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Global Catfish Biodiversity

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Abstract.—Catfishes are a broadly distributed order of freshwater fishes with 3,407 currently valid species. In this paper, I review the different clades of catfishes, all catfish families, and provide information on some of the more interesting aspects of catfish biology that express the great diversity that is present in the order. I also discuss the results of the widely successful All Catfish Species Inventory Project.

Introduction

Renowned herpetologist and ecologist Archie Carr's 1941 parody of dichotomous keys, *A Subjective Key to the Fishes of Alachua County, Florida*, begins with "Any damn fool knows a catfish." Carr is right but only in part. Catfishes (the Siluriformes) occur on every continent (even fossils are known from Antarctica; Figure 1); and the order is extremely well supported by numerous complex synapomorphies (shared, derived characteristics; Fink and Fink 1981, 1996). They are found in tropical and temperate freshwaters primarily, but some species of predominantly freshwater families get into saltwater, and two families are predominantly marine (Burgess 1989). Across this broad range of habitats, there is something that nearly everyone would be able to identify as a catfish. These fishes are generally roughly cylindrical with a gray or silver body, a large mouth, spines in front of the dorsal and or pectoral fins, no scales, and, of course, the character that gives catfishes their name, barbels (Fink and Fink 1981).

Indeed, throughout the world, the catfishes to which people are most familiar fit this general description. In South America are the Pimelodidae, in Africa and Asia are the Bagridae, in Europe and Asia are the Siluridae, and in Australia, Papua New Guinea, and tropical to temperate continental shelves around the world are the Ariidae. Because nearly every country on the planet has catfish, the concept of catfish is well known to most people. But this perception on the identity of catfish is limited because there are 37 families of catfishes currently recognized and about 3,407 species (Table 1). Approximately 10.8% of all fishes and 5.5% of all vertebrates are catfishes.

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But would every one be able to identify the loricariid catfish *Pseudancistrus pectegenitor* as a catfish (Figure 2A)? It does not have scales, but it does have bony plates. It is very flat, and its mouth has long jaws but could not be called large. There is a barbel, but you might not recognize it as one as it is just a small extension of the lip. There are spines at the front of the dorsal and pectoral fins, but they are not sharp like in the typical catfish. How about *Pygidianops* and *Typhlobelus* (Figure 3)? *Pygidianops* are vaguely identifiable as catfish (although they looks more like the leptocephalus larvae of elopiforms). However, *Typhlobelus* are very different; they lack paired fins, so they obviously do not have spines, and even lack eyes. Specimens are only about 30 mm long and a couple of millimeters in diameter. There are no scales and the barbels are large, but can catfish be so small and featureless?

With greater than 3,000 species (Table 1), perhaps it should be expected that the diversity of catfishes is great, but this diversity is bewildering when we have such a stereotypical view of what it is to be a catfish (Arratia et al. 2003). It was with this in mind that Larry Page, John Lundberg, Carl Ferraris, Mark Sabaj, John Friel, and I developed the All Catfish Species Inventory (ACSI), a project ostensibly to describe all catfish species. ACSI was funded through a then new program at the U.S. National Science Foundation called Planetary Biodiversity Inventories (PBIs) in 2003 and funding for ACSI ended in 2009. The PBIs are experimental programs to accelerate taxonomy. As species across the globe disappear due to environmental degradation, it is important to determine what species are out there.

FIGURE 1. Approximate global distribution of catfishes based on Berra (2001), Ferraris (1999), Kailola (1999), and the map constructed by M. H. Sabaj-Perez for the All Catfish Species Inventory Web page. Dark areas are freshwater distributions (exaggerated in southeast Pacific islands) and gray areas are marine distribution (exaggerated, generally limited to continental shelves). Extralimital fossil records (crosses) from Grande and Eastman (1986), Lundberg (1975, 1992), Otero and Gayet (2001) and A. D. de la Peña (personal communication). The fossil record of catfishes is reviewed in Gayet and Meunier (2003).

Without such basic knowledge, we cannot tell where to allocate resources in protecting the environment. Taxonomy is largely done piecemeal, and the PBIs are an attempt to bring together large teams of scientists to develop the tools to speed up the process. In this paper, I will review the families of catfishes providing their diversity, range, and basic ecology, and I will discuss the results of ACSI. The diversity of catfishes will follow the recent phylogeny of Sullivan et al. (2006) with additions by Lundberg et al. (2007) (Figure 4), although other phylogenies for catfishes are available (Mo 1991; de Pinna 1998; Hardman 2005). Teugels (2003) reviews the characters that define catfish families and major groups, and Diogo (2003) reviews phylogenetic relationships.

Basic Catfish Taxonomy

Catfishes are now believed to be in two distinct suborders, the Loricarioidei and the Siluroidei, with Diplomystidae currently unplaced.

Loricarioidei

The loricarioids have been recognized as a monophyletic group for a long time (Bailey and Baskin 1976) and are supported as such mainly by the derived presence of odontodes (integumentary teeth). These teeth range from minute denticles on the plates of loricariids and callichthyids to the sharp spines on the heads of blood-sucking candirus to the long structures found on many breeding male loricariids. Given that loricarioids are sister to all other catfishes, it is not surprising that none of them fit our basic image of a catfish. Despite this, 38.5% of catfishes (1,312 species) are loricarioids. Loricarioids are found only in the neotropics and temperate regions of South America and are broken up into five families: Nematogenyidae, Trichomycteridae, Callichthyidae, Scoloplacidae, Astrobepidae, and Loricariidae.

Nematogenyidae (Nematogenyid Catfish)

Nematogenyidae consists only of *Nematogenys inermis* from the mountains of Chile. The Nematogenyidae is only one of two monotypic families of catfishes (the other is the recently described Lacantuniidae).

Trichomycteridae (Pencil or Parasitic Catfishes)

Trichomycterids range throughout much of South America and southern Central America. Trichmo-

TABLE 1. Number of catfish species described (nominal species), currently valid, and the number added in the past 10 years. From Eschmeyer and Fong (2010).

Taxonomy	Common name	Range	Nominal species	Valid species	Past 10 years
Loricaroidei					
Astroblepidae	Naked suckermouth or climbing catfishes	South America, Panama	56	54	0
Callichthyidae	Armored catfishes	South America, Panama	270	199	26
Loricariidae	Suckermouth armored catfishes	South America, Costa Rica, Panama	936	813	174
Nematogenyidae	None	Chile	3	1	0
Scoloplacidae	Spiny dwarf catfishes	South America	5	5	1
Trichomycteridae	Pencil or parasitic catfishes	South America, Costa Rica, Panama	281	240	70
Total Loricarioidei			1,551	1,312	271
Diplomystidae	Velvet catfishes	Chile and Argentina	12	6	0
Siluroidei					
Akysidae	Stream catfishes	Southeast Asia	66	57	23
Amblycipitidae	Torrent catfishes	South Asia	37	33	8
Amphiliidae	Loach catfishes	Africa	98	80	16
Anchariidae	Madagascar catfishes	Madagascar	6	6	4
Ariidae	Sea catfishes	Tropical to warm temperate oceans and nearby freshwaters	343	147	15
Aspredinidae	Banjo catfishes	South America	67	39	3
Auchenipteridae	Driftwood catfishes	South America and Panama	161	105	11
Auchenoglanididae	Giraffe catfishes	Africa	37	25	1
Austroglanididae	None	Southern Africa	3	3	0
Bagridae	Naked or bagrid catfishes	Asia and Africa	314	210	44
Cetopsidae	Whale catfishes	South America	50	42	20
Chacidae	Squarehead, frogmouth, or angler catfishes	Southeast Asia	6	3	0
Clariidae	Airbreathing or walking catfishes	Southeast Asia and Africa	216	111	14
Claroteidae	None	Africa	93	66	3
Cranoglanididae	Armorhead catfishes	China and Vietnam	7	5	2
Doradidae	Thorny or talking catfishes	South America	144	88	15
Heptapteridae	None	South and Central America	289	199	15
Heteropneustidae	Air-sac catfishes	South Asia	8	4	0
Horabagridae	Sun catfishes	South Asia	8	4	0

TABLE 1. Continued.

