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Biogeography on the early distribution of cuckoos (Aves: Cuculiformes)

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ABSTRACT. Cuckoos are widely distributed, but are concentrated in the tropics, where they occupy a wide range of habitats. Both terrestrial and arboreal behaviors can be found in this group, but there is no consensus on as to whether these behaviors have arisen more than once. Moreover, the historical distribution of cuckoos is poorly understood. This paper presents a biogeographyc analysis of the early history of the distribution of these birds. The analysis was performed by using the Principle of Parsimony based on primary and secondary "Brooks Parsimony Analysis" (BPA). Despite some exceptions, the primary BPA corroborated events of vicariance (general pattern) in the early distribution of cuckoos and a terrestrial ancestor widespread in the Gondwana. The most parsimonious hypothesis suggests that the distribution of terrestrial cuckoos (basal group) is associated with the break-up of the Gondwana (Early to Mid Cretaceous), consistent with molecular data for other living birds. On the other hand, the fossil records indicate a more recent origin (Paleocene to Upper Tertiary) in the Laurasia. Nevertheless, to corroborate the fossil records, the early distribution of cuckoos would not be explained by parsimony, since additional steps on dispersion and local extinctions should be added. In addition, according to the secondary BPA, most exceptions can be explained by dispersion as the origin of the arboreal cuckoos (derived group) in South America, where they dispersed to other continents.

KEY WORDS. Parsimony analysis; BPA; Cuculidae; Evolution.

The striking heterogeneity of the cuckoos in terms of morphology, behavior and DNA structure results from a long evolutionary history and a broad geographic distribution (Sibley & Ahquist 1990, Woodbury 1998). Terrestrial cuckoos are generally considered to be the oldest (Hughes 2000, Payne 2005, Posso & Donatelli 2006), occurring in the Neotropics (Crotophaginae, Neomorphinae), Africa, Madagascar and South Asia (Centropodinae). The arboreal cuckoos (Cuculinae, Coccyzinae, Phaenicophaeinae) are cosmopolitan, but are concentrated in the tropics (Payne 1997 2005).

Cuckoos are well known because of their eccentric reproductive behaviors, as brood parasitism and cooperative breeding, and also their terrestrial and arboreal habits (Payne 2005). However, despite the increased systematic research on them in recent decades (Sibley & Ahlquist 1990, Aragón *et al.* 1999, Hughes 1996, 2000, Johnson *et al.* 2000, Posso & Donatelli 2001, 2006, Sorenson & Payne 2005), there is still no agreement on whether terrestrial and arboreal habits emerged more than once among cuckoos.

Moreover, there are no biogeography studies from which to withdraw the historical distribution of cuckoos with reasonable confidence. Cracraft (1973) notes that little is known about the distribution of cuckoos, given the large geographic area over which its members are distributed. An additional problem is the small number of fossil remains and their controversial nature (Olson 1985). Most have been dated to the Upper Tertiary and point to an origin in Laurasia (Feduccia 1996). On the other hand, the oldest is dated to the Paleocene in South America (Baird & Vickers-Rich 1997).

Thus, we set out to perform a biogeography analysis adopting a hypothetical-deductive approach (BPA) to reconstruct some hypotheses about the early historical distribution of the cuckoos.

MATERIAL AND METHODS

We used the classification proposed by Payne (1997), except for the positions of *Coua* Linnaeus, 1766 and *Carpococcyx* Temminck, 1832, which were placed in Couinae (Fig. 1), *Tapera* Linnaeus, 1766 and *Dromococcyx* Wied, 1832 placed in Taperinae, and the *Coccyzus* Vieillot, 1816 placed in Cuculinae, based on the phylogenetic analysis performed by Posso & Donatelli (2006).

