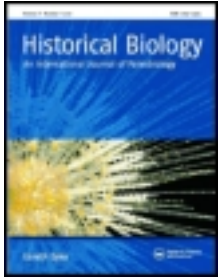


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A species-level supertree of Crocodyliformes

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A species-level supertree of Crocodyliformes

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With fossils found worldwide, Crocodyliformes stands as one of the best documented vertebrates over the Mesozoic and Cenozoic. The multiple phylogenetic hypotheses of relationship proposed for the group allow plenty of space for contentious results, partially due to the small overlapping of taxa and disagreeing homology statements among studies. We present two supertrees of Crocodyliformes, based on different protocols of source tree selection, summarising phylogenetic data for the group into a ‘synthetic consensus’. The consensus of the most parsimonious trees, containing 184 terminal taxa, has a remarkably well-resolved branching structure, which may serve as a framework for further macroevolutionary studies. In addition, the *IterPCR script* was for the first time used in the supertree context to build a reduced consensus tree with the pruning of unstable taxa.

Keywords: Crocodyliformes; phylogeny; supertree; *IterPCR script*

1. Introduction

Along an evolutionary story that spans more than 200 million years, from the Late Triassic to present days, Crocodyliformes occupied many different habitats, encompassing a broad set of morphological and behavioural traits (Clark 1994; Sereno and Larsson 2009). The group stands as one of the better documented in Vertebrate Paleontology (Brochu 2003), but its relationships have been controversial. After pioneering evolutionary works (Buffetaut 1981; Crush 1984; Benton and Clark 1988), Clark (1994) first carried out a numerical phylogenetic analysis including many different Crocodyliformes and a vast array of characters. Several of his results are still accepted nowadays (Sereno and Larsson 2009), including the paraphyletic status of traditional taxa such as ‘Protosuchia’ (Mook 1934) and ‘Mesosuchia’ (Huxley 1875), whereas Eusuchia is consensually accepted as monophyletic (Pol et al. 2009). Despite such a general agreement, the great morphological diversity of basal crocodyliforms, coupled with disagreeing homology statements and ineffective (*sensu* Sanderson et al. 2010) taxa overlapping among different analyses, produced a fruitful ground for discrepant results (Sereno and Larsson 2009). Some of the more noticeable contentious issues include the position of Thalattosuchia as basal mesoeucrocodylians (Young and de Andrade 2009) or basal neosuchians (Pol et al. 2009) and the position of sebecids within Notosuchia (Pol et al. 2009) or Sebecia (Larsson and Sues 2007).

The idea of combining phylogenies in order to obtain a more comprehensive topology comes from pre-

cladistic studies, when research was focused on recovering the ‘Tree of life’ (Bininda-Emonds 2004). Yet, the concept of supertree as currently understood was only formalised by Gordon (1986), and Sanderson et al. (1998) define supertree construction as the generation of one output tree from a subset of source trees with total or partial taxa overlap. More recently, this kind of meta-analysis has been used as a basis for studies in many different areas of biology, from genomics (e.g. Holton and Pisani 2010) to paleontology (e.g. Pisani et al. 2002).

We present here two matrix representations with parsimony (MRP; Baum 1992; Ragan 1992) species-level supertrees of Crocodyliformes, with emphasis on non-Crocodylia (*sensu* Brochu et al. 2009) forms, given that a supertree of Crocodylia was already presented by Gatesy et al. (2004). Although useful as a template for macroevolutionary studies (e.g. Lloyd et al. 2008), the primary application of supertrees is to summarise phylogenetic information in a ‘synthetic consensus’ (*sensu* Ruta et al. 2007), which can be used to evaluate pieces of competing evidence on the position of taxa in different source trees (Ruta et al. 2003; Bininda-Emonds et al. 2004).

In addition, aspects of the broadly used ‘garbage in, garbage out’ protocol (Bininda-Emonds et al. 2004) for source tree collection are discussed, along with its application in the Crocodyliformes supertree, and we propose the use of the *IterPCR script* (Pol and Escapa 2009) in supertree context.

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2. Material and methods

2.1 Source trees

Potential source trees were exhaustively searched on the electronic literature database *Web of Science* (<http://wos.mimas.ac.uk/>), in other Internet databases and search engines (e.g. *Scopus*, *Google*), as well as in the reference lists of all recovered publications. The phylogenetic trees were selected only if derived from numerical phylogenetic analyses with published data matrices. This led to the recovery of source trees ranging from Buscalioni and Sanz (1988) to Smith et al. (2010). The application of the ‘garbage in, garbage out’ protocol to identify only independent trees to compose the matrix resulted in 41 source trees. Yet, the great subjectivity of this protocol encouraged us to build another supertree using a ‘less restricted’ protocol, which resulted in 97 source trees. In this second approach, studies derived from modifications (e.g. new scoring for certain taxa; addition of taxa or characters) of previous data-sets were considered as separate analyses. If the same paper provides two or more different topologies, derived from modifications of the same data-set (e.g. addition or exclusion of taxa, different scoring for given characters), these were all included as separate source trees.