Taxonomy	Common name	Range	Nominal species	Valid species	Past 10 years
Ictaluridae	Bullhead catfishes	North America (Canada to Guatemala)	137	51	4
Lacantuniidae	Chiapas catfish	Mexico	1	1	1
Malapteruridae	Electric catfishes	Africa	27	19	14
Mochokidae	Squeaker or upside-down catfishes	Africa	261	204	22
Pangasiidae	Shark catfishes	South Asia	52	28	4
Pimelodidae	Long-whiskered catfishes	South America and Panama	187	107	23
Plotosidae	Eeltail or tandan catfishes	Indo-Pacific, Australia, New Guinea	80	40	5
Pseudopimelodidae	Bumblebee catfishes	South America	40	34	8
Schilbidae	None	Africa and South Asia	120	61	4
Siluridae	Sheatfishes	Europe and Asia	169	97	19
Sisoridae	Hill-stream catfishes	South Asia	264	218	87
Total Siluroidei			3,291	2,089	385
Total Siluriformes			4,854	3,407	656

mycterids generally are equipped with interopercles and opercles that support odontodes. They can evert these odontodes for protection and to provide friction when climbing waterfalls. The candirus are often described as the only parasitic vertebrates (Gudger 1930) and are in two subfamilies. The Stegophilinae feed on mucus and scales of other fishes, and the Vandeliinae feed on blood of other fishes. Fernández and Schaefer (2009) found that parasitism arose only once in the trichomycterids. Vandellines swim into the gills of other fishes and use a uniquely derived median upper jaw bone to pierce the dorsal or ventral aorta and rapidly fill themselves with blood (Spotte et al. 2001; Spotte 2002; Zuanon and Sazima 2004). The fishes then drink the blood and drop out of the fish when they get their fill. They are often collected engorged with blood in sandy streams (Figure 5). Although there are not that many species of hematophagous trichomycterids, legends of the candiru dominate our thoughts on this group of fishes because they have been known to mistake the human urethra for fish gills (Gudger 1930; Vezhaventhan and Jeyaraman 2007; Zuanon and Sazima 2004). The result is damaging to both fish and human.

Callichthyidae (Armored Catfishes)

Callichthyids are distributed in Neotropical South America and southern Central America, most in the genus *Corydoras*. Most *Corydoras* are small (<50 mm), detritivorous catfishes covered in two rows of bony plates. Many species occur in hypoxic water where they breathe air with the help of modified intestines capable of gas exchange (Persaud et al. 2006). This type of air breathing may have been what helped lead to the very unusual breeding strategy of *Corydoras*. It had been considered unusual that spawning *Corydoras*. would sit in a T position, with the male as the bar of the T and the female with her mouth at the vent of the male as the post of the T. After apparent spawning, the female would move off and lay one to several eggs, but it was unknown how the eggs were fertilized. Kohda et al. (1995) found that the mode of fertilization is for the female to ingest the milt, move it quickly through her gastrointestinal tract, and deposit the milt from her cloaca along with the eggs.

Scoloplacidae (Spiny Dwarf Catfishes)

The Scoloplacidae consists of a single genus of very small fishes (<25 mm). Scoloplacids are su-

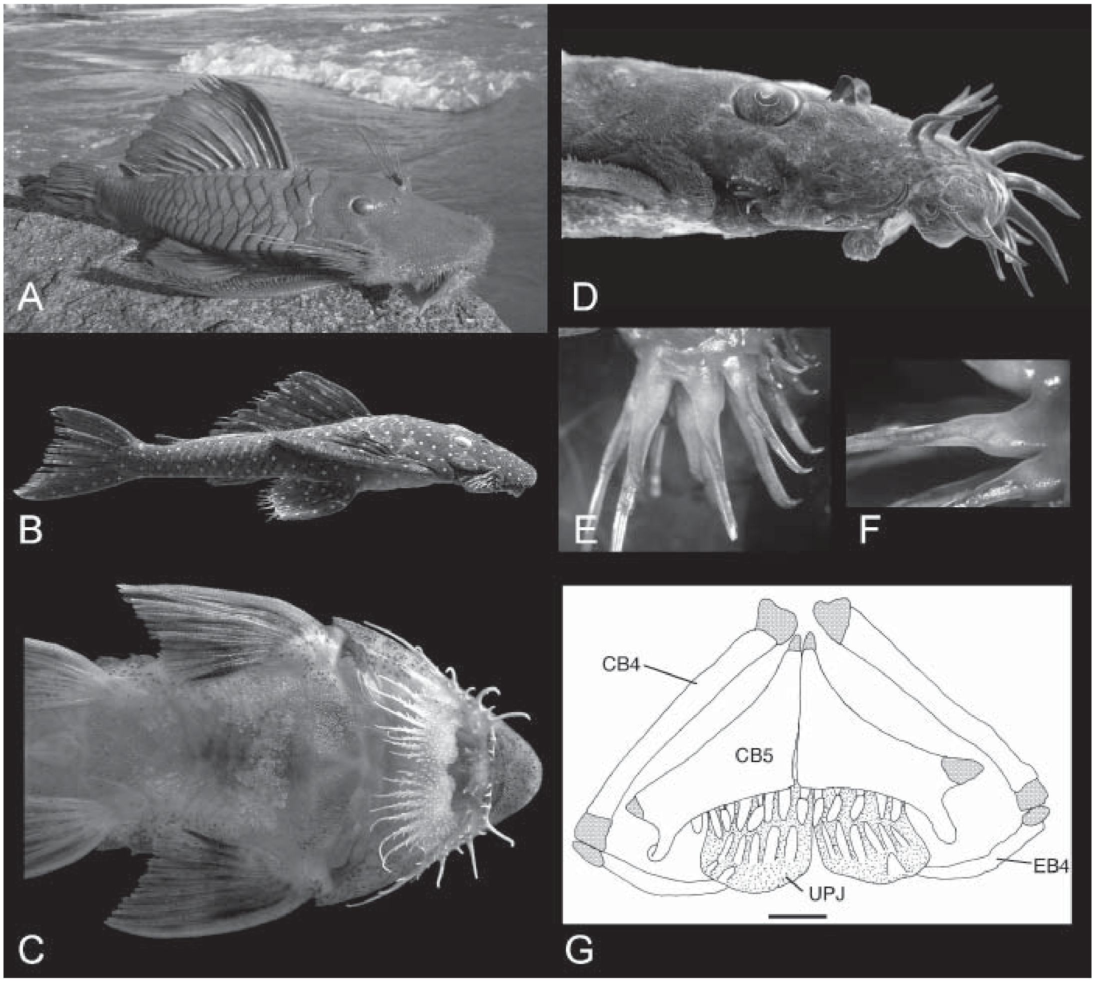

FIGURE 2. Members of the Loricariidae: A. *Pseudancistrus pectegenitor*, B. *Pseudolithoxus anthrax* (close-up of cheek odontodes in E and F), C. *Pseudohemiodon* sp. mouth (pharyngeal jaws in G, CB—ceratobranchial, EB—epibranchial, UPJ—upper pharyngeal jaw), and D. *Ancistrus macropthalmus* male with tentacles. Images by M. H. Sabaj (A–D) and J. W. Armbruster (E–G).

perficially similar to aspredinids; however, they possess odontodes like other loricarioids, particularly well developed on a plate on the snout (Bailey and Baskin 1976; Schaefer et al. 1989; Schaefer 1990). They are found in floodplain lakes and small streams and have been hypothesized to have a respiratory stomach (Armbruster 1998).

Astroblepidae (Naked Suckermouth or Climbing Catfishes)

Astroblepids have a suckermouth, but are not armor-plated. They live in torrential streams of the Andes and feed on insect larvae. Astroblepids are capable of climbing waterfalls (Nelson 2006) by using their pelvic fins, which are used almost in a walking motion. Armbruster (2004) contends that the loricariid *Lithogenes* (from the Guiana Shield of Venezuela and Guyana and from the Caribbean Andes of Venezuela) is an astroblepid, but Schaefer (2003) and Schaefer and Provenzano (2008) take an opposing view. According to Nelson (2006), the Astroblepidae is the most species-rich monogeneric family.

Loricariidae (Suckermouth Armored Catfishes)

The Loricariidae (suckermouth armored catfishes) is the largest family of catfishes with more than

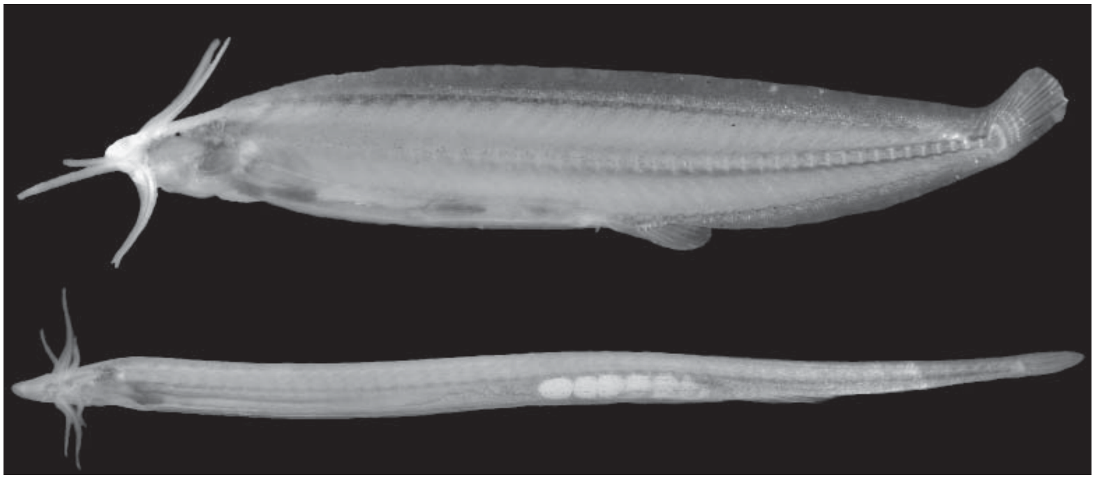

FIGURE 3. The trichomycterids *Pygidianops cuao* (top) and *Typhlobelus guacamaya* (bottom) from Venezuela. Photos by N. K. Lujan.

