A new parrot taxon from the Yucatán Peninsula, Mexico - its position within genus *Amazona* based on morphology and molecular phylogeny (#14707)

Second revision

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Michael Wink / 21 Apr 2017

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A new parrot taxon from the Yucatán Peninsula, Mexico - its position within genus *Amazona* 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 can represent a new species. However, the phylogenetic tree based on mitochondrial markers shows 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 tree topology tests and morphometric analyses, we can conclude that the new parrot represents a recently evolving species, whose taxonomic status should be further confirmed. 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*. 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 their 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 can represent a new species. However, the phylogenetic tree based on mitochondrial markers shows 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 tree topology tests and morphometric analyses, we can conclude that the new parrot represents a recently evolving species, whose taxonomic status should be further confirmed. 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*. 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 their 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 neotropical with a distribution that extends from northern 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 distinguish 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 genus *Amazona* 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 (Barrowclough et al. 2016); it was formerly regarded as a subspecies of *A. dufresniana (Forshaw 1973)*. 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), whose distinctness was first noted by the senior author (Silva 1991). 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 genus *Amazona* contains 30 species, e.g. Clements et al. (2016).

67   1.2.   *Amazona* species native to Mexico and finding the new dimorphic *Amazona*

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

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

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

71   Mexico. The Mexican Amazon parrots can be divided into three groups with different coloring:

72   1) having variable amounts of yellow on the head (*A. oratrix, A. auropalliata*); 2) predominately

73   green with only blue on the head (*A. farinosa guatemalae*); and 3) possessing various tonalities of

74   red in the head invariably accompanied by blue (*Amazona viridigenalis, A. finschi*), yellow

75   (*Amazona xantholora, A. autumnalis*) or white (*Amazona xantholora, A. albifrons*).

76   Monomorphism is the rule in the genus *Amazona*. However, two species, *Amazona albifrons* (all

77   three subspecies) and *Amazona xantholora,* display significant dimorphism: males possess much

78   more colorful heads and a more extensively red colored alula and wing speculum (Gómez Garza

79   2014; Silva 1991).

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

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

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

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

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

85   and *Amazona xantholora*.

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

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

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

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

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

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

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

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

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

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

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

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

98   phylogeography.

2. Materials and methods

2.1. The new *Amazona* sampling

101   Living specimens of known morphological types of both sexes (male holotype and female

102   paratype – see **Fig. 4-7**) of the new *Amazona* were collected in the Yucatán Peninsula in Mexico,

103   south of Becanchén in Tekax Municipality. However, the detailed location is not provided here

104   due to conservation reasons. Both individuals are now maintained as living birds in Mexico by

105   Miguel Angel Gómez Garza with the permission and authorization of the Procuraduría Federal de

106   Protección al Ambiente (PROFEPA), the national wildlife protection agency. Tail feathers from

107   both specimens were used for DNA isolation and were also deposited in the collection of the

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

109   León, Mexico. This material is assigned the following catalog numbers: MGG01-*Amazona*

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

111   feathers. Both the living holotype and paratype will be ceded with the authorization of PROFEPA

112   to the Laboratorio de Ornitología, Facultad de Ciencias Biológicas, Universidad Autonóma de

113   Nuevo León, Mexico, upon their death.

114   We checked the collections of six museums rich in Mexican birds for possibly misidentified

115   specimens of the new taxon that could have been used as type specimens: Museo Nacional de

116   Historia Natural in Madrid (Spain), the collection belonging to the Estación Biológica de Doñana

117   in Seville (Spain), the Field Museum of Natural History in Chicago (USA), Museo de las Aves de

118   México in Saltillo (Mexico), Laboratorio de Ornitología, Universidad Autónoma de Nuevo León

119   (Mexico) and the Laboratorio de Ornitología de la Universidad Nacional Autónoma de México

120   (Mexico). However, we did not find any specimens with characteristics of the new taxon.

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

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

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

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

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

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

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

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

129　D2EB3635397C. The online version of this work is archived and available from the following
130　digital repositories: PeerJ, PubMed Central and CLOCKSS.

131　In taxonomic circles, there has been much debate about the deposition of preserved voucher
132　specimens when naming a species (Donegan 2008; Dubois & Nemésio 2007; Nemesio 2009). In
133　the current case, the precarious status of the new *Amazona*, which warrants a listing of Critically
134　Endangered (CR) under IUCN (International Union for the Conservation of Nature) criteria
135　makes the collection of a preserved specimen ethically impossible; the taking of two living
136　specimens will permit their nesting biology in captivity to be studied, as the birds are held in a
137　manner that should allow them to breed; when such breeding takes place, details on incubation
138　and the development of the young can be documented.

139　A precedent for naming species without the formal deposition of such type was proposed by
140　Smith et al. (1991) and was followed by others (Athreya 2006; Gentile & Snell 2009; Jones et al.
141　2005). Three former secretaries of the International Commission on Zoological Nomenclature
142　support the view that the CODE allows the naming of a species without the collection of a
143　voucher specimen in particular circumstances, see Polaszek et al. (2005) and Wakeham-Dawson
144　et al. (2002). Moreover, Article 16.4.2 of the CODE states that where the holotype is an extant
145　individual, a statement of the intent to deposit the individual in a collection upon its death
146　accompanied by a statement indicating the name and location of that collection is sufficient.

147　Herein, the authors follow Böhme & Ziegler (1997) in naming a new species based on a living
148　specimen, but the recommendation by Dubois (2009), who suggested that museums be contacted
149　for the existence of specimens that had not erstwhile been recognized, was followed to no avail
150　for the new *Amazona*. In lieu of an onomatophore specimen of the new parrot, the authors
151　deposited feathers from the holotype and paratype as vouchers in following Smith et al. (1991),
152　per the recommendation of Donegan (2008) and in compliance with Article 72.5.1 of the CODE,
153　which states that a type may be an animal or any part of an animal. Article 16.4.2 of the CODE
154　will be met with the deposition in a secure collection of the extant, caged individuals from whom
155　the feathers were removed upon their death. The photographs and illustrations that accompany
156　this description represent the designated holotype and paratype. The authors thus believe that
157　they have met all thresholds to adequately name for the new *Amazona* taxon.

158   2.2. Morphometric and vocalization data collection and analysis

159   Adult specimens of parrots were collected evenly throughout the whole year without focusing on

160   a specific season. We observed no great variation of weights between individuals of the same

161   species. We examined them according to five metric features: body weight, total length, length of

162   wing chord, tail length and exposed culmen, as well as six morphological discrete characters:

163   coloration of forehead, lores, cheeks and crown, the presence of black ear patch and black

164   scalloping on contour feathers on the face (**Table 1, 2 and 3**). The measurements were taken by

165   one person (TS) using Fischer Scientific digital caliper with the resolution of 0.1 mm. Three

166   individuals of each sex were measured for each taxon, except for *Amazona autumnalis* in which

167   six birds of unknown sex were taken into account. In the case of the new *Amazona*, only two

168   specimens were collected and analyzed in details because of its endangered status but several

169   small groups with up to 12 individuals were additionally observed and studied in the field. To use

170   the different morphometric features simultaneously in multivariate studies, we normalized their

171   values using the minimum-maximum method: (value-min)/(max-min). The metric features were

172   first averaged per the particular taxon or sex before the normalization. The morphological

173   discrete characters were coded as 1 (when the character was present), 0 (when it was absent) or

174   0.5 (when it has an intermediate state).

175   The Principal Component Analysis (PCA) was done using the Statistica software (StatSoft_Inc.

176   2011). In the analysis, covarion matrix was used on the normalized data to calculate principal

177   components. Hierarchical clustering of parrot taxa was performed on the normalized

178   morphometric features using pvclust function in R package (R_Core_Team 2015) assuming

179   Euclidean distance and UPGMA as agglomeration method. To estimate the uncertainty in the

180   clustering, AU (Approximately Unbiased) p-value and BP (Bootstrap Probability) value were

181   calculated for each cluster with bootstrap resampling assuming 1000 replications. The AU p-

182   value, which is computed by multiscale bootstrap resampling, is considered a better

183   approximation to unbiased p-value than the standard BP value computed by normal bootstrap

184   resampling (Shimodaira 2004).

185   High quality parrots' vocalization files were downloaded from Avian Vocalizations Center

186   (AVoCet, http://avocet.zoology.msu.edu) and xeno-canto database (http://www.xeno-canto.org):

187   AV14063 (*Amazona albifrons*) recorded by Pamela C. Rasmussen, AV11523 (*Amazona agilis*)

188 recorded by Brian K. Schmidt, XC77749 (*Amazona xantholora*) recorded by Mary Beth Stowe,

189 XC282102 (*Amazona albifrons*) recorded by Oscar Humberto Marin-Gomez as well as XC97904

190 (*Amazona agilis*) and XC5942 (*Amazona xantholora*) both recorded by Richard C. Hoyer. The

191 files together with call records obtained for the new taxon were processed and analyzed in

192 Avisoft-SASLab 5.209 (Sound Analysis and Synthesis Laboratory) and Sound Analysis Pro 2011

193 (Tchernichovski et al. 2000), in which syllable units were identified (segmented by amplitude)

194 and their statistic features were derived. These features were next studied by Discriminant

195 Function Analysis (DFA) including Canonical analysis (CA) using the Statistica software

196 (StatSoft_Inc. 2011) as well as by non-parametric Kruskal-Wallis test and Dunn's test of post-hoc

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

198 (R_Core_Team 2015).

199   2.3. DNA extraction and amplification

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

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

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

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

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

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

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

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

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

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

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

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

212 GenBank database under accession numbers: KU605663-8.

213   2.4. Phylogenetic analyses

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

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

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

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

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

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

220   COI (561bp).

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

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

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

224   2004) and RAxML 8.2.3 (Stamatakis 2014). The best-fit partitioning schemes were selected

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

226   TreeFinder, we also applied these partitioning scheme using models suggested by TreeFinder

227   Propose Model module based on BIC for these partitions. Moreover, to specify appropriate

228   substitution models across the larger space in the Bayesian MCMC analysis (Huelsenbeck et al.

229   2004), we used mixed models in MrBayes analysis.

