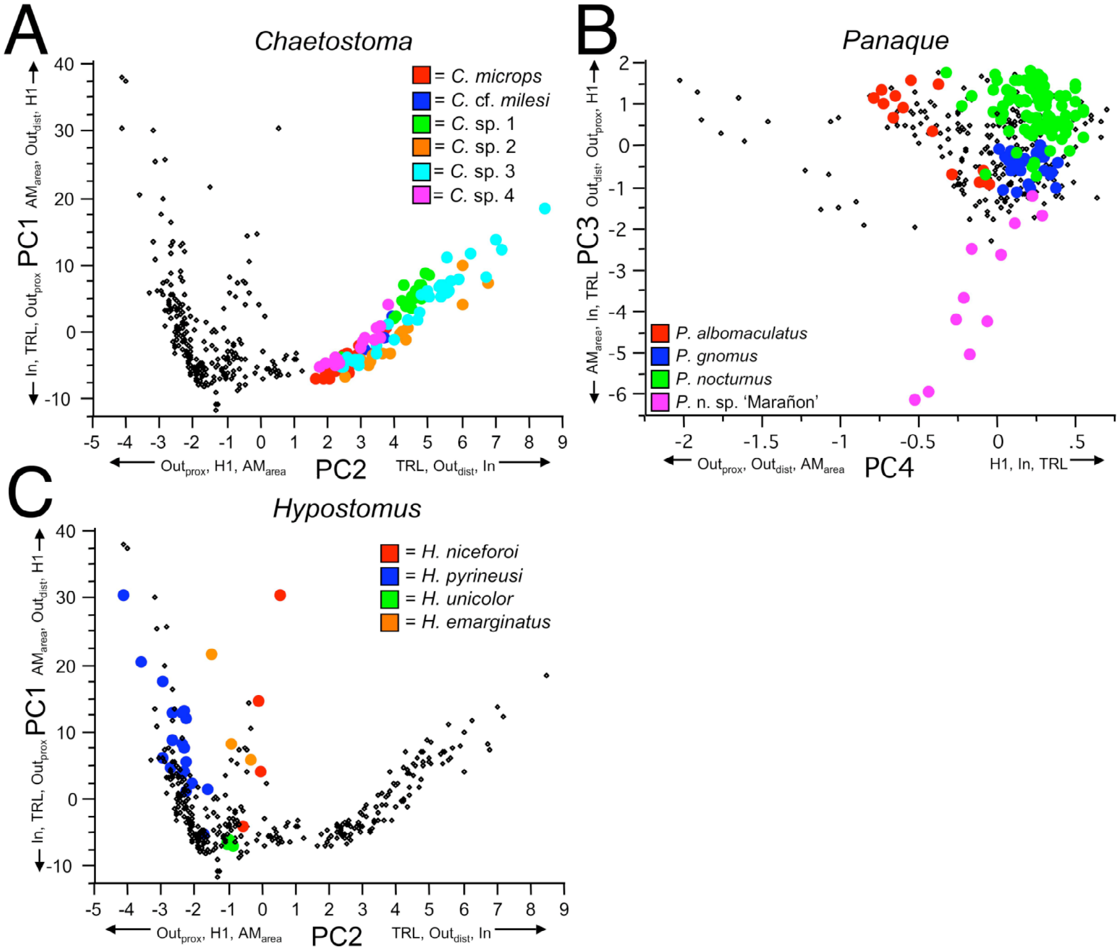


Figure 11. Adductor mandibulae area of insertion (AM_{area}) over tooth row length (TRL), hypothesized to predict force intensity, with high values indicating force concentration and low values indicating force distribution. Plotted values are means ± standard deviation. See Table 1 for species sample sizes.

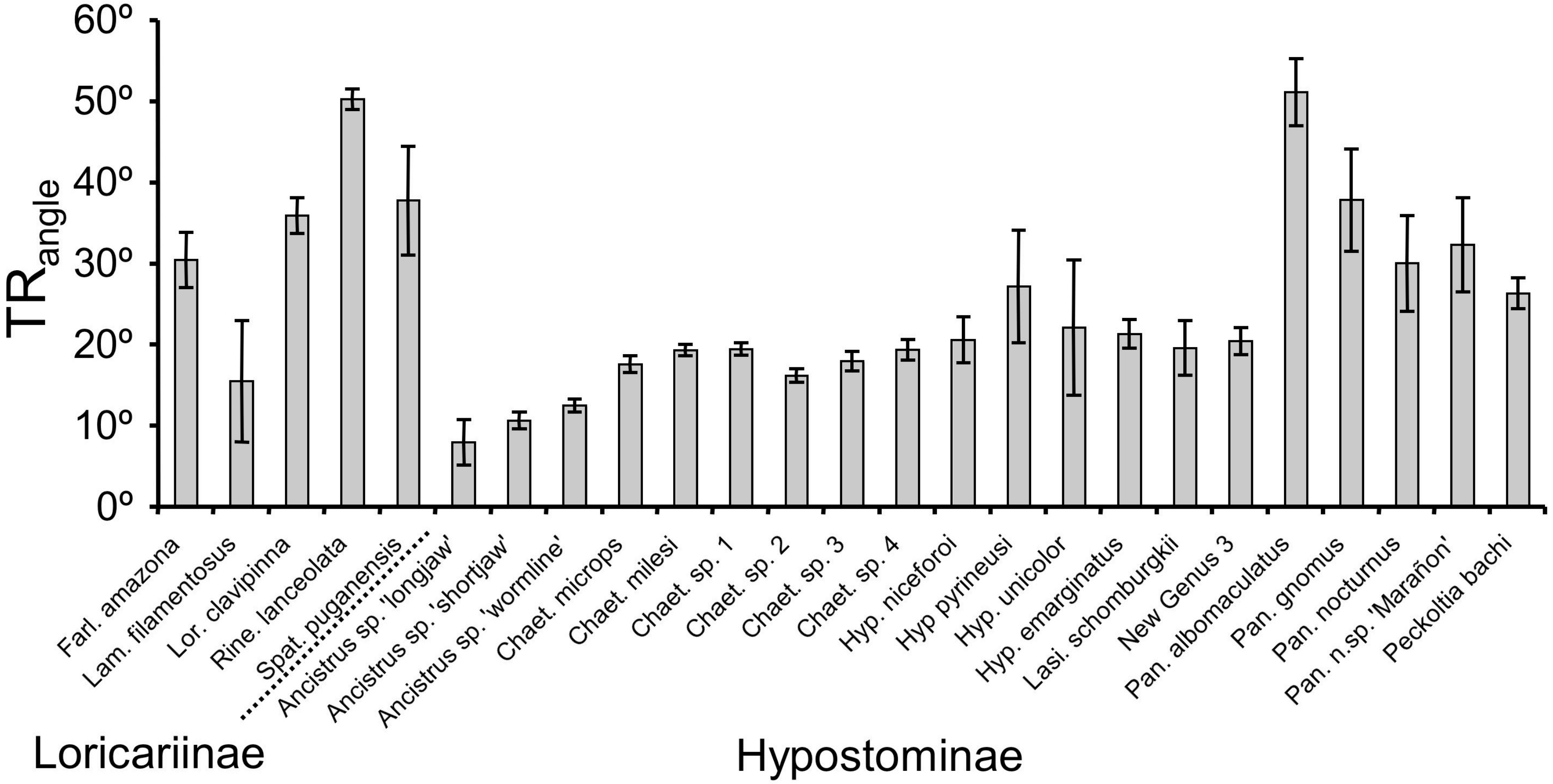


Figure 12. Examples of convergent trends in herbivorous jaw morphologies from (A) Insecta, Trichoptera (labrum in dorsal view modified from Satija & Satija, 1959), (B) fossil Sauropoda, *Nigersaurus taqueti* (lower jaw in dorsal view modified from Sereno et al., 2007), (C) Cypriniformes, Gastromyzontinae (snout in ventral view modified from Roberts, 1989), and (D) extinct Mammalia, Giraffidae (premaxillae in ventral view modified from Solounias & Moelleken, 1993). Series in (C) hypothesized to be that of a carnivore (narrowest, bottom) to herbivore (broadest, top). Series in (D) hypothesized to represent a foraging spectrum from browser (narrowest, bottom) to mixed grazer (middle) to grazer (broadest, top), with support provided by fecal data (Solounias & Moelleken, 1993). See Fig. 2 for similar spectrum of jaw morphologies in Loricariidae.

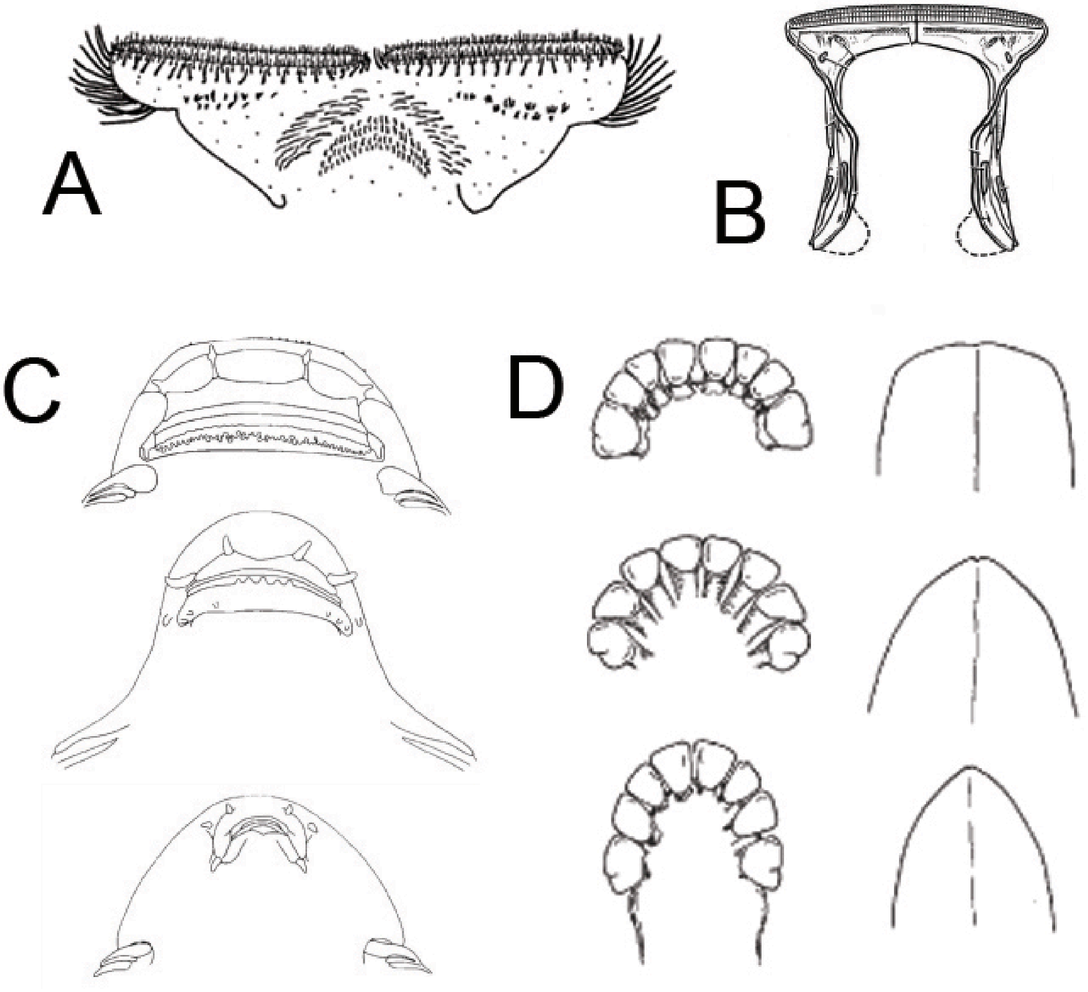


Figure 13. The novel metric of force intensity AM_{area}/TRL (see Fig. 11) plotted against traditional metrics of mechanical advantage: distance from anguloarticular condyle to center of adductor mandibulae insertion area (In) over respective distances from anguloarticular condyle to distalmost (Out_{dist}) and proximalmost (Out_{prox}) tooth insertions. Capital letters indicate jaws illustrated in Fig. 3. Plotted values are means ± standard deviation. See Table 1 for species sample sizes.

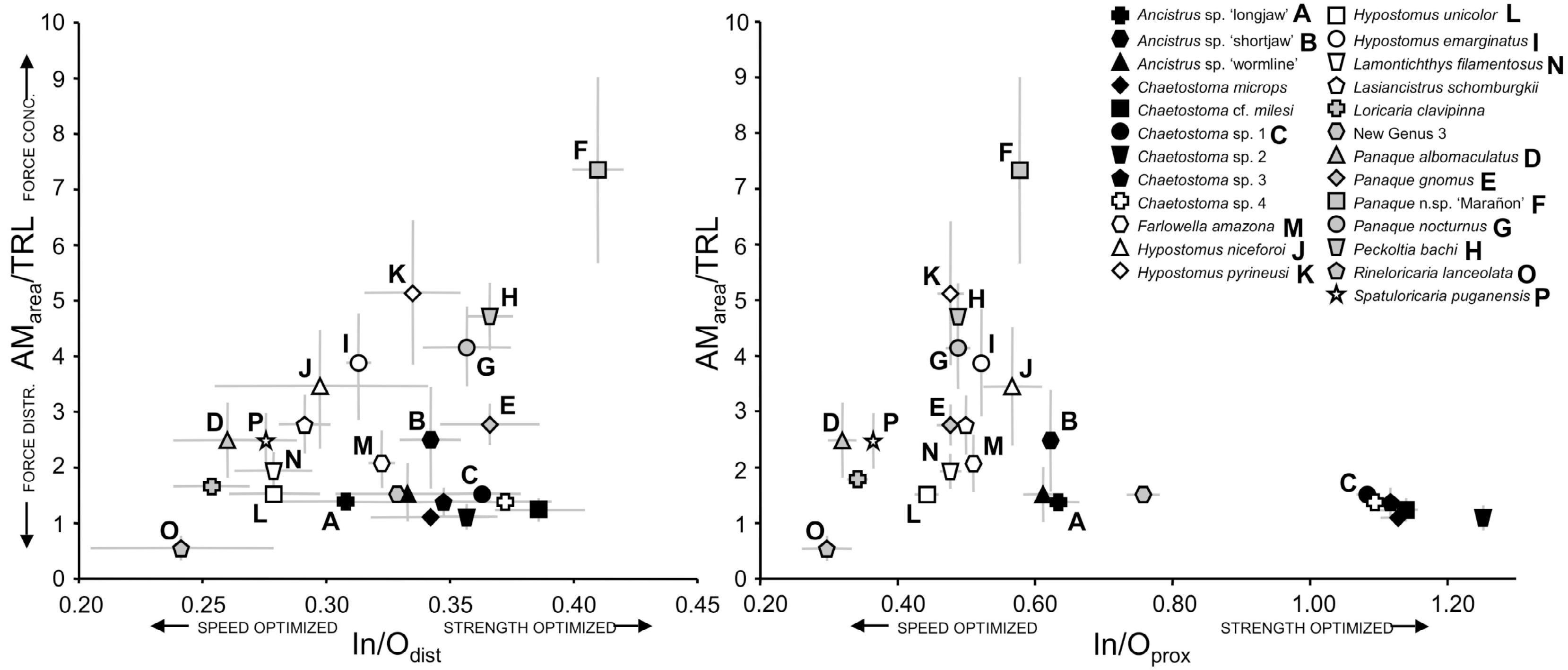


Figure 14. Three novel metrics of lower jaw morphological diversity hypothesized to be linked to function: (1) Adductor mandibulae area of insertion (AM_{area}) over tooth row length (TRL) – hypothesized to be a measure of force distribution versus force concentration; (2) distance parameter H1 (see Fig. 6) over TRL – hypothesized to be a combined measure of mechanical advantage (force vs. speed optimization) and force distribution; and (3) the distal out-lever arm (Out_{dist}, see Fig. 5) over H1 – a measure of the gross length (Out_{dist}) versu height (H1) dimensions of the lower jaw and hypothesized to be an indicator of the predominant plane of torque through the lower jaw. Capital letters indicate jaws illustrated in Fig. 3. Plotted values are means ± standard deviation. See Table 1 for species sample sizes.

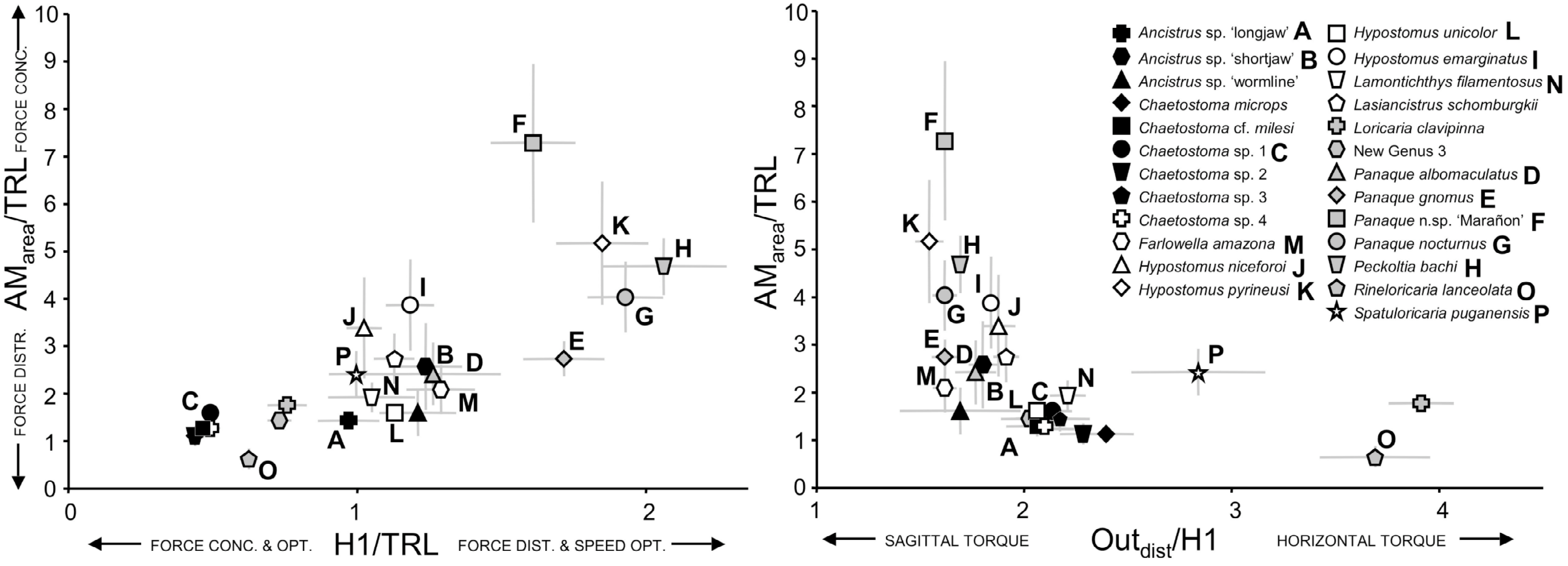


Figure 15. Mean angles and angular standard deviations between the tooth row and distalmost output lever for species examined in this study. Plotted values are means ± standard deviation. See Table 1 for sample sizes.

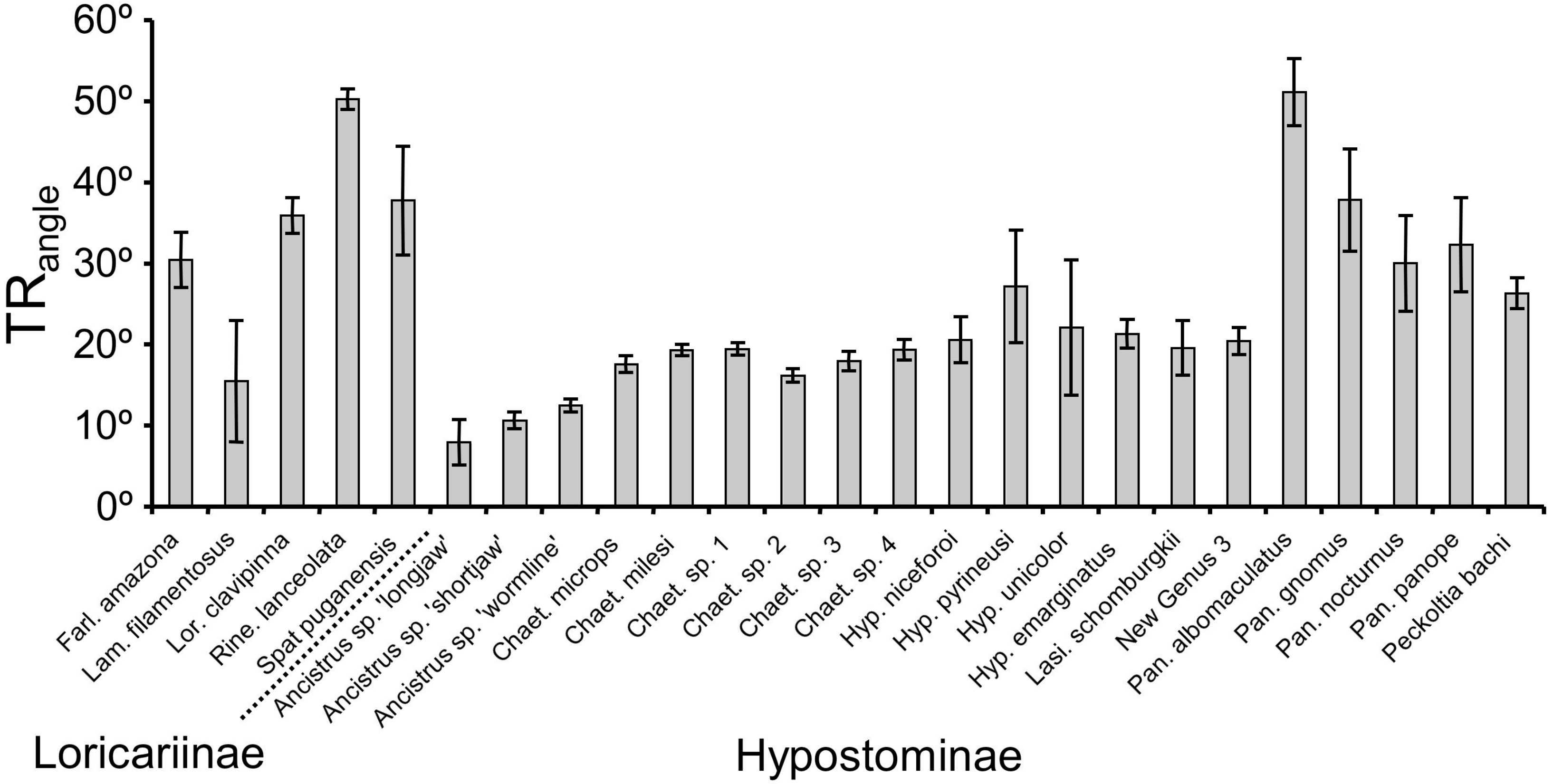
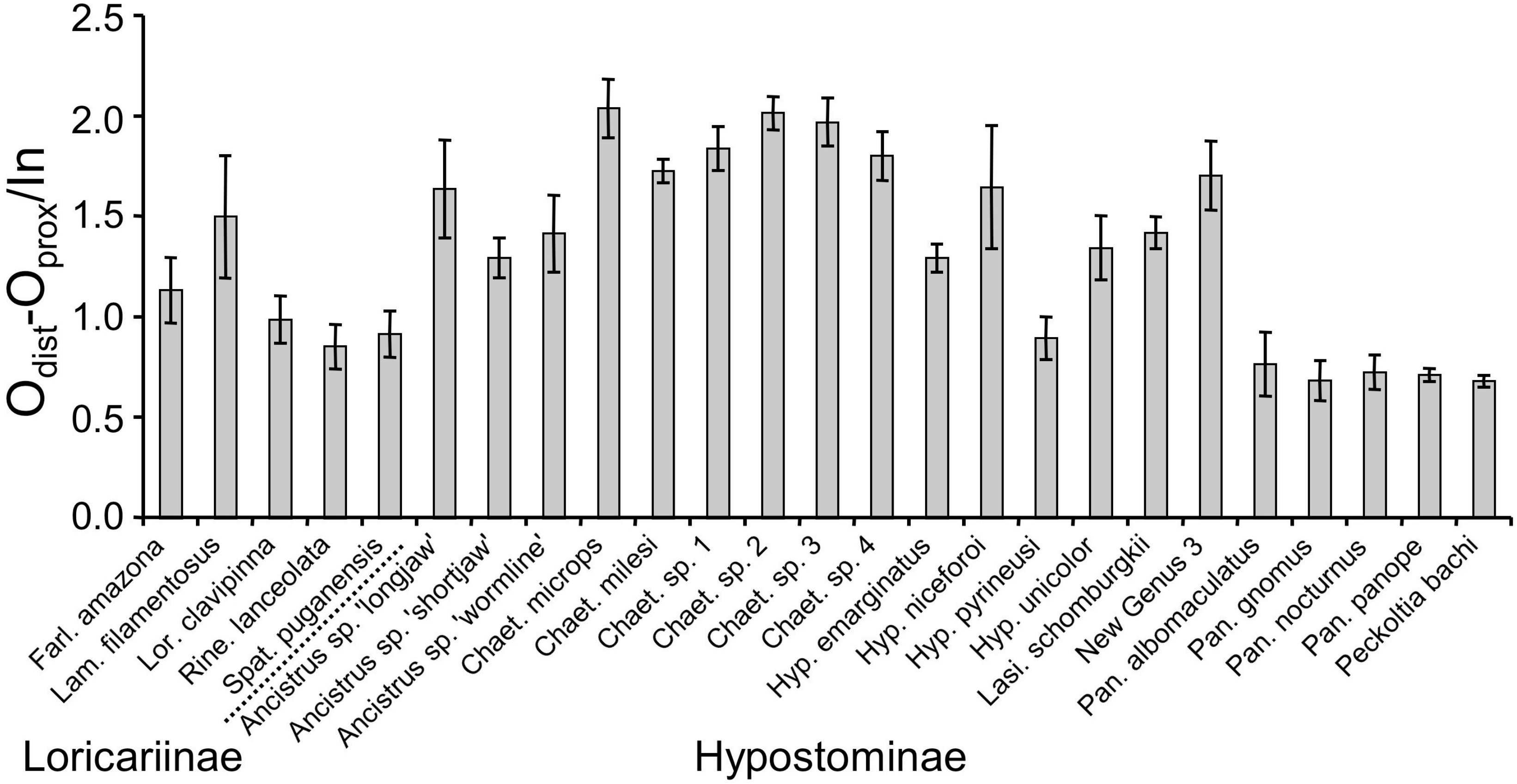


Figure 16. The metric Out$_{dist}$-Out$_{prox}$/In, a measure of torque differential across the tooth arcade. Plotted values are means ± standard deviation. See Table 1 for sample sizes.



CHAPTER 3. STABLE ISOTOPES REVEAL TROPHIC STRUCTURE WITHIN SYMPATRICALLY DIVERSE ASSEMBLAGES OF NEOTROPICAL DETRIVOROUS FISHES

3.1 INTRODUCTION

Detritus is broadly recognized as the foundation of most aquatic food webs (Mann, 1972, 1988, Wetzel et al., 1972, Cummins, 1973), yet the fine-scale use and partitioning of detrital resources, and variation in the contribution of detritus to the biodiversity and productivity of food webs, remain poorly understood (Moore et al., 2004). Prior to robust quantitative descriptions of the trophic structure of tropical freshwater fish communities (e.g. Flecker, 1992, Winemiller, 1990, Lewis et al., 2001, Layman et al., 2005), fishes were described as primarily carnivorous, and largely dependent on invertebrates for their trophic connections to either detritus or primary production (Odum, 1970, Eggers et al., 1978). This pattern is not the case for lowland tropical freshwater fish communities in general, and Neotropical riverine fish communities especially. Indeed, the detritivore niche, which is almost entirely associated with invertebrates at temperate latitudes (Anderson and Sedell, 1979, Cummins, 1979, Maltby, 1994), is filled largely by fishes in lowland tropical systems and detritivores compose most of fish biomass in most Neotropical rivers (Bonetto et al., 1969, Quirós and Baigún, 1985, Araujo-Lima et al., 1986, Bayley, 1989, Benedito-Cecilio et al., 2000, Alvim and Peret, 2004). Neotropical freshwater fish communities are among the most diverse in the world, with total fish richness estimated to be between 5000 and 8000 species (Lundberg et al., 2000). Describing major patterns of variation within the trophic structure of these highly diverse communities is a challenging but pressing goal for fish ecologists. Highly detritus-dependent Neotropical fish food webs are facing severe perturbation from overfishing (Bayley and Petrere, 1986, Galvis and Mojica, 2007, Rodríguez et al., 2007) and habitat alteration (Winemiller et al., 1996, Mol and Ouboter, 2004), just as light is beginning to be shed on the astounding diversity, distinctiveness, and complexity of these systems, particularly compared with well-studied temperate counterparts (Benedito-Cecilio and Araujo-Lima, 2002, Flecker et al., 2002, Jepsen and Winemiller, 2007).

My study focused on the Loricariidae, a diverse radiation of mostly detritivorous catfishes that are endemic to the freshwaters of tropical Central and South America. Carbon and nitrogen stable isotope data and several recently proposed metrics for the analysis and comparison of community-wide consumer isotope data (Layman et al., 2008) were used to reveal the potential for trophic differentiation within Loricariidae, upon a diet that has been largely treated as homogenous. Detrital resources are heterogeneous on a fine scale, and determination of variation in detrital composition and quality is frequently dependent not on gross taxonomic identification of component species, but on its chemical composition and nutrient ratio (Frost et al., 2002, Cross et al., 2003, Moe et al., 2005). Stable isotope techniques for food-web analysis (reviewed by Fry and Sherr, 1984, Peterson and Fry, 1987, Thompson et al., 2005, Newsome et al., 2007) have greatly improved the description of the fate and food value of detritus in aquatic ecosystems (Roman and Tenore, 1984); however, studies inferring the structure of detritus- or algae-based food webs from isotope data have traditionally struggled with both the differentiation of basal resource components and the identification of a spectrum of discrete, consistent $\partial^{13}C$ and $\partial^{15}N$ basal resource values needed for accurate association with consumers (Hecky and Hesslein, 1995, Post, 2002, Hamilton et al., 2005).

Layman et al. (2008) proposed that consumer isotopic signatures could be used to compare trophic structure among communities in the absence of either finely partitioned basal resource data or a well-supported linkage model of trophic relationships within communities. They proposed the following 6 metrics that each quantify, or correct for, a different potential aspect of variation across food webs that might be separated by space, time, and/or taxonomic composition:

1) $\partial^{15}N$ range (NR): Measured as the distance between mean $\partial^{15}N$ values of the most $\partial^{15}N$-enriched and most $\partial^{15}N$-depleted member of the community. NR is treated as a measure of vertical structure within the community, and a potential indicator of the number of trophic levels present.
2) $\partial^{13}C$ range (CR): Measured as the distance between mean $\partial^{13}C$ values of the most $\partial^{13}C$-enriched and most $\partial^{13}C$-depleted member of the community. CR is treated as a measure of the diversity of a community's basal resources.
3) Total area (TA): Measured as the area of a convex polygon, of which each vertex is the mean $\partial^{15}N$ and $\partial^{13}C$ value of a species at the perimeter of the community in $\partial^{13}C$-$\partial^{15}N$ biplot space. TA is treated as a measure of the total amount of trophic niche space occupied by the community.

4) Mean distance to centroid (CD): Calculated as the mean Euclidean distance from the community centroid (mean) to the mean ∂^{15}N/∂^{13}C value of each species in the community. CD is treated primarily as a measure of trophic diversity within the community, and, to a lesser extent, the trophic distance among species within the community.
5) Mean nearest neighbor distance (NND): Calculated as the mean Euclidean distance between mean ∂^{13}C-∂^{15}N values of each species and the species to which it is closest in ∂^{13}C-∂^{15}N bi-plot space. NND is treated primarily as a measure of species packing within community trophic niche space and, to a lesser extent, trophic diversity within the community.
6) Standard deviation of nearest neighbor distance (SDNND): Calculated as the standard deviation of NND, and treated as a measure of the evenness of species packing in community trophic niche space.

The 6 Layman et al. (2008) metrics were critiqued by Hoeinghaus and Zueg (2008), who asserted that foodweb ecologists should persist in the struggle to identify and quantify patterns of isotopic variation across basal resources and that in most ecosystems, failing to carefully consider the effect of variation in the isotopic baseline on variation in consumers largely negates any inferences that can be made about foodweb structure. Layman and Post (2008), in a reply to Hoeinghaus and Zueg (2008), questioned the latter's generalization to most ecosystems. Layman and Post (2008) acknowledged that finely partitioned gut content data and a nuanced understanding of variation in the isotopic baseline are valuable; but, they state that in most systems the resource-based standardization methods proposed by Hoeinghaus and Zueg (2008; also Newsome et al.,

2007) are not possible because of the high diversity of basal resources. Layman and Post (2008) also concluded that one of the ways to resolve problems raised by Hoeinghaus and Zueg (2008) would be to include a covariate such as species richness.

I applied the community-wide metrics of Layman et al. (2008) to ∂^{13}C and ∂^{15}N data from 19 sympatric assemblages of mostly detritivorous Neotropical catfishes (Table 1), varying in richness of species (2–16), genera (1–11), tribes (2–6), subfamilies (1–3), and families (1-2). Isotope data from a total of 79 species of Loricariidae and 3 species of Astroblepidae (sister to Loricariidae) were examined. Localities of sampled assemblages were broadly distributed across northern South America, including 2 sites in the Essequibo River Basin (Guyana), three sites in the Orinoco River Basin (Venezuela), and 12 sites in the Amazon River Basin (Brazil, Guyana, Venezuela, and Peru; Fig. 1). South American rivers have historically been divided into 3 major limnological categories according to their water chemistry and underlying geology (Sioli, 1975, 1984). My study was restricted to two of these water types: clearwater rivers draining the geologically ancient Brazilian and Guiana Shields in central and northern South America, and whitewater rivers draining the geologically younger Andes Mountains in western South America. The third major type, blackwater rivers, which typically drain low lying areas of the shields or Amazon Basin, are highly acidic with little primary productivity (Jepsen and Winemiller, 2007), and possess a depauperate fauna of loricariid catfishes, were not examined in this study.

Loricariidae is a taxonomically highly diverse family, containing over 700 described species, or 20% of the approximately 3600 fish species currently described from Neotropical freshwaters (Reis et al., 2003). Popularly known as plecos in the aquarium trade, or suckermouth armored catfishes, loricariids are distinguished by having armored plating and a ventral oral disk. Throughout their native range of tropical Central and South America, loricariids have undergone a remarkable diversification of jaw, tooth, and oral disk morphologies (Fig. 2). Trophic ecological data are generally lacking for most loricariid species and, where available, are typically qualitative. A review of the taxonomic and ecological literature yields diet descriptions for 82 species (Chapter 1, Table 1). Most of these (39 species) are described primarily as detritivores (e.g. Saul, 1975, Kramer and Bryant, 1995, Vaz et al., 1999, Jepsen and Winemiller, 2002, Alvim and Peret, 2004, Melo et al., 2004, Ferreira, 2007). Other food items reported from various numbers of loricariid species include wood (19 spp.; Schaefer and Stewart, 1993, Armbruster, 2003, Nonagaki et al., 2003), algae (11 spp.; Zaret and Rand, 1971, Hood et al. 2005, Nonogaki et al., 2007, Jepsen and Winemiller, 2007), benthic macroinvertebrates (8 spp.; Mérona et al., 2008, Forsberg et al., 1993, Winemiller, 1990, Saul, 1975, Kramer and Bryant, 1995, Melo et al., 2004), mosses and plants (3 spp.; Saul, 1975, Delariva and Agostinho, 2001), fruits and seeds (3 spp.; Armbruster, 2002, 2004, Melo et al., 2004), and sponges (2 spp.; DeLariva and Agostinho, 2001). The consensus is that loricariid diets have remained largely restricted to basal resources, a set of trophic niches frequently associated with derived morphologies (Kramar and Bryant, 1995, Bellwood, 2003, Konow et al., 2008) and physiologies (Buddington et al., 1987, Choat and Clements, 1998). Numerous oral and jaw specializations described for Loricariidae are shared by their sister lineage, Astroblepidae, which has a geographic range restricted to high elevation hillstream habitats in the Andes. Together, the derived trophic morphologies shared only by Loricariidae and Astroblepidae support the distinctiveness of their ecological niche, and the assumption that any trophic competition they might face is greatest from other members of these same families.

Precise descriptions of trophic structure within diverse assemblages of basal consumers face numerous challenges. Detritivores and herbivores, for example, are characterized by having fast gut passage rates (Cummins, 1979, Horn, 1992), which limit the relevance of any given gut sample to a brief period prior to capture. Gut passage times measured for loricariids range from 40 minutes to four hours, through intestines that can be >10 times standard body length (Delariva and Agostinho, 2001, Hood et al., 2005, German, 2008). Most material ingested by detritivores, including substantial inorganic material, is not assimilated (Yossa and Araujo-Lima, 1998, Bowen et al., 2006), further limiting the relevance of any given gut content sample, and suggesting that large sample sizes would be needed for dietary studies to reveal consumer nutrition (Hyslop, 1980, Bowen, 1983). These problems are exacerbated when patterns are sought across a large geographic and taxonomic range of consumers in the Neotropics, where vertebrate taxonomies and that of their algal and microbial food resources are poorly resolved (Lundberg et al., 2000); and where food availability undergoes strong seasonal shifts (Lowe-McConnell, 1964, Winemiller, 1990). The dry season, when water levels are lowest, is the only time when many species can be collected; however, this is also when food resources are extremely limited, and when many species switch from preferred to low-quality, detrital foods and/or begin to starve (Lowe-McConnell, 1964, Prejs and Prejs, 1987, Winemiller, 1990). For these reasons, and for the purpose of quantifying trophic structure based on the energy or nutritive value of resources consumed, gut content data from loricariids collected in the dry season can be highly imprecise and potentially misleading.

Attempts to link specific detritivores to distinct subsets of detrital resources using ∂^{13}C signatures face similar challenges to the differentiation of basal resources (Benedito-Cecilio et al., 2000, Leite et al., 2002, Jepsen and Winemiller, 2007). In addition, ∂^{13}C signatures of detritus can vary seasonally (McCutchan and Lewis, 2001) and variations in the detrital qualities that are most biologically significant to consumers may not correspond with variation in their ∂^{13}C signatures. These challenges largely preclude robust linkage of detritivorous consumers to subsets of the detrital resource base as recommended by Hoeinghaus and Zueg (2008), yet isotopes remain a powerful tool for investigation of trophic structure across detritivore assemblages because of their unique capacity to quantify time-integrated patterns of resource assimilation (Perga and Gerdeaux, 2005). The 6 metrics proposed by Layman et al. (2008) offer a means by which variation in ∂^{13}C and ∂^{15}N signatures of sympatric assemblages of detritivores like the Loricariidae may be analyzed and compared across broad limnological, geographical, temporal, and taxonomic ranges.

