A new parrot taxon from the Yucatán Peninsula, Mexico - its position within *Amazona* genus based on morphology and molecular phylogeny

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Parrots (Psittaciformes) are a diverse group of birds, which need urgent protection. However, many taxa from this order have an unresolved status, which makes their conservation difficult. One of species-rich parrot genus is *Amazona*, which is widely distributed in the New World. Here we describe a new *Amazona* form, which is endemic to the Yucatán Peninsula. This parrot is clearly separable from other *Amazona* species in eleven morphometric characters as well as call and behavior. The clear differences in these features imply that the parrot could represent a new species. However, phylogenetic analyses based on mitochondrial markers show that this parrot groups with strong support within *A. albifrons* from Central America, which would suggest that it is a subspecies of *A. albifrons*. Taken together phylogenetic and morphometric analyses, we can conclude that the new parrot represents a recently evolving lineage, whose taxonomic status should be further verified. This lineage diverged from its closest relative about 120,000 years ago and was subjected to accelerated morphological and behavioral changes like some other representatives of the genus *Amazona*, which makes difficult to establish its taxonomic status and need further studies. Our phylogenies, which are so far the most comprehensive for *Amazona* taxa enabled us to consider the most feasible scenarios about parrot colonization of the Greater and Lesser Antilles and Central America from South America mainland. The molecular dating of these migrations and diversification rate were correlated with climatic and geological events in the last 5 million years giving an interesting insight into Amazon parrot phylogeography and evolution in general.

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Abstract

Parrots (Psittaciformes) are a diverse group of birds, which need urgent protection. However, many taxa from this order have an unresolved status, which makes their conservation difficult. One of species-rich parrot genus is *Amazona*, which is widely distributed in the New World. Here we describe a new *Amazona* form, which is endemic to the Yucatán Peninsula. This parrot is clearly separable from other *Amazona* species in eleven morphometric characters as well as call and behavior. The clear differences in these features imply that the parrot could represent a new species. However, phylogenetic analyses based on mitochondrial markers show that this parrot groups with strong support within *A. albifrons* from Central America, which would suggest that it is a subspecies of *A. albifrons*. Taken together phylogenetic and morphometric analyses, we can conclude that the new parrot represents a recently evolving lineage, whose taxonomic status should be further verified. This lineage diverged from its closest relative about 120,000 years ago and was subjected to accelerated morphological and behavioral changes like some other representatives of the genus *Amazona*, which makes difficult to establish its taxonomic status and need further studies. Our phylogenies, which are so far the most comprehensive for *Amazona* taxa enabled us to consider the most feasible scenarios about parrot colonization of the Greater and Lesser Antilles and Central America from South America mainland. The molecular dating of these migrations and diversification rate were correlated with climatic and geological events in the last 5 million years giving an interesting insight into Amazon parrot phylogeography and evolution in general.

1. Introduction

1.1.   The genus *Amazona* and its taxonomic changes

Amazona (Amazon parrots) is the most species-rich genus within the Androglossini tribe (Schodde et al. 2013). The Amazon parrots are strictly neo-tropical with a distribution that extends from southern Mexico through Mesoamerica and the Caribbean to much of South America, with the southernmost distribution reaching the provinces of Santa Fé and Córdoba in Argentina (Darrieu 1983). They are characterized by medium to large size, strong-heavy bill, short-rounded tail, prominent naked cere and a distinct notch in the upper mandible (Forshaw 1973; Juniper & Parr 1998). Their body plumage is predominantly green with variable colorations on the head, breast, shoulders, and/or flight feathers. Red, yellow, white and blue are dominating colors in their head. The tail is squared in shape and often banded with red and blue stripes. The variation of these accenting colors is one of the morphological features commonly used to separate the species and subspecies. However, phylogenetic analyses of mitochondrial DNA (mtDNA) have not always supported the current classification of the *Amazona* group (Eberhard & Bermingham 2004).

When Forshaw published the first edition of his *Parrots of the World* (Forshaw 1973), the *Amazona* genus contained 27 species. No one refuted this arrangement until 1981, when the species number increased to 28 with the elevation of *A. rhodocorytha* to species status; it was formerly regarded as a subspecies of *A. dufresniana (Forshaw 1973; Forshaw 1984)*. The first substantial change in the taxonomy of this genus was the transfer of *Amazona xanthops* to the new genus *Alipiopsitta* (Caparroz & Pacheco 2006; Duarte & Caparroz 1995). These results opened the floodgates for a series of partial (Eberhard & Bermingham 2004; Ribas et al. 2007; Silva 2014; Urantowka et al. 2014) or complete revisions of the genus *Amazona* (Russello & Amato 2004). Many of these changes have elevated *Amazona* subspecies to the species rank, as in the case of *A. oratrix* and *A. auropalliata* (Clements et al. 2016; Gill & Donsker 2017), and four new *Amazona* subspecies have been named (Lousada 1989; Lousada & Howell 1997; Reynolds & Hayes 2009).

While the taxonomic changes were ongoing (H. Sick *in litt*. to T. Silva, 1988), an additional new species, *A. kawallii,* was described (Grantsau & Camargo 1989). Its validity was firstly questioned (Vuilleumier et al. 1992) but reaffirmed soon afterwards by other authors (Collar & Pittman 1996; Martuscelli & Yamashita 1997; Silva 2015). Currently, most of the present checklists assume that the *Amazona* genus contains 30 species, e.g. Clements et al. (2016).

68   1.2.   *Amazona* species native to Mexico and finding the new dimorphic *Amazona*

69   Mexico is the home of 23 parrot species of which six are endemic (Gómez Garza 2014; Herminio

70   Plasencia-Vazquez & Escalona-Segura 2014; Juniper & Parr 1998). Eight of these species belong

71   to the genus *Amazona* and two of them (*Amazona viridigenalis* and *A. finschi*) are found only in

72   Mexico. The Mexican *Amazona* species can be divided into three groups: 1) species having

73   variable amounts of yellow on the head (*A. oratrix, A. auropalliata*); 2) species that are

74   predominately green with only blue on the head (*A. farinosa guatemalae*); and 3) species

75   possessing various tonalities of red in the head invariably accompanied by blue (*Amazona*

76   *viridigenalis, A. finschi*), yellow (*Amazona xantholora, A. autumnalis*) or white (*Amazona*

77   *xantholora, A. albifrons*). Monomorphism is the rule in the genus *Amazona.* However, two

78   species, *Amazona albifrons* (all three subspecies) and *Amazona xantholora,* display significant

79   dimorphism: males possess much more colorful heads and a more extensively red colored alula

80   and wing speculum (Gómez Garza 2014; Silva 1991).

81   In the beginning of 2014, during a visit to a remote part of the Yucatán Peninsula, in south of

82   Becanchén in Tekax Municipality (**Fig. 1**), Miguel A. Gómez Garza sighted parrots with

83   coloration completely different from that of other known species. The birds' appearance and

84   behavior suggested that they belong to the genus *Amazona.* The individuals of this unknown

85   taxon also exhibited sexual dimorphism (**Fig. 2** and **Fig. 3**) like the sympatric *Amazona albifrons*

86   and *Amazona xantholora*.

87   To verify the taxonomic status of the new parrot, we performed a detailed morphological study

88   comparing it with other Mexican *Amazona* species that possess red feathers in the head.

89   Moreover, to establish its phylogenetic position within the genus *Amazona*, we also sequenced

90   three typical mitochondrial markers from the new form and also from *Amazona xantholora*,

91   which had not been previously studied at the molecular level.

92   This new parrot can be confused with *A. albifrons* and *A. xantholora* in the field when observed

93   at a distance, by their similar size and general appearance. However, its call and other

94   morphological features are very distinctive and could be used in discrimination of this parrot as a

95   new species, at least under typological, morphological and phenetic species concepts. On the

96   other hand, molecular phylogenetic analyses imply that this parrot could be a subspecies of *A.*

97   *albifrons*. Therefore, we discussed the pros and cons of these two taxonomic concepts and

98   presented its phylogenetic position in the wide framework of *Amazona* genus evolution and

99   phylogeography.

2. Materials and methods
2.1. The new *Amazona* sampling

102   Living specimens of known morphological types (male holotype and female allotype – see **Fig.**

103   **4-7**) of the new *Amazona* were collected in the Yucatán Peninsula in Mexico, south of Becanchén

104   in Tekax Municipality. However, the detailed location is not provided here due to conservation

105   reasons. Both individuals are now maintained as living birds in Mexico by Miguel Angel Gómez

106   Garza with the permission and authorization of the Procuraduría Federal de Protección al

107   Ambiente (PROFEPA), the national wildlife protection agency. Tail feathers from both specimens

108   were used for DNA isolation and were also deposited in the collection of the Laboratorio de

109   Ornitología, Facultad de Ciencias Biológicas, Universidad Autonóma de Nuevo León, Mexico.

110   This material is assigned the following catalog numbers: MGG01-*Amazona gomezgarzai*-

111   Holotipo- for male feathers and MGG02-*Amazona gomezgarzai*-Alotipo- for female feathers.

112   Both the living holotype and allotype will be ceded with the authorization of PROFEPA to the

113   Laboratorio de Ornitología, Facultad de Ciencias Biológicas, Universidad Autonóma de Nuevo

114   León, Mexico, upon their death.

115   The electronic version of this article in Portable Document Format (PDF) will represent a

116   published work according to the International Commission on Zoological Nomenclature (ICZN),

117   and hence the new names contained in the electronic version are effectively published under that

118   Code from the electronic edition alone. This published work and the nomenclatural acts it

119   contains have been registered in ZooBank, the online registration system for the ICZN. The

120   ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed

121   through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The

122   LSID   for   this   publication   is   urn:lsid:zoobank.org:act:C4AA8659-8077-4195-9E11-

123   D2EB3635397C and urn:lsid:zoobank.org:act:A8F38A42-6F3A-4453-8730-1D2FDCE3D44A.

124   The online version of this work is archived and available from the following digital repositories:

125   PeerJ, PubMed Central and CLOCKSS.

126   In taxonomic circles, there has been much debate about the deposition of preserved voucher

127   specimens when naming a species (Donegan 2008; Dubois & Nemésio 2007; Nemesio 2009). In

128   the current case, the precarious status of the new *Amazona*, which warrants a listing of Critically

129   Endangered (CR) under IUCN (International Union for the Conservation of Nature) criteria

130   makes the collection of a preserved specimen ethically impossible; the taking of two living

131   specimens will permit their nesting biology in captivity to be studied, as the birds are held in a

132   manner that should allow them to breed; when such breeding takes place, details on incubation

133   and the development of the young can be documented.

134   A precedent for naming species without the formal deposition of such type was proposed by

135   Smith *et al. Smith et al. (1991)* and was followed by others (Athreya 2006; Gentile & Snell 2009;

136   Jones et al. 2005). Three former secretaries of the International Commission on Zoological

137   Nomenclature support the view that the CODE allows the naming of a species without the

138   collection of a voucher specimen in particular circumstances, see Polaszek et al. (2005) and

139   Wakeham-Dawson et al. (2002). Moreover, Article 16.4.2 of the CODE states that where the

140   holotype is an extant individual, a statement of the intent to deposit the individual in a collection

141   upon its death accompanied by a statement indicating the name and location of that collection is

142   sufficient.

143   Herein, the authors follow Böhme & Ziegler (1997) in naming a new species based on a

144   living specimen, but the recommendation by Dubois (2009), who suggested that museums be

145   contacted for the existence of specimens that had not erstwhile been recognized, was followed to

146   no avail for the new *Amazona*. In lieu of an onomatophore specimen of the new parrot, the

147   authors deposited feathers from the holotype and allotype as vouchers in following Smith et al.

148   (1991), per the recommendation of Donegan (2008) and in compliance with Article 72.5.1 of the

149   CODE, which states that a type may be an animal or any part of an animal. Article 16.4.2 of the

150   CODE will be met with the deposition in a secure collection of the extant, caged individuals from

151   whom the feathers were removed upon their death. The photographs and illustrations that

152   accompany this description represent the designated holotype and allotype. The authors thus

153   believe that they have met all thresholds to adequately name for the new *Amazona* taxon.

154   2.2. Morphometric and vocalization data collection and analysis

155   We examined five metric features: body weight, total length, length of wing chord, tail length and

156   exposed culmen, as well as six morphological discrete characters: coloration of forehead, lores,

157   cheeks and crown, the presence of black ear patch and black scalloping on contour feathers on the

158   face (**Table 1, 2 and 3**). The measurements were taken by one person (TS) using Fischer

159   Scientific digital caliper with the resolution of 0.1 mm. Three individuals of each sex were

160 measured for each taxon, except for *Amazona autumnalis* in which six birds of unknown sex
161 were taken into account. In the case of the new *Amazona*, only two specimens were collected and
162 analyzed in details because of its endangered status but several small groups with up to 12
163 individuals were additionally observed and studied in the field. To use the different morphometric
164 features simultaneously in multivariate studies, we normalized their values using the minimum-
165 maximum method: (value-min)/(max-min). The metric features were first averaged per the
166 particular taxon or sex before the normalization. The morphological discrete characters were
167 coded as 1 (when the character was present), 0 (when it was absent) or 0.5 (when it has an
168 intermediate state).

169 The Principal Component Analysis (PCA) was done using Statistica software (StatSoft_Inc.
170 2011). In the analysis, covarion matrix was used on the normalized data to calculate principal
171 components. Hierarchical clustering of parrot taxa was performed on the normalized
172 morphometric features using pvclust function in R package (R_Core_Team 2015) assuming
173 Euclidean distance and UPGMA as agglomeration method. To estimate the uncertainty in the
174 clustering, AU (Approximately Unbiased) p-value and BP (Bootstrap Probability) value were
175 calculated for each cluster with bootstrap resampling assuming 1000 replications. The AU p-
176 value, which is computed by multiscale bootstrap resampling, is considered a better
177 approximation to unbiased p-value than the standard BP value computed by normal bootstrap
178 resampling (Shimodaira 2004).