800 species (23.9% of catfishes). They are found in Neotropical South America and southern Central America. The range of size and diversity of these fishes is astounding. Fishes range from 20 to nearly 700 mm (with nearly this entire size range seen in one clade of approximately 16 species, the Acanthicus group of Armbruster 2004). Males of many species have hypertrophied odontodes over various parts of their bodies, and in some species, females have them as well.

Among the most unusual loricariids are members of *Ancistrus*, where males have long, fleshy tentacles on the tips of their snouts. We have hypothesized that these tentacles are larval mimics (Sabaj et al. 1999) and are used by males to trick females into thinking that they have young in their nests; this is because *Ancistrus* males protect the young until they absorb the yolk sac, and having young may signify that the male is a good parent. Recently, I have discovered what looks like larval mimics among the hypertrophied odontodes that are held on evertible cheek plates in *Ancistrus*, as well as closely related genera (*Lasiancistrus* and *Pseudolithoxus*). These cheek larval mimics have a rounded base that is yellow in life and a darkened region that proceeds distally from this base and forks near the end of the odontode (Figure 2E–F).

The only two instances of lignivory (wood eating) among fishes occur in the Loricariidae. Members of *Panaque* and the *Hypostomus cochliodon* species group have teeth modified into short, wide, spoon-shaped structures that they use like adzes to remove chunks of wood (Schaefer and Stewart 1993; Armbruster 2003). But do they digest it? Nelson et al. (1999) suggest that they do; however, the wood looks the same in the anterior part of the intestine as the posterior part. Recently, German (2009) and German and Bittong (2009) did not find that loricariids could digest wood because they lacked the ability to harbor symbiotic microorganisms, the gut passage rate was much too fast to digest wood, and there was not the right enzyme activity to digest wood. So, the fishes may be consuming the wood only for the microorganisms that are themselves eating the wood.

Also unusual among loricariids are members of the tribe Loricariina (Figure 2C). These extremely dorsoventrally flattened fishes usually have small tentacles around their mouths and very few teeth. They do, however, have large, molariform pharyngeal teeth (Figure 2G). I have found only seeds in the stomachs of the specimens I have dissected (Armbruster 2004), but some species are known to also consume insect larvae (Thomas and Rapp Py-Daniel 2008). Although insectivory is common in fishes, loricariids are generally considered algivores (technically, this is incorrect as they mainly scrape biofilm and should be classified as detritivores). Granivory in fishes is more unusual but can be seen in many South American fishes, including other catfishes (particularly doradids, Goulding 1980).

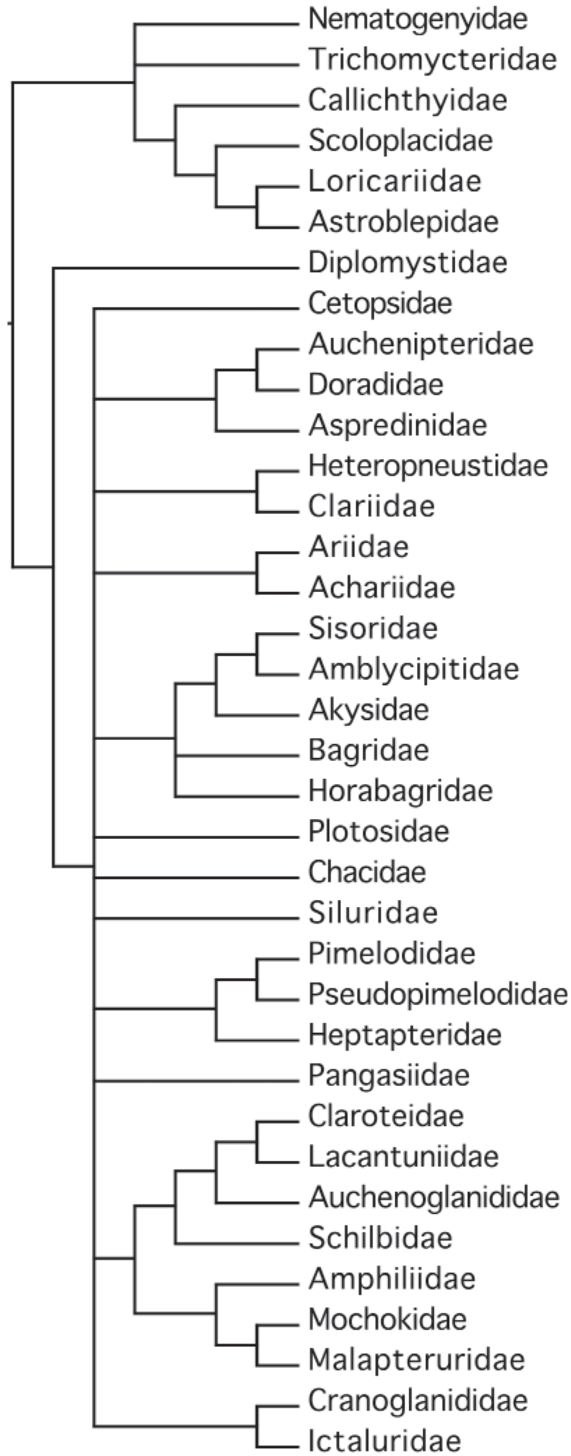

FIGURE 4. Phylogeny of the Siluriformes from Sullivan et al. (2006) and as modified for the Big Africa clade by Lundberg et al. (2007).

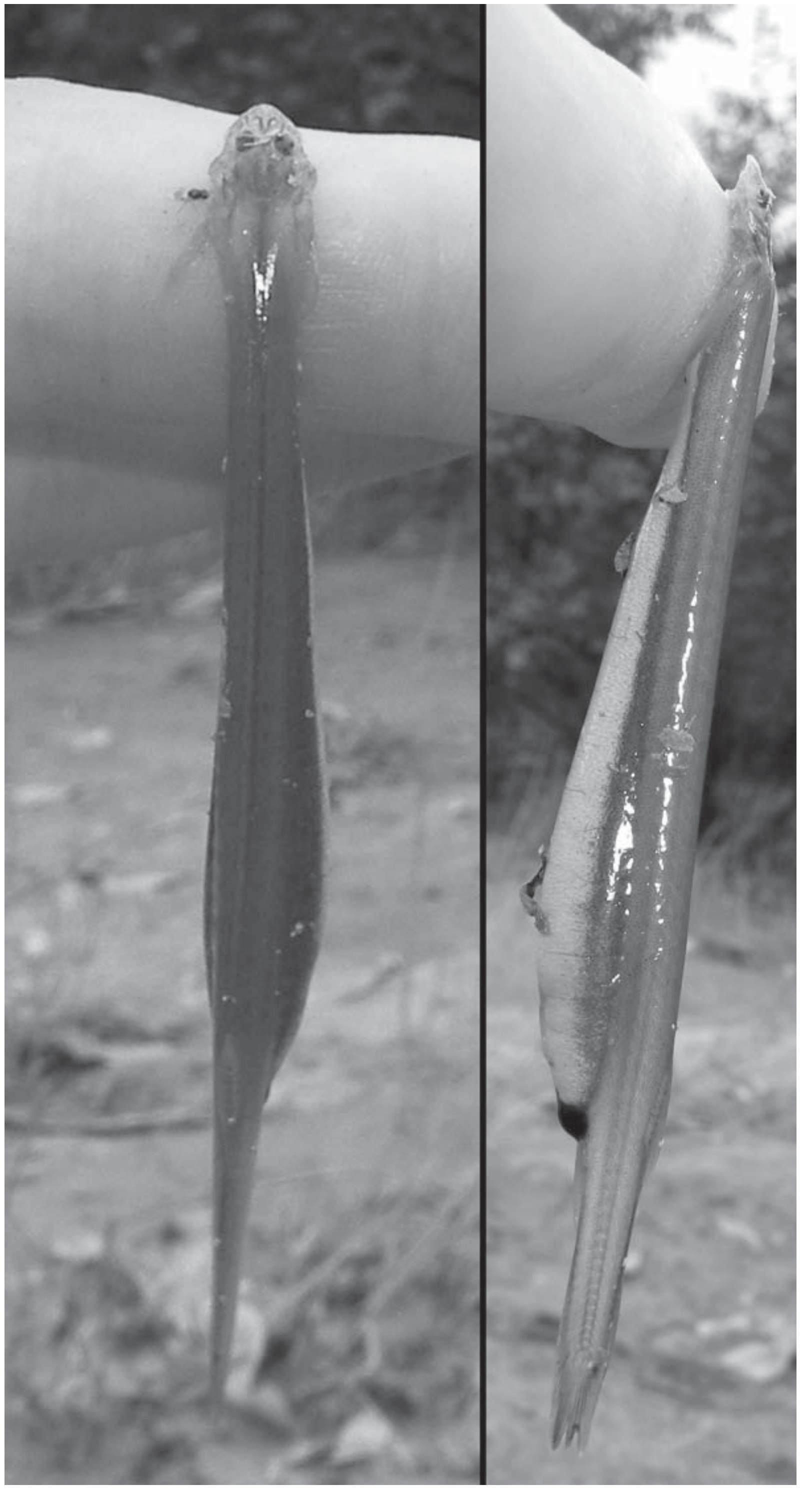

FIGURE 5. The Trichomycterid *Vandellia sanguinea* from Guyana with belly distended with blood. The fish is hanging by means of odontodes (integumentary teeth) on its interopercles and opercle. Photos by L. S. de Souza.