230   In the MrBayes analysis, two independent runs starting from random trees were applied, each

231   using 4 Markov chains. Trees were sampled every 100 generations for 10,000,000 generations. In

232   the final analysis, we selected trees from the last 4,082,000 generations that reached the

233   stationary phase and convergence (i.e. the standard deviation of split frequencies stabilized and

234   was lower than the proposed threshold of 0.01). In PhyloBayes, we used CAT-GTR model with

235   rate variation across sites modeled by five discrete rate categories of gamma distribution. The

236   number of components, weights and profiles of the model were inferred from the data. Two

237   independent Markov chains were run for 100,000 generations in each of these analyses. The last

238   85,000 trees from each chain were collected to compute posterior consensus trees after reaching

239   convergence, when the largest discrepancy observed across all bipartitions (maxdiff) was below

240   recommended 0.1. We set search depth to 2 in TreeFinder and applied 1000 distinct ML searches

241   on 1000 randomized stepwise addition parsimony trees in RAxML. To assess significance of

242   particular branches, non-parametric bootstrap analyses were performed on 1000 replicates in

243   these two programs.

244   Tree topologies assuming different relationships between parrots from the Greater Antilles and

245   Central America as well as the alternative position of the newly described *Amazona* were

246   compared according to approximately unbiased (AU), Shimodaira-Hasegawa (SH) and weighted

247   Shimodaira-Hasegawa (wSH) tests, which were performed in Consel v0.20 (Shimodaira &

248 Hasegawa 2001) assuming 10,000,000 replicates. Site-wise log-likelihoods for the analyzed trees

249 were calculated in TreeFinder under the best fitted substitution models.

250 Divergence times were estimated with Beast software. As constraints for tree calibration, we

251 assumed the uniform prior distribution of the separation time between *Pionus menstruus* and

252 *Amazona* dated from 5.646 to 16.553 million years ago, and the divergence time of *A. aestiva*, *A.*

253 *dufresniana* and *A. pretrei* as dating from 2.877 to 10.502 million years ago, according to

254 Schweizer et al. (2011). We tested both strict and lognormal relaxed clock models assuming the

255 calibrated Yule model and separate substitution schemes for particular data partitions according to

256 PartitionFinder results (**Table S2**). Finally, we applied the relaxed clock model for the second

257 codon position and the strict clock model for rRNA genes as well as the first and third codon

258 positions. The decision about the selection of clock model was made based on the inspection of

259 the standard deviation of the relaxed clock assuming that its value exceeding 1 indicates a

260 significant variation among branches. The clock and substitution rates were estimated in the

261 analyses. Posterior distributions of parameters were estimated for 100,000,000 generations with a

262 sampling frequency of 1000 steps. The convergence and sufficient sampling was checked using

263 Tracer 1.6 (Rambaut et al. 2014). Effective sample size (ESS) for all parameters was larger than

264 the assumed threshold 200, which indicated sufficient convergence, sampling and chain mixing.

265 Phylogenetic trees were summarized in TreeAnnotator 2.3.1 (Drummond et al. 2012) with 10%

266 burn-in of total trees using maximum clade credibility tree and common ancestor heights. The

267 generated tree was visualized in FigTree 1.4.2 (Rambaut 2012).

268 The number of base differences per site (p-distance) between selected pair of sequences was

269 calculated in MEGA6 (Tamura et al. 2013). The analysis involved all 1485 positions in the

270 alignment. The distance was expressed as percent. Standard error was estimated by bootstrap

271 method assuming 1000 replicates.

272   2.5. Diversification rate estimation

273 The maximum clade credibility tree obtained from Beast and associated branching times were

274 used for calculation diversification rate using R package LASER 2.4 (Rabosky 2006a). In order

275 to test whether diversification rates decreased with time, we calculated the γ statistic (Pybus &

276 Harvey 2000). We also tested 11 likelihood models for diversification rates (Rabosky 2006b;

277 Rabosky & Lovette 2008) – **Table S3**. The models were compared according to the values of the

278   Akaike information criterion (AIC). Temporal variation in diversification rates was visualized

279   with yuleWindow (Nee 2001) within overlapping periods of 400 thousand years. The results of

280   diversification were compared with the $\delta^{18}O$ curve (Lisiecki & Raymo 2005), which is a good

281   climate proxy. For better visualization of climate oscillations, we calculated the variance in the

282    $\delta^{18}O$ records within the same overlapping periods.

3. Results

283   3.1. Multivariate analyses of morphometric and vocalization features

284

285   One of the most distinctive metric features that can be used to differentiate the *Amazona* parrots

286   from Mexico possessing red feathers in the head area are the length of the wing chord, tail and

287   exposed culmen (**Table 1**). To visualize these differences, we performed PCA analysis (**Fig. 8**).

288   The first two factor coordinates explained in total 94% of variance (86% and 8%, respectively).

289   In the PCA plot obtained, the first component is responsible for the separation of the species,

290   whereas the second one applies to sexual dimorphism. The first component was highly correlated

291   with all three variables: wing chord (-0.90), tail (-0.96) and exposed culmen (-0.91). Generally,

292   parrots with the largest dimensions of studied characters (*A. autumnalis* and *A. viridigenalis*) are

293   located on the left of the plot, whereas parrots characterized by smaller length values (*A.*

294   *albifrons* and *A. xantholora*) are placed on the right. The new *Amazona* with the intermediate

295   length of the wing chord, tail and exposed culmen occurs between these two extremes. The

296   second component showed the highest correlation with exposed culmen (-0.42) and is responsible

297   for the separation of sexes. Males of almost all the species are located at the lower part of the plot

298   and are characterized by the larger length of exposed culmen than females, which are placed

299   above them in the plot. Only the male of *A. a. saltuensis* is placed among females of other

300   species. In fact, the difference in this parameter between *A. a. saltuensis* sexes is smallest. This

301   taxon shows also the shortest distance between two sexes, whereas *A. viridigenalis* shows the

302   largest. The latter species is also farthest from the parrots of Central America, which are grouped

303   on the right site of the plot. The individual of *A. autumnalis* without assigned sex is closest to the

304   *A. viridigenalis* male. The male of the new *Amazona* quite clearly separates from males of other

305   Mexican taxa, whereas the female of this new form is located near the *A. a. saltuensis* male and

306   *A. xantholora* female in the plot.

307   We also compared the studied parrot taxa in PCA analysis (**Fig. 9**) using both five metric (**Table**

308   **1**) and six morphological features (**Table 2**). The first two factor coordinates explained almost

309   81% of variance (63% and 17%, respectively). The first component showed the highest

310   correlation with metric features: the total length (-0.96), wing chord (-0.94), tail (-0.94), exposed

311   culmen (-0.94) and weight (-0.90), as well as some morphological characters: coloring of

312   forehead (0.84), the presence of black scalloping contour feathers (0.79) and coloring of cheeks

313   (0.73). The second component was highly correlated with crown coloring (0.83), coloring of the

314   lores (-0.59) and the presence of a black ear patch (0.59). The first component is responsible for

315   the distinct separation of *A. autumnalis* and *A. viridigenalis* from the other Mexican parrots

316   because of their larger weight and length of studied characters as well as the absence of black

317   scalloping contour feathers. The Mexican parrots are differentiated by the second component into

318   the group of *A. albifrons* subspecies and the cluster of the new *Amazona* and *A. xantholora*. The

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

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

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

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

323   agreement with these results, the hierarchical clustering based on five metric parameters clearly

324   separates *A. autumnalis* and *A. viridigenalis* from Central America parrots (**Fig. 10**). At the base

325   of the latter group, *A. xantholora* is placed and next the new *Amazona* branches off. The

326   subspecies of *A. albifrons* create a significant cluster with *A. albifrons nana* at the base.

327   The proposed new taxon is characterized by a unique vocalization in comparison to other

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

353   (1.184), mean amplitude (1.094) and mean pitch goodness (-1.160). The largest correlations with

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

355   3.2. Molecular phylogenetic studies

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

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

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

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

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

361   region.

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

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

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

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

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

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

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

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

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

371   and *A. barbadensis*.

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

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

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

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

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

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

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

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

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

381   parrots making ==them== paraphyletic. The sister taxon to the Central American parrots is *A. agilis*

382   from the Greater Antilles. The position of *A. agilis* received no support larger than 0.5 posterior

383   probability and 50% bootstrap percentage but was indicated by all four applied methods, two

384   Bayesian and two maximum likelihood approaches. The other Greater Antillean parrots ==already==

385   form a clear monophyletic clade. To assess stability of phylogenetic position of *A. agilis*, we

386   carried out tree topology tests. They showed that trees in which *A. agilis* is clustered with other

387   Greater Antillean parrots (**Fig. 13B**) or placed at the base to all parrots from Central America and

388   the Greater Antilles (**Fig. 13C**) were not significantly worse that the best topology (**Fig. 13A**).

389   The Mexican *Amazona* taxa are also monophyletic with *A. xantholora* placed at the base to the

390   clade with the largest possible support including three subspecies of *A. albifrons* and the new

391   *Amazona*. The taxa are split into two sister subclades that are well supported. One includes *A. a.*

392   *albifrons* and *A. a. saltuensis*, whereas the newly described ==taxon== ==*Amazona*== groups with *A.*

393   *albifrons nana,* with which it is sympatric. We also tested alternative topologies with different

394   placement of the new taxon (**Fig. 13**). Interestingly, the tree assuming earlier divergence of the

395   new taxon before differentiation of *A. albifrons* subspecies (**Fig. 13D**) was not significantly worse

396   than the best one (**Fig. 13A**). However, trees with clustering the new *Amazona* to *A. xantholora*

397   (**Fig. 13E**) or the basal placement of the new parrot to the rest Central America parrots (**Fig. 13F**)

398   were significantly worse.

399   The branch leading to the new *Amazona* seems relatively short indicating a very small number of

400   substitutions in comparison to other lineages. The number of base differences per site (p-distance

401   ± standard error) expressed as percent calculated for the three markers is 0.135 ± 0.091 between
402   the new *Amazona* and *A. albifrons nana*. However, it is about two times greater than the distance
403   between two subspecies, *A. a. albifrons* and *A. a. saltuensis*, which is 0.067 ± 0.067. Similar
404   conclusions can be drawn from distance calculation for individual markers but we decided to
405   present results for the concatenated sequences because of smaller stochastic error.

