

Evolution, Ecology and Taxonomy of the Corydoradinae revisited

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General Introduction

At the time of the publication of Identifying Corydoradinae Catfishes (Fuller and Evers, 2005), little was known about the relationships among different species in the Callichthyidae as a whole and even less was known about the relationships among the Corydoradinae. This has changed recently with the publication of the first comprehensive molecular phylogeny of the group (Alexandrou et al., 2011). Here we discuss the advances made in the phylogenetics and ecology of the Corydoradinae, and review the status of the group as a whole from a historic perspective.

The Callichthyidae

The family Callichthyidae (Bonaparte, 1838) are armoured catfishes widely distributed in South America defined by having two longitudinal rows of lateral body plates which completely cover the sides and two or three (basal) barbels at the junction of the lips on either side of the mouth (Gosline, 1940). Their name is derived from the Greek words *kallis* (beauty) and *ichthys* (fish). The family consists of two subfamilies, the Callichthyinae (genera: *Callichthys*, *Dianema*, *Hoplosternum*, *Leptoplosternum* and *Megalechis*) and the Corydoradinae (*Aspidoras*, *Scleromystax*, *Corydoras*, and *Brochis*). The Corydoradinae make up the majority (90% of the species within the Callichthyidae) with more than 170 valid species, and many more undescribed taxa with C-numbers or CW numbers. The group are likely to be very old, with a fossilized *Corydoras* (*Corydoras revelatus*) described from the Maiz Gordo Formation of Argentina (Cockerell, 1925), dated from the late Paleocene.

Taxonomic history

The first callichthyid was described by Linnaeus (Linnaeus, 1758) as *Silurus callichthys* (subsequently redesignated as *Callichthys callichthys*). The first *Corydoras* species was described by Lacépède in Histoire Naturelle des Poissons (Lacépède, 1803), designating *Corydoras geoffroyi* as the type species for the new genus. Subsequently, the genera *Brochis* (Cope, 1872) and *Aspidoras* (Ihering, 1907) were erected. In comparison with *Brochis* (Cope, 1872) and *Aspidoras* (Ihering, 1907), *Corydoras* differs by its laterally compressed head, short rictal barbels, and a single pair of short mental barbels at the lower lip. The genus *Brochis* can be distinguished by its greater number of soft dorsal rays (up to 12 in *Brochis*; 6-8 in *Corydoras* and *Aspidoras*). *Aspidoras* differs from *Corydoras* by having a short supra occipital crest, not separating the nuchal plates (Nijssen, 1970). Hoedeman defined the subfamilies Callichthyinae and Corydoradinae in 1952 (Hoedeman, 1952).

Taxonomic relationships of the Callichthyidae

Until recently, the majority of the taxonomic and systematic study of the Callichthyidae

has been based on morphological characters and cladistic analyses. Many attempts have been made to classify Corydoradinae species into groups that reflect their evolutionary history using a variety of techniques including morphology, colour patterns, chromosome numbers and characteristics and most recently, genetic markers. We briefly review the work that has been conducted in each of these areas.

Morphology

The first comprehensive studies of the Corydoradinae were conducted by Nijssen (1970) and Nijssen & Isbrücker (Nijssen, 1970; Nijssen and Isbrücker, 1980). These studies used meristic counts and morphological ratios to try and assemble species into meaningful groups. However, with a few exceptions most species overlapped in these characters and their morphological analyses were largely unsuccessful in grouping taxa (although successful in terms of characterising species). Because of the lack of differentiation, Nijssen (1970) and later Nijssen and Isbrücker (1980) suggested grouping taxa based on colour patterns (discussed below).

The next attempt to provide some order to the Corydoradinae was published by Strauss (Strauss, 1985). Using the tables of counts and measurements from Nijssen and Isbrücker (Nijssen and Isbrücker, 1980), Strauss performed a multivariate statistical analysis that indicated changes in morphology are the result of subtle changes in relative growth rates among body structures (Strauss, 1985). The author found that four out of the five groups proposed by Nijssen (1970) could not be discriminated properly due to overlap in body form and meristics. Therefore, the results conflicted with Nijssen's original proposed species groups that relied heavily on ratios and colour patterns.

