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Phylogeny, origin and biogeography of catfishes: support for a Pangean origin of ‘modern teleosts’ and reexamination of some Mesozoic Pangean connections between the Gondwanan and Laurasian supercontinents

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Abstract—The wide geographical distribution of the mainly freshwater catfishes has long intrigued the scientific community. This work provides a new insight into the phylogeny and the puzzling biogeographical distribution of catfishes. The important implications for teleost biogeography and plate tectonics are discussed. The results of the author’s cladistic study on catfish higher level phylogeny, together with a revision of the data available concerning different fields such as palaeobiogeography, phylogeny, ecology and molecular biology, as well as the growing evidence supporting the existence of some remaining Pangean connections between Gondwana and Laurasia extending into the Early Cretaceous, strongly support a rather complex biogeographic scenario with multiple pre-drift and post-drift continental dispersions, vicariations, and, possibly, some marine migrations. According to this scenario: 1) catfishes originated in the South American region at a moment when there were still some remaining Pangean connections between Gondwana and Laurasia; 2) after this, there was a relatively rapid pre-drift continental dispersion of several, but not all, main groups of Siluriformes from the South-American region to Africa and other Gondwanan areas, with some of those groups succeeding in radiating ultimately via the remaining continental Pangean connections between Gondwana and Laurasia to this latter super-continent; 3) the final separation between Laurasia and Gondwana, and posteriorly between the regions constituting each of these super-continent, contributed to important vicariant events; 4) this scenario was still further complicated by numerous events such as the collision of India with Asia, the re-establishment of certain land connections between previously separated continents (e.g., between the Americas), and eventually also by some marine migrations, thus explaining the highly complex biogeographical distribution of the Siluriformes. In sustaining such a scenario, this work thus supports that, contrary to what is often accepted, some groups of ‘modern teleosts’ did have a Pangean origin.

Keywords: biogeographical distribution; catfish origin; Cretaceous; Gondwana; Laurasia; Mesozoic; Ostariophysi; Pangea; palaeobiogeography; phylogeny; Siluriformes; tectonics; teleosts.

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INTRODUCTION

The catfishes, or Siluriformes, with 34 families (Diogo, 2004), about 437 genera and more than 2700 species (e.g., Teugels, 2003), represent about one third of all freshwater fishes and constitute one of the most diverse vertebrate taxa. The great majority of Siluriformes, as well as of the other Ostariophysa — Gymnotiformes, Characiformes, Cypriniformes and Gonorynchiformes — are effectively primary division freshwater fishes according to Myers (1938), with only three of the 32 extant catfish families, Ariidae, Plotosidae, and, to a much lesser extent, Aspredinidae, possessing marine species. Moreover, it should be noted, and this is an important aspect that is, unfortunately, not often remembered, that the extant marine species of these three families essentially are confined to coastal areas (Burgess, 1989). The particularly wide geographical distribution of catfishes — they are found in North, Central and South America, Africa, Eurasia, South-East Asia, Japan and Australia, with fossil catfishes having even being reported in Antarctica (Grande and Eastman, 1986) — has, thus, long intrigued ichthyologists and biogeographers in general. Researchers such as Briggs (1979: 111) have stressed that catfishes and other ostariophysans are “particular useful for studying past continental relationships”.

The biogeographic hypothesis that is nowadays most commonly accepted to explain catfish geographical distribution postulates a Gondwanan siluriform origin and a somewhat implicit, but usually not clearly stated, mainly continental ulterior passage from the Gondwanan regions to the northern (Laurasian) areas, i.e., Europe, North America and Asia (Gayet and Meunier, 2003; Teugels, 2003). According to this hypothesis, which I will call the ‘traditional hypothesis’ throughout this paper, the presence of catfishes in these three continents could, thus, be essentially due, respectively, to: the Eocene connection between Africa and Europe; the Paleocene connection between South America and North America; and the Eocene collision between India and Asia and/or the Eocene passage from Africa to Asia through Europe (Gayet and Meunier, 2003). Another hypothesis defended by some authors, which I will call the ‘marine hypothesis’ in this text, defends an essentially marine origin/dispersion to explain catfish wide distribution (Chardon, 1967; Gayet and Meunier, 2003).

However, it should be noted that these hypotheses have been mostly formulated outside an explicit phylogenetic framework on catfish intra-relationships. In fact, as stressed by authors such as Weitzman and Weitzman (1982), Lundberg (1998) or Lundberg et al. (1998), there is unfortunately a tendency in several biogeographic works, and particularly in those concerning major groups of freshwater fishes, to assume certain biogeographic scenarios outside an explicit phylogenetic context. But, as stated by Weitzman and Weitzman (1982), the current distribution of fishes of a given geographical area can best be explained only when our systematic and phylogenetic knowledge on that fish fauna reaches a high level of sophistication. Therefore, a typical problem for biogeographic studies is precisely the lack of available detailed phylogenetic studies on the relationships among the groups to be

analysed. As a typical example of a narrow focus, many authors have emphasised the 'final' (usually meaning Miocene to Pleistocene) uplift of the Andes as the quintessential event in cis/trans Andean vicariance and in the formation of the Amazonas watershed. But, as pointed out by Lundberg et al. (1998: 41), "such emphasis precedes or overlooks knowledge of the far deeper history of neotropical fishes, even at fairly fine taxonomic levels".

The main aim of this work is to re-examine the biogeographical distribution of catfishes in the light of the author's cladistic analysis of catfish higher-level phylogeny, as well as of an up-to-date revision of the data available in different fields such as palaeobiogeography, phylogeny, ecology/physiology, molecular biology, and plate tectonics. I shall argue that the results of this cladistic study and the revision of the available data in these fields strongly support an alternative hypothesis on siluriform origin and distribution consisting of a rather complex scenario with multiple pre-drift and post-drift continental dispersions, vicariations and, possibly, some marine migrations. According to this hypothesis: 1) catfishes had a rather earlier origin in the South American region than is usually stated, i.e., than the Late Cretaceous period, at a time when there were still some remaining Pangean connections between Gondwana and Laurasia; 2) subsequently, there was a relatively rapid pre-drift continental dispersion of several, but not all, the siluriform main groups from the South American region to Africa and eventually to other Gondwanan areas, with some of those groups succeeding in undertaking a continental dispersion to the Laurasian continents via the remaining continental Pangean connections existing between the Gondwanan and Laurasian supercontinents; 3) the separation between these two supercontinents, and ulteriorly between the different areas constituting each of them, contributed to important vicariant events; 4) this scenario was further complicated by ulterior events, such as the collision of India with Asia, the ulterior re-establishment of certain continental connections that were previously separated (e.g., between the Americas), and eventually also by some marine migrations, thus explaining the highly complex biogeographical distribution of Siluriformes.

HIGHER LEVEL PHYLOGENY OF CATFISH

The only works published so far that provide an explicit cladogram of the higher-level phylogeny of this group are those of Mo (1991) and de Pinna (1998). However, as stressed recently by authors such as Teugels (2003), these cladograms are rather unresolved, with "the position of numerous families being uncertain", thus seriously obstructing discussions on the general evolution and biogeographic distribution of this important group. In order to try precisely to surpass such restrictions, I have undertaken, over the last years, a cladistic work on the higher-level phylogeny of catfishes. This work is based on a phylogenetic comparison of 440 morphological characters concerning the configuration of the osteological and myological structures of the cephalic region and the pectoral girdle of 120 species

grouped in 87 genera representing the 32 extant catfish families. A detailed list of these characters is given in Diogo (2004). The phylogenetic analysis resulted in an almost completely resolved strict consensus cladogram with a length of 902 steps, CI = 0.52, and RI = 0.78. The main results of this analysis are illustrated in figure 1, in which, apart from the relationships between the different catfish families represented, is shown the current biogeographic distribution of these families. The cladogram presented in this figure is more resolved than those of de Pinna (1993) and Mo (1991) studies, presenting a single polytomy — that leading to the Akysidae, the Amblycipitidae and the remaining Sisoroidea — and providing some interest points for discussion of the biogeographical distribution of some major catfish clades. Before analysing these points, I would like to pay tribute to the previous work of authors such as de Pinna and Mo, as well as of many other researchers, who have paved the way and made possible my own studies on the morphology and phylogeny of catfishes.

