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Muscles versus bones: catfishes as a case study for a discussion on the relative contribution of myological and osteological features in phylogenetic reconstructions

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Abstract—The levels of homoplasy and phylogenetic reliability of different types of data sets have since long intrigued evolutionary scientists. This paper provides, to the author's knowledge, the first assessment of the relative contribution of a large set of myological and osteological characters in simultaneous phylogenetic analyses. The biological taxon used as a case study for this comparison was the highly diverse and cosmopolitan teleost Siluriformes (catfishes) which, with 34 families, about 437 genera and more than 2700 species, represents about one third of all freshwater fishes and one of the most diverse vertebrate groups. Such a direct comparison of the relative contribution of these two types of data sets has the advantage that the homoplasy levels and the phylogenetic trees being compared refer to the same group and, more importantly, to the very same terminal taxa. The overall analysis of the results presented in this work seems to indicate that: (1) osteological structures display a greater morphological variation than myological ones; (2) this difference (which is very likely overenhanced by the fact that the phylogenetic variation of osteological structures has historically been the subject of many more studies and descriptions than myological ones) is particularly notable in small taxa, such as genera or species; (3) myological characters provide, however, a high proportion of informative characters for disclosing the relationships between larger taxa, and, thus, for disclosing the phylogeny of the higher clades in which these taxa are included. These results raise some puzzling, general questions. For instance, what are the reasons for the seemingly greater morphological variation of osteological structures? And why is this greater morphological variation of osteological structures in relation to myological structures particularly pronounced in low ranking taxa? Does natural selection eventually act, in certain cases, more on bones than on muscles? Is the development of myological structures eventually more constrained than that of osteological features? What explains the apparently high reliability of muscular characters to disclose the higher-level phylogeny of higher taxa? More direct comparisons, either of other major groups of teleosts or of vertebrates in general, are clearly needed to infer if the patterns found in the direct comparison of this work correspond to a more general phylogenetic pattern, or instead refer to a particular situation found in the order Siluriformes.

Keywords: bones; catfish; Consistency and Retention Indexes; evolution; homoplasy; morphology; muscles; phylogeny; Siluriformes; Teleostei; vertebrates.

INTRODUCTION

The levels of homoplasy found in different types of data sets have since long intrigued evolutionary scientists. The comparison of the homoplasy levels found in phylogenetic studies of animals vs. that found in studies of plants, for example, was discussed with some detail by Sanderson and Donoghue (1989). As noted by these authors, it is usually “widely believed that plants are more homoplastic than most animals” (Sanderson and Donoghue, 1989, 1790). For instance, Wagner (1984: 115) stated that “plants are evidently unusually inclined to have parallelisms”, while Cronquist (1987: 24) suggested that “the relative lack of morphological integration in plants, and poor correlation of evolutionary advances with adaptive zones and ecological niches, combine to permit rampant parallelism, in contrast to the more rigid evolutionary channelling in animals”. However, the comparison promoted by Sanderson and Donoghue (1989: 1790) between explicit cladistic analyses using, respectively, data from plants and animals indicates “that the levels of homoplasy (between plants and animals) are remarkably similar”. Another issue that has been, and continues to be widely discussed (Doyle, 1998; Smith, 1998; Benton, 1999a, b; Easteal, 1999; Mallet and Willmott, 2003; Dunn, 2003; etc.) is the use of molecular vs. morphological data in phylogenetic studies. As noted by Sanderson and Donoghue (1989: 1791), the “value of morphological data in elucidating phylogeny has frequently been questioned because of the ‘susceptibility’ of morphology to convergent evolution in natural selection”. In order to analyse this, these authors elaborated a comprehensive comparison of 18 molecular and 42 morphological phylogenetic studies, concluding that “there is no evidence to date that molecular data are less homoplastic than morphological data” (Sanderson and Donoghue, 1989: 1791).

As stressed by these and other authors, there are, however, other kinds of different data sets that deserve to be compared in a phylogenetic context, such as reproductive vs. nonreproductive, sequence vs. electrophoretic, or myological vs. osteological. This paper provides a discussion on the different contributions of these two latter types of data sets, i.e., of myological versus osteological characters, in phylogenetic studies. As far as the author is aware, this is, in fact, the first direct comparison between the homoplasy levels and the phylogenetic relevance of a great number of myological characters (91: see below) and a great number of osteological characters (303: see below) within the same phylogenetic analysis.

As noted by Borden (1999: 191), very few phylogenetic studies focus on myology for a variety of reasons: “investigators may be reluctant to use myology due, for example, to the plethora of names that have been used to describe the same muscles, to the realisation that osteological proficiency is mandatory in order to identify muscle, leading them to concentrate only on osteology, or to the requirement of potentially finer dissection to preserve muscle bundles and nerves; furthermore, fossil fishes leave few if any myological clues, complicating hypotheses between extinct and extant fishes”. In consequence, as also noted by Borden (1999: 191), “of those studies using myology as a basis of information, most are functional works

often analysing the role of various muscles in feeding or locomotion or comparing a muscle or specific group across a number of taxa systematically and/or ecologically related”.

Explicit cladistic analyses based on muscular data are, thus, rather rare. Some examples, within teleost fishes, listed by Borden (1999) are those of Winterbottom (1993) using 46 muscular characters to reconstruct the relationships among the acanthurid genera and of Borden (1998) using about ten myological characters to investigate the phylogeny inside the acanthurid genus *Naso*. As these studies are essentially restricted to myology, they do not allow a direct comparison between the homoplasy and phylogenetic relevance of myological versus osteological data. In a study of the Cottoidea, Yabe (1985) included, as noted Borden (1999), some myological characters together with some osteological ones. But the total number of muscular characters was rather small (only 14, together with an also relatively small — 46 — number of osteological characters), and, moreover, Yabe (1985) did not provide a direct comparative analysis of the homoplasy levels and phylogenetic relevance of the two different kind of characters. In what refers to the teleost order Siluriformes, or catfishes, which constitute the case study discussed in the present paper, the only relevant phylogenetic analyses published so far including a relatively significant number of myological characters are those of Howes (1983) (11 myological characters out of a total of 34 used) and Schaefer (1990) (seven muscular characters out of a total of 72 used) concerning the Loricarioidea. But, again, the total number of muscular characters included in those two studies is rather small and not representative, and neither do these studies provide a direct comparative analysis between the homoplasy levels and phylogenetic relevance of these two types of data sets. With regard to non-teleost taxa, some authors have discussed the phylogenetic utility of myological characters for inferring the relationships of groups such as, for example, Aves (McKittrick, 1991), hadrosaurian dinosaurs (Dilkes, 2000), or primate mammals (Shoshani et al., 1996; Collard and Wood, 2000; Gibbs et al., 2000, 2002). However, again, none of these studies had as its main objective to compare directly the phylogenetic relevance of myological versus osteological structures, nor provided a direct comparison between the homoplasy levels and the partial contribution of these two types of structures within the same phylogenetic analysis.