3.2 METHODS

Nineteen geographically, hydrologically, and taxonomically distinct loricariid assemblages (Table 1) were sampled during expeditions to Venezuela (March 2004, March 2005), Guyana (October 2005), Peru (August 2006), and Brazil (October 2007; Fig. 1). Specimens were collected by hand or with seines, gillnets, castnets, or a backpack electroshocker. Small (<1 g) samples of postdorsal-fin epaxial or postanal-fin hypaxial muscle were excised from specimens in the field and preserved in salt according to Arrington and Winemiller (2002). Most whole specimens from which tissues were removed were fixed in 10% formalin and have been deposited in museums in South America (Brazil: MZUSP; Guyana: UG; Peru: MUSM; Venezuela: MCNG) and the United States (ANSP, AUM). Many loricariid species collected during these expeditions were undescribed, and have either recently been described (e.g. Lujan et al., 2009), or are being described. As a means of differentiation, general descriptors are provided for those species whose taxonomy is uncertain (e.g. *Ancistrus* sp. 'wormline'). Generic assignments within Loricariidae are also often poorly resolved (e.g. Lujan et al., 2009), and/or poorly correlated with phylogeny (e.g. Armbruster, 2008). Tribes were therefore used as a proxy for higher phylogenetic relations among species, following the taxonomies of Armbruster (2004) for subfamily Hypostominae, and Rapp Py-Daniel (1997) for subfamily Loricariinae.

Salt-preserved tissue samples were rinsed, soaked, dried, and ground according to the methods of Arrington and Winemiller (2002). Subsamples of each sample were weighed to 10^{-5}g, pressed into Ultra-Pure tin capsules (Costech), and sent for analysis of stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) to the Analytical Chemistry Laboratory, Institute of Ecology, University of Georgia, Athens, USA. Encapsulated samples were dry-combusted (micro Dumas technique) with a Carlo Erba CHN elemental analyzer. Purified gases (CO_2 and N_2) were introduced into a Finnigan Delta C mass spectrometer, and the isotopic composition was quantified relative to a standard reference material. Standards were carbon in the PeeDee Belemnite and molecular nitrogen gas in the air. Results were reported as parts per mille (‰) differences from the corresponding standard:

$$\partial X = [(R_{sample}/R_{standard}) - 1] \times 10^3$$

where $R = {}^{15}N/{}^{14}N$ or ${}^{13}C/{}^{12}C$.

Assemblages were defined as all members of the Loricariidae plus Astroblepidae (the sister family to Loricariidae; only present in three Andean assemblages) sampled during the same expedition and from the same stream or river channel. Samples from multiple localities in the same river channel were combined, except in the upper Orinoco River main channel in southern Venezuela, and in the Siasme River in northern Peru. Sampling localities in the upper Orinoco main channel were divided into two separate reaches, respectively dowstream (Orinoco-1) and upstream (Orinoco-2) of the mouth of the Ventuari River, a major tributary of the upper Orinoco known to have relatively enriched particulate $\partial^{13}C$ values relative to the Orinoco River (Tan and Edmund, 1993). Loricariid/astroblepid assemblages in the Siasme River were also separated into respective headwater (Siasme-upr) and lower reaches (Siasme-lwr) because sampling localities were taxonomically and limnologically distinct and separated by several kilometers.

$\partial^{13}C$ and $\partial^{15}N$ signatures for all specimens (if >1) of a given species in a given assemblage were pooled, and mean $\partial^{13}C$ and $\partial^{15}N$ values for each species were used to compute metrics described by Layman et al. (2008). Instead of calculating total area (TA, metric 3) according to Cornwall et al. (2006), areas were measured empirically from scatterplots with standardized X and Y-axes. In addition to determining the metrics of Layman et al. (2008) for species in each assemblage, mean Euclidean distances to centroid (CD) and mean nearest neighbor distances (NND) were computed for the taxonomic rank of tribe (trCD and trNND, respectively). To calculate trCD, assemblage centroid remained defined as the species mean, and Euclidean distances from this centroid to each tribe mean were determined. To calculate trNND, mean Euclidean distances from each species to its nearest neighbor within its own tribe were calculated. Differences between tribe and species values were interpreted as a measure of how phylogenetic rank might influence trophic diversity within loricariid assemblages (cf. niche conservatism; Peterson et al., 1999, Wiens and Graham, 2005).

3.3 RESULTS

Relationships between loricariid/astroblepid assemblage species richness and the 6 metrics of trophic structure proposed by Layman et al. (2008) are presented in Table 1 and Fig. 3. Metrics 1-3 (NR, CR, and TA; Fig. 3A-C) showed a significant ($p<0.001$) positive correlation with richness. As richness increased, trophic niche space of the entire assemblage increased both vertically, indicating trophic level expansion, and horizontally, indicating basal resource expansion. Correlation between richness and centroid distance was also positive (Fig. 3D), albeit less significantly ($p=0.09$), suggesting that as species are added to an assemblage, they occupy trophic positions further from the most common, shared resource. Correlations between richness and NND and SDNND (Fig. 3E, F) were both negative, although only significantly so ($p=0.05$) in the first case. These patterns suggest that niche packing is occurring, and that as species are added to the assemblage, basal resources are increasingly shared among multiple species.

Plots showing relationships between species richness and CD, NND, and SDNND (Fig. 3D-F) show considerable variation among species-poor assemblages that appear to be inversely related to richness. Correlation between richness and variation from predicted relationships was examined explicitly by regressing absolute values of the residuals of CD and NND against richness (Fig. 4A, B). Significance of these relationships (CD: p=0.06; NND: p=0.007) suggest that rules potentially governing the trophic structure of loricariid assemblages become increasingly strict as richness increases, and that trophic structure within species-poor assemblages is less predictable.

Relationships between assemblage tribe richness and trCD and trNND likewise showed considerable diminution in variability with increasing species richness (Fig. 5A, B), but otherwise showed no significant correlation (p>0.60). When compared with species metric NND (Fig. 3E), tribe NND (Fig. 5B) was higher in most assemblages (Fig. 6), suggesting that higher level taxa (clades) are more divergent from one another than lower level taxa.

No divergent patterns were observed between whitewater and clearwater limnological categories in any of the analyses.

3.4 DISCUSSION

Ricklefs and Travis (1980) first compared communities using metrics similar to those proposed by Layman et al. (2008; e.g. total niche volume, NND, SDNND), except the former applied their metrics to ordinations of 8 ecomorphological correlates of niche space, rather than to direct descriptions of the realized trophic niche (as provided herein by isotopes; Newsome et al., 2007). Regardless, Ricklefs and Travis (1980) observed similar relationships between richness and niche structure as that observed among loricariid assemblages in my study. They found that across 11 passerine bird assemblages in temperate-zone scrub habitats of North and South America, total assemblage hypervolume increased, and NND and SDNND decreased in direct proportion to number of species. They interpreted these observations as providing no support for the hypothesis that density or regularity of species spacing are caused by species interactions (i.e. competition).

Ricklefs and Travis (1980) remained confident that species are added to communities in a decidedly non-random manner and they attributed the lack of support for interspecific interactions provided by their data to two sources of sampling error: (1) the problem of low sample sizes when data from each whole community contribute only a single data point, and (2) artifacts of treating all members within a given spatially defined habitat as equivalent members of the community. In communities of highly mobile species like birds, the species encountered in any given habitat likely vary in the degree to which they are optimized for the specific habitat being sampled and, therefore, the degree to which they regularly interact with other species in that habitat. My study at least partially corrects for these potential sources of error in the Ricklefs and Travis (1980) study by increasing overall sample size from 11 to 19 communities, and by examining taxa that are relatively non-vagile (e.g. Power, 1984). The presence of any given loricariid species in one of the assemblages defined herein is an indicator that it is a permanent member of the assemblage, and regularly interacts with other sampled species.

Unfortunately, divergent geochemical and watershed characteristics of the different habitats sampled in this study contributed new potential sources of variability that

Ricklefs and Travis (1980) were able to minimize by restricting their study to similar (scrub) habitats. Sioli's (1964, 1967, 1975) classic typology of South American rivers as black-, clear-, or whitewater according to watershed and geochemical characteristics has provided a common context for comparative examination of trophic dynamics in Neotropical rivers (e.g. Fisher, 1979, Bayley, 1981, Rodríguez and Lewis, 1990, Henderson and Crampton, 1997, Putz and Junk, 1997, Saint-Paul et al., 2000, Melack and Forsberg, 2001, Jepsen and Winemiller, 2007). Whitewater rivers are highly turbid, have relatively high conductance and alkalinity, slight acidity, and carry high suspended and dissolved loads. In contrast, both black- and clearwaters have very low turbidity and little to no suspended or dissolved solids. Blackwaters are distinguished from clear by having high levels of dissolved organic matter, little to no alkalinity, and high acidity. These limnological characteristics are closely linked to each river's watershed, with whitewater rivers draining the geologically younger and rapidly eroding Andean uplands of western South America; and black- and clearwater rivers draining the highly weathered and geologically ancient shield areas to the north (Guiana Shield) and south (Brazilian Shield) of the Amazon Basin. High acidity, alkalinity and DOM of blackwater rivers is due to their origination in poorly drained, low lying shield areas that promote extended residence times and the leaching of humic acids. In contrast, most clearwater rivers originate in well-forested shield uplands. Concentrations of major ions and nutrients in both black- and clearwater rivers draining shield uplands fall near or even below those expected in precipitation, indicating minimal contributions from geology and significant nutrient sequestration by forests (Lewis and Weibezahn, 1981).

Most studies comparing trophic structure within these water types have focused on blackwater versus whitewater river channels or floodplains since these are the dominant habitat types in the central Amazon Basin. Whitewater habitats have generally been demonstrated to be more productive, but some studies (e.g. Henderson and Crampton, 1997) have observed either consistently greater fish abundance in blackwater habitats, or seasonal shifts with respect to which is more productive. In one of the few studies to examine differences in trophic structure across all three water types using stable isotopes, Jepsen and Winemiller (2002) concluded that food chain length was higher in nutrient-poor rivers than in more productive whitewater rivers. These results are questionable however, because their methods for inferring trophic position and food chain length assumed a ∂^{15}N enrichment factor (2.8‰) nearly half the rate (5.08‰) recently determined experimentally for the loricariid *Pterygoplichthys disjunctivus* (German, 2008). Indeed, the avoidance of potentially inter- and intraspecifically variable enrichment factors is one advantage of using total ∂^{15}N range (NR) as a measure of vertical structure rather than attempting to define distances from a standardized baseline.

Regardless, these divergent interpretations of whitewater versus black- or clearwater systems with respect to productivity and resource diversity make the spectrum of white- and clearwater habitats sampled in this study a potentially confounding variable. Niche expansion in response to increases in species richness (Fig. 3A-C) could be a response to interspecific competition (i.e. niche diversification), or it could simply reflect a bottom-up response to habitats (whitewater or clearwater) that contain more resources. A prediction consistent with the latter hypothesis is that assemblages would assort to trophic space above or below the regression line according to their limnology. If we were to assume, for example, that whitewater habitats are more productive, and feature a broader diversity of resources, and that an increase in resource diversity or abundance is the true driver of observed relationships, then we would predict that at any given species richness, whitewater assemblages would occupy greater niche space than clearwater habitats. Instead of this pattern (or the opposite pattern in which clearwater habitats are greater than predicted), assemblages appear to be evenly distributed with respect to the regression line in all metrics of trophic niche breadth (Fig. 3A-C).

Potential increases in basal resource diversity could also be inferred from the spectrum of stream orders sampled in this study. All of the sampled regions (Fig. 1) were in uplands or piedmont zones where stream order is loosely, and inversely correlated with frequency of disturbance and degree of scour. Patrick (1964), for example, surveyed the macroinvertebrate fauna of upland stream habitats in Peru and noted the almost complete absence there of gastropods and trichopteran and plecopteran larvae. One reason she hypothesized for this was that high suspended and bed loads of these Andean systems scoured the bottom too intensely to allow persistence of these elements of the macroinvertebrate fauna. In comparison, large river habitats are relatively stable and feature of diversity of both autochthonous primary production and allochthonous detrital resources (e.g. Putz and Junk, 1997, Roelke et al., 2006). An increase in resource diversity with increase in stream order is a more difficult alternative hypothesis to attempt to falsify with the given data set. My study concentrated on regions within the range of Loricariidae known to exhibit relatively high levels of species richness, but future studies should contrast the results reported herein with data from habitats that are relatively depauperate in loricariid diversity.

Even if increases in resource diversity and abundance across the sampled taxa are playing a role in the observed expansion of niche space, contemporaneous decreases in NND (Fig. 3E) suggest that resources are not expanding at quite the same rate as species are being added to the assemblage, and that individual trophic niches are becoming increasingly packed. This suggests that loricariids in species rich assemblages may be beginning to fully occupy the fundamental loricariid trophic niche, and that limited opportunities exist for loricariids to expand beyond this fundamental niche. Likewise, decreases in variation from predicted relationships of CD and NND to species richness (Fig. 4) indicate that with increasing species richness, assemblages approach a limit to the amount of variability that can be tolerated; that is, the realized niche of loricariids is expanding to fully occupy their fundamental niche.

Decreases in variability and convergence upon predicted trophic structure observed at the species level are mirrored at the level of tribe for both CD and NND (Fig. 5), despite relatively poor correspondence between species richness and tribe richness across the sampled assemblages (Table 1). Although not significant ($p>0.6$), possibly due to considerable variation among tribe poor assemblages, the flat relationship between tribe richness and inter-tribe spacing as measured by trCD and trNND (Fig. 5), in conjunction with generally greater inter-tribe spacing than inter-species spacing (Fig. 6), indicates that taxa at higher taxonomic ranks are more divergent from each other than species are from each other regardless of rank. This is consistent with niche conservation theory, which generally supports the conclusion that extent of niche divergence is correlative with taxonomic rank (Peterson et al., 1999, Wiens and Graham, 2005). That is, families are more divergent from each other than tribes, which are more divergent from each other than species.

My study has presented the first data suggesting the existence of rules governing the trophic structure of loricariid assemblages. When viewed in light of the highly successful models of river function (e.g. river continuum concept, Vannote et al., 1980) that grew out of a basic understanding of the diversity of functional roles of temperate detritivores, the importance of a more detailed understanding of trophic diversity in Loricariidae is magnified. Traditional stream ecological paradigms must be adjusted to the scale of tropical river systems, whose scale and trophic and taxonomic diveristy is orders of magnitude larger than temperate zone ecosystems. As an example of scale and trophic diversity from among detritivores, two species of macroinvertebrate shredders (the calamoceratid caddisfly *Heteroplectron californicum* and the elmid *Lara avara*; Anderson et al., 1978, Anderson and Sedell, 1979) are known to specialize on large-scale detrital resources, like tree boles, in north temperate rivers. Among Loricariidae, two different lineages (*Panaque* and the *Hypostomus cochliodon* group) have converged upon a wood gouging trophic morphology featuring teeth shaped like carpentry instruments (Fig. 2B). And in the most species rich of the assemblages sampled in this study (Marañon, Fig. 14), five species of these wood-eating loricariids coexist. ∂^{13}C and ∂^{15}N signatures and unpublished jaw morphological data from these wood-eaters suggest that even across such challenging detrital resources, loricariids have diversified.

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Table 1. 19 loricariid assemblages sampled in this study, their taxonomic diversity, and results of community-wide stable isotope analyses proposed by Layman et al. (2008).

	N species	N tribes	NR	CR	TA	CD	NND	SDNND	trCD	trNND
Shaapan	2	2	0.5	0.9	0.0	0.5	1.0	0.0	0.5	1.0
Huancabamba	3	2	1.0	4.7	0.8	2.4	1.8	2.2	1.3	4.4
Peixoto	3	2	2.4	1.3	0.1	1.2	1.0	1.5	1.4	0.1
Siasme-lwr	3	2	1.8	3.8	0.8	1.7	1.9	0.6	1.7	1.6
Siasme-upr	3	2	0.8	0.6	0.0	0.5	0.5	0.2	0.3	0.7
Almendro	5	4	2.0	5.3	3.3	1.5	1.4	1.4	1.7	1.1
Bununi	5	5	0.8	2.6	1.0	0.9	0.6	0.5	0.8	0.6
Utcubamba	5	3	1.4	3.9	2.8	1.8	1.3	1.0	0.9	2.1
Takutu	6	3	3.3	3.2	7.5	1.8	1.4	0.8	1.0	1.9
Casiquiare	7	3	3.6	2.1	5.5	1.4	1.0	0.9	1.6	0.5
Essequibo	7	5	3.0	4.8	7.1	1.6	1.0	0.8	1.5	1.3
Nieva	7	4	1.6	4.0	1.3	1.6	0.7	0.5	1.1	1.7
Jamanxim	11	3	2.7	4.3	4.2	1.2	0.6	0.4	0.6	1.2
Orinoco-1	11	2	2.1	4.6	3.8	1.0	0.6	0.5	1.5	0.5
Orinoco-2	11	3	3.1	6.0	9.4	1.7	1.0	1.0	2.4	1.0
Rupununi	12	4	3.6	6.8	14.9	1.8	0.9	0.6	1.3	2.1
Curuá	14	4	4.0	5.1	12.2	1.9	0.7	0.5	0.6	2.2
Ventuari	14	3	3.6	5.8	12.1	1.7	0.9	0.6	1.2	0.9
Marañon	16	6	3.0	5.9	10.9	1.6	0.8	0.7	1.0	1.6

Figure 1. Drainage map of northern South America with regions sampled in this study marked by dotted ovals. Region 1 (Venezuela) included the Casiquiare Assemblage (7 spp.), the Orinoco-1 Assemblage (11 spp.), the Orinoco-2 Assemblage (11 spp.), and the Ventuari Assemblage (14 spp.). Region 2 (Guyana) included the Bununi Assemblage (5 spp.), Rupununi Assemblage (12 spp.), and the Takutu Assemblage (6 spp.). Region 3 (Peru) included the Almendro Assemblage (5 spp.), the Huancabamba Assemblage (3 spp.), the Marañon Assemblage (16 spp.), the Nieva Assemblage (7 spp.), the Siasme-lwr Assemblage (3 spp.), the Siasme-upr Assemblage (3 spp.), and the Utcubamba Assemblage (5 spp.). Region 4 (Brazil) included the Peixoto Assemblage (3 spp.), the Jamanxim Assemblage (11 spp.), and the Curuá Assemblage (14 spp.).

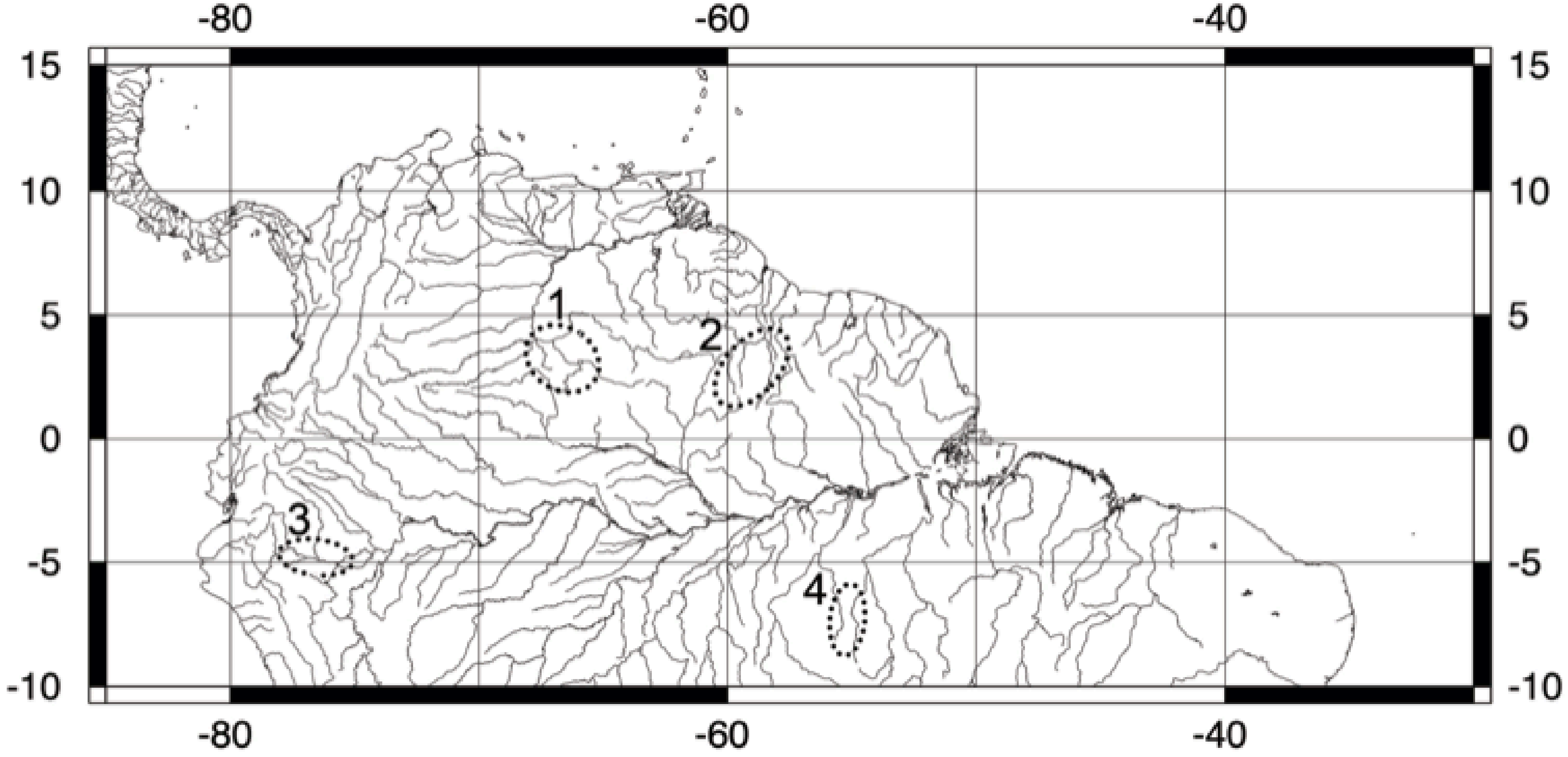


Figure 2. Representative diversity of loricariid upper and lower jaw morphologies: A. *Leporacanthicus*, B. *Panaque*, C. *Chaetostoma*.

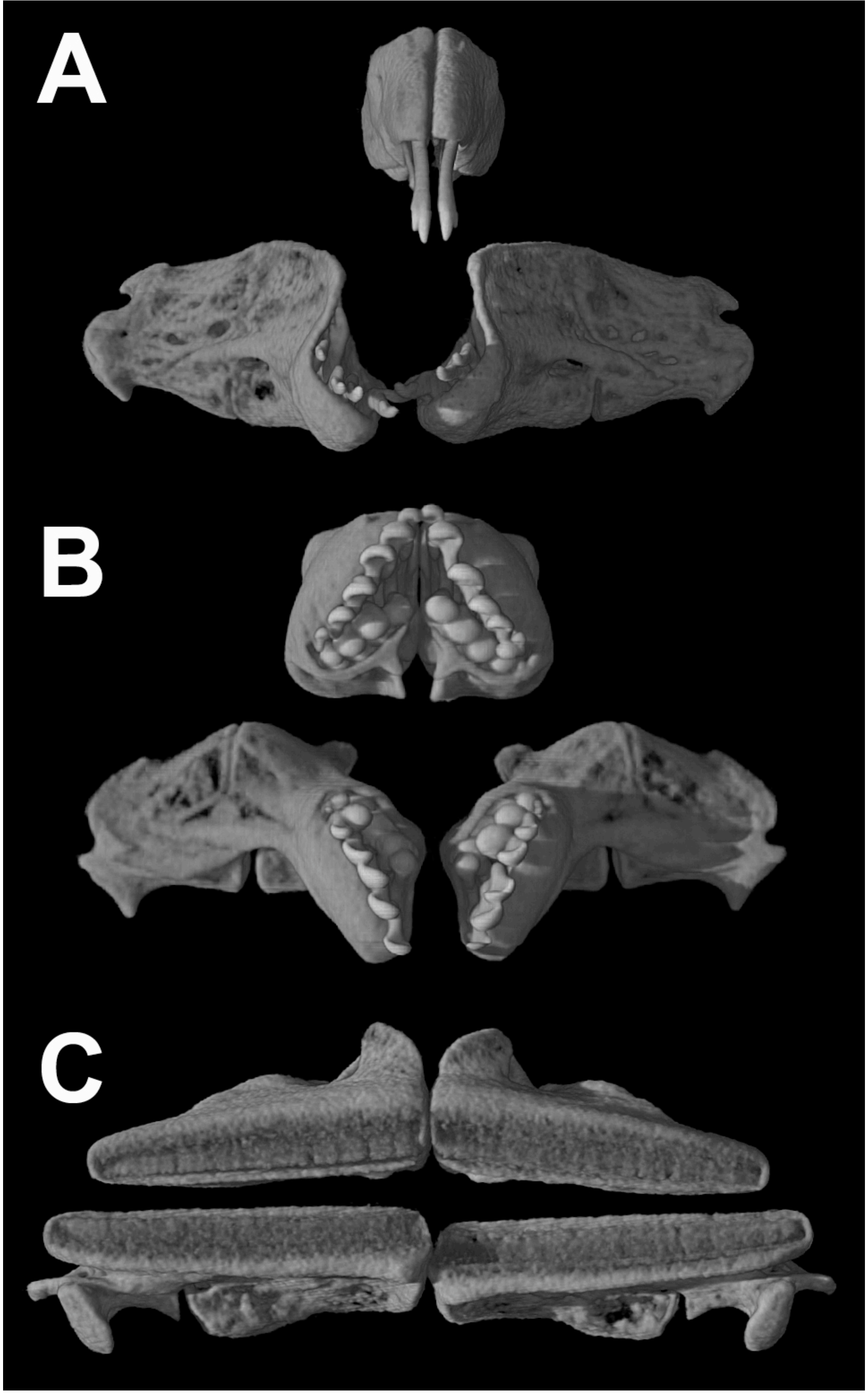


Figure 3. Relationships between loricariid assemblage species richness and six metrics of trophic structure proposed by Layman et al. (2008; see *Introduction*): (A) NR, (B) CR, and (C) TA are indicators of whole assemblage trophic niche breadth, whereas (D) CD, (E) NND, and (F) SDNND are indicators of species niche breadth and spacing within each assemblage. Squares represent clearwater shield habitats and circles represent whitewater Andean habitats.

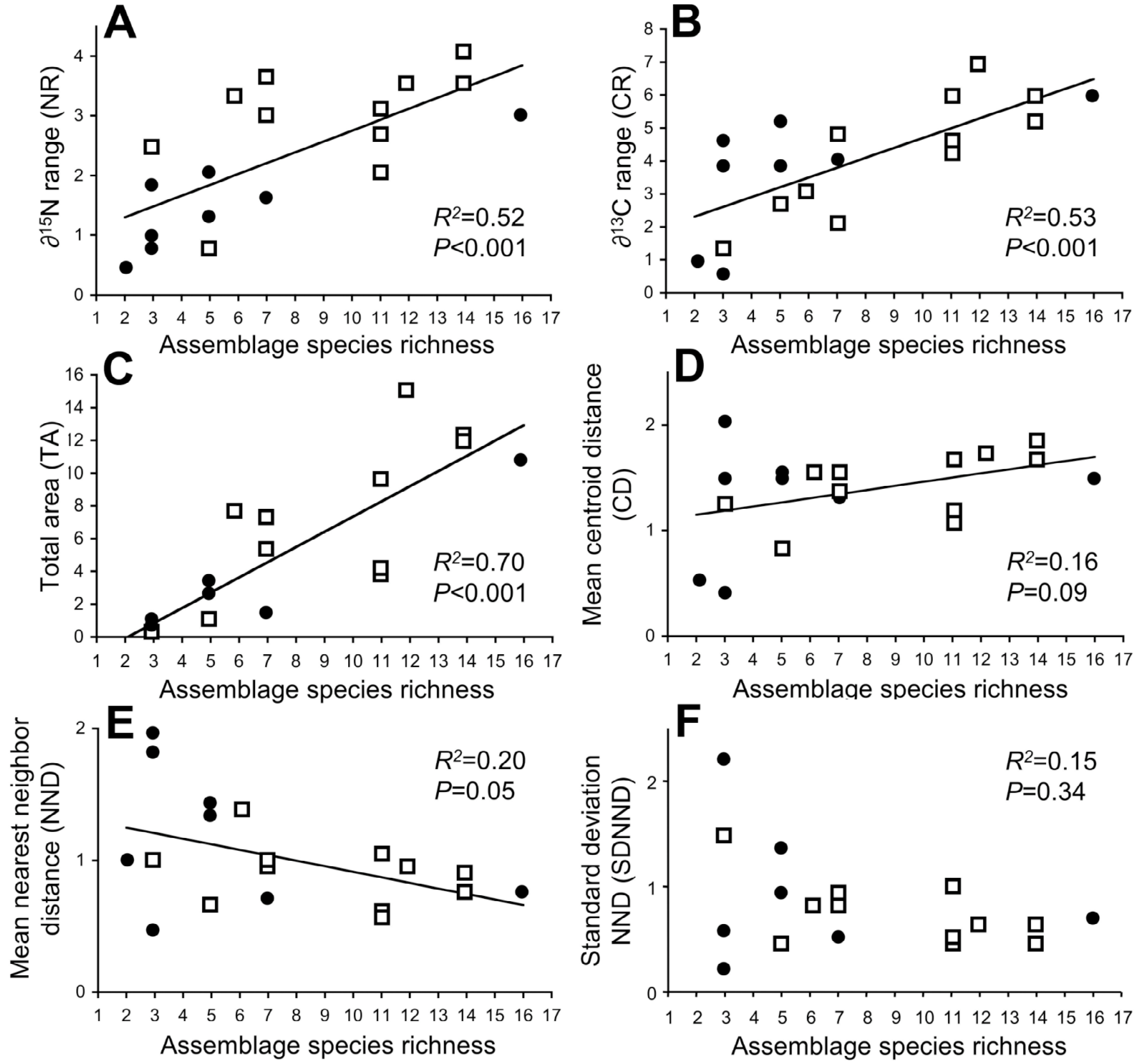


Figure 4. Relationships between loricariid assemblage species richness and the absolute values of (A) CD and (B) NND residuals. Squares represent clearwater shield habitats and circles represent whitewater Andean habitats.

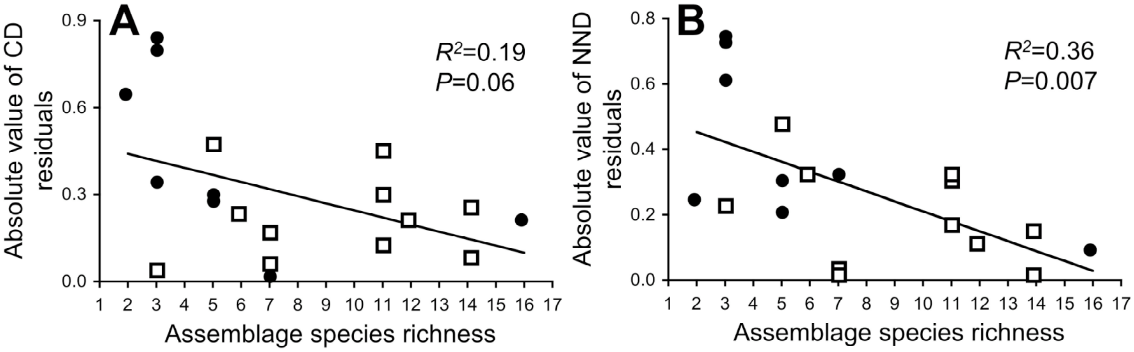


Figure 5. Relationships between loricariid assemblage tribe richness and (A) CD calculated as the mean distance from the species centroid to each tribe mean (trCD); and (B) NND calculated as the mean distance from each species to its nearest neighbor within its own tribe (trNND). Squares represent clearwater shield habitats and circles represent whitewater Andean habitats.

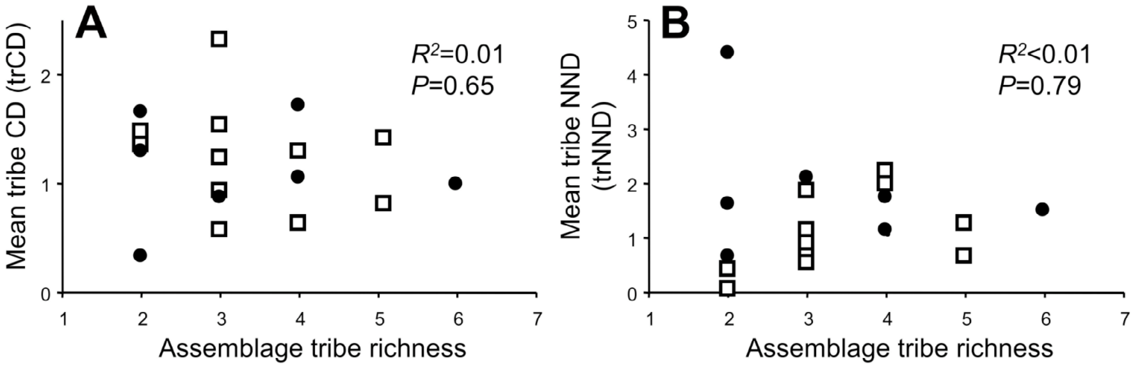


Figure 6. Comparison of species versus tribe NND for each assemblage sampled in this study. Assemblages in ascending order of species richness from left to right.

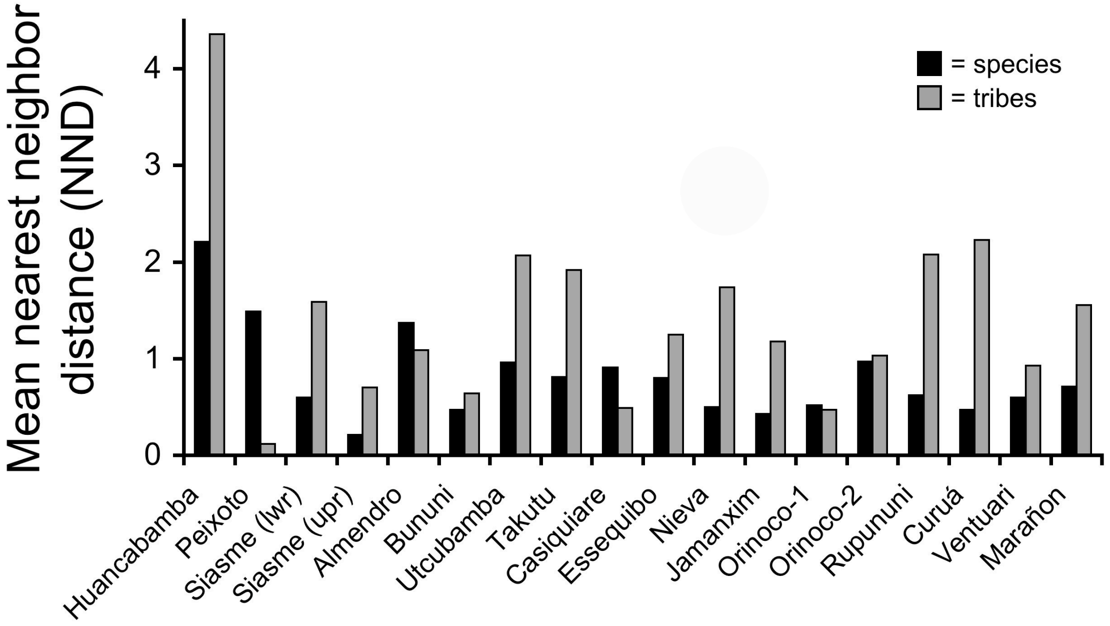


Figure 7. ∂^{15}N and ∂^{13}C relationships of loricariid plus astroblepid consumers in (A) Shaapan creek, Marañon (Amazon) drainage, northern Peru; (B) Peixoto river, Tapajós (Amazon) drainage, Brazil; (C) upper Siasme creek, Marañon (Amazon) drainage, northern Peru; and (D) Bununi creek, Rupununi (Essequibo) drainage, Guyana. Sample sizes in parentheses.

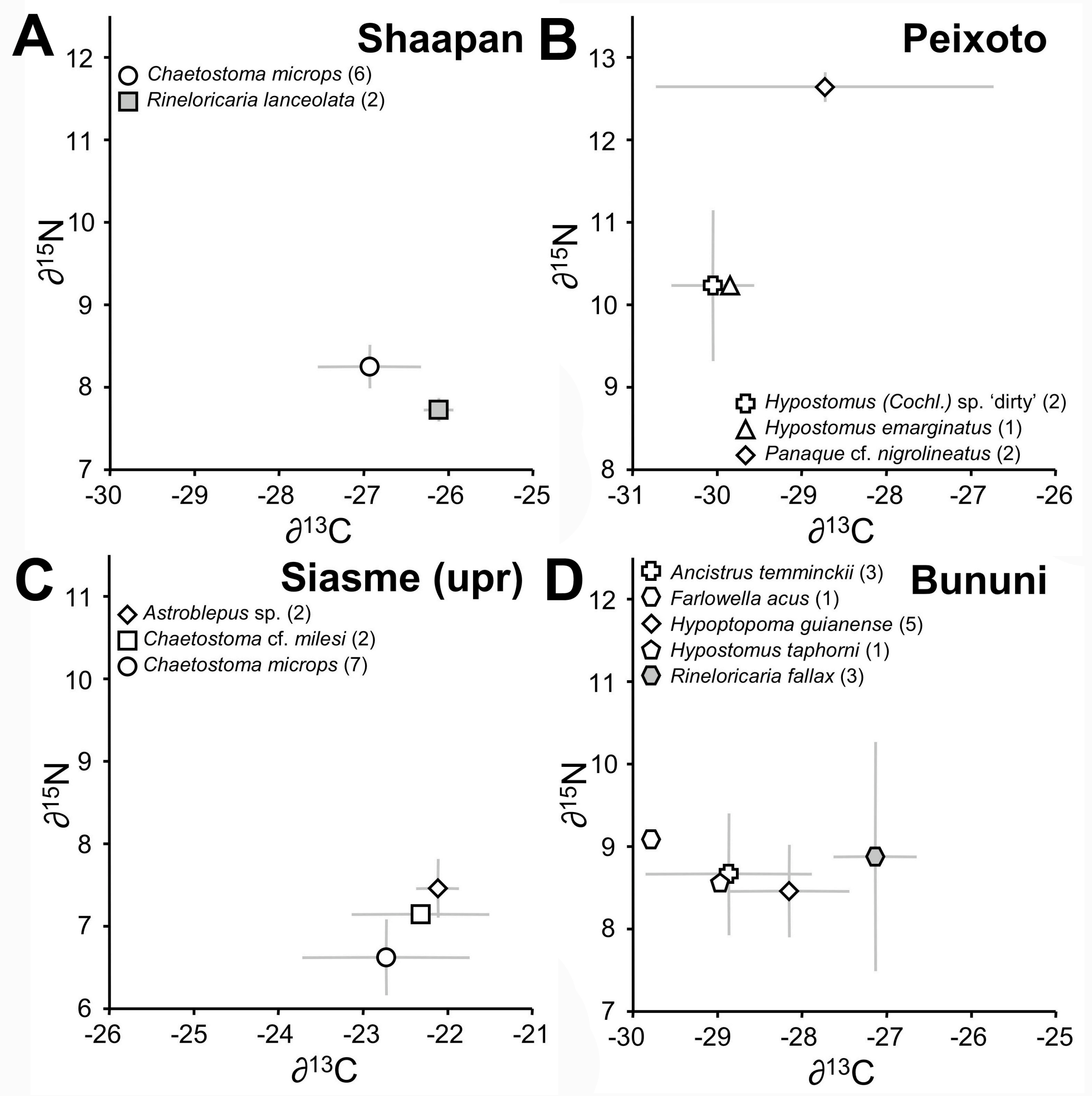


Figure 8. ∂^{15}N and ∂^{13}C relationships of loricariid consumers in (A) the Utcubamba river, Marañon (Amazon) drainage, northern Peru; (B) Casiquiare canal, Negro (Amazon) drainage, southern Venezuela; and (C) Takutu river, Branco (Amazon) drainage, Guyana. Sample sizes in parentheses.

