

TRACKING EVOLUTIONARY TRENDS IN SILURIFORMES
(TELEOSTEI; OSTARIOPHYSI)

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Introduction

Phylogenetic hypotheses have proven to be instrumental in assessing if morphological novelties are advantageously adaptive or exaptations. Darwin (1859) pioneered the use of an evolutionary framework in behavior. The advent of a rigorous method for determining genealogical relationships, cladistics (sensu Hennig, 1966), has triggered more studies on behavior evolution. Phylogenetic works, however, are still in their relative infancy. Large groups are still to be phylogenetically analyzed, and most published studies are preliminary or cover a diffuse array of topics (McLennan, 1994).

In fishes, the vast majority of phylogenetic studies are based on osteological, external morphological or molecular characters. Molecular systematics is attractive for providing a time frame for diversification events: however anatomical/osteological features provide grounds for comparative anatomy, behavior, and analyses of sequence of evolutionary novelties.

The ordinary way to reconcile phylogenetic relationships and behavior is by optimizing the character of interest in a given phylogeny. The main goal is to find the best hypothesis of the evolution of the character that fits in parsimoniously with the given phylogenetic hypothesis. The fact that a derived trait appeared at the same time as the development of a certain function may be the evidence necessary to recognize an adaptation (Greene, 1986; Coddington, 1988). On the other hand, if the function predates the evolutionary novelty, we may almost certainly affirm that the trait is irrelevant for the function - Donoghue (1989, p. 1147) illustrates the issue very clearly and states that "...besides assessing sequence of character change, cladograms may provide means of testing ideas concerning changes in flexibility during evolution".

The present paper is a preliminary attempt to track putative adaptational traits on Siluriformes based on recent phylogenetic hypotheses. According to available hypotheses of Siluriformes relationships, different tests could be made comparing behavior and morphological or physiological/biochemical traits. Two tentative tests are going to be analyzed: air-breathing capacity and sexual dimorphism.

1. Air-breathing capacity – correlation with swimbladder encapsulation

Swimbladder encapsulation is an overgrowth of bony tissue from skull parts that ended enclosing the bladder in bone. This modification is a synapomorphy for a set of Neotropical catfish families (Baskin, 1973; Schaefer and Lauder, 1986). The physiological importance of such modification has never been properly appreciated. One possible consequence of encapsulation could have been the loss of an organ to perform gas exchange, which could have forced their bearers to develop a new evolutionary pathway such as capturing O₂ from the air, giving rise to the air-breathing behavior in these fishes. In this test, I try to identify the possible correlation between these two traits, air-breathing and gas bladder encapsulation, based on the hypothesis that if these characters co-evolved, one might have predated the other in appearance, the origin of one trait may have been advantageous for the second and it should be present in the same taxa.

2. Sex dimorphism - modifications on skull and mouth parts

In this analysis, I try to evaluate the importance of certain derived features with the presence of sex dimorphism. This analysis is restricted to the armored catfish family Loricariidae because sex dimorphism and morphological novelties in this family have been receiving closer attention lately and some information is currently available in the literature.

Methods

Siluriformes comprise an extremely successful group of freshwater fishes. With around 30 families, only 1 is exclusively marine, 2 have freshwater and marine representatives, and the vast majority occurs exclusively in freshwater. Siluriformes are present in all continents, except Antarctica, being mainly concentrated in tropical areas (low latitudes). Siluriformes originated in the early Cretaceous, before or about the time of the break-up of Gondwana. These

fishes have colonized all kinds of water and habitats (except oceanic depths and below-freezing waters) and have certainly a long pathway of historical, phylogenetic and structural constraints still to be uncovered. The high number of Siluriformes species and their morphological and environmental diversity make this group of fishes an excellent source of information on character evolution.

The first step for accomplishing this kind of enterprise is to find robust and reasonably resolved phylogenies. The phylogenetic hypothesis of Neotropical Siluriformes relationships used as the background for this analysis was summarized from de Pinna (1993, 1998). Loricarioidea phylogeny was based on Lundberg & Baskin (1969), Baskin (1973), Schaefer & Lauder (1986), Schaefer (1990), de Pinna (1992, 1998). Loricariinae phylogeny is based on Rapp Py-Daniel (1997). These three sets of cladograms were based on morphological/osteological characters.