Diplomystidae (Velvet Catfishes)

Diplomystids were found by Sullivan et al. (2006) to be sister to the Siluroidei, but they did not provide a higher ranking for the family. Diplomystids are from Chile and Argentina and are the only living catfishes to retain maxillary teeth, a trait that causes some to believe that diplomystids are the most primitive catfishes (Arratia 1987; de Pinna 1998).

Siluroidei

All of the remaining catfish families are siluroids, but the relationships of the families are poorly known. Sullivan et al. (2006) found little structure to the relationships of the families but noted some important clades, including the groups mentioned below. Although most siluroids are readily recognized as catfishes, several groups push the definition of catfish quite far.

Cetopsidae (Whale Catfishes)

This small, South American family consists of the whale catfishes. Cetopsids are generally small (<60 mm, but some reach ~30 cm). Some cetopsids feed on larger fishes by biting chunks out of their flesh and swimming away (Burgess 1989).

Aspredinidae + Auchenipteridae + Doradidae

This clade of South American catfishes includes some generalized catfishes (like *Trachelyopterus*, *Auchenipteridae*) but generally are stranger fishes with many species armor-plated.

Aspredinidae (Banjo Catfishes)

Aspredinids are found in tropical South America. The skin of aspredinids is keratinized and is shed like in reptiles (Friel 2009). These bizarre fishes (Figure 6C) are often found in leaf litter, although some prefer high montane streams and some, like *Aspredo*, are found in estuaries and marine waters. Females of some species hold their eggs on outgrowths of their skin called cotylephores, which may aid in gas exchange for the embryos (Wetzel et al. 1997).

Auchenipteridae (Driftwood Catfishes)

Auchenipterids are found in tropical South America up to the Tuira River of Panama. They are often found in crevices or hollow logs. Many of the species can be relatively easily collected by removing hollow logs from rivers and letting the fishes fall out. Others, such as *Ageniosus*, are generally found in open water. Specimens of the unusual auchenipterid *Gelanoglanis* are less than 30 mm standard length (SL; Figure 6A), and thus far, each discovered population appears to be a different species. These rare, pink fishes only come out at night where they can be seen swimming through the middle of the water column. Male auchenipterids, like guppies, have a modified anal fin that they use for internal fertilization (Meisner et al. 2000).

Doradidae (Thorny or Talking Catfishes)

Doradids are found in tropical South America. Although most doradids have a generalized catfish form, they generally have at least a single row of plates with large spikes running down their sides (Figure 6B). Birindelli et al. (2009) described the swim bladder variation of doradids and found it to be extreme, with some bladders having many thin diverticula of unknown function coming off of a generally heart-shaped chamber. The function of these diverticula is unknown.

Heteropneustidae + Clariidae

This clade has long been recognized, with heteropneustids occasionally placed within the Clariidae.

Heteropneustidae (Air-Sac Catfishes)

Heteropneustidae is from Southeast Asia and has just four species. *Heteropneustes* has one of the most powerful toxins in catfishes (Wright 2009), as well as paired outgrowths of the buccal cavity that they use to breathe air (Munshi 1962).

Clariidae (Air-Breathing or Walking Catfishes)

The clariids include a diverse array of species from Asia and Africa. Most species are like the walking catfish *Clarias batrachus* that has been introduced throughout the world (including Florida), but some have elongated or anguilliform bodies like *Chanallabes* (Figure 7). Species of *Clarias* are able to leave water and walk to other bodies of water. Unusual among fishes, clariids can breathe air with their gills because they have bony stays within the gills that keep them from collapsing in air (Graham 1997), and species of *Chanallabes* are known to actually feed on land (Van Wassenbergh et al. 2006).

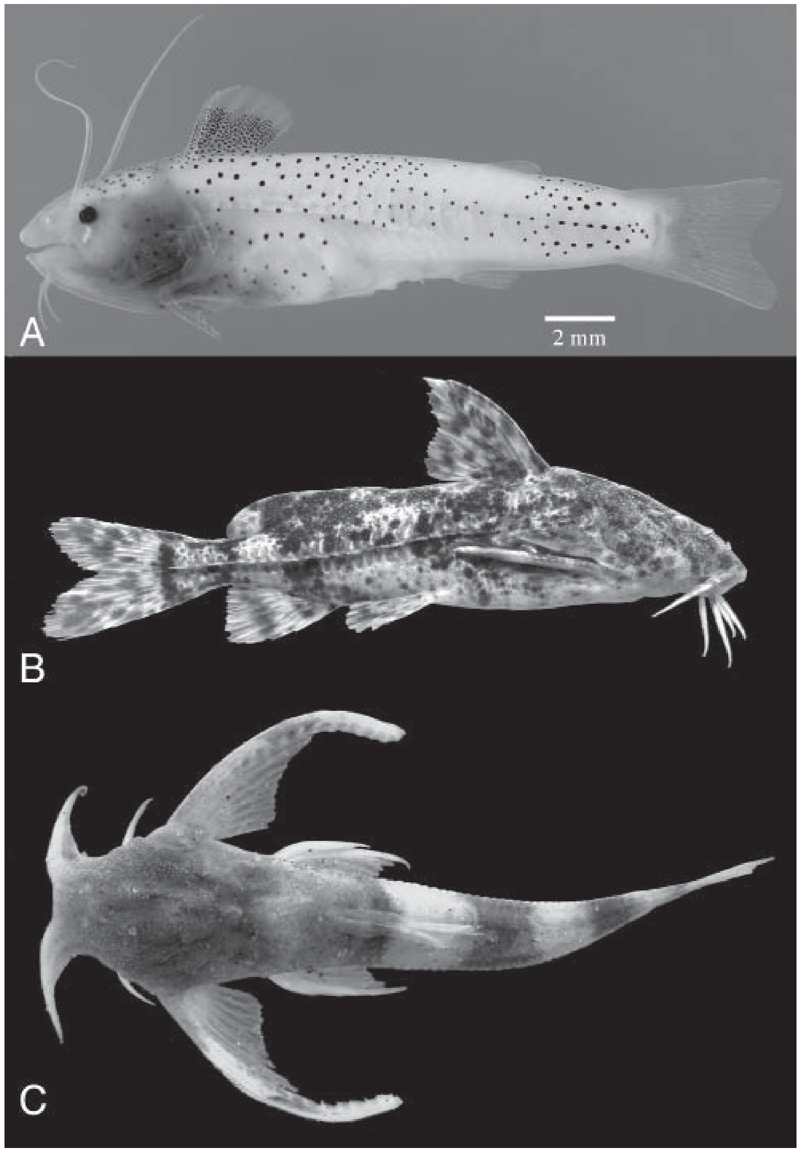

FIGURE 6. A. The auchenipterid *Gelanoglanis* sp. (Photo by P. Petri), B. the doradids *Rhinodoras armbrusteri* (Photo by M. H. Sabaj), and C. the aspredinid *Ernstichthys* sp. (photo by N. K. Lujan).

Anchariidae + Ariidae

The anchariids and ariids have long been thought to be related, with the anchariids occasionally placed in the Ariidae.

Anchariidae (Madagascar Catfishes)

Anchariids are a small group of fishes found in freshwaters of Madagascar, but they are sister to the widest-ranging family of catfishes, the Ariidae or sea catfishes. Like the ariids, they have few, very large eggs, but it is unknown what they do with the eggs (Ng et al. 2008).

Ariidae (Sea Catfishes)

Ariids (Figure 8) are found on continental shelves off of all continents except Antarctica (Betancur and Armbruster 2009; Kailola 1999). Ariids are

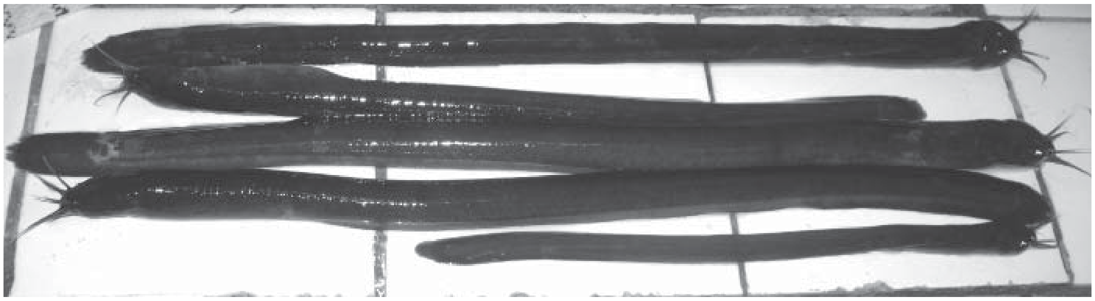

FIGURE 7. A group of anguilliform clariids, *Chanallabes* sp. (Photo by J. W. Armbruster).