In the present paper I provide a direct comparison between the homoplasy levels and phylogenetic contribution of a large set of myological and osteological characters in the reconstruction of the higher level relationships of the order Siluriformes, as a basis for a broader discussion on the contribution of osteological and muscular characters in phylogenetic reconstructions. The Siluriformes, or catfishes, found in North, Central and South America, Africa, Europe, Asia and Australia, with fossils in Antarctica even, constitute a cosmopolitan and particularly diverse 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 diverse vertebrate taxa (see e.g., Burgess, 1989; Diogo, 2003a; Teugels, 2003). The

detailed study of the order Siluriformes can therefore effectively provide useful data and illustrative examples for broader discussions on theoretical biology, phylogeny, and macroevolution in general.

The direct comparison provided here has the advantage that the homoplasy levels and the phylogenetic trees being compared concern the same group and, more importantly, the same terminal taxa. This substantially facilitates not only the discussion on the contribution of each of these two types of characters for the phylogenetic analysis, but also the comparison between the levels of homoplasy displayed by the two different data sets. In fact, the variable that most correlates with homoplasy levels clearly seems to be the number of terminal taxa, the number of characters (which is the only variable to change in the present study: see below) having apparently very little or no influence at all on these levels of homoplasy, particularly when both data sets have a markedly high number of characters, as is the case of the present study (Sanderson and Donoghue, 1989; Poe, 1998). This comparison is based on the phylogenetic results of a recently published, extensive phylogenetic analysis of 440 morphological characters concerning the configuration of the bones, muscles, cartilages and some soft tissues of the cephalic region and the pectoral girdle of species of 87 genera representing the 32 extant siluriform families (Diogo, 2004). That phylogenetic analysis resulted in an almost completely resolved strict-consensus cladogram (fig. 1), more resolved than those of previous published analyses on siluriform higher-level (Mo, 1991; de Pinna, 1998), presenting three polytomies, of which only one directly concerns interfamilial relationships within the order (fig. 2).

MATERIALS AND METHODS

In the present work, two main strategies were used to compare the phylogenetic reliability of the 91 myological and 303 osteological characters used in the overall phylogenetic analysis provided by Diogo (2004). The first was to elaborate tables 1 and 2, which show, respectively, the individual Consistency Index (CI) and Retention Index (RI) of each of these myological (table 1) and osteological (table 2) characters in that phylogenetic analysis. Those characters that are *autapomorphic*, i.e., derived and *unique for a single terminal taxa* (for each one of the 87 catfish genera shown in the cladogram of fig. 1), and, thus, that were not informative of the phylogenetic relationships between different terminal taxa, are, respectively, indicated as 'AUT' in these tables. The analysis of tables 1 and 2, therefore, will allow discussion of some points regarding the different performances of myological vs. osteological characters in phylogenetic studies, such as the different proportions of autapomorphic and informative characters or the different averages of the Consistency and Retention Indexes displayed by each of these two types of data sets. All statistical analyses and comparisons provided in the present work were performed using the computer program SPSS, version 8.0.

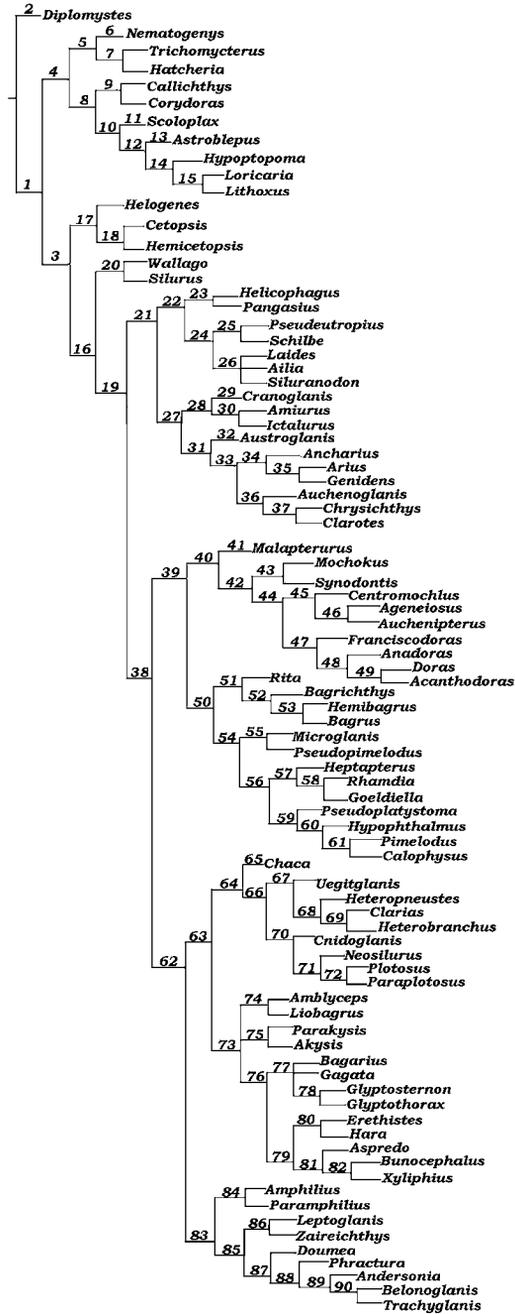


Figure 1. Strict consensus tree of 12 equally parsimonious trees obtained in the cladistic analysis of catfish higher-level phylogeny promoted by Diogo (2004) (440 characters; 87 terminal taxa; CI = 0.52; RI = 0.78; numbers on the cladogram correspond to the numbers used in the original work to identify the different clades of the cladogram, which are also followed in the present text: for more details, see text).