179 High quality parrots' vocalization files were downloaded from Avian Vocalizations Center
180 (AVoCet, http://avocet.zoology.msu.edu) and xeno-canto database (http://www.xeno-canto.org):
181 AV14063 (*Amazona albifrons*) recorded by Pamela C. Rasmussen, AV11523 (*Amazona agilis*)
182 recorded by Brian K. Schmidt, XC77749 (*Amazona xantholora*) recorded by Mary Beth Stowe,
183 XC282102 (*Amazona albifrons*) recorded by Oscar Humberto Marin-Gomez as well as XC97904
184 (*Amazona agilis*) and XC5942 (*Amazona xantholora*) both recorded by Richard C. Hoyer. The
185 files together with call records obtained for the new taxon were processed and analyzed in
186 Avisoft-SASLab 5.209 (Sound Analysis and Synthesis Laboratory) and Sound Analysis Pro 2011
187 (Tchernichovski et al. 2000), in which syllable units were identified (segmented by amplitude)
188 and their statistic features were derived. These features were next studied by Discriminant
189 Function Analysis (DFA) including Canonical analysis (CA) using Statistica software
190 (StatSoft_Inc. 2011) as well as by non-parametric Kruskal-Wallis test and Dunn's test of post-hoc

191   multiple comparisons with Benjamini-Hochberg correction for p-values using R package

192   (R_Core_Team 2015).

193   2.3. DNA extraction and amplification

194   Total genomic DNA was extracted from tail feather from the living specimens of the new

195   *Amazona* and *A. xantholora* using Qiagen DNeasy® tissue extraction kits (Valencia, CA) and

196   following the manufacturer´s protocol. Afterwards, amplification of sex specific *CHD*-Z and

197   *CHD*-W introns was performed for molecular sexing of the new *Amazona* individuals. The pair

198   of 2550F and 2718R primers was used in PCR reactions according to the protocol previously

199   described by Fridolfsson and Ellegren (Fridolfsson & Ellegren 1999). Obtained amplicons were

200   analyzed with the Agilent 2200 TapeStation System (**Fig. S1**).

201   Three mitochondrial genes, COI, 12S and 16S rRNA, were amplified using the previously

202   published protocol described by Russello & Amato (2004). PCR products were purified and

203   sequenced in both directions at the sequencing service Macrogen® (Rockville, MD). Full

204   complementary strands of each gene were unambiguously aligned using CodonCode Aligner

205   (CodonCode Corporation®, Dedham, MA). The newly obtained sequences are available in

206   GenBank database under accession numbers: KU605663-8.

207   2.4. Phylogenetic analyses

208   The obtained new mitochondrial sequences were aligned with all corresponding sequences of

209   *Amazona* taxa available in GenBank, including *Pionus menstruus* as an outgroup (**Table S1**).

210   Most of the sequences were obtained by Russello & Amato (2004) and one by Eberhard &

211   Wright (2016). In their papers is provided further information about geographic origin and

212   vouchers for them. The final alignment used in phylogenetic studies comprised 45 sequences

213   with the length of 1485 bp including three markers: 12S rRNA (390bp), 16S rRNA (534bp) and

214   COI (561bp).

215   For reconstructing phylogenetic trees, we applied four algorithms: Bayesian inference in

216   MrBayes 3.2.3 (Ronquist et al. 2012), PhloBayes MPI 1.5 (Lartillot et al. 2013) and Beast 2.4.0

217   (Bouckaert et al. 2014), as well as maximum likelihood (ML) analyses in TreeFinder (Jobb et al.

218   2004) and RAxML 8.2.3 (Stamatakis 2014). The best-fit partitioning schemes were selected

219   according to PartitionFinder 1.1.1 based on BIC criterion (Lanfear et al. 2012) – **Table S2**. In

220   TreeFinder, we also applied these partitioning scheme using models suggested by TreeFinder
221   Propose Model module based on BIC for these partitions. Moreover, to specify appropriate
222   substitution models across the larger space in the Bayesian MCMC analysis (Huelsenbeck et al.
223   2004), we used mixed models in MrBayes analysis.

224   In the MrBayes analysis, two independent runs starting from random trees were applied, each
225   using 4 Markov chains. Trees were sampled every 100 generations for 10,000,000 generations. In
226   the final analysis, we selected trees from the last 4,082,000 generations that reached the
227   stationary phase and convergence (i.e. the standard deviation of split frequencies stabilized and
228   was lower than the proposed threshold of 0.01). In PhyloBayes, we used CAT-GTR model with
229   rate variation across sites modeled by five discrete rate categories of gamma distribution. The
230   number of components, weights and profiles of the model were inferred from the data. Two
231   independent Markov chains were run for 100,000 generations in each of these analyses. The last
232   85,000 trees from each chain were collected to compute posterior consensus trees after reaching
233   convergence, when the largest discrepancy observed across all bipartitions (maxdiff) was below
234   recommended 0.1. We set search depth to 2 in TreeFinder and applied 1000 distinct ML searches
235   on 1000 randomized stepwise addition parsimony trees in RAxML. To assess significance of
236   particular branches, non-parametric bootstrap analyses were performed on 1000 replicates in
237   these two programs.

238   Tree topologies assuming different relationships between parrots from the Greater Antilles and
239   Central America as well as the alternative position of the newly described *Amazona* were
240   compared according to approximately unbiased (AU), Shimodaira-Hasegawa (SH) and weighted
241   Shimodaira-Hasegawa (wSH) tests, which were performed in Consel v0.20 (Shimodaira &
242   Hasegawa 2001) assuming 10,000,000 replicates. Site-wise log-likelihoods for the analyzed trees
243   were calculated in TreeFinder under the best fitted substitution models.

244   Divergence times were estimated with Beast software. As constraints for tree calibration, we
245   assumed the uniform prior distribution of the separation time between *Pionus menstruus* and
246   *Amazona* dated from 5.646 to 16.553 million years ago, and the divergence time of *A. aestiva*, *A.*
247   *dufresniana* and *A. pretrei* as dating from 2.877 to 10.502 million years ago, according to
248   Schweizer et al. (2011). We tested both strict and lognormal relaxed clock models assuming the
249   calibrated Yule model and separate substitution schemes for particular data partitions according to
250   PartitionFinder results (**Table S2**). Finally, we applied the relaxed clock model for the second
251   codon position and the strict clock model for rRNA genes as well as the first and third codon

252 positions. The decision about the selection of clock model was made based on the inspection of
253 the standard deviation of the relaxed clock assuming that its value exceeding 1 indicates a
254 significant variation among branches. The clock and substitution rates were estimated in the
255 analyses. Posterior distributions of parameters were estimated for 100,000,000 generations with a
256 sampling frequency of 1000 steps. The convergence and sufficient sampling was checked using
257 Tracer 1.6 (Rambaut et al. 2014). Effective sample size (ESS) for all parameters was larger than
258 the assumed threshold 200, which indicated sufficient convergence, sampling and chain mixing.
259 Phylogenetic trees were summarized in TreeAnnotator 2.3.1 (Drummond et al. 2012) with 10%
260 burn-in of total trees using maximum clade credibility tree and common ancestor heights. The
261 generated tree was visualized in FigTree 1.4.2 (Rambaut 2012).

262 The number of base differences per site (p-distance) between selected pair of sequences was
263 calculated in MEGA6 (Tamura et al. 2013). The analysis involved all 1485 positions in the
264 alignment. The distance was expressed as percent. Standard error was estimated by bootstrap
265 method assuming 1000 replicates.

266 2.5. Diversification rate estimation

267 The maximum clade credibility tree obtained from Beast and associated branching times were
268 used for calculation diversification rate using R package LASER 2.4 (Rabosky 2006a). In order
269 to test whether diversification rates decreased with time, we calculated the γ statistic (Pybus &
270 Harvey 2000). We also tested 11 likelihood models for diversification rates (Rabosky 2006b;
271 Rabosky & Lovette 2008) – **Table S3**. The models were compared according to the values of the
272 Akaike information criterion (AIC). Temporal variation in diversification rates was visualized
273 with yuleWindow (Nee 2001) within overlapping periods of 400 thousand years. The results of
274 diversification were compared with the $\delta^{18}O$ curve (Lisiecki & Raymo 2005), which is a good
275 climate proxy. For better visualization of climate oscillations, we calculated the variance in the
276 $\delta^{18}O$ records within the same overlapping periods.

3. Results
277
278 3.1. Multivariate analyses of morphometric and vocalization features

279 One of the most distinctive metric features that can be used to differentiate the *Amazona* parrots
280 from Mexico possessing red feathers in the head area are the length of the wing chord, tail and

281   exposed culmen (**Table 1**). To visualize these differences, we performed PCA analysis (**Fig. 8**).
282   The first two factor coordinates explained in total 94% of variance (86% and 8%, respectively).
283   In the PCA plot obtained, the first component is responsible for the separation of the species,
284   whereas the second one applies to sexual dimorphism. The first component was highly correlated
285   with all three variables: wing chord (-0.90), tail (-0.96) and exposed culmen (-0.91). Generally,
286   parrots with the largest dimensions of studied characters (*A. autumnalis* and *A. viridigenalis*) are
287   located on the left of the plot, whereas parrots characterized by smaller length values (*A.*
288   *albifrons* and *A. xantholora*) are placed on the right. The new *Amazona* with the intermediate
289   length of the wing chord, tail and exposed culmen occurs between these two extremes. The
290   second component showed the highest correlation with exposed culmen (-0.42) and is responsible
291   for the separation of sexes. Males of almost all the species are located at the lower part of the plot
292   and are characterized by the larger length of exposed culmen than females, which are placed
293   above them in the plot. Only the male of *A. a. saltuensis* is placed among females of other
294   species. In fact, the difference in this parameter between *A. a. saltuensis* sexes is smallest. This
295   taxon shows also the shortest distance between two sexes, whereas *A. viridigenalis* shows the
296   largest. The latter species is also farthest from the parrots of Central America, which are grouped
297   on the right site of the plot. The individual of *A. autumnalis* without assigned sex is closest to the
298   *A. viridigenalis* male. The male of the new *Amazona* quite clearly separates from males of other
299   Mexican taxa, whereas the female of this new form is located near the *A. a. saltuensis* male and
300   *A. xantholora* female in the plot.

301   We also compared the studied parrot taxa in PCA analysis (**Fig. 9**) using both five metric (**Table**
302   **1**) and six morphological features (**Table 2**). The first two factor coordinates explained almost
303   81% of variance (63% and 17%, respectively). The first component showed the highest
304   correlation with metric features: the total length (-0.96), wing chord (-0.94), tail (-0.94), exposed
305   culmen (-0.94) and weight (-0.90), as well as some morphological characters: coloring of
306   forehead (0.84), the presence of black scalloping contour feathers (0.79) and coloring of cheeks
307   (0.73). The second component was highly correlated with crown coloring (0.83), coloring of the
308   lores (-0.59) and the presence of a black ear patch (0.59). The first component is responsible for
309   the distinct separation of *A. autumnalis* and *A. viridigenalis* from the other Mexican parrots
310   because of their larger weight and length of studied characters as well as the absence of black
311   scalloping contour feathers. The Mexican parrots are differentiated by the second component into
312   the group of *A. albifrons* subspecies and the cluster of the new *Amazona* and *A. xantholora*. The

313 outlying position of the new *Amazona* results from its unique green coloring of crown versus blue

314 and bluish in other parrots. In turn, *A. xantholora* separates because it has yellow lores and black

315 ear patch as the only species of the studied species. The three subspecies of *A. albifrons* are

316 clustered together because of white forehead and subtle black scalloping contour feathers.

317 In agreement with these results, hierarchical clustering separate *A. autumnalis* and *A.*

318 *viridigenalis* from Central America parrots into two groups (**Fig. 10**). At the base of the latter

319 group is placed *A. xantholora* and next the new *Amazona* branches off. The subspecies of *A.*

320 *albifrons* create a significant cluster with *A. albifrons nana* at the base.

321 The newly described taxon is characterized by a unique vocalization in comparison to other

322 Amazon parrots inhabiting Central America (**Fig. 11**, Supporting information **Files S1** and **S2**). In

323 this comparison, we also included *Amazona agilis* from the Greater Antilles because it appears

324 the sister taxon to the Central American parrots (see section Molecular phylogenetic studies). The

325 most distinct feature of the new *Amazona* is a relatively long duration of syllables, which is

326 almost 5 times longer in comparison to *A. albifrons* and more than 3 times longer than in *A.*

327 *xantholora* (**Fig. 11**). For each of 12 considered vocalization features, the new taxon differs

328 significantly ($p < 0.05$) from at least one of three other analyzed *Amazona* parrots (Supporting

329 information **Fig. S2** and **Table S4**). Besides syllable duration, it is also significantly different

330 from all three parrots in mean FM (frequency modulation), mean Wiener entropy (a measure of

331 the width and uniformity of the power spectrum) and variance of mean frequency (the center of

332 gravity of the power spectrum). In total, the new *Amazona* differs significantly in seven features

333 from *A. albifrons*, nine from *A. xantholora* and ten from *A. agilis*.

334 In agreement with that, Discriminant Function Analysis with Canonical Analysis shows the clear

335 separation of the four parrots according to the twelve statistical features of their syllables, which

336 indicates that they are characterized by disparate vocalizations (**Fig. S3**). The analysis proposes

337 three discriminant functions (root) explaining 75.5%, 16.9% and 7.6% of variance, respectively.

338 The first root distinctly separates *A. agilis* and the new *Amazona* from *A. albifrons* and *A.*

339 *xantholora*. The greatest contribution (expressed by standardized function coefficients) to the first

340 discriminant function has mean entropy (-1.210), syllable duration (-1.065), mean FM (0.969)

341 and mean of mean frequency (0.877). Syllable duration is most correlated (-0.686) with the first

342 root. The second discriminant function makes separate sets of syllables from *A. agilis* and the

343 new *Amazona*, whereas the sets of *A. albifrons* and *A. xantholora* overlap partially. The second

344 function is mostly associated with mean entropy (2.302) and mean of mean frequency (-2.227) as

345 well as correlated with mean amplitude (-0.313) and syllable duration (-0.308). The third root

346 separates *A. albifrons* and *A. xantholora* and is most related with variance of pitch goodness

347 (1.184), mean amplitude (1.094) and mean pitch goodness (-1.160). The largest correlations with

348 this function show mean AM^2 (-0.502) and variance of AM (-0.501).

349   3.2. Molecular phylogenetic studies

350 Phylogenetic analyses were conducted on concatenated alignment of three genes: 12S rRNA, 16S

351 rRNA and COI. Both Bayesian and maximum likelihood analyses showed the same quite well-

352 resolved tree topology and relationships among the studied taxa (**Fig. 12**). Interestingly, none of

353 recognized biogeographic groups (Central and South America as well as the Greater and Lesser

354 Antilles) creates a strictly monophyletic clade that would include all members from the given

355 region.

356 The South America parrots are mixed with samples from the Lesser Antilles and Central America

357 (**Fig. 12**). The Lesser Antillean parrots are clearly separated into three independent lineages. *A.

358 guildingii* from the Lesser Antilles is significantly placed within the very significant group

359 including also the South American parrots, *A. amazonica* and *A. brasiliensis*. A sister lineage to

360 these species is *A. imperialis* from the Lesser Antilles. All four parrots form a group very well

361 supported by all methods. The third Lesser Antillean lineage contains *A. arausiaca* and *A.