A morphological approach was used in the first modern comprehensive phylogenetic analysis covering all callichthyid genera within a siluriform framework (Reis, 1998). The author set out to describe the skeletal anatomy of the Callichthyidae, to study the phylogenetic interrelationships among species and to test the monophyly of the family and its genera. The study supported the monophyly of the family Callichthyidae, and the division of the subfamilies Callichthyinae and Corydoradinae. Within the Corydoradinae, the genus *Aspidoras* was the sister-group of a clade formed by *Corydoras* and *Brochis*. There were no characters that supported the genus *Corydoras*, whereas four derived features supported the monophyly of the genus *Brochis*. The author provides a key to all callichthyid genera based on the morphological features described, and discusses the species groupings as described by Nijssen (1970) and Nijssen & Isbrücker (1980). Although the analysis was robust, it lacked taxonomic sampling within the Corydoradinae, most notably within the genus *Corydoras* and *Scleromystax*.

In 2003, Britto published a phylogenetic analysis of the Corydoradinae based on 83 morphological characters (Britto, 2003). Going one step further than Reis (1998), Britto expanded the number of morphological characters used and total taxonomic coverage within the genera *Corydoras*, *Scleromystax*, and *Aspidoras*. One of the outcomes of this study was the suggestion of the non-monophyletic nature of *Corydoras*. Instead of

Brochis and *Corydoras* forming a clade with *Aspidoras* as its sister group (Britto, 2003), Britto proposed a clade consisting of *Aspidoras* and *Scleromystax*. This resulted in the proposal of two tribes within the Corydoradinae: Aspidoradini and Corydoradini. Despite thorough analysis using a large number of morphological characters, the study did not resolve relationships within the Corydoradinae and raised the possibility that osteological characters may not resolve relationships among the group.

Colour patterns

From the early 19th century to the present, taxonomic descriptions of *Corydoras* have been primarily based on colour patterns. These tend to be variable both within and between species, thus making them difficult to quantify objectively (Nijssen, 1970). This results in both the ‘lumping’ of species with similar colour, when in reality they are genetically, morphologically and geographically distinct, and also the ‘splitting’ of geographic variants of single species. In his revision of the Surinam catfishes of the genus *Corydoras*, Nijssen (1970) proposed a number of species groups based on colour pattern, morphometry, and meristic characters. These were later refined by Nijssen and Isbrücker (1980) to five groups. However, these groups did not reflect phylogenetic relatedness among species as subsequently recognized by Isbrücker (Isbrücker, 2001). Taxonomic issues also arise when dealing with mimetic species, where type and paratype material belong to different lineages and have been placed together solely due to their similarity in colour.

Chromosomes

The Corydoradinae display high variation in chromosome number among species, making them potentially useful characters for grouping species. The first study reporting karyotypic and cytogenetic diversity within *Corydoras* was published by (Scheel et al., 1972) and detailed chromosome counts of 14 species of *Corydoras* which ranged from 44 in *C. paleatus* to 134 in *C. aeneus*. The authors compared these results to the groups proposed by Nijssen (1970), but found no obvious connection between their chromosome data and Nijssen’s groups. Further studies on chromosomes identified 58-64 chromosomes in four populations of *C. aeneus* (Oliveira et al., 1988) and 40, 42 and 44 chromosome in three populations of *C. nattereri* (Oliveira et al., 1990). When compared to the results by Scheel et al. (Scheel et al., 1972), differences in *C. aeneus* data indicated the existence of a possible diploid-tetraploid system within the *C. aeneus* group (58-64 vs. 134 chromosomes). Further work included *Corydoras* species from a wider geographic area, detailing chromosome characteristics and genome sizes for 11 species from a variety of localities across the South American continent (Oliveira et al., 1992). This study increased the total number of *Corydoras* species with known karyotypes to 30. The study provided a hypothetical framework for chromosome and genome size evolution within the group. Subsequently, additional callichthyid species were analysed by Oliveira et al. with additional hypotheses concerning genome evolution within the Callichthyidae as a whole (Oliveira et al., 1993a; Oliveira et al., 1993b; Oliveira et al., 1993c). These studies allowed species to be grouped based on chromosome numbers, but the relationships among groups and the mechanisms leading to chromosome changes were still far from clear.

