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Evolutionary convergences and parallelisms: their theoretical differences and the difficulty of discriminating them in a practical phylogenetic context

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Abstract. The importance of evolutionary parallelisms and their differences from evolutionary convergences have been historically underappreciated, as recently noticed in Gould's last book '*The structure of evolutionary history*'. In that book, Gould make an effort to distinguish and to reinterpret these concepts in the light of the new discoveries of the last decades on developmental biology and genetics, presenting the elegant metaphor of 'Pharaonic bricks versus Corinthian columns'. In this paper I will briefly discuss these concepts, and will argue that, despite the advances that have been made to define them in theory, it is rather hard to differentiate them in a practical phylogenetic context. In order to do so, I will provide some few examples from my own empirical studies on the last years of one of the most morphologically and taxonomically diverse groups of Vertebrates, the catfishes.

The theoretical definition of evolutionary convergences and parallelisms and Gould's metaphor: a brief introduction

As extensively explained in Gould's masterpiece '*The structure of evolutionary history*' (2002), the importance of parallelism for evolutionary theory has been historically underappreciated. One of the reasons for this is precisely due, as described in the historical and conceptual overview on this subject given by Gould, to the difficulty of defining properly the limits between parallelisms and convergences, and even between parallelisms and homologies. In fact, as noted that author, although we now usually make, in a somewhat simplistic way, a general, central distinction between *homologies* and *homoplasies*, with parallelisms and convergences being ranked in the category of homoplasies, this was not always the case.

One should recall that, when Lankester(1870) proposed the concept of homoplasy, he defined homoplasy as a subcategory of homology. According to Lankester, many similarities not directly due to inheritance of common ancestral structures nonetheless arise as consequences of the inheritance of unique, phylogenetically constrained building patterns. Therefore, according to

this author, these similarities deserve inclusion within a broader category of similarity upon descent (as opposed to similarity derived purely by independent adaptation, with no contribution by constraint from an organism's past history: see Gould 2002). These independently evolved, but historically constrained, similarities defined by Lankester as 'homoplasy' correspond to what we call now parallelisms.

Thus, homoplasy has suffered a conceptual, historical movement 'from a subcategory of homology, where it was placed before, to become the diametric opposite of homology, with the domain of homology then shrinking to encompass only Lankester's narrower category of homogeny' (Gould 2002: p. 1074). Thus, the domain of homoplasy has been historically expanded to include all similarities evolved independently, and not only those directly inherited from a common ancestral structure. But 'what looks like an enormous difference – the expulsion of homoplasy as a subcategory of homology (*sensu lato*), and its establishment as a phenomenon directly contrary to homology (*sensu stricto*) actually rests upon a small point: the migration of convergence *into* the category of homoplasy as now defined' (Gould 2002: p. 1074).

As stressed Gould (2002), a detailed reanalysis of the meaning of parallelisms, particularly attending to advances in the last two decades on the field of developmental biology, has important evolutionary implications.

One significant implication is, precisely, the recognition that constraints are fundamental, 'positive' actors, and not only mere 'negative' intervenients of evolution. This because the discoveries of the last years have pointed out that these constraints are, in fact, directly responsible of homoplastic parallelisms, and, consequently, of a great number of evolutionary changes. Of course, constraints are not only related to homoplastic parallelisms. The recent discoveries of 'deep homology', i.e. the discovery that major phyla, separated by more than 500 millions years of independent evolutionary history, still share substantial, if not predominant channels of development based on levels of genetic retention, has also clearly contributed to understanding the marked importance of historical constraints. Evolutionary constraints also modulate, indirectly, homoplastic convergences. In fact, in markedly reducing the total number of possible evolutionary options, constraints are augmenting the probability that the same evolutionary option will be taken by different, distantly related groups of organisms. Thus, constraints consequently augment the frequency of homoplastic convergences.