We adopted the BPA ("Brooks Parsimony Analysis") *sensu* Wiley (1988a, b) and Brooks *et al.* (2001) for the biogeography analysis. The reasons for choosing BPA are the following: a) it does not permit modifications in the cladogram of taxa (hypothesis "0" *sensu* Wiley 1988b) and absent areas are considered as non-informative; b) it is *a posteriori* method, i.e., it considers the Principle of Parsimony to find the most probably hypothesis, just after the establishment of the taxa/area cladogram (Brooks *et al.* 2001); c) it comprises a hypothetical-deductive model rather than an inductive reasoning for analysis in biogeography; d) it provides a complex of speciation, dispersal and extinction events without removing or modifying data included from previous phylogenies, at least three clades were analyzed simultaneously. This simultaneous analysis can provide a distinction between general and specific elements of distribution; e) it adoptes the cladistics biogeography paradigm, where both disjunct distribution of endemic most related taxa and the most parsimonious topologies of area/taxa cladograms are considered to perform biogeographical approaches; f) it follows the Popperian Principle of Falsification, since it only infers about dispersion or extinction after the test of falsification of both. Episodes of extinction do not provide distortion in a hypothesis of simple vicariance and the lack of evidence can never confirm or falsify a hypothesis.

The most parsimonious cladograms were obtained by using the PAUP 4.0b10 version (Swofford 2001). The DELTRAN was adopted for character optimization in order to minimize the numbers of reversals, as recommended by Wiley (1988b).

The cladograms of Posso & Donatelli (2006) (Fig. 1) and Cracraft (2001) (Fig. 2) were used as basis for the taxa cladogram and the cladogram area, respectively. However, in the cladogram area, the Australian and Antarctic were omitted to simplify the analysis.

In addition, we did not make any inference about the cladogenesis among Neomorphinae, Crotophaginae and Taperinae in South America. We considered their distribution in a single event in order to make the explanation shorter in the analysis of historical biogeography. This exception demands further explanations in future papers.

RESULTS

Data matrix to the primary BPA is found in the table I and the primary most parsimonious taxa/area cladogram in the figure 2.

Data matrix to the secondary BPA included 17 characters (Tab. II). According to the matrix (Tab. II) and the taxa/area cladogram (Fig. 3), South America was considered as only two reticulated area. It regards to the fact that Neomorphinae, Crotophaginae and Taperinae are basal taxa of the 13, 14 and 15 internodes (Fig. 3). Hence, the analysis was simplified by considering them a single area and omitting the events of speciation in South America.

Table I. Matrix listing the geographical distribution of cuckoos subfamilies, along with the binary codes representing the phylogenetic relationships among the subfamilies.

Area	Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Southeast Asia	1, 3, 7, 9	1	0	1	0	0	0	1	0	1	1	1	0	0	0	0	0	0
Madagascar	2,3	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Africa	3, 7, 9	0	0	1	0	0	0	1	0	1	1	0	1	1	1	1	1	1
South America	4, 5, 6, 8	0	0	0	1	1	1	0	1	0	1	0	1	1	1	1	1	1

Table II. Matrix listing the geographical distribution of cuckoos subfamilies, along with the binary codes representing the phylogenetic relationships among the subfamilies. The areas were considered reticulated.

Area	Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Southeast Asia 1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Southeast Asia 2	3	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Southeast Asia 3	7	0	0	0	0	0	0	1	0	0	1	0	1	1	1	1	1	0
Southeast Asia 4	9	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1
Madagascar 1	2	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Madagascar 2	3	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Africa 1	3	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Africa 2	7	0	0	0	0	0	0	1	0	0	1	0	1	1	1	1	1	0
Africa 3	9	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1
South America 1	4, 5, 6	0	0	0	1	1	1	0	0	0	1	0	1	1	1	1	0	0
South America 2	8	0	0	0	0	0	0	0	1	0	1	0	1	1	1	1	1	1