406   The performed molecular dating enabled to estimate divergence time of important events in the
407   evolution of Amazon parrots (**Fig. 14**). According to these estimations, the radiation of the
408   present lineages of *Amazona* started about 5 million years ago (mya). The South American
409   parrots begun their differentiation about 4.4 mya. The Lesser Antilles were settled from South
410   America independently three times about 3.2, 1.5 and 1.3-0.8 mya. The South American parrots
411   migrated also to Central America between 4.1 to 2.9 mya and also much later between 0.95 to
412   0.55 mya giving two separate lineages. The radiation of the third Central America clade is dated
413   to 2.5 mya, whereas the whole group including additionally the Greater Antillean parrots started
414   its evolution about 3.5 mya. The small number of substitution indicates quite recent divergence of
415   the new *Amazona* from *A. albifrons nana*. Accordingly, molecular dating showed that their
416   lineages split by average 119 thousand years ago (kya) with 95% credibility interval 9 - 270 kya
417   (**Fig. 14**). The two subspecies, *A. albifrons albifrons* and *A. albifrons saltuensis* diverged slightly
418   later about 89 kya.

419   3.3. Diversification rate analyses

420   To assess if and when Amazon parrots (including the newly described taxon) were subjected to
421   increase speciation rate, we performed diversification rate analyses. The calculated γ statistic was
422   1.509 (p-value = 0.934) indicating no evidence for significant slowdown in the diversification.
423   Among eleven tested methods, a yule4rate appeared the best-fitted (**Table S3**). According to this
424   model, the first shift to a higher speciation rate (from 0.138 to 0.934) happened in $t_1 = 5.099$ mya
425   and lasted to $t_2 = 3.199$ mya, when the rate decreased to 0.229. Since $t_3 = 1.305$ mya, the
426   speciation rate again have increased to 0.644. The first increase is associated with radiation of the
427   basal *Amazona* lineages (**Fig. 14**). The period between t_1 and t_2 corresponds to the lowest
428   speciation of this genus. The final increase in diversification rate is related with emergence of
429   closely related species and subspecies. Interestingly, this period corresponds to the more intensive
430   climate fluctuations in the Pleistocene started about 2 mya (**Fig. 14A**). In agreement with the

431 observation, we found significant positive correlation (Pearson correlation coefficient = 0.795

432 with p-value = 0.006) between the rate of newly diverged lineages and the variance in the climate

433 fluctuations based on the δ^{18}O curve from 2 mya to the present (**Fig. 14B, C**).

434   3.4. Description of the new taxon

435 As a consequence of carried out analyses, we decided to propose the taxonomic position of the

436 new *Amazona*. The significant differences in morphometry, morphology, behavior and vocal

437 features imply that the new parrot can obtain a species status under the typological,

438 morphological, phenetic, as well as biological and evolutionary species concepts. However,

439 genetic analyses suggest a subspecies level. Therefore, the phylogenetic species concept and

440 integrative species delimitation (Aleixo 2007; Helbig et al. 2002; Padial et al. 2010) cannot be

441 applied in the species elevation.

442 *Amazona gomezgarzai,* sp. nov. (**Figs 2-7**)

443 *Holotype.* Adult male, MEXICO, the Yucatán Peninsula, south of Becanchén in Tekax

444 Municipality. The holotype is represented by the feathers of the male, which were deposited in

445 the collection of the Laboratorio de Ornitología, Facultad de Ciencias Biologícas, Universidad

446 Autonóma de Nuevo León, Mexico and were assigned catalog number: MGG01-*Amazona*

447 *gomezgarzai*-holotipo. Article 72.5.1 of the Code of Zoological Nomenclature (henceforth

448 CODE) permits the use of animal parts in the designation of a type specimen. Upon death of the

449 living bird, its preserved body will be paired to the feathers for a complete body. This complies

450 with Article 16.4.2 of the CODE, which states that where the holotype is an extant individual, a

451 statement of the intent to deposit the individual in a collection upon its death accompanied by a

452 statement indicating the name and location of that collection is sufficient.

453 *Paratype.* Adult female collected in the same locality as the holotype. Like the holotype, feathers

454 from this specimen have been deposited in the collection and have assigned catalog number:

455 MGG02-*Amazona gomezgarzai*-alotipo. Upon its death, it will be added to the collection in

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

457 León, Mexico.

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

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

480   A very distinctive feature of the new taxon is its call, which is loud, sharp, short, repetitive and
481   monotonous; one particular vocalization is more reminiscent of an *Accipiter* than of any parrot
482   we know (Supporting information **Files S1** and **S2**). In flight, the call is a loud, short, sharp and
483   repetitive *yak-yak-yak* that is never repeated in pairs like in *A. xantholora.* While perched, the call
484   is mellow and prolonged, sharper and more melodious than that of *Amazona albifrons.* Perched
485   birds always respond to the call of another flock member, insuring that the parrots always
486   maintain contact with one another.

487   In general appearance, the new *Amazona* demonstrates a similarity to *A. vittata* of Puerto Rico
488   and to a lesser extent to *A. tucumana* from Bolivia and Argentina and *Amazona pretrei* from
489   Brazil and Argentina. *A. vittata* can be distinguished from the female of the new *Amazona* by the

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

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

492   of rose-red feathers around the orbital ring.

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

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

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

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

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

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

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

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

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

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

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

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

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

506   and the new *Amazona*.

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

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

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

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

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

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

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

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

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

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

517   *Description*

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

519   89.6 mm. The sex has been determined with molecular methods (**Fig. S1**). Upperparts, including

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

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

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

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

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

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

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

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

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

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

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

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

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

533   grey, darkest at tip.

534   *Female (paratype).* Total length 24.7 cm; wing (chord) 170.4 mm; exposed culmen 25.7 mm; tail

535   83.7 mm. The sex has been determined with molecular methods (**Fig. S1**). Like male but rose-red

536   confined to forehead.

537   3.5. Additional characteristics

538   *Distribution.* The new *Amazona* is endemic to the Yucatán Peninsula in southern Mexico. To date,

539   its presence is confined to an area roughly 100 km^2 that is centered south of Becanchén in Tekax

540   Municipality, Yucatán. No part of the range is presently protected in any form.

541   *Habitat.* The new *Amazona* is found in tropical caducifolius and subcaducifolius forest. It is also

542   found in disturbed patches of native vegetation and in small, cultivated fields with scattered trees.

543   It is found below 300 m above sea level.

544   *Natural history.* Miguel A. Gómez Garza first sighted this parrot in the field in trees of the

545   *Leucaena* genus at heights of approximately 6 meters in the beginning of 2014 during a visit to

546   the south of Becanchén, in the municipality of Tekax. The parrots occurred in small flocks of

547   three to five individuals and fed on the tender pods produced by this tree. During a follow up visit

548   in August 2014, Gómez Garza also sighted pairs with their fledged young. This field work

549 confirmed the rarity of the species and that it was far less common than the other two species
550 found in the same area, *Amazona albifrons nana* and *Amazona xantholora*.

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

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

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

566 ## 4. Discussion
567 4.1. Taxonomic position of the newly described *Amazona*

568 In this study, we proposed the new taxon of *Amazona* at the species level, *Amazona gomezgarzai*
569 sp. nov. However, it has not been easy to take up the final decision because available data are
570 contradictory. The species level is supported by morphometrical and behavioral data, whereas
571 mitochondrial genetic analyses imply the subspecies level. Below we discussed the pros and cons
572 of these two taxonomic concepts in an objective way.

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

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

589   Nonetheless, the new *Amazona* is clearly different from *A. albifrons*. Although the three Mexican
590   parrots found in the Yucatán Peninsula (*A. albifrons nana, A. xantholora* and the new *Amazona*)
591   share the same habitat and come into frequent physical contact, they live commensally and show
592   substantial differences in their morphology, plumage, call and behavior (**Table 1-3, Fig. 3, 11,**
593   **S3**). The features used here to discriminate the proposed taxon are of the same type as those
594   utilized in elevation of other *Amazona* species. The characters described allow the species to live
595   sympatrically without hybridizing (Pettingill 1970). This suggests that these three forms could be
596   separate species. The differentiation in characters involved in mate choice, such as song,
597   plumage, and behavior play a central role in avian speciation (Edwards et al. 2005). The role of
598   song is particularly interesting because multiple factors influence vocal evolution and this feature
599   is subjected to rapid change through learning and behavioral evolution.

600   Studies of geographic variation in the vocalizations of the crimson rosella (*Platycercus elegans*)
601   parrot species complex showed that vocal variation, in a species with vocal learning, can coincide
602   with areas of restricted gene flow across geographically continuous populations. These results
603   suggest that vocalization can be associated with reduced gene flow between populations, and
604   therefore may promote speciation, even in the absence of other barriers (Ribot et al. 2012). On
605   the other hand, several local dialects were documented for *Amazona auropalliata* with no
606   significant relationship with genetic variations (Wright & Wilkinson 2001) indicating a high
607   degree of gene flow and individual dispersal across the dialect boundaries. Experimentally
608   simulated dispersals with *Amazona auropalliata* individuals moving within and across dialect
609   regions showed that both vocal learning (in the case of juveniles) and limited dispersal (in the
610   case of adults) are responsible for the dialect maintenance (Salinas-Melgoza & Wright 2012).

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

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

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

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

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

616   On the other hand, it could be possible that the studied individuals of the new taxon are hybrids

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

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

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

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

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

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

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

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

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

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

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

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

629   when a ban was introduced on export of parrots.

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

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

632   1997). Nevertheless, more extensive studies including larger number of *A. albifrons* specimens

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

634   The distinct morphological and behavioral features seem incongruent with molecular

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

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

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

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

639   **13D**). It suggests that the new taxon could have emerged before differentiation of *A. albifrons* to

640   subspecies and has reached a species level. Interestingly, such alternative topology was obtained

641   for hierarchical clustering of parrots based on all morphometric characters (**Fig. 10**). Moreover,

642   the molecular distance between the new *Amazona* and *A. albifrons nana* measured by the number

643 of base differences per site (0.135) is even about two times greater than the distance (0.067)

644 between two *A. albifrons* subspecies, *A. a. albifrons* and *A. a. saltuensis*.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

669 Omland 2003).

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

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

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

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

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

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

676   and *A. a. nana* is two times larger <mark>than their closest relatives between</mark> *A. a. albifrons* and *A. a.*

677   *saltuensis*.