Molecular Phylogenetic Studies

The first molecular phylogeny of the family Callichthyidae was presented by Shimabukuro-Dias et al. (Shimabukuro-Dias et al., 2004). The authors sequenced mitochondrial genes from 28 representative callichthyids (Genera: *Corydoras* (12), *Aspidoras* (3), *Brochis* (2), *Dianema* (2), *Leptoplosternum* (2), *Megalechis* (2), *Callichthys* (2), and *Hoplosternum* (2)). The authors concluded that the callichthyids form a monophyletic assemblage comprising two natural groups: the subfamily Corydoradinae (Genera: *Aspidoras*, *Brochis*, and *Corydoras*) and the subfamily Callichthyinae (Genera: *Callichthys*, *Dianema*, *Hoplosternum*, *Leptoplosternum*, and *Megalechis*). This molecular phylogeny conflicted with previously proposed morphological relationships. The addition of karyotypic data added a unique phylogenetic perspective, supporting basal relationships of diploid progenitors and the monophyly of polyploid species groups within *Corydoras*.

In 2011, Alexandrou et al. published the first comprehensive molecular phylogeny of the Corydoradinae (Alexandrou et al., 2011). This study used sequences from a variety of genes with different characteristics to construct a phylogeny of the group. These regions include mitochondrial markers that are widely used in phylogenetic studies in fishes and other organisms and nuclear genes. Mitochondrial markers are inherited through the maternal line; so all offspring (male and female) from a female inherit solely her mitochondrial genes. Mitochondrial genes can be misleading in a phylogenetic perspective if hybridization has occurred. Nuclear genes are inherited from both the mother and the father of an individual, and are useful for investigating hybridization of species and groups. By using a combination of markers, a consensus can be drawn about the most likely relationships among species. The Alexandrou et al. (2011) study used sequences from six different regions within the genome and a total of 435 individual taxa including multiple individuals when available.

The Alexandrou et al. (2011) phylogeny identified nine major lineages of Corydoradinae (Figure 1). In order of time since common ancestor these are: Lineage 1 (saddle snouted species such as *C. fowleri*), Lineage 2 (*Aspidoras*), Lineage 3 (*Scleromystax*), Lineage 4 (dwarfs + some others), Lineage 5 ('elegans' group), lineage 6 (*C. paleatus* and others), Lineage 7 ('aeneus' group), Lineage 8 (*Brochis* and species such as *C. haraldshultzi*), Lineage 9 (*C. adolfoi* and other short snouted species). These results conflict with the morphological hypothesis put forward by Britto (Britto, 2003) which separated the Aspidoradini and Corydoradini tribes into monophyletic assemblages. Firstly, the position of the Aspidoradini tribe (*Aspidoras* and *Scleromystax*, Lineages 2 & 3 respectively) as sister group of the remaining Corydoradinae was rejected. All molecular phylogenies inferred in this study fully support Lineage 1 as the sister group of all other Corydoradinae, with the Aspidoradini (Lineages 2 & 3) derived in relation to Lineage 1. As a result of the morphological phylogeny (Britto, 2003), *Brochis* was synonymised with *Corydoras*, which is fully supported by the Alexandrou et al. (2011) study (however, a future revision would involve the resurrection of the genus *Brochis*). There are other differences with the proposed morphological phylogeny in the structure of smaller clades within the

Corydoradinae, with respect to the placement of *C. garbei*, *C. undulatus*, *C. gracilis*, *C. flaveolus*, *C. ephippifer*, *C. hastatus*, *C. pygmaeus*, *C. maculifer*, *C. reticulatus*, *C. agassizi*, *C. ambiacus* and *C. ornatus*. The basal positioning of Lineage 1 that includes the type species of *Corydoras* (*C. geoffroy*) means that the genus is currently paraphyletic with respect to the Aspidoradini.