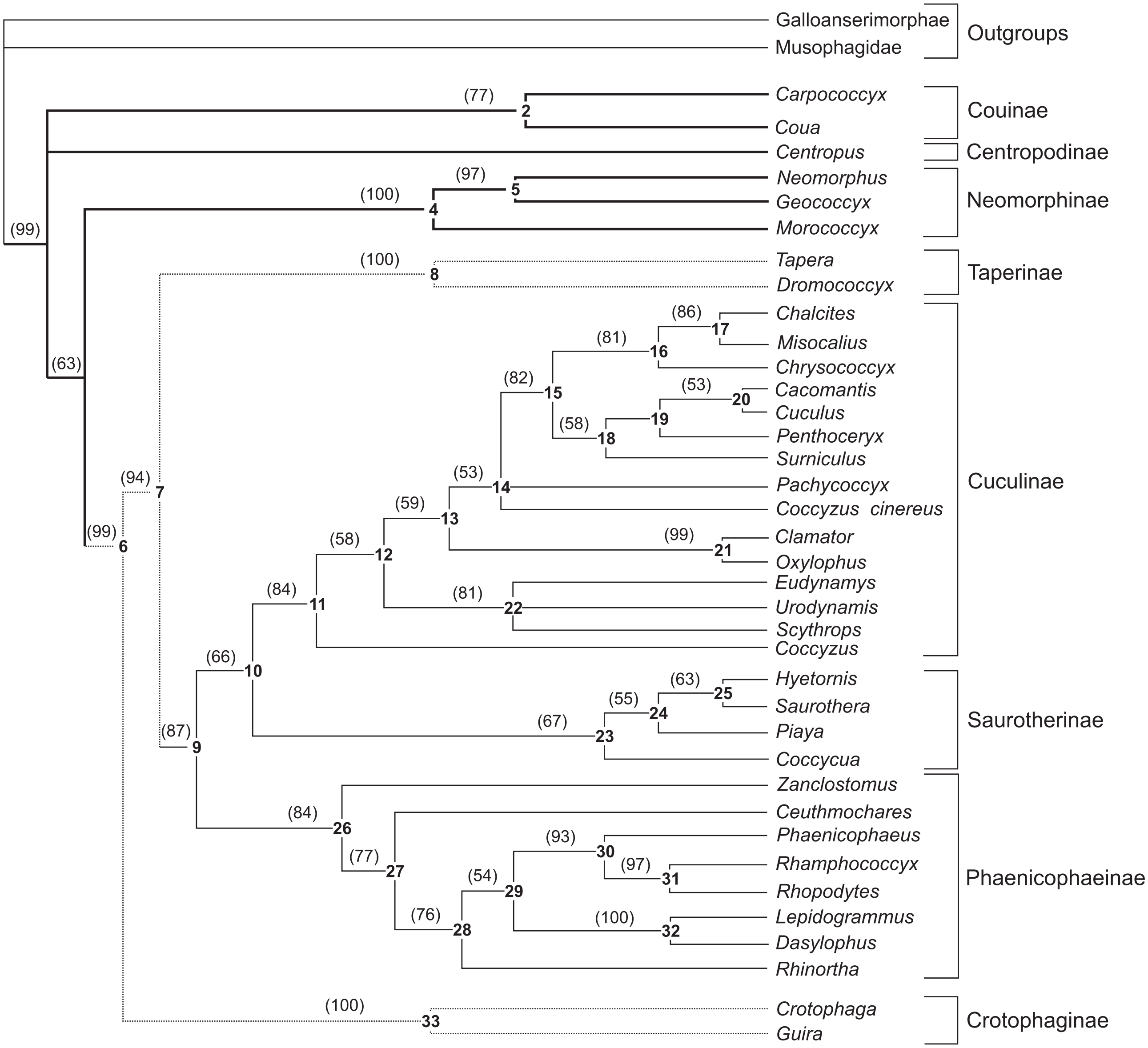

Figure. 1. Strict consensus cladogram (Posso & Donatelli 2006). 1-33: internodes; (51-100): percentages of Bootstrap analysis; spotted lines: terrestrial/arboreal habits; thick lines: terrestrial cuckoos; thin lines: arboreal cuckoos.

The secondary most parsimonious taxa/area cladogram is shown in figure 3.

By superimposing the taxa and area cladograms (Figs 1-3), it can be seen that vicariance is the most parsimonious distribution hypothesis for the early evolution of cuckoos. Moreover, the vicariant hypothesis indicates that the initial distribution of cuckoos is explained by the disruption of Gondwana at the Early Cretaceous (Figs 4 and 5). The exceptions are discussed below.

DISCUSSION

The early distribution of cuckoos: The Gondwanan origin?

Some patterns of Gondwanan distribution have been suggested for many avian groups (Cracraft 2001), including the most derived birds, the passerines (Ericson *et al.* 2002). Cracraft (2001) argued that the biogeography of many groups of Neoaves could be explained in terms of Gondwanan pat-