2.2 Replacement of supra-specific terminal taxa in source trees

Higher rank terminal taxa within source trees were standardised by operational taxonomic units at the species rank. In this study, two distinct approaches were taken for the substitution of taxa. Both of which are modifications of the ‘all-encompassing’ substitution of Ruta et al. (2003),

with the replacement taxa incorporated in a polytomic clade. The substitution was carried out only when the inclusiveness of higher taxa was not explicitly provided in the publication.

Genus rank terminal taxa were replaced by all species of that genus included in at least one of the source trees. Yet, the species was only included if proposed at least 1 year prior to the publication of the source tree whose terminal is to be replaced. Due to the instability in Crocodyliformes phylogenetic proposals, substitution of supra-generic terminal taxa includes an additional step. Each of them was replaced by all species included in the taxon in at least one of the source trees, but not explicitly excluded from it in any of the other employed studies (Figure 1).

2.3 In-group selection

Based on the definition/circumscription of Crocodyliformes and Crocodylia used for each source tree, terminal taxa were scored in the supertree data-matrix if unambiguously nested within Crocodyliformes, but not within Crocodylia (Figure 2). Taxa within the crown-group Crocodylia (*sensu* Brochu et al. 2009) were collapsed as a single terminal taxon. In order to circumscribe Crocodylia and Crocodyliformes in publications that do not explicit the circumscription of these taxa, the definitions of Sereno et al. (2001) and Brochu (2003) were, respectively, applied. In addition, for phylogenies that lack the specifiers of the above definitions (e.g. Buscalioni and Sanz 1988; Hastings et al. 2010), the position of the source tree taxa within ‘non-Crocodylia Crocodyliformes’ was accepted following the current knowledge, and the topologies were entirely scored into the data-matrix.

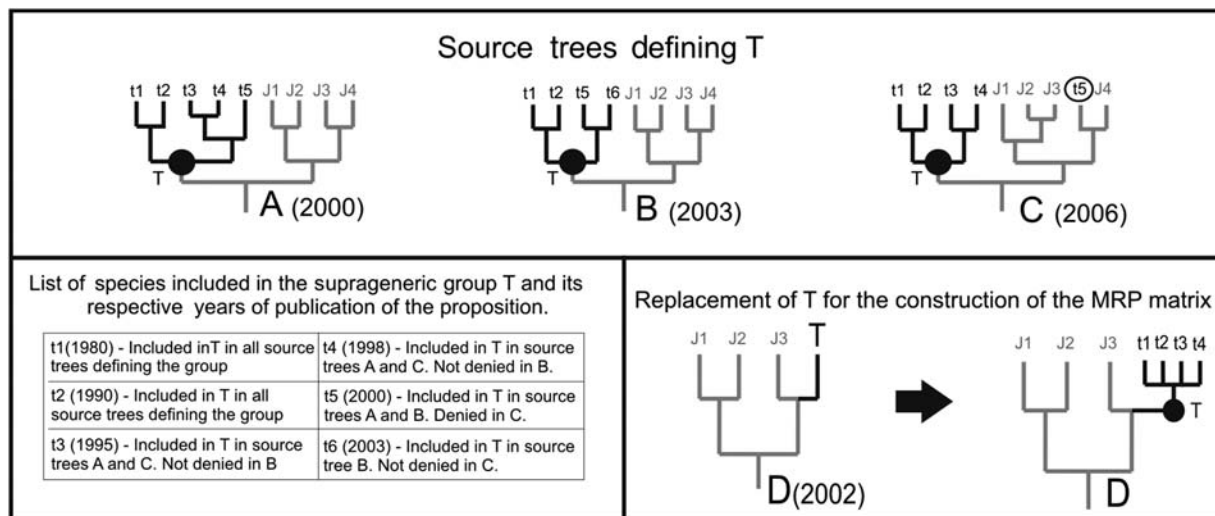


Figure 1. Example of the procedure for the replacement of supra-generic terminal taxa. Step 1: search for species included in the respective supra-generic group (T) in at least one ‘source tree’, but not excluded in any other. Step 2: identify the year of proposition of the previously selected species. Step 3: replace the supra-generic taxon by the species published at least 1 year before the year of publication of the ‘source tree’.