Ecology of the Corydoradinae

Mimicry

Aquarists have known for a long time that *Corydoras* species frequently share colour patterns when living together. What was missing was an understanding of how the different species were related genetically and how they managed to coexist. Alexandrou et al. (2011) demonstrated that species living together with the same colour patterns are almost always genetically distantly related and come from different genetic lineages. Some known exceptions include *S. barbatus*, *S. macropterus* and *C. ehrhardti*, *C. paleatus* that are members of the same lineage (*Scleromystax* and Lineage 6 respectively). This allowed a number of hypotheses that may have led to sympatric species sharing colour patterns to be ruled out (ecological speciation, sympatric speciation via polyploidy and the possibility that sympatric species were actually different morphotypes of the same species). The Corydoradinae are well defended with armour plates, lockable sharp spines and toxins, thus Müllerian mimicry appears to be the most likely explanation for colour pattern sharing. Müllerian mimicry occurs when two or more defended species adopt the same colour pattern for mutual benefit. This mutualistic relationship evolves because predators need to sample a certain number of individuals to learn that a certain colour pattern signals unprofitability. By sharing colour patterns, species share the cost of educating predators. This differs from Batesian mimicry where undefended prey mimic defended model species. Examples of Batesian mimicry include *Corydoras diphyes* and *Otocinclus mimulus* (Axenrot and Kullander, 2003) and *Corydoras hastatus* and various Characiformes (e.g. *Serrapinnus kriegi*) where the undefended *Otocinclus* and Characiformes mimic defended *Corydoras* species.

Investigating diet using stable isotopes

Studying the diet of detritivorous fishes directly can be challenging due to the difficulty in identifying fragmented and partially digested items found in the stomachs of fishes. The Alexandrou et al. (2011) study used $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ and stable isotopes found in muscle tissue to investigate dietary differences of wild caught Corydoradinae. Stable isotopes are particularly useful when investigating diet, as they retain a signature over a long time period, as opposed to stomach contents that indicate what the organism was eating on the day of capture. Nitrogen ($\delta^{15}\text{N}$) increases in a stepwise manner between trophic levels; for example carnivore tissues have higher $\delta^{15}\text{N}$ values than herbivore tissues due to their higher position in the food web (Peterson and Fry, 1987). Carbon ($\delta^{13}\text{C}$) may change slightly with trophic level, but the major source of variation are the sources of primary production, and $\delta^{13}\text{C}$ values are typically more useful in deriving

foraging locations (Rubenstein and Hobson, 2004; West et al., 2006). The results from the Alexandrou et al. (2011) study demonstrate that sympatric species from different genetic lineages feed at different trophic levels, and therefore that co-mimics with different snout morphology are able to partition resources and do not compete for food. These differences determine community structure of mimetic groups (Figure 2). Larger, long-snouted species always occupy a lower relative trophic level than smaller short snouted species (which can be seen behaviourally where long snout species forage by digging their heads deep into the benthos while short snouts forage on the substrate surface). Some representatives from lineage 4 (e.g. *C. hastatus*) are not benthic feeders like their relatives, occupying a mid-water position in the rivers water column.

Morphology

In order to investigate differences in snout morphology and body size between different Corydoradinae species, we used a geometric morphometric approach based on landmarks (Alexandrou et al., 2011). Briefly, multiple landmarks are placed on identifiable morphological regions of a fish profile. Software is used to transform distances between landmarks, allowing the user to visually explore and identify areas that differ in shape between species. In the Alexandrou et al. (2011) study, a total of 200 preserved individuals, representing over 120 different species (including all mimetic taxa), were photographed and used for digital landmark-based morphometric analysis of body shape. Major differences between species belonging to different Corydoradinae lineages were identified in snout morphology, position of the eye and vertical body depth. As mentioned above, differences in snout morphology are important in terms of feeding differences. The position and size of the eye would be a useful character to differentiate between species belonging to different lineages, as the eyes of species within Lineages 4 and 5 occupy a comparatively lower position relative to other Lineages. The sensitivity of the geometric morphometric approach is great enough to assign any species to its respective lineage with an accuracy of 99%. This is a useful approach as the only data required for these analyses are profile pictures of a fish with measurement scale. Furthermore, morphological differences within the Corydoradinae are conserved within lineages. For example, all species within Lineage 9 are short snouted, while all species in Lineage 1 are long snouted. Even within lineage 8 where there is some morphological variation (see sub-clade structure below), species can be identified by their body depth.