362 versicolor*. It also obtained very high posterior probability and bootstrap values but clearly

363 separates from the other Lesser Antillean parrots. The third lineage is very significantly related

364 with Yellow-headed Amazon parrots from South America, namely *A. aestiva*, *A. ochrocephala*

365 and *A. barbadensis*.

366 The parrots from Central America are also split into three very well supported clades (**Fig. 12**).

367 The one including *A. viridigenalis*, *A. finschi* and *A. autumnalis* is placed within South America

368 parrots. The second clade including Yellow-headed Amazon parrots is closely affiliated to their

369 relatives from South America, namely *A. aestiva* and *A. ochrocephala* with a moderate support,

370 whereas the third clade is very significantly grouped with the Greater Antillean parrots, i.e. *A.

371 agilis*, *A. collaria*, *A. vittata*, *A. leucocephala* and *A. ventralis*.

372 This third clade contains parrots from Mexico and northern Central America, i.e., *A. albifrons

373 albifrons, A. albifrons saltuensis, A. albifrons nana* as well as the newly studied *A. xantholora*

374 and the newly described *Amazona* (**Fig. 12**). This clade branches off within the Greater Antillean

375   parrots making them paraphyletic. The sister taxon to the Central American parrots is *A. agilis*
376   from the Greater Antilles. The position of *A. agilis* received no support larger than 0.5 posterior
377   probability and 50% bootstrap percentage but was indicated by all four applied methods, two
378   Bayesian and two maximum likelihood approaches. The other Greater Antillean parrots already
379   form a clear monophyletic clade. To assess stability of phylogenetic position of *A. agilis*, we
380   carried out tree topology tests. They showed that trees in which *A. agilis* is clustered with other
381   Greater Antillean parrots (**Fig. 13B**) or placed at the base to all parrots from Central America and
382   the Greater Antilles (**Fig. 13C**) were not significantly worse that the best topology (**Fig. 13A**).

383   The Mexican *Amazona* taxa are also monophyletic with *A. xantholora* placed at the base to the
384   clade with the largest possible support including three subspecies of *A. albifrons* and the new
385   *Amazona*. The taxa are split into two sister subclades that are well supported. One includes *A. a.*
386   *albifrons* and *A. a. saltuensis*, whereas the newly described taxon *Amazona* groups with *A.*
387   *albifrons nana,* with which it is sympatric. We also tested alternative topologies with different
388   placement of the new taxon (**Fig. 13**). The tree assuming earlier divergence of the new taxon
389   before differentiation of *A. albifrons* subspecies (**Fig. 13D**) was not significantly worse than the
390   best one (**Fig. 13A**). However, trees with clustering the new *Amazona* to *A. xantholora* (**Fig. 13E**)
391   or the basal placement of the new parrot to the rest Central America parrots (**Fig. 13F**) were
392   significantly worse.

393   The branch leading to the new *Amazona* seems relatively short indicating a very small number of
394   substitutions in comparison to other lineages. The number of base differences per site (p-distance
395   ± standard error) expressed as percent calculated for the three markers is 0.135 ± 0.091 between
396   the new *Amazona* and *A. albifrons nana*. However, it is about two times greater than the distance
397   between two subspecies, *A. a. albifrons* and *A. a. saltuensis*, which is 0.067 ± 0.067. Similar
398   conclusions can be drawn from distance calculation for individual markers but we decided to
399   present results for the concatenated sequences because of smaller stochastic error.

400   The performed molecular dating enabled to estimate divergence time of important events in the
401   evolution of Amazon parrots (**Fig. 14**). According to these estimations, the radiation of the
402   present lineages of *Amazona* started about 5 million years ago (mya). The South American
403   parrots begun their differentiation about 4.4 mya. The Lesser Antilles were settled from South
404   America independently in three ways about 3.2, 1.5 and 1.3-0.8 mya. The South American
405   parrots migrated also to Central America between 4.1 to 2.9 mya and also much later between
406   0.95 to 0.55 mya giving two separate lineages. The radiation of the third Central America clade is

407   dated to 2.5 mya, whereas the whole group including additionally the Greater Antillean parrots
408   started its evolution about 3.5 mya. The small number of substitution indicates quite recent
409   divergence of the new *Amazona* from *A. albifrons nana*. Accordingly, molecular dating showed
410   that their lineages split by average 119 thousand years ago (kya) with 95% credibility interval 9 -
411   270 kya (**Fig. 14**). The two subspecies, *A. albifrons albifrons* and *A. albifrons saltuensis* diverged
412   slightly later about 89 kya.

413   3.3. Diversification rate analyses

414   To assess if and when Amazon parrots (including the newly described taxon) were subjected to
415   increase speciation rate, we performed diversification rate analyses. The calculated γ statistic was
416   1.509 (p-value = 0.934) indicating no evidence for significant slowdown in the diversification.
417   Among eleven tested methods, a yule4rate appeared the best-fitted (**Table S3**). According to this
418   model, the first shift to a higher speciation rate (from 0.138 to 0.934) happened in t_1 = 5.099 mya
419   and lasted to t_2 = 3.199 mya, when the rate decreased to 0.229. Since t_3 = 1.305 mya, the
420   speciation rate again have increased to 0.644. The first increase is associated with radiation of the
421   basal *Amazona* lineages (**Fig. 14**). The period between t_1 and t_2 corresponds to the lowest
422   speciation of this genus. The final increase in diversification rate is related with emergence of
423   closely related species and subspecies. Interestingly, this period corresponds to the more intensive
424   climate fluctuations in the Pleistocene started about 2 mya (**Fig. 14A**). In agreement with the
425   observation, we found significant positive correlation (Pearson correlation coefficient = 0.795
426   with p-value = 0.006) between the rate of newly diverged lineages and the variance in the climate
427   fluctuations based on the $\delta^{18}O$ curve from 2 mya to the present (**Fig. 14B, C**).

428   3.4. Description of the new taxon

429   As a consequence of carried out analyses, we decided to propose the taxonomic position of the
430   new *Amazona*. The significant differences in morphometry, morphology, behavior and vocal
431   features imply that the new parrot can obtain a species status under the typological,
432   morphological, phenetic, as well as biological and evolutionary species concepts. However,
433   genetic analyses suggest a subspecies level. Therefore, the phylogenetic species concept and
434   integrative species delimitation (Aleixo 2007; Helbig et al. 2002; Padial et al. 2010) cannot be
435   applied in the species elevation.

436   *Amazona albifrons gomezgarzai,* ssp. nov. Silva, Guzmán, Urantówka and Mackiewicz

437   or *Amazona gomezgarzai,* sp. nov. Silva, Guzmán, Urantówka and Mackiewicz (**Figs 2-7**)

438   *Holotype.* Adult male, MEXICO, the Yucatán Peninsula, south of Becanchén in Tekax
439   Municipality.

440   *Allotype.* Adult female collected in the same locality as the holotype.

441   *Etymology.* We take extreme pride in naming this parrot after Miguel Angel Gómez Garza, a
442   Mexican veterinarian born in Monterrey (Nuevo León, Mexico) in 1960. Gómez Garza´s interest
443   in the ecology of the parrots of Mexico spans decades and culminated in the publication of a
444   work specifically dealing with the psittacines of that country (Gómez Garza 2014). During his
445   professional lifetime, Gómez Garza has been deeply involved in rehabilitating confiscated
446   wildlife. For the last thirty years, in his private veterinary clinic (Veterinaria del Valle) in
447   Monterrey, he has honorably supported the wildlife protection agency of the Republic of Mexico,
448   Procuraduría Federal de Protección al Ambiente (PROFEPA), providing medical attention to
449   confiscated wildlife suitable for being returned to their natural habitat. As a researcher in the
450   Facultad de Medicina Veterinaria y Zootecnia of the Universidad Autonóma de Nuevo León, he is
451   presently working on a veterinary protocol for confiscated psittacines intended for reintroduction
452   to the wild. He brought the existence of this unique member of the genus *Amazona* to our
453   attention and to him science and we owe a debt of gratitude. We suggest the common name in
454   English: Blue-winged Amazon and in Spanish: Loro de alas azules.

455   *Diagnosis.* The studied specimens show all of the characteristics of the genus as described by
456   Lesson (1831): "Rugged beak, very hooked, thick, banded edge or forming a flattened
457   depression, narrow, which follows the curvature of the beak, swollen sides, the scalloped edges;
458   the fringed lower mandible forward; nostrils rounded, very open in the wax and with protruding
459   flange; wings extending until one third of the tail; the tarses very short, reticulate, robust." Their
460   behavior, including display, is consistent with that of the genus and is closer to *A. viridigenalis*
461   than *A. xantholora* or *A. albifrons,* the birds being active and very vocal (pers. obs. senior author;
462   M.A. Gómez Garza, *in litt.,* 2015).

463   A very distinctive feature of the new taxon is its call, which is loud, sharp, short, repetitive and
464   monotonous; one particular vocalization is more reminiscent of an *Accipiter* than of any parrot
465   we know (Supporting information **File S1** and **S2**). In flight, the call is a loud, short, sharp and

466 repetitive *yak-yak-yak* that is never repeated in pairs like in *A. xantholora*. While perched, the call

467 is mellow and prolonged, sharper and more melodious than that of *Amazona albifrons*. Perched

468 birds always respond to the call of another flock member, insuring that the parrots always

469 maintain contact with one another.

470 In general appearance, the new *Amazona* demonstrates a similarity to *A. vittata* of Puerto Rico

471 and to a lesser extent to *A. tucumana* from Bolivia and Argentina and *Amazona pretrei* from

472 Brazil and Argentina. *A. vittata* can be distinguished from the female of the new *Amazona* by the

473 paler colored bill, larger and purer white orbital ring and more prominent grey bordering to the

474 feathers. Male of the new *Amazona* can be separated from *A. vittata* in addition by the presence

475 of rose-red feathers around the orbital ring.

476 *A. pretrei* exhibits dimorphism like the new *Amazona* but the male of *A. pretrei* displays

477 significantly redder feathering on the head and considerable red on the bend of the wing and

478 carpal edge; the red tone in *A. pretrei* is also richer. Indeed, both sexes of *A. pretrei* possesses

479 more extensive red feathering in the head, the color extending to forecrown and covering a

480 broader area around the orbital region; red feathers tend to appear scattered on the head; the bend

481 of wing and carpal area are covered in red as previously mentioned; the grey bordering to the

482 feathers is more prominent; and the bill is smaller, more proportionate and tends to have a

483 orangish hint, a color which intensifies with the breeding cycle.

484 The new *Amazona* is more phlegmatic in its behavior compared to the highly excitable and vocal

485 *A. pretrei*. In turn, *A. tucumana* differs by having a reddish triangle on the head, extending from

486 forehead to crown (a feature seen only in male of the new *Amazona*); there is an absence of

487 dimorphic head coloration; the grey bordering to the feathers is very prominent; the head is more

488 proportionate and the bill is whitish. In behavior, there are some affinities between *A. tucumana*

489 and the new *Amazona*.

490 Of the Mexican species, the new *Amazona* can easily be separated from *A. xantholora* by the

491 absence of yellow, white and blue from the head, from the green ear coverts and by the absence

492 of the prominent barring to the body feathers. The new taxon can be differentiated from *A.*

493 *albifrons* by the absence of white and blue from the head and by the green alula in both sexes, as

494 well as a larger size when compared to the sympatric *A. albifrons nana*.

495 The new *Amazona* resembles *A. albifrons albifrons* in size. Although its general color scheme is

496 closer to *A. viridigenalis* from northern Mexico (**Table 2**), the size difference is significant and

497   diagnostic as pointed out in **Table 1** and **3**. Moreover, the new *Amazona* has less red on the head

498   and possess neither the distinctive yellowish nape feathers that appear in elderly male *A.*

499   *viridigenalis* nor the red wing speculum found in *A. viridigenalis*.

500   *Description*

501   *Male (holotype).* Total length 26.6 cm; wing (chord) 175.3 mm; exposed culmen 27.8 mm; tail

502   89.6 mm. The sex has been determined with molecular methods (**Fig. S1**). Upperparts, including

503   nape, auriculars, dorsum, tertials, wing-coverts, rump and upper tail coverts parrot green, the

504   feathers of the head, nape, neck and mantle subtlety bordered black; forehead, forecrown and

505   feathers surrounding naked periophthalmic ring rose-red. Rear crown feathers subtlety bordered

506   in blue. Underside, chin, throat, breast and belly parrot green, the feathers from chin to vent

507   subtlety bordered in blue. Thigh feathers also washed in blue. Primaries (numbered descendently)

508   dark blue with flight feathers numbers 10 and 9 green on outer webs near base. Secondaries blue

509   with green margin on outer webs. Primary coverts blue, except along shaft, which is green.

510   Upperside of tail: two central feathers green; other feathers blue on outer web, red on inner web,

511   then yellowish green towards tip; all tail feathers are bordered in blue. Underside of tail: two

512   central feathers green, reddish hinted near feather shaft; other tail feathers rose-red on inner web,

513   yellowish at base and green towards tip; outer webs greyish-blue. Bill yellow, whitish at tip of

514   upper mandible. Tongue flesh grey, exposed nares naked and grey colored, periophthalmic ring

515   naked and greyish-white colored, iris pale mustard yellow, feet greyish-flesh colored and nails

516   grey, darkest at tip. Feathers from this specimen have been deposited in the collection of the

517   Laboratorio de Ornitología, Facultad de Ciencias Biologícas, Universidad Autonóma de Nuevo

518   León, Mexico and have assigned catalog number: MGG01-*Amazona gomezgarzai*-holotipo.

519   Article 72.5.1 of the Code of Zoological Nomenclature (henceforth CODE) permits the use of

520   animal parts in the designation of a type specimen.

521   Upon death of the living bird, its preserved body will be deposited in the same institution. This

522   complies with Article 16.4.2 of the CODE, which states that where the holotype is an extant

523   individual, a statement of the intent to deposit the individual in a collection upon its death

524   accompanied by a statement indicating the name and location of that collection is sufficient.

525 *Female (allotype)*. Total length 24.7 cm; wing (chord) 170.4 mm; exposed culmen 25.7 mm; tail
526 83.7 mm. The sex has been determined with molecular methods (**Fig. S1**). Like male but rose-red
527 confined to forehead. Like with the Holotype this individual will, upon its death, be presented to
528 the Laboratorio de Ornitología, Facultad de Ciencias Biologícas, Universidad Autonóma de
529 Nuevo León, Mexico. In the interim, feathers from this specimen have been deposited in the
530 collection and have assigned catalog number: MGG02-*Amazona gomezgarzai*-alotipo.