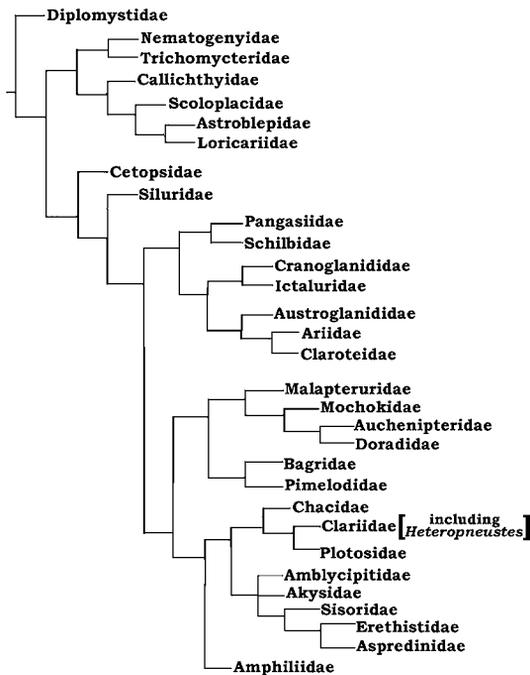
Table 1.

List of the 91 myological characters (Char.) included in the cladistic analysis of Diogo (2004) and their respective CI and RI; the number of these characters correspond to their number in the character list provided in that paper. AUT means that the character is autapomorphic for a single genus; the last cells, indicated with TN, MC and MR represent, respectively, the sum total of the number of myological characters (TN), the arithmetical mean of the consistency indexes of these characters (MC), and the arithmetical mean of the retention index of these characters (MR) (for further explanations and more details, see text).

Char.	CI	RI	Char.	CI	RI
16	AUT	AUT	214	100	100
18	33	77	215	66	75
19	25	81	216	100	100
20	100	100	217	66	75
21	100	100	218	AUT	AUT
22	AUT	AUT	219	28	68
23	100	100	220	25	40
24	100	100	221	50	50
26	100	100	222	100	100
27	20	76	223	25	40
28	AUT	AUT	224	25	72
29	AUT	AUT	225	50	75
30	100	100	226	66	93
31	100	100	227	16	61
32	33	33	228	33	50
33	33	60	229	100	100
34	100	100	230	100	100
35	22	68	231	50	80
36	100	100	232	100	100
37	33	78	233	100	100
38	100	100	234	AUT	AUT
39	50	0	235	50	66
40	AUT	AUT	236	33	88
41	AUT	AUT	237	33	50
42	10	77	238	AUT	AUT
43	50	0	239	50	75
44	100	100	240	66	85
45	AUT	AUT	241	100	100
46	AUT	AUT	242	50	50
47	14	72	243	AUT	AUT
48	66	95	244	100	100
49	100	100	245	100	100
50	66	85	246	50	60
51	100	100	247	14	82
52	100	100	248	25	88
53	25	77	249	AUT	AUT
54	100	100	250	25	25
55	50	80	251	14	77

Table 1.
(Continued).

Char.	CI	RI	Char.	CI	RI
206	33	33	252	100	100
207	100	100	253	100	100
208	33	60	254	20	75
209	100	100	255	AUT	AUT
210	20	88	256	100	100
211	50	66	257	100	100
212	40	70	258	100	100
213	66	80	TN = 91	MC = 0.64	MR = 0.80

**Figure 2.** Relationships among the extant catfish families, derived from the strict consensus tree shown in figure 1 (for more details, see text).

The second strategy followed here to compare the phylogenetic reliability of the 91 myological and 303 osteological characters in the overall phylogenetic analysis promoted by Diogo (2004) was simply to compare the phylogenetic trees generated directly from these two different kinds of data. It should be noted that the 303 osteological characters exclusively deal with the configuration of bones and associated cartilages constituting a certain osteological component (e.g., main body of the autopalatine plus the autopalatal cartilages), and not of ligaments connecting different osteological components. The Implicit Enumeration algorithm (ie^*) of

Table 2.

List of the 303 myological characters (Char.) included in the cladistic analysis of Diogo (2004) and their respective CI and RI; the number of these characters corresponds to their number in the character list provided in that paper. AUT means that the character is autapomorphic for a single genus; the last cells, indicated with TN, MC and MR represent, respectively, the sum total of the number of myological characters (TN), the arithmetical mean of the consistency indexes of these characters (MC), and the arithmetical mean of the retention index of these characters (MR) (for further explanations and more details, see text).