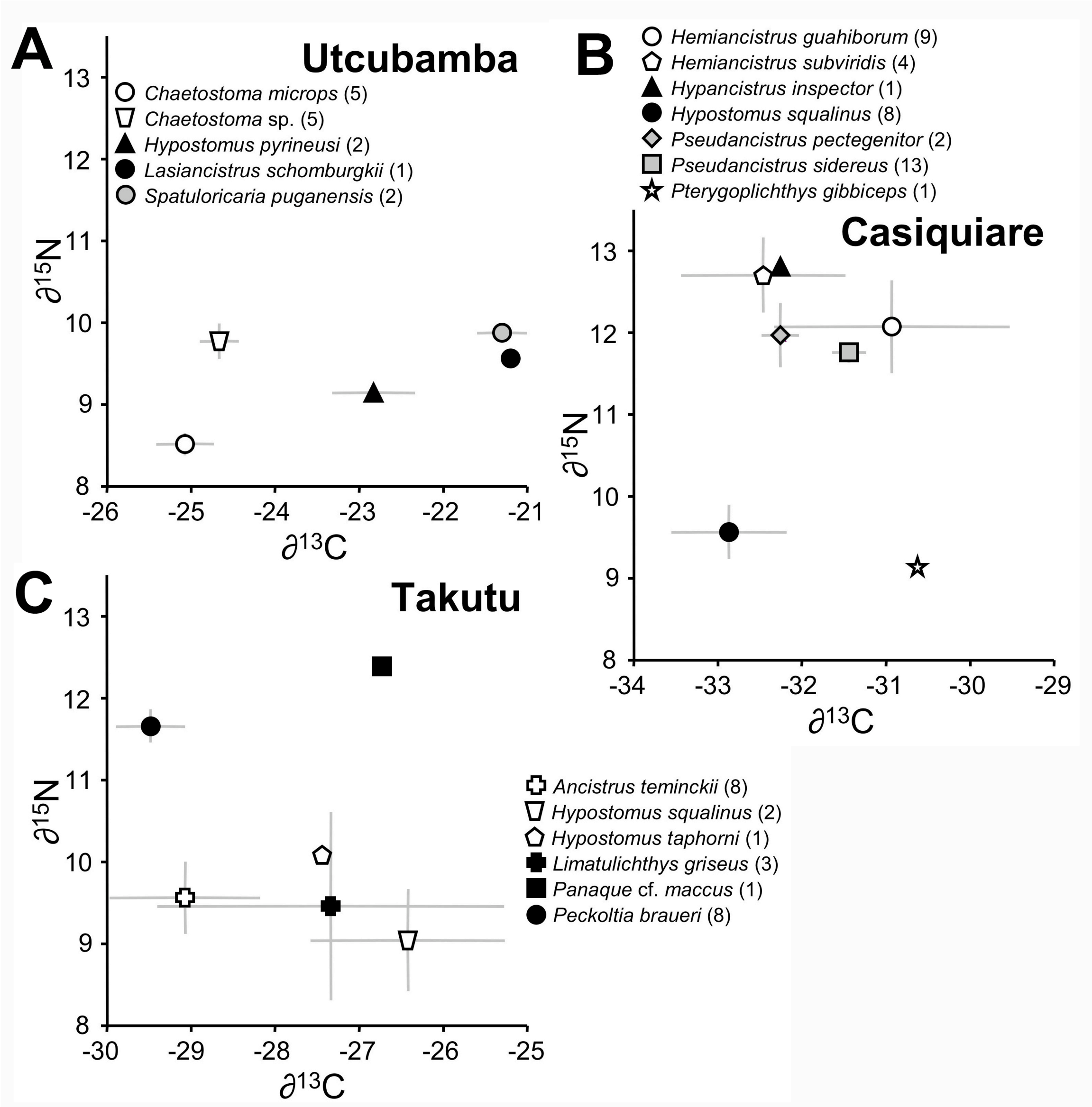


Figure 9. ∂^{15}N and ∂^{13}C relationships of loricariid plus astroblepid consumers in (A) the Huancabamba river, and (B) lower Siasme creek, both Marañon (Amazon) drainages in northern Peru. Sample sizes in parentheses.

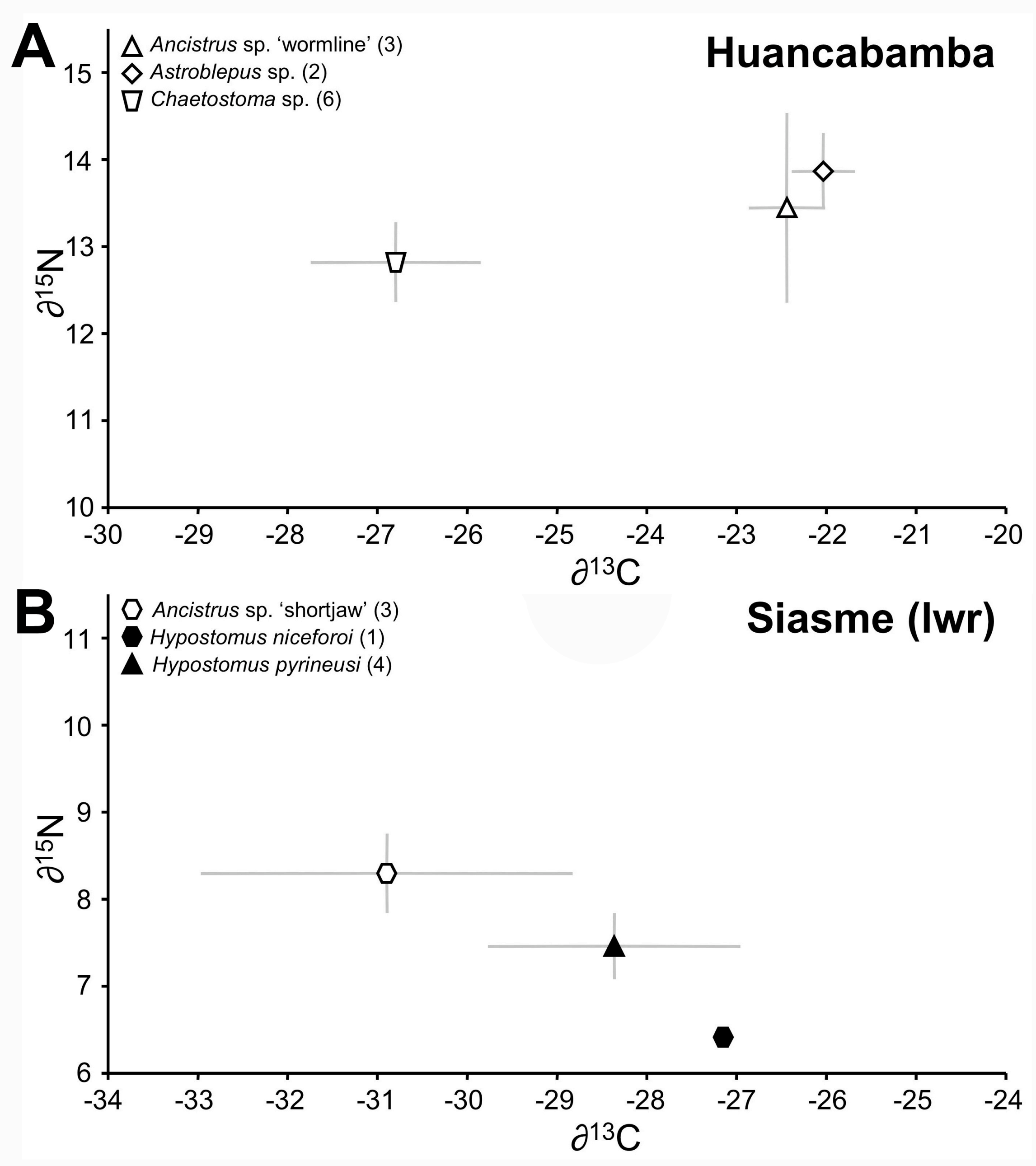


Figure 10. ∂^{15}N and ∂^{13}C relationships of loricariid plus astroblepid consumers in (A) Almendro creek, and (B) the Nieva river, both Marañon (Amazon) drainages in northern Peru. Sample sizes in parentheses.

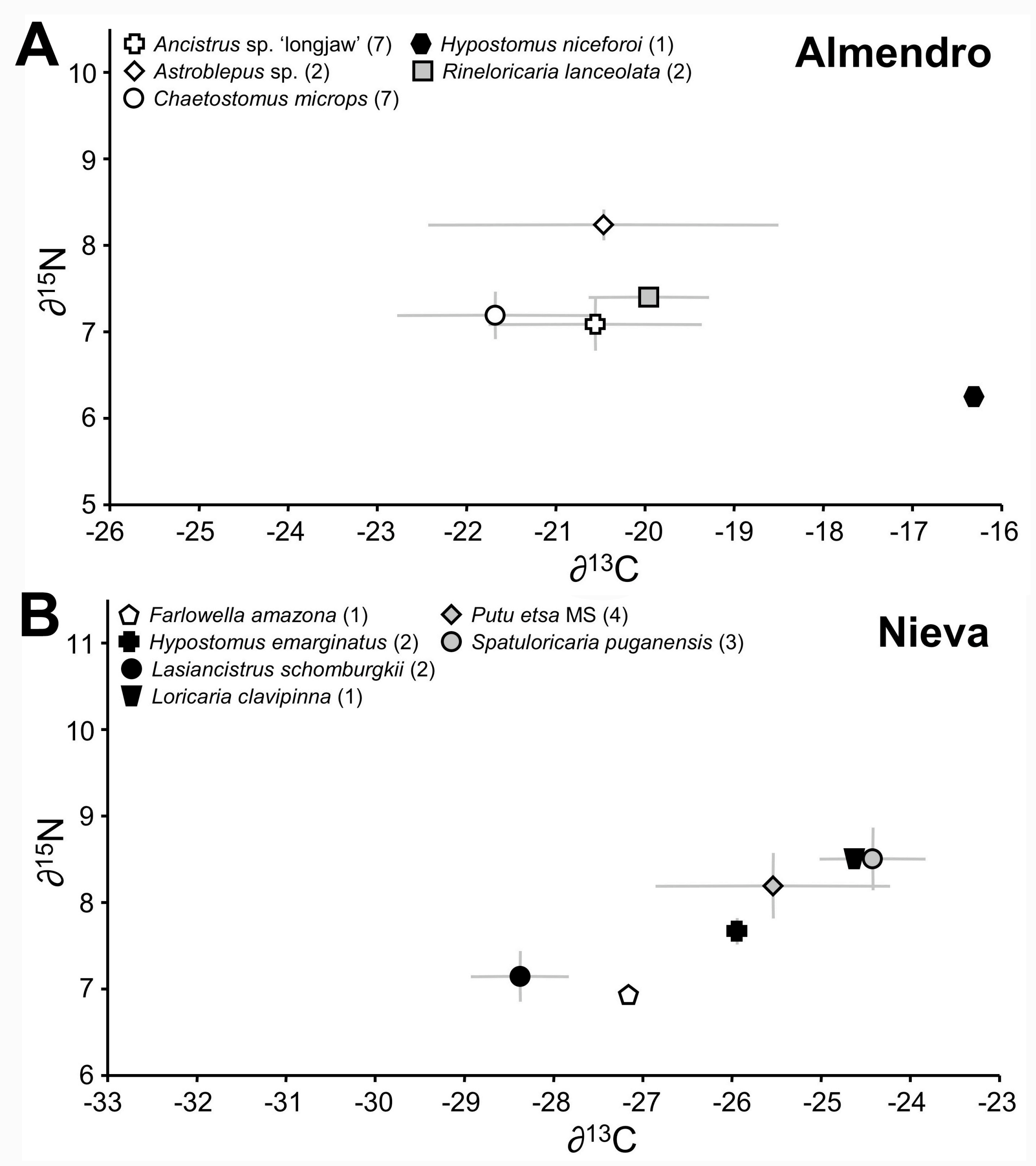


Figure 11. ∂^{15}N and ∂^{13}C relationships of loricariid consumers in the (A) Essequibo river, Guyana, and (B) the Jamanxim river, Tapajos (Amazon) drainage, Brazil. Sample sizes in parentheses.

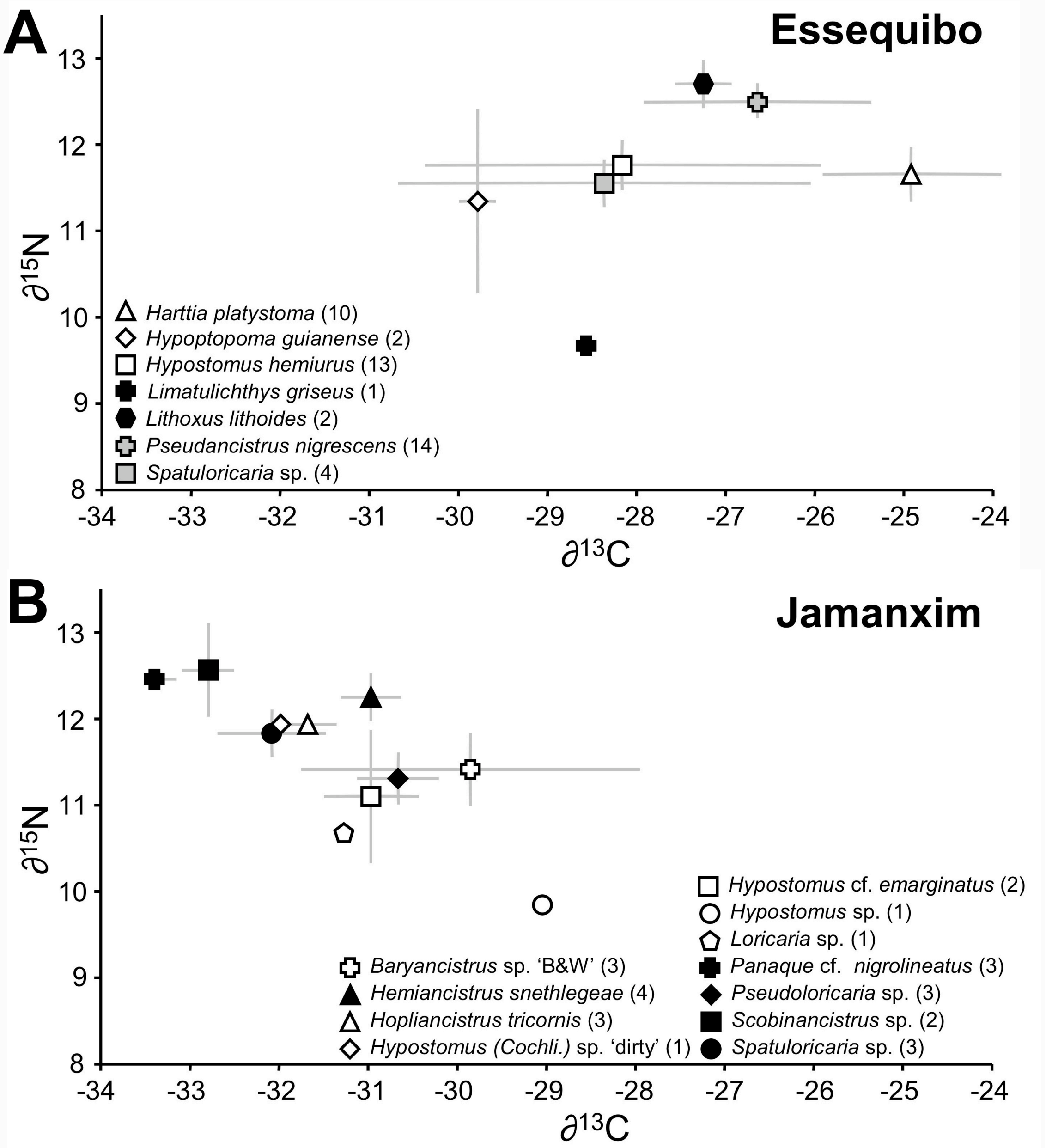


Figure 12. ∂^{15}N and ∂^{13}C relationships of loricariid consumers in the Orinoco river main channel, (A) below and (B) above the mouth of the Ventuari river. Sample sizes in parentheses.

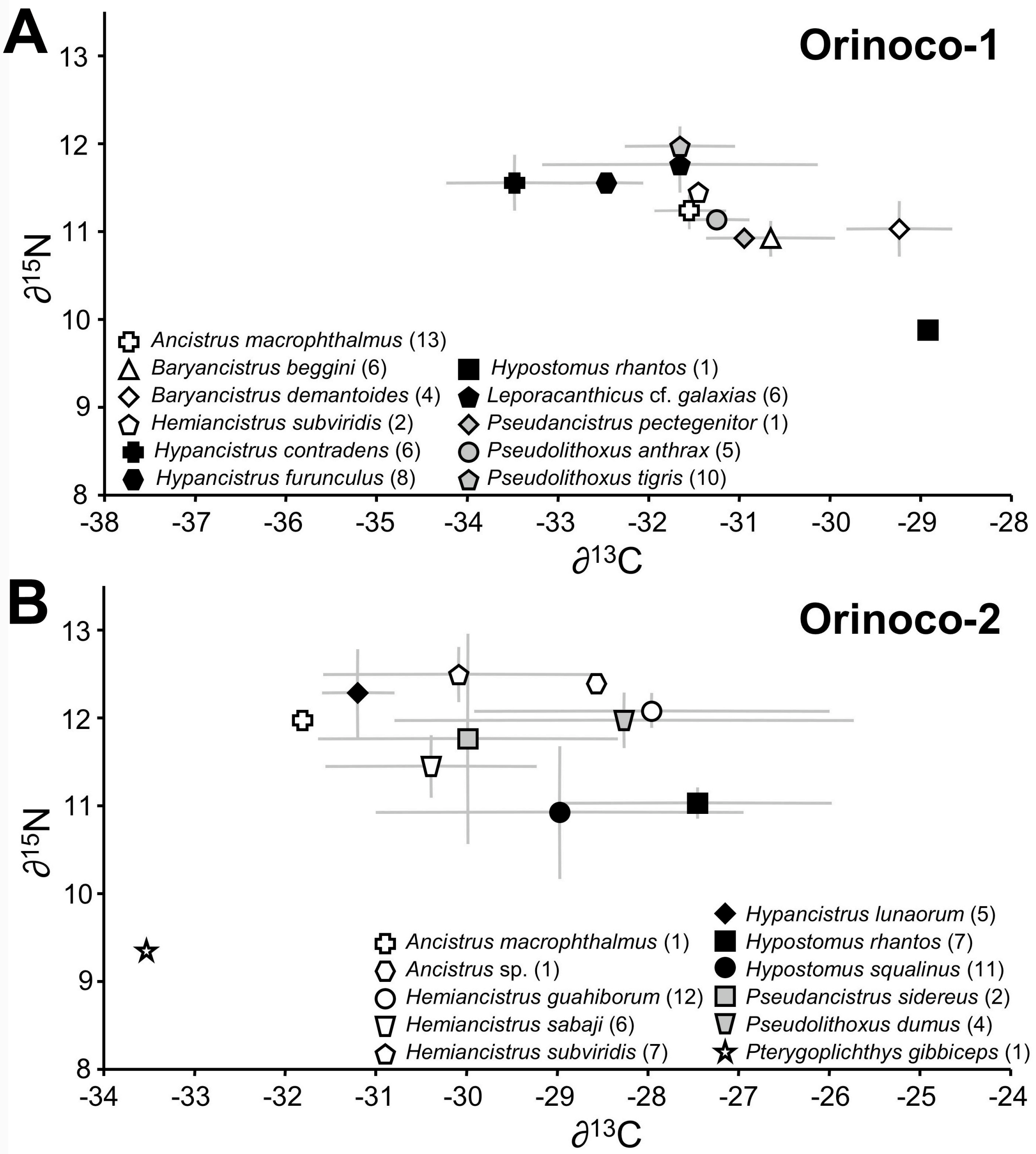


Figure 13. ∂^{15}N and ∂^{13}C relationships of loricariid consumers in (A) the Rupununi river, Essequibo drainage, Guyana; and (B) the Curuá river, Xingu drainage, Brazil. Sample sizes in parentheses.

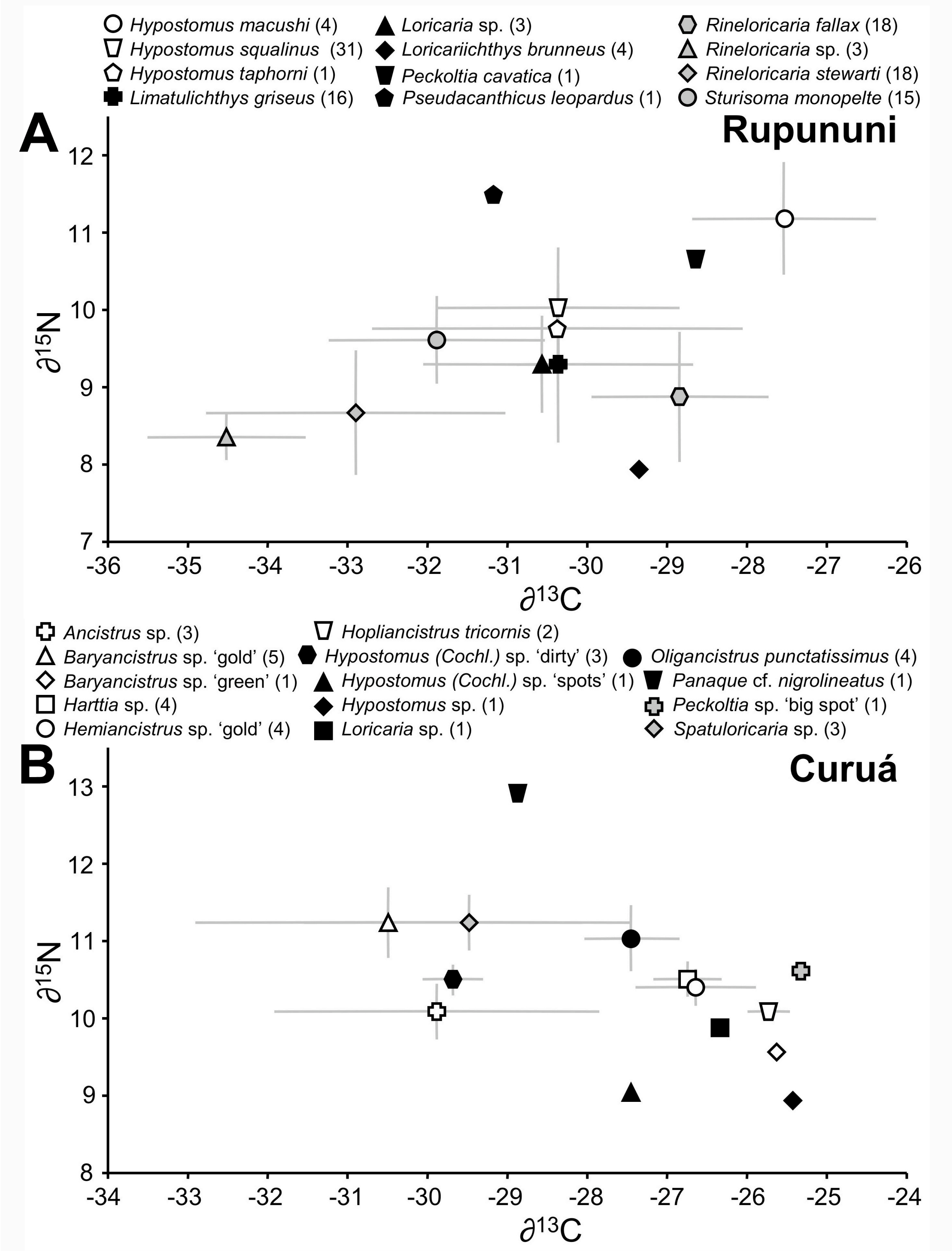
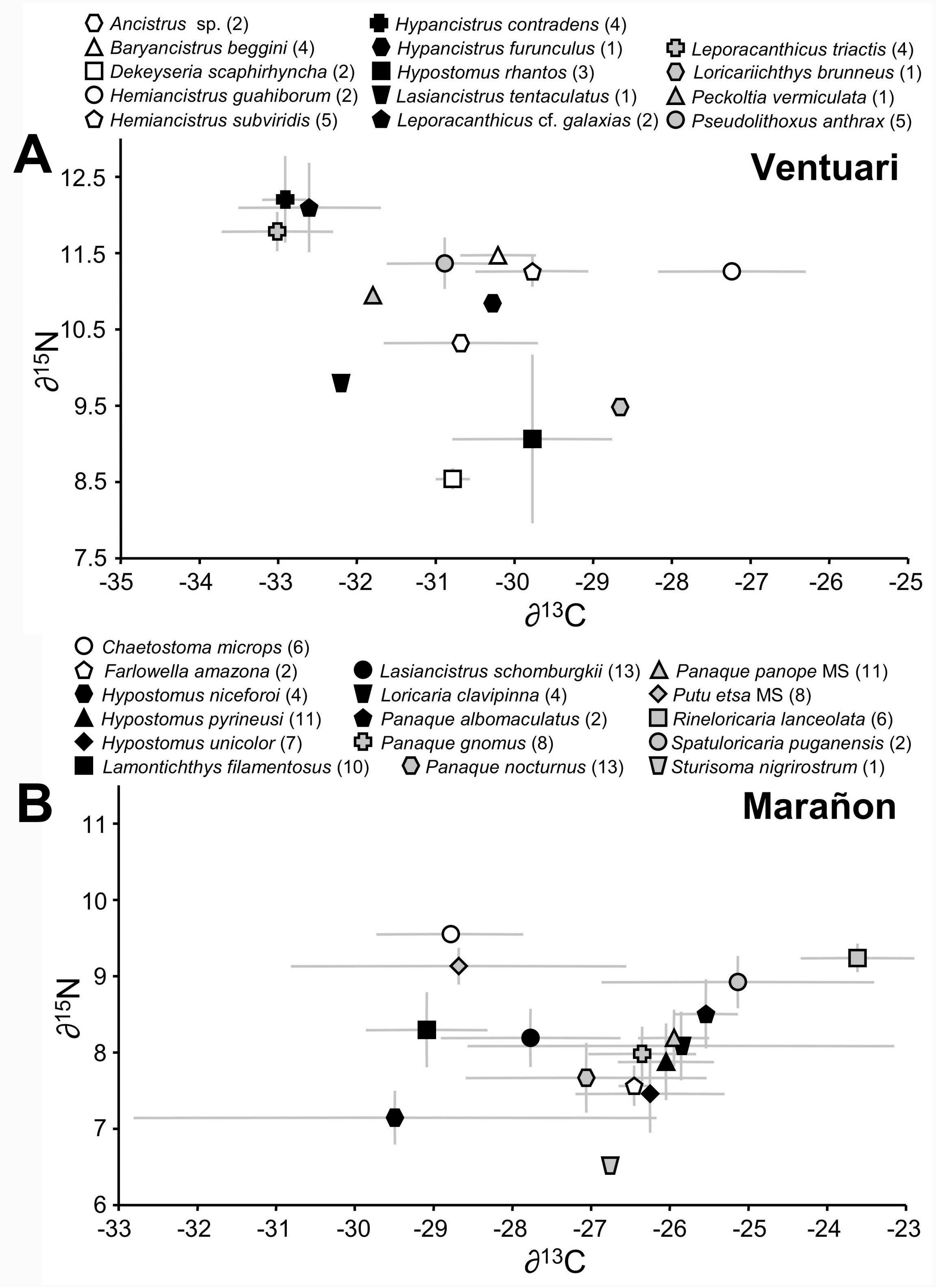


Figure 14. ∂^{15}N and ∂^{13}C relationships of loricariid consumers in (A) the Ventuari river, Orinoco drainage, southern Venezuela; and (B) the Marañon river, Amazon drainage, northern Peru. Sample sizes in parentheses.



CHAPTER 4. GEOLOGICAL AND HYDROLOGICAL HISTORY OF THE GUIANA SHIELD, AND HISTORICAL BIOGEOGRAPHY OF ITS FISHES

4.1 SUMMARY

The Guiana Shield is a geologically ancient region of high to middle elevation terrain covering approximately 2,288,000 km^2 of northern South America, from French Guiana west across northern Brazil, Suriname, Guyana, southern Venezuela, and eastern Colombia. The Guiana Shield is drained by most of the major rivers of South America including upper and right bank tributaries of the Orinoco River (including the Ventuari, Caura, and Caroni), upper and left bank tributaries of the Essequibo River (including the Rupununi, Potaro, and Mazaruni/Cuyuni), upper and left bank tributaries of the Negro River (including the Branco, Uraricoera, Takutu, and Ireng), left bank tributaries of the lower Amazon River (including the Uatuma, Trombetas, Paru do Oeste, Paru, and Jari), and an east-to-west series of Atlantic coastal rivers north of the Amazon including the Oyapock, Marone, Coppename, and Corantijne. Topography of the Guiana Shield is largely the result of approximately six periods of non-deformational uplift and tilting since at least the Early Cretaceous, each uplift period followed by a period of drainage reorganization, erosion, and downcutting. High elevation parts of the shield are now concentrated like an east-west ridge down its center. Elevations are particularly high in the west, in southern Venezuela, where a concentrated region of isolated massifs or

cerros over 2000 m-asl is known as Pantepui or the Guayana Highlands. Sediments from erosion of the Guiana Shield have been distributed in all directions around the highlands, creating peneplanar savannas to the northwest, west, and south, and coastal lowlands to the northeast and east.

Headwaters of most Guiana Shield rivers interdigitate throughout the highlands, and the biogeographic patterns of Guiana Shield fishes indicate a strong historical influence of river capture both in the highlands and the lowlands. The Guiana Shield has an ancient history of cyclical uplift followed by drainage reorganization, which has allowed for an abundance of both recent vicariant speciation and relictual persistence of narrowly endemic basal lineages. Vicariant speciation and relictual persistence is particularly evident among the suckermouth armored catfishes (family Loricariidae), a radiation of over 700 species broadly distributed across tropical Central and South America. Loricariid assemblages in the Guiana Shield are particularly species rich and they are frequent occupants of upland habitats, making them an ideal group in which to examine the biogeographic importance of modern topographic patterns and historical geological events. Several genera in the loricariid tribes Hartiini (*Harttia*) and Ancistrini (*Pseudancistrus, Pseudacanthicus, Leporacanthicus*) are shared between the Guiana and Brazilian Shields, but are absent from highlands of the Andes. Several other ancistrin genera (*Exastilithoxus, Lithoxus, Neblinichthys,* New Genus 2) have ranges restricted only to uplands of the Guiana Shield, where their distributions across isolated and restricted ranges serves as important clues to the historical continuity of many currently disconnected headwaters.

At the center of the Guiana Shield, until at least the Plio-Pleistocene, a river called the proto-Berbice is hypothesized to have united modern headwaters of the Orinoco, Branco and Essequibo into a single paleodrainage that exited into the Atlantic near the modern border between Guyana and Suriname. Progressive stream capture by the Orinoco, Amazon, and Essequibo led to modern drainage patterns. Highlands of the Guiana Shield also appear to have functioned as an incubator and source for upland specialized taxa that have radiated into more recently uplifted terrains along the Andean flanks. Phylogenetic analysis of morphological data indicate that a predominantly Andean upland radiation of four ancistrin genera (*Chaetostoma, Cordylancistrus, Dolichancistrus*, *Leptoancistrus*) is nested within a clade of Guiana Shield endemic genera (*Exastilithoxus, Lithoxus,* New Genus 2). Morphological data likewise indicate that *Lithogenes*, which is currently or recently known only from the Guiana Shield and the nearby Coastal Mountain range of northern Venezuela, is either sister to the Andean upland genus *Astroblepus* (family Astroblepidae, sister to Loricariidae), or sister to all remaining Loricariidae.

In addition to historical geologic events and basal radiations, distributional patterns of several widespread fish groups support the broad taxonomically significance of several modern, permanent or seasonal connections between major drainage basins. The network of major modern and historical avenues for dispersal between drainages conforms, roughly, to a prone number 8 laid atop the Guiana Shield. Major modern lowland connections among Guiana Shield rivers include: the Casiquiare Canal, linking the upper Orinoco with the upper Negro; the seasonally flooded Rupununi Savannas, linking the Essequibo with the Branco; Atlantic coastal connections consisting of flooded lowlands and freshwater plumes from the Amazon mouth northwest to the Orinoco mouth; and both southern and northern tributaries of the lower Amazon, which drain respective northern and southern slopes of the Brazilian and Guiana Shields. High resolution phylogenetic hypotheses and fish distributional data that might provide greater resolution to the rank importance of these drainage connections are generally lacking.

4.2 INTRODUCTION

Highland areas that serve as sources and boundaries for the great rivers of South America can be broadly divided into two categories based on their geologic age and origin. As reviewed elsewhere in this volume (Chapters 15 and 16), the allochthonous terrains and massive crustal deformations of the Andes Mountains that comprise the extremely high-elevation western margin of South America have their origins in diastrophic (distortional) tectonic activity largely limited to the Late Paleogene and Neogene (<25 Ma; Gregory-Wodzicki, 2000). In contrast, vast upland regions across much of the interior of the continent have been relatively tectonically quiescent since the Proterozoic (>550 Ma; Gibbs and Baron, 1993) and exhibit a topography that is instead largely the result of epeirogenic (non-distortional) uplift of the Guiana and Brazilian Shields and subsequent erosion of overlying sedimentary formations.

Topographic and hydrologic evolution of both the Andes and the Amazon Platform advanced within the late Mesozoic to Cenozoic timeframe recognized as largely encompassing the evolutionary radiations of Neotropical fishes (Lundberg *et al.*, 1998); however, early uplifts of the Amazon Platform predate significant Andean orogeny by several hundred million years. Lundberg (1998), in his review of the temporal context for diversification of Neotropical freshwater fishes, made it clear that, despite the prevailing attention given to Andean orogeny and the various vicariant speciation events that it spawned, most major Neotropical fish lineages were already extant long before the Miocene surge in Andean uplift, and the search for geologic events relevant to basal nodes in the evolutionary history of Neotropical fish lineages should extend deeper in time.

In this chapter we describe the geologic, topographic, and hydrologic evolution of the Guiana Shield since at least the Cretaceous. We then compare these historical processes with evolution of the region's fishes. The primary taxonomic focus of this chapter is on suckermouth armored catfishes (Loricariidae), due to their great diversity, comprising over 700 described species, their ancient ancestry as part of a superfamily sister to all other Siluriformes, and their biogeographic tractability due to distributions across headwater habitats and associated allopatric distribution patterns among sister taxa. We conclude that the diverse loricariid fauna of the Guiana Shield accumulated gradually over tens of millions of years over the whole continent, and not as the result of a rapid, geographically restricted adaptive radiation. We demonstrate the role of the Guiana and Brazilian shields as ancient highland regions in the origin of frequently rheophilic loricariid taxa. We also show how diversification was influenced by a restricted number of landscape scale features; especially dispersal and vicariance across several geologically persistent corridors, expansion and contraction of ranges due to tectonic alterations in prevailing slope, and patterns of local and regional climate change. Continued progress in this area will require increased sampling, especially in the southern and western portions of the Guiana Shield, both to more fully understand the alpha taxonomy and distribution of species, and for the reconstruction of detailed species-level phylogenies.

4.3 GEOLOGY AND HYDROLOGY

4.3.1 Overview

Surficial outcrops of the Amazon Platform can be observed as bedrock shoals in many northern and southern tributaries of the Amazon River, but rarely at elevations higher than 150 meters above sea level (m-asl). Topography higher than this is largely comprised by the Roraima Group, an aggregation of fluviolacustrine sediments deposited over much of the northern Amazon Platform during the Proterozoic and subsequently uplifted along with the basement. Portions of this formation resistant to erosion now comprise most of the striking topographic elements for which the shield regions are famous, including the fabled Mount Roraima (2810 m-asl) and South America's highest non-Andean peak, Pico Neblina (3014 m-asl) at the frontier with Brazil in the southwestern corner of Amazonas State, Venezuela. The relatively recent discovery of Pico Neblina in the mid-twentieth century illustrates both the long standing inaccessibility of much of the Guiana Shield, and the tremendous gaps in knowledge that still challenge summaries of shield geology and biogeography.

Separating the Guiana Shield from the Brazilian Shield is the Amazon Graben, a structural downwarp underlying the Amazon Basin. This major divide is 300 to 1000 km wide (from North-South) and is filled with sediments up to 7000 m deep. South of the

Amazon Graben to about 20ºS latitude, stretches the larger of the Amazon Platform's two subunits: the Brazilian (or Guaporé) Shield, whose highlands delineate watershed boundaries of the major southern Amazon River tributaries Tocantins, Tapajos and Xingu, as well as northwestern headwaters of the south-flowing Parana River. Middle reaches of the Madeira River are also interrupted by several major rapids due to their transect of a western arm of the Brazilian Shield.

The Guiana Shield, the smaller, more northern subunit of the Amazon Platform, is elongated nearly east to west and roughly oval in shape (Fig. 1). From its eastern margin along the Atlantic coast, it stretches across French Guiana, Suriname, Guyana, and Venezuela, to southeastern Colombia in the west (approximately 2000 km distance). Bounded by the Amazon Basin to its south, and the Orinoco River to its north (approximately 1000 km distance) and west, the Guiana Shield occupies some 2,288,000 km^2 (Hammond, 2005). The average elevation of the Guiana Shield is approximately 270 m-asl but disjunct and frequently shear-sided formations exceeding 2000 m-asl, known variously as tepuis, cerros, massifs, sierras, and inselbergs are common, particularly near Venezuela's frontier with Brazil in a region of concentrated high elevation terrain known as Pantepui. The Pantepui region slopes more or less gently to the north but has a striking southern scarp boundary along the Venezuela-Brazil border. Ridges along this border comprise the Sierras Pakaraima and Parima, which stretch some 800 km ENE–WSW and rarely drop below 1000 m-asl. The Pakaraima and Parima ranges have their eastern origin in Mount Roraima at the tricorners between Guyana, Brazil, and Venezuela, and their western terminus in Sierra Neblina.