678   The taxon described here, morphologically and behaviorally different from other members of the

679   genus found in Mexico, is not an exception regarding the small genetic distance. There are many

680   examples of birds with minor genetic differences that are treated as valid species, e.g. *Apus*

681   *apus/A. pallidus* (Packert et al. 2012), *Clanga clanga/C. pomarina* (Helbig et al. 2005; Lerner et

682   al. 2017) and *Falco rusticolus/F. biarmicus/F. cherrug* (Nittinger et al. 2007). Recent estimates of

683   avian diversity suggest that the current taxonomy of birds underestimates their species number by

684   at least a factor of two (Barrowclough et al. 2016). Nevertheless, the taxonomic status of the new

685   *Amazona* should be verified in subsequent studies which are conditioned by a possibility of

686   finding and studying more individuals of this rare parrot.

687   4.2. Implication on general phylogeny and migration of Amazon parrots

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

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

690   indicate that Central America was settled three times independently at different times from

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

706   (2004) proposed also two colonization events but both directed to Jamaica.

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

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

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

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

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

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

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

714   (2014), the Central America clade was also placed within the Greater Antillean parrot group but

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

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

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

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

719   account that the first topology (**Fig. 13A**) was inferred by all four applied methods and the

720   Greater Antillean parrot clade, including *A. agilis,* shows a greater genetic variation and older

721   divergence time than the Central America clade, it is possible that a migration happened from the

722   Greater Antilles to Mexican territory. In this scenario, the Greater Antillean parrots would be

723   derived from species inhabiting northern South America, whose lineages became extinct and

724   therefore are not present in inferring phylogenies. According to our molecular dating, the

725   colonization of the Central America could happen between 3.4 to 2.5 mya (**Fig. 14**). These event

726   is in agreement with dating of decrease in sea level, which started to systematically fall since 3

727   mya and in the period 3.4 to 2.5 mya descended even 50 m below the present level (Hansen et al.

728   2013), which could have facilitated the migrations.

729   In the case of the Lesser Antillean parrots the situation seems clearer. The presence of three

730   separated clades placed within South American parrots suggests independent migrations from the

731   mainland to the islands as proposed by Bond (1963). Our estimations indicate that it could have

732   happened about 3.2, 1.5 and 1.3-0.8 mya, which well correspond with the decrease in sea level

733   initially by 25 m and after 2.5 mya by more than 50 m with relation to the Pleistocene glaciations

734   (Hansen et al. 2013). However, we cannot exclude the opposite direction of migrations, from

735   islands (the Lesser Antilles) to the mainland (the northern coast of Venezuela) as it was recently

736   proposed for the origin of Yellow-headed Amazon parrots (Urantowka et al. 2014). Nevertheless,

737   the obtained results show a complex history for parrots within the Caribbean region (Russello &

738   Amato 2004) related probably with the refugial and insular character of its habitats. Additional

739   studies are required to solve in detail the migration routes.

740   The Amazon parrots have been subjected to evolutionary expansion since the last 5 mya. Their

741   earliest diversification may be associated with adaptive radiation which has been triggered by the

742   arrival of Arini parrots in South America from Africa (Schweizer et al. 2014). Other important

743   factors could be drainage evolution in Amazonia and Pleistocene climatic oscillations (**Fig. 14**)

744   causing alterations and partitioning of habitats, sea level changes influencing colonization of

745   islands (and again mainland) as well as recurrent elevational migrations (Ribas et al. 2012; Rull

746   2011; Schweizer et al. 2014). These processes could cause the differentiation of populations into

747   new lineages. One of such recently evolving lineage could represent the newly described Amazon

748   parrot. Schweizer et al. (2014) studying the diversity of Neotropical parrots (including members

749   of Arini and Androglossini clades) found no evidence of the slowdown in their speciation rate and

750   discovered two young, unexpectedly species-rich clades represented by *Pyrrhura* and *Aratinga*.

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

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

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

754   ## 5. Conservation aspects

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

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

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

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

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

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

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

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

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

764   alerting government authorities, conservationists and local inhabitants that implementing

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

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

767 *Amazona.* Because of this precarious status, the Mexican government would not allow the
768 collection of voucher specimens. Instead the authorities permitted that two individuals
769 maintained locally as pets be transported for safe keeping under the care of Dr Miguel Angel
770 Gómez Garza.

6. Acknowledgements

787 **Table 1.** Morphometric data (in millimeters) of the new *Amazona* compared with other similarly
788 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)

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

803   **Table 2.** Comparison of differences in face coloration of the new *Amazona* and other similarly
804   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

805 **Table 3.** Morphological traits of the new *Amazona* compared with other similarly red-fronted and
806 -faced species of *Amazona,* including other species occurring in the Yucatán Peninsula (*A.*
807 *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 (range 198.1-213.0)	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 (range 207.4-244.4)	26	As *A. a. nana*, but green slightly darker.	As *A. a. nana*.	As *A. a. nana*.
A. a. saltuensis	230 (range 211.9-233.5)	26	As *A. a. albifrons*, but blue crown extends to nape.	As *A. a. nana*.	As *A. a. nana*.
A. xantholora	200 (range 197.1-238.2)	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 (range 338.9-369.0)	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 (range 266.4-299.2)	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.

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

810 **Fig. 1.** Map of Yucatán Peninsula with the location of site (asterisk), where the new *Amazona* was
811 found.