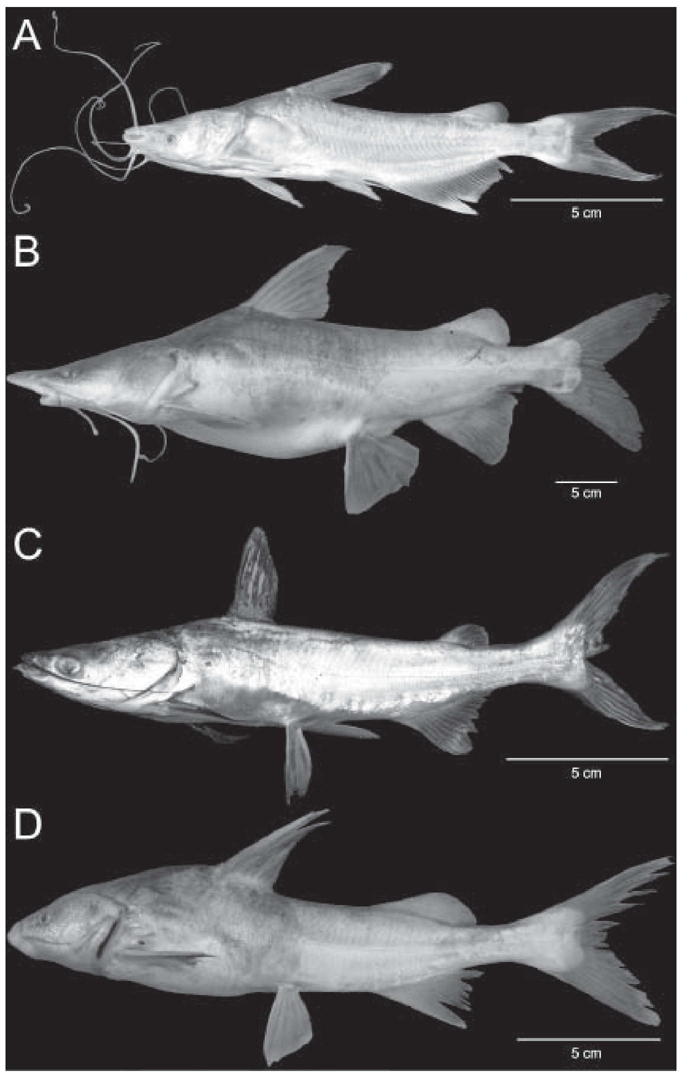

FIGURE 8. Unusual Papua New Guinea ariids: A. *Doiichthys novaeguineae*, B. *Cochlefelis spatula*, C. *Brustiarius nox*, D. *Pachyula crassilabris* (photos by R. Betancur-R.).

mouth-brooding fishes and have very few, very large eggs; eggs up to 13 mm in diameter have been reported (Coates 1988). They are almost always generalized catfishes, but in the Indo-Pacific, they have their greatest diversity in morphology. Perhaps the greatest diversity is ironically found in freshwaters of New Guinea, where ariids have speciated tremendously (Allen 1991). The most unusual species that my graduate student (R. Betancur) and I collected in Papua New Guinea is *Doiichthys*, a small ariid (<200 mm) with a very flattened head (Figure 8A).

Big Asia

Sullivan et al. (2006) describe the "Big Asia" clade for the most speciose groups in Asia: the Horabagridae, Bagridae, Akysidae, Amblycipitidae, Sisoridae, and Erethistidae (now placed in the Sisoridae). *Rita*, generally considered a bagrid, was not found to be related to other bagrids.

Horabagridae (Sun Catfishes)

Horabagrids have been placed with the bagrids and schilbids up until recently. The family contains just three genera and six valid species. Superficially, Horabagrus are similar to *Ictalurus* or to the bagrid *Mystus*. Both species of Horabagrus are considered threatened (Anvar Ali et al. 2007; Prasad et al. 2008).

Bagridae (Naked or Bagrid Catfishes)

Bagrid diversity is centered in tropical Southeast Asia; however, the type genus *Bagrus* are from Africa (Mo 1991). Bagrids are mostly generalized catfishes (Figure 9A), and many of the bagrids are similar in appearance to the North American Ictaluridae or the South American Pimelodidae.

Some bagrids have unusual reproductive behaviors. *Sperata* are known to feed its young with mucous secretions. Kampango *Bagrus meridionalis* from Lake Malawi have biparental care of nests of young, the female produces unfertilized eggs to feed the young, and the parents will even bring invertebrates to the nest to feed the young (LoVullo et al. 1992). Cichlids will often lay their eggs in the nests of kampango, and both the cichlids and the catfish will mutually defend the nest (McKaye 1985). Even more complexly, a clariid, *Bathyclarias nyasensis*, is known to occasionally brood parasitize kampango nests where the bagrid feeds the clariid young to the detriment of its own (Stauffer 2010).

Akysidae (Stream Catfishes)

Akysids are cryptically colored, small catfishes (generally less than 50 mm SL) from Southeast Asia that have tubercles all over their bodies and extremely small eyes. Superficially, they resemble aspredinids. There have been many new akysids described in the past 15 years due to collection efforts in new places.

Amblycipitidae (Torrent Catfishes)

The Amblycipitidae is a small family of Southeast Asian catfishes that occur in swift waters as far north as Japan. They are generally elongate, resembling some members of the Heptapteridae or Trichomycteridae. Sullivan et al. (2008) corroborated Hardman's (2005) suggestion that the akysids are not monophyletic and suggest that either one new family needs to be described or that the amblycipitids and akysids need to be placed in the Sisoridae.

Sisoridae (Hill-Stream Catfishes)

Sisoridae is a large family of fastwater fishes from Southeast Asia (Figure 9B–C). Among the more interesting adaptations in the Big Asia clade is the presence of an attaching structure made of folds of epidermis on the thorax in some sisorids, with *Pseudecheneis* also having the pelvic fins connected to forming a sucking attachment similar to that in gobies (Figure 9C).

Plotosidae (Eeltail or Tandan Catfishes)

The plotosids of the Indo-Pacific are the other marine family of catfishes but are actually more diverse in freshwater as in Australia and Papua New Guinea (Allen 1991; Ferraris 1999). Plotosids have heads that look like typical catfishes, but generally the adipose fin has rays and is connected to the caudal and anal fins, giving the common name of eeltail catfishes. (Figure 10A). *Plotosus lineatus* often lives in compact schools on coral reefs when they are juveniles; thus, at least in the Indo-Pacific, catfishes are even reef fishes.

Chacidae (Squarehead, Frogmouth, or Angler Catfishes)

The Chacidae of Southeast Asia is a small family of three species that are ambush predators with a very large mouth (Figure 10B). Superficially, they are similar (although flatter) than the North Ameri-