Systematic relationships and suggestions for a revision of the Corydoradinae (Hoedeman, 1952)

It is clear from the molecular phylogeny that the Corydoradinae are in need of taxonomic revision (Alexandrou et al., 2011). The need for this revision has been recognized for some time (Isbrücker, 2001), although it is only now that the genetic relationships among species are clear, allowing species to be grouped into phylogenetically meaningful and monophyletic groups. Here we present suggestions for revision of the Corydoradinae (both formally described and undescribed taxa). This is intended as an outline proposal for a future taxonomic revision, and does NOT

represent a formal revision. All species should continue to be referred to as *Corydoras*, *Aspidoras* or *Scleromystax* until a thorough peer-reviewed revision incorporating both morphological and genetic data has been published.

Lineage 1. The basal ‘saddle nosed’ species remain as *Corydoras*, as first described by Lacépède in 1803 (Lacépède, 1803). *C. geoffroy* would remain the type species for the genus. Long snouted ‘Saddle nosed’ species such as *Corydoras fowleri* occur at the base of the Corydoradinae. Species included in this lineage include:

Described species: *C. coriatae*, *C. fowleri*, *C. semiaquilus*, *C. treitlii*, *C. narcissus*, *C. serratus*, *C. simulatus*, *C. amapaensis*, *C. solox*, *C. cortesi*, *C. septentrionalis*, *C. stenocephalus*, *C. aurofrenatus*, *C. ellisae*, *C. blochi*, *C. pastazensis*, *C. acutus*, *C. areio*, *C. cervinus*, *C. geoffroy*, *C. heteromorphus*, *C. maculifer*, *C. negro*, *C. sararensis*, *C. vittatus*, *C. ourastigma*, *C. oxyrhynchus*, *C. orcesi*, *C. saramaccensis*.

Undescribed species: c8, c16, c24, c28, c29, c38, c42, c47, c51, c53, c61, c63, c77, c78, c86, c92, c94, c95, c99, c109, c115, c116, c124, c127, c145, c146, c149, c153, cw5, cw11, cw12, cw17, cw53, cw55, cw59.

Lineage 2. *Aspidoras*. This group would remain as *Aspidoras* (Ihering, 1907) with the designated type species: *A. rochai*. All known *Aspidoras* belong to lineage 2 with the exception of *A. pauciradiatus*. Furthermore, recently described *C. gladysae* and *C. petrarcini* seem closely related to *Aspidoras*, yet they lack certain synapomorphies that define *Aspidoras*, thereby potentially requiring a new generic name (Calvino and Alonso, 2009). Genetic data are required to better understand the relationships of these species to *Aspidoras*.

Described species: *A. albater*, *A. belenos*, *A. brunneus*, *A. carvalhoi*, *A. depinnai*, *A. eurycephalus*, *A. fuscoguttatus*, *A. lakoi*, *A. maculosus*, *A. menezesi*, *A. microgaleus*, *A. poecilus*, *A. psammatides*, *A. raimundi*, *A. rochai*, *A. spilotus*, *A. taurus*, *A. velites*, *A. virgulatus*.

Undescribed species: c35, c36, c37, c118, c119, c125, c158, cw52.

Lineage 3. All known *Scleromystax* belong to lineage 3 and thereby this groups would remain as *Scleromystax* (Günther, 1864) with the designated type species: *S. barbatus*.

Described species: *S. barbatus*, *S. macropterus*, *S. prionotus*, *S. kronei*, *S. salmaccis*, *S. lacerdai*.

Undescribed species: c112, c113, cw38, cw42.

Lineage 4. This lineage includes two of the dwarf species, and therefore we would suggest resurrection of the disused *Microcorydoras* (Myers, 1953), with the designated type species: *C. hastatus*. Not all species within this group are dwarfs per se, but they are closely related and share similar colour pattern throughout larval development.

Described species: *C. hastatus*, *C. pygmeus*, *C. mamore*, *C. guapore*, *C. paucerna*.

Lineage 5. Lineage 5 contains species that have been known as the ‘*elegans*’ group *sensu* Nijssen (Nijssen, 1970) with some additions and corrections. A revision could involve the resurrection of the genus name *Gastrodermus* (Cope, 1878), with the designated type species: *C. elegans*. *C. gracilis* is the basal species in this lineage and *A. pauciradiatus* also belongs to this lineage rather than *Aspidoras* (Lineage 2).