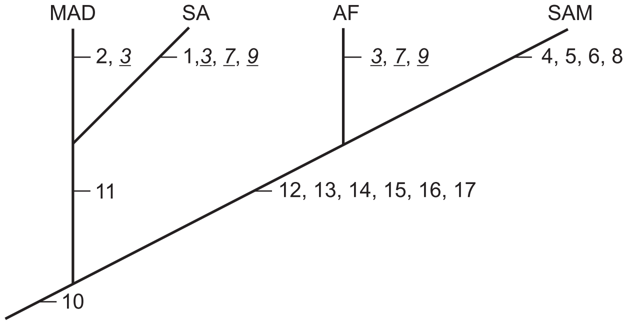

Figure 2. Cladogram presenting the general pattern of distribution among cuckoos subfamilies and Gondwanaland areas (*sensu* Cracraft 2001), except for Australia and Antarctic. (AF) Africa, (MAD) Madagascar, (SA) Southeast Asia, (SAM) South America, (1) *Carpococcyx*, (2) *Coua*, (3) *Centropus*, (4) Neomorphinae, (5) Crotophaginae, (6) Taperinae, (7) Phaenicophaeinae, (8) Saurotherinae, (9) Cuculinae, (10-17) arbitrary numbers showing the relationships among taxa. The numbers in italic and underlined represent the homoplasies.

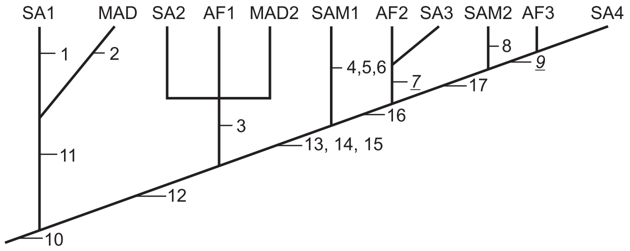

Figure 3. Taxa/area cladogram presenting the general pattern of distribution among cuckoos subfamilies and reticulated Gondwanaland areas, except for Australia and Antarctic. (AF) Africa, (MAD) Madagascar, (SA) Southeast Asia, (SAM) South America, (1) *Carpococcyx*, (2) *Coua*, (3) *Centropus*, (4) Neomorphinae, (5) Crotophaginae, (6) Taperinae, (7) Phaenicophaeinae, (8) Saurotherinae, (9) Cuculinae, (10-17) arbitrary numbers showing the relationships among taxa. The numbers in italic and underlined represent the homoplasies where areas duplications are required.

terns. He did not mention cuckoos, in a previous study however, he suggested same patterns of such origin for cuckoos (Cracraft 1973).

The hypothesis regarding the distribution of cuckoos presented here corroborates the vicariance patterns for Neoaves suggested by Cracraft (2001). The parsimonious hypothesis means cuckoos first emerged in Gondwana, a conclusion reinforced by: a) the endemism of their probable closest relatives – *Opisthocomus hoazin* (Statius Müller, 1776) (Opisthocomidae) in South America and turacos (Musophagidae), in Africa (Hughes & Baker 1999, Hughes 2000, Livezey & Zusi 2001); b) most basal cuckoos (terrestrial) are distributed in the Gondwanan components (Sorenson & Payne 2005, Posso & Donatelli 2006).

Although Hughes (2000) did not use a methodology capable of testing biogeographic patterns, she suggested that the distribution of cuckoos reflects dispersion long after the break-up of Gondwana. However, given that most basal cuckoos analyzed biogeographically in this study are largely terrestrial or weak fliers at best, in theory, they cannot cover medium and long distances such as crossing the Atlantic. Moreover, these cuckoos are not adapted to polar climates (Norris & Elder 1982), as evidenced by the fact that their current distribution is concentrated in the tropics (Payne 2005). Thus a transition via the North Pole (sensu Hughes 2000) is improbable. Considering these premises, it is difficult to sustain the hypothesis of transatlantic migration by cuckoos from the Old to the New World or migration via the Bering Strait indeed (*sensu* Hughes 2000).

Except for Sorenson & Payne (2005), the Couinae (Fig. 1, internode 2), shows several plesiomorphic characters (Posso & Donatelli 2006), generally recognized as most basal cuckoos (Hughes 1996, 2000, Johnson *et al.* 2000, Posso & Donatelli 2006). Taxa/area cladogram suggests that this group occupied the northeast of Gondwana and its taxa separated when this part of Gondwanan mass broke up to form what is now Madagascar (*Coua*) and Southeast Asia (*Carpococcyx*) – to which Gondwanan origin is widely acknowledged for (Archbold *et al.* 1982, Audley-Charles 1984).