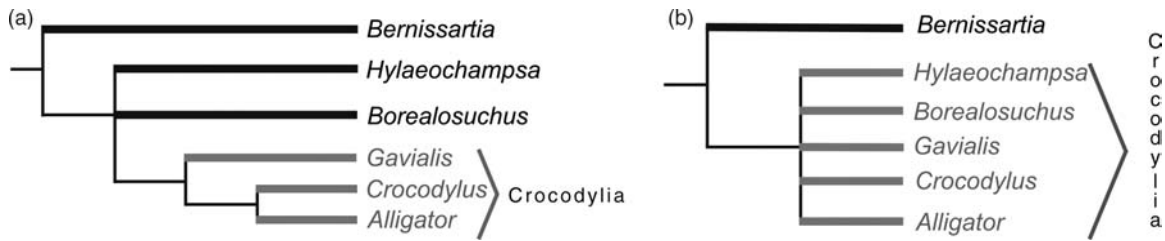


Figure 2. Examples of the procedure for selection of taxa from the source trees. Only taxa (black branches) undoubtedly nested within ‘non-Crocodylia Crocodyliformes’ were included in the MRP data-matrix, whereas the others (grey branches) were replaced by Crocodylia as a terminal taxon. (a) Unambiguous example (modified from Pol and Norell 2004a); (b) ambiguous example (modified from Pol and Norell 2004b), *Hylaeochampsia* and *Borealosuchus* were not selected because they might belong to Crocodylia.

2.4 Data-matrices, numerical and script analyses

The data-matrices were built following the MRP protocol of Baum (1992) and Ragan (1992), and using the software *Mesquite 2.6* for Microsoft Windows (Maddison and Maddison 2009). The data-matrices were exported into the software *TNT 1.1* (Goloboff et al. 2008) and analysed under a heuristic search with 10,000 replicates, ‘hold’ 20, and tree bisection and reconnection (TBR) as the branch swapping algorithm. After the parsimony analysis, the most parsimonious trees (MPTs) resulting from both protocols were analysed using the *IterPCR* script (Pol and Escapa 2009) implemented on *TNT*.

3. Results and discussion

3.1 Source trees selection

Most of phylogenetic analyses of Crocodyliformes are clearly extensions of previous studies (Jouve et al. 2006), with most published character–taxon matrices based on either Clark (1994) or Ortega et al. (2000). Many also use combinations of previous data-sets to compose the matrix.

There is no explicit dependence threshold between analyses, and a strict application of current protocols would neglect a huge amount of data from the MRP matrix. Accordingly, our experience building the Crocodyliformes supertree suggests that the restricted approach towards source tree collection oversimplifies phylogenetic controversies, summarising in few analyses gradients of dependence among source trees. It also ignores reinterpretations of previously published data, ignoring that even if based on related data-sets, each phylogenetic analysis can provide very different results. In any case, it is clear that a more interactive approach to source tree collection for the building of MRP-matrices is needed. This should take into account the peculiarities of each group and, if possible, of each source tree database.

3.2 Structure of the supertree

A total of 722 MPTs of 3380 steps were obtained from the parsimony analysis of the data-matrix derived from the ‘less

restricted’ protocol, whereas the parsimony analysis of the data-matrix derived from the ‘garbage in garbage out protocol’ resulted in 487 MPTs of 1036 steps. The majority-rule consensus of the analyses is presented in Figures 3 and 4, respectively. A similar arrangement of major Crocodyliformes subgroups is seen in both topologies (see Supplementary Materials for more detailed results). *Protosuchus*, *Orthosuchus*, *Hemiprotosuchus*, ‘Kayenta Form’ and *Edentosuchus* form a basal clade as in nearly all recent proposals (Pol and Norell 2004a, 2004b; Jouve et al. 2006), whereas other taxa traditionally regarded as ‘Protosuchia’ are placed as consecutive sister groups of Mesoeucrocodylia. The basal dichotomy of that clade leads to notosuchians and to a lineage including peirosaurids, Mahajangasuchidae (Serenó and Larsson 2009), ‘trematochampsids’ (Buffetaut 1994) and Neosuchia (*sensu* Benton and Clark 1988). Notosuchia includes all the forms originally assigned to the group (Gasparini 1971) as well as Sebecosuchia.

As recovered by Clark (1994), Neosuchia includes a branch of longirostrine forms such as ‘pholidosaurids’, thalattosuchians and dyrosaurids. The former corresponds to a paraphyletic array (Pol and Gasparini 2009) of successive sister groups to the Dyrosauridae clade (Hastings et al. 2010). Goniopholididae fits into the Eusuchia branch, which also includes taxa often nested within the Crocodylia crown-group, such as *Allodaposuchus*, *Borealosuchus*, *Leidyosuchus* and *Pristichampsus*.