812   **Fig. 2.** Illustration of the new *Amazona*. Male holotype (left) and female paratype (right).
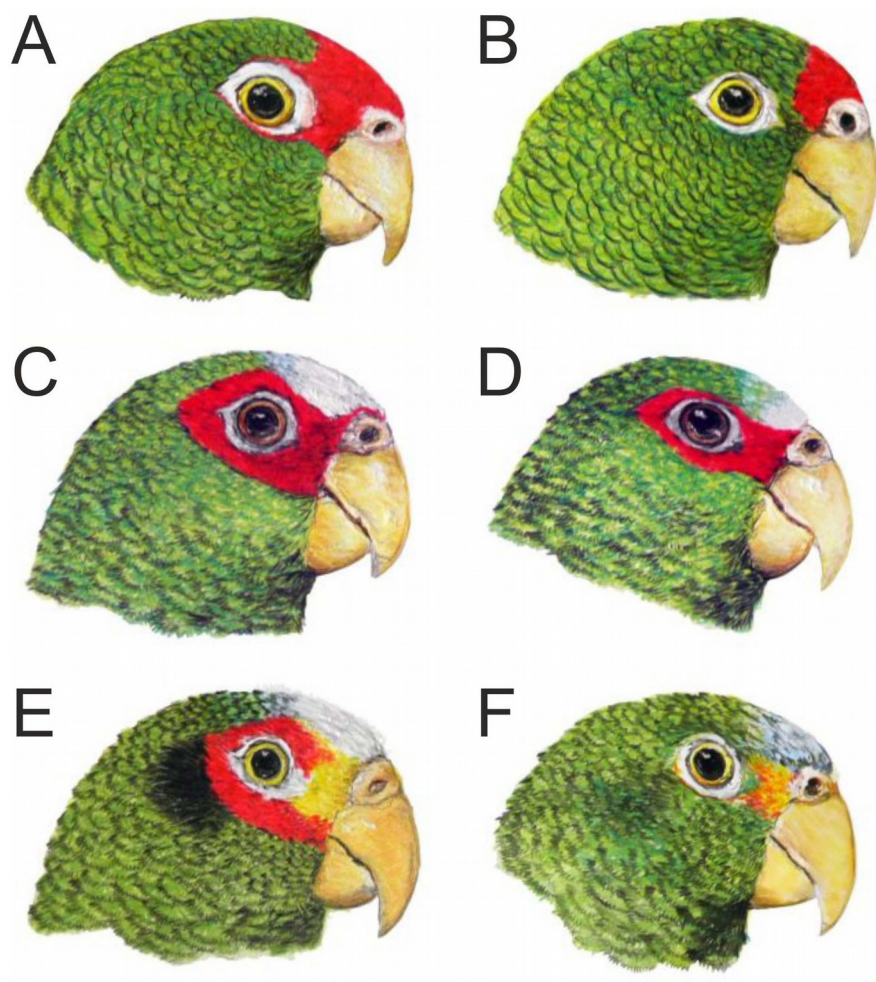
813   **Fig. 3.** Head coloration in the male (A) and female (B) of the new *Amazona* in comparison to
814   both sexes of congeners *Amazona albifrons nana* (C – male; D – female) and *Amazona*
815   *xantholora* (E – male; F – female), also from the Yucatán Peninsula, Mexico. The three taxa are
816   the smallest members of the genus *Amazona*.
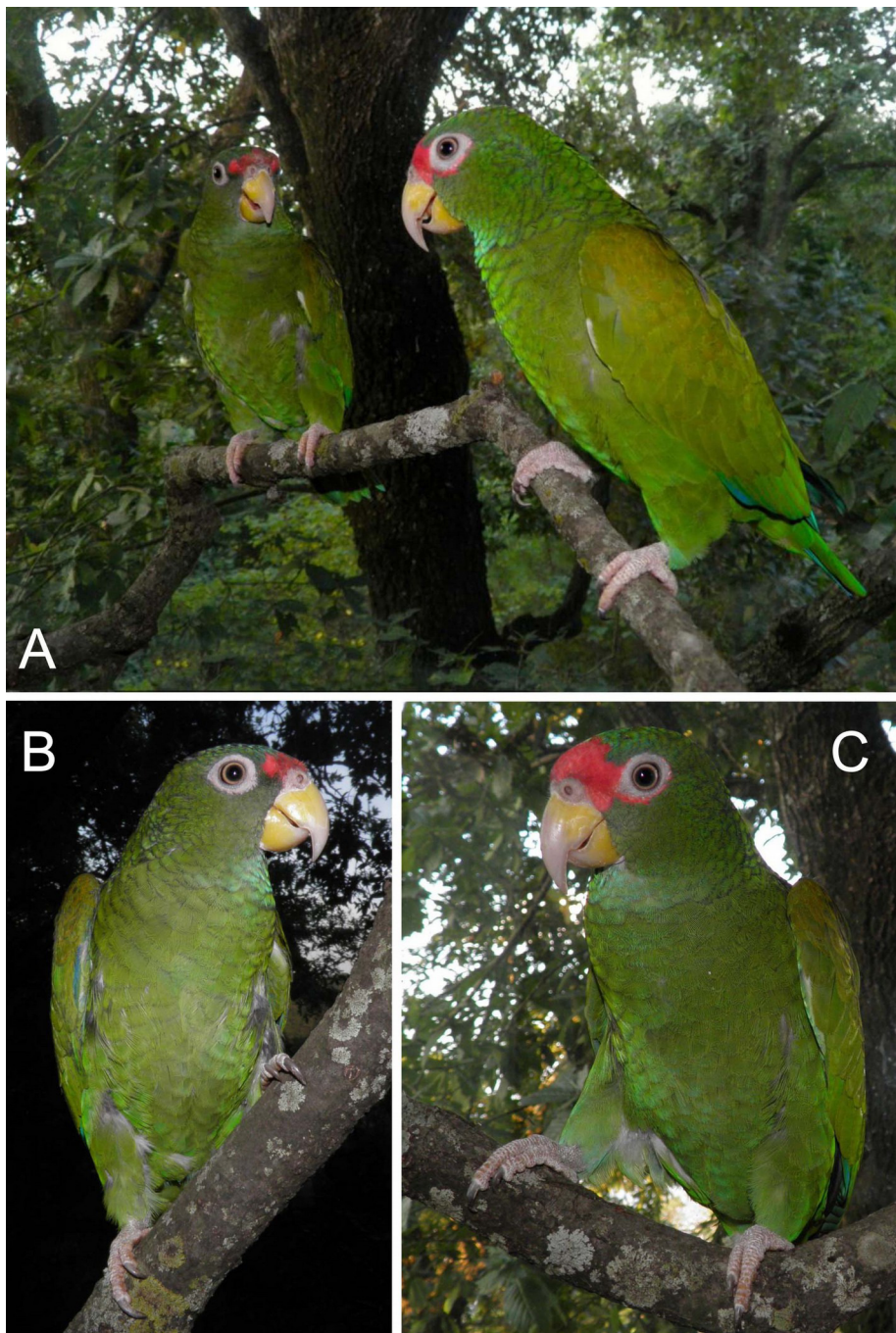
817 **Fig. 4.** Photograph of the male holotype (panel C and panel A - individual on the right) and
818 female paratype (panel B and panel A - individual on the left) of the new *Amazona*.
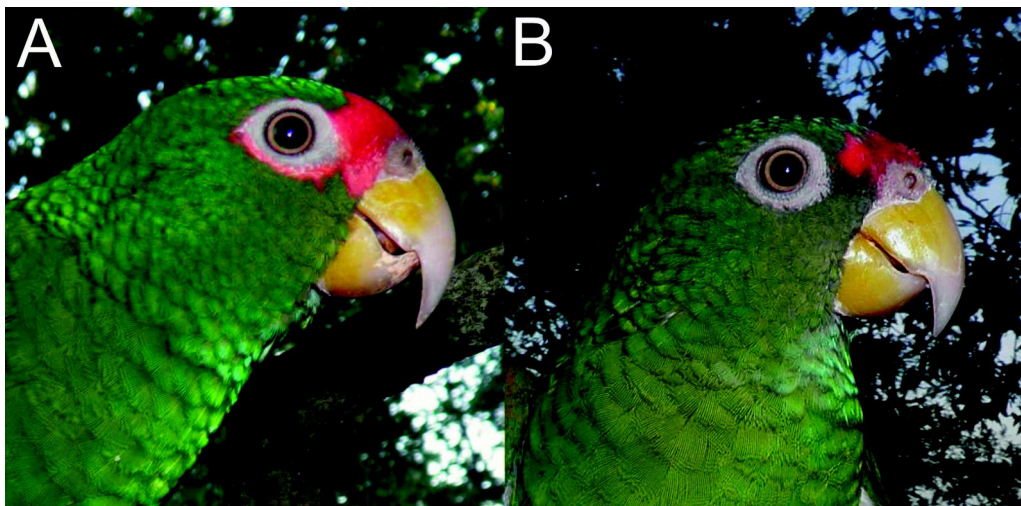
819 **Fig. 5.** Photographs of the head of male holotype (A) and female paratype (B) of the new
820 *Amazona.*
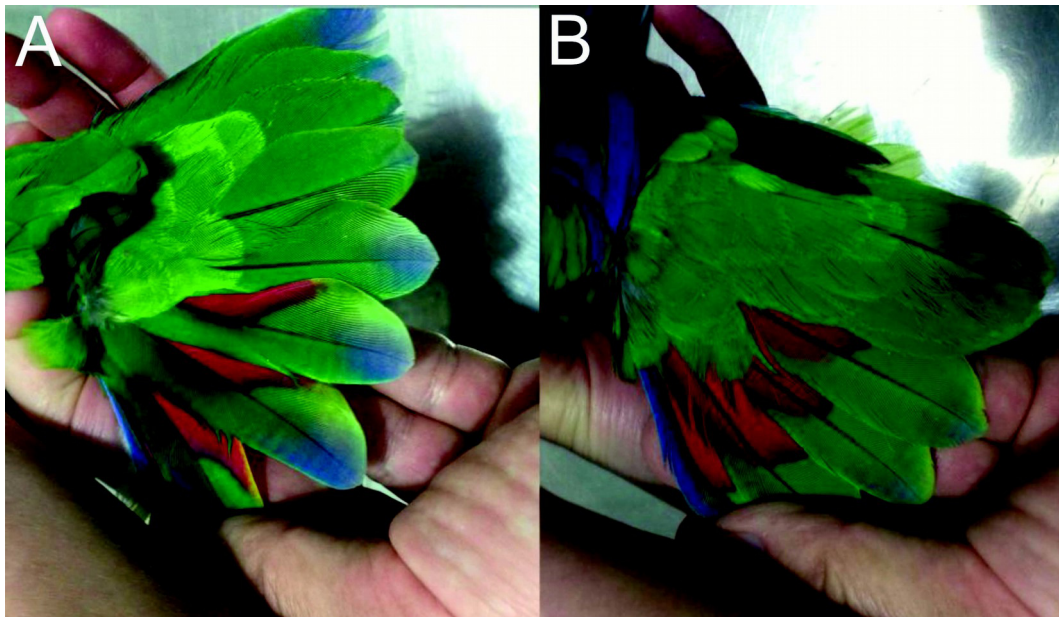
821   **Fig. 6.** Open tails showing colored bands of male holotype (A) and female paratype (B) of the
822   new *Amazona*.
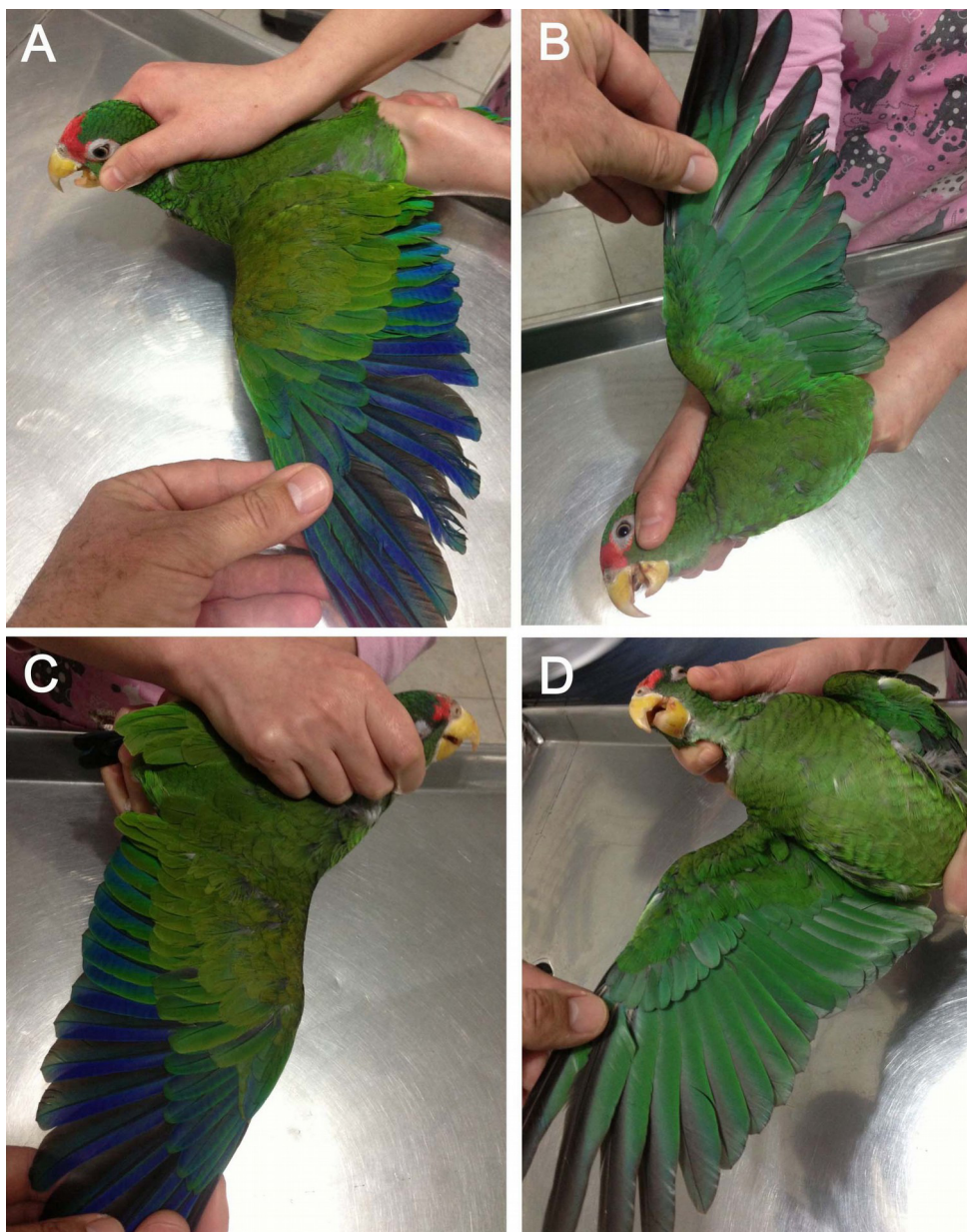
823   **Fig. 7.** Open upper (A) and underside of wing (B) of male holotype as well as open upper (C) and
824   underside of wing (D) of female paratype of the new *Amazona*.

Fig. 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.