According to Lundberg (1998), because of the widespread distribution of catfishes and the poorly solved cladograms on the higher-level phylogeny of these fishes available at the time, there was no evidence to assume that ancestral siluriforms “have been in South America or on the American side of the united southern continents”. The phylogenetic results illustrated in figure 1 revise this. In fact, the eight most basal extant catfish families of the cladogram of this figure are from South America, with only the neotropical Pimelodidae, Doradidae and Auchenipteridae, appearing, together with the Aspredinidae, in more apomorphic clades. In the cladograms of Mo (1991) and de Pinna (1998), the most basal catfish were also from South-America, but this exclusively neotropical basal distribution applied only to two groups (diplomystids and cetopsids). It should be noted here that, as my cladistic analysis referred to the 32 extant catfish families, it did not include the fossil family Hysidoridae, a North American group that has been considered rather basal by some authors (see the cladograms of de Pinna, 1993; Grande and de Pinna, 1998), but more derived by others (cladogram 2, Mo, 1991). As the phylogenetic position of the Hysidoridae is thus still unclear, only a more conclusive future work on this subject will confirm if this North American family is, or not, eventually more basal than the eight extant basal South American families referred to above.

Also importantly, the phylogenetic results of the present work strongly support the existence of four relatively apomorphic catfish groups with members in both South America and the Old World, and which are indicated, respectively, in figure 1 by ‘Y1’, ‘Y2’, ‘Y3’ and ‘Y4’. These are: 1) the Ariidae (Y1), a family of mostly marine (but restricted to coastal areas) catfishes actually found in South America, but also in Africa and Asia, as well as in Australia and North America; 2) the clade including the South American auchenipterids + doradids and the African mochokids (Y2); the clade including the South American pimelodids and the Afro-Asiatic bagrids (Y3); and the clade, particularly apomorphic within the Siluriformes, formed by the South American Aspredinidae and the Asian Erethistidae (Y4). The existence of an also relatively apomorphic clade formed by the New World family Ictaluridae (not from

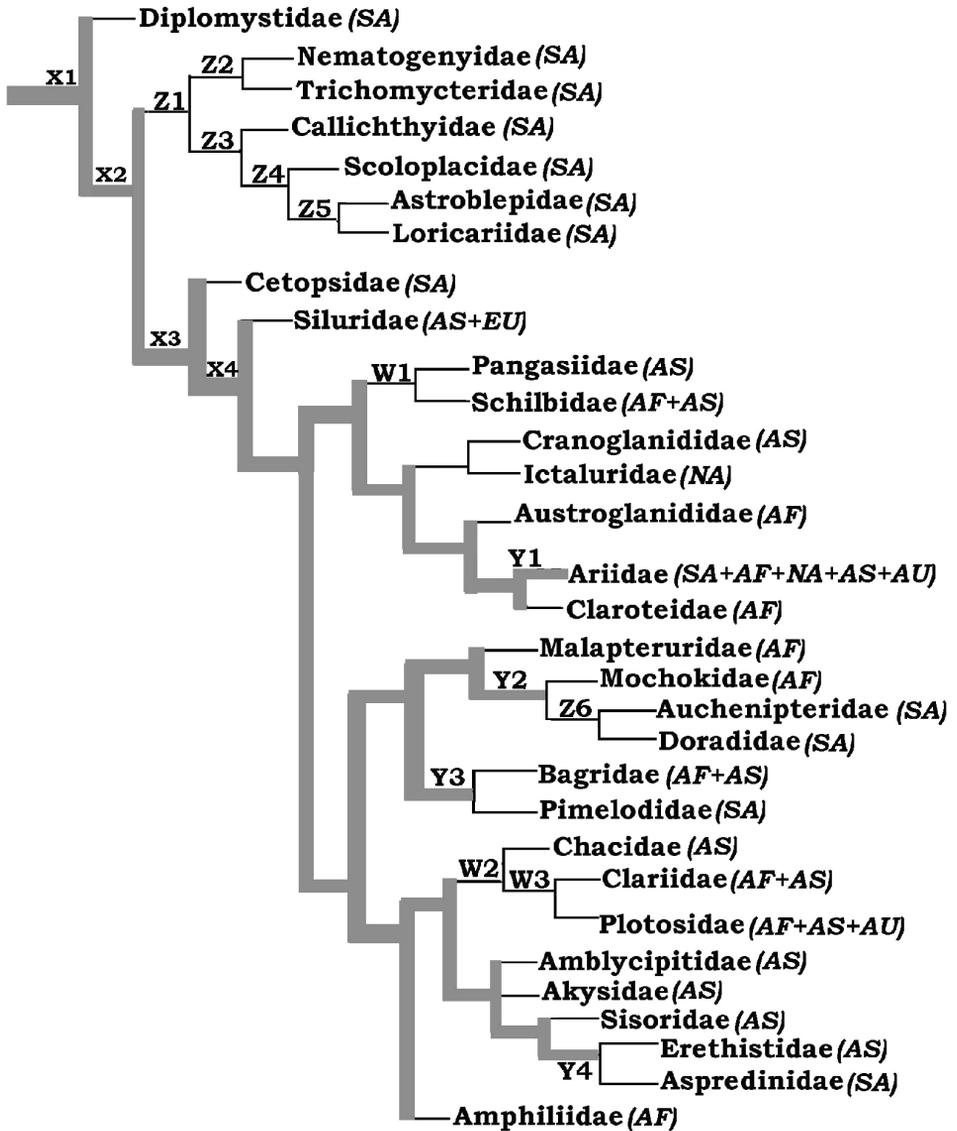


Figure 1. Scheme illustrating the biogeographic hypothesis presented in this paper concerning the distribution of the major siluriform clades in view of the phylogenetic results obtained in the author's cladistic analysis on the higher level phylogeny of the order: SA = South America; AF = Africa; NA = North America; EU = Europe; AS = Asia; AU = Australia (for more details and further explanations, see text).

South but from North America) and the Old World family Cranoglanididae (from Asia) should also be noted.

One of the clades referred to above, namely the one formed by the South American aspredinids and the Asiatic erethistids, was precisely put into question in Gayet

and Meunier's (2003: 513-515) excellent up-to-date overview on catfish palaeontology and palaeobiogeography, since "the placement of the South American Aspredinidae as the sister-group of the Asian Erethistidae is unlikely outside the Pangean hypothesis", a hypothesis seen as "unthinkable given the evolutionary level of siluriforms". In fact, as recognised by Gayet (pers. comm.), a sister-group relationship between the Aspredinidae and a group of Asiatic catfishes is not only problematic for the 'traditional hypothesis' commonly accepted nowadays to explain catfish biogeography, but also for the 'marine hypothesis' in the way it was formulated by authors such as Gayet and Meunier (2003) or Chardon (1967) (see above). However, it should be noted that the close relationship between aspredinids and Asiatic sisoroids appears not only strongly supported in the author's cladistic analysis, but also in several other studies (Ferraris, 1989; Mo, 1991; Chen, 1994; de Pinna, 1993, 1996, 1998).