This could help to explain the high levels of homoplasy usually found in most cladistic analyses. During a long time evolutionary papers often referred to evolution as somewhat 'linear' process, with homoplasies being, of course, admitted, but somehow considered as peculiar, 'extraordinary' cases. However, the results obtained in most cladistic analyses seem to indicate that evolution is a rather complex, highly homoplastic process, with homoplasies constituting a markedly high fraction of evolutionary changes, particularly in higher taxa such as the Siluriformes (see Diogo 2004).

But one other implication of the reinterpretation of the meaning of parallelisms is precisely the reinforcement of the idea that *all* evidence available should be taken into account in phylogenetic evolutionary studies. Evolutionary parallelisms, although having an independent origin, are, by definition, channelled by *certain common* internal constraints of homologous genes or developmental pathways (see above). Therefore, the occurrence of homoplastic parallelisms in different taxa *of a certain major group* could somehow indicate that these different taxa share ‘common internal constraints of homologous genes or developmental pathways’, and, consequently, that these taxa are, in fact, phylogenetically associated. This point, concerning the particularly interesting, and apparently paradoxical, relation between homoplastic parallelisms and phylogenetic reconstructions, lead, for example, Saether (1983: 343) to propose the cladistic concept of ‘underlying synapomorphies’. These are defined as ‘the capacity to develop synapomorphy’, or, ‘close parallelism as a result of inherited factors within a monophyletic group’.

In order to try to reinterpret and to explain the concepts of convergence and parallelism in the light of the new discoveries of the last decades on developmental biology and genetics, Gould (2002: p. 1134–1142), known by his analogies between biological concepts and non-biological themes, presented the interesting metaphor of ‘*Pharaonic bricks versus Corinthian columns*’. According to Gould, in view of our increasing knowledge of genetic sequences and their actions, homology of some sort or level will always be found in underlying generators of similar end products, if only because all organisms share the same genetic code by common ancestry. But, as stressed Gould (2002: p. 1136), ‘no one would argue that we should redescribe a classic range of convergence as parallelism simply because the markedly different developmental pathways of the two adaptations both rest upon the action of genes made of DNA!’. One needs thus to develop theoretical criteria for ordering and evaluating the highly varied and ever-growing compendium of homoplastic results generated along homologous developmental pathways, since these cases fall along a continuum from narrow and controlling channels of constraint to insignificant sharing of non-specific building blocks. This is where it appears Gould’s interesting discussion on ‘*Pharaonic bricks versus Corinthian columns*’ (Gould 2002: p. 1134):

When Pharaoh ‘made the children of Israel serve with rigor’ (Exodus 1:13), they fabricated bricks to use in a full range of buildings: ‘and they built for Pharaoh treasure cities, Pithom and Raamses’ (Exodus 1:11). Now if these bricks built every structure in the city, from great pyramids to public toilets, we might identify a homologous generator of all final products (bricks of the same composition made by the same people in the same way over a continuous stretch of time). But we could scarcely argue that these homologous generators exercised any important constraint over the differing forms of Pharaoh’s final products – if only because all realized architectural diversity shared the same building blocks. But if I note a majestic portico of Corinthian columns in front of a building in modern Manhattan, I recognise a strong internal constraint imposed by an

architectural module of very different status (...). Like Pharaonic bricks, Corinthian columns hold clear status as homologous underlying generators for their continuous phyletic history and stable form. Pharaonic bricks did little to constrain a resulting building by their form or structural character, and would not therefore sustain an interesting interpretation of parallelism for two similar buildings that happened to employ them in construction (if only because many other, very unsimilar, buildings in town also use the same bricks). Corinthian columns do exert a strong structural constraint from an inherited past (a homology) that can help us to identify and distinguish buildings, even after 2500 years after the invention of this unchanged form.