531   3.5. Additional characteristics

532 *Distribution*. The new *Amazona* is endemic to the Yucatán Peninsula in southern Mexico. To date,
533 its presence is confined to an area roughly 100 km^2 that is centered south of Becanchén in Tekax
534 Municipality, Yucatán. No part of the range is presently protected in any form.

535 *Habitat*. The new *Amazona* is found in tropical caducifolius and subcaducifolius forest. It is also
536 found in disturbed patches of native vegetation and in small, cultivated fields with scattered trees.
537 It is found below 300 m above sea level.

538 *Natural history*. Miguel A. Gómez Garza first sighted this parrot in the field in trees of the
539 *Leucaena* genus at heights of approximately 6 meters in the beginning of 2014 during a visit to
540 the south of Becanchén, in the municipality of Tekax. The parrots occurred in small flocks of
541 three to five individuals and fed on the tender pods produced by this tree. During a follow up visit
542 in August 2014, Gómez Garza also sighted pairs with their fledged young. This field work
543 confirmed the rarity of the species and that it was far less common than the other two species
544 found in the same area, *Amazona albifrons nana* and *Amazona xantholora*.

545 In normal parrot fashion, the new *Amazona* is diurnal, beginning the day at sunrise. It is generally
546 secretive when resting, using its plumage as camouflage. In contrast, it is vocal and noisy in
547 flight. The flight is moderately fast with the mechanism that is typical of the genus *Amazona* with
548 wing-beats never exceeding the horizontal axis.

549 The new *Amazona* is found in small flocks of less than 12 individuals, which were studied in the
550 field. Pairs and their progeny have a tendency to remain together and are discernible in groups.
551 Like all members of the genus *Amazona*, this parrot is herbivore. Its diet consists of seeds, fruits,
552 flowers and leaves obtained in the tree canopy. It also consumes tender shoots of native trees and
553 the pods of leguminous trees including uaxim (*Leucaena glauca*), bukut (*Cassia grandis*) and
554 katsín (*Acasia gaumeri*).

555 Very little is known about this parrot's biology. There is no conservation program currently in
556 effect to preserve this parrot but its long-term existence impinges on the local communities and
557 making them aware of this parrot's value as a result of its uniqueness, its potential as a bird
558 watching attraction and the fact that it is present only locally. Its small range and rarity should
559 make its conservation a priority.

4. Discussion
560
561 4.1. Taxonomic position of the newly described *Amazona*

562 In this study, we proposed the new taxon of *Amazona* at the species (*Amazona gomezgarzai* sp.
563 nov.) or subspecies level (*Amazona albifrons gomezgarzai* ssp. nov.). It is not easy to take up the
564 final decision because available data are contradictory. The species level is supported by
565 morphometrical and behavioral data, whereas mitochondrial genetic analyses imply the
566 subspecies level. Below we tried to discuss the pros and cons of these two taxonomic concepts in
567 an objective way.

568 Multivariate analysis incorporating both metric and morphological features clearly separated the
569 new *Amazona* from the other Mexican parrots, which in turn differed distinctly from *A.*
570 *autumnalis* and *A. viridigenalis* (**Fig. 8-10**). The newly described taxon showed the closest
571 morphometric similarity to *A. xantholora*. However, it clearly separates in vocalization features
572 from two other Central American parrots (*A. albifrons* and *A. xantholora*) and their Greater
573 Antillean relative *A. agilis* (**Fig. 11** and **Fig. S3**).

574 Based on the phylogenetic analysis performed, this new taxon is undoubtedly grouped within the
575 clade of Mexican congeners, namely *Amazona albifrons albifrons, A. a. nana, A. a. saltuensis* and
576 *A. xantholora* (**Fig. 14**). Although the new *Amazona* shows some morphological similarity to *A.*
577 *vittata*, these two taxa are clearly separated into two clades in the phylogeny. The closest relative
578 of the new *Amazona* is *A. a. nana*, also from the Yucatán Peninsula. The other two subspecies of
579 *Amazona albifrons* (*A. a. albifrons* and *A. a. saltuensis*) included in the same clade are distributed
580 along the Pacific slope of Mexico (Gómez Garza 2014) and surely share the same ancestors as
581 the forms from the Yucatán Peninsula. The common origin of these taxa, along with the newly
582 described form, is concordant in several common features, such as sexual dimorphism and similar
583 plumage coloration with the presence of red on the head (**Fig. 3**).

584   Nonetheless, the new *Amazona* is clearly different from *A. albifrons*. Although the three Mexican

585   parrots found in the Yucatán Peninsula (*A. albifrons nana, A. xantholora* and the new *Amazona*)

586   share the same habitat and come into frequent physical contact, they live commensally and show

587   substantial differences in their morphology, plumage, call and behavior (**Table 1-3, Fig. 3, 11,**

588   **S3**). The features used here to discriminate the proposed taxon are of the same type as those

589   utilized in elevation of other *Amazona* species. The characters described allow the species to live

590   sympatrically without hybridizing (Pettingill 1970). This suggests that these three forms could be

591   separate species. The differentiation in characters involved in mate choice, such as song,

592   plumage, and behavior play a central role in avian speciation (Edwards et al. 2005). The role of

593   song is particularly interesting because multiple factors influence vocal evolution and this feature

594   is subjected to rapid change through learning and behavioral evolution.

595   Studies of geographic variation in the vocalizations of the crimson rosella (*Platycercus elegans*)

596   parrot species complex showed that vocal variation, in a species with vocal learning, can coincide

597   with areas of restricted gene flow across geographically continuous populations. These results

598   suggest that vocalization can be associated with reduced gene flow between populations, and

599   therefore may promote speciation, even in the absence of other barriers (Ribot et al. 2012). On

600   the other hand, several local dialects were documented for *Amazona auropalliata* with no

601   significant relationship with genetic variations (Wright & Wilkinson 2001) indicating a high

602   degree of gene flow and individual dispersal across the dialect boundaries. Experimentally

603   simulated dispersals with *Amazona auropalliata* individuals moving within and across dialect

604   regions showed that both vocal learning (in the case of juveniles) and limited dispersal (in the

605   case of adults) are responsible for the dialect maintenance (Salinas-Melgoza & Wright 2012).

606   Although recent studies on contact calls of Neotropical parrots from the tribe Arini (related to

607   Androglossini) showed evolutionary rates similar (but not accelerated) to those of morphological

608   traits, the calls contained significant levels of phylogenetic signal and evolution of some acoustic

609   parameters correlated with evolution of body mass and bill length (Medina-Garcia et al. 2015).

610   The coordinated evolution of these features can facilitate speciation of parrots.

611   On the other hand, it is possible that the studied individuals of the new taxon are hybrids or

612   aberrant forms of *Amazona albifrons* and the observed morphometric differences result from

613   intraspecific variation in *A. albifrons*. However, the length of wings and tail of the newly

614   described parrots are out of the range of these characters in all three *Amazona albifrons*

615   subspecies. The red forehead, green crown and distinct black scalloping contour feathers were not

616 observed in *A. albifrons* too. Field studies carried out by Miguel A. Gomez Garza and others

617 during the past 30 years have revealed no individuals of *A. albifrons* showing such mixed

618 characters. Similarly, local informants and the staff at PROFEPA (Procuraduría Federal de

619 Protección al Ambiente) and CIVIS (Center for the Conservation and Research of Wildlife),

620 which is managed by the government in the same municipality of Tekax, have never seen such

621 potential hybrids or *A. albifrons* with the atypical features among the hundreds of all parrots

622 confiscated in the range area each year, either. Such forms were not observed also among the

623 hundreds of all parrot specimens imported through the US quarantine system from 1973 to 2008,

624 when a ban was introduced on export of parrots.

625 The Kawall's Amazon (*Amazona kawalli*) was also initially considered an aberrant form of Mealy

626 Parrot (*Amazona farinosa*) before it was recognized as the new species (Martuscelli & Yamashita

627 1997). Nevertheless, more extensive studies including larger number of *A. albifrons* specimens

628 are necessary to verify its variation because aberrant forms are not unusual in parrots.

629 The distinct morphological and behavioral features seem incongruent with molecular

630 phylogenetic results, in which the new *Amazona* and *A. albifrons nana* are clustered together

631 leaving outside the two *A. albifrons* subspecies. It would suggest that the new taxon should be a

632 subspecies within *A. albifrons*. However, the alternative placement of the new *Amazona* at the

633 base to the monophyletic *A. albifrons* clade is not significantly worse than the best tree (**Fig.

634 13D**). It suggests that the new taxon could have emerged before differentiation of *A. albifrons* to

635 subspecies. Interestingly, such alternative topology was obtained for hierarchical clustering of

636 parrots based on all morphometric characters (**Fig. 10**).

637 Moreover, the molecular distance between the new *Amazona* and *A. albifrons nana* measured by

638 the number of base differences per site (0.135) is even about two times greater than the distance

639 (0.067) between two *A. albifrons* subspecies, *A. a. albifrons* and *A. a. saltuensis*.

640 The acceptance of the new *Amazona* as a species, would imply that the *A. albifrons* taxon would

641 be paraphyletic. In consequence, *A. albifrons nana* could be also obtained a species status.

642 However, it is not sufficiently different in morphology and morphometry from other subspecies

643 of *A. albifrons* to be elevated to the new species. It should be noted that the paraphyly of

644 *Amazona* taxa is not an exceptional case because the same situation concerns Central American

645 *A. oratrix* and *A. auropalliata*, whose sequences are mixed and do not form one-species

646 monophyletic clades (**Fig. 12**). Similarly, paraphyletic is also *A. ochrocephala* whose

647 representatives group with *A. aestiva*, *A. barbadensis* and the clade *A. oratrix* - *A. auropalliata*. It

648 cannot be excluded that some specimens (e.g. *A. ochrocephala*) were misidentified and the

649 taxonomy of the *Amazona* genus should be substantially revised.

650 The resulted paraphyly of *A. albifrons* with nested the new *Amazona* does not have to be an

651 extraordinary case, either. In agreement with that comprehensive surveys and meta-analyses of

652 mitochondrial gene phylogenies showed that such paraphyletic or polyphyletic species constitute

653 a substantial fraction (19-23%) of thousands animal taxa studied, including an additional four

654 species from the *Cacatuidae* family (Funk & Omland 2003; Ross 2014). The major natural

655 reasons of species-level paraphyly and polyphyly can be introgression and incomplete lineage

656 sorting following recent speciation. However, following Haldane's rule (Haldane 1922), the

657 introgression of maternally inherited mtDNA is restricted between heterogametic avian species

658 because female hybrids are characterized by a reduced viability (Brumfield et al. 2001; Carling &

659 Brumfield 2008; Rheindt & Edwards 2011; Saetre et al. 2001; Saetre et al. 2003; Tegelstrom &

660 Gelter 1990; Turelli & Orr 1995). Mitochondrial genes are also less prone to the incomplete

661 sorting than nuclear loci because they are present in a haploid genome and maternally inherited

662 (Hudson & Turelli 2003). However, it cannot be excluded that this effect can influence mitDNA

663 in rapidly radiating taxa, in which on-going speciation occurs before genetic sorting (Funk &

664 Omland 2003).

665 Assuming that the current phylogeny reflects real relationships between Amazon parrots, we

666 could accept that the parrot paraphyletic species have emerged quite recently within others from

667 one of their isolated subspecies. Consequently, the same would concern the new *Amazona*. Its

668 lineage diverged most probably about 120,000 years ago within *A. albifrons* (**Fig. 14**). During

669 this time, the taxon differentiated sufficiently to be clearly recognizable by many morphometric

670 and behavioral features. In agreement with that, the genetic distance between the new *Amazona*

671 and *A. a. nana* is two times larger than their closest relatives between *A. a. albifrons* and *A. a.*

672 *saltuensis*. Nevertheless, the final taxonomic status (species or subspecies) of the new *Amazona*

673 should be determined in subsequent detailed studies which are conditioned by a possibility of

674 finding and studying more individuals of this rare parrot.

675   4.2. Implication on general phylogeny and migration of Amazon parrots

676   Our results have also interesting implications for phylogeography of the whole genus *Amazona*

677   and colonization of Central America as well as Lesser and Greater Antilles. The obtained results

678   indicate that Central America was settled by three ways independently at different times from

679   distinct ancestral lineages. Two times their ancestors were South American parrots and the

680   immigrations happened 4-3 mya and 1-0.5 mya. It is in good agreement with the standard

681   assumption on the formation of the Panama Isthmus, whose final closure is proposed to have

682   occurred just 4-3 mya (see (Montes et al. 2015) for the much earlier dating, which also supports

683   our estimations). The third case is more controversial because the clade does not cluster directly

684   with any South American parrots but with those from Greater Antilles. The observed proximity of

685   the Mexican *Amazona albifrons* clade with the Greater Antillean clade composed of *Amazona*

686   *collaria, A. vittata, A. leucocephala, A. ventralis* and *A. agilis* suggests the continental origin of

687   the island parrots (Bond 1963; Lack 1976; Lantermann 1997; Ottens-Wainright et al. 2004;

688   Russello & Amato 2004; Snyder et al. 1987; Wiley 1991). Two colonization events of the Greater

689   Antilles from Central America, i.e. Yucatan Peninsula and Honduran-Nicaraguan Bulge were

690   proposed (Bond 1963; Lack 1976; Lantermann 1997; Snyder et al. 1987; Wiley 1991). It was

691   hypothesized that one invasion could have occurred through Jamaica (by lineage of *A. agilis*) and

692   the second through Cuba (by *A. leucocephala* from which other Jamaica parrot *A. collaria* would

693   derive) (Lack 1976; Lantermann 1997; Snyder et al. 1987; Wiley 1991). Ottens-Wainright et al.

694   (2004) proposed also two colonization events but both directed to Jamaica.

695   Our phylogenies including the largest number of *Amazona* representatives from Central America

696   do not split the Greater Antillean parrot clade into two groups as it would be expected in the case

697   of the two-colonization scenario. Just the opposite, they show that the Central America clade is

698   nested within the Greater Antillean parrot group. Such branching order results from the basal

699   position of the quite diverged lineage of *A. agilis* to the Central American parrots. In the LogDet

700   model-based tree by Ottens-Wainright et al. (2004), the consensus of 12 equally most

701   parsimonious trees by Russello & Amato (2004), and Bayesian Beast tree by Schweizer et al.