Described species: *C. gracilis*, *C. sp.* *A. pauciradiatus*, *C. nijsseni*, *C. bilineatus*, *C. elegans*, *C. nanus*, *C. napoensis*, *C. undulatus*.

Undescribed species: c41, c88, c89, c123, c126, c132, cw8, cw18, cw19, cw22, cw29, cw44, cw48, cw56.

Lineage 6. Species within this group have always been classified under the genus *Corydoras*, with no synonymous disused generic names available. Thereby, it would be necessary to describe a new genus with a new type species.

Described species: *C. carlae*, *C. cochui*, *C. nattereri*, *C. potaroensis*, *C. diphyes*, *C. ehrhardti*, *C. micracanthus*, *C. paleatus*, *C. flaveolus*, *C. reynoldsi*, *C. tukano*, *C. albolineatus*, *C. longipinnis*, *C. ortegai*, *C. steindachneri*.

Undescribed species: c7, c40, c73, c114, c144, cw3, cw24.

Lineage 7. This lineage comprises all species from the ‘*aeneus*’ group. A revision would involve the resurrection of the genus name *Osteogaster* (Cope, 1871), with the designated type species: *C. eques*. The most basal species in this group are *C. melanotaenia* and *C. aeneus* from Trinidad, which are found in the Orinoco drainage. *C. zygatus* and *C. rabauti* are found within this group and appear to be more closely related to each other than they are to other species in the lineage. Most closely related to these species are *C. aeneus* spp. from the Parana drainage that were originally known as *C. macrosteus*. The Amazonian species form a group within the lineage, with *C. aeneus* from Suriname and Guyana separate from species from Peru where the ‘laser’ species are found.

Described species: *C. rabauti*, *C. aeneus* (spp.), *C. eques*, *C. melanotaenia*, *C. zygatus*, *C. schultzei*, *C. venezuelanus*.

Undescribed species: cw7, cw9, cw10, cw14, cw16, cw23, cw26, cw41, cw43.

Lineage 8. This lineage comprises mainly the ‘intermediate long-snouts’ - the long snouted but deep bodied species, but also includes *Brochis*, that was recently synonymized with *Corydoras* (Britto, 2003). A revision would involve the resurrection of the name *Brochis* (Cope, 1871), with the designated type species: *B. splendens*. Furthermore, another three genera would have to be named for sub-clades within this species rich lineage.

Described species:

Sub-clade 1: *Brochis*: *B. britskii*, *B. multiradiatus*, *B. splendens*.

Undescribed species: cw34, cw35.

Sub-clade 2: *C. garbei*, *C. diffluviatilis*, *C. filamentosus*.

Undescribed species: c57, c67.

Sub-clade 3: *C. latus*, *C. sodalis*, *C. reticulatus*, *C. geryi*, *C. pantanalensis*.

Undescribed species: c81, cw33.

Sub-clade 4: *C. crypticus*, *C. imitator*, *C. virginiae*, *C. amandajanea*, *C. condisciplus*, *C. ornatus*, *C. orphnopterus*, *C. pulcher*, *C. agassizii*, *C. ambiacus*, *C. crimmeni*, *C. delphax*, *C. ephippifer*, *C. incolicana*, *C. robustus*, *C. leopardus*, *C. geryi*, *C. gomezi*, *C. haraldschultzi*, *C. isbrueckeri*, *C. noelkempffi*, *C. pinheiroi*, *C. robinae*, *C. seussi*, *C. spectabilis*, *C. approuaguensis*, *C. filamentosus*, *C. sychri*, *C. melanistius*, *C. lamberti*, *C. spilurus*, *C. bifasciatus*.

Undescribed species: c9, c10, c13, c18, c34, c39, c49, c52, c66, c68, c71, c74, c75, c80, c87, c97, c98, c101, c102, c103, c110, c117, c122, c128, c130, c131, c135, c138, c140, c143, c152, c155, c156, c157, c159, cw2, cw6, cw13, cw20, cw25, cw40, cw57, cw58.

Lineage 9. Species in lineage 9 are the classic ‘short snouted’ species such as *C. adolfoi*. A revision would likely involve the resurrection of name *Hoplosoma* (Agassiz, 1846), with the designated type species: *C. punctatus*. This is a very species rich lineage and many of the species are relatively recently evolved.