Although clades 'Y1', 'Y2' and 'Y3' are not as problematic as 'Y4' for the 'traditional' and 'marine' hypotheses, their presence, together with that of clade 'Y4', in the figure 1 cladogram also indicates a siluriform origin significantly older than is usually accepted. This is because it emphasises that not only a few, but rather the great majority of the major interfamilial cladogenetic events of catfish evolutionary history, very likely occurred before the separation of the South American and African continents (at about 112 MY; see Lundberg, 1998). (These cladogenetic events are indicated by thick, grey lines in fig. 1.) In fact, this strongly supports the view of Lundberg (1993, 1998), who, based on the distribution of one of these groups (the group made up of mochokids + doradids + auchenipterids), pointed out that considerable diversification within Siluriformes already occurred before the final separation of these two continents. It also corroborates the results presented by Orti and Meyer (1997). Based on genetic divergent values derived from mitochondrial DNA sequences, these authors pointed out that **most** of the major groups of another otophysan order, the Characiformes, were already present **before** the separation of Africa and South America (see below).

One other major indication of a much older origin of the catfishes than is usually accepted (i.e., a Gondwanan origin in the Late Cretaceous) concerns the biogeographic distribution and phylogenetic relationships of those catfishes inside clade 'X4' in figure 1. In fact, besides the distribution of the eight most basal extant catfish families, all endemic to South America, indicating that the cladogenetic events leading to 'X1', 'X2' and 'X3' probably occurred in the South American area (see above), there is no strong phylogenetic relationship, after 'X4', between the different families of each continent. Indeed, within the 31 catfish families shown in figure 1 (in the cladogram in this figure, the Clariidae includes the genus *Heteropneustes*, previously assigned to family Heteropneustidae), there is not even a monophyletic clade constituted by two sister-group African families, or by two sister-group Asian families. The only cladogenetic event separating two families endemic to the same continent, after 'X4', is that indicated by 'Z6' leading to the neotropical families Auchenipteridae and Doradidae.

The overall analysis of the cladogram in figure 1 does, therefore, seriously contradict the most commonly accepted theories to explain catfish biogeography. If the Siluriformes originated in Gondwana at a moment where there were no remaining connections between it and Laurasia, and had evolved almost exclusively in Gondwanan areas for a long time before continental connections between these regions and the Laurasian continents were again available much later, a particularly strong phylogenetic relationship between Gondwanan catfishes would be expected, particularly between the South American and African ones. However, of all those clades represented in the cladogram of figure 1, only two are exclusively constituted of South American-African families, namely the one uniting the Auchenipteridae + Doradidae + Mochokidae, and the one formed by these three families plus the Malapteruridae.

The cladogram in figure 1 also contradicts some of the arguments often used by defenders of the 'marine hypothesis'. One of these arguments is that many of the oldest catfish fossil records, i.e., of the Late Cretaceous, refer to 'plesiomorphic arioids' (a group which includes the mostly marine, heavily ossified ariids and also often other groups of heavily ossified siluriforms such as doradids or auchenipterids) that were reported from deltaic and marine deposits (see Gayet and Meunier, 2003). However, the results of the author's cladistic analysis of catfish higher level phylogeny not only contradicts a supposedly close relationship between the ariids and the doradids and/or auchenipterids, as did also those of de Pinna (1993), but also points out that the Ariidae occupy a rather apomorphic position within the Siluriformes (fig. 1). This is also the case for the Plotosidae, a family which also presents a large number of marine species, and for the Aspredinidae, the other catfish family that includes some marine members (see above). Therefore, under the phylogenetic paradigm, attending to the rather apomorphic position of these three groups, it is far more plausible to consider the ability to live in marine environments as an apomorphic, rather rare feature than as a plesiomorphic and rather common character within siluriform evolutionary history.

This draws attention to an issue often discussed in biogeographic and theoretical studies: 'contemporary importance to historical priority' (Gould, 1983). I agree that (as noted by Gould and others) the presence of certain physiological/ecological characteristics in a particular extant group does not invalidate the possibility that the members of this group presented, in the past, different physiological/ecological traits. The freshwater extant distribution of most catfish groups surely does not refute that these groups could have been adapted to marine environments in the past. However, I also believe that one should not consider as simply irrelevant a) the data from current ecology/physiology, or b) that only three rather apomorphic families among all extant catfish groups present some marine species nowadays, and particularly that, as mentioned above and discussed in more detail below, these extant 'marine species' seem to be confined to coastal areas and to be unable to live and cross the high seas. It is surely not, or at least should not be, as easy to advance a possible marine origin/dispersion for a group of currently mainly freshwater

members, such as catfishes, than for a currently mostly marine group, such as sharks. Amongst the reasons for this, a simple one is that, as mentioned above, under an explicit phylogenetic framework (fig. 1) the number of evolutionary steps needed to postulate such a marine origin/dispersion for catfishes is simply much larger and, thus, less parsimonious, than that needed to explain an essentially freshwater origin/dispersion. This stresses the importance of discussing such biogeographic subjects against an explicit phylogenetic scheme on the relationships of the groups analysed.

In fact, in my opinion, the reports of fossil ariids not only from the Maastrichtian but already on the Campanian (see Gayet and Meunier, 2003: fig. 17.2), far from supporting the 'marine hypothesis', support instead that Siluriformes are very likely much older than is usually accepted, due to the rather apomorphic position of the Ariidae within this order (fig. 1, see also Mo, 1991; de Pinna, 1993). The relatively high proportion of ariid and/or 'Arioid' fossils among the older catfishes, could, in reality, be due to one or more of the following three reasons. Firstly, because ariids and/or 'Arioids' are more heavily ossified than most other catfishes, which could therefore facilitate the fossilisation and/or the discovery of these fishes, as stressed by authors such as Chardon (1968). Secondly, as recognised by authors such as Gayet et al. (1993: 863), "it is moreover very frequent to find continental vertebrates in coastal marine deposits; such deposits, although formed in a marine environment, are often among the most rich deposits for continental vertebrates" (translation from French, by the author). It is interesting to note that Gayet et al. (1992: 785) did, in fact, explicitly state that the old ariid fossils from the Campanian-Maastrichtian of South-America "lived mainly in freshwaters, their presence in marine waters resulting thus from a post-mortem displacement" (translation from French, by the author). Thirdly, as Romer (1966) emphasised, the discovery of relatively few ostariophysan fossils from freshwater deposits of the Cretaceous could be related to the also relatively scarce number of these type of deposits during this period. In fact, it is striking to note that some of the Cretaceous fossils of the also otophysan Characiformes, a group of currently exclusively freshwater fishes, are also from marine deposits (Gayet et al., 2003; Filleul and Maisey, in press). As discussed above for catfishes, I have no problem in admitting that some Characiformes were, indeed, marine at the Cretaceous, but it is rather difficult to conceive that the great majority, or even all major characiform clades were marine during that period, since this would imply a rather impressive number of independent ulterior homoplasious reversion to freshwater environments. And, even more puzzling, if this was the case, why would all those characiform groups perfectly adapted to marine environments at that time actually lose, without a single exception (since there is not a single marine characiform group today), an ability that was so important for their own evolution and geographical radiation?

PHYSIOLOGY/ECOLOGY

Apart from the old ariid and/or 'arioid' catfish fossil records, a typical argument used by defenders of the 'marine hypothesis' is, as referred above, the high tolerance to salinity of several extant catfish species, and particularly the fact that among these species, those of the families Ariidae, Plotosidae, and, to a much lesser extent, Aspredinidae, are indeed able to live in marine environments. However, these authors usually seem to forget that, as stressed by authors such as Rivas (1986) or Gosline (1975), a high physiological tolerance to salinity does not necessarily confer on a fish the ability to live and/or cross high seas. As these authors noted, salinity is not the only, and probably not the most important, barrier to live and cross open seas, since the latter differ also in the nature of their food supplies, predators, competitors, parasites, physical parameters such as temperature, cover, etc. This seems to be supported by the direct empirical observation of the geographical distribution of the extant marine catfishes: seemingly they are restricted to coastal areas and to "never venture to go to the high seas", as noted by Gayet et al. (1992: 785). An important point should be noted here: the 'marine hypothesis' defended by certain authors to explain catfish distribution requires that several catfish groups had, in the past, an ability that not a single group, not even extant ariids, plotosids or aspredinids, seems to display today: the ability to live in and/or cross high seas.