702   (2014), the Central America clade was also placed within the Greater Antillean parrot group but

703   in these cases *A. agilis* was basal to both Central America and Greater Antilles clades. These two

704   alternative topologies are not statistically different but the first one is favored (**Fig. 13A, C**). The

705   topology assuming the separation and monophyly of the Central American and the Greater

706   Antillean parrots was not rejected by the applied tests, either (**Fig. 13B**). However, taken into

707 account that the first topology (**Fig. 13A**) was inferred by all four applied methods and the
708 Greater Antillean parrot clade, including *A. agilis,* shows a greater genetic variation and older
709 divergence time than the Central America clade, it is possible that a migration happened from the
710 Greater Antilles to Mexican territory. In this scenario, the Greater Antillean parrots would be
711 derived from species inhabiting northern South America, whose lineages became extinct and
712 therefore are not present in inferring phylogenies. According to our molecular dating, the
713 colonization of the Central America could happen between 3.4 to 2.5 mya (**Fig. 14**). These event
714 is in agreement with dating of decrease in sea level, which started to systematically fall since 3
715 mya and in the period 3.4 to 2.5 mya descended even 50 m below the present level (Hansen et al.
716 2013), which could have facilitated the migrations.

717 In the case of the Lesser Antillean parrots the situation seems clearer. The presence of three
718 separated clades placed within South American parrots suggests independent migrations from the
719 mainland to the islands as it as proposed by Bond (1963). Our estimations indicate that it could
720 have happened about 3.2, 1.5 and 1.3-0.8 mya, which well correspond with the decrease in sea
721 level initially by 25 m and after 2.5 mya by more than 50 m with relation to the Pleistocene
722 glaciations (Hansen et al. 2013). However, we cannot exclude the opposite direction of
723 migrations, from islands (the Lesser Antilles) to the mainland (the northern coast of Venezuela) as
724 it was recently proposed for the origin of Yellow-headed Amazon parrots (Urantowka et al.
725 2014). Nevertheless, the obtained results show a complex history for parrots within the Caribbean
726 region (Russello & Amato 2004) related probably with the refugial and insular character of its
727 habitats. Additional studies are required to solve in detail the migration routes.

728 The Amazon parrots have been subjected to evolutionary expansion since the last 5 mya. Their
729 earliest diversification may be associated with adaptive radiation which has been triggered by the
730 arrival of Arini parrots in South America from Africa (Schweizer et al. 2014). Other important
731 factors could be drainage evolution in Amazonia and Pleistocene climatic oscillations (**Fig. 14**)
732 causing alterations and partitioning of habitats, sea level changes influencing colonization of
733 islands (and again mainland) as well as recurrent elevational migrations (Ribas et al. 2012; Rull
734 2011; Schweizer et al. 2014). These processes could cause the differentiation of populations into
735 new lineages. One of such recently evolving lineage could represent the newly described Amazon
736 parrot. Schweizer et al. (2014) studying the diversity of Neotropical parrots (including members
737 of Arini and Androglossini clades) found no evidence of the slowdown in their speciation rate and
738 discovered two young, unexpectedly species-rich clades represented by *Pyrrhura* and *Aratinga*.

739   Although these two clades originated in the late Miocene/Pliocene, speciation within each clade

740   took place mainly during the Pleistocene. The same can be observed in the case of at least some

741   *Amazona* lineages (**Fig. 14**).

742   ## 5. Conservation aspects

743   If the newly described *Amazona* represents the species status must be regarded as critically

744   endangered (CR) based on IUCN (International Union for the Conservation of Nature) Red List

745   of Species criteria, as all new species described in recent decades. Its habitat has been

746   significantly altered. This parrot is confined to a small area and no parts of its range are currently

747   protected. Because of this precarious status, the Mexican wildlife authorities are urged to regard

748   it as "Especie en Peligro de Extinción" (Endangered species), in following established guidelines

749   (Norma Oficial Mexicana NOM-059-SEMARNAT-2010). This *Amazona* does not undergo

750   displacement, making them confined to a small area of lowland native forest and interspersed

751   altered plots containing native vegetation. Through the publication of this description, we are

752   alerting government authorities, conservationists and local inhabitants that implementing

753   conservation measures is imperative to provide refuge for a broad array of species found within

754   the range of *Amazona (albiforns) gomezgarzai*, including this unique new member of the genus

755   *Amazona.* Because of this precarious status, the Mexican government would not allow the

756   collection of voucher specimens. Instead the authorities permitted that two individuals

757   maintained locally as pets be transported for safe keeping under the care of Dr Miguel Angel

758   Gómez Garza.

775 **Table 1.** Morphometric data (in millimeters) of the new *Amazona* compared with other similarly
776 red-fronted and –faced species of *Amazona*.

Feature	New *Amazona*	*A. a. nana*	*A. a. albifrons*	*A. a. saltuensis*	*A. xantholora*	*A. autumnalis*	*A. viridigenalis*
Wing	175.3 ♂ 170.4 ♀	167.3 ♂ (Range 149.9-170.3) 152.9 ♀ (Range 133.8-162.53)	180.9 ♂ (Range 179.3-191.0) 174.2 ♀ (Range 170.7-177.9)	182.8 ♂ (Range 175.4-191.3) 180.0 ♀ (Range 177.4-184.2)	165.1 ♂ (Range 153.0-170.8) 169.3 ♀ (Range 166.8-170.3)	217.8 * (Range 212.7-223.0)	202.4 ♂ (Range 197.1-209.1) 197.8 ♀ (Range 189.9-201.3)
Tail	89.6 ♂ 83.7 ♀	73.8 ♂ (Range 71.9-80.1) 76.5 ♀ (Range 74.6-80.1)	76.1 ♂ (Range 73.5-83.2) 77.9 ♀ (Range 75.7-81.9)	76.8 ♂ (Range 72.9-83.1) 78.8 ♀ (Range 76.1-80.8)	77.2 ♂ (Range 74.8-79.9) 77.4 ♀ (Range 75.3-79.3)	100.8 * (Range 95.1-106.5)	104.6 ♂ (Range 89.2-117.1) 105.3 ♀ (Range 103.5-107.4)
Exposed culmen	27.8 ♂ 25.7 ♀	26.4 ♂ (Range 24.9-30.5) 24.9 ♀ (Range 24.7-25.2)	26.5 ♂ (Range 24.0-28.1) 24.2 ♀ (Range 23.6-25.2)	25.1 ♂ (Range 23.8-27.3) 24.0 ♀ (Range 23.8-27.5)	26.1 ♂ (Range 25.4-26.6) 24.8 ♀ (Range 24.7-25.0)	30.4 * (Range 27.9-32.9)	29.9 ♂ (Range 28.5-31.7) 27.0 ♀ (Range 24.2-28.6)

777 Three individuals of each sex were measured for each taxon, except for *Amazona autumnalis* in which six
778 birds of unknown sex were taken into account. Data were collected from living birds of known
779 provenance and preserved skins in the collection of the Museo de las Aves de México (MAM), in Saltillo.
780 The museum specimens are identified as: *Amazona albifrons albifrons* MAM 1076; *A. albifrons nana*
781 MAM 2780, MAM 2217, MAM 2988, MAM 2433, MAM 1726*; A. viridigenalis* MAM 132, MAM 133,
782 MAM 2725, MAM 1878, MAM 1548, MAM 1715, MAM 1723, MAM 1775, MAM 1377, MAM 2216,
783 MAM 1547*; A. autumnalis autumnalis* MAM 2989, MAM 2987, MAM 1883, MAM 2448, MAM 1827,
784 MAM 134; *A. xantholora* MAM 1948, MAM 737; * Unsexed specimens. Geographic origin of studied
785 individuals: *A. albifrons nana*: Zoologico de Merida, from the local population; *Amazona albifrons*
786 *albifrons*: Planetaro Alfa, Monterrey, from the Guerrero population; *Amazona albifrons saltuensis*:
787 Acuario de Mazatlán (a public aquarium that also displays birds), from Sinaloa specimens; *A. xantholora*:
788 Zoologico de Merida, from the local population; *A. autumnalis autumnalis*: Planetario Alfa, from the
789 southern Tamaulipas population; *A. viridigenalis*: Planetario Alfa, from the southern Tamaulipas
790 population.

791   **Table 2.** Comparison of differences in face coloration of the new *Amazona* and other similarly
792   red-fronted and –faced species of *Amazona* from Mexico and Mesoamerica.

Species	Forehead	Lores	Cheeks	Crown	Black ear patch	Black scalloping contour feathers (face)
New *Amazona*	red	red	green	green	absent	present
A. albifrons nana	white	red	green	bluish	absent	subtle
A. a. albifrons	white	red	green	blue	absent	subtle
A. a. saltuensis	white	red	green	blue	absent	subtle
A. xantholora	white	yellow	green	bluish	present	present
A. autumnalis autumnalis	red	red	yellow	bluish	absent	absent
A. viridigenalis	red	red	green	bluish	absent	absent

793 **Table 3.** Morphological traits of the new *Amazona* compared with other similarly red-fronted and
794 -faced species of *Amazona,* including other species occurring in the Yucatán Peninsula (*A.*
795 *albifrons nana, A. xantholora, A. autumnalis*).

| Species	Average weight (grams)	Average length (cm)	Head coloration	Wing coloration	Tail coloration
New *Amazona*	200	25	Male: Forehead and forecrown red; rear crown feathers subtle bluish tipped; periophthalmic ring red. Female: Forehead red.	Underside of wings green, except tips of primaries which are bluish green.	Green, bluish tipped; three lateral tail feathers red on inner part.
A. albifrons nana	205	23	Male: forehead and forecrown white, posterior border blue; periophthalmic ring and lores red. Female: white on forehead and red of periophthalmic ring greatly reduced.	Primary coverts red in male, green or red greatly reduced in most females; primaries green, dark blue towards tip; secondaries blue; under-wing coverts green.	Green, yellowish-green towards tip; base of lateral feathers red.
A. a. albifrons	230	26	As *A. a. nana*, but green slightly darker.	As *A. a. nana.*	As *A. a. nana.*
A. a. saltuensis	230	26	As *A. a. albifrons*, but blue crown extends to nape.	As *A. a. nana.*	As *A. a. nana.*
A. xantholora	200	23	Male: Forehead and forecrown white, posterior blue; lores yellow; periophthalmic ring red; ear coverts preeminently black. Female: all head colors significantly reduced, except for the crown, which is blue.	Primary and secondary flight feathers green, blue towards tip; underside of wings greenish-blue; red on shoulder present in some individuals, mainly males.	Tail green, yellowish-green towards edge; lateral tail feathers red at base.
A. autumnalis autumnalis	350	34	Forehead and upper part of lores red, lower part of lores and cheeks yellow, strongly hinted with red in some individuals from Mexico; crown blue	Primary and secondary flight feathers green, becoming dark blue towards tips; first five secondaries with red wing-speculum.	Green with greenish-yellow tips; outer webs of outer tail feathers blue.
A. viridigenalis	270	33	Forehead, upper lores and crown red; dark blue extends from rear part of eye and occiput to encircle cheeks, which are lighter green. Females have less red on head and some old males acquire several yellow feathers to the nape.	Outer webs of primaries violet-blue; secondaries with blue tips; first five secondaries with red wing-speculum.	Green, with green-yellow tips.

796 Three individuals of each sex were measured for each taxon, except for *Amazona autumnalis* in which six
797 birds of unknown sex were taken into account.