Char.	CI	RI												
56	100	100	119	AUT	AUT	181	14	61	309	25	72	378	50	0
57	100	100	120	50	75	182	66	66	310	100	100	379	100	100
58	100	100	121	AUT	AUT	183	66	75	311	100	100	380	AUT	AUT
59	AUT	AUT	122	100	100	184	AUT	AUT	312	66	75	381	16	44
60	33	75	123	40	80	185	20	69	314	AUT	AUT	382	AUT	AUT
61	100	100	124	AUT	AUT	186	AUT	AUT	315	AUT	AUT	383	AUT	AUT
62	100	100	125	100	100	187	100	100	317	AUT	AUT	384	AUT	AUT
64	AUT	AUT	126	50	80	188	50	66	318	50	75	385	100	100
65	100	100	127	AUT	AUT	189	100	100	319	AUT	AUT	386	10	50
66	AUT	AUT	128	100	100	190	50	90	320	AUT	AUT	387	AUT	AUT
67	AUT	AUT	129	AUT	AUT	191	33	60	321	100	100	388	AUT	AUT
68	100	100	130	100	100	192	20	33	322	AUT	AUT	389	66	0
69	25	35	131	16	71	193	50	50	323	AUT	AUT	390	100	100
70	AUT	AUT	132	100	100	194	14	68	324	50	0	391	100	100
71	AUT	AUT	133	100	100	195	AUT	AUT	325	23	65	392	100	100
72	50	88	134	100	100	196	100	100	326	100	100	393	100	100
73	25	60	135	100	100	197	50	0	327	12	46	394	AUT	AUT
74	100	100	136	50	87	198	25	84	328	100	100	395	100	100
75	33	60	137	50	50	199	AUT	AUT	329	AUT	AUT	396	50	75
76	33	66	138	100	100	200	50	80	330	50	0	397	100	100
77	AUT	AUT	139	50	85	201	50	50	331	66	50	398	14	40
78	100	100	140	100	100	202	66	66	332	20	42	399	AUT	AUT
79	100	100	141	50	66	203	100	100	333	AUT	AUT	400	100	100
80	50	0	142	50	85	204	100	100	334	33	63	401	50	83
81	20	20	143	AUT	AUT	205	AUT	AUT	335	100	100	402	50	66
83	AUT	AUT	144	33	50	259	100	100	336	100	100	403	100	100
84	16	68	145	100	100	260	100	100	337	AUT	AUT	404	100	100
85	100	100	146	33	71	261	AUT	AUT	338	100	100	405	100	100
86	20	75	147	100	100	262	AUT	AUT	339	100	100	406	AUT	AUT
87	AUT	AUT	148	30	74	263	50	80	340	100	100	407	33	81
88	66	87	149	100	100	264	50	0	341	33	60	408	25	90
89	100	100	150	15	75	265	14	25	342	100	100	409	AUT	AUT
90	33	60	151	50	0	266	25	76	343	50	80	410	100	100
91	50	50	152	50	66	267	100	100	344	AUT	AUT	411	66	0
92	AUT	AUT	153	50	95	268	100	100	345	100	100	412	66	0
93	25	40	154	AUT	AUT	269	AUT	AUT	346	50	85	413	AUT	AUT
94	AUT	AUT	155	16	70	276	50	0	347	AUT	AUT	414	14	45
95	66	0	156	100	100	277	25	76	348	14	14	415	AUT	AUT
96	33	60	157	33	81	278	50	75	349	AUT	AUT	416	100	100
97	16	66	158	100	100	279	100	100	350	66	80	417	66	66

Table 2.
(Continued).

Char.	CI	RI	Char.	CI	RI									
98	100	100	159	20	55	280	AUT	AUT	351	33	50	418	AUT	AUT
99	50	0	160	50	80	281	100	100	353	AUT	AUT	419	20	82
100	100	100	161	100	100	282	AUT	AUT	354	AUT	AUT	420	100	100
101	AUT	AUT	162	25	50	283	33	88	356	100	100	421	50	85
102	33	66	163	AUT	AUT	284	100	100	357	50	0	422	100	100
103	50	75	165	20	66	285	50	75	358	50	75	423	28	79
104	AUT	AUT	166	50	50	286	50	94	360	75	66	424	50	87
105	100	100	167	50	80	287	100	100	363	AUT	AUT	425	50	80
106	50	0	168	20	73	288	75	85	364	AUT	AUT	426	AUT	AUT
107	100	100	169	100	100	289	100	100	365	100	100	427	66	0
108	100	100	170	100	100	290	28	84	366	66	83	428	AUT	AUT
109	16	41	171	100	100	291	AUT	AUT	367	AUT	AUT	430	100	100
110	AUT	AUT	172	AUT	AUT	292	AUT	AUT	368	AUT	AUT	431	50	75
111	AUT	AUT	173	50	88	293	40	62	369	100	100	432	AUT	AUT
112	50	66	174	50	83	294	50	88	370	AUT	AUT	433	100	100
113	100	100	175	100	100	295	100	100	371	AUT	AUT	434	100	100
114	66	87	176	AUT	AUT	296	100	100	372	AUT	AUT	437	50	87
115	100	100	177	AUT	AUT	297	AUT	AUT	373	AUT	AUT	439	50	75
116	100	100	178	AUT	AUT	298	100	100	375	100	100	440	AUT	AUT
117	33	50	179	AUT	AUT	306	20	20	376	AUT	AUT			
118	100	100	180	33	80	308	20	73	377	AUT	AUT	TN =	MC =	MR =
												303	0.66	0.77

Hennig86 (Farris, 1988) was employed in the search for the most parsimonious cladograms, with Nona and Winclada (Nixon, 2002) being used to confirm the most parsimonious results found with this algorithm. Tree manipulations and diagnostics were done with the help of the program Nona and Winclada (Nixon, 2002). Autapomorphies for the different terminal taxa examined were actively searched for and included in the analysis. For a detailed account on the list of characters and the phylogenetic methodology used by the author to elaborate the overall cladogram shown in figure 1, to which the cladograms of figures 3 and 4 will be compared, please refer to Diogo (2004).

RESULTS AND DISCUSSION

One result from analysis of tables 1 and 2 is that there is a much higher proportion of autapomorphic characters characterising the terminal taxa of the strict-consensus cladogram of Diogo (2004) (fig. 1) within the osteological characters (83 autapomorphies in a total of 303 osteological characters, i.e., about 27.4%) than within the myological ones (14 autapomorphies out of a total of 91 characters, i.e., about 15.4%). This seems to corroborate the opinion of Borden (1999), who suggested that muscular structures seemingly provide fewer characters to characterise low ranking

taxa such as species or genera. According to Borden (1999), muscular structures are somewhat more 'conservative' than osteological ones, with these latter demonstrating a higher variability, particularly in taxa such as genera or species, and, therefore, usually providing more autapomorphic characters to characterise such low ranking taxa. The osteological structures included in the cladistic analysis of Diogo (2004) exhibit, in fact, a much greater morphological variation than the myological ones. The 65 different osteological structures of the cephalic region and the pectoral girdle included in that analysis provided, as referred to above, 303 phylogenetic characters (i.e., 4.7 phylogenetic characters per each osteological structure examined). The 39 muscles of the cephalic region and the pectoral girdle included in that analysis provided 91 phylogenetic characters (i.e., 2.3 phylogenetic characters for each muscular structure examined).