The name ‘Guiana’ is believed to be derived from an Amerindian word meaning ‘water’ or ‘many waters’ (Hammond, 2005). Indeed, as many as 47 medium to large rivers drain the greater Guiana Shield region (Fig. 1), including the Negro, Orinoco, Essequibo, Trombetas, Caqueta (Japurá), Jatapu, Marone (Marowijne), and Corentyne (Correntijne). Discharge from rivers draining or traversing the Guiana Shield totals an estimated average of 2,792 km^3 per year, which amounts to approximately a quarter of South America’s total volume of freshwater exported to the oceans (Hammond, 2005). This volume of water carries with it considerable erosive power, which, with sporadic periods of epeirogenic uplift, are primary forces responsible for the region’s remarkable topography.

4.3.2 Topographic Evolution

Granitic basement rocks that comprise most of the Amazon Platform formed during orogenic events of the Paleoproterozoic (1,700-2,200 Ma), although the Imataca Complex of northeastern Venezuela is exceptional for its Archean age (>2,500 Ma). For much of this time, it is hypothesized based on once-contiguous fault lines that the Amazon Platform was united with the West African craton, and that together they were part of a single tectonic plate forming parts of the supercontinents Gondwana, Pangea, and Columbia. Approximately 1,800 Ma, a major orogenic episode somewhere to the east and north of the Guiana Shield in what would have been the Supercontinent Columbia, turned what is now the shield into a foreland basin and depositional zone (Santos *et al.*, 2003). Over the course of a few hundred million years the northern Amazon Platform accumulated up to over 3,000 m (avg. 500 m; Gansser, 1974) of sediment from rivers flowing off of this ancient mountain range into fluvio-deltaic and lacustrine environments (Edmond *et al*. 1995). The resulting sandstone formations, known as the Roraima Group, feature ripple marks and rounded pebbles indicating their fluvial origin and the original east to west direction of deposition (Gansser, 1954; Ghosh, 1985). Now uplifted at least 3000 m and constituting highlands throughout the Guiana Shield, these sediments still cover a vast area but are much reduced from their original range, which surpassed 2,000,000 km^2 and stretched about 1,500 km from an eastern origin in or near Suriname (largely exclusive of French Guiana) to Colombia and across northern Brazil. Eastern Roraima formations such as the Tafelberg in east-central Suriname and Cerro Roraima itself are older and deeper than western Roraima sediments now evident as shallow sandstone caps of the central Colombian Macarena and Garzon massifs, and the southeastern Colombian mesas of Inirida, Mapiripan, and Yambi (Gansser, 1974).

Transition from the once contiguous, fluvially deposited Roraima formation to the now disjunct Guiana Shield highlands required loss of an enormous volume of intervening sediment via erosion. The modern highlands constitute approximately 200,000 km^3 of comparatively resistant sediment, but this is a small remnant of what was originally an approximately 1,000,000 km^3 formation averaging approximately 500 m in depth (Gansser, 1974). Erosional redistribution of Roraima Group sediments, along with younger Andean sediment, into structural basins encircling the shield has created peneplainer savannas north, west, and south of the highlands. To the north, the structure of the flat Eastern Venezuelan Llanos is that of a basin filled with sediments over 12 km deep (Hedberg, 1950). This Eastern Venezuela Basin is narrowly contiguous with the Apure-Barinas back arc basin underlying the Apure Llanos northwest of the Guiana

Shield (see *Eastern Venezuela Basin* below). Around the western side of the Guiana Shield, the Apure-Barinas basin and a back arc basin underlying the Colombian Llanos just southeast of the Andes are contiguous with a low-lying cratonic subduction or suture zone approximately coincident with the Colombia-Venezuela border (Gaudette and Olszewski, 1985; Hammond, 2005). Lowlands of the Amazon Graben form the shield's southern boundary, and the Rupununi Savannas in the middle of the Guiana Shield are comprised of Cenozoic sediments filling a rift valley up to 5400 m deep (see *Proto-Berbice* below). Even basins of the Western Amazon have, since the Cretaceous, been filling with sediments from the Guiana and Brazilian shields (Räsänan *et al*., 1998). Despite the dramatic topographic results of a long history of erosion and sediment redistribution, the modern shield highlands are subject to chemical weathering almost exclusively and shield rivers carry very little sediment (Lewis and Saunders, 1990; see *Limnology and Geochemistry of Shield Rivers* below).

Epeirogenic uplift of the Guiana Shield has occurred sporadically almost since its formation in the Paleoproterozoic. Since at least the middle Paleozoic, when the region was first exposed at the surface, cycles of uplift and stasis during which erosion occurred have resulted in elevated erosional surfaces (pediplains or planation surfaces) that are now observed throughout the northern interior of South America (Table 1; Schaefer and do Vale, 1997, Gibbs and Barron, 1993). At lower elevations, these appear as steps or stages of Roraima Formation sediments, vertically separated from each other by 60 to 200 m elevation. At higher elevations, collections of peaks can be identified that share similar elevations (Fig. 2). Berrangé (1975:813), for example, described the "remarkable concordance of summits" of the Kanuku Mountains, which are mostly between 900 and

946 m-asl. The heights of Kanuku peaks can be correlated with heights of the Pakaraima-Parima ranges to the northwest, Wassari Mountains to the south, and several other peaks to the north and east, each separated from the other by hundreds of kilometers. Five surfaces, one higher and four lower than that of the Kanuku Mountains, have been identified and assigned tentative ages (Table 1; Schubert *et al*., 1986).

The ages and history of Guiana Shield uplift provide important clues to the origin and evolution of topographic formations such as drainage divides and waterfalls particularly relevant to the distribution patterns of aquatic faunas. Kaieteur Falls (226 m high) in Guyana, for example, isolates the only known habitats of *Lithogenes villosus*, a basal astroblepid or loricariid, and *Corymbophanes andersoni* and *C. kaiei*, the only two species of this basal genus of hypostomin loricariid (Armbruster *et al*., 2000). Fossil calibrated relaxed molecular clock data (Lundberg *et al*., 2007) suggest that these relictual taxa predate the Oligocene uplift of the Kaieteur planation surface and may therefore owe their continued existence to isolation via uplift of this barrier (see *Relictual Fauna* below).

4.3.3 Proto-Berbice (Central Shield)

The hydrologic history of South America is a dynamic one, and a large body of evidence indicates that many of the paleofluvial predecessors of modern drainages were substantially different from rivers seen today. Regardless, the Guiana Shield has been embedded among headwaters of the Amazon, Orinoco, Essequibo and their paleofluvial predecessors, since their inception. Late Mesozoic and Paleogene terrigenous sediments recorded from the Caribbean Sea (Kasper and Larue, 1986) and Atlantic Ocean (Dobson *et al*., 2001) are derived from Proterozoic and Archean age sources, indicating that, prior to Neogene acceleration of Andean uplift, the Guiana and Brazilian Shields were the continent's major uplands, and likely the continent's most concentrated regions of high-gradient lotic habitat (Galvis, 2006). One of the largest drainages of the central Guiana Shield during much of the Cenozoic was the proto-Berbice, a northeast-flowing river draining portions of Roraima State, Brazil, most of Guyana, and parts of southern and eastern Venezuela and western Suriname (Sinha, 1968, Schaefer and do Vale, 1997).

Central to the historical geography and hydrology of the proto-Berbice is the Takutu Graben, a deep structural divide between eastern and western lobes of the Guiana Shield approximately 280 km long by 40 km wide and up to 7 km deep, centered on the town of Lethem, Guyana. The modern graben is a valley between the Pakaraima and Kanuku Mountains trending ENE to WSW and approximately equally divided between Brazil and Guyana. Early rifting of the graben resulted in volcanism in the Late Triassic to Early Jurassic but the depression has received freshwater sediments since the Middle to Late Jurassic. Lake Maracanata, an endorheic lake approximately 75 to 100 m deep (though progressively shallower through time and fluctuating greatly in depth through periods of aridity) occupied the graben until the Early Cretaceous (Crawford *et al*., 1985). This ancient lake received predecessors of the modern Ireng, Cotinga, Takutu, Uraricoera, Rupununi, Rewa, and Essequibo Rivers (McConnell, 1959, Sinha, 1968, Berrangé, 1975, Crawford *et al*., 1985).

From Late Cretaceous to Paleogene, Lake Maracanata transitioned to a fluvial environment with a trunk stream, the proto-Berbice, that flowed northeast through the

North Savannas Gap and exited to the Atlantic between the modern towns of New Amsterdam, Guyana and Nickerie, Suriname (McConnell, 1959). Head-cutting by the Branco River, a south-flowing tributary of the Amazon River, into the western end of what had been Lake Maracanata robbed the proto-Berbice of the Cotinga and Uraricoera first, at the end of the Pliocene, then the Ireng and Takutu in the Pleistocene. The broader, flatter bed now apparent in the Takutu relative to the Ireng indicates that the former was captured and rejuvenated first, whereas the latter, with its entrenched, meandering bed, is still accommodating to its new slope (Sinha, 1968). The modern Berbice River itself has withered, and is now dwarfed by its former tributaries the Essequibo and Corentyne to its northwest and southeast, respectively. Evidence of a shift away from the lower Berbice as the more important trunk stream can be observed in an elbow of capture near Massara, at the eastern edge of the Maracanata Basin. This is the point at which the modern upper Essequibo shifts abruptly westward, away from a nearby north-flowing Berbice tributary, that has aggraded in response – raising the level of the stream bed (Gibbs and Baron, 1993).

It seems likely, given their considerable endemism (see *Caroni (Orinoco) to Cuyuni/Mazaruni Corridors* below), that the Mazaruni and Cuyuni rivers were also only recently linked with the Essequibo, and that they historically exited to the Atlantic via their own mouth, separate from that of the proto-Berbice. In the southern Guiana Shield highlands of Venezuela, strongly recurved elbows of capture are regular features of the upper Caroni, Caura, and Erebato (Caura), which, along with biogeographic evidence (Lujan, 2008), indicate historical confluence of these headwaters with the southeasterly flowing upper proto-Berbice, now the Uraricoera River.

The North Rupununi Savannas occupy the modern Maracanata depression and form a shallow continental divide between the northeastern versant of South America, drained in this area predominantly by the Essequibo, and a more southern versant that drains to the Amazon via the Branco and Negro. Seasonal (May to August) rains regularly flood this divide, forming a lentic connection extending to over 6,000 km^2 and centered between the north-flowing Rupununi River and headwaters of the Pirara River, a west-flowing tributary of the Ireng. Lake Amuku is the name sometimes applied to the broad areal extent of these floodwaters (Lowe-McConnell, 1964), as well as to one or more restricted ponds into which floodwaters retreat (NKL pers. obs.). Lacustrine sedimentation from the annual inundation continues to contribute to a shallowing of the Maracanata basin (Sinha, 1968) and a possible long-term reduction of its role as biogeographic portal between the Essequibo and Negro watersheds.

Tilting of the underlying basement both in the North Rupununi Savannas and across the Guiana Shield has occurred as recently as the Holocene (Gibbs and Baron, 1993) and is likely a frequent driver of head cutting and stream capture. Evidence of this can be seen in the disproportionate incision of tributaries on one side of rivers flowing perpendicular to the direction of tilt, and aggradation of tributaries on the opposite side. Tilting to the west in the South Rupununi Savannas, for example, has led to rejuvenation and steepening of eastbank tributaries, and aggradation and sluggishness in westbank tributaries of the north flowing Takutu, Rupununi, and, in part, Kwitaro rivers (Gibbs and Baron, 1993). In Southeastern Venezuela, a gradual shift in the prevailing tilt of the Gran Sabana from north to south is thought by López *et al*. (1942) to be responsible for remarkably complex drainage patterns in the upper Caroni River. Abrupt and localized orthogonal shifts in channel direction, with streams of the same drainage flowing in parallel but opposite directions are common features, as are biogeographic patterns indicative of frequent stream capture (Lasso *et al*., 1990; see *Caroni to Cuyuni/Mazaruni Corridors* below).

4.3.4 Proto-Orinoco (Western Shield)

The western Guiana Shield features one of the largest and most notable river capture events in the Neotropics: that of the ongoing piracy of the northwest-flowing Upper Orinoco River by the southeast-flowing Negro River, via the southwest-flowing Casiquiare Canal. The Casiquiare Canal diverts up to 20% of the Upper Orinoco's discharge away from the Orinoco trunk and into the Amazon via the Negro. This is a relatively recent phenomenon, however, in the dynamic history of the Orinoco River, which has given rise to the upper-Amazon and Magdalena Rivers while its own main channel migrated progressively eastward from an ancestral north-south orientation. Prior to consolidation by any trunk stream, from at least the Campanian to the Maastrichtian, westward flowing drainages from highlands of the Guiana and Brazilian Shields likely followed short, anastomosing channels across a broad coastal plain, into shallow marine environments that occupied much of what is today Colombia, Ecuador, and Peru. The Panamanian Isthmus was not yet present and the northern Andes were just beginning to form.

By the Middle Eocene, uplift of the Central Cordillera had progressed to the extent that it formed the western margin of a large south to north trending valley, drained by a single fluvial system, then expanded by coalescence of both high gradient left bank tributaries draining the eastern slope of the young Central Cordillera and right bank tributaries flowing west from Guiana Shield uplands. The mainstem of this proto-Orinoco was a large, low-energy, meandering river that deposited “vast amounts of sediment” (Villamil, 1999: 245) in a geological formation called the Misoa Delta in what is now the Maracaibo Basin (Díaz de Gamero, 1996). From Late Eocene to Oligocene, marine incursions pushed the mouth of the proto-Orinoco back as far south as the modern town of Villavicencio, Colombia up to five times (Díaz de Gamero, 1996; Villamil, 1999). In the Late Oligocene, the proto-Orinoco expanded longitudinally to the north-northeast (Shagam *et al.*, 1984; Villamil, 1999), and by the Early Miocene, it was flowing into the eastern end of the La Pascua-Roblecito marine basin, a deep seaway occupying much of modern-day Falcon State in northwest Venezuela. The proto-Orinoco and its mouth were isolated at this time from the Maracaibo Basin by uplift of the Merida Andes (Shagam *et al.*, 1984; Villamil, 1999) and from the Eastern Venezuela Basin by the El Baul structural arch (Kiser and Bass, 1985; Díaz de Gamero, 1996).

4.3.5 Eastern Venezuela Basin (Northern Shield)

The Eastern Venezuela Basin is a structural depression located between the northern edge the Guiana Shield and the northern coast of South America that receives lower portions of the northern shield drainages Caura, Aro and Caroni. The basin is asymmetric in bottom profile, growing shallower to the south and west and opening to the northeast, where the basement is over 12 km deep. The entire basin is filled and leveled with Mesozoic to Cenozoic sediments now zero to 50 m-asl and comprising the eastern half of the Venezuelan Llanos. Approximately 800 km east to west and 250 km north to south, the basin is bounded in the east by the Sierra Imataca, a northern arm of the Guiana Shield, and in the south by the Guiana Shield proper. In the north, it is bounded by the Sierra del Interior and Coastal mountain ranges; and in the east, it has an opening to the Apure-Barinas basin that is constricted as between a thumb and forefinger by the coastal mountain ranges in the north and the El Baul structural arch in the south.

From at least the Lower Cretaceous to the Early Eocene, the Eastern Venezuela Basin was a marine environment that received rivers draining the northern slope of the Guiana Shield directly. In the Early Eocene, however, tectonic convergence of the Caribbean Plate caused widespread emergence of the Eastern Venezuela Basin and northward expansion of the coastal plain. In response, the Caura extended its lower course north-northeast so that it formed a delta in the Sucre region of Venezuela between the modern islands of Margarita and Trinidad (Rohr, 1991; Pindell *et al*., 1998). Emergent, coastal plain conditions largely prevailed in the Eastern Venezuela Basin throughout the Eocene and into the Oligocene but convergence of the Caribbean Plate in the Late Oligocene caused southeastward migration of the La Pascua-Roblecito seaway. While the proto-Orinoco continued to discharge into the seaway's closed southwestern end, the Caura and Caroni coalesced in a more restricted coastal plain and delta near the seaway's eastern opening, in the northern portion of Anzoategui State, Venezuela (Rohr, 1991; Pindell *et al*., 1998).

In the Early Miocene, regression of the seaway, and consequent eastward progradation of the proto-Orinoco placed deltas of the proto-Orinoco and Caura in close proximity at the western margin of the Eastern Venezuela Basin, but uplift of the El Baul arch at this time ensured that they remained separate until at least the Middle Miocene (Pindell *et al*., 1998). In the Late Middle Miocene, southward propagation of rapid uplift in the Serrania del Interior, along with a possible decrease in the significance of the El Baul arch, pushed the proto-Orinoco southward to capture the lower course of the Caura (Pindell *et al*., 1998). Further progradation and eastward movement of the Orinoco put its delta in the region of modern Trinidad in the mid-Pliocene. Final conformation to its modern course, adhering closely to the northern edge of the Guiana Shield, occurred in the Late Pliocene to Pleistocene (Rohr, 1991; Hoorn *et al*., 1995; Díaz de Gamero, 1996).

4.3.6 Proto-Amazon and eastern Atlantic drainages (Southern and Eastern Shield)

The Amazon River's birth as a distinctly South American, versus Gondwanan, river can be dated to at least the Middle Aptian, approximately 120 Ma. Fossil evidence indicates that by the Late Aptian, an equatorial seaway linked the North and South Atlantic, thereby dividing the once-contiguous landmass of Gondwana into South America and Africa (Maisey, 2000). Given the much older Proterozoic structural evolution of the Amazon Graben as a regional lowland, and its sediment fill dating at least to the Cambrian (Putzer, 1984), it can be assumed that from the moment the South Atlantic Seaway opened, a paleofluvial predecessor of the Eastern Amazon drained the southeastern Guiana and northeastern Brazilian shields east through a mouth approximately coincident with its modern delta. This proto-Amazon was much smaller than the modern Amazon-Solimões system. For over 100 My following the breakup of Gondwana, upper and lower portions of the modern Amazon Basin (approximately coincident with the modern Solimões and Amazonas reaches), were separated by the Purus Arch, a continental divide within the Amazon Graben located near the modern mouth of the Purus River. Lowland portions of those proto-Amazon tributaries draining the southern slope of the Guiana Shield would have also been separated by the Purus continental divide into western and southeastern paleo-drainages. The upper Negro, Caqueta (Japurá), and upper Orinoco would have flowed west or northwest during this period, either directly into the Pacific or into the Caribbean via the proto-Orinoco (see *Proto-Orinoco* above).

Southeastern drainages of the Guiana Shield would have been further limited in areal extent, and distanced from the western lobe of the Guiana Shield relative to their modern pattern by the expanded proto-Berbice draining the central Guiana Shield region (see *Proto-Berbice* above). Paleodrainages of the southeastern Guiana Shield that would have been south of the proto-Berbice's approximate watershed boundaries, and east of the Purus Arch, and therefore still been northern tributaries of the proto-Amazon, would have included the lower Branco/Negro below the Mucujai River, and the Uatuma, Trombetas, and Paru Rivers. A series of ridges with peaks in the range of 400 to 1000 m extends east from the Kanuku Mountains and forms another continental divide within the eastern lobe of the Guiana Shield, in this case separating south-flowing Amazon tributaries from northeast flowing Atlantic Coastal drainages. Headwaters of respective northern and southern rivers interdigitate across these highlands, though, rendering them largely porous to fish dispersal (Nijssen, 1970, Cardoso and Montoya-Burgos, 2009; see

Atlantic Coastal Corridors below). The westernmost of these east-to-west ranges, forming the border between Brazil and Guyana, are the Wassari and Acarai Mountains which give rise to the Trombetas, the fourth largest watershed on the Guiana Shield (drainage area 136,400 km^2). The easternmost of these ranges, forming the southern borders of Suriname and French Guiana, are the Tumucumaque Mountains, which give rise to the Paru River (44,250 km^2). North of this divide, in order from west to east, flow the Correntyne (68,600 km^2), Coppename (21,900 km^2), Suriname (17,200 km^2), and Marone (70,000 km^2) rivers. Finally, draining the eastern slope of the eastern Guiana Shield is the Oyapok River (32,900 km^2), which forms the border between French Guiana and Brazil, and the Approugue River (10,250 km^2) just to its northwest inside French Guiana (Fig. 1; drainage area data from Hammond, 2005).

In the Late Miocene, paroxysms of Andean uplift shifted the prevailing slope of the Andean back arc basin eastward and caused Andean-derived watercourses to breach the Purus Arch, vastly expanding the proto-Amazon's watershed westward. New regions of the Amazon Basin included vast swaths of the modern western and southwestern Amazon Basin that had been tributary to the proto-Orinoco and are now tributary to the upper Amazon mainstem (Solimões). New northern tributaries of the expanded Amazon included drainages of the western lobe of the Guiana Shield such as the Caqueta and upper Río Negro. Uplift of the Vaupes Arch and Macarena Massif contemporaneous with the Late Miocene Western Cordillera uplift also created a new drainage divide segregating the upper Negro from the upper Orinoco (Galvis, 2006).

Orographic rainfall effects of the rapidly rising Andes Mountains also contributed to the expansion of the Amazon in the Late Neogene by increasing its discharge beyond that predicted by its areal expansion alone. With the increase in discharge came an increase in erosional potential and further watershed expansion via head cutting. The southeast flowing Branco River, for example, sequentially captured headwater tributaries of the northeast flowing proto-Berbice throughout the Pliocene and Pleistocene. Indeed, the Amazon is still expanding, as seen in the ongoing capture of the upper Orinoco by the Rio Negro. The initiation of this capture and opening of this portal has been hypothesized to be fairly recent, possibly due to Late Pleistocene or even Holocene tilting (Stern, 1970; Gibbs and Barron, 1993). Under this scenario, the Orinoco is estimated to have been largely isolated from the Amazon for some 5–10 My, from the Late Miocene uplift of the Vaupes Arch to the Pleistocene-Holocene formation of the Casiquiare Canal. The future seems to be one in which a new drainage divide forms within the Orinoco downstream of the Tama-Tama bifurcation, and the current headwaters of the Orinoco become entirely adopted by the Amazon (Stern, 1970).

4.3.7 Aridity and Marine Incursions

We have thus far described, in broad strokes, major trends and events in the drainage evolution of four hydrologic regions around the Guiana Shield, but we have done so at the expense of dwelling in too great detail on global cycles and climatological events that had periodic, widespread effects across all hydrologic units. Aridity and marine incursions are treated here together because of their similar effects on rivers and riverine biota – that of reducing and isolating habitats over a broad geographic range. The two phenomena are also correlated in their response to global cycles of glaciation with a periodicity of 20–100 thousand years (Milankovitch cycles; Bennett, 1990). In general, warmer, interglacial climates correspond to higher sea levels, more extensive marine incursions, and higher levels of precipitation. Cooler, glacial periods result in reduced precipitation, retreat of the sea, expansion of the coastal plain, and incision of river channels.

Many lines of geologic and biogeographic evidence indicate that the climate of South America was much drier in the recent past than it is today. The last major glacial period, the Würm or Wisconsin glaciation, lasted throughout the Late Pleistocene, from approximately 110,000 BP to between 10,000 and 15,000 BP. Several authors (*e.g.* Krock, 1969, Hammen, 1972, Tricart, 1985, Schubert *et al.*, 1986, Schubert, 1988) describe the substantial paleobotanical and geomorphological evidence of aridity in South America during this period. Hammen (1972) states that within the overall trend of late Pleistocene aridity, the period from approximately 21,000 to 13,000 BP was the driest.

Terrestrial vegetation throughout much of the Guianas in the Late Pleistocene was of an open savanna or grassland type, with rainforests likely limited to a few highland refugia, including parts of the Pantepui highlands, and riparian margins. These refugia feature heavily in explanations of patterns of terrestrial plant and animal diversity (*e.g.,* Haffer, 1969, 1997, Prance, 1973, Vanzolini, 1973, Brown and Ab'Sáber, 1979, Kelloff and Funk, 2004), but do not appear to useful in explaning freshwater fish distributions (Weitzman and Weitzman, 1982; see reviews in Chapters 1 and 18). Loss of major forest cover along with a decrease in sea level had major effects on the geomorphic evolution of South American rivers. Without forest cover to keep soil intact, and because of lowered river base levels due to lower sea levels, many rivers cut deeply into their channels

(Sternberg, 1975, Tricart, 1985, Latrubesse and Franzinelli, 2005). Channel bottom in the lower reaches of some Amazon tributaries, for example, can be up to 80 m below modern sea level (Sioli, 1964, Latrubesse and Franzinelli, 2005). Rapids would have been more widespread during periods of aridity, and deep-channel habitats that may currently function as barriers to rheophilic taxa would have been reduced. Decreases in total discharge would have lead to shallowing, sedimentation and aggradation or braiding of low gradient habitats where they persisted (Schubert *et al.*, 1986, Latrubesse and Franzinelli, 2005). Garner (1966) also suggests that the complex drainage pattern of the upper Caroni in the Gran Sabana may be the result of anastomosing channel development during a more arid climatic regime, and that the latest humid period has not lasted long enough for the Caroni to consolidate into a more stable drainage pattern.

Marine incursions have inundated much of northwestern South America during interglacial periods of globally high sea level since at least the Maastrichtian (Gayet *et al.*, 1993, Hoorn, 1993; see review in Chapter 17). During much of the Miocene, from approximately 23–11 Ma, the llanos basins of Colombia and Venezuela were dominated by coastal and lagunal conditions with occasional marine episodes (Hoorn *et al.*, 1995). Given their similar elevations and exposure to the coast, it is likely that similar conditions prevailed in the Rupununi Savannas and coastal plain of Guyana. A more recent marine incursion, approximately 6–5 Ma, was hypothesized by Hubert and Renno (2006) to have affected the distribution and diversity of characiform fishes in northeastern South America by isolating a series of upland freshwater refuges in respective eastern and western portions of the eastern Guiana Shield highlands. Further support for such an incursion is provided by Noonan and Gaucher (2005, 2006), who recovered a temporally and spatially congruent vicariance pattern in their molecular phylogenetic studies of *Dendrobates* and *Atelopus* frogs.

4.3.8 Limnology and Geochemistry of Shield Rivers

Rivers of the Guiana Shield are a heterogeneous mix of white-, black-, and clearwater, with most tributaries initially trending toward black- and clearwater then mixing to form intermediate main stems. In heavily forested and largely uninhabited regions such as the shields and the Amazon Basin of South America, topography, climate, geology and a watershed's terrestrial vegetative cover are the main influences on a river's limnological character. Because of their origins in watersheds of ancient, highly weathered, and forest covered basement rock, rivers of the Guiana Shield tend to be nutrient poor with very low levels of suspended solids and alkalinity, but relatively high levels of dissolved silica. Limestones and evaporates are completely absent in the Guiana Shield, so the chemical signature of its rivers are largely influenced by primary weathering of silica-rich felsic granitoids that are the dominant rock type (Edmond *et al*., 1995, Hammond, 2005). Concentrations of major ions and nutrients in the Orinoco mainstem and its Guiana Shield tributaries fall near or even below those expected in precipitation, though, indicating minimal contributions from geology and significant sequestration by forests (Lewis and Weibezahn, 1981).

Extreme blackwater conditions of low acidity (pH <5.5), negative to low alkalinity, and low conductivity (<25 μohms) prevail in the Atabapo, Guainia, Negro, Pasimoni, and other tributaries of the Casiquiare that drain low-lying peneplains between the upper Orinoco and Negro. Adjacent higher-gradient headwaters of the Orinoco such as the Ventuari, Ocamo, Mavaca, and Guaviare are white- to clearwater, with near neutral pH, alkalinity up to 85 μeq/kg, and up to 29 μohms conductance (Thornes, 1969, Edmond *et al*., 1995). Rivers draining the northern slope of the Guiana Shield, such as the Caura, Caroni, and Cuyuni, as well as rivers further east in Suriname and French Guiana, trend toward blackwater conditions despite also having higher gradients. Drainages in the central, south and southeast of the Guiana Shield, such as the Essequibo, Branco, Trombetas, and Paru Rivers are clear to whitewater. Guiana Shield whitewater rivers, it should be noted, are defined based largely on alkalinity and pH, being considerably lower in suspended solid load relative to those Andean drainages on which the traditional definition of whitewater rivers is based (Sioli, 1964).

4.4 BIOGEOGRAPHY OF GUIANA SHIELD FISHES

4.4.1 Modern Corridors: the Prone-8

Phylogeography of South American fishes is hampered by a lack of collections and a lack of studies, and the problems of amassing specimens for phylogeographic studies have been particularly acute in the Guiana Shield. Most of the region is difficult to access with few or no roads to important habitats. Among the better-sampled areas are the lowlands of Amazonas, Venezuela, the lower and upper Caroni of Venezuela (although not the middle reaches or of the Paragua, a large tributary), the Cuyuni of Venezuela, the Rupununi and Takutu of Guyana, and much of French Guiana. The western highlands, the Mazaruni, the Corantijne, and most rivers of the southern edge of the Guiana Shield have been poorly sampled. Phylogeographic studies are especially hampered by the scarcity of collections from headwaters throughout the Guiana Shield.

Most molecular phylogenetic studies inclusive of the Guiana Shield, including those by Lovejoy and Araújo (2000) of *Potamorrhaphis*, Turner *et al*. (2004) and Moyer *et al*. (2005) on prochilodontids, and Willis *et al*. (2007) on *Cichla*, are based on lowland taxa potentially capable of great vagility that could obscure fine-scale biogeographic patterns within the Guiana Shield.

To observe fine-scale biogeographic patterns within and between drainages, low-vagility taxa that are less likely to have biogeographic patterns erased via migration and panmixis should be examined. Rheophilic fishes whose movement between drainages would be expected to be hampered in the absence of stream capture or lowered main channel base levels are good examples of such taxa. The phylogenetic patterns of rheophilic taxa distributed allopatrically across isolated headwaters may be particularly informative when trying to understand the biogeographic significance of such historical events. Among rheophilic Neotropical fishes, loricariid catfishes of the tribe Ancistrini (Hypostominae) are a group with several genera and species that appear to be both most common and most diverse in shield regions. Ancistrin catfishes are, as a whole, also highly territorial with relatively low vagility (see Power, 1984), and are a group that we have studied most. We will therefore focus on them in the discussion below.

For the purpose of our discussion, we refer to taxa known only from the Guiana and/or Brazilian Shields as Shield Endemic Taxa. Taxa that are only most common within the Guiana and/or Brazilian Shields, but have ranges extending beyond these regions, are considered Shield Specialist Taxa. Although our discussion of biogeographic patterns will focus on species in the tribe Ancistrini and Hypostomini that we have studied, published examples from other taxa will also be discussed.

Problematically, the phylogeny and taxonomy of Loricariidae are in their infancy and are complicated by gross morphological similarity. In many of our studies (Armbruster, 2005; 2008; Armbruster *et al*. 2007), we have found little morphological variability within genera upon which to base robust phylogenies; however, by using what is known of ancistrin phylogenetics, distributions, and historical and current corridors between river systems, we support below a conceptual model of biogeographically significant hydrologic corridors around the Guiana Shield. This model approximates the appearance of a prone number 8 (Fig. 3). Corridors between hydrologically contiguous segments of this Prone-8 consist of both recently formed portals such as the Casiquiare Canal (see *Proto-Orinoco* above), recently closed or altered corridors such as the Rupununi Savannas, and numerous intermittent corridors that have likely been present in the recent past. These corridors allow for dispersal around the shield, and their intermittent nature serves as the basis for allopatric speciation. Given that our understanding of the geologic and hydrologic evolution of the Guiana Shield extends beyond the node-age estimates for most Neotropical taxa, especially ancistrin loricariids, we assume that such geophysical evolution has been relevant to the dispersal of extant taxa. The alternative argument that modern Neotropical fish distributions are the result of widespread extinction versus dispersal will be discussed under *Relictual Taxa* below, but will not be considered in the majority of our discussion.

4.4.2 Caroni (Orinoco) to Cuyuni/Mazaruni Corridors

Streams of the lower Caroni interdigitate with streams of the upper Cuyuni, and streams of the upper Caroni interdigitate with the upper Mazaruni, allowing the possibility of stream capture between Orinoco and Essequibo drainages. Lasso *et al.* (1990) found a close similarity between whole fish communities of the Caroni in the Gran Sabana and those of the Cuyuni-Essequibo system and hypothesized frequent stream capture as a cause. Despite the relative richness of the loricariid fauna in the Orinoco and Essequibo basins, there seems to be little evidence that the Caroni to Cuyuni and Caroni to Mazaruni corridors are particularly important for loricariids. Armbruster and Taphorn (2008) suggest that the ancestor of *Pseudancistrus reus* (Ancistrini) may have entered the Caroni from the Cuyuni as it is the only member of *Pseudancistrus sensu stricto* currently known from the Orinoco (all other Orinoco *Pseudancistrus* are basal species); however, *P. reus* has some unique characteristics that make its relationship to other *Pseudancistrus* unclear. The only species of *Pseudancistrus* we know of in the Cuyuni is a species with large white blotches that may be undescribed, and that is relatively common in the Essequibo.

Exchange of loricariids between the upper Caroni and upper Mazaruni also seems to be rare, and consistent with a general tend in which many fish taxa seem to be endemic to the Mazaruni alone. An undescribed species of *Exastilithoxus* (Ancistrini) from the upper Mazaruni has been reported in aquarium literature although we have not examined specimens, and *E. fimbriatus* is restricted to the upper Caroni. Two undescribed species of *Neblinichthys* (Loricariidae: Ancistrini) were collected during recent fieldwork in the upper Mazaruni by H. Lopez and D. Taphorn (pers. comm.), while the congeneric *N. yaravi* is only known from the upper Caroni. Non-loricariid taxa endemic to the Mazaruni include a recently described new species, possibly new genus, of parodontid (*Apareiodon agmatos*, Taphorn *et al.*, 2008), a basal crenicarine cichlid (*Mazarunia mazarunii*;

Kullander, 1990), a lebiasinid, possibly sister to the Pyrrhulininae (*Derhamia hoffmannorum*; Géry and Zarske, 2002), and a basal *Nannostomus* (*N. espei*; Weitzman and Cobb, 1975). The basal crenuchid *Skiotocharax meizon* was also described largely from the Mazaruni (Presswell *et al*., 2000). Taken together, these taxa provide strong evidence of long-term isolation of the Mazaruni River. Indeed, if the proto-Berbice paleodrainage hypothesis is correct, it seems like that the Mazaruni would have maintained its own mouth to the Atlantic through much of the Miocene-Pliocene when the proto-Berbice is thought to have exited further to the east.

4.4.3 Casiquiare Portal

The Casiquiare Canal is a large and permanent (navigable year round) corridor between the upper Orinoco and the upper Rio Negro (Amazon). Distributions of species across the Casiquiare have been studied by Chernoff *et al*., (1991), Buckup (1993), Schaefer and Provenzano (1993), Lovejoy and Araújo (2000), Turner *et al*. (2004), Moyer *et al*. (2005), and Willis *et al*. (2007). Winemiller *et al*. (2008) and Winemiller and Willis (Chapter 11 this volume) review this literature and supplement it with fish community ecology data transecting the entire Casiquiare. They suggest several distinct distribution patterns: broad distribution in the Orinoco and Negro, distribution in the upper Orinoco and upper Casiquiare (but not lower Casiquiare or Negro), and distribution in the lower Casiquiare and the Negro (but not upper Casiquiare or Orinoco). They attribute the second two distributional patterns to an environmental gradient from clearwater (Upper Orinoco) to blackwater (Negro). In addition to this limnological gradient, upper portions of the Orinoco and Negro are isolated from lower portions of their respective drainages by the high energy rapids Atures and Maipures (Orinoco) and São Gabriel (Negro). Several Amazonian species conspicuously absent from the Orinoco basin (*e.g., Osteoglossum* spp., *Arapaima gigas*, *Parapteronotus hasemani, Orthosternarchus tamandua*, *Symphysodon* spp.) are likely more subject to exclusion by the rapids at São Gabriel than by shifts in limnology.

Turner *et al*. (2004) and Moyer *et al*. (2005) reported complete segregation between mitochondrial genotypes of *Prochilodus mariae* and *P. rubrotaineatus* in the Orinoco and *P. rubrotaineatus* in the Negro and Essequibo. Likewise Lovejoy and Araújo (2000) identified basal haplotypes of *Potamorrhaphis* that were isolated in the upper Orinoco and not shared with Negro populations, indicating a barrier at the Casiquiare. Willis *et al*. (2007), however, observed that three of the four *Cichla* taxa present in the upper Orinoco (*C. monoculus, C. orinocensis, C. temensis*) were genetically similar to conspecifics in the upper Negro. Chernoff *et al*. (1991) list 16 species (11 Characiformes, four Siluriformes, one Gymnotiform) distributed from the upper Orinoco, across the Casiquiare, into the upper Negro, and the revision of characidiin fishes by Buckup (1993) gives eight more species whose distribution at least encompasses this divide.

Several loricariids have broad distribution patterns that include the Orinoco, Casiquiare, Negro, and possibly even northern tributaries of the Brazilian Shield. We have studied five species (two shield endemics and three shield specialists) of hypostomines that occur in the Orinoco, Casiquiare/Negro, and drainages of the Brazilian Shield - Shield Endemics: *Hemiancistrus sabaji* (Armbruster, 2008) and *Leporacanthicus galaxias*; Shield Specialists: *Hypostomus hemicochliodon* (Armbruster, 2003), *Lasiancistrus schomburgkii* (Armbruster, 2005), and *Peckoltia vittata* (Armbruster, 2008). Two of these species (*H. sabaji* and *L. schomburgkii*) are also found in the Essequibo. These species may offer the best insights into potentially recent movements of taxa among drainages of the Guiana Shield and between the Brazilian and Guiana Shield; however, intra-taxon relationships must be explored with genetic techniques to determine the relative timing of current distributions and degree of population structure. Three Shield Endemic genera have ranges similar to those outlined for the species above (*Baryancistrus, Hypancistrus,* and *Leporacanthicus*; Werneke *et al*., 2005a; Armbruster *et al*., 2007, Lujan et al., 2009) as do two Shield Specialist genera (*Hemiancistrus* and *Peckoltia*; Armbruster, 2008).

Several loricariids have distributions limited to the Upper Orinoco and upper Casiquiare. *Hemiancistrus guahiborum, H. subviridis, Hypostomus sculpodon, Pseudancistrus orinoco, P. pectegenitor,* and *P. sidereus* all occur in the upper Orinoco and Casiquiare, but are not currently known from elsewhere in the Amazon. A few recently described species from the Orinoco have putative sister species in the Casiquiare: *Hypancistrus inspector* (Casiquiare) vs. *H. contradens* and *H. lunaorum* (Orinoco) and *Pseudolithoxus nicoi* (Casiquiare) vs. *P. anthrax* (Orinoco). Given the relatively recent formation of the Casiquiare Portal (Late Pleistocene to Holocene; see *Proto-Amazon* above), these species may represent recent invasions from the Orinoco to the Casiquiare and/or relatively recent speciation events. Aside from a few widespread, blackwater adapted species (*e.g.,, Dekeyseria niveata, D. pulchra*), most ancistrin loricariids appear to be excluded from the lower Casiquiare and upper Negro by extremely blackwater limnology.