The methodology used here (Section 2.3) fails to incorporate all the phylogenetic data available for taxa such as *Kayentasuchus walkeri*. This was originally considered a ‘sphenosuchian’ by Clark and Sues (2002), i.e. outside Crocodyliformes, but regarded as a ‘protosuchian’ Crocodyliformes by Jouve et al. (2006) and Jouve (2009). Following the ‘in-group selection’ procedure, phylogenies that place *K. walkeri* outside Crocodyliformes were not taken into account, and its position in the supertree is biased towards the studies that nest *K. walkeri* within the group. An analogous situation occurs for more apical taxa such as *Borealosuchus* spp., *Leidyosuchus canadensis* and *Pristichampsus vorax* which were already proposed as members of the crown-group Crocodylia (Gatesy et al. 2004). In this case, the supertree is

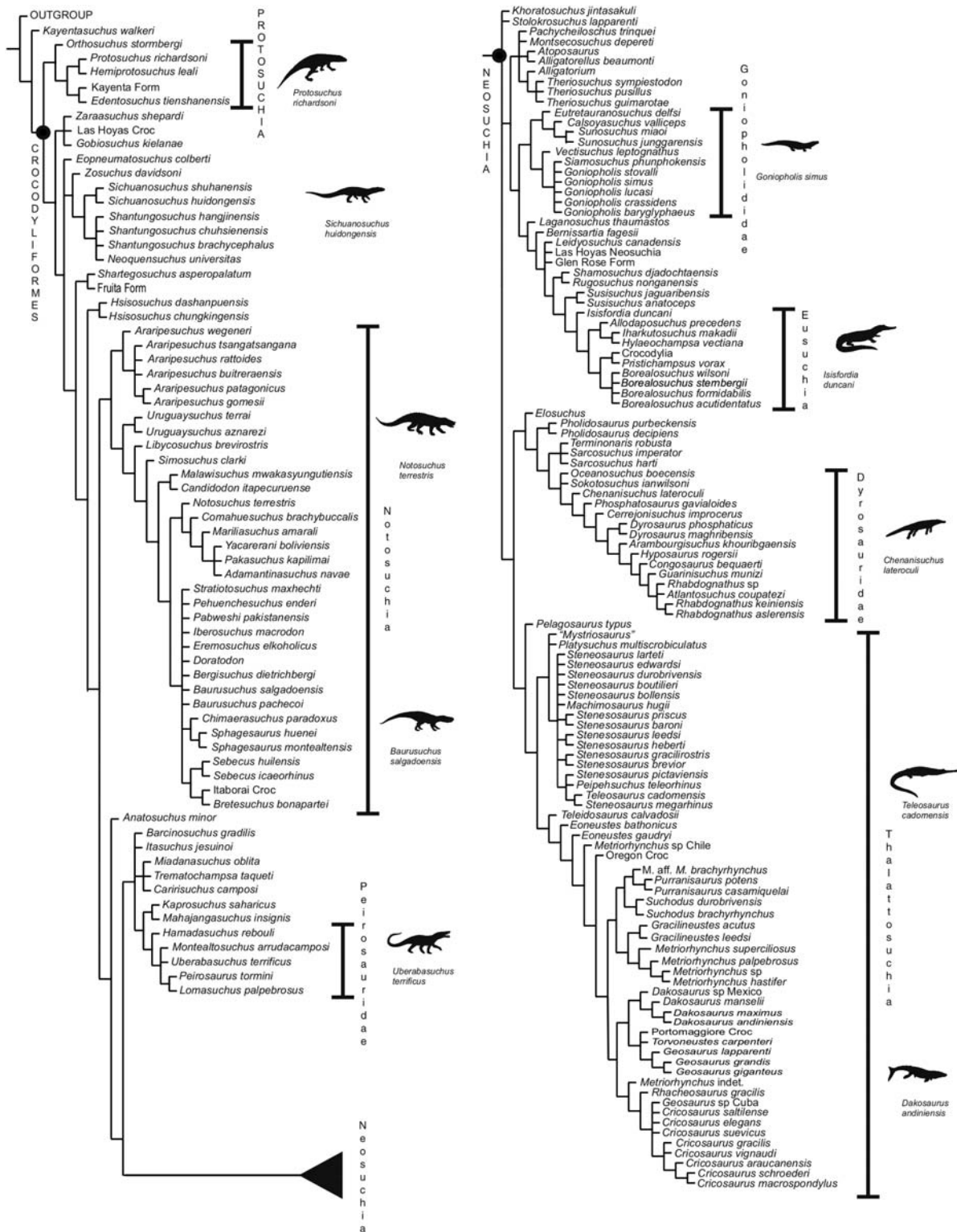


Figure 3. Majority-rule consensus of the 722 MPTs depicting the relationships of Crocodyliformes, derived from a MRP supertree study based on 97 source trees using the ‘less restricted’ protocol in source trees selection from the literature.