However, this does not mean that osteological structures are simply more appropriate than myological ones for phylogenetic reconstructions. In fact, in phylogenetic studies of major groups, such as the Siluriformes, the osteological characters, by providing a greater percentage of autapomorphies to characterise low taxa such as genera, consequently reveal a smaller percentage of informative characters to infer the phylogenetic relationships between these taxa. To say that about 27.4% of the osteological characters (against 15.4% of the myological ones) refer to autapomorphies characterising terminal taxa is equivalent to saying that only 72.6% of these characters (against 84.6% of the myological ones) were shown to be informative for disclosing the relationships between these terminal taxa, and, thus, for disclosing siluriform higher level phylogeny.

In consequence, to 'counterbalance' to an extent the fact that osteological structures provided, in proportion, more phylogenetic characters per structure observed than myological ones, the myological characters obtained seem to be, in proportion, at least in the present case study, more informative on the higher level phylogeny of a major group such as the Siluriformes. It should be noted, however, that, despite this 'counterbalance', each osteological structure did provide, in proportion, more informative characters to reveal the general phylogenetic relationships of the Siluriformes. The 65 osteological components included in that analysis provided, as mentioned above, 303 phylogenetic characters, of which 220 were informative in disclosing the higher-level phylogeny of this order (in a proportion of 3.4 informative characters per osteological component examined). The 39 myological structures included in that analysis provided 91 phylogenetic characters, of which 77 were informative on the higher-level phylogeny of this order (in a proportion of 2.0 informative characters per myological structure examined).

It is also important to draw attention here to another important point. The 39 myological structures provided 91 phylogenetic characters, with 2.3 phylogenetic characters per muscle examined, against the 4.7 phylogenetic characters per osteological component examined. Although very likely indicating a true higher osteological variation, as suggested by Borden (1999), this is also clearly related to the historical fact that there are, as was also stressed by Borden, many fewer phyloge-

netic studies available based on myology (see Introduction). In fact, a significant number of the osteological characters included in Diogo's 2004 study were inspired by phylogenetic characters previously provided in analyses of other authors. This is due to the fact that there are, in the literature, a great number of phylogenetic studies on catfish relationships, and particularly on the relationships within certain particular, low ranking catfish taxa, based on osteological data. Those studies thus drew the attention of the author towards several interesting osteological characters. However, a completely different picture is found with myological characters: there is not a single published, explicit catfish phylogeny based on myological data, with only one or two authors eventually including a few muscular characters in their analyses mainly based on osteological data. This point clearly should be kept in mind in a detailed discussion on the 'variation' of, and the consequent number of informative phylogenetic characters provided by osteological vs. myological structures.

Another interesting point revealed through analysis of tables 1 and 2 is that amongst the informative characters pointed out by these two types of structures, those referring to the myological ones exhibit a higher mean Retention Index (=0.80: see table 1, MR) than those that refer to the osteological ones (=0.77: see table 2, MR). However, a statistical analysis reveals that these means are not significantly different at a significance level of 0.05. Contrarily to what happens with the Retention Index, the arithmetical mean of the Consistency Index of those informative characters referring to myological structures (=0.64: see table 1, MC) is somewhat inferior to that of those informative characters referring to the osteological ones (=0.66: see table 2, MC). But again, these means are statistically not significantly different at a significance level of 0.05.

In order to explain to the reader who is not familiar with the terms Consistency Index (CI) and Retention Index (RI) why it is interesting to compare, in a study such as this, the arithmetical means of the CI and RI seen in tables 1 and 2, as carried out above, as well as to compare the CI and RI of the 'osteological' and 'myological' trees of figures 3 and 4 (see below), I consider it appropriate to provide a short, simplified, introductory example of the difference between these Indexes. The CI of a character simply relates to the level of homoplasy exhibited by that character, while the RI also considers if the character helps to retain a certain clade in the cladogram of the group being studied (thence the name Retention Index). If, for example, a certain feature X is found in the loricariid genus *Lithoxus* and in the distantly related plotosid genus *Paraplotosus*, the respective character will have a CI of 0.5 (feature X was independently acquired twice in the cladogram) and an RI of 0.0 (the character does not help to retain any of the clades illustrated in the cladogram) (see fig. 1). However, if a certain feature Z is found i.e., in *Lithoxus* and *Paraplotosus*, but also in the doradid genera examined, *Doras*, *Anadoras*, *Acanthodoras* and *Franciscodoras*, the respective character Z will have a CI of 0.33 but a RI of 0.6 (feature Z was independently acquired in three different, non-related groups, i.e. *Lithoxus*, *Paraplotosus*, and the clade *Doras* + *Anadoras* + *Acanthodoras* + *Franciscodoras*; but the character helps to