Of course, as authors such as Unmack (2001: 1065) stated, it is possible for fishes that are not actually adapted to live in high seas to eventually undertake random transoceanic dispersions, such as "rains and accidental movements by other organisms, whole fish being dropped by birds, or hurricanes". However, I wonder if such rare phenomena really could have contributed in an important way for the biogeographical history of the major siluriform clades shown in figure 1. Another hypothesis that is occasionally advanced by some authors to explain transoceanic dispersions of mainly freshwater groups such as catfishes is the existence of 'freshwater oceans'. For example, some authors have hypothesised that some freshwater cypriniforms may have undertaken a dispersion "across the present-day Mediterranean Sea during a 'freshwater phase' that followed the Messinian salinity crisis, during which the basin was transformed into a network of freshwater lakes" (Tsigenopoulos et al., 2003: 208). Other authors consider that a similar salinity crisis might have occurred in the arctic ocean during the Late Paleocene/Early Eocene, thus referring to a 'freshwater arctic ocean' (Chang and Maisey, 2003). Again, I have no problem in accepting that some catfishes might have eventually undergone a dispersion across these 'freshwater oceans'. However, one should note that these examples of 'freshwater oceans' mostly refer to a time when the major siluriform lineages were already differentiated and already had a rather cosmopolitan distribution (see below, 'palaeobiogeography'). Therefore, and since at least to my knowledge there are no reports of such large, geographically important 'freshwater oceans' in periods such as the Cretaceous, the eventual dispersion across these 'freshwater oceans' again does not seem able to explain the geographical distribution of most of the major catfish lineages.

PLATE TECTONICS

The phylogenetic results discussed above seem to indicate an origin of the Siluriformes considerably older than the usually accepted, i.e., than the Late Cretaceous (Gayet and Meunier, 2003). Also, contrary to what would be expected for an origin on an isolated Gondwana, the relationships between the catfish groups from the different Gondwanan regions do not appear to be stronger than those existing between these groups and the taxa occurring on the Laurasian areas, i.e., Europe, North America and Asia (see above). Thus, one could speculate that catfishes might have originated at a time when there were still some remaining Pangean connections between Gondwana and Laurasia, with the existence of those remaining connections explaining the lack of special relationships between the groups of the different Gondwanan continents and the wide Pangean distribution that these fishes effectively display. This is not an easy question. In fact, the more I investigated and read about plate tectonics, the more I realised the striking lack of consensus that still dominates several fundamental questions related to this field. This is clearly exemplified by several recent papers, such as the Philippe et al. (2003) study that questions the timing and location of the latest Pangean connections between Laurasia and Gondwana, Briggs' (2003) article criticising the commonly accepted theories on the biogeographic and tectonic history of India, Dobson's (2003) comments on a supposed Palaeozoic link between eastern Australia and eastern North America, and Bosellini's (2002) study which rewrites the geodynamics of the eastern Mediterranean, etc.

However, as stressed in the paper by Philippe et al. (2003), there is, effectively, growing evidence, based on paleobiogeographic data on several dinosaur groups, but also on other organisms such as ferns or lizards, that in the Early Cretaceous there were still some remaining Pangean connections between Gondwana and Laurasia, and namely between North Africa and the North American and/or European continents (Galton and Taquet, 1982; Buffetaut, 1989; Weishampel, 1990; Le Loeuff, 1991; Buffetaut and Le Loeuff, 1991; Sereno et al., 1994, 1996, 1998; Morell, 1994; Holtz, 1998; Barale et al., 2000; Chure, 2001; Perez-Moreno et al., 1999; Philippe et al., 2003 and references cited in these papers). Such evidence inclusively led authors such as Le Loeuff (1991) to introduce an explicit Afro-Euro-American palaeobioprovince for the Early Cretaceous. Apart from this strongly supported Pangean connection between Africa and the North American and/or European continents, some researchers point out other possible connections on the Early Cretaceous between the southern continents and some regions currently situated in the north, such as the connection between Africa and the Apulia Platform, a sort of Florida peninsula that migrated north, forming the Italy of today (Bosellini, 2002). But the problem, identified by authors such as Briggs (2003), is that, unfortunately, many researchers insist on continuing to use general geological maps that often date from a considerable time ago and hence do not reflect recent available scientific data. Thus, they continue to ignore, in their paleobiogeographic discussions, all the new data currently available. Also, as Ebach (2003: 3) stressed

recently, many authors, although recognising the importance and the advances of plate tectonics, seem to have a tendency to see continental drift “purely as a geological phenomenon that had virtually no impact on modern distribution of plants and animals”.

According to Sereno et al. (1996: 989), the remaining Pangean connections between North Africa and the North America and/or European continents have “continued well into the Early Cretaceous”, thus explaining why, contrary to what was expected, the relationships between Early Cretaceous dinosaurs from Gondwana are not stronger than between these dinosaurs and some dinosaurs from the Early Cretaceous of Laurasia (see Morell, 1994). In this aspect, the situation of Early Cretaceous dinosaurs is, in fact, quite similar to that of Siluriformes, in which there are no special phylogenetic affinities between the different Gondwanan groups (see above). Therefore, it seems plausible to consider that catfishes, as Early Cretaceous dinosaurs, could have eventually passed through the last remaining Pangean connections between Gondwana and Laurasia. The question is: could catfishes have already been there in the Early Cretaceous, or even before? Available data on catfish higher level phylogeny provide several arguments suggesting an origin of the Siluriformes significantly older than the late Cretaceous and recent paleobiogeographic and molecular data also provide evidence to support this.

PALAEOBIOGEOGRAPHY OF SILURIFORMS AND OTHER OSTARIOPHYSANS

The defenders of the traditional and marine hypotheses usually consider that the direct paleobiogeographic data available for the Siluriformes contradicts a Pangean origin of these fishes (see Gayet and Meunier, 2003). This argument, in fact, is often provided as the ‘one’ that most contradicts the diverse remaining evidence, coming from fields such as phylogenetics or molecular biology (see below), supporting a rather old, Pangean origin. However, in my opinion, such an argument should be regarded with caution. In fact, this issue relates to an old and much discussed question concerning paleobiogeographic studies: is the absence of evidence, evidence of absence? This subject has indeed been widely discussed, and was analysed in Lundberg’s (1998) overview on the temporal context of the diversification of neotropical fishes. This author (1998: 64), referring to the otophysan fishes, stated: “one possible answer, especially for the absence in the Early Cretaceous record of taxa like cichlids placed high up in the tree of acanthomorphs, is yes, they just had not evolved by then; the other possible answer perhaps more applicable to otophysans (which include catfish) for which there is a basis for predicting a ghost-like existence, is no, some had originated and perhaps diversified but they have escaped preservation or detection”. One particularly elucidative example given by Lundberg concerns precisely catfishes: †*Corydoras revelatus*, a callichthyid record from the late Palaeocene, ca. 58.5 MY, was described more than three-quarters of a century ago by Cockerell (1925), but,

despite the heavy bony armour in which callichthyids are encased, there are no subsequent fossil records of these fishes at least until 20 millions of years later.

As Lundberg (1998) stated, one of the problems related to paleobiogeographic hypotheses is that, although palaeontologists acknowledge, in theory, that 'absence of evidence' does not correspond to 'evidence of absence', they often do refer, in practice, to the absence of evidence as evidence of absence. This is precisely the case concerning the origin of Siluriformes, in which the defenders of the traditional and marine hypotheses use the absence of catfish fossils older than the Late Cretaceous as 'evidence' of the absence of this group before this period. However, as noted in the Stiassny et al. (in press) up-to-date overview on Gnathostome fishes, within the rayfin groups it is not the exception, but rather the rule, that the estimated age of a taxon (indicated by phylogenetic data, molecular clocks, etc.) differs considerably from the age of the oldest fossil known for that group.