According to the BPA, others ancestor cuckoos split apart from *Carpococcyx* and *Coua* ancestors during the separation of Africa/South America from Madagascar/Southeast Asia, about 100 million years ago (m.y.a.) (Cracraft 2001). Moreover, the *Centropus* Illiger, 1811 (Centropodinae) ancestor, whose probable origin is Africa, split apart from the ancestor of Neomorphinae, Crotophaginae and arboreal cuckoos by the break up between Africa and South America, about 80 m.y.a. (Cracraft 2001).

One of the exceptions for the vicariance distribution is that *Centropus* is a widespread genus. While some species of *Centropus* are found in Africa, other species inhabit the entire southern portion of Asia and northern Australia and one species, *Centropus toulou* (Statius Muller, 1776), is found in Madagascar (Payne 1997). According to the secondary BPA, the most parsimonious hypothesis required to explain their current distribution is the dispersion across a continuous landmass (Africa-Asia). Such fact is also supported considering that most basal *Centropus* species (terrestrial) are endemic in Africa and derived species (arboreal) in the Southeast of Asia e North of Australia (Payne 1997). The vicariant hypothesis also suggests that the *C. toulou* transition from Africa to Madagascar occurred by dispersion across some islands between these two areas long after the break-up of Gondwana.

In any event, the parsimony suggests that the initial distribution of cuckoos took place about 100 m.y.a., dating from the probable break-up of Gondwana (Cracraft 2001). Johnson *et al.* (2000) compared molecular differentiation patterns in species of *Coua* with those of other cuckoos and other bird species. They concluded that *Coua* was the most basal of the cuckoos analyzed (*Centropus* and *Carpococcyx* are missing in their analysis) and had diverged from other cuckoos a long time ago. Moreover, while comparative studies of skulls of arboreal cuckoos (Coccyzinae, Cuculinae, Phaenicophaeinae) show little difference between the skulls of congeneric species (Posso & Donatelli 2006), the species of *Coua*, *Carpococcyx* and *Centropus* show conspicuous skull variation, as well as most species diversity when compared with other cuckoo genera.

According to Brooks *et al.* (2001), any different hypothesis of taxa relationships could falsify the results from an analysis in biogeography. So we compare the phylogenies performed within cuckoos among each other, looking for differences between cladogram topologies.

One of the few differences between molecular (Sibley & Ahlquist 1990, Aragón *et al.* 1999, Sorenson & Payne 2005) and morphological data (Posso & Donatelli 2006) refers to the relationships between terrestrial cuckoos. In molecular studies, Crotophaginae is the most close related with terrestrial cuckoos and *Tapera* and *Dromococcyx* are considered in the Neomorphinae. However, even in these cases, the vicariance is still the most parsimonious hypothesis from the Gondwana rupture. It only modifies the interpretation of same origin among Crotophaginae, Taperinae and arboreal cuckoos (Phaenicophaeinae, Saurotherinae e Cuculinae) in South America. The explanation for it would be the two distinct events of cladogenesis: one giving arises to Neomorphinae, Crotophaginae and Taperinae and other to the arboreal cuckoos. The number of steps (3) and the origin (South America) would be the same.

Except for Cuculinae and Crotophaginae, the monophyly of each subfamily of cuckoos (*sensu* Payne 1997) is not supported. The strict consensus cladogram from Posso & Donatelli (2006) diverges from the molecular data of Sorenson & Payne (2005), and osteological data from Hughes (2000) also concerning the controversy regarding Taperinae position (Posso & Donatelli 2010). Phylogenetic studies (Sibley & Ahlquist 1990, Aragón *et al.* 1999, Sorenson & Payne 2005) alternatively indicate them to be the most close related to Neomorphinae. But even if in this case the hypothesis of distribution by vicariance is more parsimonious, and also we are not considering the cladogenesis events of Neotropical cuckoos that took place in South America.

Another alternative hypothesis can be found in the ambiguous relationships of *Centropus* (Fig. 1). In some equally most parsimonious trees, *Centropus* is more closely related to the Neomorphinae, Crotophaginae and arboreal cuckoos (Hughes 2000, Posso & Donatelli 2010). On the other hand, some trees indicate *Centropus* to be close related to Couinae (Posso & Donatelli 2010), as in Sibley & Ahlquist (1990) and Sorenson & Payne (2005). We considered *Centropus* more close related to Neomorphinae, Crotophaginae and arboreal cuckoos, since it is the most parsimonious hypothesis: a) the same historical biogeography between these taxa and the areas evolved (Africa and South America) and b) the basal *Centropus* species (terrestrial) are found in Africa. However, even if *Centropus* is considered to be close to Couinae, there is not any modification in the hypothesis of distribution by vicariance. In this case, itcould only be interpreted that alternatively *Centropus* would have splitted from the Couinae in Southeast Asia and it would have dispersed to Africa afterwards.