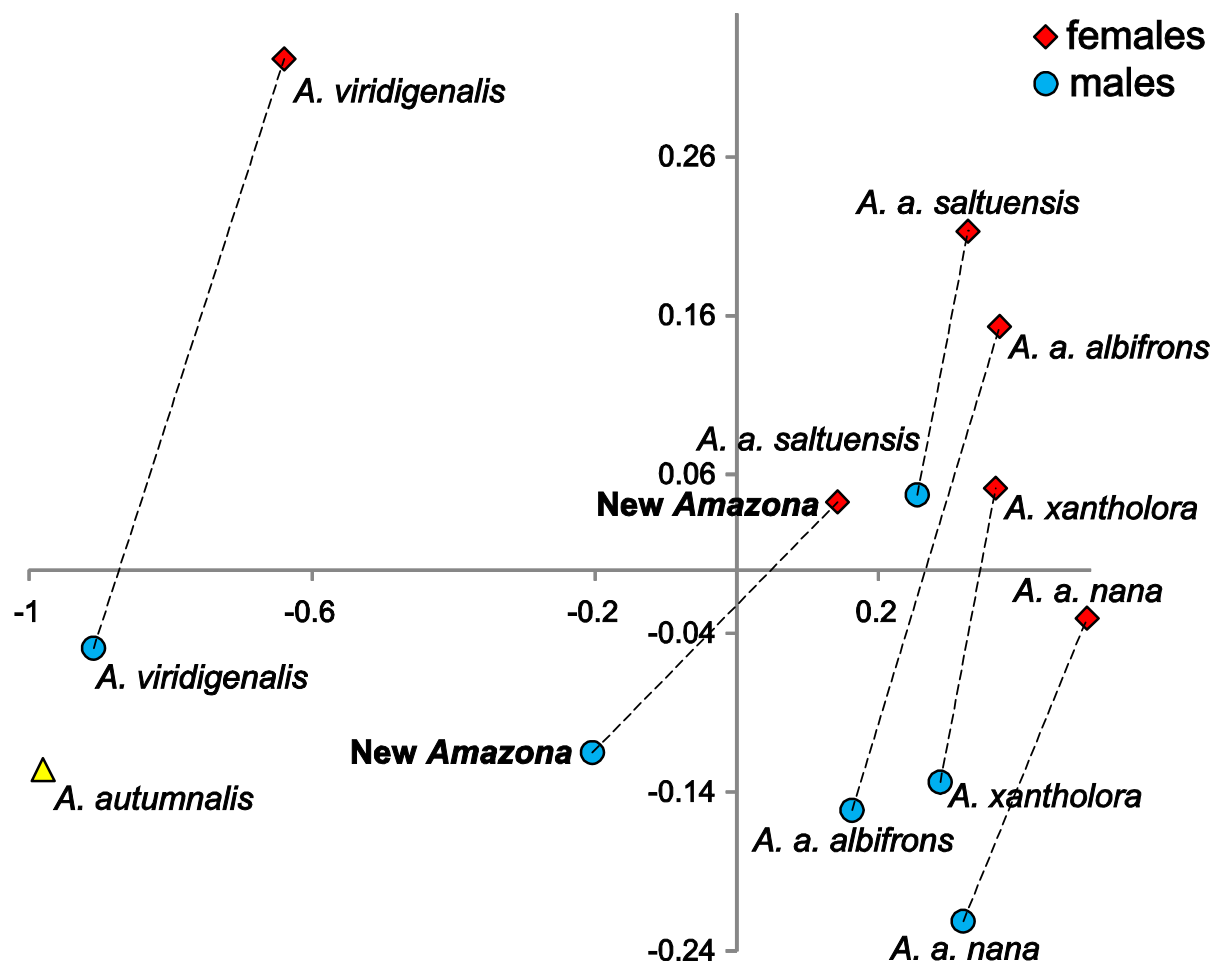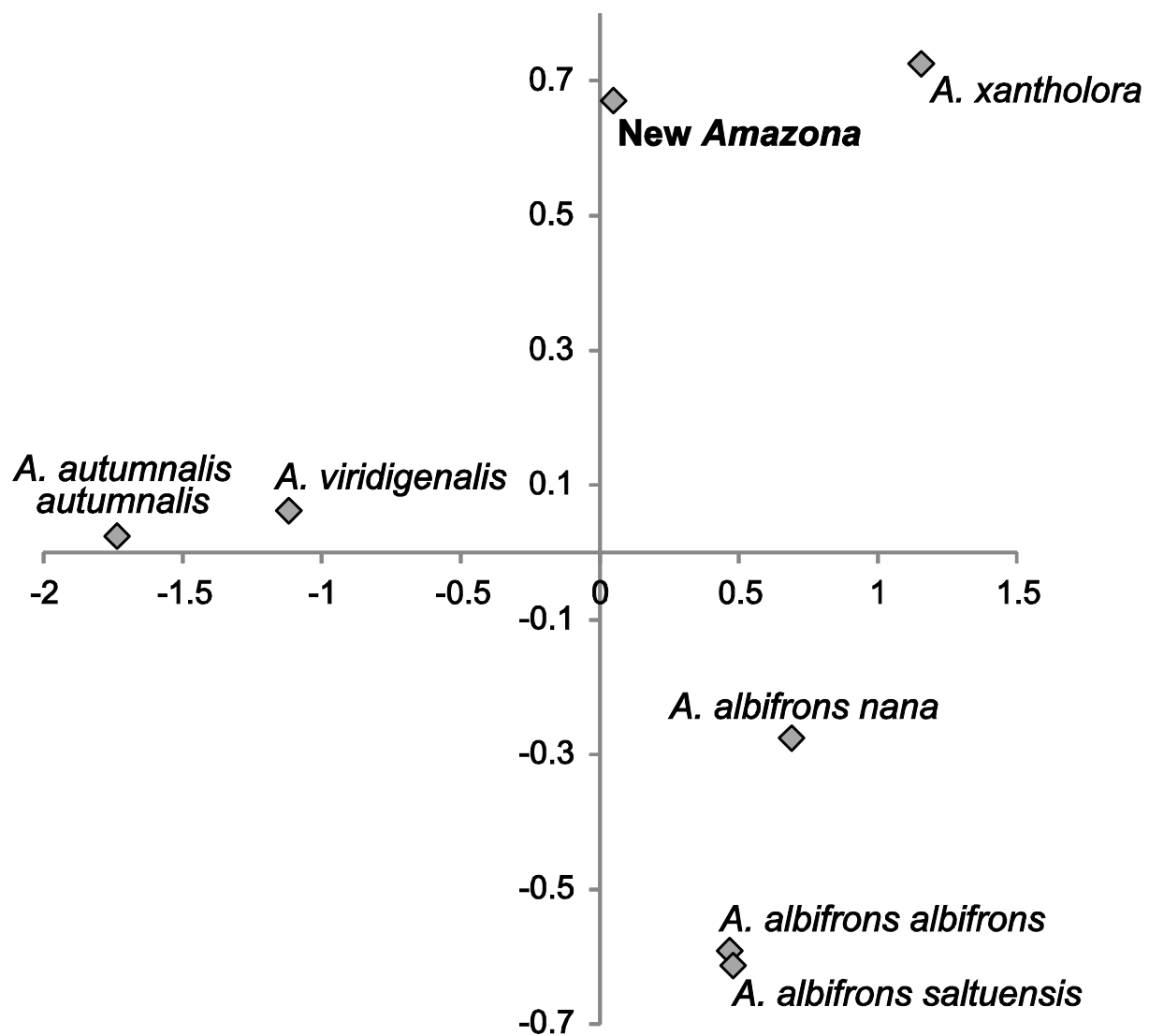Fig. 9. The plot of the two-factor coordinates from Principal Component Analysis for *Amazona* species displaying red head feathers from Mexico and Mesoamerica based on all morphometric features.

Distance

2.0 1.5 1.0 0.5 0.0

A. a_autumnalis autumnalis

81/80

A. viridigenalis

A. xantholora

New *Amazona*

83/59

70/45

A. albifrons nana

99/86

A. albifrons albifrons

AU/BP

100/99

81/80

A. albifrons saltuensis
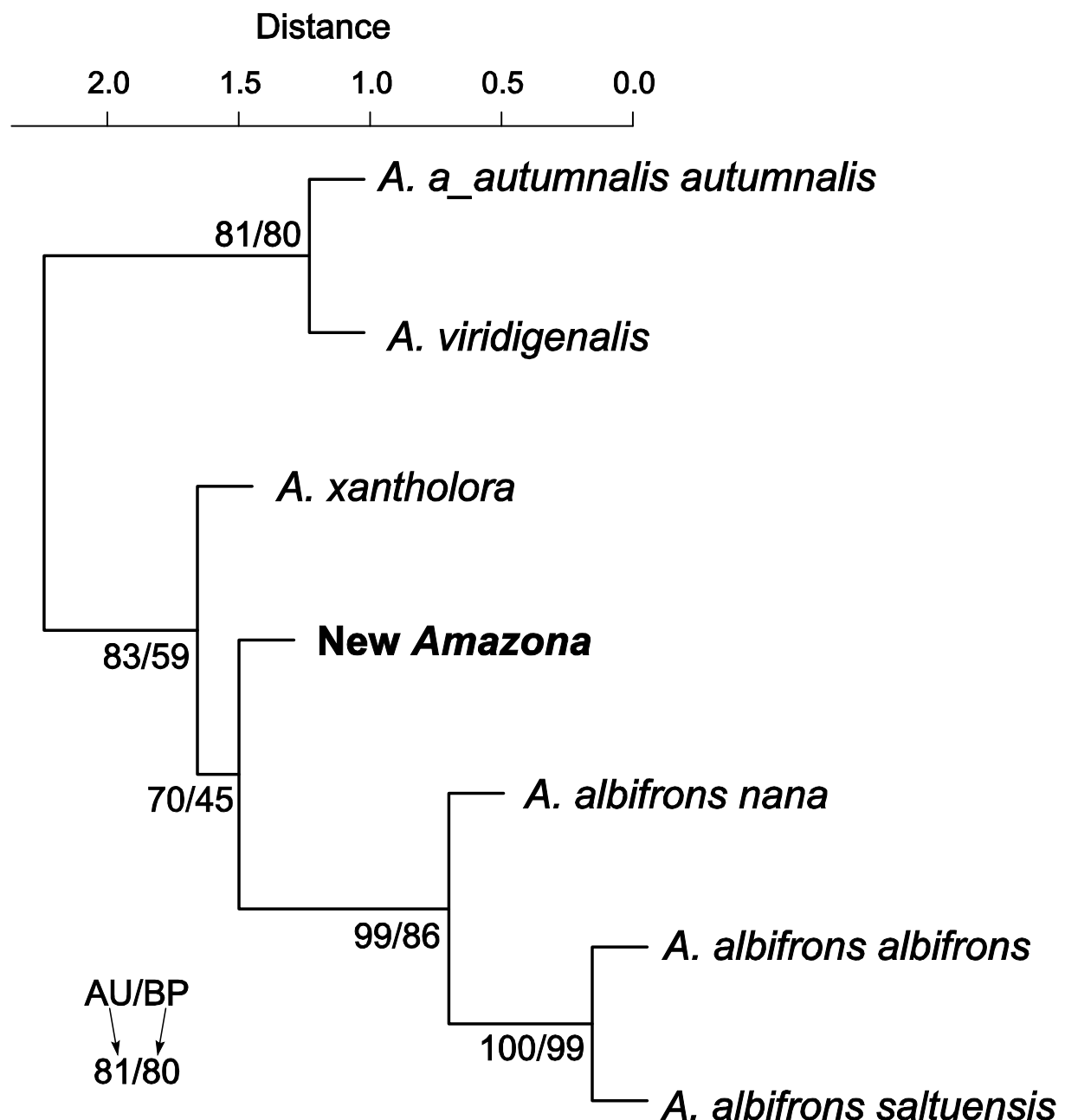
833　**Fig. 10.** UPGMA dendrogram clustering parrot taxa according to five metric parameters (body
834　weight and length, length of wing chord, tail and exposed culmen) and six morphological discrete
835　characters (body weight, total length, length of wing chord, tail length, exposed culmen).
836　Numbers at nodes correspond to p-values expressed as percentages calculated using
837　approximately unbiased test (AU) and bootstrap resampling (BP), respectively.