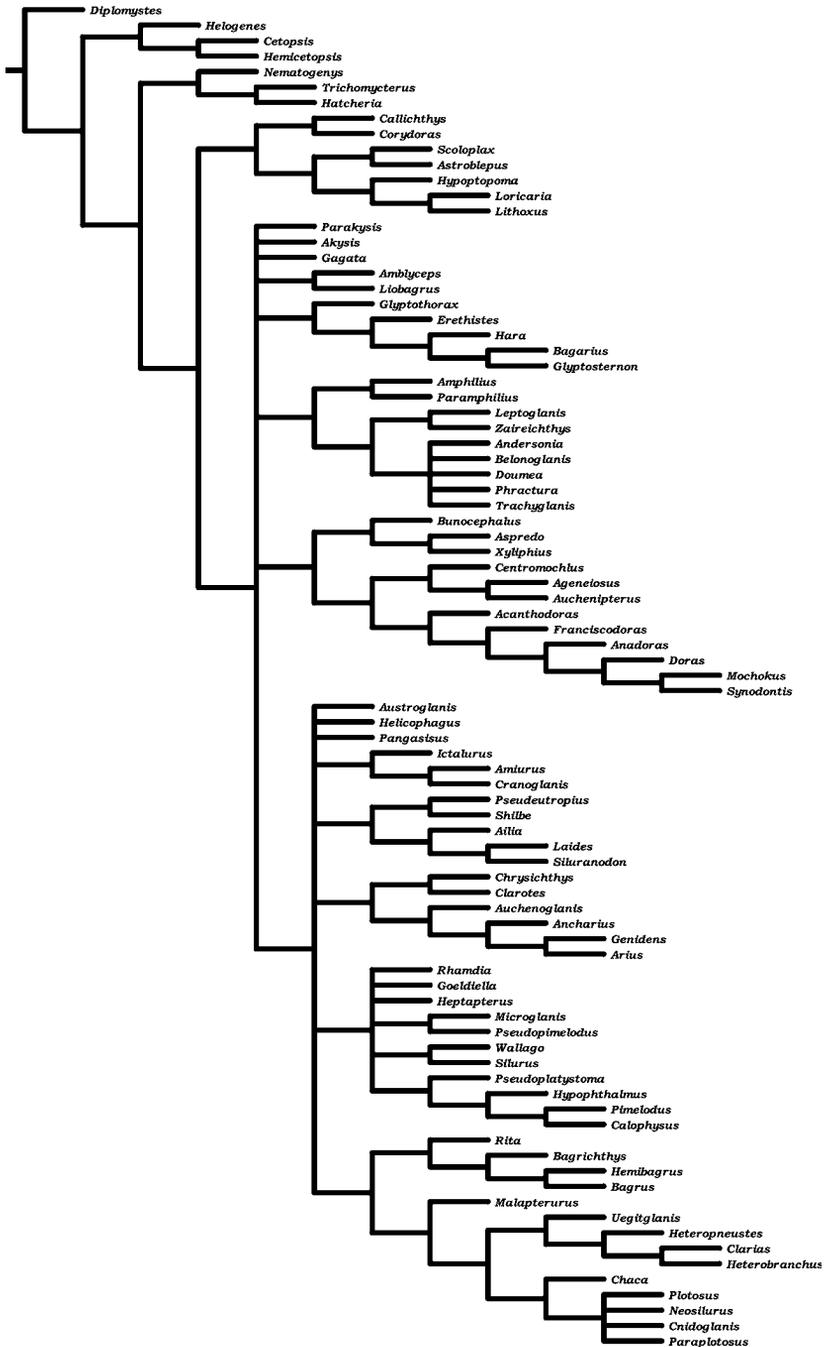


Figure 3. Strict consensus tree of 640 equally parsimonious cladograms obtained from the cladistic analysis of the 91 myological characters used in Diogo's 2004 phylogenetic study (91 characters; 87 terminal taxa; CI = 0.48; RI = 0.81: for more details, see text).