In my view the palaeontological data for catfishes provides indirect evidence in support of (as do also phylogenetic and molecular data (see below)) a rather older origin of these fishes. As explained above, defenders of the traditional hypothesis usually argue that the presence of these fishes in the Laurasian regions of Europe, North America and Asia can be explained by, respectively: the Eocene connection between Africa and Europe; the Paleocene connection between South America and North America; and the Eocene collision between India and Asia and/or the Eocene passage from Africa to Asia through Europe. But it is important to note that ariid fossil otoliths were reported from North America in the late Campanian, long before the Palaeocene (Gayet and Meunier, 2003: fig. 17.2). Ariid fossil otoliths were also reported from Europe in the Palaeocene, that is, before the Eocene (Gayet and Meunier, 2003: fig. 17.2). These records, referring to otoliths, have sometimes been questioned, but the problem is that it is not clear whether they are refuted because they refer to otoliths or because they merely do not fit into the scenario proposed by the traditional hypothesis (Gayet and Meunier, 2003). But the important point is that, besides the otolith fossils, there are records which refer not to otoliths but to bone remains of undetermined siluriform fossils from the Maastrichtian of Europe, long before the Eocene, as shown in Gayet and Meunier (2003: fig. 17.4). To this should be added the report of ariid fossils, also referring not to otoliths but to bone remains, on the Maastrichtian of Asia, that is, again long before the Eocene (Gayet and Meunier, 2003: fig. 17.2).

Of course, the defenders of the traditional hypothesis could argue that perhaps this means that the land contacts allowing the passage of catfishes from Gondwana to these Laurasian continents occurred earlier than they stated. For example, they could argue that the passage to Europe, and thus to Asia, could have been carried out by means of an eventual land contact between Africa and Europe on the Maastrichtian (Gayet, pers. comm.). However, the presence of catfish fossils on the Campanian of North America would continue to be particularly problematic for the traditional hypothesis. Some authors do stress that the 'Paleocene' connection between South America and North America might have occurred, in reality, on the Paleocene

but also on the Maastrichtian (Gayet, 2001); however, this would not explain the Campanian catfish fossils of North America. The defenders of the marine hypothesis could, in turn, argue that these ariid Campanian fossils might have passed from South America to North America via a direct marine dispersion (see above). This issue regarding possible transoceanic dispersions of catfish taxa was discussed earlier. But what is more important here is that, be that as it may, the reality is that at the Late Cretaceous catfishes effectively had already a worldwide distribution, with the fossils found in the various continents at that period being from phylogenetically derived groups such as ariids and presenting a morphology similar to that of extant siluriforms (see above). Thus, the paleobiogeographic data available for catfishes, evidence of an already worldwide distribution by the Late Cretaceous, does not refute that these fishes originated before this epoch. One other important detail pointing towards a rather older origin of catfishes is that the amazing distribution of recent catfishes, in itself an indication of a Pangean siluriform origin, appears still more complex at a paleobiogeographic level, with, for example: 1) 'bagrid' fossils reported from North America (Gayet and Meunier, 2003), while extant bagrids are only found in Africa and Asia (fig. 1); 2) bagrid, clariid and ariid fossils reported from Europe (Gayet and Meunier, 2003), a continent where these three groups are now absent (fig. 1); 3) apparent 'ictalurid' fossil forms reported from Asia (Stucky, 1982), a continent lacking extant ictalurids (fig. 1); and 4) undetermined fossil catfishes found in Antarctica, a continent with no extant Siluriformes (Grande and Eastman, 1986). The case of bagrids is particularly worth mentioning. These fishes are now found in Asia and Africa, but: bagrid fossils were reported from Miocene and Pliocene of Europe; 'bagrid' fossils, although somewhat dubious, were reported from Eocene of North America; with some researchers even reporting seemingly extant bagrids from the neotropical region (Lundberg, pers. comm.). If this is so, bagrids would demonstrate a cosmopolitan distribution perhaps only comparable to that of the Ariidae, being reported, thus, from Africa, Asia, and possibly South America (extant forms) and from Europe and North America (fossil forms).

Paleobiogeographic data on other ostariophysan groups also provide interesting indirect evidence supporting that catfishes might have originated before the Late Cretaceous. In fact, Arratia (1997) described an ostariophysan fossil, †*Tichlingichthys*, from the Late Jurassic, ca. 150 Ma, and Poyato-Ariza (1996) described a chanid fossil from the order Gonorynchiformes, that is, the sister-group of the Otophysi, of about 140 MY, which is particularly remarkable since this means that ca. 140 MY there were already fishes from an extant ostariophysan family, i.e., the Chanidae. Thus, if members of this extant gonorynchiform family were already there at about 140 MY, this must mean that the first Gonorynchiformes, and, thus, the bifurcation between the Anatophysi and the Otophysi, occurred well before that (if the sister-group between the Otophysi and the Anatophysi is accepted: see below). In fact, it is relevant to mention that, while I was writing this paper defending a catfish origin older than the Late Cretaceous, Filleul and Maisey (in press) precisely described a characiform fossil, i.e., a fossil from the otophysan

order that is seemingly the sister-group of the clade Gymnotiformes + Siluriformes (see below), from the Early Cretaceous. This, as Maisey (pers. comm.) stressed, does not only make “us recalibrate the origin of the Otophysi and of the different otophysan orders”, but also gives a clear example on how erroneous it is to use the ‘absence’ of records of a certain group in a certain epoch as ‘evidence’ of the absence of that group at that epoch since, in fact, older fossils of existing groups can be, and often do continue to be, discovered.

CATFISH SISTER-GROUP

As the reader might have noted, when referring to the sister-group of the Siluriformes, I was particularly prudent, referring that this sister-group is seemingly the order Gymnotiformes. I agree with most authors that the Fink and Fink (1981) first explicit cladistic analysis of ostariophysan relationships, and the paper by the same authors in 1996 corroborating this 1981 study, have indeed largely contributed to our knowledge on this subject. I also agree that the phylogenetic scheme provided by these authors constitutes a solid, well-grounded working hypothesis, and I am aware that this scheme is the one most commonly accepted nowadays.

However, I also think that one cannot simply neglect the cladistic studies on ostariophysan phylogeny done by other authors after that first cladistic study by Fink and Fink (1981). And, concerning this, one is obliged to admit that most of these studies have indeed contradicted some of the sister-group relationships supported by Fink and Fink. In fact, apart from the 1997 analysis by Orti of molecular data from mtDNA and all codon-positions of the ependymin gene, which indeed supported Fink and Fink’s scheme, the only published works, at least to my knowledge, that theoretically supported this scheme, i.e., Dimmick and Larson (1996) and Arratia (1992), did, in reality, only support it after the Fink and Fink characters were introduced in the phylogenetic analysis. The independent analysis promoted by Dimmick and Larson (1996), based on molecular characters, but not including the morphological characters of Fink and Fink, suggested, in fact, that the sister-group of the Siluriformes is a clade formed by both Gymnotiformes and Characiformes, and not by Gymnotiformes alone as suggested by Fink and Fink. The independent analysis promoted by Arratia (1992), based only on her morphological characters of the suspensorium, without those characters of Fink and Fink (1981), suggested that the characiforms are the sister-group of the cypriniforms, and not of the clade gymnotiforms + siluriforms as suggested by Fink and Fink (see above). It is important to note that the independent results based exclusively on Dimmick and Larson’s molecular data indicating a sister-group relationship between the Siluriformes and the clade Characiformes + Gymnotiformes were also supported by Orti’s (1997) analysis of the first and second codon positions of the ependymin gene. These results were also supported by analysis carried out by Saitoh et al. (2003) based on the mitochondrial genome. Thus, one cannot say that the relationships among the otophysan orders constitute a completely consensual issue nowadays.