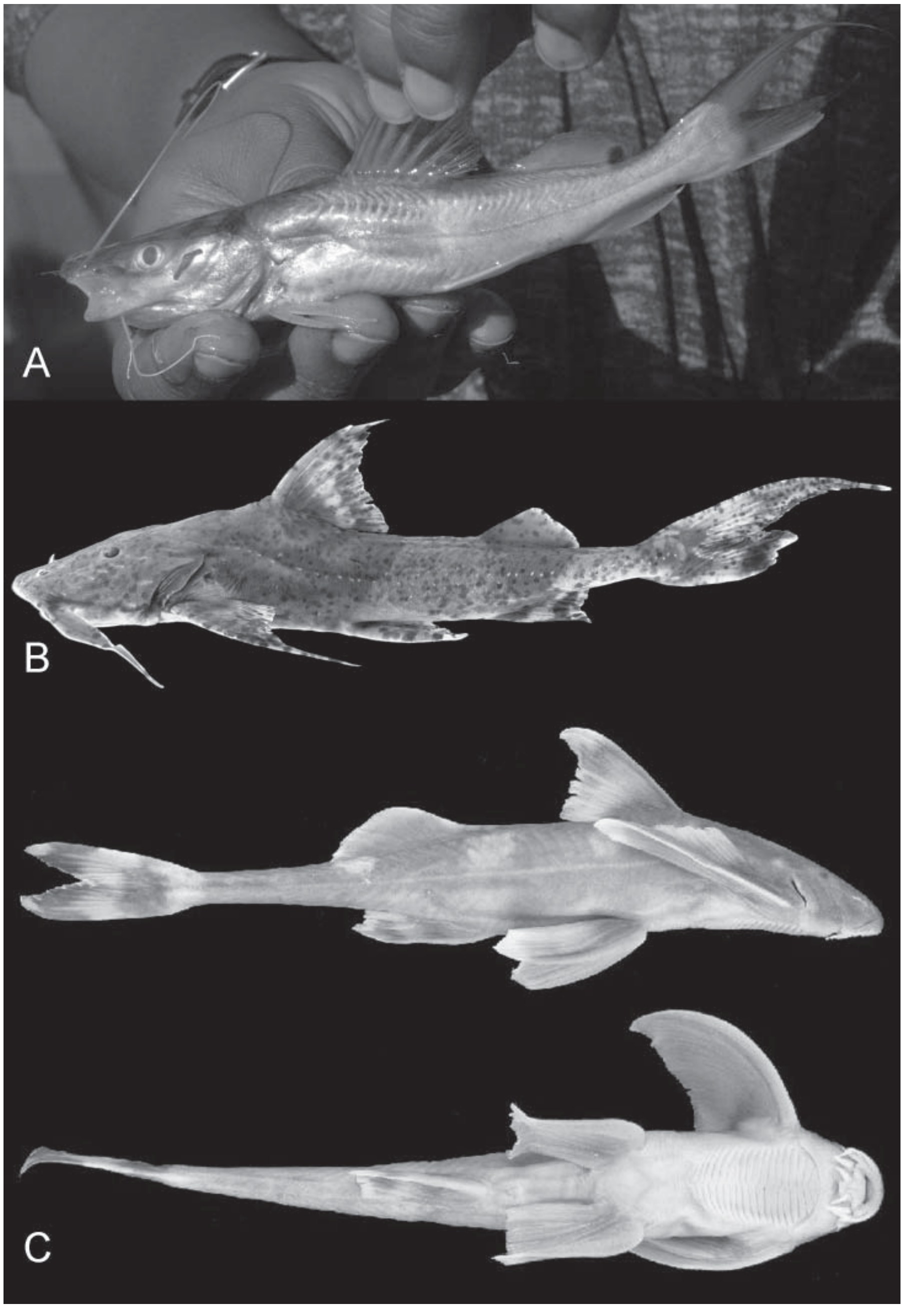

FIGURE 9. Members of the Big Asia clade: A. the bagrid *Sperata aor* (photo by S. Ferdous) and the sisorids B. *Bagarius yarrelli* (photo by M. H. Sabaj), and C. *Pseudecheneis longipectoralis* showing fused pelvic fins and thoracic attaching region (photos by H. H. Ng).

can flathead catfish *Pylodictus olivaris*. Chacid are called angler catfishes because they are known to use their maxillary barbels as lures to attract fishes for food (Roberts 1982).

Siluridae (Sheatfishes)

Silurids range through much of Europe and Asia. They differ from the typical catfish morphology

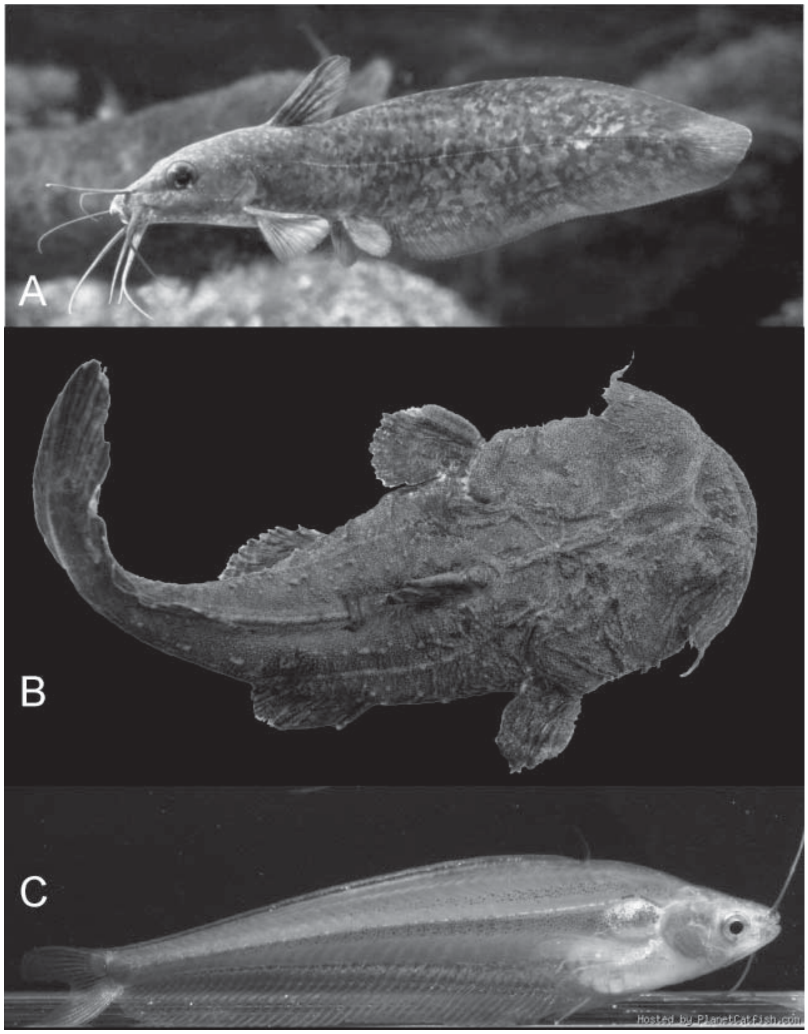

FIGURE 10. A. The plotosid *Tandanus* sp., B. (photo by P. J. Unmack), the chacid *Chaca chaca* (photo by S. Ferdous), and C. the silurid *Kryptopterus macrocephalus* (photo by H. H. Ng).

in that they lack dorsal spines and an adipose fin and have a very long anal fin. The family contains the longest catfish, wels *Silurus glanis*, which can reach 5 m (Kottelat and Freyhof 2007). Silurids do push the definition of the typical catfish a little bit, but perhaps the most unusual of them are the small fishes of *Kryptopterus* or glass catfishes. *Kryptopterus* have transparent bodies and live in schools in midwater. Their clear bodies make them difficult to spot in turbid water (Figure 10C).

Pseudopimelodidae + Pimelodidae + Heptapteridae

These three Neotropical families had been recognized in a single family, Pimelodidae, for most of their existence, but morphological studies suggested that they were three separate clades (de Pinna 1998). Molecular studies put these families into a single clade, but they are still recognized as separate families, and a fourth might be necessary for *Conorhynchos*, which does not fit comfortably into any family (Sullivan et al. 2006).

Pseudopimelodidae (Bumblebee Catfishes)

The pseudopimelodids contain small fishes like *Microglanis* and considerably larger fishes such as *Cephahlosilurus*, which reach 40 cm and look similar to the North American flathead catfish. Pseudopimelodids are found in slow to swift water but are generally not found at higher elevations.

Pimelodidae (Long-Whiskered Catfishes)

Pimelodidae are typical catfishes for the most part, with some notable exceptions (Figure 11). *Sorubim* (shovelnose catfish; Figure 11B) are particularly flattened and some contain a very potent toxin in their pectoral fins, and *Platystomatichthys* have a very flattened snout (Figure 11D). Some pimelodids like *Brachyplatystoma* and *Pseudoplatystoma* undergo basin-wide migrations within the Amazon. This process takes many years, with juveniles moving upstream to eventually spawn in the Andes (see Baras and Lalèyè 2003 for review).

Heptapteridae (Heptapterid Catfishes)

Heptapterids are the generally smaller species of the three-family group, and it is within this family