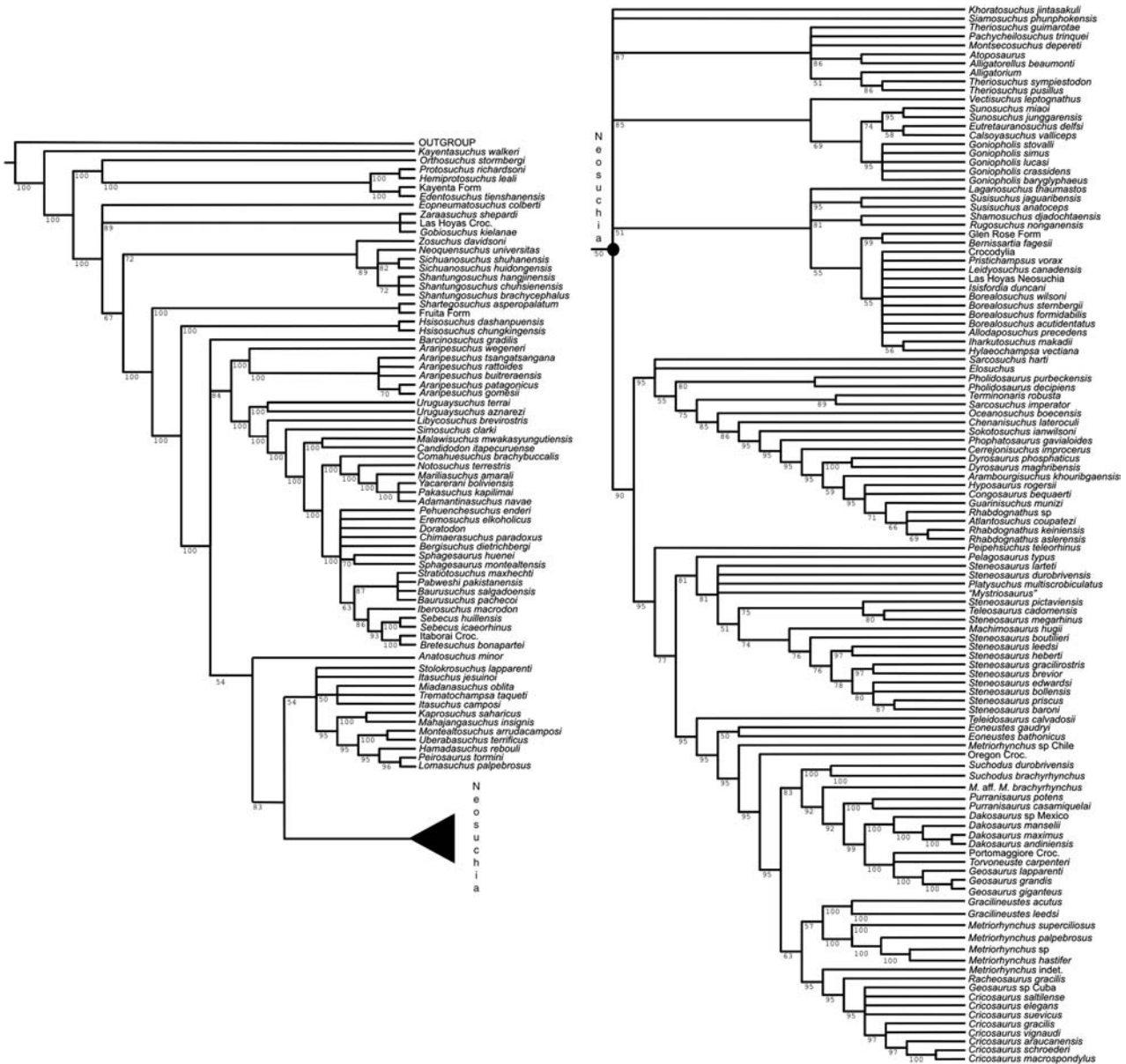


Figure 4. Majority-rule consensus of the 487 MPTs depicting the relationships of Crocodyliformes, derived from a MRP supertree study based on 41 source trees using the ‘garbage in, garbage out’ protocol in source trees selection from the literature.

biased towards studies that exclude them from that clade. Accordingly, only more inclusive supertree analyses (which are beyond the scope of this paper) can comprehensively evaluate the phylogenetic position of those boundary taxa.

3.2.1 Results of IterPCR

Running the *IterPCR script* for the MPTs of the analysis carried out using the ‘less restricted’ protocol shows that 18 taxa are unstable due to the lack of information, and could have their stability increased by scoring missing entries in the matrix. Instead, the instability of three taxa is a result of missing entries plus conflicting ‘characters’, which support

alternative placements for these taxa. From the MPTs obtained in the analysis using the ‘garbage in, garbage out’ protocol, 27 taxa were considered as unstable due to the lack of information in the matrix and 6 because of missing entries plus conflicting ‘characters’ (see Figures 5 and 6 for the list of pruned taxa in both analyses). The *script* detects unstable taxa based on the agreement of triplets within each polytomy of the strict consensus tree. This evaluation is based on an index retrieved by dividing, for each taxon, the number of triplets containing a given hypotheses of relationship by the total number of triplets (Pol and Escapa 2009).