In synthesis, the alternative phylogenetic hypotheses from literature do not refute the distribution by vicariance in the early evolution of cuckoos. However, it is strongly suggested that the matter requires alternative hypotheses of distribution in some particular groups without any additional steps, as mentioned above.

Hypothetical ancestor and the early age of cuckoos

The evidence of molecular data (Sibley & Ahlquist 1990, Hedges *et al.* 1996, Cooper & Penny 1997, Van Tuinen *et al.* 2000, van Tuinen & Hedges 2001, Cooper *et al.* 2001, Ericson *et al.* 2002) suggests that main bird groups existing today separated in the Cretaceous, i.e., a longer time ago than indicated by the fossil record (Tertiary). Johnson *et al.* (2000) analyzed patterns of molecular differentiation between cuckoos and other birds, and came to the conclusion that cuckoos are among the oldest bird groups alive today, as also found by Woodbury (1998). Payne (2005) analyzed the parameters used by several authors to estimate the age of cuckoos and did not rule out the possibility that the ancestor cuckoos lived during the Cretaceous.

The vicariance hypothesis and the basal terrestrial habit suggest that the cuckoos ancestor was terrestrial and widely distributed throughout Gondwana, where the group cladogeneses began some 100 m.y.a. This age is in agreement with molecular studies that pointed out Gondwanan as origin of modern birds, suggesting that extant avian orders diverged in the Early-Mid Cretaceous (Sibley & Ahlquist 1990, Hedges *et al.* 1996, Cooper & Penny 1997, van Tuinen *et al.* 2000, van Tuinen & Hedges 2001, Cooper *et al.* 2001, Ericson *et al.* 2002).

The fact that no bird fossils are known in the Cretaceuos would be an evidence of a very young age for this group. However, the fossil record just tells us about minimal age (Heads 2012). In fact, the palaeontological, molecular and biogeographic studies indicate an earlier, Cretaceous diversification of bird lineages (Hedges *et al.* 1996). These results mean that the birds are older than indicated by fossil records. Most notably, Ericson *et al.* (2002) hypothesis supports a Gondwanan origin and early radiation of a derived group of birds, the New Zealand wrens (Acanthisittidae), a sister taxa to all other extant passerines. They proposed that these birds were isolated when New Zealand separated from Gondwana (82-85 m.y.a.).

In addition, the new molecular and cladistic biogeography evidences emphasize the major gaps in the fossil record. Acctually, fossil records may erroneously point to an origin in

Laurasia (Feduccia 1996). According to Cracraft (2001), inferences based on the fossil record indicating that certain groups of birds originated in Laurasia may be mistaken, owing above all to the fact that fossils in the southern hemisphere have been insufficiently recorded or their significance has been underestimated. It seems to happen within the cuckoos, except for the oldest fossil record from the Late Paleocene of Brazil (Baird & Vickers-Rich 1997).

Early history of distribution of New World cuckoos: South America as cradle of arboreal cuckoos?

According to BPA hypothesis, terrestrial cuckoos of the Neotropics (Neomorphinae) and the intermediate terrestrial/arboreal Taperinae and Crotophaginae inhabited the western portion of Gondwana and separated from other terrestrial cuckoos when Africa and South America split apart (Figs 4 and 5). The osteological data indicate major variations among genera in each subfamily that can be indicative of a long history of cladogenesis (Posso & Donatelli 2006). In addition, the phylogenetic analysis based on morphological, ecological and behavioral characters (Posso & Donatelli 2006) shows parsimonious hypotheses for the evolution of the following behaviors: a) the terrestrial habit is basal and emerged only once in cuckoo; b) it provides strong support to demonstrate the transition of terrestrial to arboreal to be considered Crotophaginae and Taperinae (Neotropical cuckoos) as intermediary groups between terrestrial and arboreal cuckoos. Other studies (Sibley & Ahlquist 1990, Aragón *et al.* 1999, Hughes 1996, 2000, Johnson *et al.* 2000, Sorenson & Payne 2005) provide additional steps to the origin of the terrestrial and/or arboreal habits.