4.4.4 Southern Guiana Shield and Northern Brazilian Shield Corridors

The mainstem Amazon River likely acts as a partial barrier for both Shield Endemic and Shield Specialist taxa on the respective Guiana and Brazilian Shields. Genera known to withstand more lowland conditions (*e.g.,, Ancistrus, Lasiancistrus,* and *Hypostomus*) may be able to cross the Amazon Basin, but such dispersal is unlikely among most ancistrins. East-West dispersal around the southern part of the Guiana Shield may be via either southern Guiana Shield drainages or drainages of the northern part of the Brazilian Shield. Currently, the fauna of the northern Brazilian Shield is much better known than that of the southern part of the Guiana Shield. Species and genera mentioned above from both the Guiana and Brazilian shields offer potential examples of movement across the northern Brazilian Shield at least to the Tocantins. Dispersal along the southern flank of the Guiana Shield may be exemplified by *Pseudancistrus* sensu stricto as several undescribed species are known from these drainages; however, undescribed species are also known from the northern Brazilian Shield. Demonstration of ancistrin biogeographic patterns across the southern Guiana Shield and northern Brazilian Shield must, therefore, await further collections and analysis of genetic data. Amongst other fishes, the range of *Psectrogaster essequibensis* (Characiformes: Curimatidae; Vari, 1987) and *Parotocinclus ariapuanensis* and *P. britskii* (Loricariidae: Hypoptopomatinae) support dispersal via the northern Brazilian Shield, although we reiterate that collection data in this region are poor.

4.4.5 Rupununi Portal

The Rupununi Savanna floods seasonally, creating a lentic corridor between the Essequibo and Takutu Rivers, the latter of which was lost to the Negro via stream capture as recently as the Pleistocene (see *Proto-Berbice* above). Loricariids of the Essequibo are nearly identical to those of the Takutu, indicating either regular, recent dispersal across the flooded savanna or insufficient time for differentiation since stream capture. Among hypostomines we have examined, *Hemiancistrus sabaji*, *Hypostomus squalinus, H. macushi, Lasiancistrus schomburgkii, Lithoxus lithoides,* and *Pseudacanthicus leopardus* are well-represented in collections on either side of the Rupununi Portal and show no morphological differentiation between drainages. Many other fishes also have ranges that extend across the Rupununi Portal including *Osteoglossum bicirrhosum*, *Arapaima gigas, Psectrogaster essequibensis* (Vari, 1987), and *Rhinodoras armbrusteri* (Sabaj *et al*., 2008). Molecular phylogenetic studies by Lovejoy and Araújo (2000), Turner *et al.* (2004), and Willis *et al*. (2007) support transparency of the Rupununi Portal for *Potamorrhaphis*, *Prochilodus rubrotaeniatus*, and *Cichla ocellaris,* respectively.

The relative importance of the Rupununi Savannas as either portal or barrier is difficult to demonstrate. Collections of *Hypostomus taphorni* have been made from throughout the Essequibo, but from only one location in the Pirara River, a tributary of the Ireng (Negro) near the drainage divide, seemingly indicative of recent immigration. The existence of sister species *Peckoltia braueri* (Takutu) and *P. cavatica* (Essequibo) on either side of the divide seems to support the Rupununi's role as barrier. An undescribed species of both *Hypancistrus* and *Panaque* have only been collected on the Takutu River side, as has *Cichla temensis* (Willis *et al*., 2007), further supporting its role as barrier.

JWA's lab is currently investigating gene flow across the Rupununi Portal in several fish groups to determine both relative transparency of this portal for various taxa, and when it may have become closed to rheophilic species intolerant of conditions in the flooded savanna.

4.4.6 Atlantic Coastal Corridors

The exchange of fishes between Atlantic coastal drainages of the eastern Guianas (Guyana, Suriname, French Guiana) and the eastern Amazon Basin may be accomplished via either a coastal marine corridor with reduced salinity due to the westerly deflected Amazon River discharge, coastal confluences during times of lower sea level and expanded coastal plains, and/or headwater interdigitation and stream capture. The region can be broadly divided into the Western Atlantic Coastal Corridor (from the mouth of the Orinoco to the mouth of the Essequibo) and the Eastern Atlantic Coastal Corridor (from the mouth of the Essequibo to (and possibly beyond) the mouth of the Amazon.

The Atlantic Coastal region is poorly represented in molecular biogeographic studies of northern South America. Willis *et al*. (2007) report a single species of *Cichla* (*C. ocellaris*) distributed from the Essequibo in the west to the Oyapock in the east, but the aforementioned studies of *Potamorrhaphis* and *Prochilodus* do not cover this region. In a morphology based taxonomic revision demonstrating a similar pattern to that of *C. ocellaris*, Mattox *et al*. (2006) identified the single species *Hoplias aimara* in Atlantic coastal drainages from the eastern Amazon Basin as far west as the northern Guiana Shield drainages entering the Eastern Venezuela Basin, but not entering the upper Orinoco. Renno *et al*. (1990, 1991) investigated the population structure of *Leporinus* *friderici* using genetic markers and interpreted their data as providing support for the existence of an eastern and western Pleistocene refuge from which this species has more recently expanded its range. Their data identifies the Kourou River in French Guiana as the point of convergence between historically isolated eastern and western populations.

Low gradient streams of the Western Atlantic coastal plain's lower drainages are unsuitable for most ancistrins. *Hypostomus plecostomus* and *H. watwata*, coastal plain species that can be found in some estuaries, may use the low gradient streams and near-shore marine habitats to move between drainages along the whole Atlantic Coastal Corridor (Eigenmann, 1912; Boeseman, 1968). Several more rheophilic loricariid species are restricted to upland habitats across the Eastern Atlantic versant. *Lithoxus* spp. are found in upland habitats throughout the eastern Guiana Shield, and morphological characters suggest they are divided into a western, proto-Berbice subgenus (*Lithoxus*, 2spp.), and an Eastern Atlantic Coastal subgenus (*Paralithoxus*, 5 spp.; Boeseman, 1982, Lujan, 2008). *Pseudancistrus* sensu stricto is distributed throughout the eastern Guiana and northern Brazilian shields, with only a single Orinoco species, *P. reus,* restricted to the Caroni River (Armbruster and Taphorn, 2008). *Pseudancistrus barbatus* and *P. nigrescens* are distributed from the Essequibo to French Guiana (Eigenmann, 1912; Le Bail *et al*., 2000), *P. megacephalus* is in at least the Essequibo and Suriname Rivers (Eigenmann, 1912), and *P. brevispinnis* is found from the Corantijn to the Oyapock and in several northern tributaries of the Amazon (Cardoso and Montoya-Burgos, 2009). Several species of *Pseudacanthicus* are also found across the eastern Atlantic Coastal drainages of the Guianas, but specimens of these are rare in collections and they appear to be largely restricted to main river channels. *Pseudacanthicus* and *Pseudancistrus* are both

Shield Specialists, with ranges throughout the eastern Guiana and northern Brazilian shields, and *Lithoxus* is a Shield Endemic, making these groups excellent subjects for biogeographic studies of the eastern Guiana Shield and adjacent areas.

Cardoso and Montoya-Burgos (2009) conducted a molecular phylogeographic study of *Pseudancistrus brevispinnis* and found support for the hypothesis that this species invaded the Atlantic Coastal river system from the south-flowing Jari River, a tributary of the Amazon, via headwater interdigitation and stream capture with the north-flowing Marone River. From the Marone, *P. brevispinnis* dispersed eastward as far as the Oyapock River and westward as far as the Corantijn River (Cardoso and Montoya-Burgos, 2009). Similarly, Nijssen (1970) suggests a seasonal portal between the Sipalawini River (Corantijn River basin) and the Paru do Oeste River (Amazon River basin) across the potentially flooded Sipalawini – Paru Savanna. He used as support the range of *Corydoras bondi bondi*, which is found through much of Suriname, the Essequibo of Guyana, and the Yuruari (Cuyuni-Essequibo) of Venezuela; however, given the westward extent of *C. bondi bondi*'s range, the proto-Berbice or Eastern Atlantic Coastal Corridor might provide a better explanation. Regardless, Nijssen (1970) describes a variety of potential corridors between north-northeast flowing Atlantic Coastal rivers and south-flowing Amazon Rivers, and strong support for the transit of at least the species *Pseudancistrus brevispinnis* through these corridors was found by Cardoso and Montoya-Burgos (2009).

Availability of the Eastern Atlantic Coastal Corridor as a means of distribution between mouths of the Essequibo and the Amazon is suggested by ranges of *Curimata cyprinoids*, which is a lowland species that ranges throughout Atlantic Coast drainages from the Orinoco to the Amazon (Vari, 1987), *Parotocinclus britskii*, which ranges across Atlantic Coast drainages from the Essequibo to the Amazon (Schaefer and Provenzano, 1993), and several serrasalmin species with ranges extending from the Oyapock to the Amazon (Jégu and Keith, 1999).

4.4.7 Relictual Fauna

Inspired by Thurn's (1885) first ascent of Mount Roraima, Doyle (1912) wrote his fictional novel "The Lost World" about a prehistoric landscape isolated atop a table mountain and populated with ape men and dinosaurs. Although no such archaic member of the terrestrial fauna has yet been discovered, the Guiana Shield does harbor at least one aquatic taxon among the Loricarioidea that may have been swimming with dinosaurs of the Cretaceous. The genus *Lithogenes* includes three species that currently comprise the Lithogeninae of either the Astroblepidae of Loricariidae. *Lithogenes* is similar in external appearance to basal astroblepids and loricariids (Schaefer and Provenzano, 2008), but has a morphology so distinct that it does not fit comfortably into either of these loricarioid families. Armbruster (2004, 2008) and Hardman (2005) hypothesize that *Lithogenes* is sister to astroblepids, while Schaefer (2003) hypothesizes that the genus is sister to loricariids. In a phylogeny with nodes dated by a fossil-calibrated relaxed molecular clock, Lundberg *et al*. (2007) hypothesize that the split between the Astroblepidae and Loricariidae occurred approximately 85-90 Ma (*Lithogenes* was not included in the analysis). If *Lithogenes* is the sister to loricariids, it must also be at least 65–70 million years old (age of deepest node in the Loricariidae), but if *Lithogenes* is sister to astroblepids, it may be as young as 20 million years old (age of basal node in the Astroblepidae).

Two *Lithogenes* species, *L. villosus* (Potaro-Essequibo) and *L. wahari* (Cuao-Orinoco), are found in the Guiana Shield, and the third species, *L. valencia,* is thought to be from the Lago Valencia drainage in the coastal mountains of northern Venezuela (date and collector of the *L. valencia* type series are unknown and the species is currently thought extinct; Provenzano *et al*., 2003). The disjunct distribution of *L. villosus* and *L. wahari* on opposite sides of the western Guiana Shield is shared by a number of other rheophilic taxa, and may be the product of sequential capture of proto-Berbice headwaters by north- and west-flowing tributaries of the Orinoco. Dispersal via headwater capture seems a likely avenue for *Lithogenes*, which live in clear, swift flowing streams and have a specialized pelvic fin morphology adapted to climbing vertical surfaces (Schaefer and Provenzano, 2008).

Other rheophilic loricariid taxa that seem to represent disjunct East-West relicts of a more widespread proto-Berbice distribution include *Lithoxus*, *Exastilithoxus*, *Neblinichthys*, and *Harttia*. *Lithoxus* is represented in the west by *L. jantjae* in the upper Ventuari River (Orinoco) and in the east by *L. lithoides*, its putative sister species (Lujan, 2008) in the Essequibo, upper Branco, and Trombetas. *Exastilithoxus*, the sister of *Lithoxus*, is represented in the west by *E. hoedemani* in the Marauiá River (upper Negro), and in the east by *E. fimbriatus* in the upper Caroni. *Neblinichthys* is represented by *N. pillosus* from the Baria River (lower Casiquiare) and by *N. yekuana* from tributaries of the upper Caroni River. *Harttia* is represented by *H. merevari* in the upper Caura and upper Ventuari Rivers and by *H. platystoma* in the Essequibo River.

The disjunct distribution of *Lithogenes valencia* in the Coastal Range, across the Eastern Venezuela Basin from the Guiana Shield, is more difficult to explain. At no point in the hydrologic history of the Eastern Venezuela Basin (see above) was there a period in which high gradient habitat of the coastal mountain range seems to have been contiguous with that of the Guiana Shield. Periods of low sea level during the Middle Miocene eastward expansion of the Orinoco may be one period in which such contiguity existed. Dispersal from the shield, across the Apure Llanos to the Merida Andes and from there northeast via headwaters to the Coastal Mountain range represents another possibility. Regardless, the genus seems to have had a much wider distribution at one time, of which the three known localities represent relicts (Schaefer and Provenzano, 2008).

If *Lithogenes* is the sister lineage to astroblepids, a Guiana Shield origin is indicated for this diverse group of Andean-restricted loricarioids. Likewise, competition with and replacement by more highly derived astroblepids throughout the Merida Andes provides a compelling explanation for the possible extirpation of *Lithogenes* from Andean habitat between the Guiana Shield and the Coastal Mountains. The dispersal of rheophilic taxa from the Guiana Shield to the Andes, followed by radiation along the Andean flanks, is a pattern also apparent in the ancistrin clade comprising *Chaetostoma, Cordylancistrus, Dolichancistrus, Leptoancistrus, Exastilithoxus, Lithoxus,* and New Genus 2. New Genus 2 is known only from the upper Orinoco of Venezuela. It is sister to two clades: *Exastilithoxus* + *Lithoxus* and the *Chaetostoma* group (*Chaetostoma* + *Cordylancistrus* + *Dolichancistrus* + *Leptoancistrus*; Fig. 4; Armbruster, 2008).

Exastilithoxus and *Lithoxus* are endemic to the Guiana Shield, but all except two species of *Chaetostoma* are distributed across Andean drainages ranging from Panama to southeastern Peru. Species of *Cordylancistrus, Dolichancistrus,* and *Leptoancistrus* are distributed largely across the Northern Andes of Panama, Colombia, and Venezuela, although two species currently placed in *Cordylancistrus* (*C. platycephalus* and an undescribed species) are known from the Napo and Marañon of Ecuador and Peru. *Cordylancistrus torbesensis* is basal within the *Chaetostoma* group (Fig. 4), and it hails from southeastern slopes of the Merida Andes, across the Apure Llanos from the northwestern corner of the Guiana Shield. The distribution of sister clades across the Guiana Shield, a basal species in an adjacent region of the Andes, an intermediate radiation in the Northern Andes, and derived taxa across the Andes from north to south, supports a Guiana Shield origin for the *Chaetostoma* group. This largely Andean radiation has even contributed two species back to the ancistrin fauna of the Guiana Shield. *Chaetostoma jegui* and *C. vasquezi* are the only two non-Andean *Chaetostoma*, and they are present on the respective southern and northern slopes of the western Guiana Shield. *Chaetostoma jegui* is from the Uraricoera River (Branco) and *C. vasquezi* is from the Caura and Caroni (Orinoco). The derived position of both these species within *Chaetostoma* is supported by the presence of a fleshy excrescence (or keel) behind the head (Armbruster, 2004; Salcedo, 2006).

Another possible relict in the Guiana Shield is the loricariid *Corymbophanes* (Armbruster *et al*., 2000), which was found to be sister to all other hypostomines by Armbruster (2004, 2008). There are two species of *Corymbophanes*, both known only from the Potaro River above Kaieteur Falls where they are sympatric with *Lithogenes* *villosus*, and live in habitats occupied elsewhere by members of the Ancistrini. No ancistrins are present in the upper Potaro, likely because of their restriction to downstream habitats by Kaieteur Falls, a 226 m drop in the Potaro river over a scarp of the Guiana Shield uplifted in the Oligocene (Table 1).

The most basal loricariid subfamily (if *Lithogenes* is not a loricariid) is the Delturinae (Montoya-Burgos *et al*., 1997; Armbruster, 2004; 2008), which is known only from swift rivers of the southeastern Brazilian tributaries of the Brazilian Shield (Reis *et al*., 2006). With *Lithogenes* and the Delturinae in shield regions, it could be speculated that at least the loricariids (or loricariids + astroblepids) originated in the shields and subsequently spread through the rest of northern South and southern Central America. We doubt that the current ranges of the Lithogeninae and Delturinae represent the full historical distributions of these taxa, and suggest that the modern ranges represent relictual distributions. The fact that these two basal taxa are on opposite sides of the shield regions suggest that they or their ancestors had a range that may have included at least both shields. The origin of the Loricariidae in the shield regions is consistent with the hypothesis (*e.g.,,* Galvis, 2006) that shield areas were the most concentrated areas of high gradient aquatic habitat prior to significant uplift of the Andes. Loricariids share many elements of their highly-derived morphology with rheophilic specialist taxa in other parts of the world (*e.g.,,* sucker-like mouth with *Garra* and balitorid species in Asia and *Chiloglanis* in Africa, and encapsulated swimbladders with *Glyptothorax*, *Glyptosternum* and *Pseudecheneis* in Asia; Hora, 1922), indicating the selective pressures required for origination of these structures and supporting the origin of Loricariidae in high gradient habitats (Schaefer and Provenzano, 2008).

4.5 CONCLUSIONS

The Prone-8 biogeographic patterns of the Guiana Shield, coupled with more ancient drainage patterns within the Amazon-Orinoco basins, provide a conceptual framework upon which to build phylogeographic hypotheses for stream organisms in northern South America. The Guiana Shield is not merely an island of upland habitat, but shares extensive biogeographic connections with upland habitats of the Brazilian Shield, the Andes, and the Coastal Mountains. Distributions of loricariid taxa suggest that these connections to other areas have been important, but that within the Guiana Shield there has been little mixing of upland faunas via the Western Atlantic Coastal, and Caroni–Cuyuni/Mazaruni corridors. Most distributions within the Guiana Shield can be explained via currently contiguous rivers, stream capture events in the uplands of larger systems, and/or ancient river systems such as the proto-Berbice.

Because of temporal fluctuations in these connections, and their differential use by various taxa, there is no single hypothesis explaining biogeographic patterns across the Guiana Shield and neighboring uplands. We present a null hypothesis for biogeographic patterns based solely on our descriptions of basin evolution and geologic evidence of historical watershed boundaries (Fig. 5). Differential use of modern corridors of the Prone-8 can obscure these relationships, however, and give rise to a variety of divergent phylogeographic patterns. The disjunct distribution of *Lithogenes*, for example, could represent relicts from a broader Oligocene distribution, or could be due to more recent distribution via the proto-Orinoco, proto-Caura, or proto-Berbice. Figure 6 provides examples of three such alternative phylogeographic patterns.

Multiple biogeographic hypotheses described herein work for most taxa of the Guiana Shield, but no single explanation works for all taxa. Diverse, species-level phylogenies will be required to work out the timing and relative importance of proposed corridors. Further investigations of Guiana Shield biogeographic patterns will require genetic datasets that can be subjected to molecular-clock analyses, and studies of upland taxa are especially important because of their frequently smaller ranges, and corresponding potential for finer-scale resolution. The timing and dispersal rates of the *Chaetostoma* group, for example, from the Guiana Shield to the Andes and back again offer an intriguing opportunity to understand not only the relative importance of the Andes as a novel upland habitat, but also more general mechanisms of upland fish dispersal and evolutionary radiation. In today's advanced age of scientific understanding, the discoveries of primitive taxa and ancient biogeographic patterns still waiting to be made among fishes of the Guiana Shield are just as exciting as those fictionalized in Doyle's (1912) "The Lost World."

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Table 1. Planation surfaces, their age, elevation, and name in each country of the Guiana Shield (after Schubert et al., 1986, Briceno and Schubert, 1990, Gibbs and Barron, 1993).

Age of Uplift	Country	Surface	Elevation (m asl)
Pre-Late Cretaceous	Venezuela	Auyantepui	2000-2900
	Brazil	Roraima Sedimentary Plateau	1000-3000
Pre-Late Cretaceous	Venezuela	Kamarata-Pakaraima	1000-1200
	Guyana	Kanuku	900-1200
	Brazil	Gondwana	900-1200
Late Cretaceous-Paleocene	Venezuela	Imataca-Nuria	600-700
	Guyana	Kopinang	600-700
	Suriname	E.T.S.-Brownsberg	700-750
	French Guiana	First Peneplain	525-550
	Brazil	Sul-Americana	700-750
* no uplift from Lower Eocene to Lower Oligocene indicated by bauxite formations (McConnell, 1968)			
Oligocene-Miocene	Venezuela	Caroni-Aro	400-450
	Guyana-North	Kaieteur	250-350
	Guyana-South	Marudi	400-500
	Suriname	Late Tertiary I	300-400
	French Guiana	Second to Third Peneplain	200-370
	Brazil	Early Velhas	200-450
Plio-Pleistocene	Venezuela	Llanos	80-150
	Guyana-North	Rupununi	110-160
	Guyana-South	Kuyuwini	up to 200

	Suriname	Late Tertiary II	80-150
	French Guiana	Fourth Peneplain	150-170
	Brazil	Late Velhas	80-150
Holocene	Venezuela	Orinoco floodplain	0-50
	Guyana	Mazaruni	>80
	Suriname	Quaternary fluvial cycle	0-50
	Brazil	Parguaçu	0-50

Figure 1. Major rivers and drainage basins of the Guiana Shield: 1. Orinoco River, 2. Caroni River with Paragua River as its eastern tributary, 3. Caura River, 4. Ventuari River, 5. Orinoco headwater rivers, from north to south: Padamo, Matacuni, Ocamo, Orinoco, Mavaca, 6. Casiquiare Canal, 7. Siapa River, 8. Negro River, 9. Demini River, 10. Branco River, 11. Uatuma River, 12. Trombetas River, 13. Paru do Oeste River, 14. Paru River, 15. Jari River, 16. Oyapok River, 17. Marone River, 18. Coppename River to the west and Surinam River to the east, 19. Corentyne River, 20. Essequibo River, 21. Potaro River, 22. Cuyuni River, 23. Uraricoera River, 24. Rupununi Savanna bordered on the west by the Takutu River and on the east by the Rupununi.

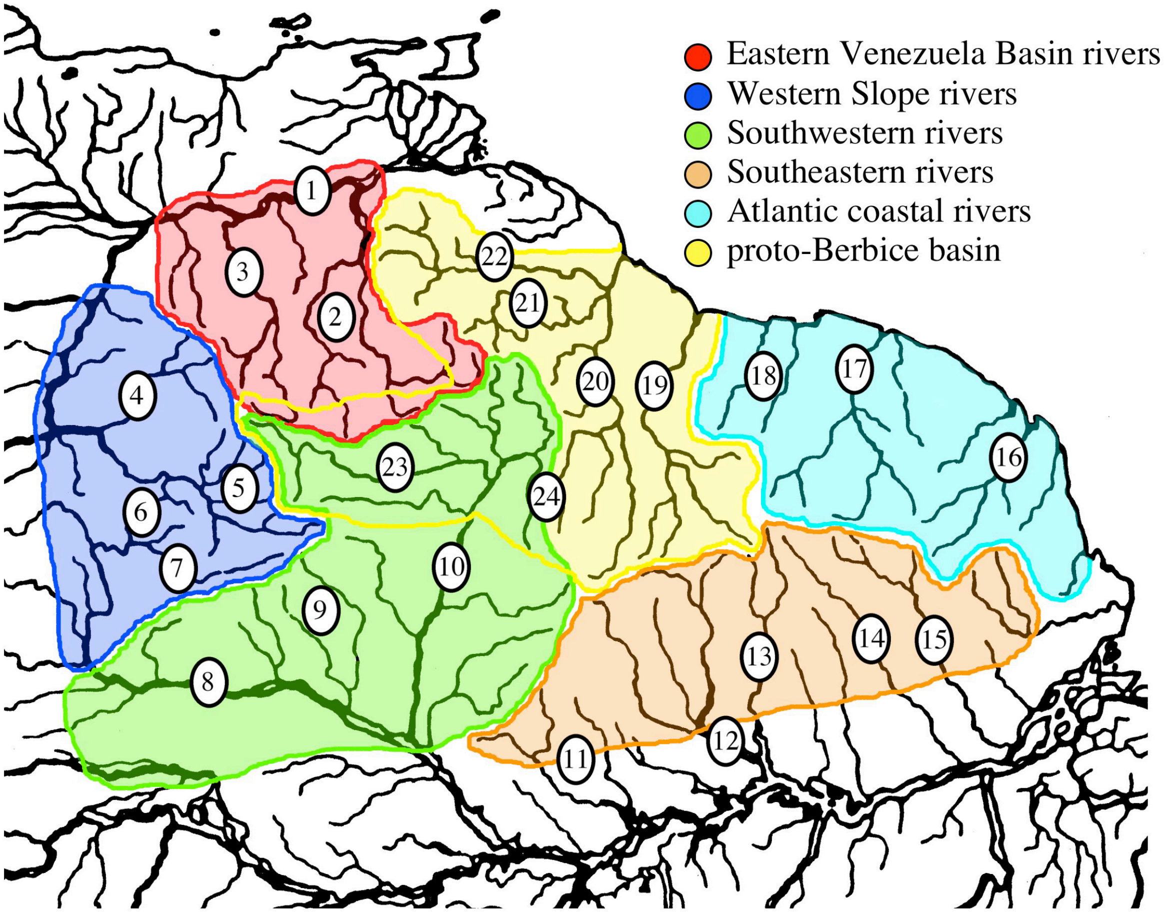
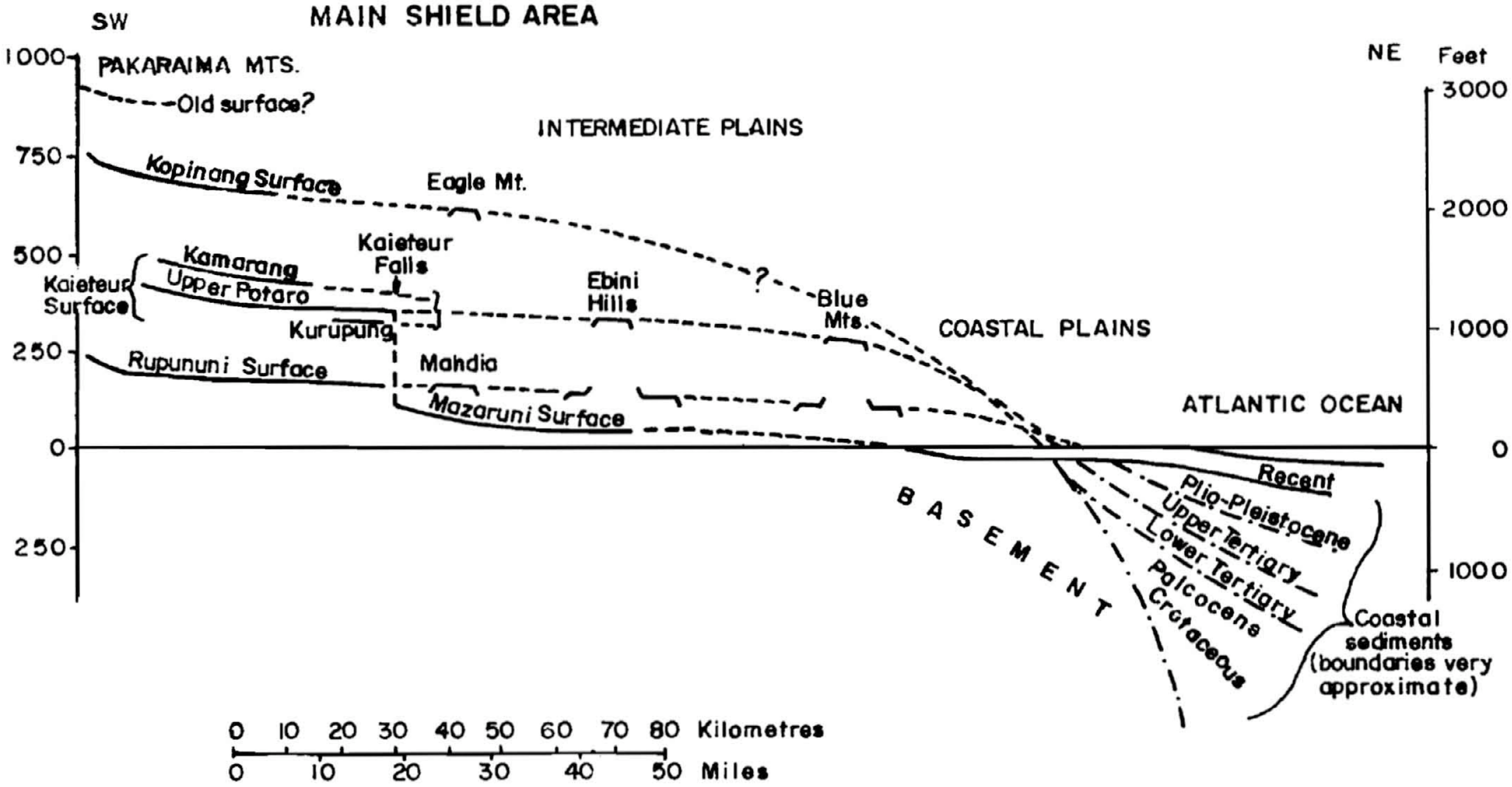


Figure 2. Schematic showing relationships among planation surfaces in Guyana, their historical contiguity (dashed lines) and their modern remnants (solid lines). Elevation of each surface relative to contemporary sea level in meters on the left and feet on the right (from McConnell, 1968).



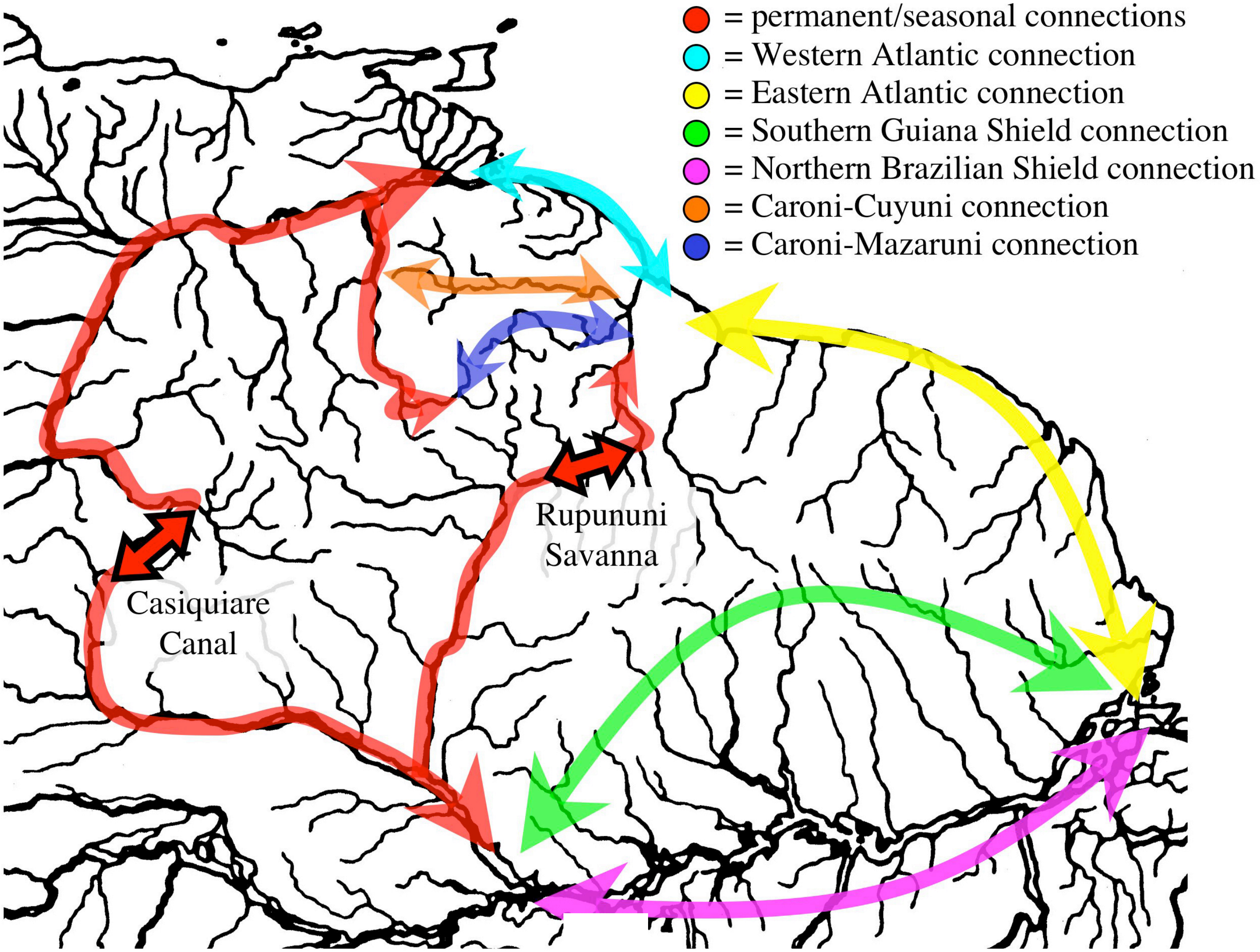


Figure 3. The Prone-8: hypothesized areas of movement between basins of the Guiana Shield. Area of some connections are approximate.

Figure 4. Phylogenetic hypothesis for the *Chaetostoma*-group (from Armbruster, 2008).

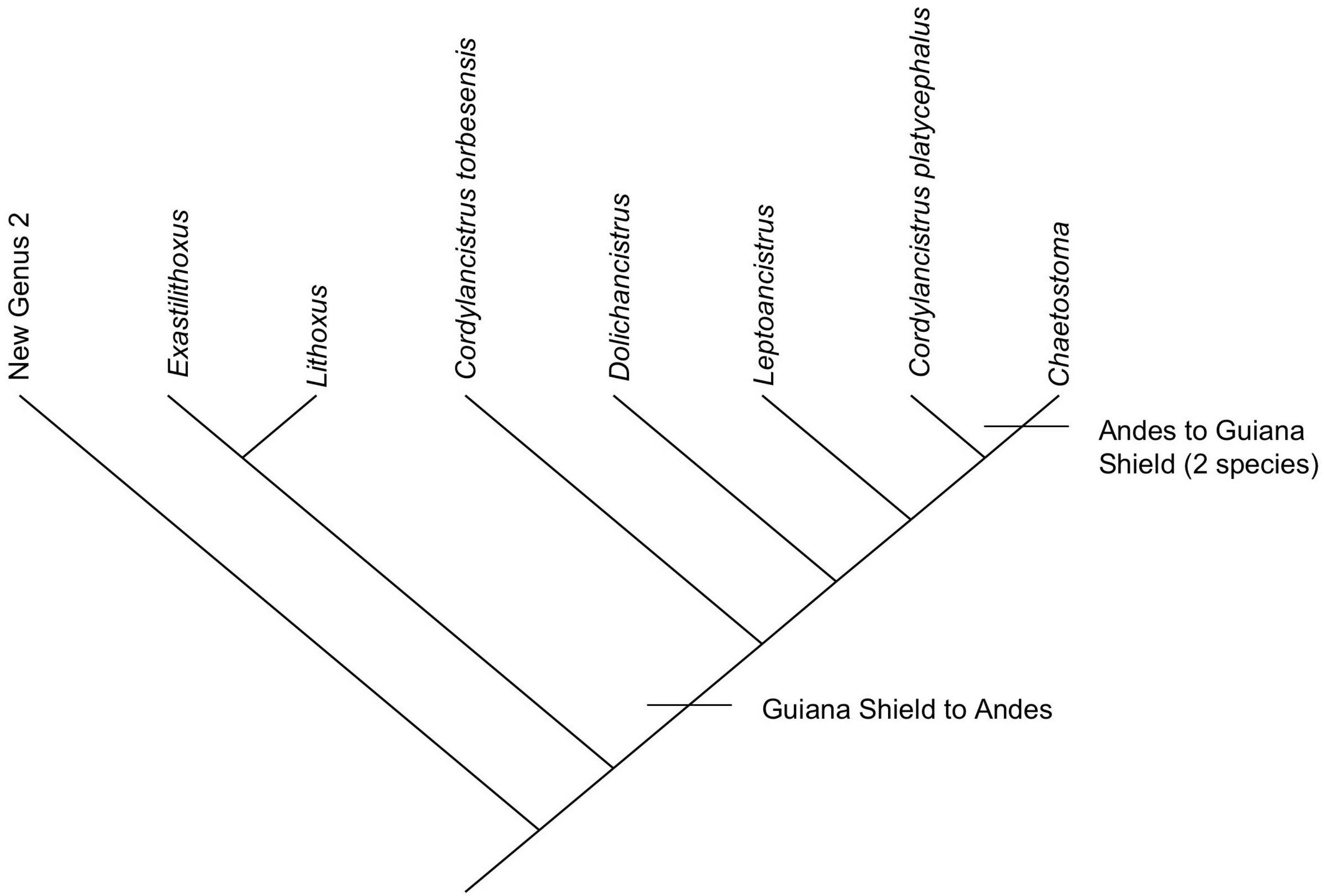


Figure 5. Null hypothesis of areal relationships among Guiana Shield fishes based only upon hydrologic history. Basal node represents the historical continental divide between eastern and western drainages at the Purus Arch. Terminal nodes represent modern river drainages with text color indicating major modern drainage basin: green = Amazon River, blue = Orinoco River. Three major clades of modern river drainages (proto-Orinoco, proto-Berbice, and NE Atlantic Coast) represent historical contiguity and regional affinities. Historical geologic and hydrologic events at internal nodes labeled accordingly.