In fact, even the sister-group relationship between the Gonorynchiformes and the Otophysi, and thus the monophyly of the Ostariophysi as a whole, has been recently put in question by molecular studies such as those of Saitoh et al. (2003) or Ishiguro et al. (2003).

What is important to note here, in my opinion, is that, either accepting the Gymnotiformes, or the clade Gymnotiformes + Characiformes as the sister-group of the Siluriformes, as suggested by some cladistic analyses, this sister-group would in any case be a group almost exclusively constituted of freshwater fishes. Extant Gymnotiformes, as well as the very few fossils known from this group, are freshwater. Concerning Characiformes, the numerous extant members of this order are freshwater, but there are, in fact, some fossils that were discovered in marine deposits (see Gayet et al., 2003), which can either be seen to indicate that at least some ancient members of this group were marine, or, instead, that marine deposits can include freshwater organisms (see above). Be that as it may, the sister-group of Siluriformes, being either the Gymnotiformes or the clade constituted of these fishes and the Characiformes, is mostly formed by freshwater fishes. This is something that, in my view, cannot simply be neglected, since, under the cladistic paradigm, the sister-group does indeed provide important information for discussion of the evolutionary history of a certain character within the group being studied. That is, if the 'first' gymnotiform or the 'first' member of the clade Gymnotiformes + Characiformes (in case we take this latter clade as the sister-group of the catfishes) were freshwater, this would imply a further extra evolutionary step for the marine hypothesis defended by some authors (i.e., we should now consider a first evolutionary transition conferring on catfishes the ability to undertake marine dispersions, and, as explained above, an ulterior series of numerous evolutionary reversions such that nowadays no catfish groups, not even taxa such as ariids or plotosids, can seemingly enter and disperse through open seas: see above).

Another argument used by some researchers to contradict a Pangean, and sometimes even a Gondwanan, origin for catfishes is that gymnotiforms, either extant or fossil, are exclusively known from South-America. There are two points I would like to mention here. One is that, as explained above, some studies have suggested that perhaps the sister-group of catfishes is constituted not only of Gymnotiformes but of these fishes plus the Characiformes. Thus, if this would be the case, the sister-group of catfishes would have a Pangean distribution, as, apart from South America and Africa (Gondwana), some characiform fossils have been found in Europe (Laurasia) (Gayet et al., 2003; Filleul and Maisey, in press). However, the most important point is that this "sister-group distribution" argument seems flawed to me. Why should two sister-groups have necessarily occupied the exact same geographical areas in the past, if this is not what most empirical data concerning current examples show us today? Why, if Gymnotiformes are indeed the sister-group of Siluriformes, should both these groups have had exactly the same geographical distribution in the Mesozoic? If one analyses the current geographical distribution of gymnotiforms and siluriforms on the South-American continent, the distribution of siluriforms is

considerably wider than that of gymnotiforms, with some catfish groups extending, for example, as far south as latitude $47^{\circ}30'$ (Berra, 2001). Thus, as a simple theoretical example to illustrate this point, if there were an eventual separation at about latitude 45° of the small South American region situated south of this latitude from the rest of the continent, catfishes would be present in that small area, while gymnotiforms would not. If we can accept this today, why is it not possible that a similar situation had occurred in the Mesozoic? Why cannot we conceive that gymnotiforms were simply less widely distributed than catfishes in that period, and, thus, did not succeed in passing from the South-American region to Africa and, hence, to reach the last remaining Pangean connections between Gondwana and Laurasia allowing them to radiate out to this last supercontinent? This seems, in my opinion, clearly the most judicious option to consider in this specific case, more than that, if catfishes had managed to do so, Gymnotiformes had necessarily also passed from South America to the other regions and ultimately were extinct in these latter regions. This hypothesis should, of course, along with all the scientific hypotheses formulated in this study, be subject to testing in the future. In fact, in the specific case of the Gymnotiformes, this scientific hypothesis can be easily contradicted: suffice to find either a fossil record or an extant species of this order in Africa or another continent other than South America to prove it wrong.

MOLECULAR CLOCKS

First of all, I would like to mention that I agree with authors such as Vences et al. (2001: 1095) in that molecular estimates of the age of divergence between major lineages should be viewed with caution, considering the “restrictions inherent in molecular clock datings”. However, again, I do think that one cannot simply neglect all those studies providing such molecular estimates. And, in fact, it is effectively interesting to note that the data provided by this type of studies does suggest, once again, a rather ancient origin for the ostariophysan lineages. For example, the recent molecular study of Saitoh et al. (2003), based on an analysis of the complete mitochondrial DNA sequences of members of the five ostariophysan orders, as well as of other teleost groups, precisely supported a Pangean origin for otophysans. According to Saitoh et al. (2003: 459) “otophysan basal divergence took place no later than the Jurassic, possibly as early as the end of Permian Period on the Pangean continent”. Moreover, it is important to note that, in this same paper, the authors pointed out that, among otophysans, siluriforms probably had a rather ancient origin, older than that of gymnotiforms and inclusively that of characiforms (Saitoh et al., 2003: 470). This, therefore, strongly supports that, as defended in the present work, catfish are a rather old group, very likely preceding the Late Cretaceous. Such an old origin of the otophysan fishes was also suggested in Orti and Meyer’s (1997: 238-239) work using genetic divergence values, according to which “most lineages of characiform fishes had originated before the vicariant event separating African and neotropical taxa”.

GENERAL CONCLUSIONS

In conclusion, I would firstly like to emphasise that a detailed review of all available data, a great part of which is provided in recent studies, from the various fields discussed above, does provide evidence to support that catfishes very likely originated before the usually accepted Late Cretaceous period, i.e., at a time when there were still some remaining Pangean connections between Gondwana and Laurasia. This origin would have been confined first to the South-American side. Then catfishes would have dispersed from the South-American area to other areas, in a rather complex and geologically rapid 'radiative' pattern, with some groups migrating, via pre-drift dispersion, to Laurasian regions. Therefore, the separation between Laurasia and Gondwana, and ulteriorly between the different areas constituting each of these supercontinents, would have contributed to important vicariant events. This scenario was probably still further complicated by events such as the collision between India and Asia, the ulterior reestablishment of certain continental bridges such as those between the Americas, and perhaps also by some marine migrations. This would thus explain the highly complex biogeographical distribution of the order Siluriformes (fig. 1). This work thus supports the remarks of Lundberg et al. (1998: 43): "the more we discover in the fossil record, and the more we resolve phylogenetic relationships of fishes, the very much older our estimates of taxic origin get".

Secondly, I would like to draw attention to the fact that, as stated by authors such as Briggs (2003: 381), although many researchers recognise important advances on plate tectonics, they continue to use, in the discussion of their biogeographic hypotheses, general maps that often do not provide "accurate representations of current scientific knowledge". In my opinion this is very likely the reason why, although there is growing evidence to support a rather old origin of modern teleost groups such as the Ostariophysi (e.g., the Late Jurassic/Early Cretaceous: see, for example, Stiassny et al., in press), there seems to be an underlying taboo when it comes to hypothesise an eventual Pangean origin for such modern groups. This is precisely because, despite the substantial amount of data supporting the existence of remaining Pangean connections between Laurasia and Gondwana in the Late Jurassic and very likely "well into the Early Cretaceous" (see above), many ichthyologists continue to use general and rather old-fashioned maps that often do not take into account such data. If there is growing evidence supporting an origin of ostariophysans in the Late Jurassic and perhaps of catfishes in the Early Cretaceous, as well as supporting that at that time there were indeed some remaining important Pangean connections between Laurasia and Gondwana, why cannot one hypothesise that such connections may have indeed played a role in the distribution of these fish groups, and, thus, of 'modern' teleost taxa? As mentioned above, this is just a scientific hypothesis that can, and should, be tested and, hopefully, stimulate further discussions, thus allowing the progress of scientific research. It is therefore hoped that this work could precisely instigate future phylogenetic, palaeontological, tectonic, biogeographical and molecular studies that might shed light on the highly

puzzling, but clearly interesting, questions relating to the origin and distribution of catfishes and other ostariophysans, as well as of the Teleostei in general.