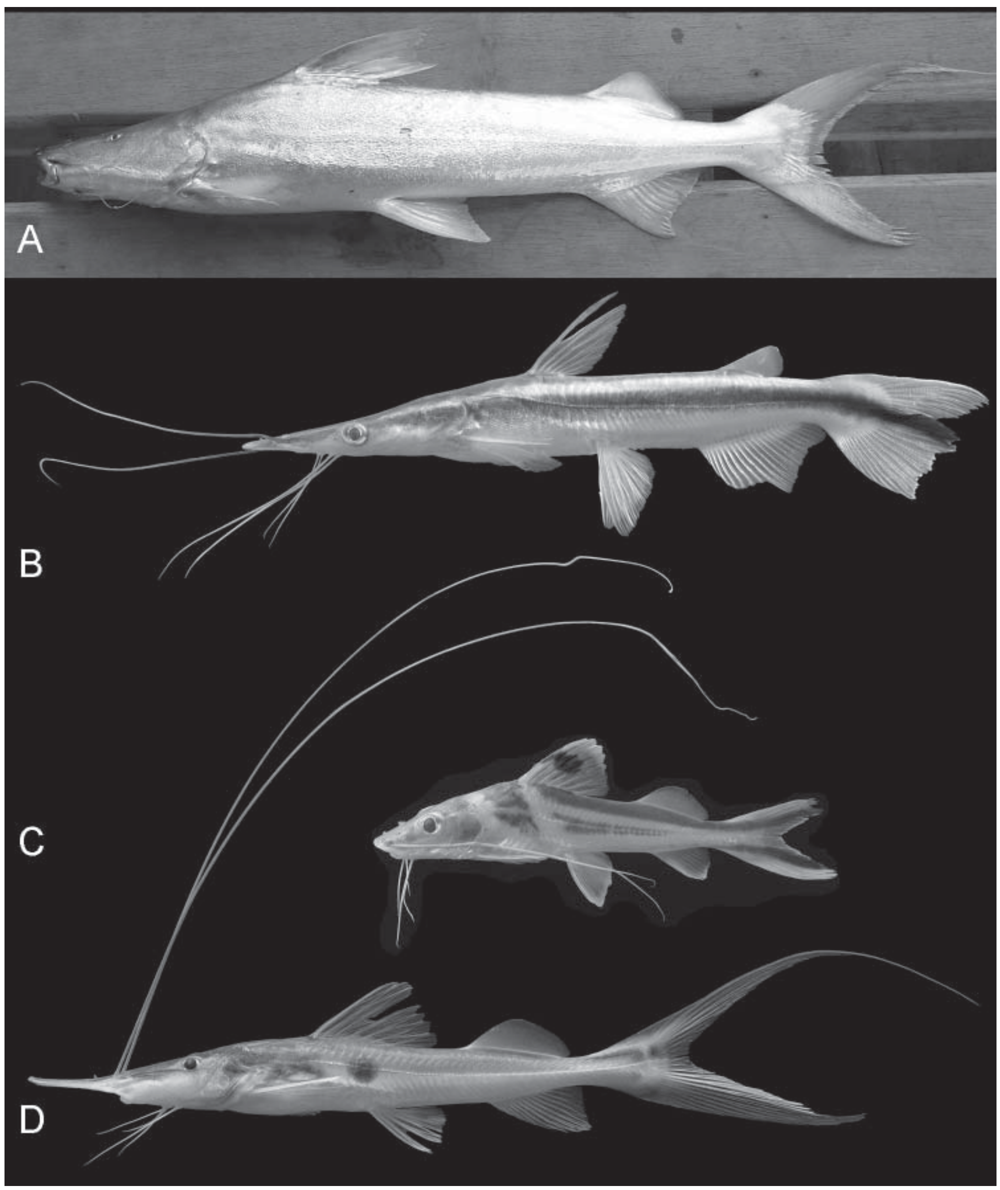

FIGURE 11. Members of the Pimelodidae: A. *Brachyplatystoma rousseauxii*, B. *Sorubim lima*, C. *Pimelodus ornatus*, and D. *Platystomatichthys sturio* (photos by M. H. Sabaj).

that the fishes play around most with the general catfish morphology. Perhaps the most unusual is *Phreatobius*, a genus of phreatic catfish. The phreatic zone is the region below the water table that is saturated with water, and these fishes can be collected in hand-dug wells but not in deeper, artesian wells (Muriel-Cunha and de Pinna 2005). Heptapterids have a large range throughout South America and as far north as Mexico.

Pangasiidae (Shark Catfishes)

The Pangasiidae of Asia contains the Mekong catfish *Pangasianodon gigas*, but also contains the common food fish of the genus *Pangasius* (the basa or tra). *Pangasius* have been introduced into the U.S. supermarket, but not without backlash from fish farmers. The U.S. Congress passed a temporary law that only the native Ictaluridae could be labeled catfish in grocery stores, and the battle between North American fish farmers and imported pangasiids continues. Juvenile *Pagasianodon* are common in the pet trade under the name "iridescent shark" (striped catfish *Pangasius hypopthalmus*), named because their dark bodies have a blue iridescence to them when young and a generalized shark shape.

Big Africa

Sullivan et al. (2006) recognize a clade consisting of the African families Mochokidae, Malapteruridae, Amphiliidae, Schilbidae, Auchenoglanidae ,and Claroteidae. Lundberg et al. (2007) found the newly discovered and described Mexican family Lacantuniidae (Rodiles-Hernández et al. 2005) in this clade as well, but this family occurs in Mexico.

Mochokidae (Squeaker or Upside-Down Catfishes)

Mochokidae is the largest family in the Big Africa clade and had been considered related to the South American families Doradidae and Auchenipteridae to which they are superficially similar (Mo 1991; de Pinna 1998). Mochokids often have dramatic patterns of spots that make them attractive aquarium fishes. Some mochokids have evolved into similar morphologies as the South American loricariids by having a ventral mouth, jaws used for scraping submerged surfaces, and a sucker-like mouth (Vigliotta 2008; Figure 12C). In another instance of brood parasitism, the cuckoo catfish *Synodontis multipunctatus* spawns over cichlid nests in Lake Tanganyika. Male cichlids mouthbrood the eggs along with their own young, but the catfish hatch earlier. Upon absorption of their yolk sacs, the catfish young eat the larval cichlids (Sato 1986). The upside-down catfishes (*Synodontis*) are unusual fishes popular in the aquarium trade that can be usually found swimming upside-down at the surface of the water. They are actually aligning themselves with the substrate and will usually swim right-side up when near the bottom (called a ventral substrate response). An experiment was done that subjected the fishes to microgravity to see if this changed their behavior, but they still ignored light and responded only to surfaces (Anken and Hilbig 2009).

Malapteruridae (Electric Catfishes)

Perhaps the most unusual family of the Big Africa clade is the Malapteruridae or electric catfishes (Figure 12B). Malapterurids have their lateral musculature modified into an electrical organ that is strong enough to shock prey and, from personal experience, cause quite a bit of pain to humans. Although for much of its history the Malapteruridae had been recognized as a single species, the diversity of form within the species was recently found to represent about 14 species in two genera.

Amphillidae (Loach Catfishes)

Amphiliids are fast-water fishes whose basal members are rather typical catfishes. Some of the derived species develop bony plates and an elongate appearance, with specimens of one genus, *Belonoglanis*, looking much like a stick.

Schilbidae (Schilbeidae) (Schilbid Catfishes)

The Schilbidae is a large family of mostly open-water fishes that are superficially similar to silurids, and unlike other families in the Big Africa clade, they range into southern Asia. *Paralia*, African glass catfish, are transparent, just as in the glass catfishes of Siluridae (*Kryptopterus*). Given that we do often define catfishes based on the presence of a dorsal-fin spine, it is unusual that several schilbids lack spines (not unique to schilbids), and some completely lack the dorsal fin (*Ailia* and *Paralia*). There is currently an argument among taxonomists on whether to spell the family name Schilbidae or Schilbeidae (based on the genus Schilbe), and both names are commonly used (Nelson 2006).

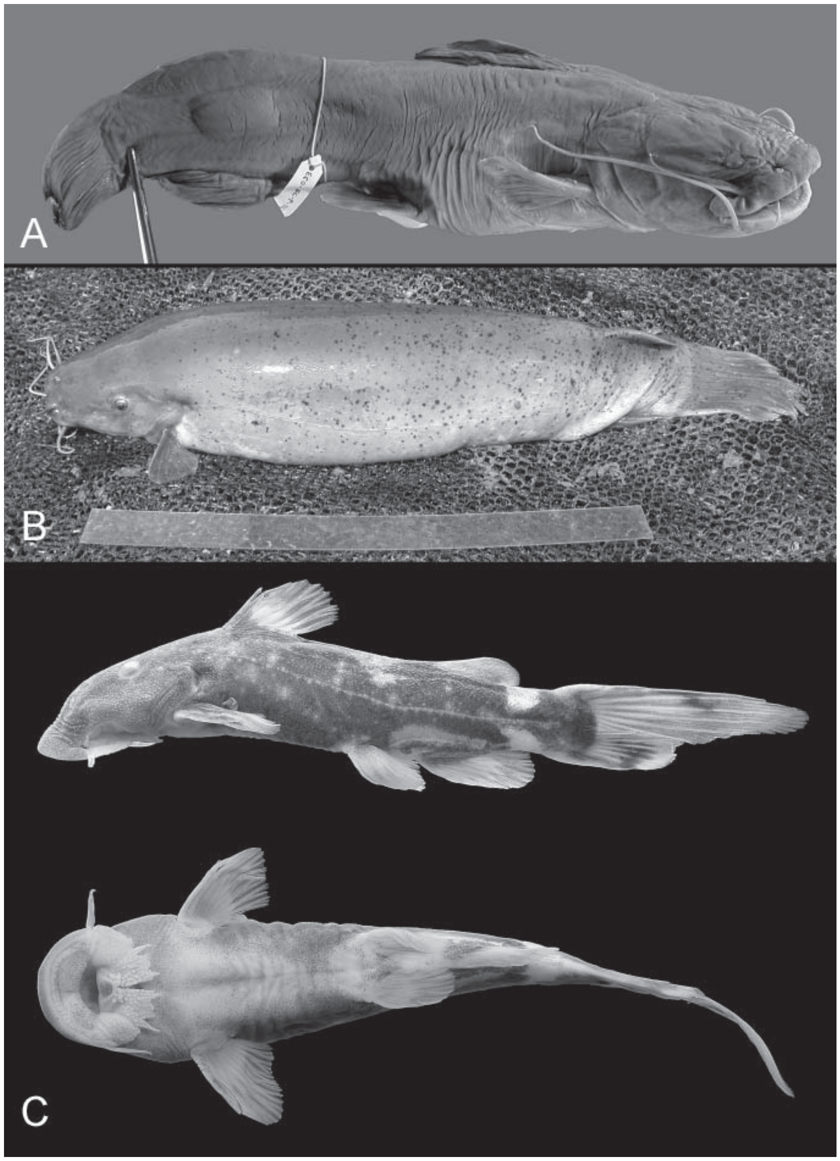

FIGURE 12. Members of the Big Africa clade: A. *Lacantunia enigmatica* (photo by J. W. Armbruster), B. *Malapterurus monsembeensis*, and C. *Chiloglanis asymetricaudalis* (photos by J. P. Friel).