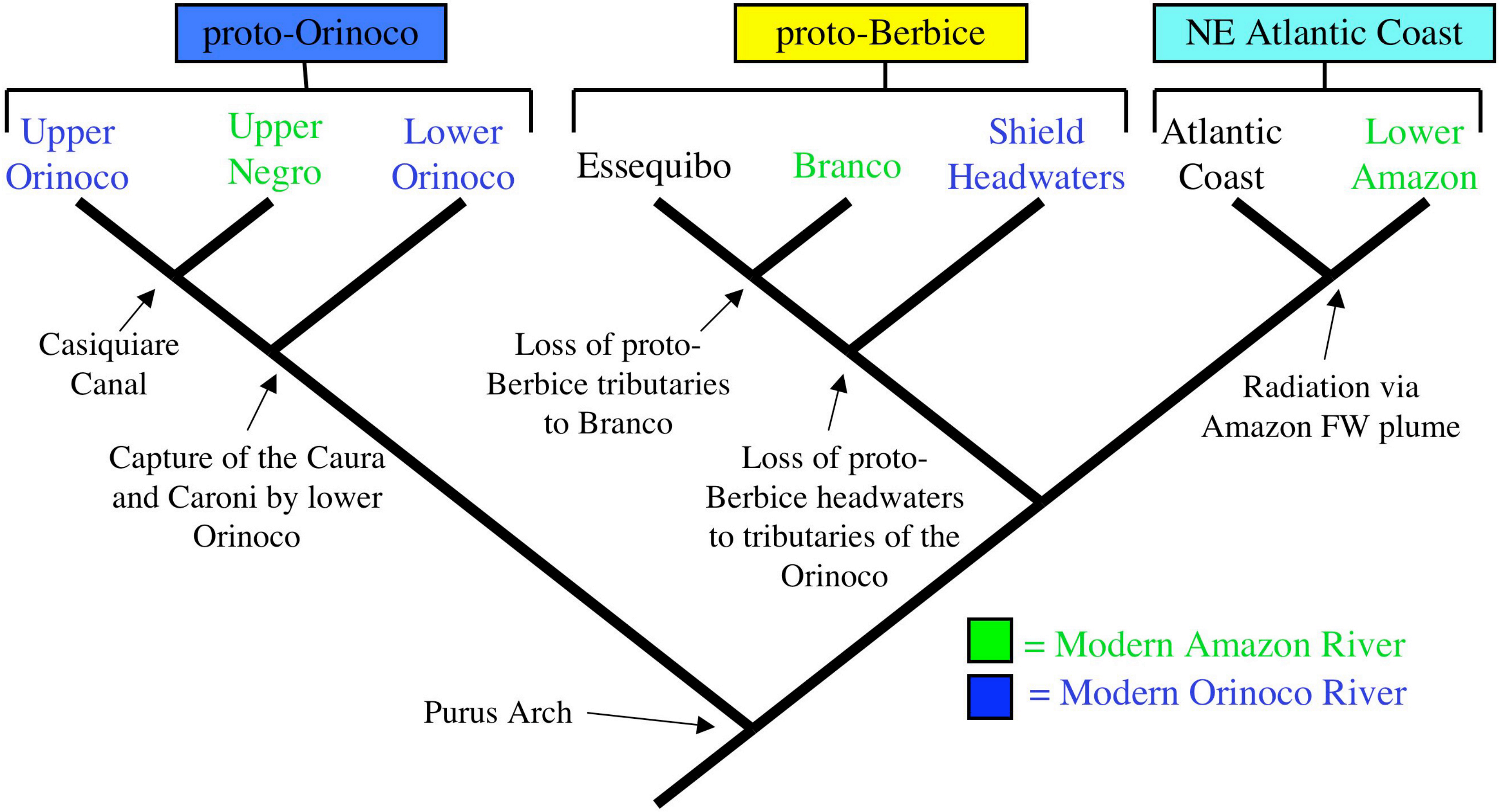
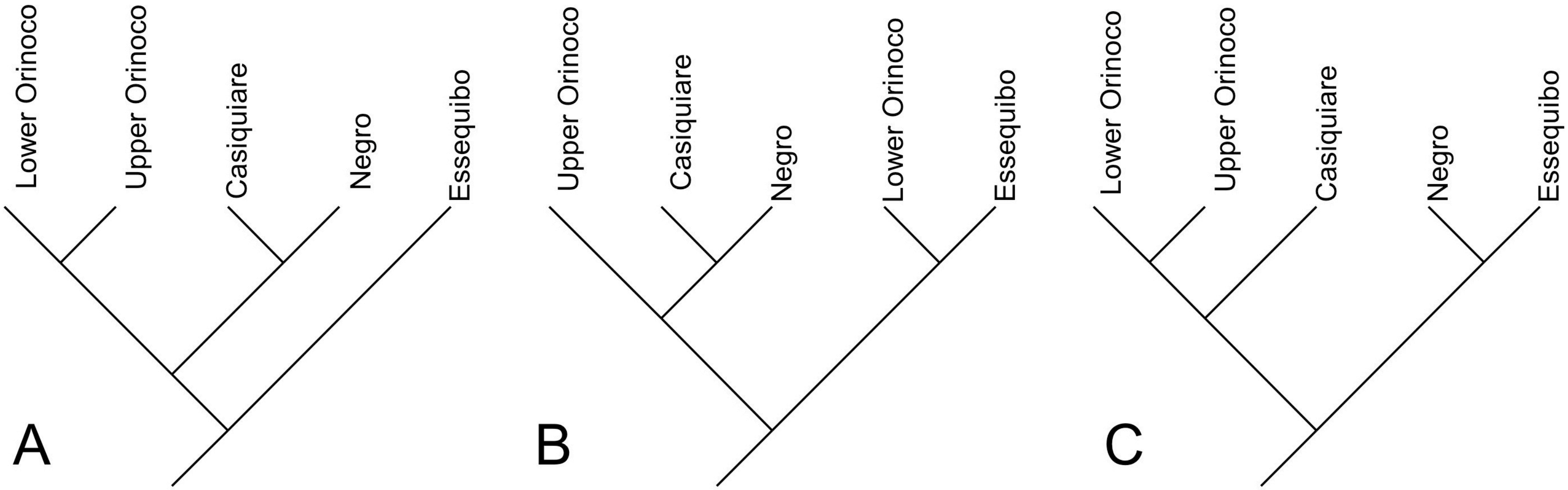


Figure 6. Three different biogeographic hypotheses based on differential use of connections in the Prone-8. A. Hypothesis based on current drainage patterns. B. Hypothesis if the Mazaruni-Caroni, Cuyuni- Caroni or Western Atlantic Coastal Connections were used. C. Hypothesis considering the Casiquiare to be Orinoco in origin.



APPENDIX I. Citations and abstracts of published or submitted manuscripts.

Armbruster, J. W., L. A. Tansey, and N. K. Lujan. 2007. *Hypostomus rhantos* (Siluriformes: Loricariidae), a new species from southern Venezuela. Zootaxa 1553:59–68.

Hypostomus rhantos is described for a uniquely pigmented species of loricariid catfish from the upper Río Orinoco of Amazonas, Venezuela. *Hypostomus rhantos* can be separated from all other *Hypostomus* except *H. micromaculatus* by having its head and dorsal and lateral surfaces of body densely covered in very small spots (greater than 15 spots on the first plate in the dorsal series of specimens less than 100 mm SL vs. less than 10; greater than 30 spots in specimens greater than 100 mm SL vs. less than 15). The new species is distinguished from *H. micromaculatus* by having round spots (vs. longitudinally oval) that are unordered (vs. in longitudinal lines), by having well-developed keels on the lateral plates (vs. keels weak), by the presence of a ridge on the pterotic that is contiguous with the supraorbital ridge (vs. pterotic ridge absent), and by having the abdomen fully plated (vs. partially plated or naked).

Armbruster, J. W., N. K. Lujan, and D. C. Taphorn. 2007. Four new *Hypancistrus* (Siluriformes: Loricariidae) from Amazonas, Venezuela. Copeia 2007:62–79.

Hypancistrus contradens, H. debilittera, H. furunculus, and *H. lunaorum* are described based on specimens from the upper Río Orinoco of southern Venezuela. *Hypancistrus furunculus* differs from other *Hypancistrus* based on color pattern: distinct dark oblique stripes ending at posterior insertion of dorsal fin and vertical bands in caudal fin (vs. oblique stripes ending at end of caudal fin in *H. zebra* and thin, indistinct, light-colored bands and vermiculations on a dark background in *H. debilittera*) and color pattern dark with white spots in *H. contradens, H. inspector*, and *H. lunaorum*. *Hypancistrus contradens* and *H. lunaorum* differ from *H. inspector* by having the dorsal fin reaching the adipose fin when adpressed (vs. not reaching), having spots on the head the same size as the body or spots absent (vs. spots smaller on head) and by usually having 22–23 mid-ventral plates (vs. 24); and from *H. debilittera, H. furunculus*, and *H. zebra* by lacking bars, saddles, or stripes on the body and bands in the fins. *Hypancistrus lunaorum* differs from *H. contradens* by having white spots on the body smaller than nasal aperture diameter (vs. white spots larger than the nasal aperture diameter).

Lujan, N. K. 2008. Description of a new *Lithoxus* (Siluriformes: Loricariidae) from the Guayana Highlands with a discussion of Guiana Shield biogeography. Neotropical Ichthyology 6:413–418.

Lithoxus jantjae, new species, is described from above Tencua Falls in headwaters of the Ventuari River, a white- to clearwater river flowing west from the Maigualida and Parima mountains in the Guayana Highlands of southern Venezuela. *Lithoxus jantjae* represents a nearly 600 km westward range expansion for a genus historically known only from Guyana, Suriname, French Guiana, and Brazil. *Lithoxus jantjae* shares with other species of *Lithoxus* a dorsoventrally depressed body and a large, papilose oral disk with small toothcups and few teeth. It can be distinguished from congeners by a unique combination of characters including 12 branched caudal-fin rays, medial premaxillary tooth cusps enlarged, and a convex posterior margin of the adipose-fin membrane. With the discovery of *L. jantjae*, *Lithoxus* becomes the most recent example of a growing list of rheophilic loricariid genera with disjunct distributions on east and west sides of the Guayana Highlands. A biogeographic hypothesis relying on the existence of a proto-Berbice River uniting the southern Guayana Highlands with rivers of the central Guiana Shield is advanced to partially explain the modern distribution of these species.

Lujan, N. K., and C. C. Chamon. 2008. Two new species of Loricariidae (Teleostei: Siluriformes) from main channels of the upper and middle Amazon Basin, with discussion of deep water specialization in loricariids. Ichthyological Exploration of Freshwaters 19:271–282.

Hemiancistrus pankimpuju, new species, and *Panaque bathyphilus*, new species, are described from the main channel of the upper (Marañon) and middle (Solimões) Amazon River respectively. Both species are diagnosed by having nearly white bodies and fins, long filamentous extensions of both simple caudal-fin rays, small eyes, absence of an iris operculum and unique combinations of morphometrics. The coloration and morphology of these species, unique within Loricariidae, are hypothesized to be apomorphies associated with life in the dark, turbid depths of the Amazon mainstem. Extreme elongation of the caudal filaments in these and a variety of other main channel catfishes is hypothesized to have a mechanosensory function associated with predator detection.

Lujan, N. K., and J. W. Armbruster. 2009a. Geological and hydrological history of the

Guiana Shield and historical biogeography of its fishes. In press *in* J. Albert and R. Reis, editors. Historical Biogeography of Neotropical Freshwater Fishes. Pfeil-Verlag, Munich.

See Chapter 4.

Lujan, N. K., and J. W. Armbruster. 2009b. Two new ancistrin genera and species (Siluriformes: Hypostominae) from the western Guiana Shield with discussion of swimbladder and jaw morphological variation across the Loricariidae. Ichthyological Exploration of Freshwaters in review.

Two new ancistrin genera and species are described from the upper Orinoco River watershed in Amazonas, Venezuela. *Micracanthicus vandragti* is black with white spots and distinguished by its small body-size, large swimbladder capsules, and highly protrusible lower jaws with short tooth cups and five to eight long teeth. The known range of *Micracanthicus vandragti* is restricted to the confluence of the Ventuari and Orinoco Rivers. *Soromonichthys stearleyi* is green with small yellow-gold spots on the head and thin vertical bars on the body, and has long jaw rami with 39 to 69 teeth. It is distinguished by its coloration and by its unique pattern of snout deplatation (plates missing from mesethmoid surface, anteriormost margin of snout, and small region posterior from anterolateral snout margin; plates present in column along either side of mesethmoid). *Soromonichthys stearleyi* is known only from Soromoni Creek, a tributary of the upper Orinoco draining southern slopes of Mount Duida. Phylogenetic analysis recovered *Micracanthicus* at the base of the *Acanthicus* clade within the larger *Panaque* clade, and *Soromonichthys* at the base of the *Lithoxus* clade within the larger *Ancistrus* clade. *Micracanthicus* and *Soromonichthys* represent near opposite ends of the spectrum of jaw and swimbladder morphologies in their respective clades, and are discussed in relation to variation and functional evolution in these characters across Loricariidae.

Lujan, N. K., J. W. Armbruster, and M. H. Sabaj. 2007. Two new species of *Pseudancistrus* from southern Venezuela (Siluriformes: Loricariidae). Ichthyological Exploration of Freshwaters 18:163–174.

Two new species of the loricariid genus *Pseudancistrus* are described from the upper Río Orinoco and Río Negro in Southern Venezuela. *Pseudancistrus pectegenitor* was collected in the main channel of the Río Orinoco near the mouth of the Río Ventuari and in the middle reaches of the Río Casiquiare. It differs from congeners by having 10-11 dorsal-fin rays (vs. seven), adpressed cheek odontodes reaching to three or more plates beyond the opercle in adults (vs. maximally to rear edge of the opercle), plates of ventral row of caudal peduncle with dorsal laminae strongly concave, accentuating the medial keel of the ventral plate row (shared with *P. sidereus*), and large oral papillae internal to the dentary tooth cup (shared with *P. coquenani, P. orinoco,* and *P. yekuana*). *Pseudancistrus yekuana* is known only from the type locality, immediately upstream of Salto Tencua in the upper Río Ventuari. It differs from congeners by having large oral papillae internal to the dentary tooth cup (shared with *P. coquenani, P. orinoco,* and *P. pectegenitor*), lower lip reaching to middle of pectoral girdle (vs. to anterior edge of pectoral girdle), pectoral-fin spine maximally reaching posterior base of the pelvic-fin spine when adpressed ventral to the pelvic fin (vs. at least halfway through pelvic-fin insertion) and by several morphometric differences.

Lujan, Nathan K., M. Arce, and Jonathan W. Armbruster. 2009. A new black *Baryancistrus* with blue sheen from the upper Orinoco (Siluriformes: Loricariidae).

Copeia 2009:50–56.

Baryancistrus beggini, new species, is described from the upper Río Orinoco and lower portions of its tributaries, the Río Guaviare in Colombia and Río Ventuari in Venezuela. *Baryancistrus beggini* is unique within Hypostominae in having a uniformly dark black to brown base color with a blue sheen in life, and the first three to five plates of the midventral series strongly bent forming a distinctive keel above the pectoral fins along each side of the body. It is further distinguished by having a naked abdomen, two to three symmetrical and ordered predorsal plate rows including the nuchal plate, and the last dorsal-fin ray adnate with adipose fin via a posterior membrane that extends beyond the preadipose plate up to half the length of the adipose-fin spine.

Rengifo, B., N. K. Lujan, D. Taphorn, and P. Petry. 2008. A new species of *Gelanoglanis* (Siluriformes: Auchenipteridae) from the Marañon River (Amazon Basin), northeastern Peru. Proceedings of the Academy of Natural Sciences of Philadelphia 157:181–188.

We describe a new species of driftwood catfish, *Gelanoglanis travieso,* (Siluriformes: Auchenipteridae) from the Marañon River, a whitewater tributary of the Amazon River in northeastern Perú. It shares with the two described species in this genus, *G. stroudi*, from left bank whitewater tributaries of the Orinoco River in Colombia and Venezuela, and *G. nanonocticolus* from blackwater tributaries of the upper Orinoco and Negro Rivers in Amazonas, Venezuela and northern Brazil, the following synapomorphies: reduced size, compressed body, conical snout, a single pair of mental barbels, premaxillae widely separated at rostral border of upper jaw, premaxillary and dentary tooth patches narrow, posterior naris long and narrow and positioned immediately anterior to orbit, and small eyes. *Gelanoglanis travieso* differs from all congeners in having second dorsal-fin lepidotrichium filamentous, simple, not a spine, and not serrate (shared with *G. nanonocticolus*); pectoral-fin spine stout, serrate along posterior margin (shared with *G. stroudi*); and a terminal mouth (vs. subterminal in *G. nanonocticolus* and *G. stroudi*).

Werneke, D. C., J. W. Armbruster, N. K. Lujan, and D. C. Taphorn. 2005. *Hemiancistrus guahiborum*, a new suckermouth armored catfish from Southern Venezuela (Siluriformes: Loricariidae). Neotropical Ichthyology 3:543–548.

Hemiancistrus guahiborum, new species, is described from the Orinoco River drainage of Venezuela. *Hemiancistrus guahiborum* can be separated from all other *Hemiancistrus* and all *Peckoltia* except *P. braueri* and *P. cavatica* by having an orange edge to the dorsal and caudal fins. *Hemiancistrus guahiborum* can be separated from *Peckoltia cavatica* and *P. braueri* by having the dorsal fin with separated light spots or uniformly colored (*vs.* with dark spots forming bands) and the sides either solidly colored or with tan blotches (*vs.* with dark dorsal saddles).

Werneke, D. C., M. H. Sabaj, N. K. Lujan, and J. W. Armbruster. 2005. *Baryancistrus demantoides* and *Hemiancistrus subviridis*, two new uniquely colored species of catfishes from Venezuela (Siluriformes: Loricariidae). Neotropical Ichthyology 3:533–542.

Baryancistrus demantoides and *Hemiancistrus subviridis* are two new species of uniquely pigmented loricariids from southern Venezuela with an olive ground coloration and white to cream-colored or golden-yellow spots. *Baryancistrus demantoides* is known only from the upper río Orinoco drainage while *H. subviridis* is also known from the río Casiquiare drainage. In addition to its coloration, *B. demantoides* can be distinguished from all other ancistrins by having dorsal and adipose fins connected by an expanded posterior section of the dorsal-fin membrane, lemon-colored spots confined to the anterior portion of the body, and greater than 30 teeth per jaw ramus. *H. subviridis* can be separated from all other ancistrins by lacking a connection between the dorsal and adipose fins and by having fewer than 30 teeth per jaw ramus.

APPENDIX II. Vectors from loricariid assemblage ∂^{13}C and ∂^{15}N centroids to species means. Data from 19 localities and 83 species pooled and sorted according to taxon. When data permit, direction of mean vector for each taxon shown as dashed radius, and 95% circular confidence intervals are shown as either dashed (significant, $p<0.05$) or dotted (not significant, $p \geq 0.05$) arcs. Vectors for species represent individual samples. Vectors for all higher taxa represent species means.

Figure 1. Hypostominae: Ancistrini, Hypostomini, Pterygoplichthyini; and Hypoptopomatinae: Hypoptopomatini.

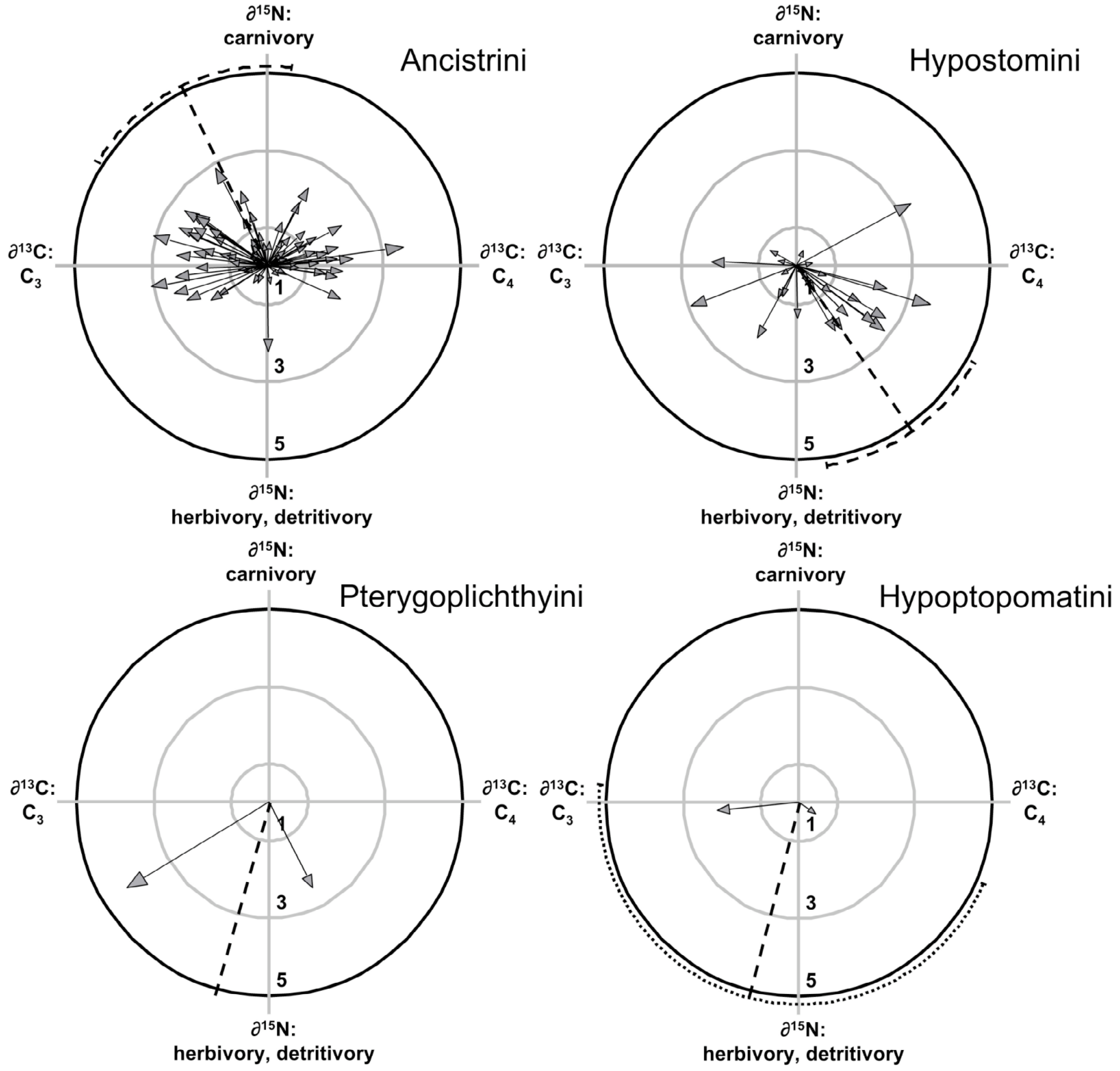


Figure 2. Loricariinae: Loricariini, Harttiini, Farlowellini.

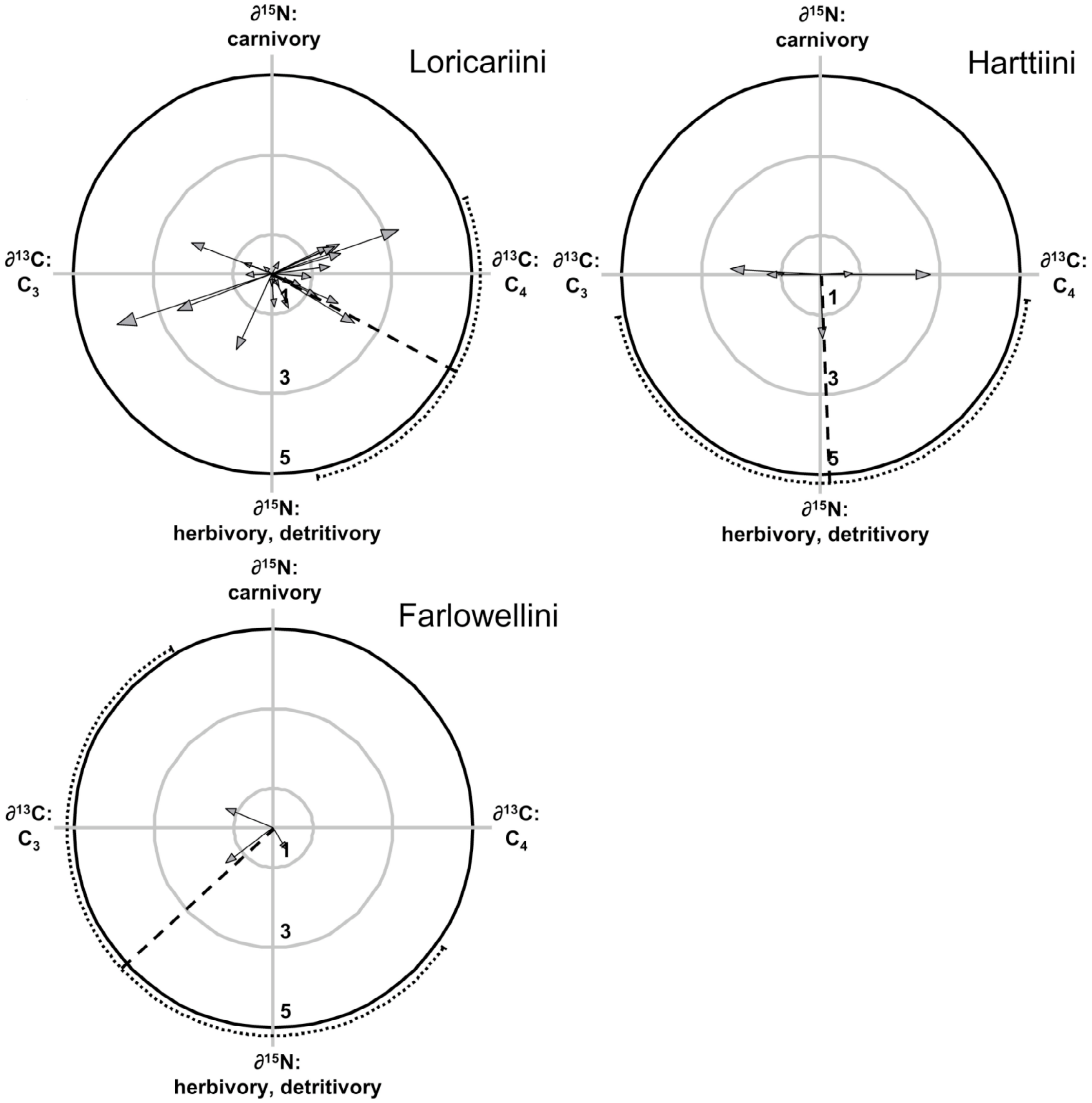


Figure 3. Hypostominae, Ancistrini: *Ancistrus, Chaetostoma, Lasiancistrus*, and *Dekeyseria*.

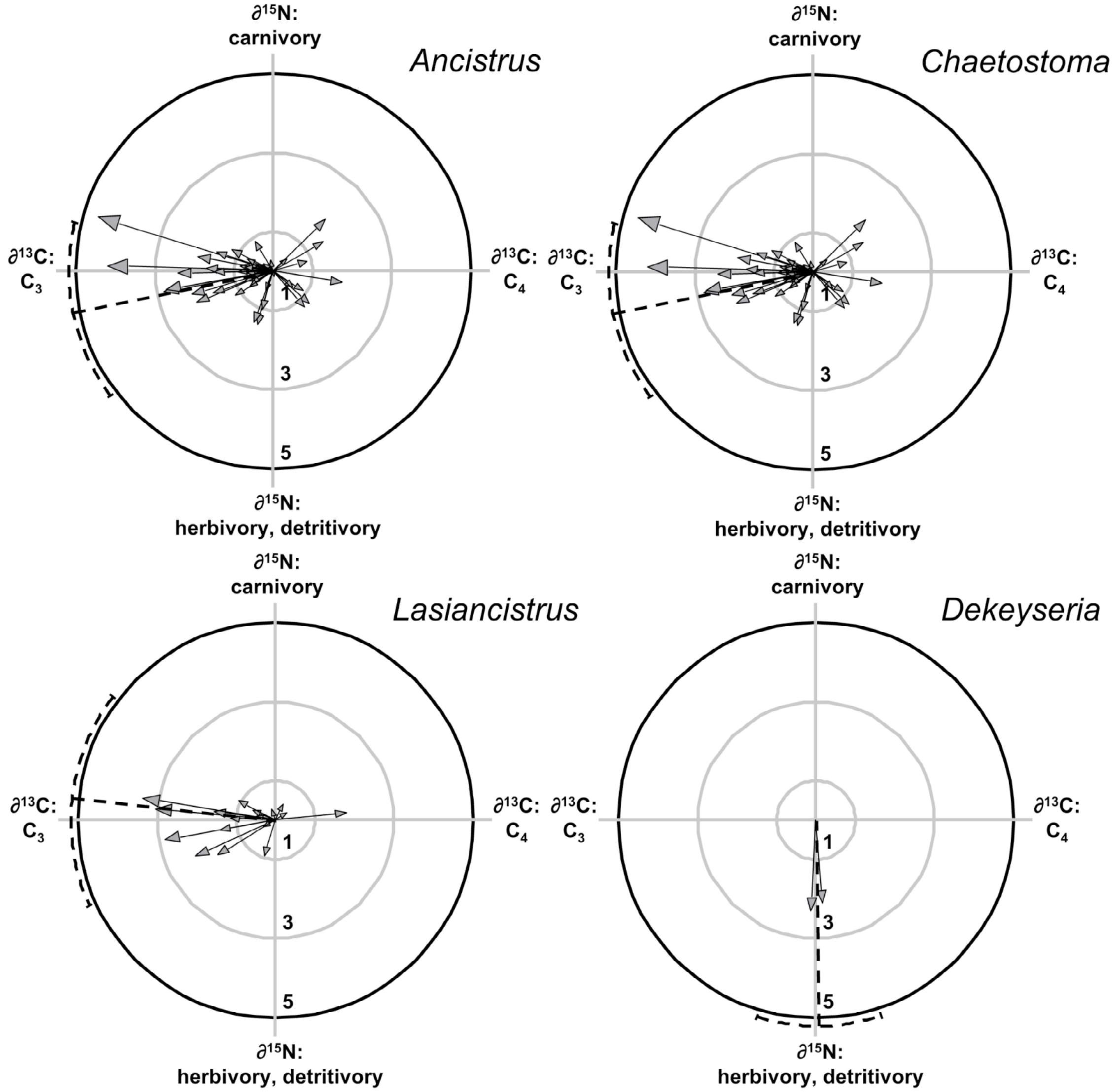


Figure 4. Hypostominae, Ancistrini: *Baryancistrus, Hemiancistrus, Hopliancistrus, Lithoxus, Oligancistrus*, and *Pseudancistrus*.

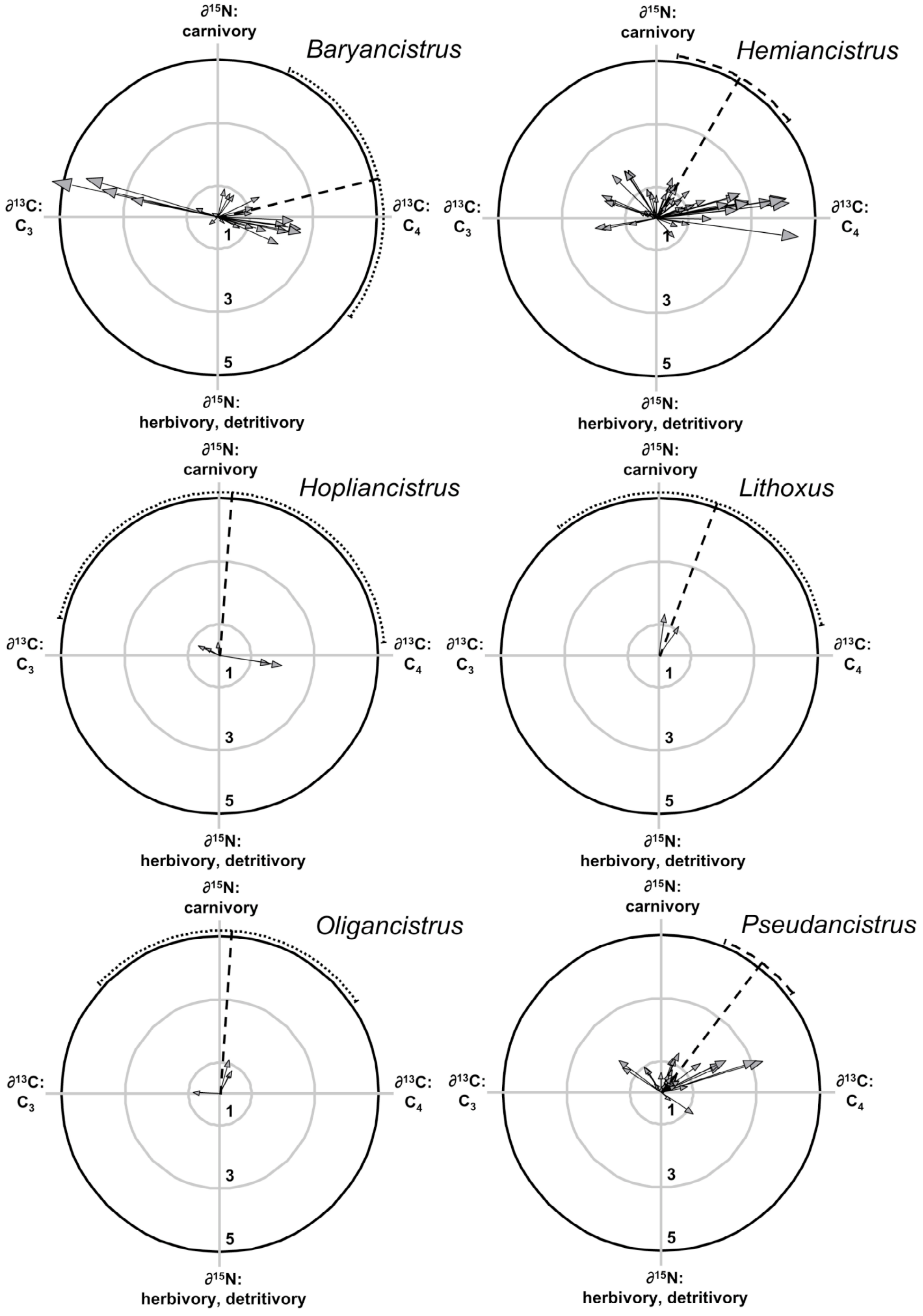


Figure 5. Hypostominae, Ancistrini: *Peckoltia, Pseudacanthicus, Pseudolithoxus*, and New Genus 3.

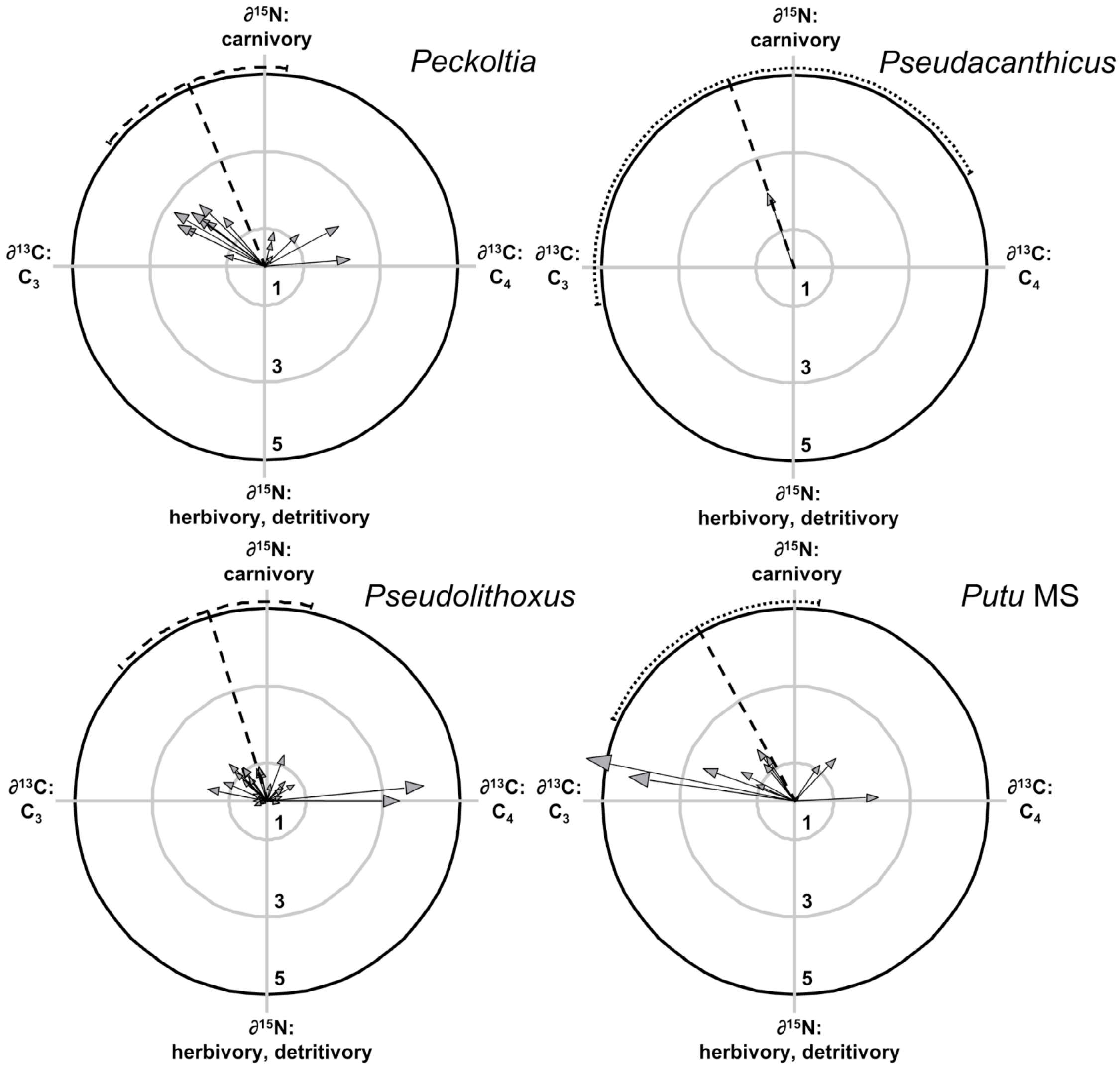


Figure 6. Hypostominae, Ancistrini: *Hypancistrus, Leporacanthicus*, and *Scobinancistrus*.