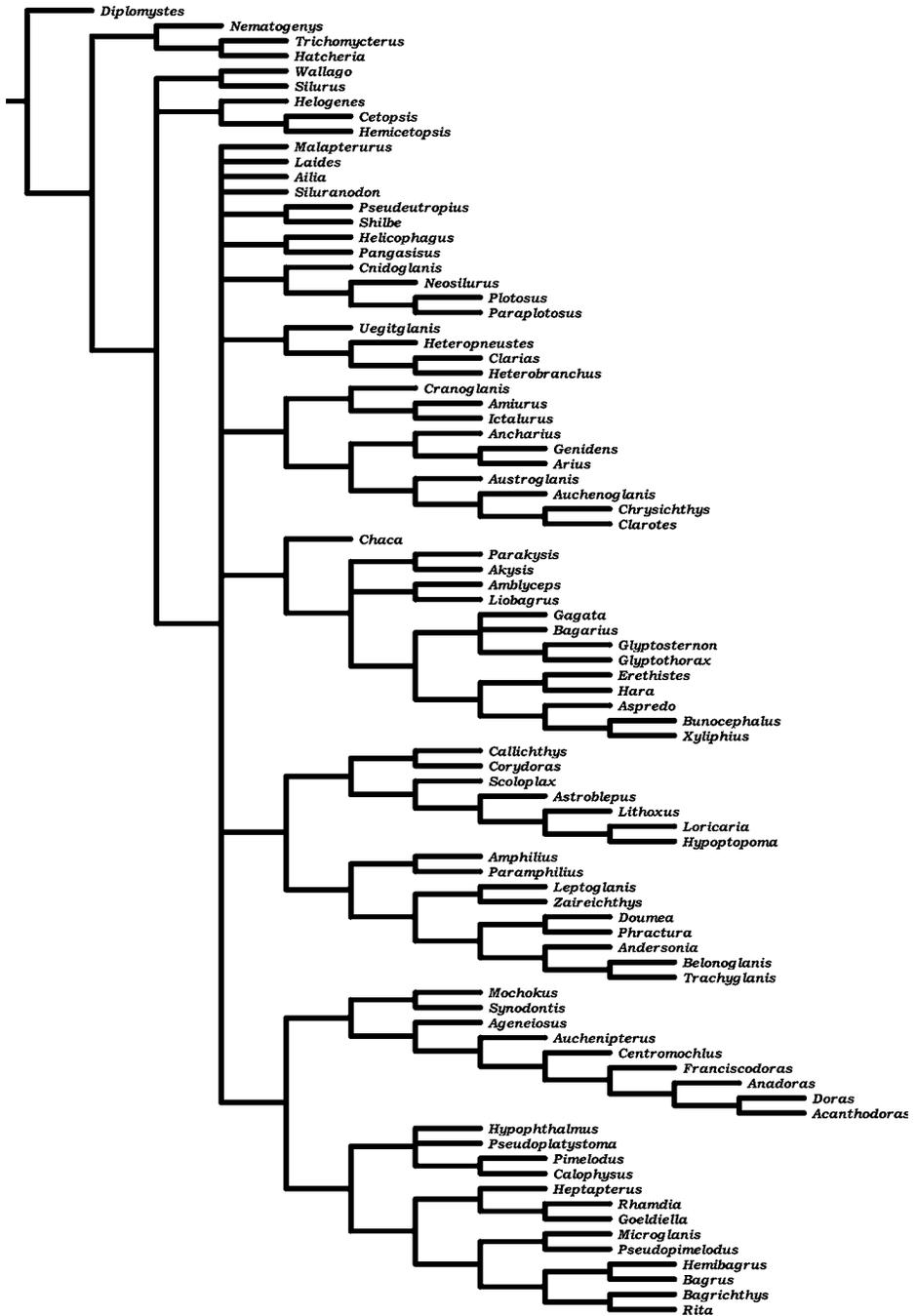


Figure 4. Strict consensus tree of 40 equally parsimonious cladograms obtained from the cladistic analysis of the 303 osteological characters used in Diogo's 2004 phylogenetic study (303 characters; 87 terminal taxa; CI = 0.50; RI = 0.73; for more details, see text).

retain, as a synapomorphy, this last clade in the cladogram) (see fig. 1). Thus, if the mean Retention Index of the myological characters were eventually higher than that of the osteological ones, this would imply that the informative myological characters would behave, in a certain way, more as feature Z than as feature X, i.e., that they would provide more evidence to retain the clades of the cladogram in figure 1.

The overall interpretation of the analysis of tables 1 and 2 thus seems to indicate: (1) osteological structures seemingly display a greater morphological variation than myological ones; (2) this difference (which is very likely overenhanced by the fact that the phylogenetic variation of osteological structures has been historically the subject of many more studies and descriptions than that of myological ones) is particularly notable in low ranking taxa, such as genera; (3) myological characters provide a high proportion of characters able to disclose the relationships between these low rank taxa, and, therefore, the higher-level phylogeny of the group in which these taxa are included.

As explained above, one other way to analyse the phylogenetic contribution of the myological vs. osteological structures examined is simply to compare the phylogenetic trees generated directly from these two different data sets. These trees are shown in figures 3 and 4. Figure 3 illustrates the strict-consensus tree obtained from a cladistic analysis of the 91 myological characters used in Diogo's 2004 work. Figure 4 illustrates the strict consensus tree resulting from the cladistic analysis of the 303 osteological characters used in that work. As can be seen, although the CI of the consensus tree obtained from the muscular characters ($CI = 0.48$) is somewhat smaller than that of the consensus tree based on osteological characters ($CI = 0.50$), the RI of the 'myological' tree ($RI = 0.81$) is considerably higher than that of the 'osteological' tree ($RI = 0.73$). As explained above, the only variable change in this comparison is the number of characters analysed to produce the 'osteological' and 'myological' trees. According to authors such as Sanderson and Donoghue (1989) or Poe (1998), this has very little, if any, influence on the levels of homoplasy being compared, particularly when both data sets have a high number of characters, as is the case in the present study.

The consensus tree obtained from the myological characters (fig. 3) appears strikingly resolved, appearing apparently more congruent, in some cases, than the consensus 'osteological' tree (fig. 4). For example, the loricarioids, a group of catfishes including nematogenyids, trichomycterids, callichthyids, scoloplacids, astroblepids and loricariids (fig. 1: clade number 4) that was supported in a series of phylogenetic studies (Howes, 1983; Schaefer, 1990; Mo, 1991; de Pinna, 1998; Diogo, 2004), although appearing as non-monophyletic, appear in a somewhat similar, and markedly basal position. In the 'osteological' tree the loricarioid callichthyids + scoloplacids + loricariids + astroblepids (clade 8 of fig. 1) appear in a markedly derived position within the Siluriformes, being separated from the nematogenyids + trichomycterids (clade 5 of fig. 1) by the vast majority of the remaining catfish groups (fig. 4). As Loricarioidea monophyly has been supported by several independent studies, in this respect the 'osteological' tree appears less

congruent than the 'myological' one. In fact, it is important to note that it was the muscular characters (fig. 3), but principally the combination of these characters with all the other characters included in the cladistic analysis, that provided evidence for the grouping and the markedly basal position of the Loricarioidea in that analysis (see fig. 1) (Diogo, 2004). This emphasises that the inclusion of muscular characters, and particularly the conjugation of the complementary information provided by these characters and others referring to osteological components or soft tissues (or other anatomical components, whenever possible), allows a much broader, and, very likely, more resolved phylogenetic reconstruction of the relationships between the groups being studied.

The cladogram illustrated in figure 1 based on all the 440 characters is, in fact, significantly more resolved than that one illustrated in figure 4 based exclusively on the 303 osteological characters used in that cladistic analysis. The 'osteological' tree of figure 4 presents a large number of polytomies, particularly of the higher catfish clades, in a similar scenario as that seen on the resulting trees of the cladistic works of Mo (1991) and de Pinna (1998), which were almost exclusively based on osteological characters. In the 'osteological' tree of figure 4 all the extant catfish families except the Diplomystidae, Nematogenyidae, Trichomycteridae, Siluridae and Cetopsidae are included in a largely unresolved polytomy leading to 12 different catfish nodes. In the tree incorporating all 440 characters, almost the totality of the nodes appear resolved, with only three trichotomies being found, of which only one concerns interfamilial nodes (fig. 2).

In agreement with the results of the analysis of tables 1 and 2, the 'osteological' tree of figure 4 only appears more resolved when it refers to lower, less inclusive catfish groups such as genera. For example, the 'myological' tree supports the monophyly of the family Amphiliidae (clade 83 of fig. 1), and even the monophyly, inside this family, of the group constituted by subfamilies Leptoglanidinae + Doumeinae, as suggested by Diogo (2003b) (clade 85 of fig. 1), but it fails to resolve the relationships between the different genera inside the subfamily Doumeinae (clade 87 of fig. 1) (fig. 3, compare with fig. 4).