Besides evaluating floating taxa, *IterPCR script* also provides a strict reduced consensus after pruning the most

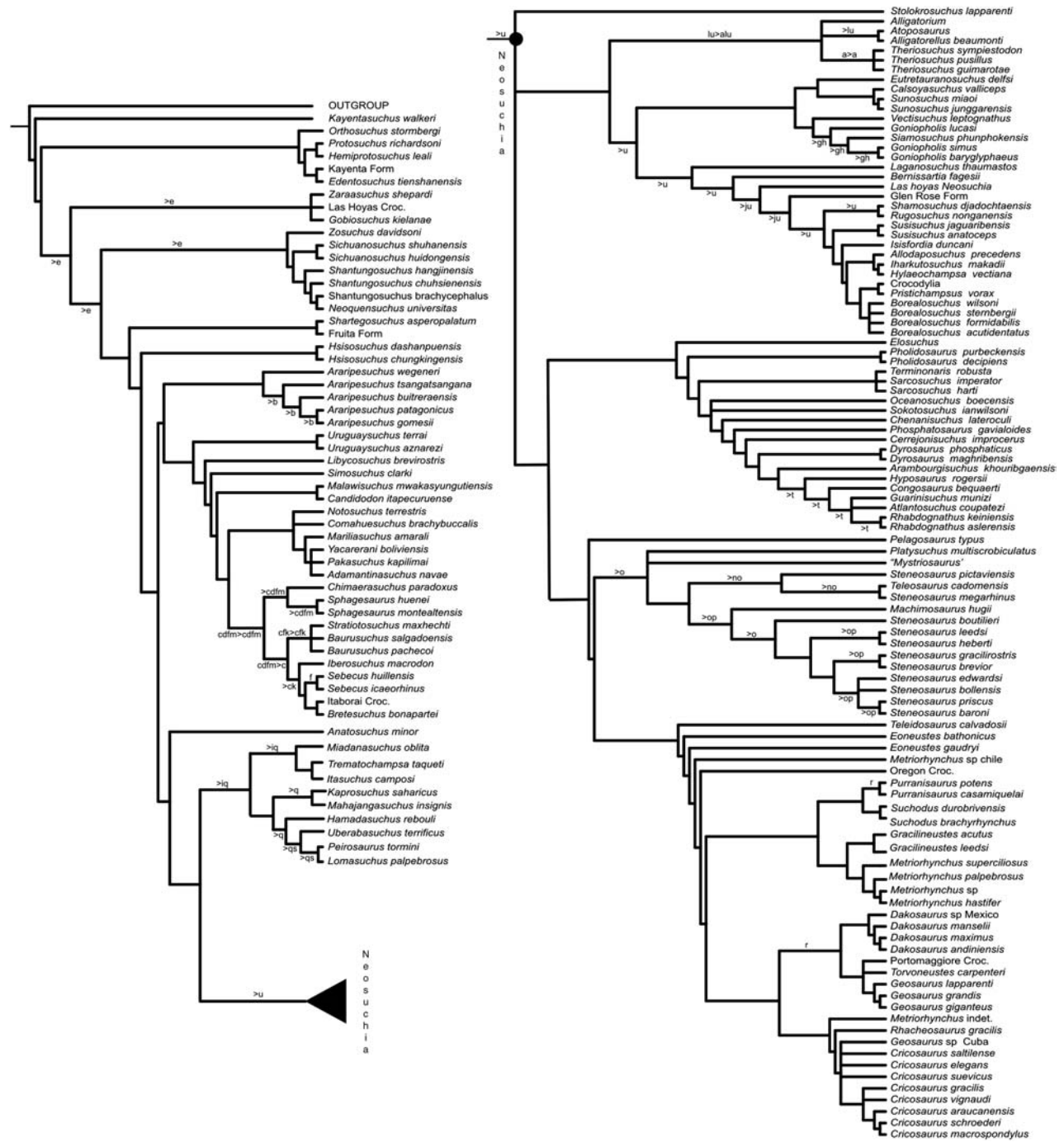


Figure 5. Strict reduced consensus obtained after running the *IterPCR script* in the MPTs derived from the MRP supertree study based on 97 source trees using the 'less restricted' protocol in source trees selection from the literature. The alternative positions of the unstable taxa are indicated in the tree as: a, *Montsecosuchus depereti*; b, *Araripesuchus rattoides*; c, *Bergisuchus dietrichbergi*; d, *Doratodon*; e, *Eopneumatosuchus colberti*; f, *Eremosuchus elkoholicus*; g, *Goniopholis crassidens*; h, *Goniopholis stovalli*; i, *Itasuchus jesuinoi*; j, *L. Canadensis*; k, *Pabweshi pakistanensis*; l, *Pachycheilosuchus trinquei*; m, *Pehuenchesuchus enderi*; n, *Peipehsuchus teleorhinus*; o, *Steneosaurus durobriivensis*; p, *Steneosaurus larteti*; q, *Barcinosuchus gradilis*; r, *Metriorhynchus* aff. *M. brachyrhynchus*; s, *Montealtosuchus arrudacamposi*; t, *Rhabdognathus* sp; u, *Khoratosuchus jintasakuli*.