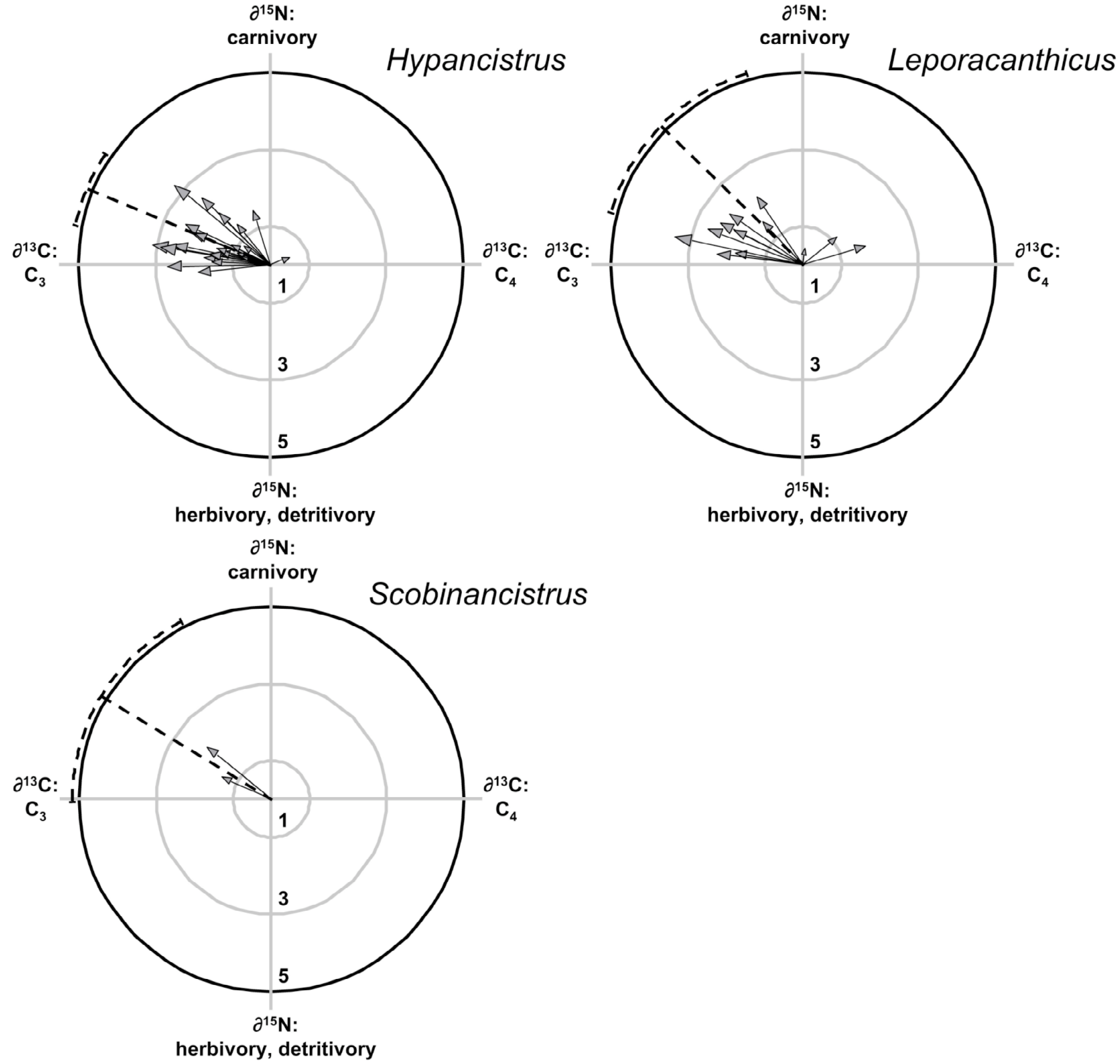


Figure 7. Loricariinae, Hartiini: *Harttia, Lamontichthys*, and *Sturisoma*; Farlowellini, *Farlowella*; and Hypoptopomatinae, Hypoptopomatini, *Hypoptopoma*.

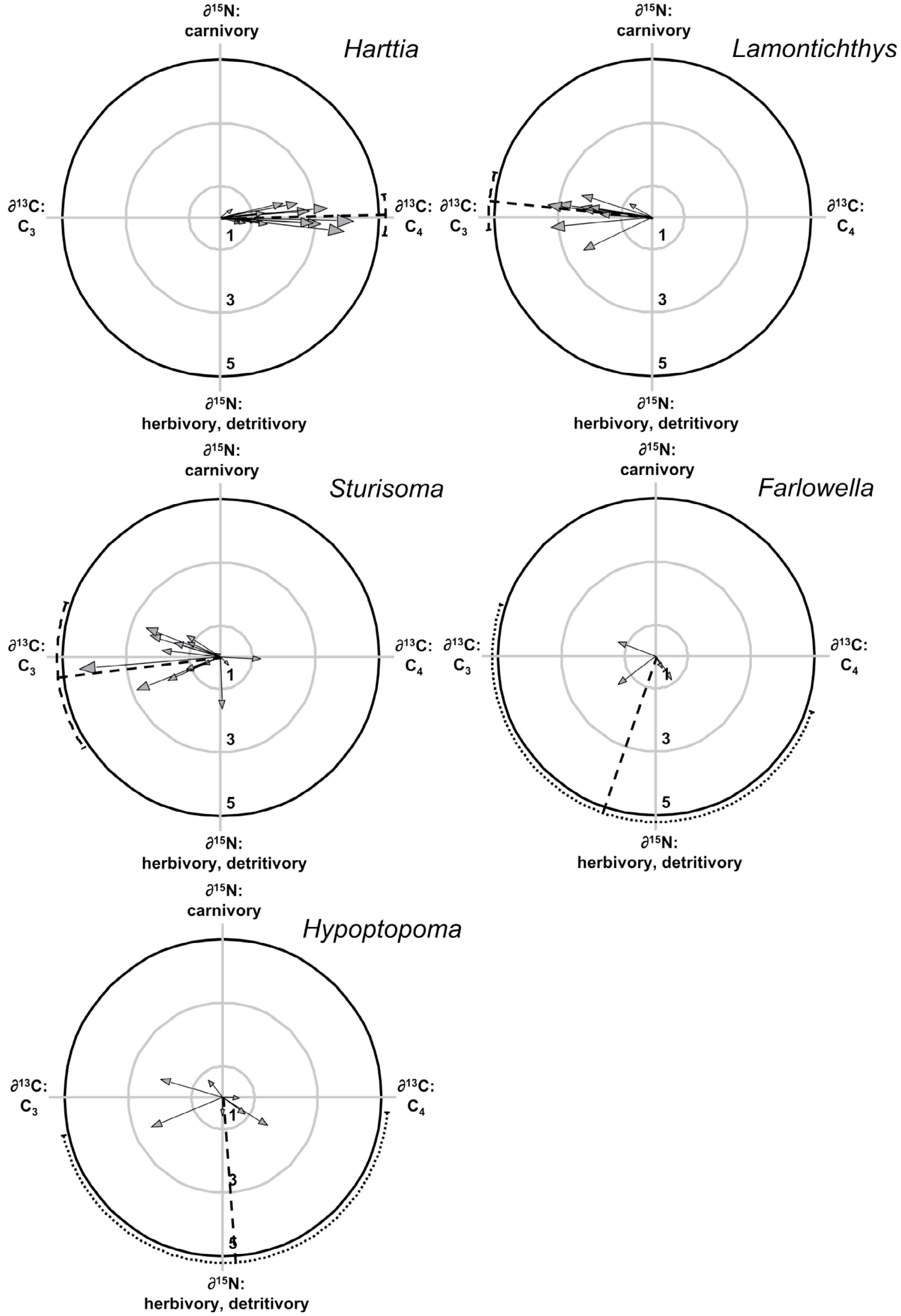


Figure 8. Loricariinae, Loricariini: *Loricaria, Pseudoloricaria, Limatulichthys, Rineloricaria, Loricariichthys*, and *Spatuloricaria*.

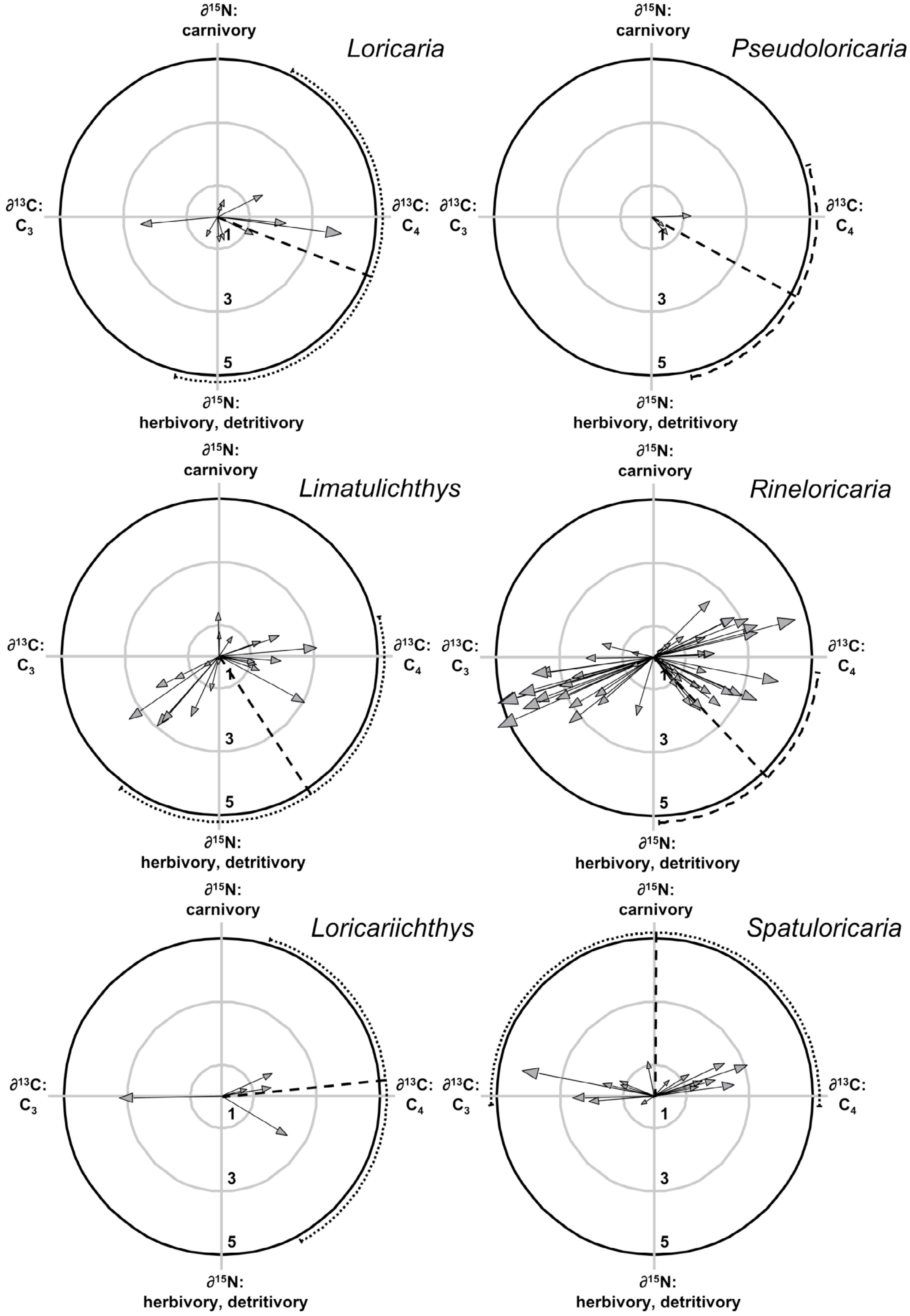


Figure 9. Hypostominae, Ancistrini: *Ancistrus macrophthalmus*, *A. temminckii*, *Ancistrus* sp. 'longjaw', *Ancistrus* sp. 'shortjaw', *Ancistrus* sp. 'wormline', and *Ancistrus* sp.

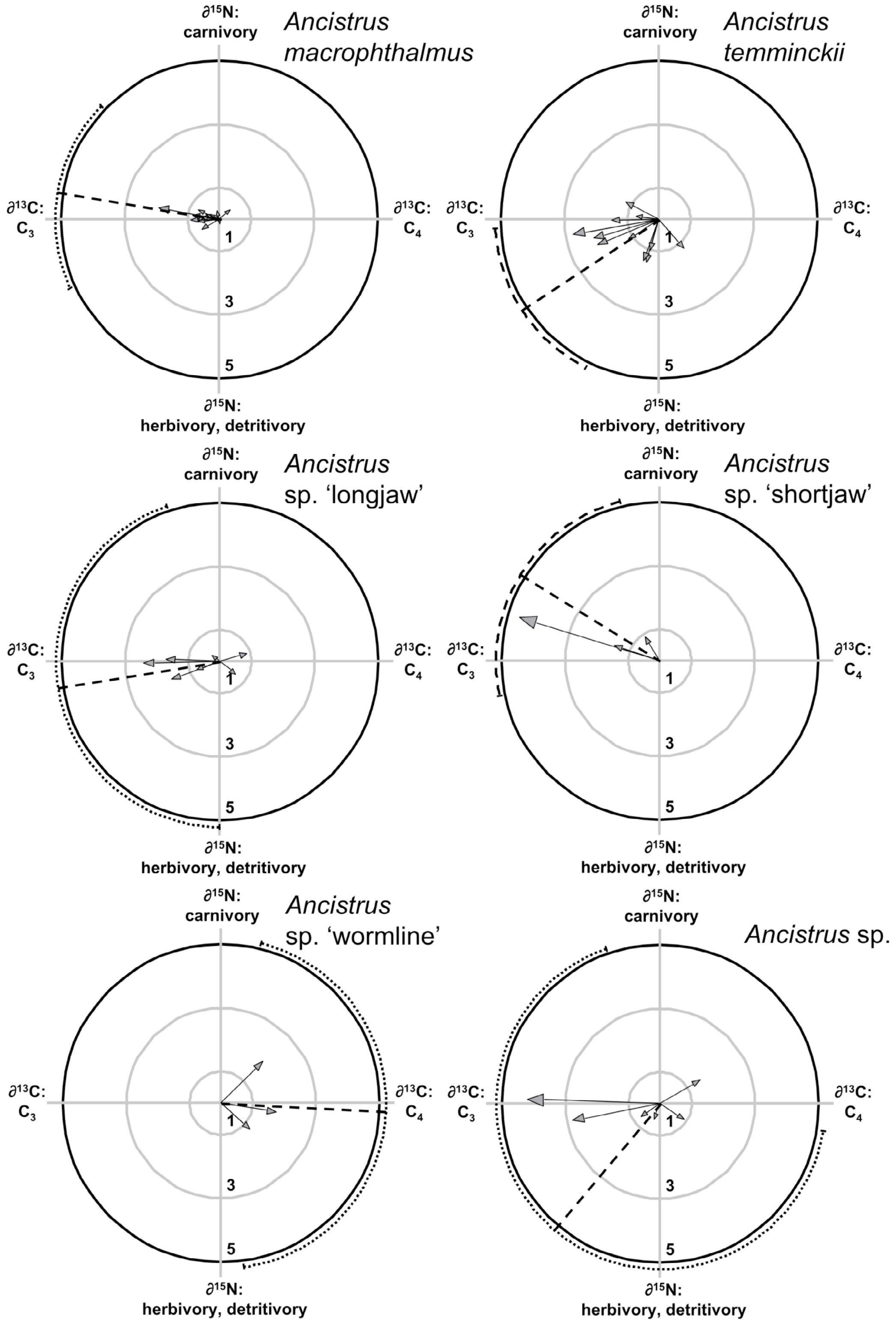


Figure 10. Hypostominae, Ancistrini: *Baryancistrus beggini*, *B. demantoides, Baryancistrus* sp. 'B&W', *Baryancisrus* sp. 'gold nugget', and *Baryancistrus* sp. 'green nugget'.

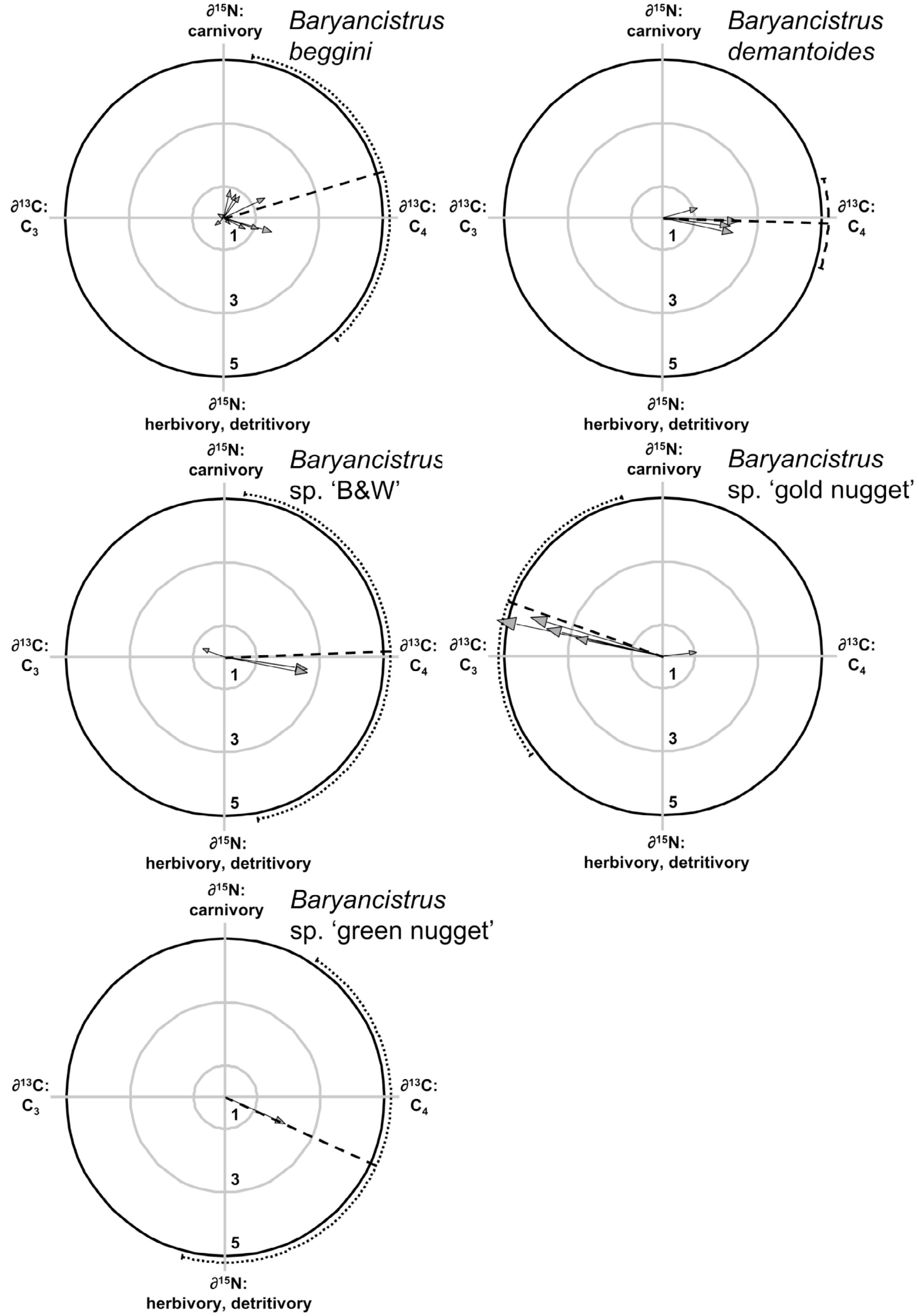


Figure 11. Hypostominae, Ancistrini: *Chaetostoma microps*, *C.* cf. *milesi*, and *Chaetostoma* sp.

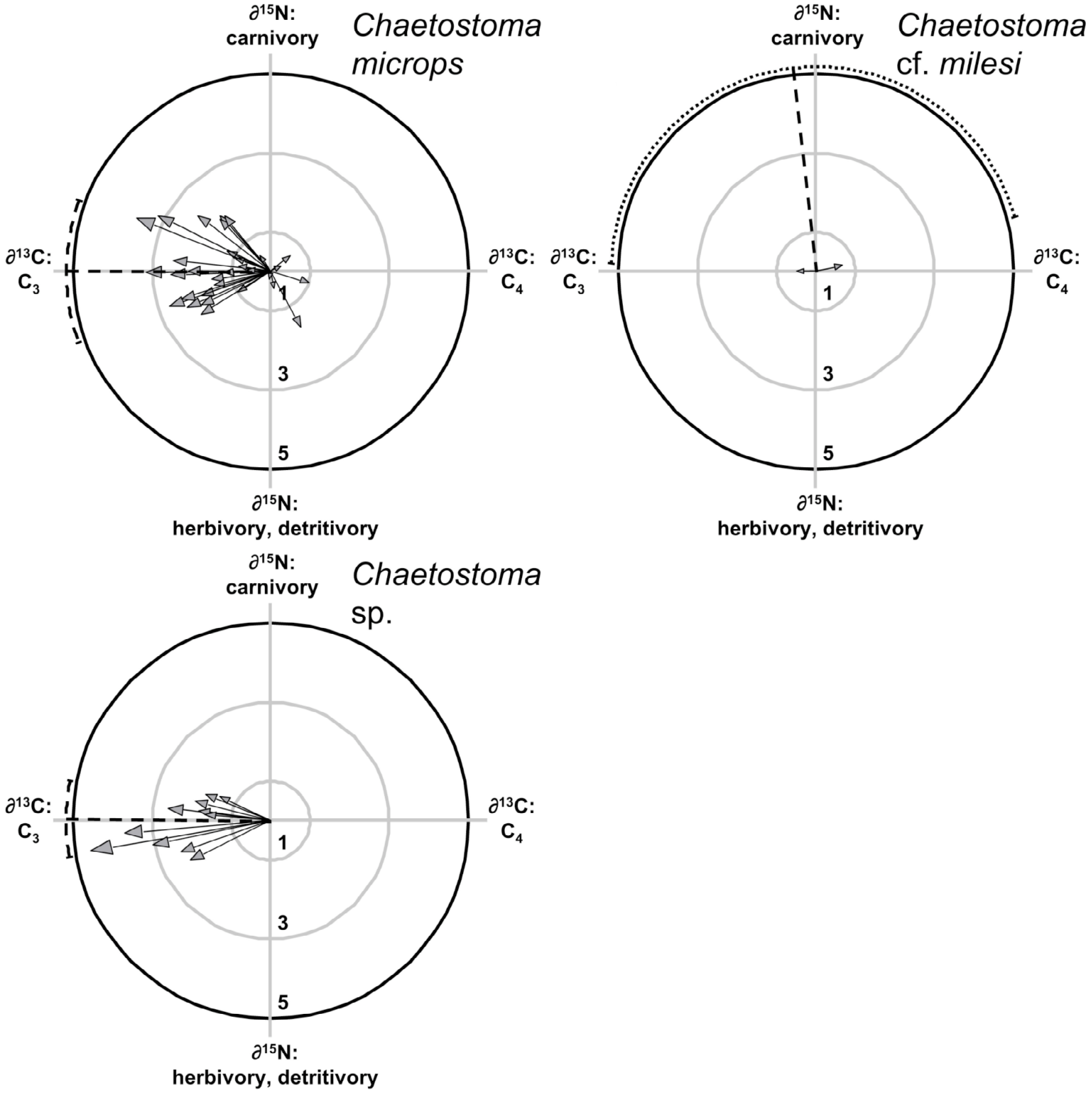


Figure 12. Hypostominae, Ancistrini: *Hemiancistrus guahiborum, H. sabaji, H. snethlageae, H. subviridis*, and *Hemiancistrus* sp. ‘gold spot’.

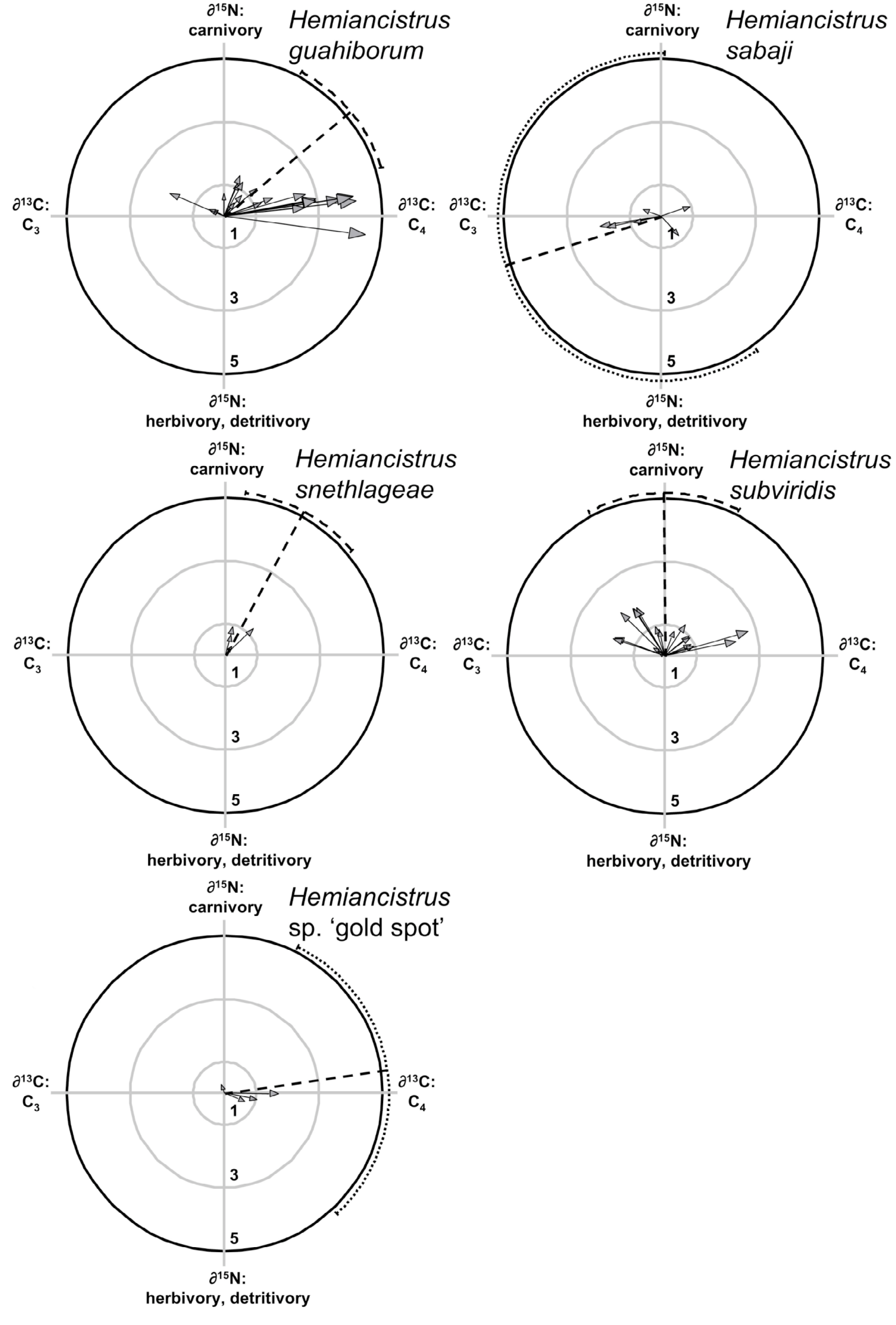


Figure 13. Hypostominae, Ancistrini: *Hypancistrus contradens, H. furunculus, H. inspector*, and *H. lunaorum*.

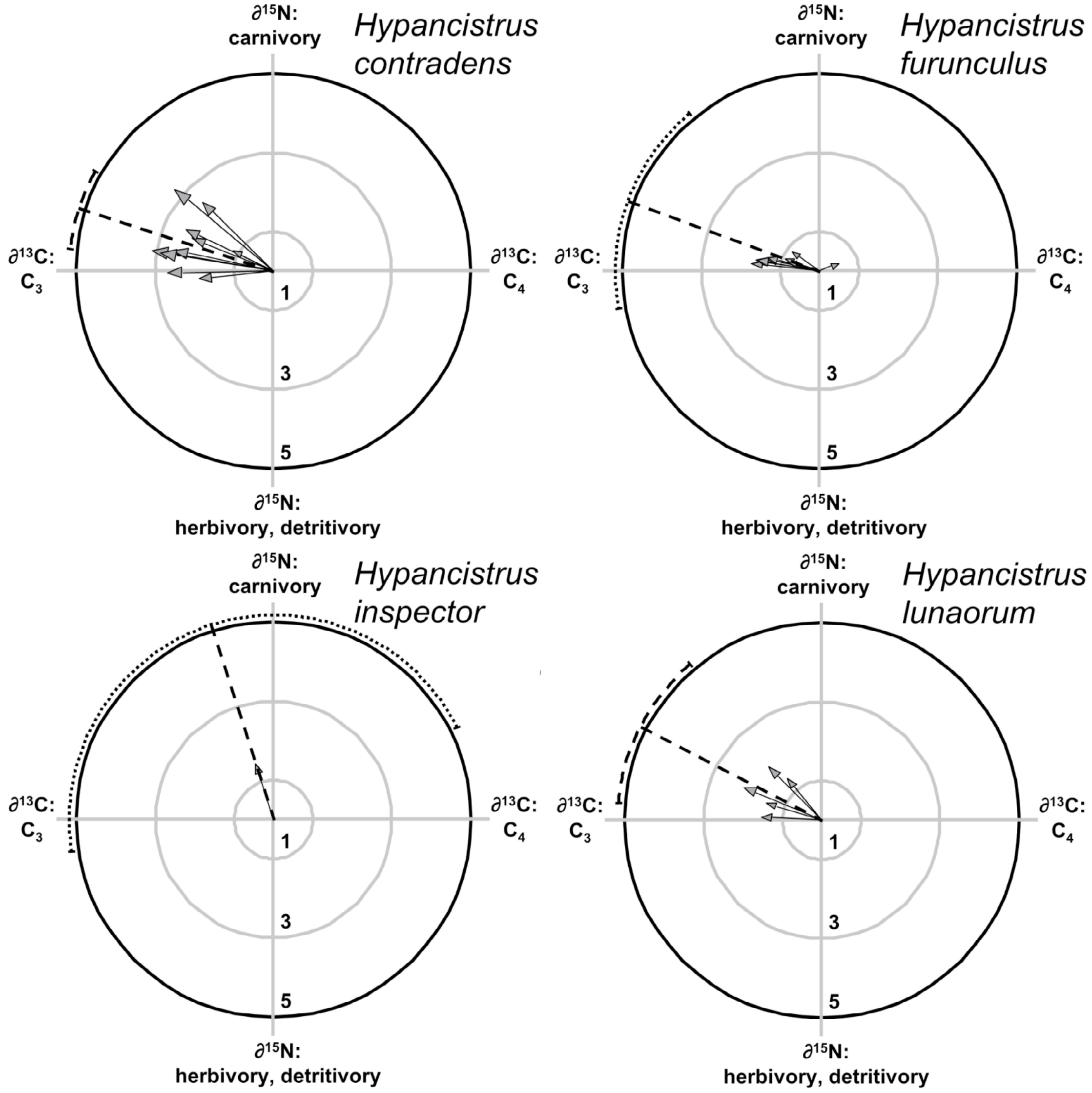


Figure 14. Hypostominae, Ancistrini: *Hopliancistrus tricornis*, New Genus 3, *Lasiancistrus schomburgkii, L. tentaculatus*, and *Dekeyseria scaphirhyncha*.

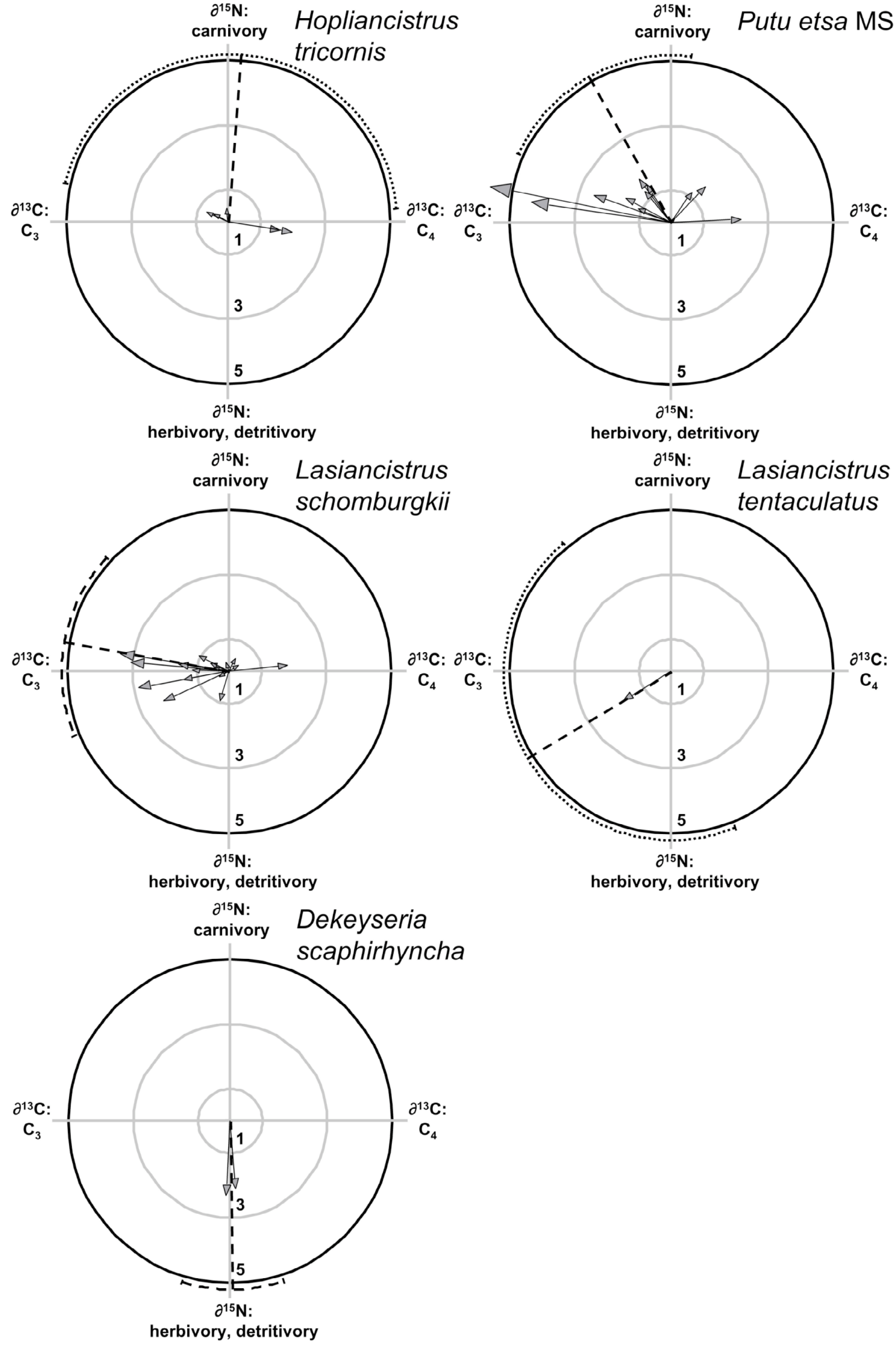


Figure 15. Hypostominae, Ancistrini: *Panaque albomaculatus, P. gnomus, P. nocturnus, P.* cf. *maccus, Panaque* n. sp. ‘Marañon’, and *P.* cf. *nigrolineatus*.

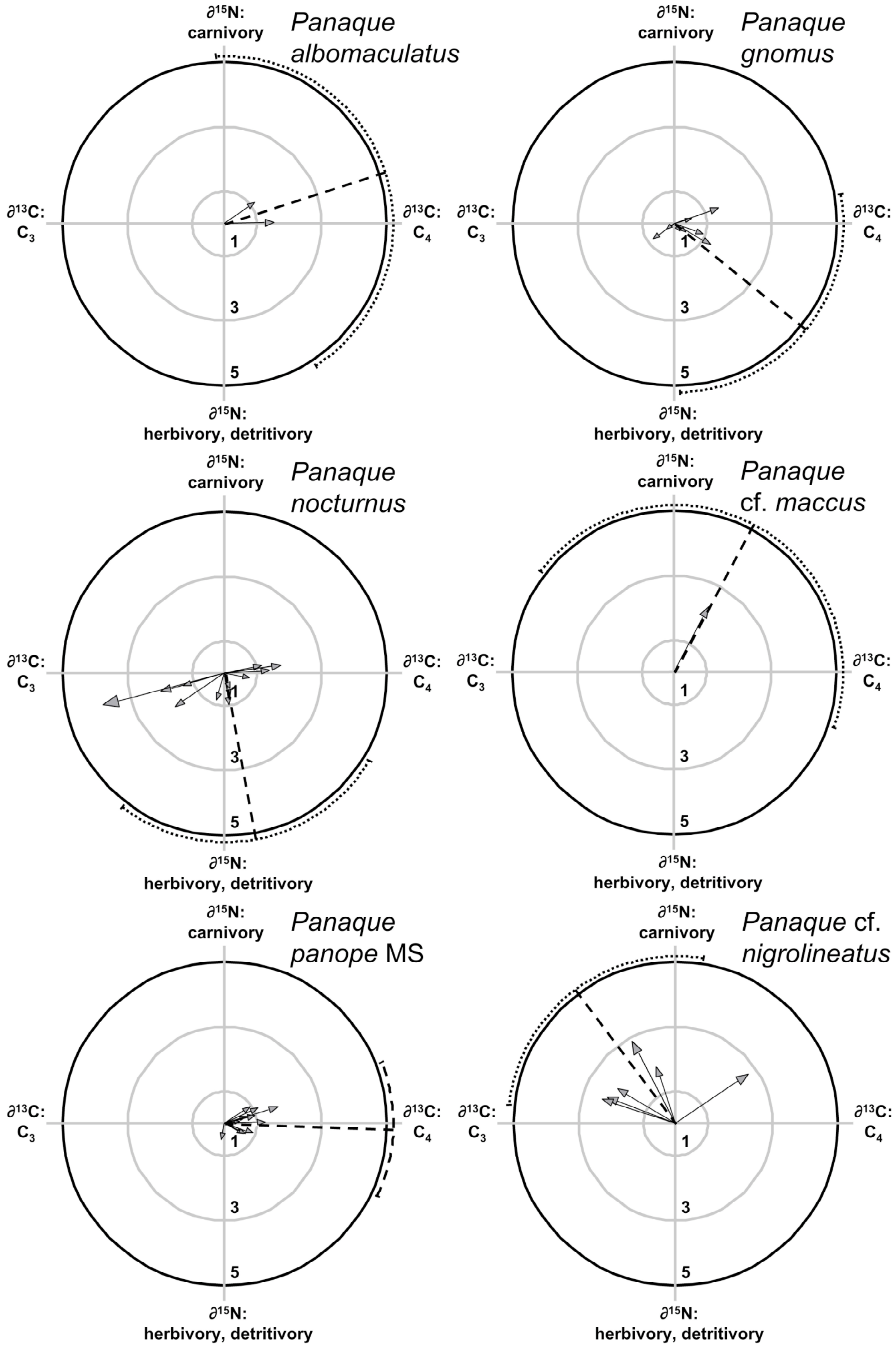


Figure 16. Hypostominae, Ancistrini: *Peckoltia braueri, P. cavatica, P. vermiculata*, and *Peckoltia* sp. 'big spot'.