To conclude this brief introduction, one can thus say that there has been a historical need to reanalyse the definition of evolutionary convergences and parallelisms, and that in the last decades a particular effort was made to redefine these concepts in view of the new discoveries on the fields of developmental biology and genetics. Therefore, theoretically one can define, in short, parallelisms as the development of similar characters separately in two or more lineages due to common internal constraints of homologous genes or developmental pathways. Convergences, by contrast, occur when distantly related organisms evolve separately to produce similarities, but these similarities are not due to specific common internal constraints. But the problem with this somewhat clear theoretical distinction between evolutionary convergences and parallelisms is that, as stressed by the discoveries on the fields of developmental biology and genetics, it is often rather difficult to apply it in a practical context. This because, as recently stressed in Wilmer's (2003) paper '*Convergence and homoplasy in the evolution of organismal form*', on a sufficiently long timescale and on a sufficiently broad phylogenetic context, all organisms share a similar genetic basis and common internal constraints.

The difficulty of discriminating evolutionary convergences and parallelisms in practice: some empirical examples from catfishes

The Siluriformes, or catfishes, found in North, Central and South America, Africa, Europe, Asia and Australia, with fossils inclusively found in Antarctica, constitute a highly diversified, cosmopolitan group, which, with 34 families, about 437 genera and more than 2700 species, represents about one third of all freshwater fishes and is one of the most morphologically and taxonomically diverse Vertebrate taxa (e.g. Burgess 1989; Diogo 2003; Teugels 2003). This remarkable group of fishes was the subject of my research in the last years. This research was mainly focused on their morphological diversity, phylogeny and macroevolution, with the main results of a broad cladistic analysis of 440 morphological characters in 87 genera representing all the 32 extant catfish families having just been published (Diogo 2004). The results obtained thus provide not only new insights on catfish evolutionary history but

also useful data and illustrative examples for broader discussions on general phylogeny and macroevolution.

With respect to the subject discussed in the present paper, the empirical case study provided by catfishes clearly pointed out the difficulties of distinguishing, in practice, in real phylogenetic analyses, evolutionary parallelisms from evolutionary convergences. How can we try to discriminate, in a practical phylogenetic context, in a certain cladogram obtained from an empirical cladistic analysis, among those characters exhibiting an homoplastic distribution according to that cladistic analysis, which constitute, in reality, evolutionary parallelisms and evolutionary convergences?

For example, among all the 87 catfish genera examined in Diogo's 2004 phylogenetic study, only three, *Nematogenys*, *Austroglanis*, and *Heptapterus*, presented a derived configuration in which the levator operculi muscle inserts not only on the dorsal surface of the opercular bone, as usually in teleosts, but also on a significant part of the lateral surface of this bone. As such a derived feature was independently acquired, inside the order Siluriformes, in three groups that appear markedly distant on the cladogram obtained in that phylogenetic study (see Figure 1), one could argue that this feature could constitute a good candidate of potential evolutionary convergence.

One could eventually compare this example with the independent acquisition, four different times, of accessory tooth-plates on the ethmoid region inside a particular, relatively restricted catfish clade including the pangasiids *Helicophagus* and *Pangasius*, the schilbids *Pseudeutropius*, *Schilbe*, *Lalax*, *Ailia* and *Siluranodon*, the cranoglanidid *Cranoglanis*, the ictalurids *Amiurus* and *Ictalurus*, the austroglanidid *Austroglanis*, the ariids *Ancharius*, *Genidens* and *Arius*, and the claroteids *Auchenoglanis*, *Chrysichthys* and *Clarotes* (see Figure 2). One could, thus, argue that this would perhaps constitute a good candidate of potential evolutionary parallelism eventually channelled by a 'common patrimony' within this catfish clade.