Auchenoglanididae (Giraffe Catfishes)

Auchenoglanidids and claroteids are often placed in the same family, but the recognition of Lacantuniidae as the sister to the Claroteidae would make this family paraphyletic. Auchenoglanidids are most similar in appearance to mochokids but typically have a longer snout.

Claroteidae (Claroteid Catfishes)

Claroteids are the large catfishes of Africa. They look superficially similar to *Bagrus* and were once considered to be bagrids. Most species are in *Chrysichthys*, which has its greatest diversity in the Congo. The most unusual claroteids are species of the Lake Tanganyika endemic genus *Phyllonemus*, the first known fishes to have biparental mouth brooding (Ochi et al. 2000).

Lacantuniidae (Chiapas Catfish)

Lacantuniidae was recently described for the newly discovered *Lacantunia enigmatica* of Chiapas, Mexico. Chiapas catfish *L. eniqmatica* sort of looks like a large madtom (Ictaluridae) but with a different number of barbels (Figure 12A). The disjunct distribution of Lacantuniidae and its proposed sister family (Claroteidae) is unusual and, if the relationship is true, requires explanation. The split between *Lancantunia* and claroteids occurred after the breakup of Gondwanaland; thus, relatives of *Lancantunia* and or Claroteids would have had to have gone extinct over large parts of the globe (Lundberg et al. 2007).

Cranoglanididae + Ictaluridae

Last in Sullivan et al.'s (2006) analysis is the clade that includes the North American bullhead catfishes or Ictaluridae. Ictalurids are found to be related to the only genus of cranoglanidid, *Cranoglanis* of China and Vietnam. This relationship is interesting because several groups of animals (such as paddlefishes , alligators, and many other groups) share a similar distribution. The linkage between eastern North America and China is sometimes referred to as a Grayan distribution after the botanist Asa Gray who published on it in the 1800s (Gray, 1846; Petersen and Hughes 2007).

Cranoglanididae (Armorhead Catfishes)

Cranoglanis (Figure 13A) has just three species from China and Vietnam. The fishes look similar to the North American bullheads of the genus *Ameiurus*.

Ictaluridae (Bullhead Catfishes)

Despite the diversity of catfishes around the world, the waters of North America north of Mexico are relatively depauperate in catfish morphologies. All ictalurids (even the boldly patterned piebald madtom *Noturus gladiator*, Figure 13B) look like typical catfishes. As this volume can attest, the ictalurids (particularly *Ictalurus* and *Pylodictis*) are probably the most widely studied catfishes in the world. Also, given the fact that there are similar fishes on every continent, the North American research will provide a lot of insight into the dynamics of catfish populations and fisheries around the world. This insight is limited by the great diversity of form, habitat, behaviors, and ecology of catfishes.

Austroglanididae (Austroglanidid Catfishes)

The three species and one genus of austroglanidids are known from southern Africa. No austroglanidids were available for either of the main molecular studies of catfishes (Hardman 2005; Sullivan et al. 2006), and morphological hypoth-

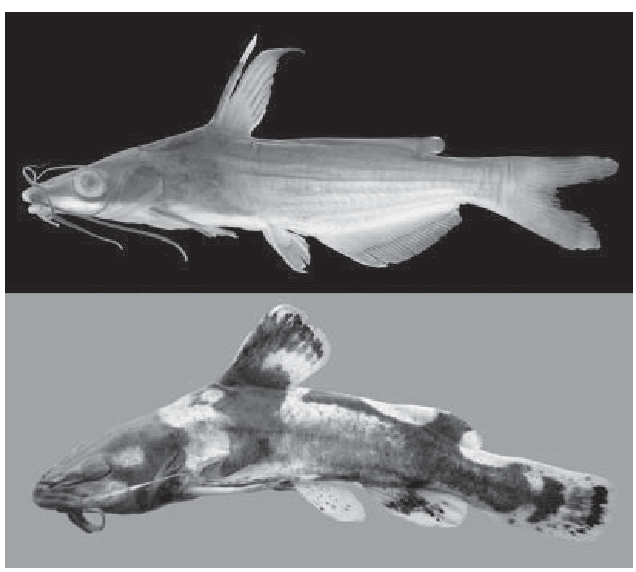

FIGURE 13. A. The cranoglanid *Cranoglanis sinensis* (Photo by H. H. Ng), and B. the ictalurid *Noturus gladiator* (Photo by M. A. Thomas).

eses differ as to their placement. Mo (1991) suggests that they are related to cranoglanidids of Asia, and de Pinna (1998) suggests that they are sister to a complex, pan-tropical clade of horabagrids, claroteids, schilbids, pangasiids, some bagrids, and pimelodids.

The Role of the All Catfish Species Inventory

ACSI was conceived in the first round of submissions for NSF's Planetary Biodiversity Inventory program, was funded in 2003, and went on to be widely successful. Although the PBIs were fashioned with the idea of discovering and describing all species in a clade dispersed across the planet, it is unreasonable to think that all undescribed species of catfishes could be described in the 6 years in which ACSI was active. What the PBIs really serve to do is to make taxonomy easier. Our results were dramatic, we developed a team of 460 participants from 53 countries and together we have increased the rate of species descriptions, especially when compared with other otophysan fishes (Figure 14). Eschmeyer and Fong (2010) keep a list of all of the described and valid species by family, as well as the species described in the past 10 years (Table 1). ACSI has been active for much of the 10 years, and we can see that the number of catfish species has increased by nearly 24% in the past 10 years.

We also developed many other products, including a database of around 10,000 photographs (mostly types) on our Web site, which enables people to see the types without having to ask for them on loan or to travel to the diverse places around the world where types are located. We began assembling PDFs of published papers on the Web site as well because a lot of the old literature is inaccessible to many people around the world. We developed auxiliary sites on the diversity of some catfish families (www.flmnh.ufl.edu/fish/freshwater/catfish/catfish_home.htm) as well as an online atlas of catfish bones (http://catfishbone.acnatsci.org). Through funds to participants, as well as funds in the laboratories of the principal investigators, we funded fieldwork in Asia, Africa, the Australian continent (Papua New Guinea), and especially South America, as well as museum visits for researchers to complete taxonomic revisions. Many of the participant awards went to graduate students, as the only way to assure the completion of taxonomy is to develop the next generation of taxonomists.

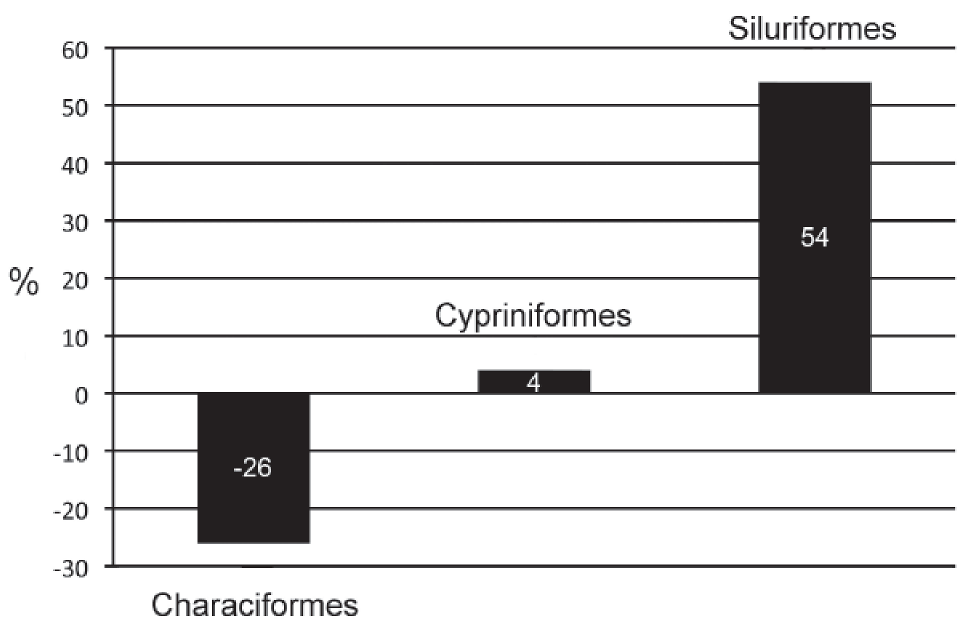

FIGURE 14. Percent change in rate of species description in the three largest orders of primary freshwater fishes in the five main years of All Catfish Species Inventory (2004–2008) compared to the previous 5 years (1999–2003).

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