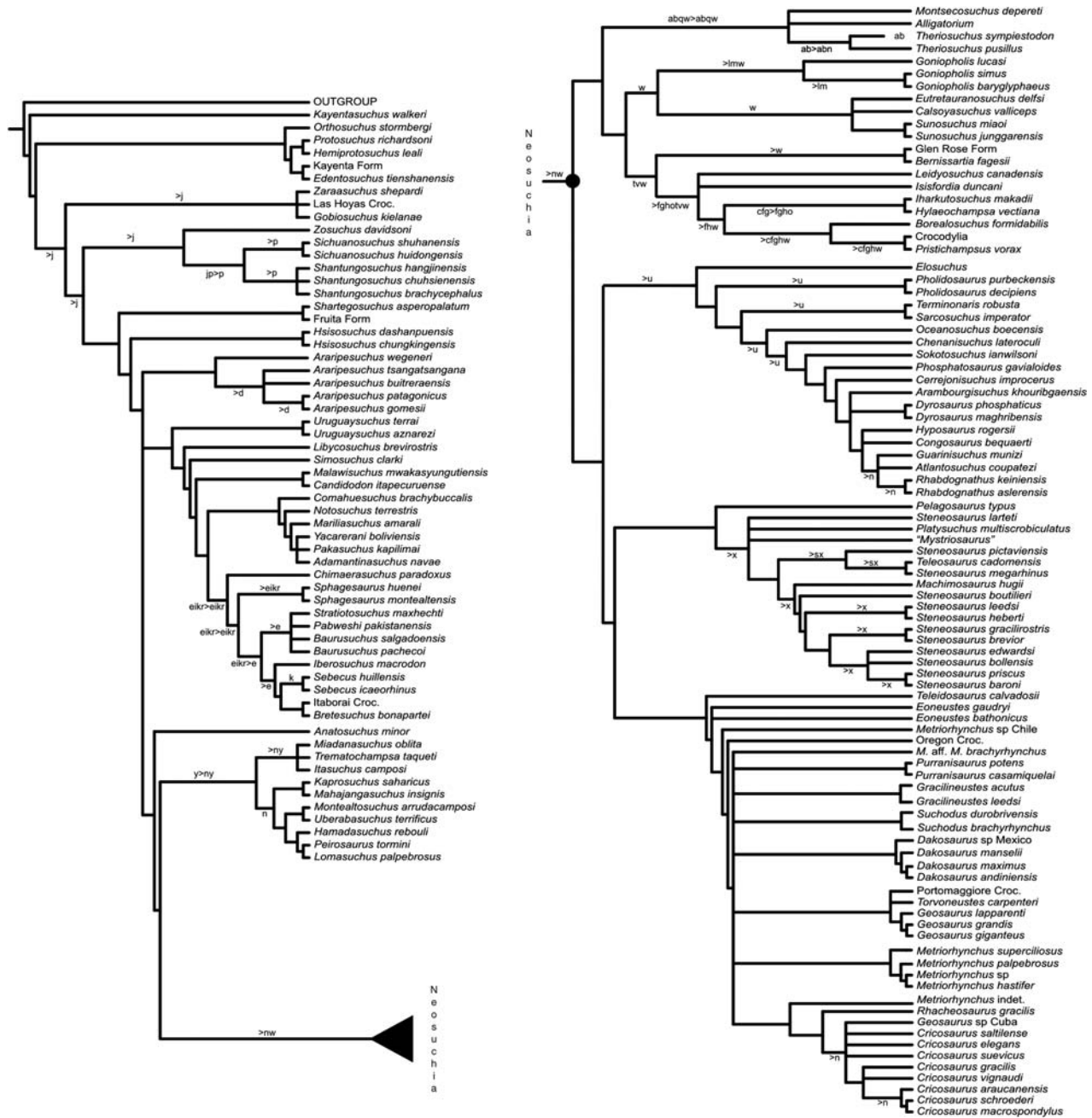


Figure 6. Strict reduced consensus obtained after running the *IterPCR script* in the MPTs derived from the MRP supertree study based on 41 source trees using the ‘garbage in, garbage out’ protocol in source trees selection from the literature. The alternative positions of the unstable taxa are indicated in the tree as: a, *Alligatorellus beaumonti*; b, *Atoposaurus*; c, *Allodaposuchus precedens*; d, *A. rattoides*; e, *B. dietrichbergi*; f, *Borealosuchus acutidentatus*; g, *Borealosuchus sternbergii*; h, *Borealosuchus wilsoni*; i, *Doratodon*; j, *E. colberti*; k, *E. elkoholicus*; l, *G. crassidens*; m, *G. stovalli*; n, *I. jesuinoi*; o, Las Hoyas Neosuchia; p, *Neoquensuchus universitatis*; q, *P. trinquei* r, *P. enderi*; s, *P. teleorhinus*; t, *Rugosuchus nonganensis*; u, *Sarcosuchus harti*; v, *Shamosuchus djadochtaensis*; w, *Siamosuchus phunphokensis*; x, *S. durobrivensis*; y, *Stolokrosuchus lapparenti*. The following taxa were excluded in the reduced strict consensus; however, its alternative positions are not depicted due to limitations of the *IterPCR script*. Nevertheless, it does not affect our conclusions. *Susisuchus anatoceps*; *Susisuchus jaguaribensis*; *Theriosuchus guimarotae*; *Vectisuchus leptognathus*; *B. gradilis*; *Rhabdognathus* sp; *Laganosuchus thaumastos*; *K. jintasakuli*.