Siluriformes are clearly monophyletic (Fink & Fink, 1981, 1996; de Pinna, 1998). Currently, loricarioids include Trichomycteridae, Nematogenyidae, Scoloplacidae, Callichthyidae, Astroblepidae and Loricariidae (Baskin, 1973; Schaefer & Lauder, 1986; de Pinna, 1993, 1998), all exclusively Neotropical. Phylogenetic relationships within loricarioids appear to have been reasonably assessed, as well as the monophyly of its inclusive families.

Based in the Loricariinae phylogeny, some taxonomic names used herein are represented between quotes. These names represent clades strongly supported cladistically, such as, 'Hemiodontichthyina' which includes three genera and six species and 'Planiloricariina' with six genera and 14 species included.

None of the behavioral characters to be analyzed were used in the reconstruction of the cladograms in order to avoid circularity or excessive weight to the same features. The characters were mapped in the phylogenies and their evolution optimized using parsimony.

Results

1. Evolution of swimbladder encapsulation and air breathing behavior

Putative questions:

- Is air-breathing related to encapsulation?

- Which character originated first?
- Are these characters plesiomorphic or apomorphic? For which levels?

Based on the existing available data (Graham, 1997), representatives of Siluriformes considered as air-breathers include Aspredinidae, Trichomycteridae, Callichthyidae, Loricariidae (figure 1), the Asian Pangasiidae and Heteropneustidae and the African/Asian Clariidae. Swimbladder encapsulation is found in Aspredinidae (not complete) and in all loricarioid catfish families Nematogenyidae, Trichomycteridae, Scoloplacidae, Calliththyidae, Astroblepidae and Loricariidae (complete) as well as in the African Amphiliidae and the Asian Akysidae, Amblycipitidae, and Sisoridae.

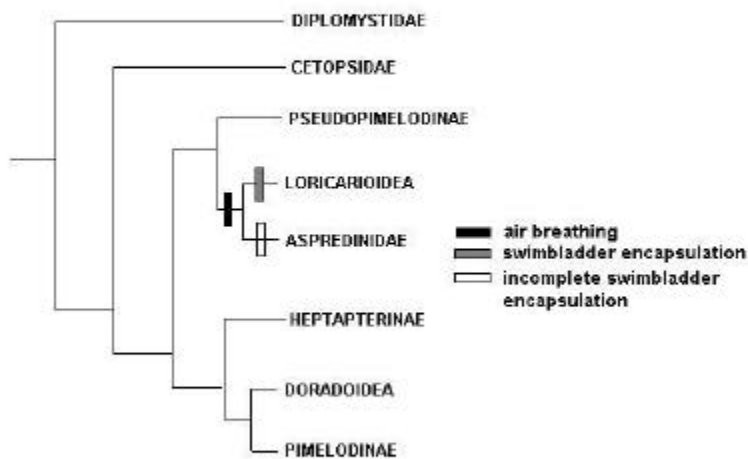


Figure 1. Distribution of air breathing and swimbladder encapsulation among Neotropical Sisoriformes (cladogram adapted from de Pinna, 1993, 1998)

In the case of loricarioids, I suggest that air-breathing behavior in these fishes could be related to the encapsulation of the swimbladder. If air breathing had originated as an alternate pathway to compensate for encapsulation of the bladder, we should expect that all families with encapsulated swimbladder should be adapted to breathe air and this is not the case (at least yet). About 50% of loricarioids families are air breathers and have encapsulated bladders. Moreover, aspredinids do not have the complete encapsulation but do perform air breathing (figure 2).

Although we may suspect of some sort of correlation between encapsulation and air breathing among Neotropical catfishes, no correlation can be made for the African/Asian catfishes. Among African/Asian catfish, the families that have air breathers are completely unrelated to the families with swimbladder encapsulation (table 1) since the families that show air-breathing behavior do not have the swimbladder encapsulated and vice-versa.

Table 1. List of Siluriformes families with air-breathing organs (ABO) and encapsulated swimbladders (SB); geographical distribution (SA = South America, AS = Asia, AF = Africa); and number of species (SP)

	AB (ABO)	SB	CONTINENT	# SP
Aspredinidae	+ (mouth)	+	SA	34
Nematogenyidae	?	+	SA	1
Trichomycteridae	+ (stomach)	+	SA	200
Scoloplacidae	?	+	SA	4
Callichthyidae	+ (intestine)	+	SA	172
Loricariidae	+ (stomach)	+	SA	>650
Astroblepidae	?	+	SA	40
Pangasiidae	+ (swimbladder)	-	AS	21
Clariidae	+ (pharyngeal sac)	-	AF + AS	90
Heteropneustidae	+ (pharyngeal sac)	-	AS	2
Amblycipitidae	?	+	AS	8
Akisidae	?	+	AS	15
Amphiliidae	?	+	AF	48
Sisoridae	?	+	AS	91