Described species: *C. boesemani*, *C. arcuatus*, *C. adolfoi*, *C. davidsandsi*, *C. duplicareus*, *C. melini*, *C. metae*, *C. panda*, *C. gossei*, *C. burgessi*, *C. griseus*, *C. oiapoquensis*, *C. baderi*, *C. concolor*, *C. axelrodi*, *C. armatus*, *C. atropersonatus*, *C. kanei*, *C. loretoensis*, *C. loxozonus*, *C. bicolor*, *C. brevirostris*, *C. evelynae*, *C. leucomelas*, *C. parallelus*, *C. schwartzi*, *C. habrosus*, *C. sterbai*, *C. trilineatus*, *C. araguaiaensis*, *C. bondi*, *C. breei*, *C. copei*, *C. coppenamensis*, *C. cruziensis*, *C. julii*, *C. multimaculatus*, *C. osteocarus*, *C. paragua*, *C. polystictus*, *C. punctatus*, *C. sipalwini*, *C. caudimaculatus*, *C. similis*, *C. weitzmani*, *C. urucu*, *C. xinguensis*, *C. sanchesii*, *C. surinamensis*, *C. boehlkei*.

Undescribed species: c3, c6, c14, c19, c21, c30, c33, c43, c44, c45, c48, c54, c62, c65, c76, c84, c85, c90, c91, c96, c100, c104, c120, c121, c129, c133, c134, c136, c137, c139, c141, c142, c147, c148, c150, c151, c154, cw1, cw4, cw15, cw21, cw27, cw28, cw30, cw31, cw32, cw36, cw37, cw39, cw45, cw46, cw47, cw49, cw50, cw51, cw54, cw60.

Acknowledgements:

We thank Juan Montoya-Burgos, Mark Sabaj Perez, Ian Fuller, Hans-Georg Evers, Mark Walters and Kim Mathiesen for providing tissue samples and photographs. We thank Claudio Oliveira who helped conduct the fieldwork, and all members of the Catfish Study Group for their enthusiasm and support.

Glossary:

Allopatric- occurring in separate non-overlapping geographical areas

Batesian mimicry- mimicry in which an edible animal is protected by its resemblance to a noxious one that is avoided by predators

Clade- a group of organisms believed to have evolved from a common ancestor, according to the principles of cladistics

Cladistics- a method of classification of animals and plants according to the proportion of measurable characteristics that they have in common

Convergence- the tendency of unrelated animals and plants to evolve superficially similar characteristics under similar environmental conditions

Cytogenetics- the study of inheritance in relation to the structure and function of chromosomes

Diploid- containing two complete sets of chromosomes, one from each parent

Karyotype- the number and visual appearance of the chromosomes in the cell nuclei of an organism or species

Meristics- counting and measuring quantitative features of fish, such as the number of fins or scales

Monophyletic- descended from a common evolutionary ancestor or ancestral group

Morphometry- the process of measuring the external shape and dimensions of landforms, living organisms, or other objects

Müllerian mimicry- a form of mimicry in which two or more noxious animals develop similar appearances as a shared protective device, the theory being that if a predator learns to avoid one of the noxious species, it will avoid the mimic species as well

Niche differentiation- the process by which natural selection drives competing species into different patterns of resource use or different niches

Niche- the relational position of a species or population in its ecosystem to each other

Paraphyletic- descended from a common evolutionary ancestor or ancestral group, but not including all the descendant groups

Polyphyletic- derived from more than one common evolutionary ancestor or ancestral group and therefore not suitable for placing in the same taxon

Polyplloid- an organism or cell containing more than two homologous sets of chromosomes

Radiation- divergence out from a central point, in particular evolution from an ancestral animal or plant group into a variety of new forms

Stable isotopes- naturally occurring stable forms of elements with differing nuclear masses, which confer disparate physical properties that cause such isotopes to behave differentially in biogeochemical processes

Sympatric- occurring within the same geographical area; overlapping in distribution

Synapomorphy- the possession by two organisms of a characteristic (not necessarily the same in each) that is derived from one characteristic in an organism from which they both evolved

Trophic Level- each of several hierarchical levels in an ecosystem, comprising organisms that share the same function in the food chain and the same nutritional relationship to the primary sources of energy

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