798   **Fig. 1.** Map of Yucatán Peninsula with the location of site (asterisk), where the new *Amazona* was
799   found.
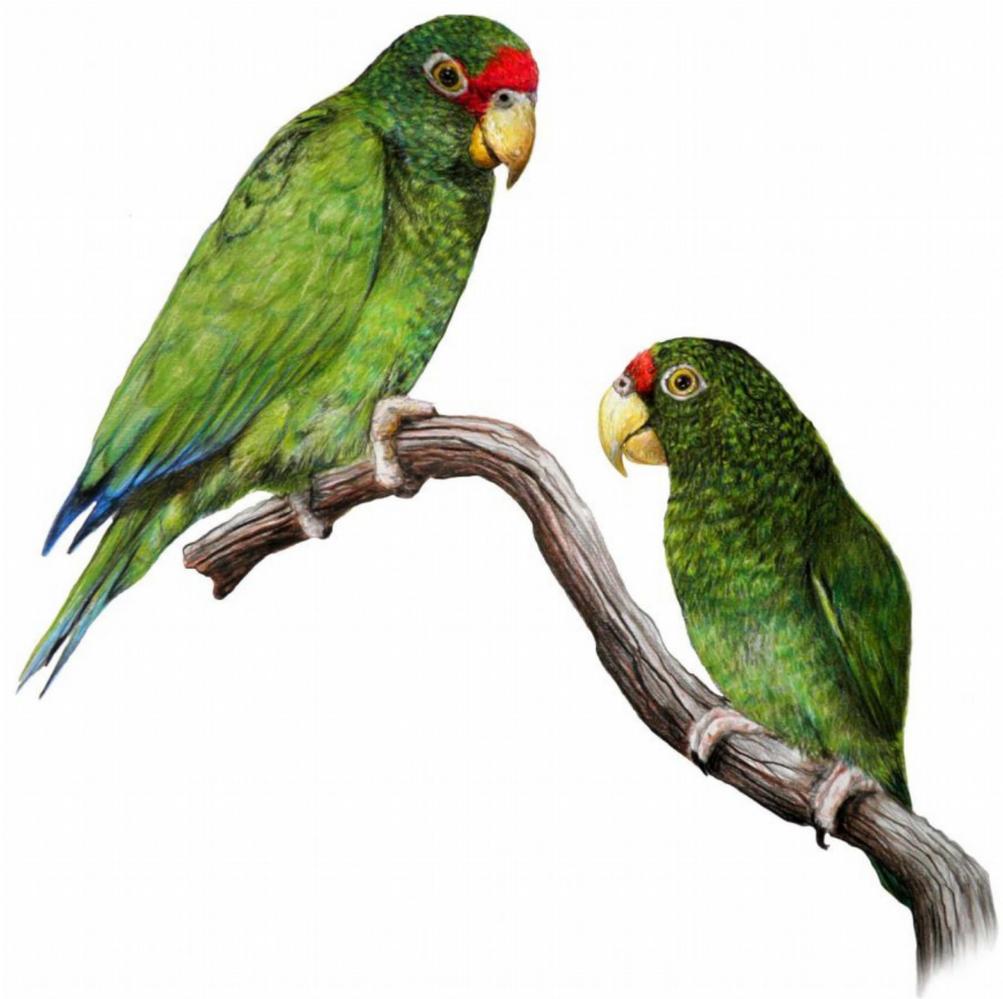
800   **Fig. 2.** Illustration of the new *Amazona*. Male holotype (left) and female allotype (right).
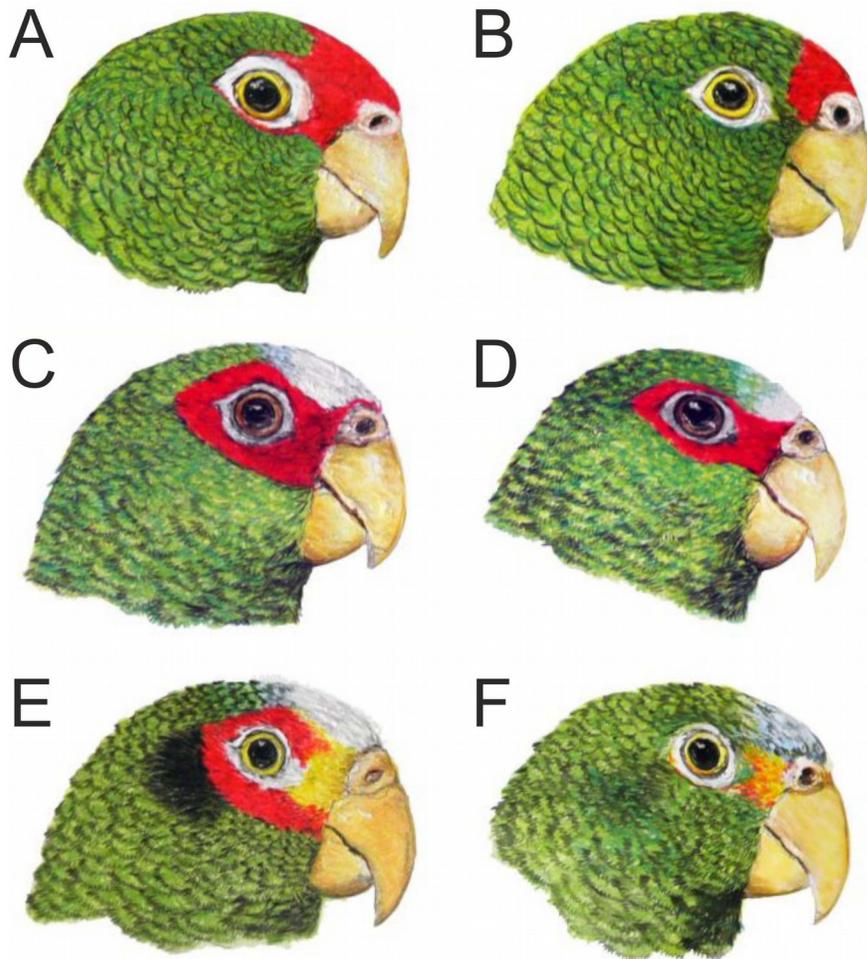
801   **Fig. 3.** Head coloration in the male (A) and female (B) of the new *Amazona* in comparison to
802   both sexes of congeners *Amazona albifrons nana* (C – male; D – female) and *Amazona*
803   *xantholora* (E – male; F – female), also from the Yucatán Peninsula, Mexico. The three taxa are
804   the smallest members of the genus *Amazona*.
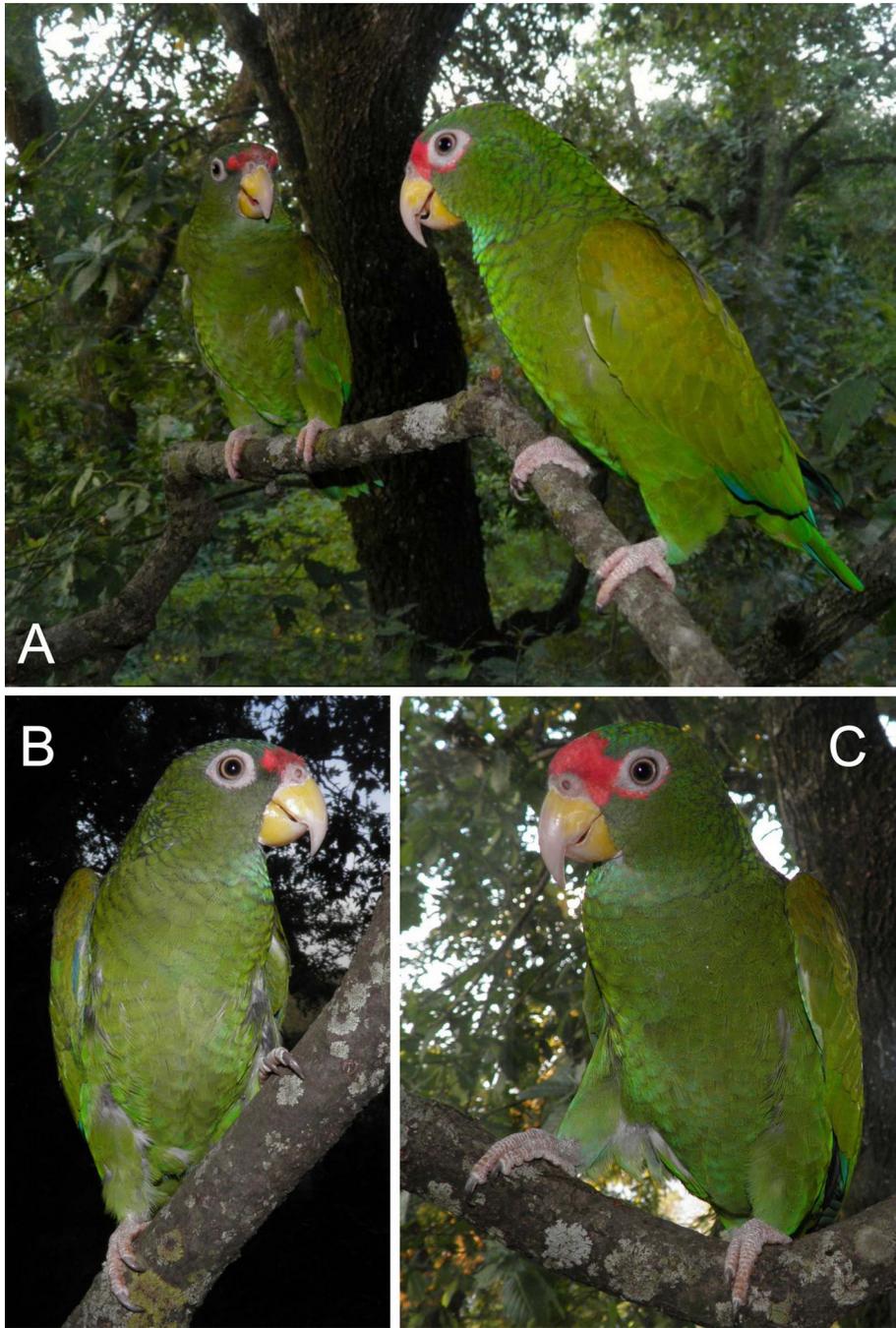
805 **Fig. 4.** Photograph of the male holotype (panel C and panel A - individual on the right) and
806 female allotype (panel B and panel A - individual on the left) of the new *Amazona*.
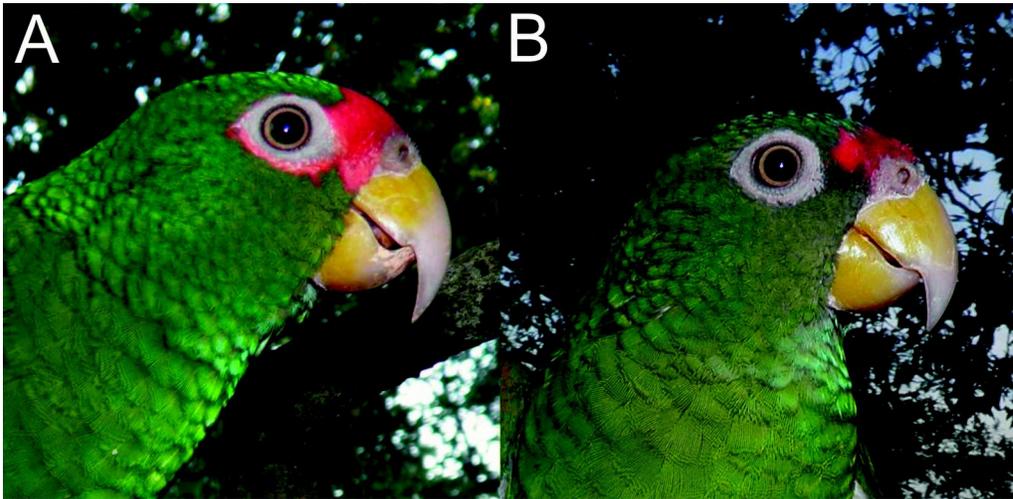
807 **Fig. 5.** Photographs of the head of male holotype (A) and female allotype (B) of the new
808 *Amazona.*
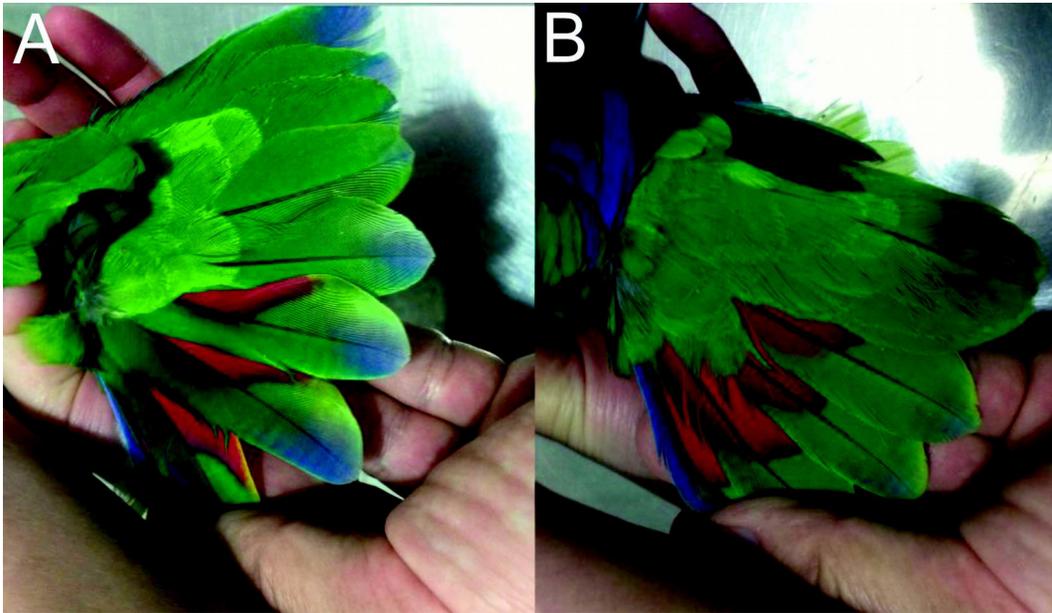
809   **Fig. 6.** Open tails showing colored bands of male holotype (A) and female allotype (B) of the
810   new *Amazona*.
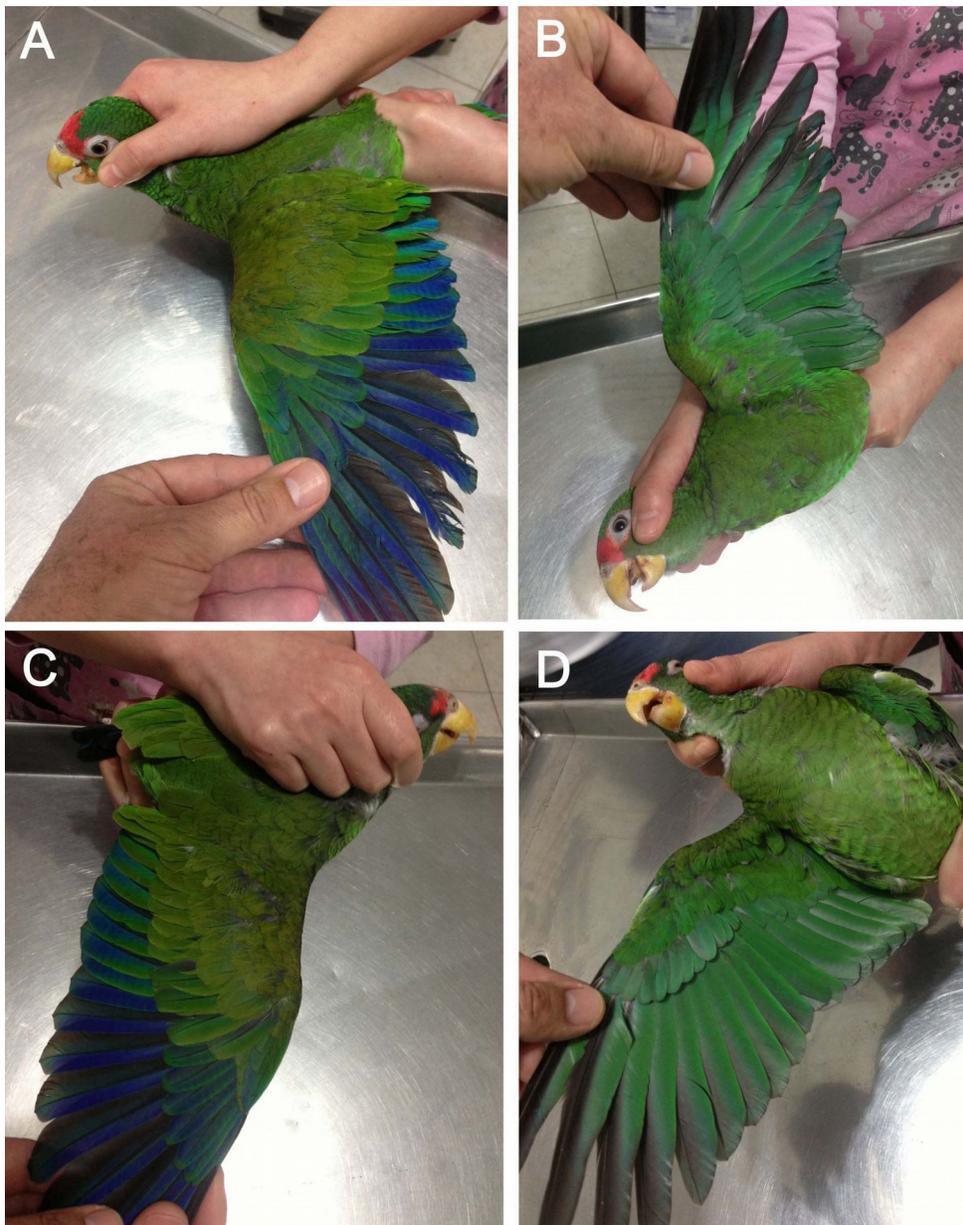
811   **Fig. 7.** Open upper (A) and underside of wing (B) of male holotype as well as open upper (C) and
812   underside of wing (D) of female allotype of the new *Amazona*.