However, this issue is rather more complex. For example, an accessory ethmoideal tooth-plate is also present, besides this clade, in the pimelodin genus *Pseudoplatystoma*, as shown in Figure 2. Of course, one could eventually argue that this was perhaps due to a true evolutionary convergence between the situation found in the node leading to this clade and that found in *Pseudoplatystoma*. However, could the anatomically similar tooth-plates found in *Pseudoplatystoma* and the members of that clade not be eventually due to an evolutionary parallelism within the whole order Siluriformes? This constitutes, in my view, one of the major problems of discriminating from homoplastic parallelisms and convergences in a phylogenetic context. In fact, if the latter option would be accepted, and, thus, one would consider the formation of ethmoideal accessory tooth-plates in five different catfish-groups as a homoplastic parallelism within the whole order Siluriformes, why would the attachment of the levator operculi on the lateral surface of the opercle found in three different catfish groups not also be eventually due to a parallelism, and not to a convergence, as hypothesised above? How many homoplastic events of a certain

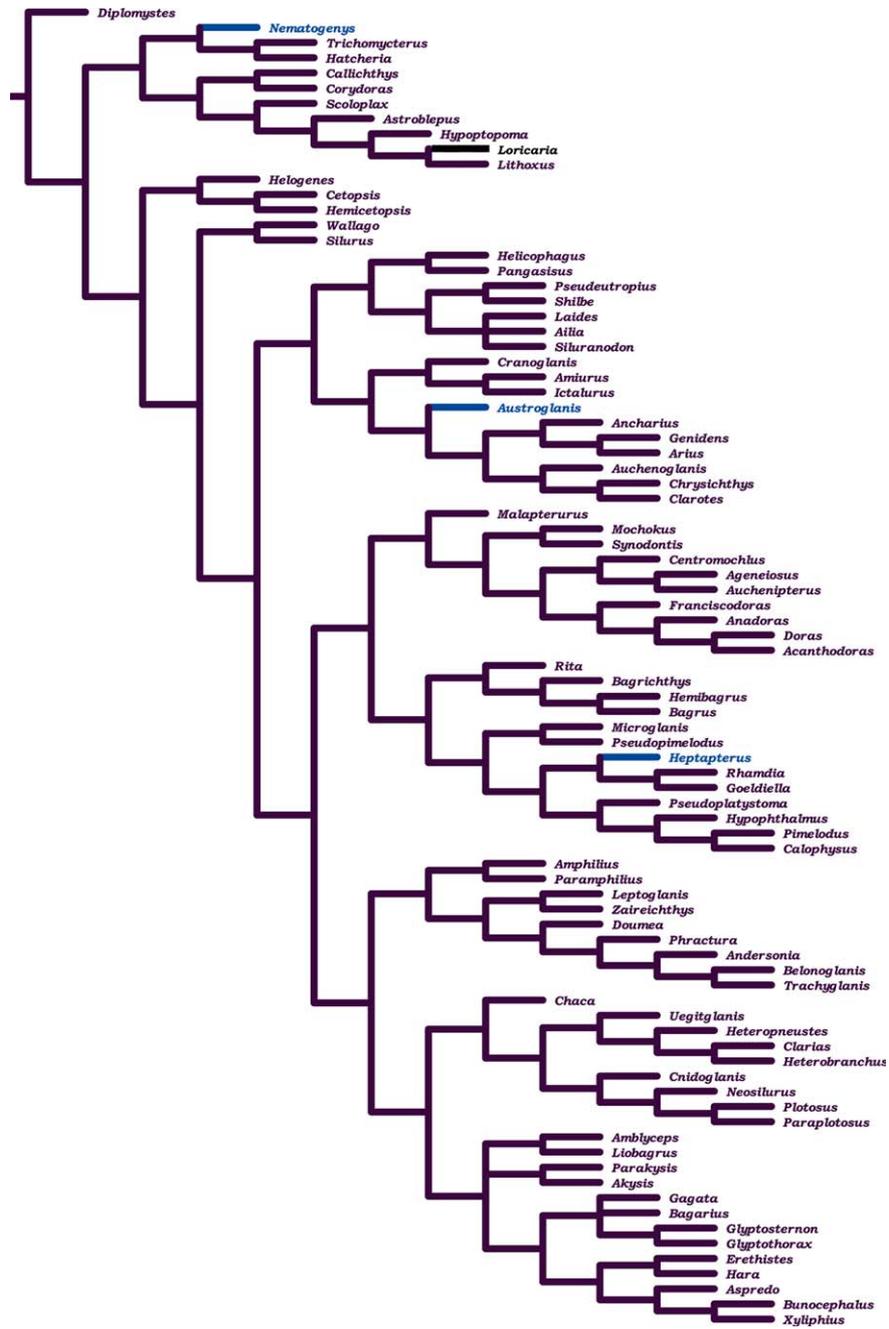


Figure 1. Hypothesis of character state evolution of insertion of levator operculi in lateral surface of opercle within Siluriformes according to the authors' phylogenetic results on the higher-level phylogeny of the order: CS0 (black) = levator operculi not attaching on a significant part of lateral surface of opercle; CS1 (blue) = levator operculi attaching on a significant part of lateral surface of opercle [for more details, see text].