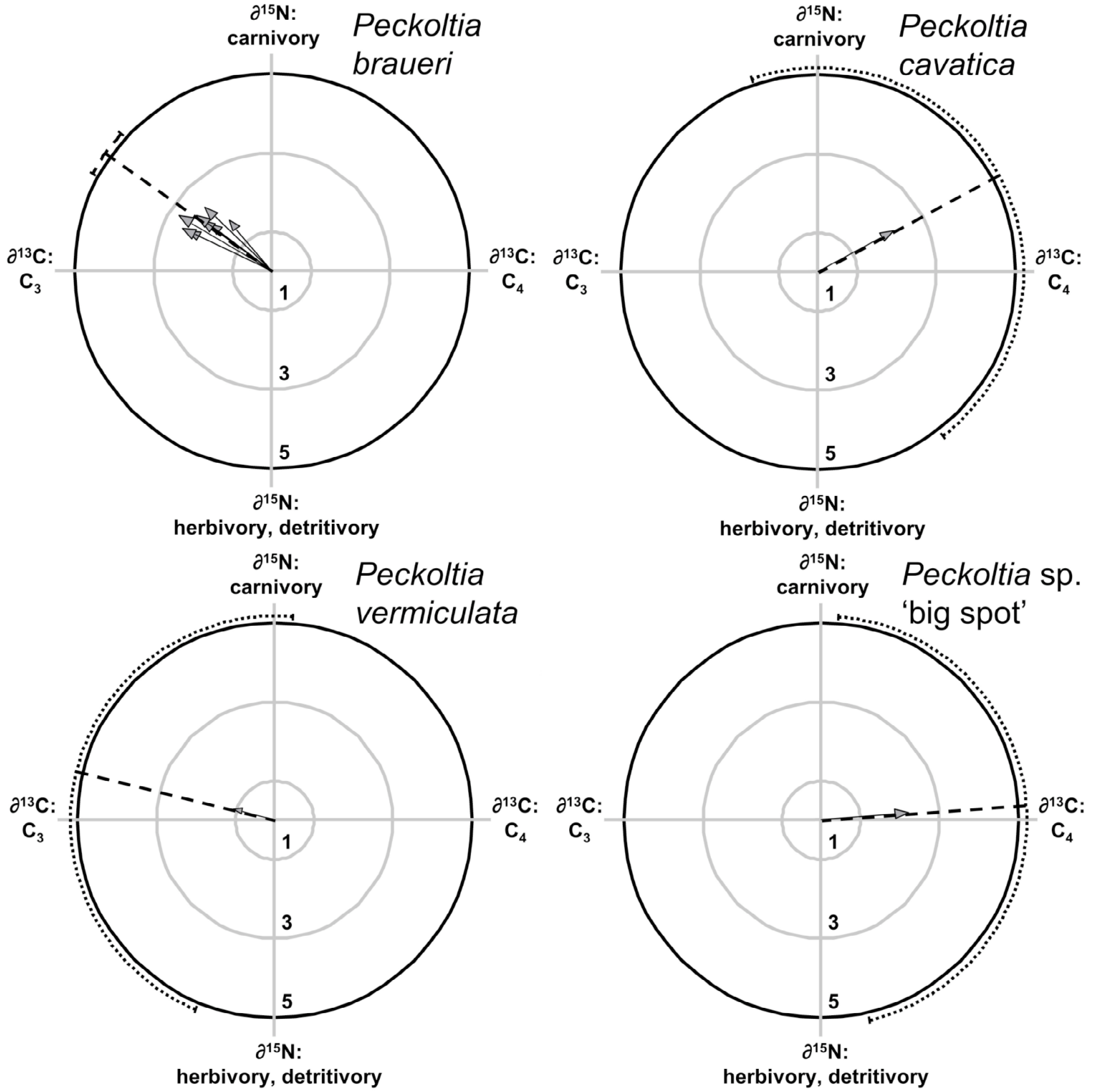


Figure 17. Hypostominae, Ancistrini: *Pseudancistrus nigrescens, Pseudolithoxus anthrax, Pseudancistrus pectegenitor, Pseudolithoxus dumus, Pseudancistrus sidereus*, and *Pseudolithoxus tigris*.

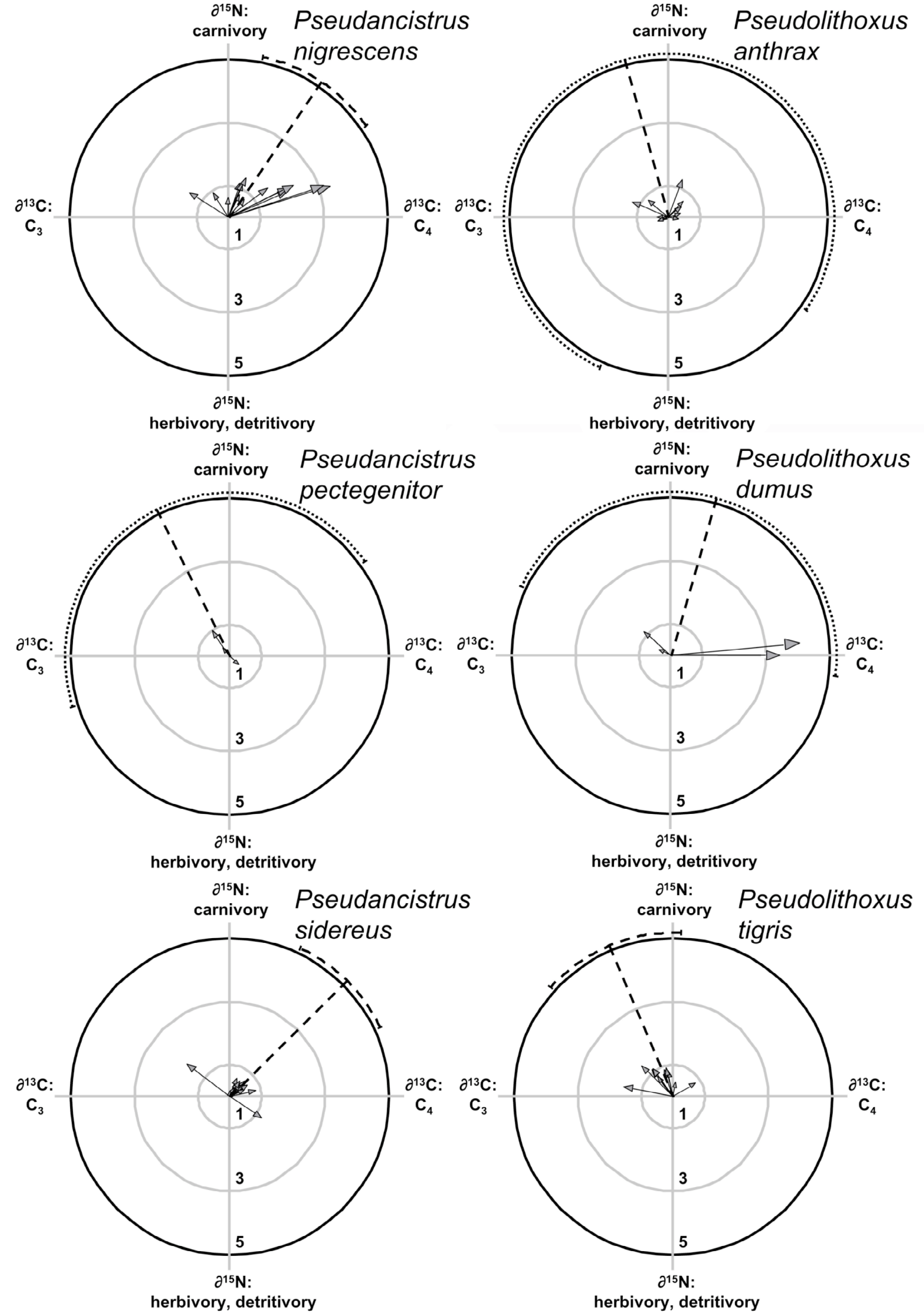
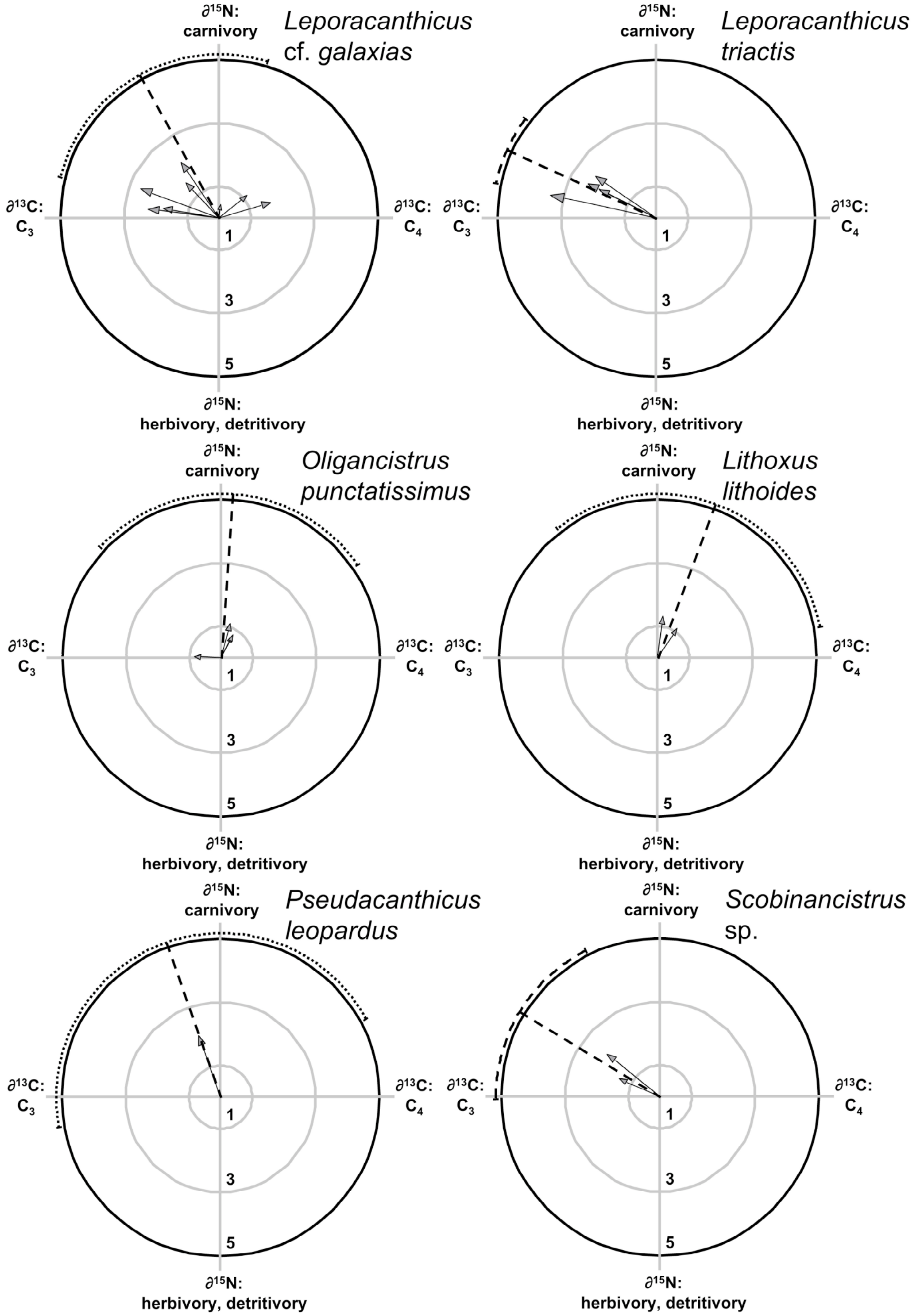


Figure 18. Hypostominae, Ancistrini: *Leporacanthicus* cf. *galaxias, L. triactis*. *Oligancistrus puctatissimus, Lithoxus lithoides, Pseudacanthicus leopardus*, and *Scobinancistrus* sp.



Leporacanthicus cf. *galaxias*

Leporacanthicus triactis

Oligancistrus punctatissimus

Lithoxus lithoides

Pseudacanthicus leopardus

Scobinancistrus sp.

Figure 19. Hypostominae, Hypostomini (*Hypostomus cochliodon*-group): *Hypostomus macushi, H. pyrineusi, H. taphorni, Hypostomus* sp. ‘dirty’, and *Hypostomus* sp. ‘spots’.

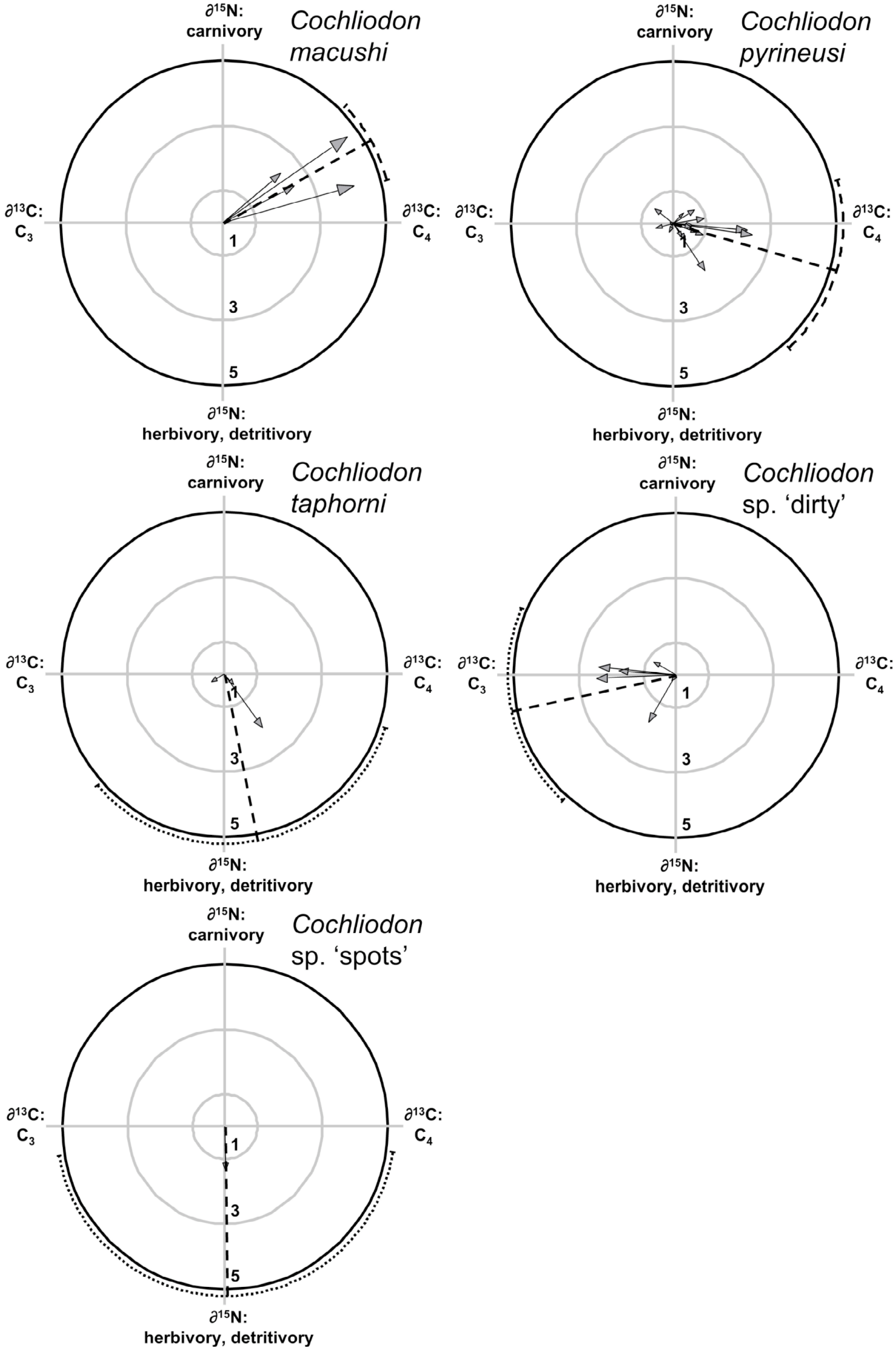


Figure 20. Hypostominae, Hypostomini: *Hypostomus hemiurus, H. niceforoi, H. rhantos,* and *Hypostomus* sp.

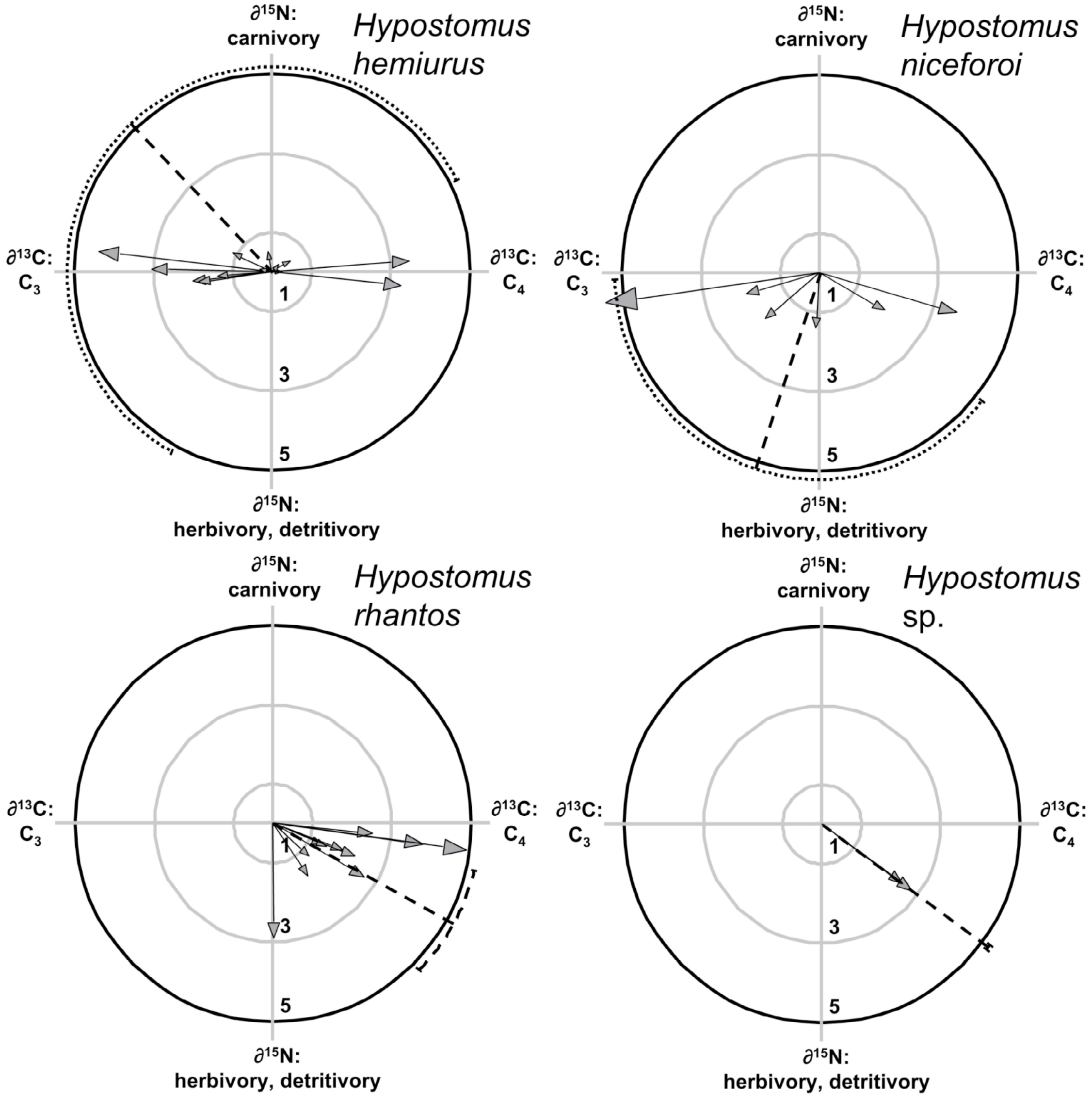


Figure 21. Hypostominae, Hypostomini (*Hypostomus emarginatus*-group): *Hypostomus emarginatus, H.* cf. *emarginatus, H. squalinus*, and *H. unicolor*.

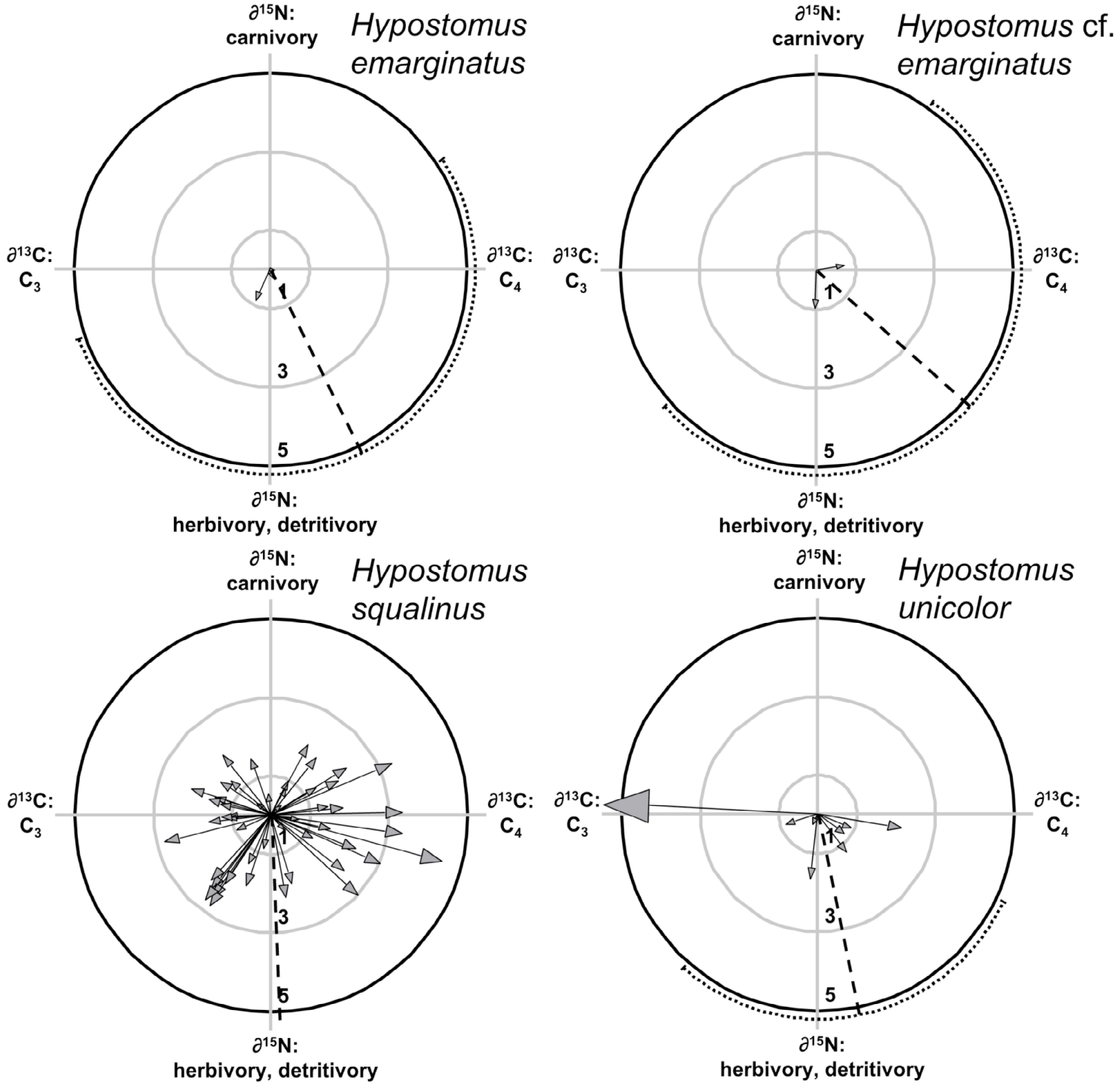


Figure 22. Loricariinae, Harttiini: *Harttia platystoma, Harttia* sp., *Sturisoma monopelte, Sturisoma nigrirostrum*, and *Lamontichthys filamentosus*.

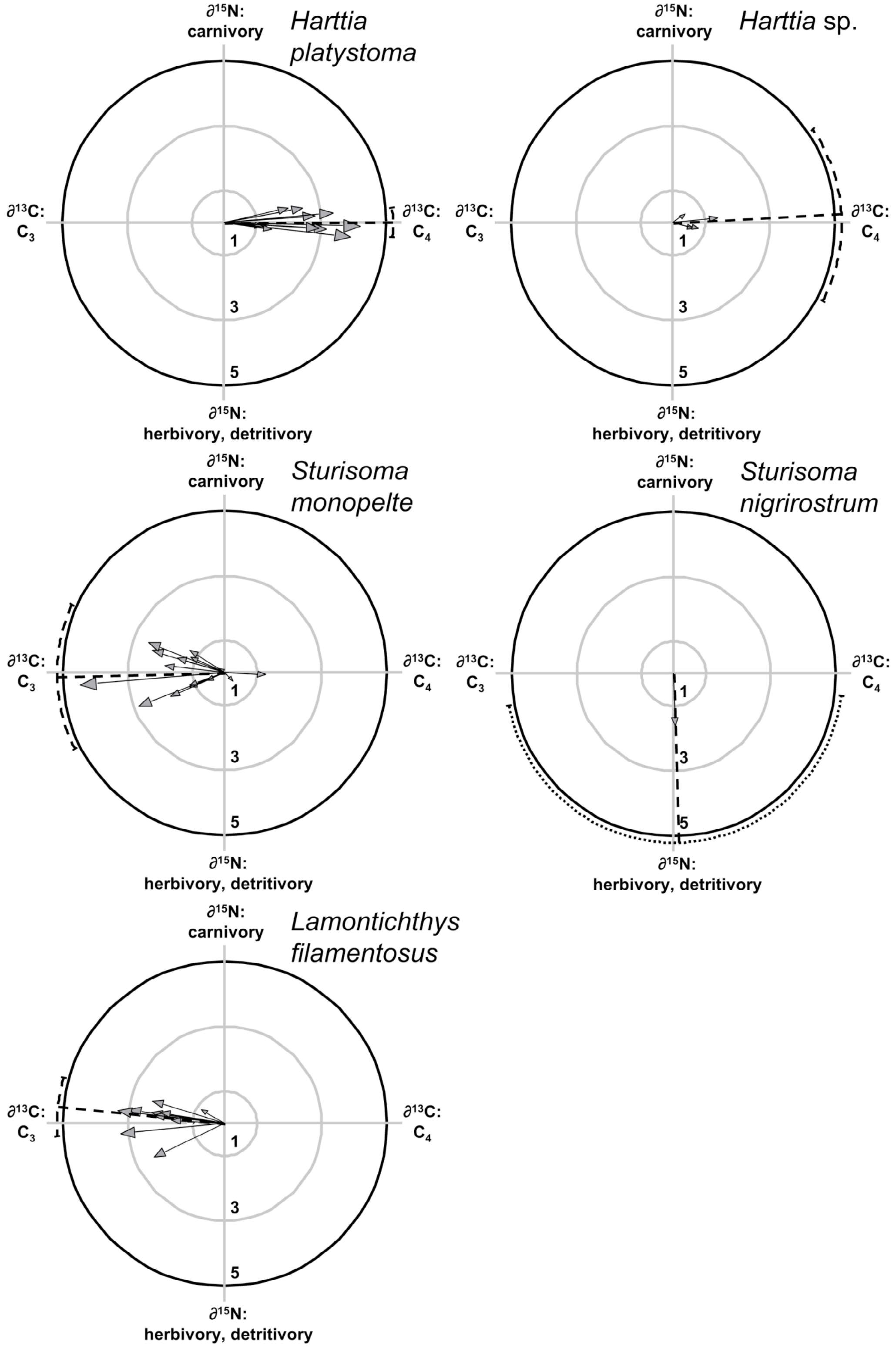


Figure 23. Loricariinae, Loricariini: *Limatulichthys griseus, Pseudoloricaria* sp., *Rineloricaria fallax, R. lanceolata, R. stewarti,* and *Rineloricaria* sp.

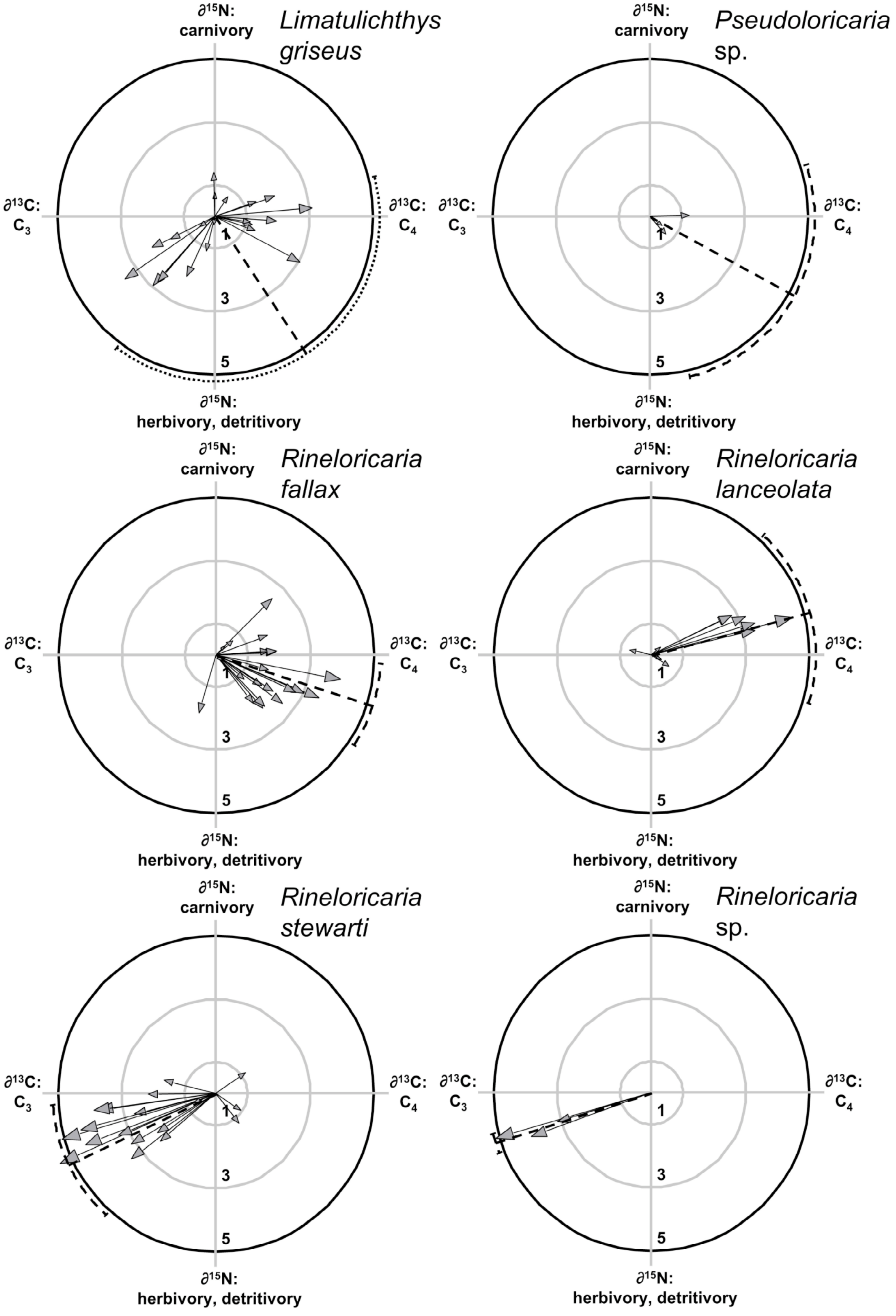


Figure 24. Loricariinae, Loricariini: *Loricaria clavipinna, Loricaria* sp. 1, *Loricaria* sp., and *Loricariichthys brunneus*.

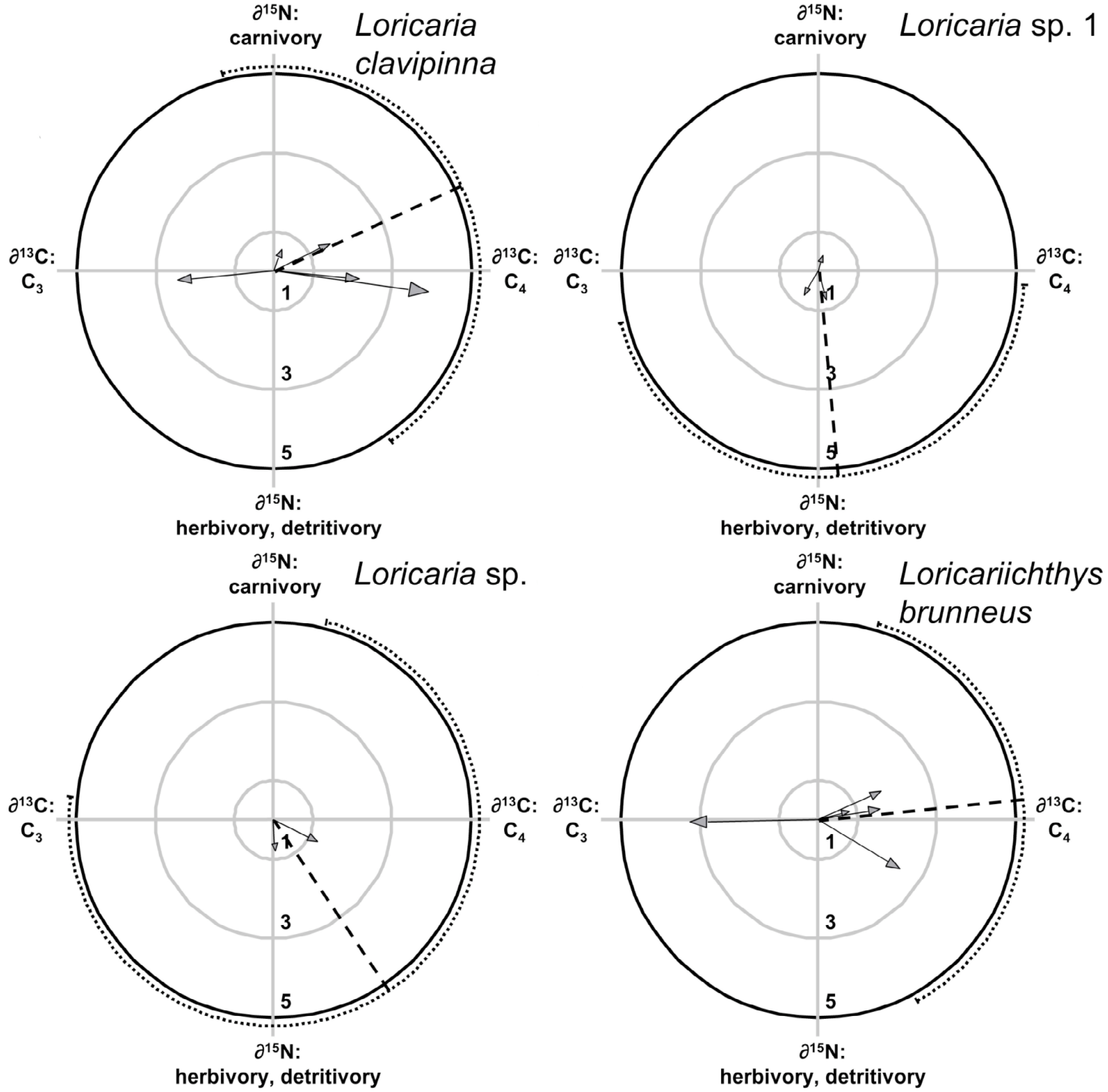


Figure 25. Loricariinae, Loricariini: *Spatuloricara puganensis, Spatuloricaria* sp. 1, and *Spatuloricaria* sp. 2.

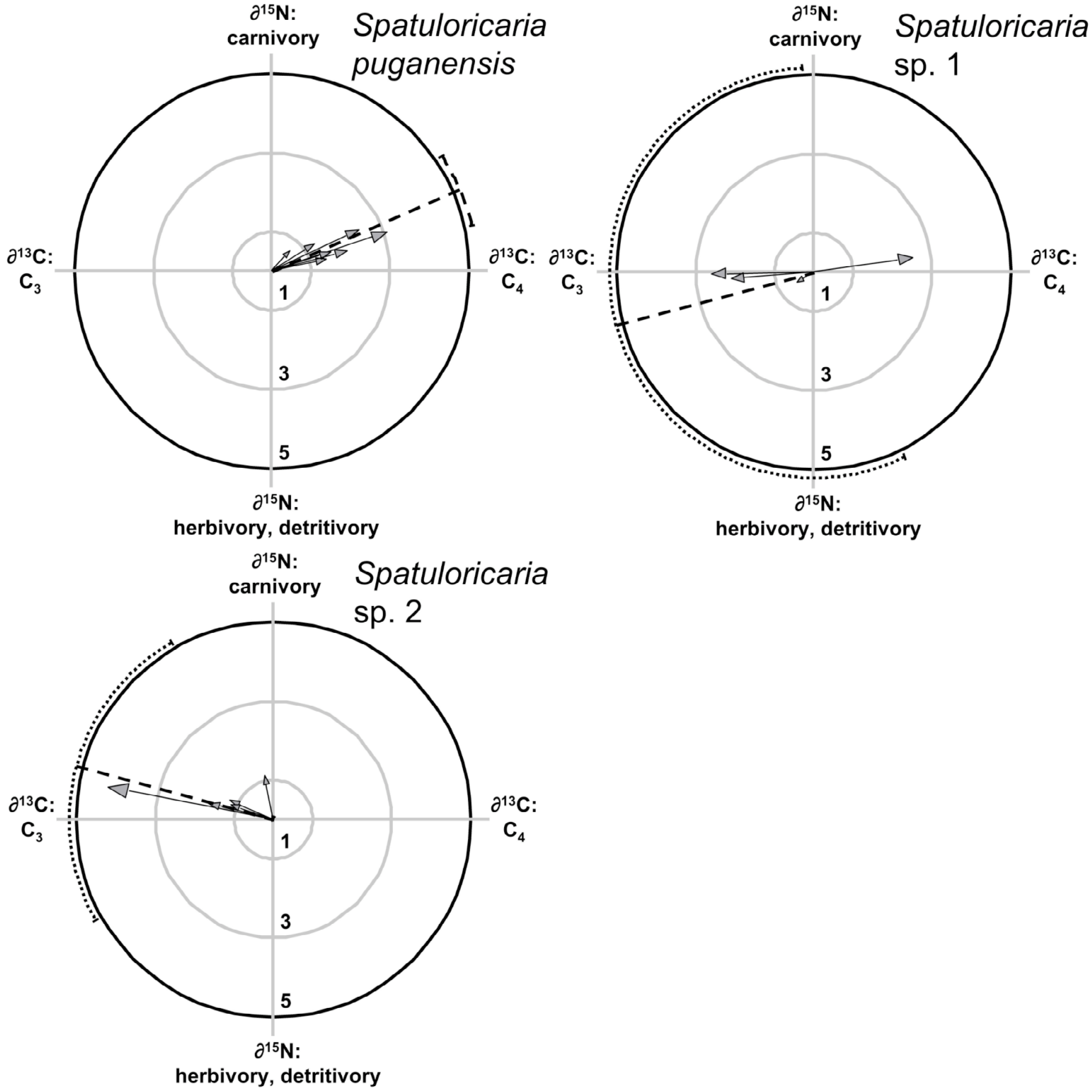


Figure 26. Loricariinae, Farlowellini: *Farlowella acus, F. amazona*; Hypoptopomatinae, Hypoptopomatini, *Hypoptopoma guianense*; and Hypostominae, Pterygoplichthyini, *Pterygoplichthys gibbiceps*.