813
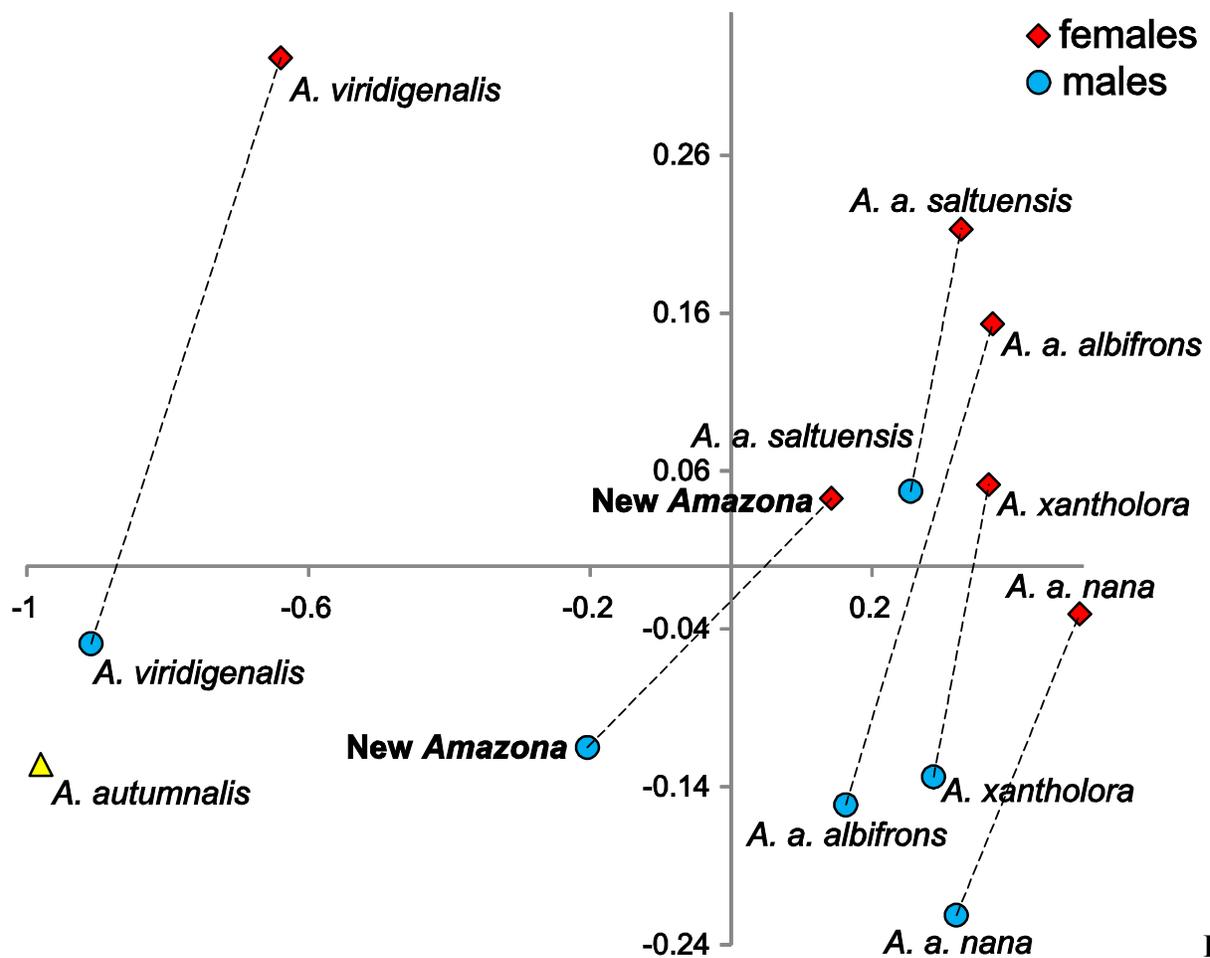
8. The plot of the two factor coordinates from Principal Component Analysis for *Amazona* parrots
displaying red in the head from Mexico and Mesoamerica separated into sexes based on three
metric parameters (length of wing chord, length of tail, culmen). Symbols represented the same
species were connected by dashed lines. The individual for *A. autumnalis* did not have assigned
sex.
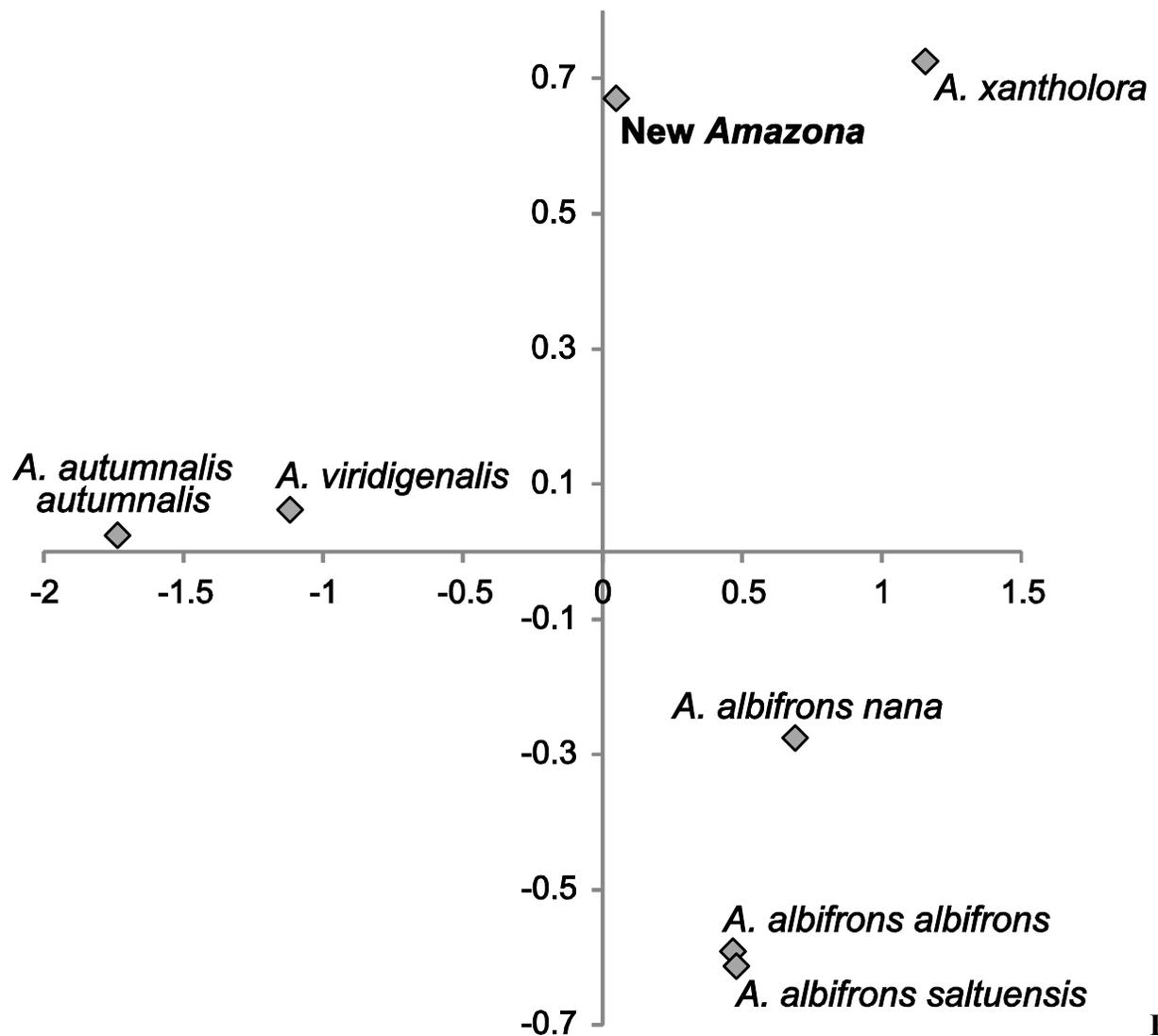
819
820 **. 9.** The plot of the two-factor coordinates from Principal Component Analysis for *Amazona*
821 species displaying red head feathers from Mexico and Mesoamerica based on all morphometric
822 features.
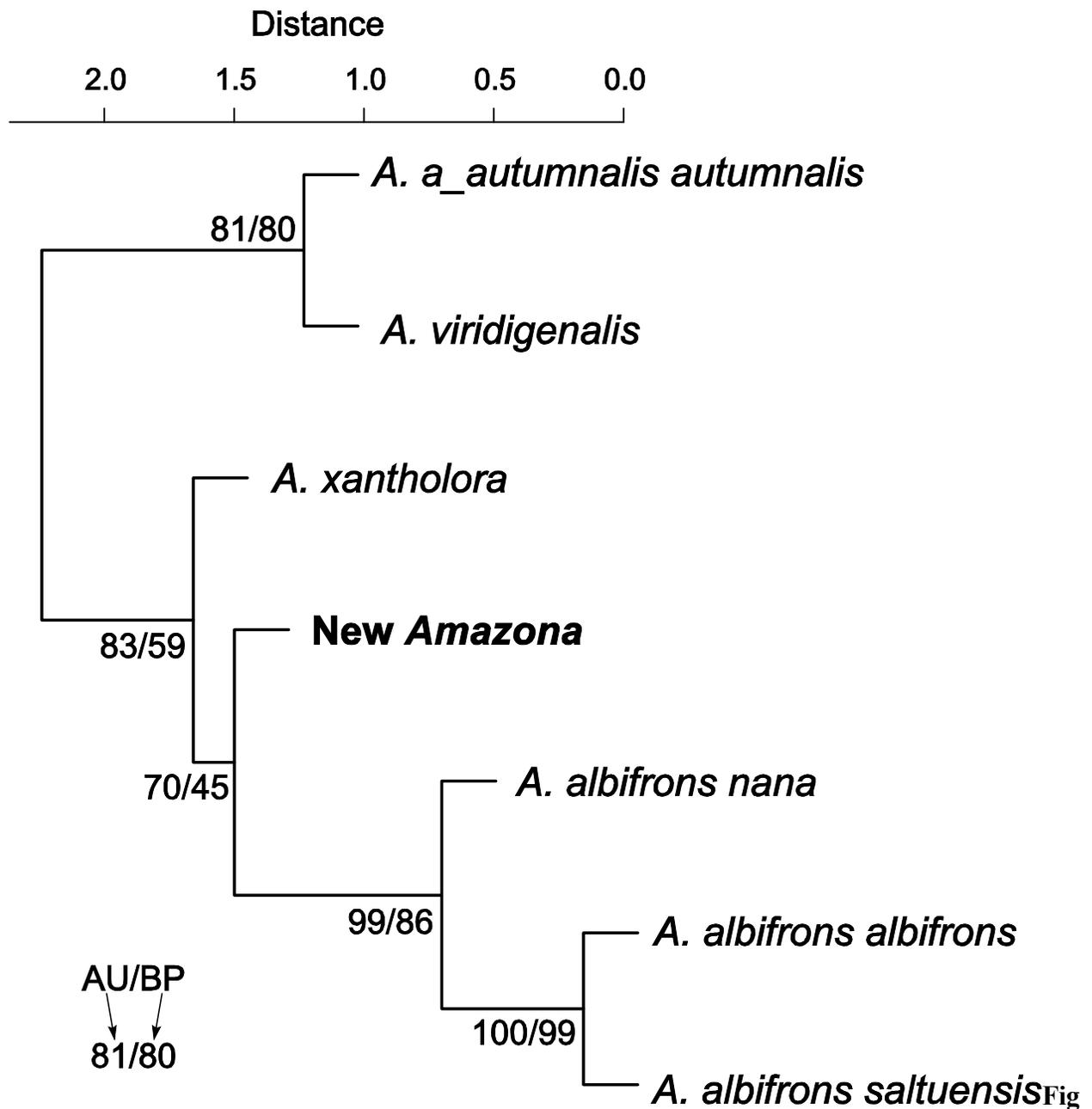
823
824 . 10. UPGMA dendrogram clustering parrot taxa according to five metric parameters (body
825 weight and length, length of wing chord, tail and exposed culmen) and six morphological discrete
826 characters (body weight, total length, length of wing chord, tail length, exposed culmen).
827 Numbers at nodes correspond to p-values expressed as percentages calculated using
828 approximately unbiased test (AU) and bootstrap resampling (BP), respectively.
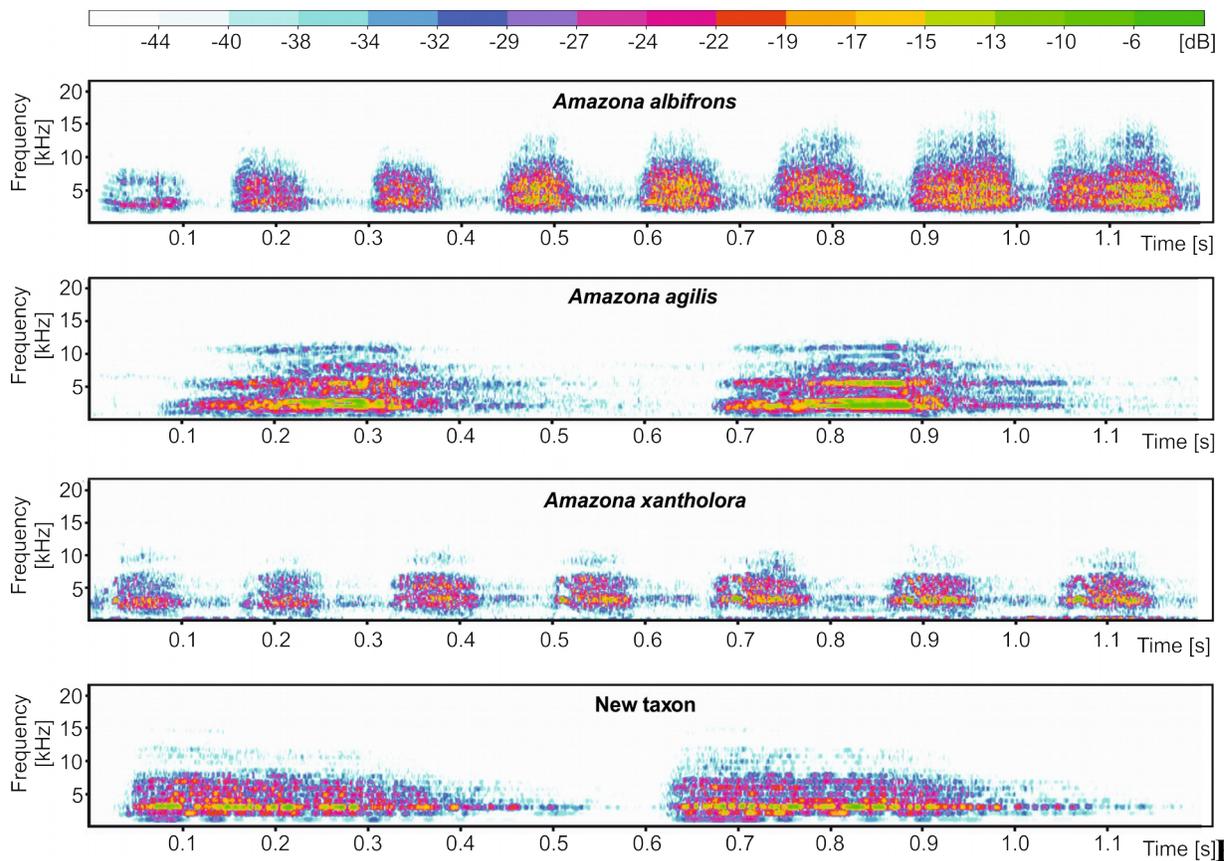
829
830   . **11.** Comparison of example sonogram for the new taxon with two other *Amazona* parrots from
831   Central America and closely related *Amazona agilis* from the Greater Antilles.
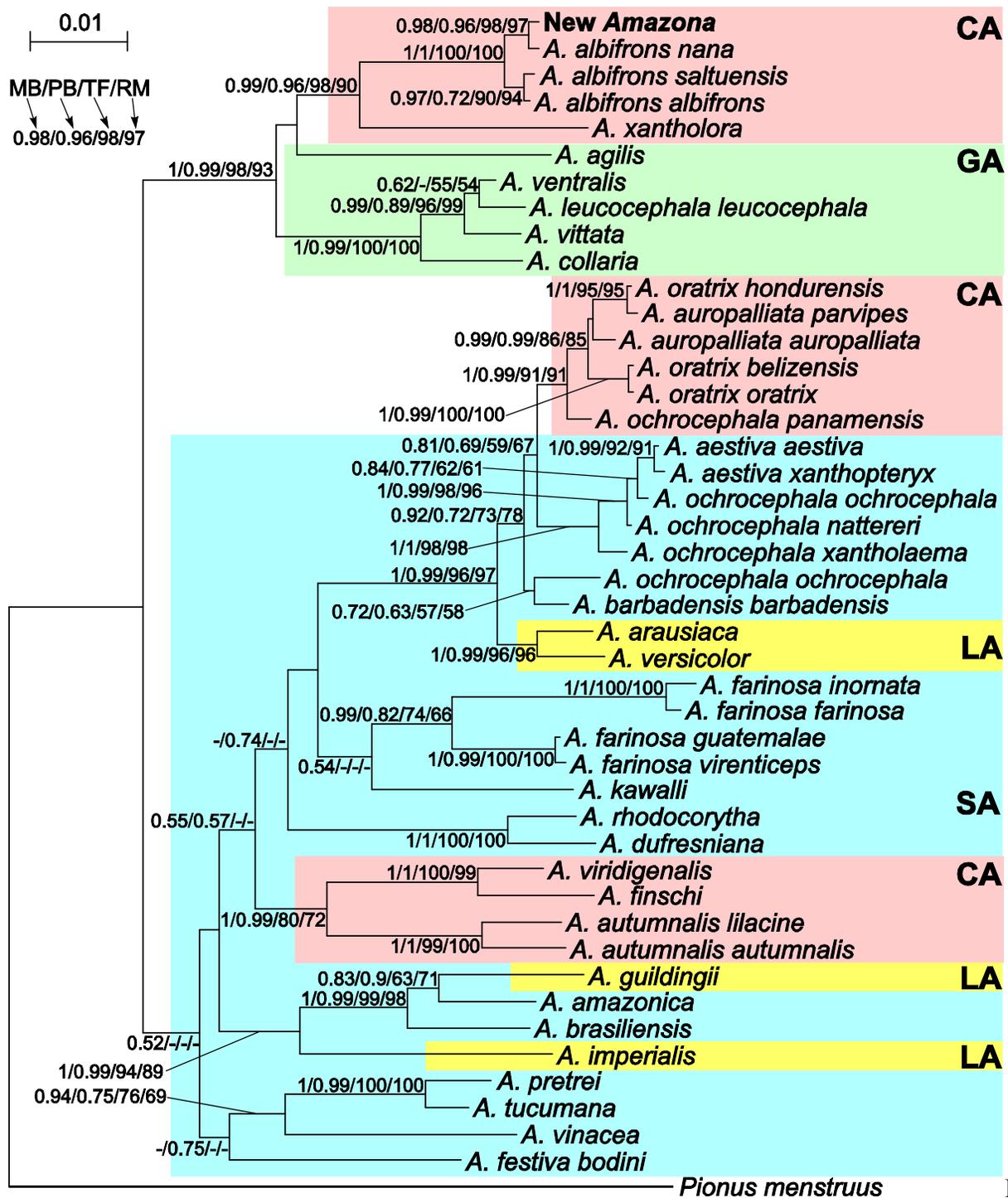
832
833 **. 12.** MrBayes maximum clade credibility tree for the concatenated alignment of genes for COI,
834 12S and 16S rRNA sequences from *Amazona* taxa and *Pionus menstruus* species (as outgroup).
835 Numbers at nodes, in the order shown, correspond to: posterior probabilities estimated in