Another illustration of this concerns the Plotosidae. The 'osteological' tree of figure 4 is much less resolved than the 'myological' one in the interfamilial relationships of the Plotosidae (clade 70 of fig. 1), with this family appearing in one of the 12 nodes of a large polytomy on the 'osteological' tree (fig. 4). The 'myological' tree (fig. 3) supports the close relationship between plotosids, chacids and clariids (clade 64 of fig. 1), as suggested by Diogo et al. (2003). However, the 'osteological' tree is much more resolved with respect to the relationships between the genera of Plotosidae, with the genus *Cnidoglanis* appearing as the sister-group of the clade *Neosilurus* + (*Plotosus* + *Paraplotosus*), as suggested by the 'all evidence' tree shown in figure 1, contrary to what happens in the 'myological' tree where the four plotosid genera appear grouped in an unresolved polytomy (fig. 3, compare with fig. 4).

It is very interesting to note that the 'myological' tree does succeed in exhibiting, in some instances, striking examples of resolution even at the level of certain lower groups. For example, in some cases the relationships inside lower groups appear, on this 'myological tree', as resolved as (Clariidae (clade 67 of fig. 1)), or even more resolved than (Pimelodinae (clade 59 of fig. 1) or Schilbidae (clade 24 of fig. 1)) on the 'osteological' tree (fig. 3, compare with fig. 4).

The overall analysis of the 'myological' and 'osteological' trees thus seems to corroborate the main points of the analysis of tables 1 and 2. The osteological structures seem to display a greater morphological variation than the myological ones, providing more characters for phylogenetic analyses (very likely overenhanced by an historical bias: see above). But this difference refers particularly to low ranking taxa such as genera or species, with the myological characters being highly useful in providing information about the relationships between higher clades, and, thus, to infer the higher level phylogeny of the groups being studied. Some previous studies have also defended the reliability of muscular characters for informing on the higher-level phylogeny of other, non-teleost major groups, such as Aves (McKittrick, 1991), hadrosaurian dinosaurs (Dilkes, 2000), or primate mammals (Shoshani et al., 1996; Collard and Wood, 2000; Gibbs et al., 2000, 2002). However, as explained above, these studies were based on indirect comparisons. For example, the phylogenetic studies on the superfamily Hominoidea based largely on myological characters supported, contrary to those studies based for the most part on osteological characters, the nowadays commonly accepted molecular cladograms indicating a sister-group relationship between the hominin tribes Panini and Hominini and between the clade formed by these two tribes and the subfamily Gorillinae (see Gibbs et al., 2002).

These points raise interesting, general questions. For instance, what can explain the seemingly greater morphological variation of osteological structures? And why is this greater morphological variation of osteological structures in relation to myological structures particularly pronounced in low ranking taxa? Does natural selection eventually act, in certain cases, more on bones than on muscles? Is the development of myological structures more constrained than that of osteological features? Why do muscular structures seem to be particularly reliable in disclosing the higher-level phylogeny of certain major groups? According to Gibbs et al. (2002), for example, one of the reasons to explain the apparently high reliability of muscular characters for disclosing the phylogeny of higher taxa may be related to the results of the experiments that used rhombomere quail-to-chick grafts to investigate the influence of hindbrain segmentation on craniofacial patterning (Köntges and Lumsden, 1996). That experimental study showed that each rhombomeric population remains coherent throughout ontogeny, with rhombomere-specific matching of muscle connective tissue and their attachment sites for all branchial and tongue muscles. As hypothesised by Gibbs et al. (2002: 13) if "a similar system operates elsewhere in the body, it would help explain how muscle gross morphology is conserved, whereas the shapes of the skeletal elements to which the muscles are attached are susceptible to changes that contrive to obscure phylogeny". In fact, at least in teleost fishes,

the principal points of muscular origin and insertion seem to be rather stable, as pointed out by authors such as Takahasi (1925) or Alexander (1965). Another contributory factor (Gibbs et al., 2002: 13) to explain the seemingly high reliability of muscular structures in phylogenetic reconstructions within higher taxa is that these structures “are not as prone to homology as skeletal characters”. As these authors explain, the term homology has been used to refer to shared character states that are phylogenetically misleading and which result from similarities in the way that genotypes interact with the environment. Thus, because bone is a dynamic tissue, “many osseous morphologies would be homologous”, with “homology playing a minor role in the generation of the phenotypes” referring to muscular and soft tissues, since “whereas the mass of a muscle may be affected by activity or inactivity, its attachments are unlikely to be” (Gibbs et al., 2002: 13). However, as is also noted by these authors, homology cannot be the whole explanation for the difference in phylogenetic reliability between osteological and myological structures, since dental enamel, for example, does not remodel and, thus, is not prone to homology. But some authors have suggested that function or developmental constraints may turn tooth morphology to be particularly prone to homoplasy, and, therefore, to be a poor guide to phylogenetic reconstructions (Hartman, 1988; Hunter and Jernvall, 1995; Jernvall, 2000).

The discussions provided in the studies mentioned in the latter paragraphs are based on indirect comparisons, and, therefore, direct comparisons of the homoplasy levels and the reliability of muscular and osteological data for phylogenetic reconstructions such as that provided in the present work are unfortunately lacking. Consequently, such direct comparisons between either other major groups of teleosts or vertebrates in general, are clearly needed to infer if the patterns found in the direct comparison of this work do correspond to a more general phylogenetic pattern, or, instead, refer to a particular situation found in the order Siluriformes, and, thus, to help clarify some of the general questions formulated above. The present study stresses that the inclusion of muscular characters, and particularly the conjugation of the complementary information provided by these and other morphological characters (referring to osteology, to soft structures, etc.), allow much broader and, very likely, more resolved phylogenetic reconstructions. Moreover, the inclusion of myological data on phylogenetic analyses allows a more complete, integrative discussion on the functional aspects and the evolution of the structural complexes being examined, and, thus, on the general macroevolution of the groups under study. Therefore, despite the intrinsic difficulties (i.e. relating to museum availability or the arduousness of muscular dissections, especially on small sized specimens), it is hoped that this work could stimulate zoologists to include myological characters in their phylogenetic reconstructions.

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