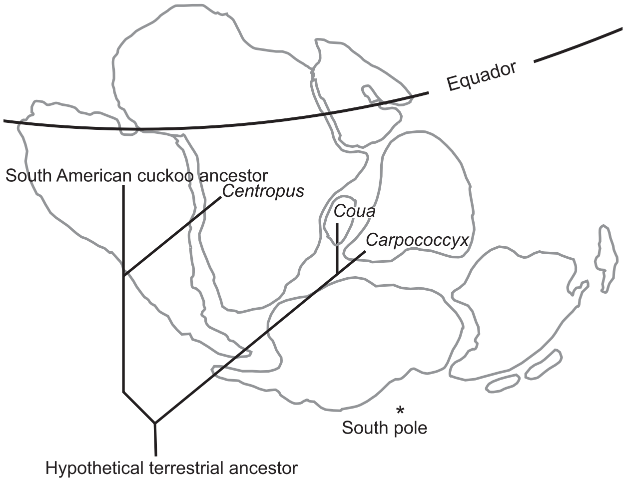

Figure 4. Hypothesis of early vicariance distribution of the cuckoos in the Early Cretaceuos.

According to the vicariance hypothesis, South America would not have been colonized by the ancestors of today's terrestrial cuckoos from North America via the Bering Strait in the Miocene, as suggested by Hughes (2000), or from Europe via Atlantic Ocean. The most parsimonious explanation indicates that terrestrial cuckoos already existed in South America (SA) when it joined North America (NA) through the Panama isthmus. The probable existence of a cuckoo fossil from the Late Paleocene of Brazil corroborates this hypothesis (Baird & Vickers-Rich 1997). Hence *Geococcyx californianus* (Lesson, 1829) (Neomorphinae) and *Crotophaga sulcirostris* Swainson, 1827 (Crotophaginae) must have gone to the south of NA (Nearctic region) from SA and not the other way around *sensu* Hughes (2000).

The strict consensus cladogram (Fig. 1) suggests that the transition between terrestrial/arboreal cuckoos occurred in South America, since the cuckoos, whose arboreal behaviors are observed (Crotophaginae and Taperinae: Fig. 1, internodes 8 and 33,) are the most basal cuckoos of the large arboreal group (internode 6). In addition, literature (Hughes 1996, 2000, Payne 1997, 2005) mentions these groups as intermediate in relation to the terrestrial and arboreal habits and considers arboreal only the Phaenicophaeinae, Coccyzinae and Cuculinae cuckoos. Both primary and secondary BPA indicate that the history of distribution of these derived cuckoos cannot be explained by vicariance from the breakup of Gondwana. The most parsimonious hypothesis indicates dispersion from South America. The extinction is more parsimonious only in rare events (see below).

According to the BPA hypothesis, these arboreal cuckoos split apart from each other only after the breakup of Gondwana. Which is also corroborated by the all cladistic analyses (Sibley & Ahlquist 1990, Aragón *et al.* 1999, Hughes 1996, 2000, Johnson *et al.* 2000, Sorenson & Payne 2005, Posso & Donatelli 2006) where Phaenicophaeinae, Coccyzinae and Cuculinae are the most derived group of cuckoos and the osteology indicates recent cladogeneses by few modifications among the genera of each group (Posso & Donatelli 2006).

In this way, the later spread of arboreal cuckoos into the other continents probably reflects the early dispersion from South America. However, the main problem with this dispersal hypothesis from South America is the historical distribution of Phaenicophaeinae. According to secondary BPA (Fig. 3), their distribution requires two additional steps: 1) dispersion from South America to Africa/South Asia and 2) extinction in South America. They are weak fliers and migration is rare in this group (Payne 2005). As a result, the Phaenicophaeinae distribution remains enigmatic.

In relation to Coccyzinae (*sensu* Payne 1997), cladistic analyses (Fig. 1) demonstrated that it is not a monophyletic group: *Coccyzus* is considered most close related with Cuculinae, in agreement with Hughes (1996, 2000) and Sorenson & Payne (2005). However, the other genera are considered within a monophyletic group, named Saurotherinae (Fig. 1, internode 23), for the fact that this group had origin in the Neotropical region. Additional steps are not required to explain their early distribution.