838 **Fig. 11.** Comparison of example sonogram for the new taxon with two other *Amazona* parrots
839 from Central America and closely related *Amazona agilis* from the Greater Antilles.

0.01

MB/PB/TF/RM

0.98/0.96/98/97

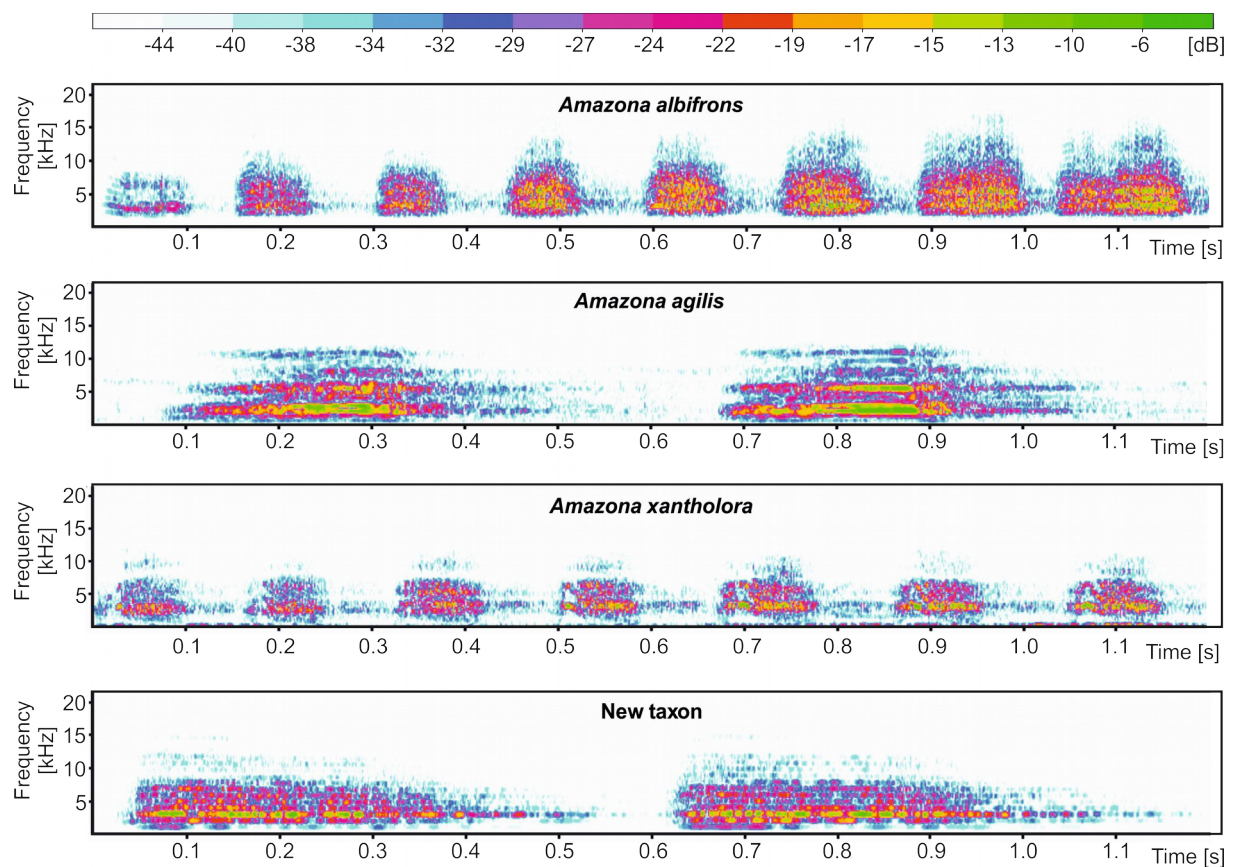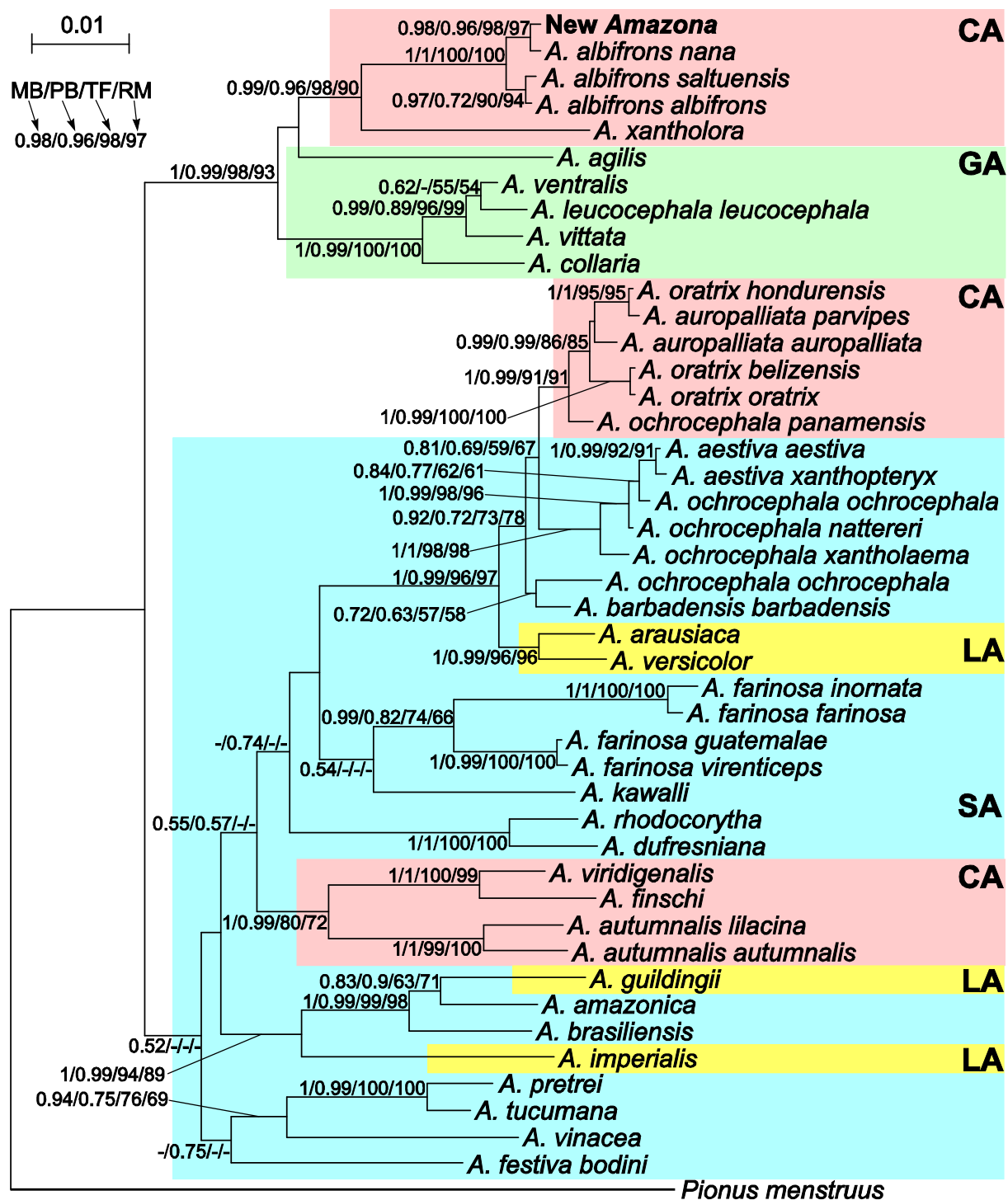**New Amazona**
0.98/0.96/98/97
1/1/100/100
A. albifrons nana
A. albifrons saltuensis
0.99/0.96/98/90
0.97/0.72/90/94
A. albifrons albifrons
A. xantholora
CA

1/0.99/98/93

A. agilis
GA
0.62/-/55/54
A. ventralis
A. leucocephala leucocephala
0.99/0.89/96/99
A. vittata
1/0.99/100/100
A. collaria

1/1/95/95
A. oratrix hondurensis
A. auropalliata parvipes
CA
0.99/0.99/86/85
A. auropalliata auropalliata
1/0.99/91/91
A. oratrix belizensis
A. oratrix oratrix
1/0.99/100/100
A. ochrocephala panamensis