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REFERENCES

- Arratia, G. (1992) Development and variation of the suspensorium of primitive catfishes (Teleostei: Ostariophysi) and their phylogenetic relationships. *Bonn Zool. Monogr.*, 32, 1-148.
- Arratia, G. (1997) Basal teleosts and teleostean phylogeny. *Palaeo Ichthyologica*, 7, 5-168.
- Barale, G., Quaja, M. & Philippe, M. (2000) Le bassin de Tataouine: une référence paléobotanique du Mésozoïque dans le domaine paraliqque du Gondwana septentrional. *Volume des communications du premier colloque du patrimoine géologique, Tunis*, 74-91.
- Berra, T.M. (2001) *Freshwater Fish Distribution*. Academic Press, San Diego, USA.
- Bosellini, A. (2002). Dinosaurs "re-write" the geodynamics of the eastern Mediterranean and the paleogeography of the Apulia Platform. *Earth-Science Rev.*, 59, 211-234.
- Briggs, J.C. (1979) Ostariophysan zoogeography: an alternative hypothesis. *Copeia*, 1979, 111-118.
- Briggs, J.C. (2003) The biogeographic and tectonic history of India. *J. Biogeogr.*, 30, 381-388.
- Buffetaut, E. (1989) Archosaurian reptiles with Gondwanan affinities in the Upper cretaceous of Europe. *Terra Nova*, 1, 69-74.
- Buffetaut, E. & Le Loeuff, J. (1991) Late cretaceous dinosaur faunas of Europe: some correlation problems. *Cretaceous Res.*, 12, 159-176.
- Burgess, W.E. (1989) *An atlas of freshwater and marine catfishes: a preliminary survey of the Siluriformes*. TFH Publications, Berkshire, USA.
- Chang, M.-M. & Maisey, J.G. (2003) Redescription of *Ellimma branneri* and *Diplomystus shengliensis*, and relationships of some basal clupeomorphs. *Am. Mus. Novitates*, 3404, 1-35.
- Chardon, M. (1967) Réflexions sur la dispersion des Ostariophysi à la lumière des recherches morphologiques nouvelles. *Ann. Soc. R. Zool. Belg.*, 97, 175-186.
- Chardon, M. (1968) Anatomie comparée de l'appareil de Weber et des structures connexes chez les Siluriformes. *Ann. Mus. R. Afr. Centr.*, 169, 1-273.
- Chen, X. (1994) *Phylogenetic studies of the amblycipitid catfishes (Teleostei, Siluriformes) with species accounts*. Unpublished Ph.D. thesis, Duke University, NC, USA.

- Chure, D. (2001) The second record of the African Theropod *Elaphosaurus* (Dinosauria, Ceratosauria) from the Western Hemisphere. *Neues Jabr. Geol. Paleont.*, 9, 565-576.
- Cockerell, T.D. (1925) A fossil fish of the family Callichthyidae. *Science*, 62, 317-322.
- De Pinna, M.C.C. (1993) *Higher-level phylogeny of Siluriformes, with a new classification of the order (Teleostei, Ostariophysii)*. Unpublished PhD thesis, University of New York, NY, USA.
- De Pinna, M.C.C. (1996) A phylogenetic analysis of the Asian catfish families Sisoridae, Akysidae and Amblycipitidae, with a hypothesis on the relationships of the Neotropical Aspredinidae (Teleostei, Ostariophysii). *Fieldiana, Zool.*, 84, 1-82.
- De Pinna, M.C.C. (1998) Phylogenetic relationships of Neotropical siluriformes: History overview and synthesis of hypotheses. In: L.R. Malabarba, R.E. Reis, R.P. Vari, Z.M. Lucena & C.A.S. Lucena (Eds.), *Phylogeny and Classification of Neotropical Fishes*, pp. 279-330. Edipucrs, Porto Alegre, Brazil.
- Dimmick, W.W. & Larson, A. (1996) [A molecular and morphological perspective on the phylogenetic relationships of the otophysan fishes](#). *Mol. Phylogenet. Evol.*, 6, 120-133.
- Diogo, R. (2003) Higher-level phylogeny of Siluriformes: an overview. In: B.G. Kapoor, G. Arratia, M. Chardon & R. Diogo (Eds.), *Catfishes*, pp. 353-384. Science Publishers Inc., Enfield, USA.
- Diogo, R. (2004) *Adaptations, homoplasies, constraints, and evolutionary trends: catfish morphology, phylogeny and evolution, a case study on theoretical phylogeny and macroevolution*. Science Publishers Inc, Enfield, USA.
- Dobson, J.E. (2003) Independent corroboration of a previously proposed Palaeozoic link between eastern Australia and eastern North America. *J. Biogeogr.*, 30, 473.
- Ebach, M.C. (2003) Area cladistics. *Biologist*, 50, 1-4.
- Ferraris, C.J. (1989) On the interrelationships between the Aspredinidae and the Akysidae (Ostariophysii, Siluriformes). *Abstracts of the 1989 Meeting, American Society of Ichthyology and Herpetology, San Francisco State University*, 86.
- Filleul, A. & Maisey, J.G. (In press) Redescription of *Santanichthys diasii* (Otophysi, Characiformes) from the Albian of the Santana formation and comments on its implications for Otophysan relationships. *Am. Mus. Novitates*.
- Fink, S.V. & Fink, W. (1981) Interrelationships of the ostariophysan fishes. *Zool. J. Linn. Soc. (Lond.)*, 72, 297-353.
- Fink, S.V. & Fink, W. (1996) Interrelationships of ostariophysan fishes (Teleostei). In: M.L.J. Stiassny, L.P. Parenti & G.D. Johnson (Eds.), *Interrelationship of fishes*, pp. 209-249. Academic Press, New York, USA.
- Galton, P.M. & Taquet, P. (1982) *Valdosaurus*, a hypsolophodontid dinosaur from the Lower Cretaceous of Europe and Africa. *Geobios*, 15, 147-159.
- Gayet, M. (2001) [A review of some problems associated with the occurrences of fossil vertebrates in South America](#). *J. South Am. Earth Sci.*, 14, 131-145.
- Gayet, M. & Meunier, F.J. (2003) Paleontology and palaeobiogeography of catfishes. In: B.G. Kapoor, G. Arratia, M. Chardon & R. Diogo (Eds.), *Catfishes*, pp. 491-522. Science Publishers Inc., Enfield, USA.
- Gayet, M., Rage, J.-C., Sempere, T. & Gagnier, P.-Y. (1992) Modalités des échanges de vertébrés continentaux entre l'Amérique du Nord et l'Amérique du Sud au Crétacé supérieur et au Paléocène. *Bull. Soc. Géol. France*, 163, 781-791.
- Gayet, M., Rage, J.-C., Sempere, T. & Gagnier, P.-Y. (1993) Réponse des auteurs. *Bull. Soc. Géol. France*, 164, 861-864.
- Gayet, M., Jegu, M., Bocquentin, J. & Negri, F.R. (2003) New characoids from the Upper Cretaceous and Paleocene of Bolivia and the Mio-Pliocene of Brazil: phylogenetic position and paleobiogeographic implications. *J. Vert. Paleont.*, 23, 28-46.
- Gosline, W.A. (1975) A reexamination of the similarities between the freshwater fishes of Africa and South America. *Mém. Mus. Natn. Hist. Nat.*, 88, 145-155.
- Gould, S.J. (1983) What, if anything else, is a zebra? *Nat. Hist.*, 90, 6-12.