unstable taxa. The resulting topologies are presented in Figures 5 and 6, for the analysis with the ‘less restricted’ protocol and for the analysis with the ‘garbage in, garbage out’ protocol, respectively. The reduced consensus trees, which are based on an explicit, non-arbitrary procedure of taxa pruning (see Pol and Escapa 2009), can be very useful for studies (e.g. macroevolutionary, tests of character correlation) that require well-resolved phylogenies.

3.2.2 Use of the *IterPCR* for supertree studies

The *IterPCR* script was developed by Pol and Escapa (2009) in the milieu of primary phylogenetic analyses, aiming at objectively evaluating unstable taxa present in polytomies of the strict consensus trees. In this context, instability is caused either by the lack of information for some taxa or by incongruent scoring of characters. In the supertree context, this happens to taxa not included in some source trees or with variable positions among source trees.

The results of the *IterPCR* script indicate that the instability of taxa in the strict consensus of both Crocodyliformes supertrees is more strongly related to the lack of information for some taxa than to contradictory information present in the data-matrix. Indeed, this even happened to the supertree derived from the analysis with the ‘less restricted’ protocol, which could be biased by data duplication. Although disagreements in homology statements certainly led to conflicting hypotheses of Crocodyliformes relationships (Serenó and Larsson 2009), our results emphasises the problem of ineffective overlapping of taxa between analyses, as also pointed out by Serenó and Larsson (2009).

A potential bias of applying the *IterPCR* script to identify floating taxa due to missing entries is related to the strategy used for replacing supra-specific terminal taxa. It is likely that the substitution procedure adopted here overestimate the content of some higher rank taxa, replacing them by a number of species higher than that actually used in the source studies. Accordingly, some species may not be as well sampled as it appears in the MRP Matrix. It is important to stress that this kind of bias occurs because many works are not explicit about the taxa used in the phylogenetic studies. Accordingly, we recommend future works to emphasise all taxa used to score the matrix. Besides evaluating the major force behind taxa floating in the supertree, the *IterPCR script* also produces a reduced strict consensus, pruning wild card taxa based on a strict methodological approach, which is preferred over an arbitrary pruning.

4. Conclusions

The supertree presented here is based on an explicit and objective procedure and represents an extensive summary

of Crocodyliformes phylogenetic hypotheses accumulated over more than 20 years. The analysis using a ‘less restricted’ approach for source trees selection fulfils the aim of source tree collection (Bininda-Emonds et al. 2004) protocol in the sense that all source trees were explicitly manipulated and the procedures adapted for the Crocodyliformes context. The supertree overcomes the problem of minor taxa overlapping among different source trees, and the extensive use of suprageneric, and even suprafamiliar taxa, in phylogenetic analyses of Crocodyliformes. The large number of source trees scored in the MRP data-matrix allowed the construction of the most comprehensive species-level phylogeny for Crocodyliformes so far, joining information from extensively sampled topologies (e.g. Larsson and Sues 2007; Pol et al. 2009) to those restricted to smaller groups (e.g. Buscalioni and Sanz 1988; Hastings et al. 2010).

Overall, the internal arrangement of the supertrees presented here agrees with the current basic structure of Crocodyliformes relationships. Main contentious issues among earlier studies of Crocodyliformes phylogeny, such the monophyly/paraphyly of Protosuchia, were resolved according to the most recent works (e.g. Jouve 2009; Pol et al. 2009; Serenó and Larsson 2009). At the same time, controversial hypotheses of relationships were corroborated, such as the Neosuchia affinity of Thalattosuchia and the nesting of *Araripesuchus* within a monophyletic Notosuchia. Yet, these results should be taken carefully, given the amount of constantly added new data that could modify this apparently stable scenario (e.g. Turner and Sertich 2010; Andrade et al. 2011). Likewise, current uncertainties, such as the monophyly/paraphyly of Sebecosuchia, were highlighted in the super-tree, suggesting further investigation in the future.

The relatively well-resolved branching structure, which can be used as a framework to trace the grand morphologic diversity of Crocodyliformes on the extensive temporal range of the group, allows supplementary macroevolutionary studies. In addition, *IterPCR* script allows recognition of the causes behind taxa instability in supertrees, and with additional empirical studies it can become a valid phylogenetic tool not only for primary morphological analysis but also for supertrees.

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