Based on Burgess (1989), Graham (1997) and de Pinna (1998)

Interestingly, Neotropical Siluriformes that breath air have their guts (stomach or intestine) used as an ABO (air breathing organ), completely different from the African/Asian Siluriformes that have pharyngeal sacs highly specialized (Clariidae and Heteropneustidae) or use the modified swimbladder as an ABO (Pangasiidae) (Graham, 1997). This different level of strategy suggests quite different origins of the air-breathing behavior among siluriformes. African/Asian and Neotropical Siluriformes have been separated for at least 100 million years, probably enough time for development of different air breathing behaviors.

On the other hand, the origin of encapsulation of the swimbladder can be interpreted either as a synapomorphy for a transatlantic group of Siluriformes (South American, African and Asian), as suggested by de Pinna, (1998) or as a

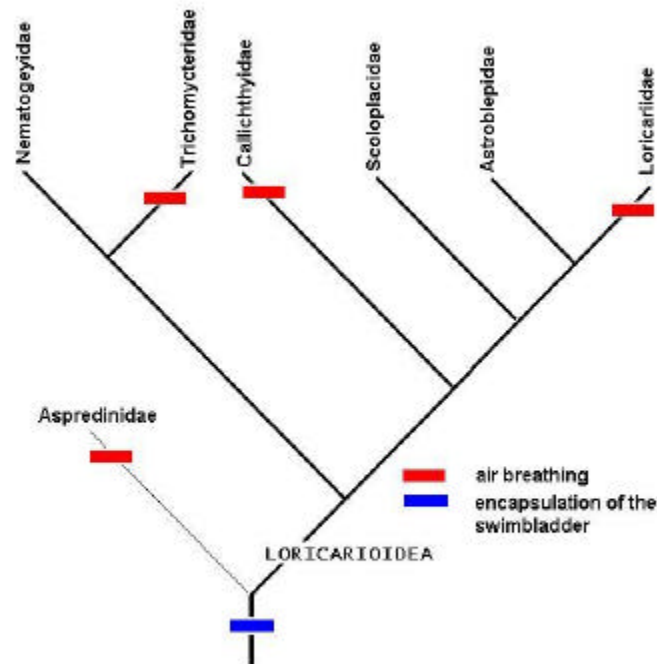


Figure 2. Distribution of air breathing behavior and swimbladder encapsulation among Loricarioidea (cladogram adapted from de Pinna, 1998)

homoplasy. The first possibility may be the correct one since the structures involved, lateral expansion of the secondary transverse process of the fifth vertebra and ventrolateral extension of the ventral surface of the Weberian complex, in the bladder encapsulation are the same in these catfishes, being consequently homologous (de Pinna, 1993).

According to the continent, you can draw different conclusions: based on African/Asian catfishes, air breathing and encapsulation are completely

unrelated. However, among South American catfishes, encapsulation seems to be related to air breathing.

Encapsulation seems to have predated air breathing in Siluriformes. Air breathing arose at least three times among Siluriformes: derived from modifications of the swimbladder (more primitive), from the guts or from pharyngeal morphological innovations (more specialized). However, we may infer that there is correlation between AB and SB in the Neotropical Siluriformes since both traits seem to have been advantageous for these fishes. The families with air breathing capacity are much more diverse than the families without these traits (table 1). Thus, gut air breathing could be seen as a putative adaptation for catfishes with bladders enclosed in bone.

2. *Sex dimorphism and evolution of the mouth parts in Loricariidae*

Loricariidae is a catfish family extremely diverse in the Neotropics, with more than 600 species occurring in all major drainages in South and Central America. These fishes are characterized by an armored body, and very specialized mandibles with suctional mouth, papillate lips for attaching to the substrate, and great mobility of the mouth parts. This great mouth specialization can be a consequence of the vital functions performed by this structure: the mouth in loricariids functions as an attachment organ, food collector and also sucks water.

Loricariidae are also known by their elaborate sexually dimorphic modifications present in mature males. Some of these sex dimorphisms are pervasive throughout loricariids and are considered generalized traits for the family. Other displays however are very distinctive and present in few selected taxa. Some of these elaborate dimorphic traits also occur on the mouth parts of these fishes, such as lips, teeth, premaxilla, etc. Since the mouth in these fishes has an extraordinarily complex role, I would like to evaluate the possibility of co-occurrence of some of the morphological modifications of the mouth with some behavior characters to assess their adaptive/evolutionary relevance for the group.