- Grande, L. & Eastman, T.J. (1986) A review of Antartical ichthyofaunas in the light of new fossil discoveries. *Paleont.*, 29, 113-137.
- Grande, L. & de Pinna, M.C.C. (1998) Redescription of *Hypsidoris farsonensis* (Teleostei: Siluriformes), with a reassessment of its phylogenetic relationships. *J. Vert. Paleont.*, 18, 451-474.
- Holtz, T.R. (1998) Spinosaurs as crocodile mimics. *Science*, 282, 1276-1277.
- Ishiguro, N.B., Miya, M. & Nishida, M. (2003) Basal euteleostean relationships: a mitogenomic perspective on the phylogenetic reality of the "Protacanthopterygii". *Mol. Phylogenet. Evol.*, 27, 476-488.
- Le Loeuff, J. (1991) The Campano-Maastrichtian vertebrate faunas from southern Europe and their relationships with other faunas in the world: paleobiogeographical implications. *Cretaceous Res.*, 12, 93-114.
- Lundberg, J.G. (1993) African-South American freshwater fish clades and continental drift: problems with a paradigm. In: P. Goldblatt (Ed.), *Biological relationships between Africa and South America*, pp. 156-199. Yale University Press, New Haven, USA.
- Lundberg, J.G. (1998) The temporal context for the diversification of Neotropical fishes. In: L.R. Malabarba, R.E. Reis, R.P. Vari, Z.M. Lucena & C.A.S. Lucena (Eds.), *Phylogeny and Classification of Neotropical fishes*, pp. 49-68. Edipucrs, Porto Alegre, Brazil.
- Lundberg, J.G., Marshall, L.G., Guerrero, J., Horton, B., Malabarba, M.C.S.L. & Wesselingh, F. (1998) The stage for Neotropical fish diversification: a history of tropical South American rivers. In: L.R. Malabarba, R.E. Reis, R.P. Vari, Z.M. Lucena & C.A.S. Lucena (Eds.), *Phylogeny and Classification of Neotropical fishes*, pp. 13-48. Edipucrs, Porto Alegre, Brazil.
- Mo, T. (1991) Anatomy, relationships and systematics of the Bagridae (Teleostei: Siluroidei) with a hypothesis of siluroid phylogeny. *Theses Zool.*, 17, 1-216.
- Morell, V. (1994) New African Dinosaurs give an old World a novel look. *Science*, 266, 219-220.
- Myers, G.S. (1938) Freshwater fishes and West Indian zoogeography. *Smithsonian Report for 1937*, 339-364.
- Orti, G.S. (1997) Radiation of characiform fishes: evidence from mitochondrial and nuclear DNA sequences. In: T.D. Kocher & C.A. Stepien (Eds.), *Molecular Systematics of Fishes*, pp. 219-243. Academic Press, San Diego, USA.
- Orti, G.S. & Meyer, A. (1997) The radiation of characiform fishes and the limits of resolution of mitochondrial ribosomal DNA sequences. *Syst. Biol.*, 46, 75-100.
- Perez-Moreno, B.P., Chure, D.J., Pires, C., Marques da Silva, C., dos Santos, V., Dantas, P., Povoas, L., Cachao, M., Sanz, J.L. & Galopim de Carvalho, A.M. (1999) On the presence of *Allosaurus fragilis* (Theropoda: Carnosauria) in the Upper Jurassic of Portugal: first evidence of an intercontinental dinosaur species. *J. Geol. Soc. Lond.*, 156, 449-452.
- Philippe, M., Cuny, G., Bamford, M., Jaillard, E., Barale, G., Gomez, B., Quaja, M., Thevenard, F., Thiebaud, M. & Von Sengbusch, P. (2003) The palaeoecological record of *Metapodocarpoxylon libanoticum* (Edwards) Dupéron-Laudoueneix et Pons and the Gondwana Late Jurassic-Early Cretaceous continental biogeography. *J. Biogeogr.*, 30, 389-400.
- Poyato-Ariza, F.J. (1996) A revision of the ostariophysan fish family Chanidae, with special reference to the Mesozoic forms. *Paleo Ichthyol.*, 6, 1-52.
- Rivas, L.R. (1986) Comments on Briggs (1984): Freshwater fishes and biogeography of Central America and the Antilles. *Syst. Zool.*, 35, 633-639.
- Romer, A.S. (1966) *Vertebrate paleontology*. University of Chicago Press, Chicago, USA.
- Saitoh, K., Miya, M., Inoue, J.G., Ishiguro, N.B. & Nishida, M. (2003) Mitochondrial genomics of ostariophysan fishes: perspectives on phylogeny and biogeography. *J. Mol. Evol.*, 56, 464-472.
- Sereno, P.C., Wilson J.A., Larsson, H.C.E., Dutheil, D.B. & Sues, H.-D. (1994) Early Cretaceous Dinosaurs from the Sahara. *Science*, 266, 267-271.
- Sereno, P.C., Dutheil, D.B., Larochene, M., Larsson, H.C.E., Lyon, G.H., Magwene, P.M., Sidor, C.A., Varricchio, D.J. & Wilson, J.A. (1996) Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science*, 272, 986-991.

- Sereno, P.C., Beck, A.L., Dutheil, D.B., Gado, B., Larsson, H.C.E., Lyon G.H., Marcot, J.D., Rauhut, O.W.M., Sadleir, R.W., Sidor, C.A., Varricchio, D.J., Wilson, G.P. & Wilson, J.A. (1998) A long-snouted predatory dinosaur from Africa and the evolution of Spinosaurids. *Science*, 282, 1298-1302.
- Stiassny, M.L.J., Wiley, E.O., Johnson, G.D. & De Carvalho, M.R. (In press). Gnathostome fishes. In: M.J. Donaghue & J. Cracraft (Eds.), *Assembling the Three of Life*. Oxford University Press, New York, USA.
- Stucky, R.K. (1982) Early fossil catfish from Mongolia. *Copeia*, 1982, 465-467.
- Teugels, G.G. (2003). State of the art of recent siluriform systematics. In: B.G. Kapoor, G. Arratia, M. Chardon & R. Diogo (Eds.), *Catfishes*, pp. 317-352. Science Publishers Inc., Enfield, USA.
- Tsigenopoulos, C.S., Durand, J.D., Unlu, E. & Berreri, P. (2003) Rapid radiation of the Mediterranean *Luciobarbus* species (Cyprinidae) after the Messinian salinity crisis of the Mediterranean Sea, inferred from mitochondrial phylogenetic analysis. *Biol. J. Linn. Soc.*, 80, 207-222.
- Unmack, P.J. (2001) Biogeography of Australian freshwater fishes. *J. Biogeogr.*, 28, 1053-1089.
- Vences, M., Freyhof, J., Sonnenberg, R., Kosuch, J. & Veith, M. (2001) Reconciling fossils and molecules: Cenozoic divergence of cichlid fishes and the biogeography of Madagascar. *J. Biogeogr.*, 28, 1091-1099.
- Weishampel, D.B. (1990) Dinosaur distribution. In: D.B. Weishampel, P. Dobson & H. Osmolska (Eds.), *The Dinosauria*, pp. 63-139. University of California Press, Berkeley, USA.
- Weitzman, S.H. & Weitzman, M. (1982) Biogeography and evolutionary diversification in Neotropical freshwater fishes, with comments on the refuge theory. In: G.T. Prance (Ed.), *Biological Diversification in the Tropics*, pp. 403-422. Columbia University Press, New York, USA.