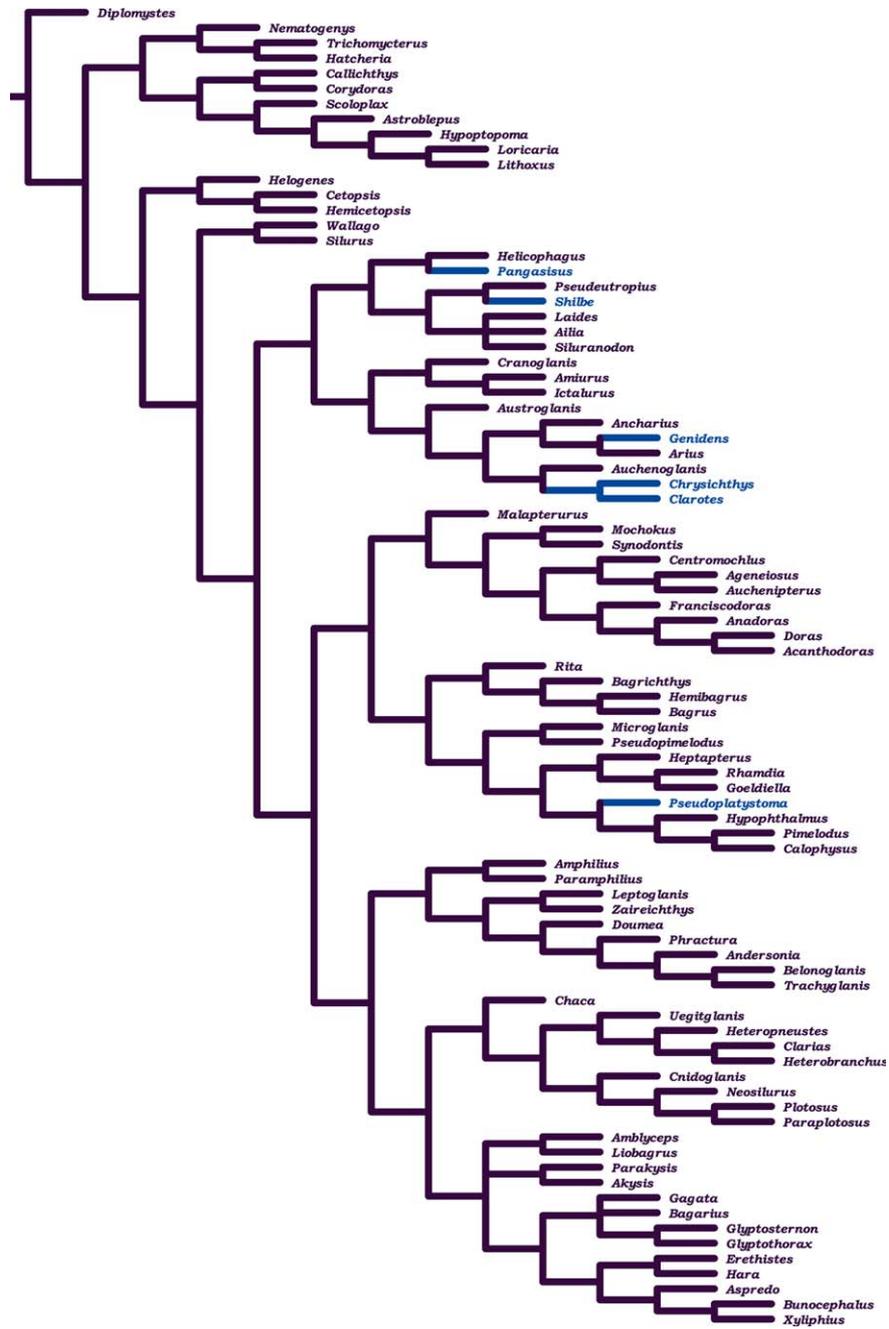


Figure 2. Hypothesis of character state evolution of presence of accessory tooth-plates on ethmoid region within Siluriformes according to the authors' phylogenetic results on the higher-level phylogeny of the order: CS0 (black) = absence of accessory tooth-plates on ethmoid region; CS1 (blue) = presence of accessory tooth-plates on ethmoid region [for more details, see text].

character should we have inside a group such as the order Siluriformes in order to hypothesise that the homoplastic development of this character was due to parallelism and not to convergence? For example, to cite another example, the homoplastic development of an elastic spring apparatus related with the production of sound and formed by the parapophysis of the 4th vertebra and a 'protractor muscle' attached to it is found in at least five different catfish clades (see Figure 3): could this constitute a potential example of convergence, or, instead, a potential example of evolutionary parallelism? If our reflection only focus on the Siluriformes, one could eventually argue that these five homoplastic events could eventually constitute a typical example of convergent evolution inside such a large and diverse order (see e.g. Alexander 1965; Chardon 1968). However, if we focus, instead, on a tree incorporating all Vertebrate taxa, one could argue that it is rather unsound that such an elastic spring apparatus was not developed even once in *all* the numerous non-siluriform Vertebrate orders, but was independently acquired by pure convergence at least five different times inside the very same order. This would, thus, likely seem to indicate that catfishes could share a certain common morphological patrimony making that the probability to develop this apparatus would be much greater in those fishes than in other Vertebrate groups.