Mouth

The generalized condition in loricariids is the presence of large jaws bearing many elongate and asymmetrically cuspidate teeth. Reduction of the number of teeth and size of the jaws occurs in very few unrelated loricariid taxa. Based on the available hypothesis of relationship within the subfamily Loricariinae (Rapp Py-Daniel, 1997), there are two large clades: one with large jaws (Harttiini) and the other with reduced jaws (Loricariini). Jaw reduction is a synapomorphy for the subfamily Loricariinae among loricariids. This reduction involves modifications in many bony structures such as palatine, premaxilla, dentary, maxilla, and branchial apparatus. For all Loricariini, the most remarkable synapomorphy is the reduction of the dentary and the coronoid process.

Within Loricariini, two large clades present different patterns of further jaw reduction (figure 3): the clade 'Hemiodontichthyina' + *Limatulichthys* + *Pseudoloricaria* and 'Planiloricariina' + *Loricaria*. *Hemiodontichthyina* + *Limatulichthys* + *Pseudoloricaria* comprise loricariines with extremely pointed to slightly prolonged snouts, palatine with large lateral expansion, long maxillae, modified gill-rakers with ossification centers, hypobranchials large and fan-shaped, premaxillae reduced to a thin sheet of bone, and number of teeth reduced (less than 20) until completely lacking (*Hemiodontichthys* and *Reganella*). *Planiloricariina* + *Loricaria* include forms with triangular to completely round snouts, palatine extremely elongate and without processes or bone expansions, powerful and completely toothed lower pharyngeal plates, mandibullary teeth round and very reduced in size and number (less than 10) until completely absent (*Planiloricaria*).

In addition to different osteological features, these clades also show different lip morphology. Fishes of the Planiloricariina + Loricaria clade have both upper and lower lip-surface and border covered by strong papilla or long filaments. These fishes have filaments even inside the mouth. Hemiodontichthyina +

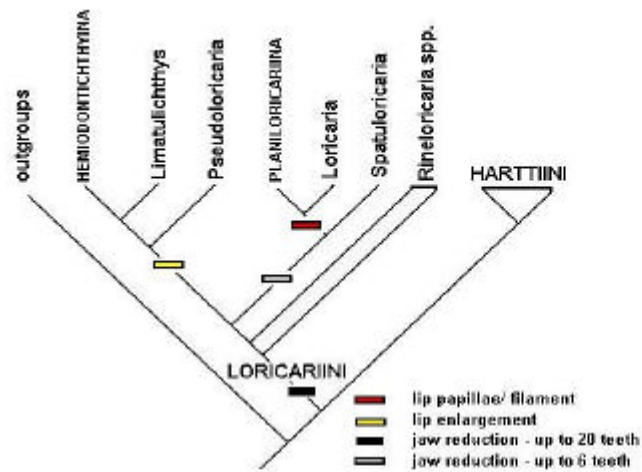


Figure 3. Distribution of mouth-related sexually dimorphic traits and jaw reduction in the subfamily Loricariinae (adapted from Rapp Py-Daniel, 1997)

Limatulichthys + Pseudoloricaria, on the other hand, have the lip-surface almost smooth or covered by delicate papillae, being *Furcodontichthys* the only exception. *Furcodontichthys*' lips are smooth but show few and long filaments on some restricted areas on the lower lip. The border of the lips, however, is straight.

Sex Dimorphism

The generalized sexually dimorphic display in loricariids is the presence of large odontodes (integumentary teeth) on head, fins and body on mature males. Neither Hemiodontichthyina+ Limatulichthys + Pseudoloricaria nor Planiloricariina+ Loricaria males have odontodes enlargement. Rather, these groups have species with other sexually dimorphic traits on the mouth during the breeding season. In the Hemiodontichthyina +L +P clade, males have an outgrowth of lip tissue providing a large soft surface used to carry the mass of fertilized eggs attached to it. This modification is present in almost all representatives, being *Reganella* the only exception. Within the Planiloricariina + Loricaria clade, sexually mature males do not have lip-enlargement but show lip-filaments reduced to papillae, whereas females keep the long lip filaments.

Putative questions:

- Can mouth-related sexually dimorphic traits be evolutionarily related to loricariine jaws reduction?
- Is jaw reduction homologous on both clades?
- What came first? Sex dimorphism or jaw reduction?