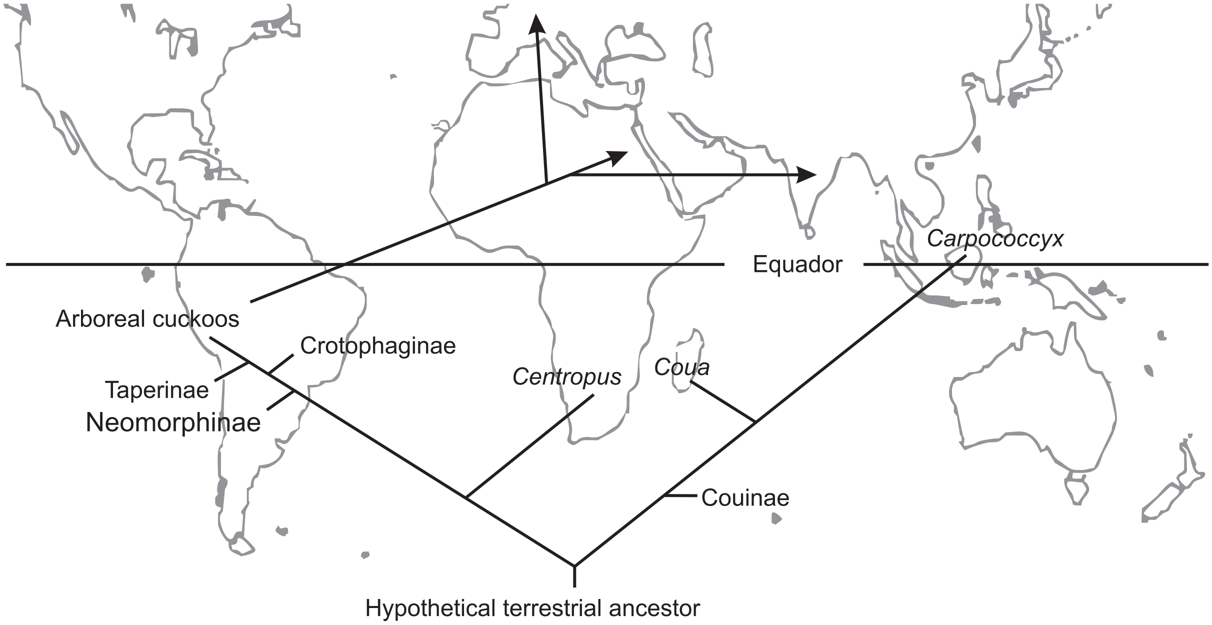

Figure 5. Current distribution of the basal cuckoos resulted from the Gondawanaland fragmentation (vicariance hypothesis). The later dispersion of arboreal cuckoos is shown in the line arrows.

The same origin in South America for Cuculinae (Fig. 1, internode 11) can be inferred, because *Coccyzus*, the most basal genus of this large group, is found in this region. The presence of other Cuculinae genera in Africa and South Asia requires two additional steps by dispersion. The hypothesis of dispersion for the Cuculinae is also plausible, since its members show a very migratory capacity of flying (Payne 2005), as in the *Coccyzus* and *Cuculus* Linnaeus, 1758 (Cuculinae) species. There are some occasional records of *Coccyzus* in Europe (Witherby 1938, American Ornithologists' Union 1983, Ellicott 1983, Moore & Abraham 1984) and of *Cuculus* in North America (American Ornithologists' Union 1983).

In synthesis, the parsimony paradigm suggests the distribution of terrestrial cuckoos (basal group) by the break-up of Gondwana (Early to Mid Cretaceous) in agreement with other group of birds (Cracraft 2001, Ericson *et al.* 2002). On the other hand, fossil records point out to a more recent origin (Paleocene to Upper Tertiary) in Laurasia. Nevertheless, many additional steps on dispersion and local extinctions should be added to corroborate the fossil records suggestions. It would indicate that the early distribution of cuckoos is not parsimonious or that the fossil records may be underestimating the group age and distribution.

Finally, it can be concluded that the early history of avian distribution seems to be an **open question still** and also an intriguing and challenging matter of research. We hope this paper will encourage ornithologists to perform further biogeography analyses on the enigmatic early distribution of birds.

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