0.81/0.69/59/67
1/0.99/92/91
A. aestiva aestiva
0.84/0.77/62/61
A. aestiva xanthopteryx
1/0.99/98/96
A. ochrocephala ochrocephala
0.92/0.72/73/78
A. ochrocephala nattereri
1/1/98/98
A. ochrocephala xantholaema
1/0.99/96/97
A. ochrocephala ochrocephala
0.72/0.63/57/58
A. barbadensis barbadensis
A. arausiaca
LA
1/0.99/96/96
A. versicolor

1/1/100/100
A. farinosa inornata
A. farinosa farinosa
0.99/0.82/74/66
A. farinosa guatemalae
1/0.99/100/100
A. farinosa virenticeps
0.54/-/-/-
A. kawalli
-/0.74/-/-
A. rhodocorytha
SA
1/1/100/100
A. dufresniana
0.55/0.57/-/-
1/1/100/99
A. viridigenalis
CA
A. finschi
A. autumnalis lilacina
1/0.99/80/72
1/1/99/100
A. autumnalis autumnalis
0.83/0.9/63/71
A. guildingii
LA
1/0.99/99/98
A. amazonica
A. brasiliensis
0.52/-/-/-
A. imperialis
LA
1/0.99/94/89
1/0.99/100/100
A. pretrei
0.94/0.75/76/69
A. tucumana
A. vinacea
-/0.75/-/-
A. festiva bodini
Pionus menstruus

Fig. 12. MrBayes maximum clade credibility tree for the concatenated alignment of genes for COI, 12S and 16S rRNA sequences from *Amazona* taxa and *Pionus menstruus* species (as outgroup). Numbers at nodes, in the order shown, correspond to: posterior probabilities estimated in MrBayes (MB) and PhyloBayes (PB), and bootstrap support values obtained in TreeFinder (TF) and RAxML (RM). Values of the posterior probabilities and bootstrap percentages lower than 0.50 and 50%, respectively, were omitted or indicated by a dash "-". CA – Central America parrots; GA – Greater Antillean parrots; LA – Lesser Antillean parrots; SA –South America parrots.
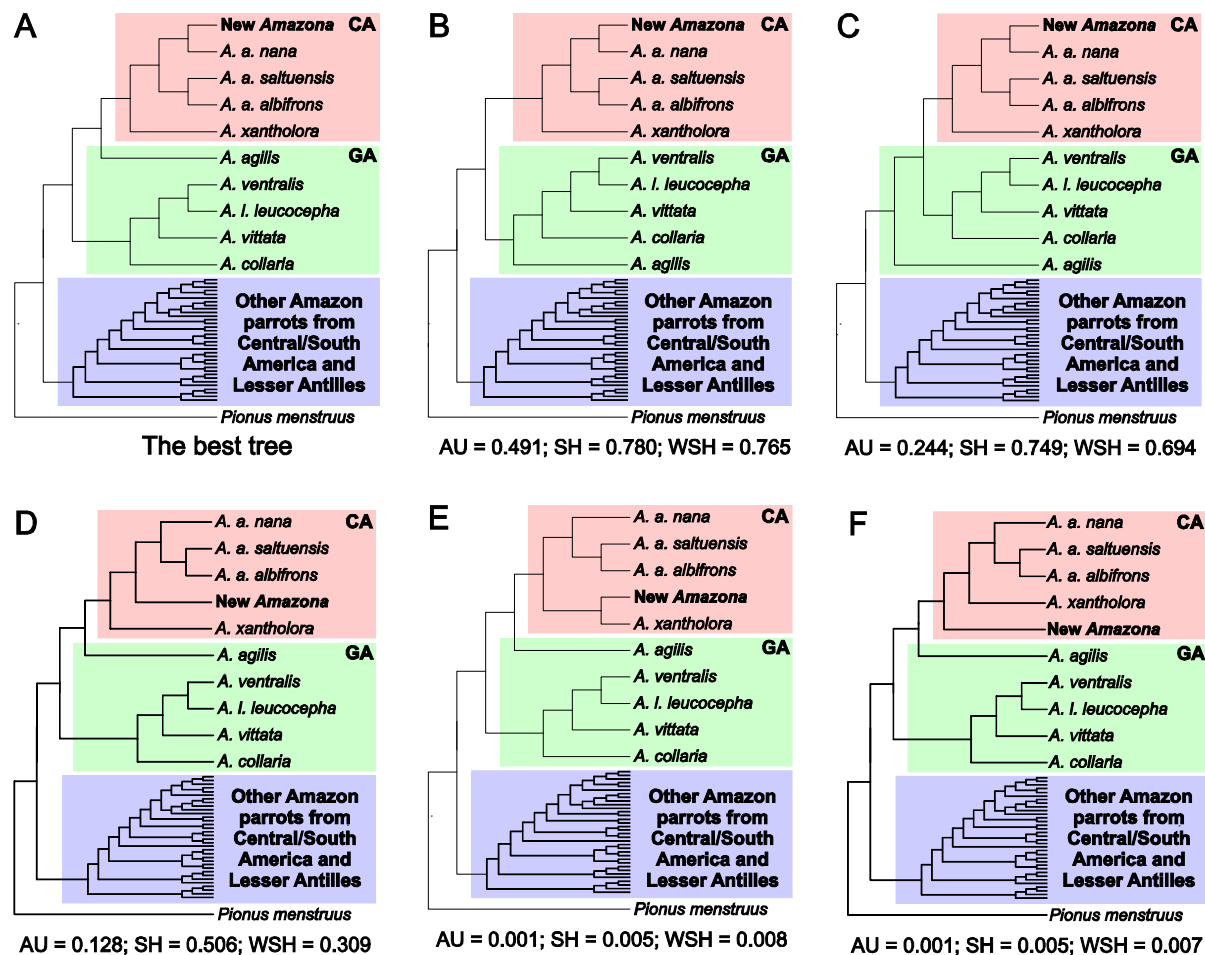
Fig. 13. Alternative tree topologies assuming different placement of *A. agilis* (B and C) and the new *Amazona* (D, E, F) in comparison to the best found tree (A). P-values of approximately unbiased (AU), Shimodaira-Hasegawa (SH) and weighted Shimodaira-Hasegawa (wSH) tests were shown. Only trees E and F are significantly worse than the best tree, whereas B, C and D cannot be rejected. SA –South America parrots; GA – Greater Antillean parrots; CA – Central America parrots.
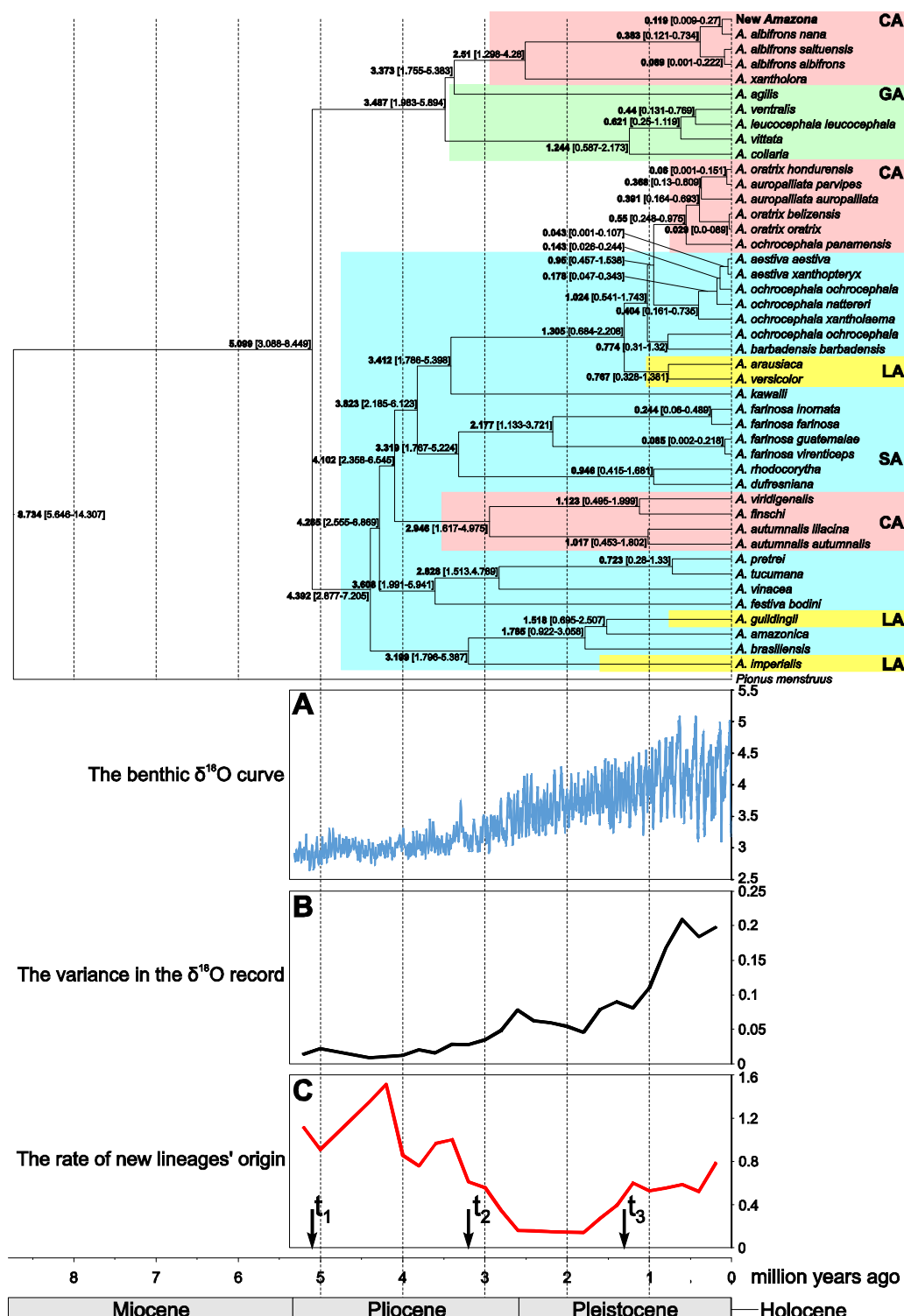
Fig. 14. Maximum clade credibility tree obtained in Beast for the concatenated alignment of genes for COI, 12S and 16S rRNA sequences from selected *Amazona* taxa and *Pionus menstruus* species (as outgroup). Mean (in bold) ages as well as the 95% highest posterior density distributions (in parenthesis) 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

861   times in which the speciation rate shifts to a new rate according to the best-fitting yule4rate
862   model.

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