It seems that jaw reduction predated the origin of mouth-related sex dimorphism because its origin is early on Loricariini evolutionary history. There are, however, several levels of jaw reduction. We can detect three levels of number of teeth reduction: the first level would be the reduction to up 20 teeth on premaxillae for all loricariinis; second level it would be the reduction to up 6 teeth in the premaxillae (only found in Planiloricariina+Loricaria + Spatuloricaria), and the third level it would be the complete loss of premaxillary teeth, found in representatives of both clades (Hemiodontichthyina + L+ P and Planiloricariina + Loricaria).

Long lip filaments, based on the hypothesis shown in figure 3, did not arise immediately after the first level of jaw reduction, or dentary reduction. Rather, long lip filaments are seen only in a subclade of Planiloricariina+ Loricaria. *Spatuloricaria*, the most basal monophyletic taxon within loricariinis, shows already a strong reduction in the number of premaxillary teeth (up to 6), however, all its representatives have papillate lips (non-filamentous) and the generalized sex dimorphic ornament of large odontodes on the sides of the head

on mature males. Moving up in the cladogram, the next taxon, *Loricaria*, already have sexually mature males with lip filaments reduced to papillae, a mouth-related sex dimorphism. On the other hand, the Hemiodontichthyina + Limatulichthys + Pseudoloricaria clade did not show such a severe reduction in the number of teeth, but rather in the size of teeth. Hemiodontichthyina + L + P have several representatives with up to 20 rather feeble teeth. This clade, however, show lip enlargement on mature males. Homoplastically, both clades have representatives without any teeth on the premaxillae and with different sexually dimorphic traits. In fact, we have three cases: *Spatuloricaria* with few teeth and no mouth-related sex dimorphism, and two clades with jaw reduction involving different anatomical parts carrying different types of mouth-related sex dimorphisms.

Since most species with mouth-related sex dimorphism have reduced jaws, it should be asked if sexually dimorphic mouth-related traits have arisen as a consequence of jaw reduction. If this would be the case, sexually dimorphic mouth-related traits could be seen as adaptative features. Based on the lack of this sort of sex dimorphic trait in *Spatuloricaria*, a jaw-reduced loricariin, one might argue that jaw reduction is decoupled from mouth-related sex dimorphism as a whole. On the other side, it could be suggested that the correlation between jaw reduction and mouth-related sex dimorphism is so strong, that even in non-homologous events of jaw reduction among loricariines, these events were followed by the arousal of different kinds of mouth-related sex dimorphism.

Conclusion

Phylogenetic hypotheses have power in orienting hypotheses of character evolution. The recognition of positive correlation between a morphological novelty and the posterior appearance of a given behavior supports the hypothesis of adaptation. On the other hand, the recognition of independent origins of morphological and behavioral traits, or non-adaptive traits, also provides useful information on character evolution.

The present work demonstrated two different situations of possible evolution of correlated characters among Siluriformes (catfishes). In the first case, swimbladder encapsulation seemed to be correlated with air breathing only within Neotropical Siluriformes. African/Asian catfishes with encapsulated bladders are completely unrelated to air breathers African/Asian catfishes. Neotropical Siluriformes have been separated from the African/Asian catfishes

for a long period (approximately 100 million years), but both groups kept an old morphological novelty, the swimbladder encapsulation. These fishes on separate continents (or in the process of separation) may have certainly been subjected to distinct selective pressures and did probably have enough evolutionary time to develop different adaptations to them. One could also argue that swimbladder encapsulation and air breathing in Neotropical Siluriformes is merely coincidental, without any adaptive value. However, the extreme success of the air breathing-encapsulated Siluriformes might be an evidence to refute this assertion.

In the second case, jaw reduction in loricariids seems to be strongly related to the appearance of mouth-related sex dimorphic traits, since two independent jaw-reduced lineages developed two independent sets of mouth-related sex-dimorphic traits. Due to the temporary or plastic nature of sex dimorphic traits, one might argue that these traits could not be seen as adaptation since they are not “genetically mediated” (Gould, 1984- in West-Eberhard, 1992) and can not be transmitted to the next generation. However, as very well put by Thompson (1991), “plasticity itself is the trait under selection”. And, that seems to be the case of sex dimorphism. There is still no evidence to suggest why some groups develop sex dimorphism and others do not. However, the capacity to develop morphological modifications during the reproductive period, other than the gonads, must be a genetically mediated trait and it might confer some sort of advantage.

Certainly, we need more information to consolidate or invalidate the conclusions cited above. Recognition of adaptation has become a very controversial issue and biologists have been treating it with caution. This kind of exercise applied to different groups of organisms and characters helps providing theoretical background for the development of new experiments in order to interpret directions of character evolution.

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