The discussion above thus stresses that it is rather difficult to try to identify evolutionary parallelisms and convergences in a practical phylogenetic context. One very important point, directly related to this issue, which probably constitutes one of the most studied topics in evolutionary biology but that clearly should also be the subject of a still much broader, encompassing integrative focus, concerns the understanding of evolutionary constraints. For example, if the presence of an elastic spring apparatus in at least five different catfish clades would, in fact, be the result of a parallel evolution channelled by a same common patrimony within the whole order Siluriformes, being present in 17 of the 87 catfish genera included in the present cladistic analysis (see Figure 3), one could ask why is such an apparatus not developed in all the other 70 genera examined? Are there some 'negative' constraints eventually limiting the expression of such a common patrimony, and, thus, limiting the acquisition of a sound production apparatus that seems rather useful in a group of mainly nocturnal fish inhabiting muddy waters (see e.g. Alexander 1965) such as the Siluriformes? These issues, concerning evolutionary constraints, parallelisms and convergences, are clearly interesting, even fundamental central issues on the study of macroevolution that will, very likely, continue to be the subject of special attention in both a short and a long term. Their study should pass more and more by an effective, broad integration of a vast range of information concerning different fields such as comparative anatomy, developmental biology, phylogenetics, functional morphology and genetics, and their increasing understanding will surely provide an important contribution for our future overall comprehension of biological evolution.