836 MrBayes (MB) and PhyloBayes (PB), and bootstrap support values obtained in TreeFinder (TF)
837 and RAxML (RM). Values of the posterior probabilities and bootstrap percentages lower than
838 0.50 and 50%, respectively, were omitted or indicated by a dash "-". CA – Central America
839 parrots; GA – Greater Antillean parrots; LA – Lesser Antillean parrots; SA –South America
840 parrots.
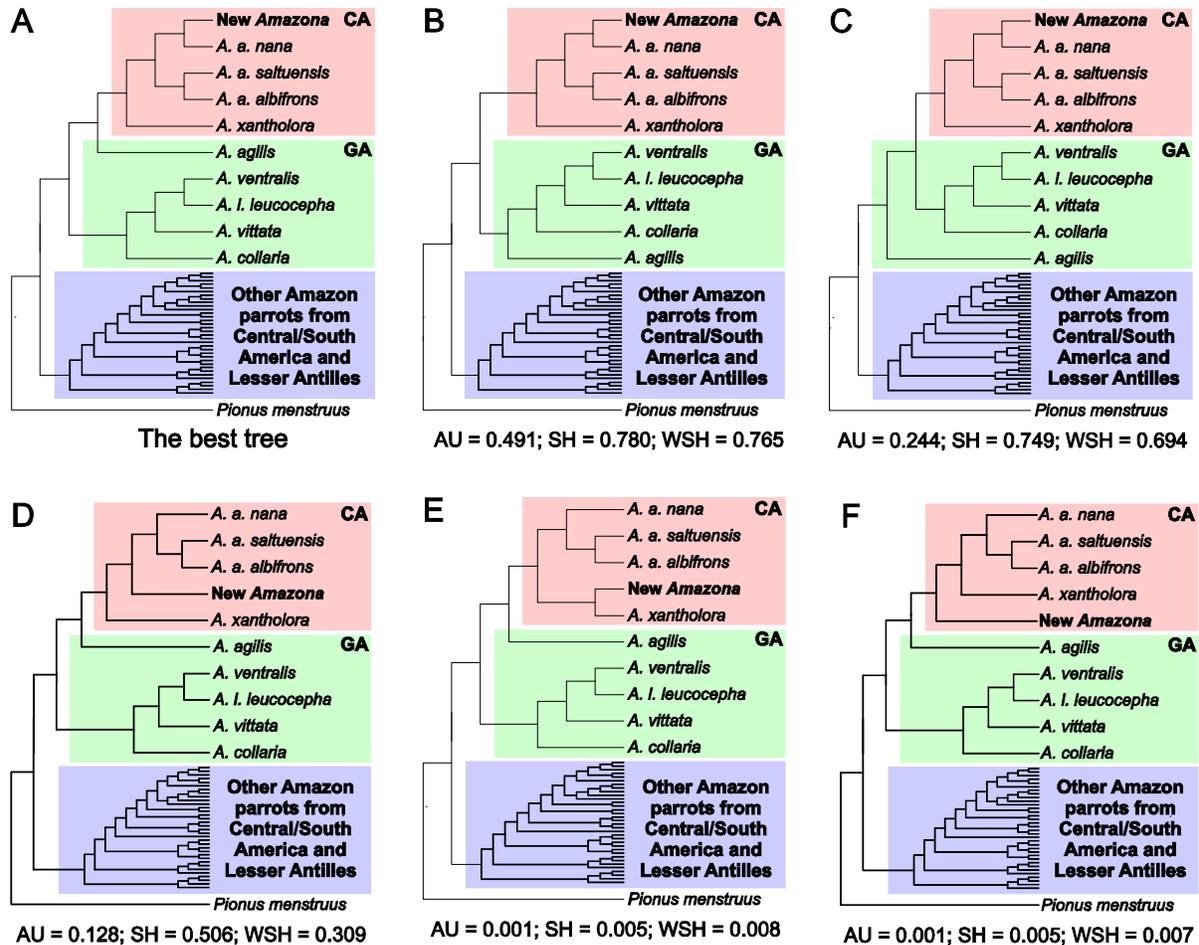
841   **Fig**
842 **. 13.** Alternative tree topologies assuming different placement of *A. agilis* (B and C) and the new
843 *Amazona* (D, E, F) in comparison to the best found tree (A). P-values of approximately unbiased
844 (AU), Shimodaira-Hasegawa (SH) and weighted Shimodaira-Hasegawa (wSH) tests were shown.
845 Only trees E and F are significantly worse than the best tree, whereas B, C and D cannot be
846 rejected. SA –South America parrots; GA – Greater Antillean parrots; CA – Central America
847 parrots.
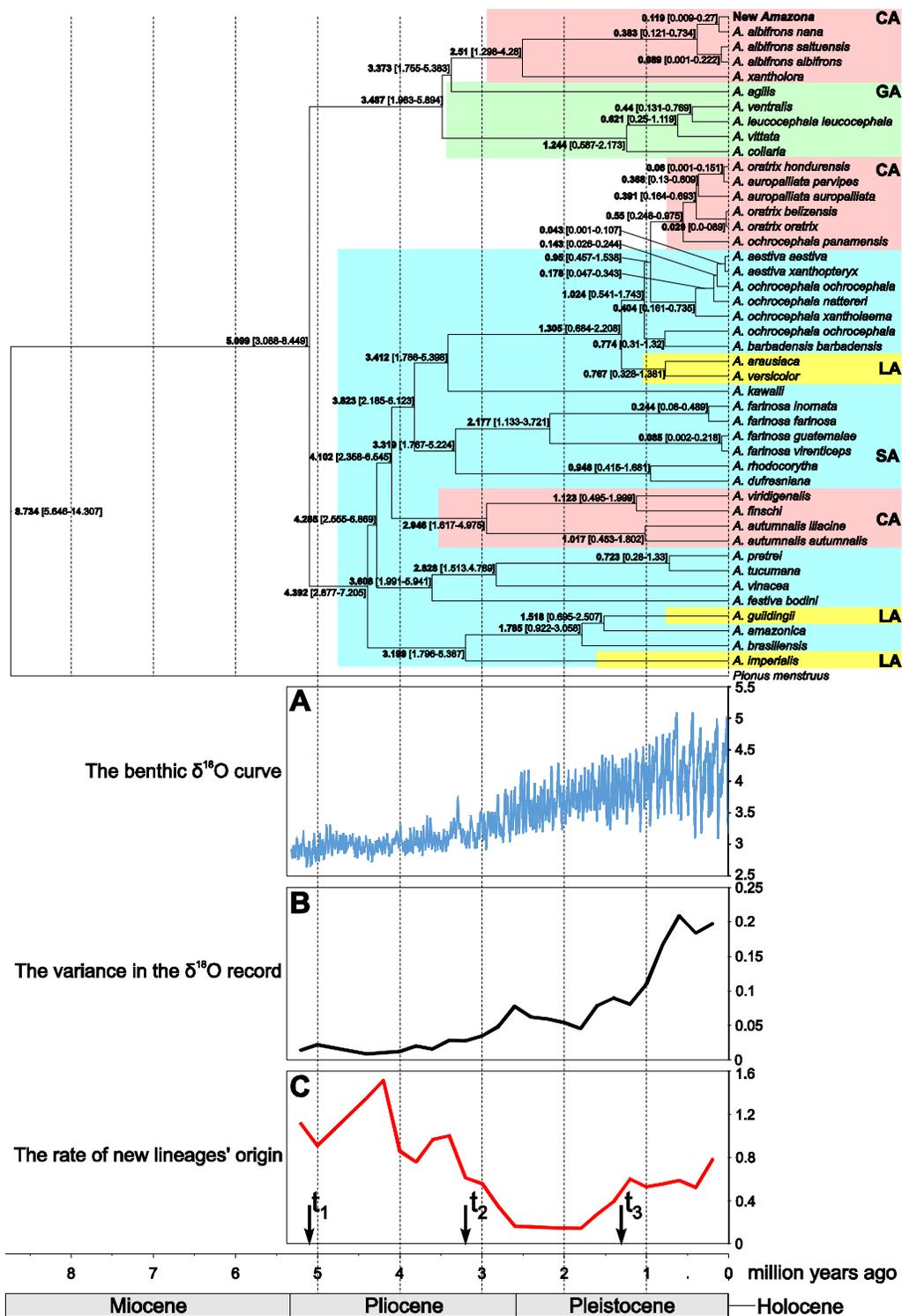
Fig. 14.
Maximum clade credibility tree obtained in Beast for the concatenated alignment of genes for COI, 12S and 16S rRNA sequences from selected *Amazona* taxa and *Pionus menstruus* species (as outgroup). Mean (in bold) ages as well as the 95% highest posterior density distributions (in parenthesis) are shown for particular nodes. CA – Central America parrots; GA – Greater Antillean parrots; LA – Lesser Antillean parrots; SA –South America parrots. The tree was compared with benthic δ18O curve according to Lisiecki & Raymo (2005) (A), the variance in the δ18O records (B) and the rate of new lineages' origin (C). Arrows t1, t2 and t3 in C indicate times in which the speciation rate shifts to a new rate according to the best-fitting yule4rate model.

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