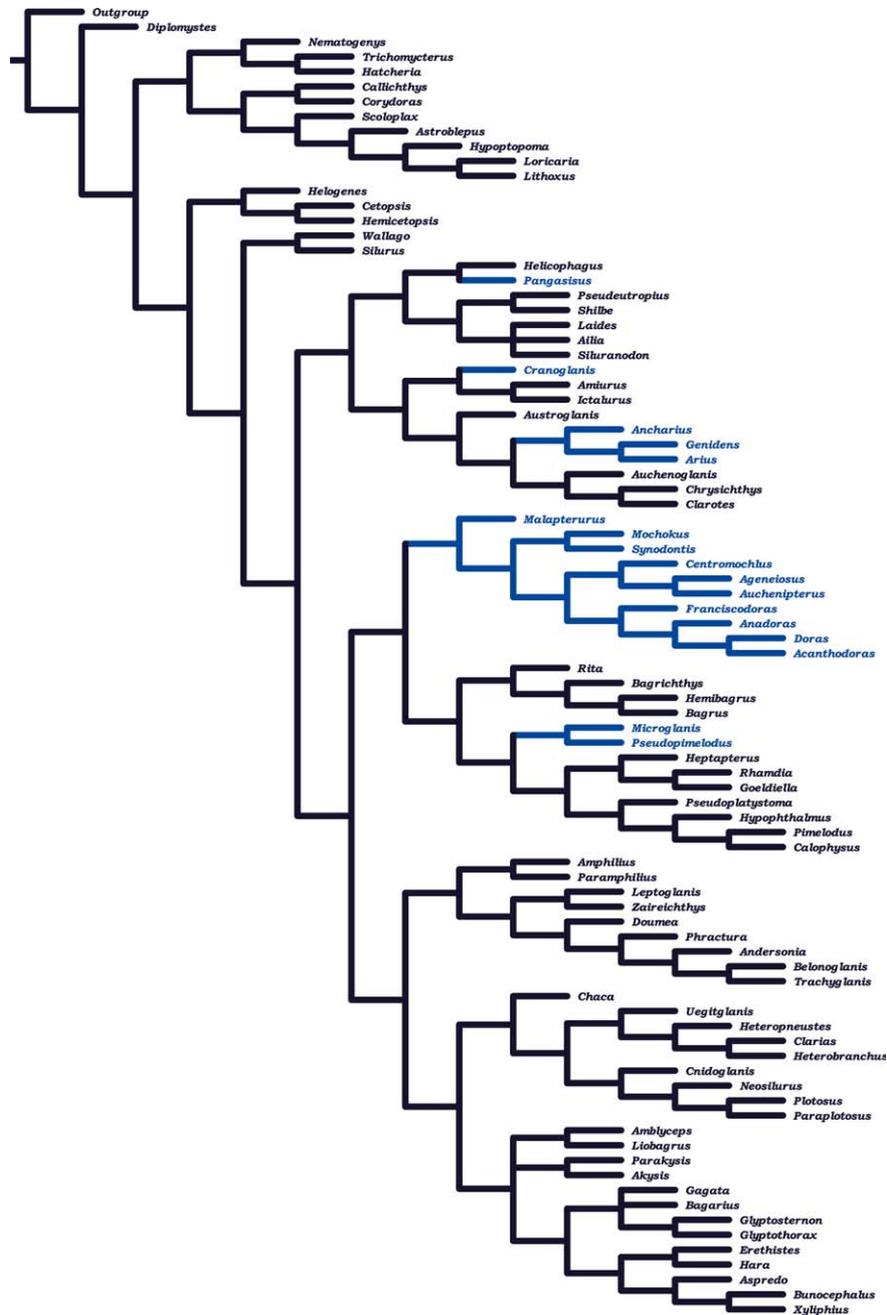


Figure 3. Hypothesis of character state evolution of presence of elastic spring apparatus within Siluriformes according to the authors' phylogenetic results on the higher-level phylogeny of the order: CS0 (black) = absence of elastic spring apparatus; CS1 (blue) = presence of elastic spring apparatus [for more details, see text].

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