



Classification of a clade of New World doves (Columbidae: Zenaidini)

RICHARD C. BANKS¹, JASON D. WECKSTEIN², J.V. REMSEN, JR.³ & KEVIN P. JOHNSON⁴

¹3201 Circle Hill Rd., Alexandria, VA 22305, USA. E-mail: rcbalone@aol.com

²Field Museum of Natural History, Chicago, IL 60605 USA. E-mail: jweckstein@fieldmuseum.org

³Museum of Natural Science and Dept. Biological Sciences, Louisiana State University, Baton Rouge, LA 70776 USA.

E-mail: najames@lsu.edu

⁴Illinois Natural History Survey, University of Illinois, Champaign, IL 61820 USA. E-mail: kpjohnso@illinois.edu

To evaluate the role of the formation of the Central American land bridge in diversification of the American avifauna, Johnson and Weckstein (2011) reconstructed a phylogeny, using DNA sequence data from four gene regions, of 24 nominal species in three putative genera of New World doves. Although a systematic revision of these doves was not a primary purpose of their study, Johnson and Weckstein (2011) provided information that helps to re-evaluate the presumed relationships among the taxa included. Their analysis supported a hypothesis of monophyly for a group containing seven species currently (American Ornithologists' Union [AOU] 1998, Gibbs *et al.* 2001, Dickinson 2003, Remsen *et al.* 2012) placed in the genus *Zenaida* Bonaparte, 1838, and for a group of 12 taxa in 6 species (of as many as 11 currently recognized species) in the genus *Leptotila* Swainson, 1837 (Gibbs *et al.* 2001, Dickinson 2003). However, the 11 species (of up to 16 [Dickinson 2003] or 18 [Gill and Wright 2006]) of the genus *Geotrygon* Gosse, 1847, occurred in three separate lineages (Johnson and Weckstein 2011: fig. 1), revealing that the genus is polyphyletic. Unfortunately, the type species of *Geotrygon*, *G. versicolor* (Lafresnaye), was excluded from their analysis because of the incomplete sequence data available for that species. The purposes of the current study are to provide molecular phylogenetic data for that species and for *G. chryisia* Bonaparte to determine which lineage includes *G. versicolor*, and to provide a taxonomic revision of the group. For the few species of the genus for which genetic data are not yet available, only tentative placement based on inference is possible.

Using the same protocols, we sequenced three (mitochondrial genes ND2 and COI and nuclear beta fibrinogen intron 7) of the four genes used by Johnson and Weckstein (2011) for captive individuals of *G. versicolor* (LSU B28878) and *G. chryisia* (LSU B20785) (GenBank Accession numbers KC881101-KC881106). Sequences for the cytochrome *b* gene could not be obtained for these species because of difficulties in PCR amplification and apparent nuclear pseudogenes. PartitionFinder (Lanfear *et al.* 2012) was used to test for the best-fit partitioning scheme and likelihood models, and indicated that the best fit resulted from partitioning into nuclear versus mitochondrial genes with a GTR+I+G model for mitochondrial genes and HKY+G model for the nuclear gene. We performed Bayesian phylogenetic analyses using MrBayes (v. 3.2.1, Ronquist and Huelsenbeck 2003). Two simultaneous runs of 10 million generations each, sampling every 500 generations, were conducted, and the first 250,000 generations were discarded as burn-in. To assess nodal support, we calculated posterior probabilities from the remaining trees.

Phylogenetic analysis of these sequences (Fig. 1) indicated that the species of *Geotrygon* comprise three distinct clades (cf. Johnson and Weckstein 2011). *Geotrygon veraguensis* was recovered as the sister species to members of the genus *Leptotila*. A clade of primarily montane *Geotrygon* species was recovered as the sister group to the genus *Zenaida*, and a third clade consisting of mainly lowland *Geotrygon* taxa was sister to the clade comprising all other taxa currently in *Geotrygon*, *Leptotila*, and *Zenaida*. Support values for most clades were similar to those in Johnson and Weckstein (2011), although support for monophyly of the clade of lowland *Geotrygon* taxa was higher (posterior probability 95%).

Three generic names are available for the species in the clade of lowland taxa. One lineage in this clade (Fig. 1) consists of two South American taxa (*saphirina* and *purpurata*) often considered conspecific (Peters 1934, Dickinson 2003) and long separated as the genus *Osculatia* Bonaparte, 1855 (type species *G. saphirina* Bonaparte, 1855). Goodwin (1958) merged *Osculatia* into *Geotrygon*, and this merger has been followed in all subsequent classifications. The other lineage consists of the Central and South American species *violacea* Temminck and the widespread continental and Caribbean species *montana* Linnaeus, the type species of *Oreopelia* Reichenbach, as well as *G. versicolor* and *G. chryisia*. The divergence between *G. purpurata* + *G. saphirina* and the other lineage of lowland *Geotrygon* is high, although support is now stronger for a sister relationship between these two sub-clades. Until further information about

relationships of these taxa becomes available, including clarification of relationships in the large *montana* complex and the status of the widely disjunct forms of *violacea*, we suggest a conservative approach by treating all these taxa as members of the genus *Geotrygon*. We also tentatively include here *G. mystacea* (Temminck, 1811), *G. caniceps* (Gundlach, 1852), and *G. leucometopia* (Chapman, 1917), lowland taxa for which no genetic data are available. Hellmayr and Conover (1942) treated *chryisia* and *mystacea* as conspecific, and both Goodwin (1967, 1983) and Gibbs *et al.* (2001) considered them to be allopecies. Further, Goodwin (1967, 1983) and Gibbs *et al.* (2001) considered *caniceps* to be closely related to *versicolor*. The Hispaniolan taxon *leucometopia* was recently treated as a species distinct from the Cuban *caniceps* (Garrido *et al.* 2002, Banks *et al.* 2004), with which it had been lumped previously.

The species originally named *Geotrygon veraguensis* was recovered as a sister to, but highly divergent from, the clade containing the several species of *Leptotila* by Johnson and Weckstein (2011; see also Fig. 1), quite distinct from any other taxon placed in *Geotrygon*. In plumage and morphology, *veraguensis* differs so much from the relatively homogeneous *Leptotila* that we consider its merger into that genus as untenable. This relationship necessitates the placement of this species in a distinct monotypic genus, for which no name is available. We propose:

***Leptotrygon*, new genus**

Type species. *Geotrygon veraguensis* Lawrence, 1866

Diagnosis. Differs from *Leptotila* by lacking the attenuation of the inner vane of the outer primary, by the presence of facial stripes, and by the absence of white terminal spots on the outer rectrices. The pale throat patch is sharply defined by dark stripes on both sides rather than blending gradually.

Comments. When Lawrence (1866) described *G. veraguensis*, he wrote that “It seems entirely unlike any species of which I can find a description.” Thus, it is perhaps not unexpected that it would deserve its own genus. The year of publication of *G. veraguensis* is given as 1867 by Peters (1934), Hellmayr and Conover (1942), and those who follow those sources (e.g., AOU 1998). The paper is dated June, 1866, and that date is indicated by Deignan (1961) for six of the holotypes of the seven species named therein, by the Peters volumes for five of the seven species, and by Wetmore (1968:49) for *G. veraguensis*. June 1866 is also the date provided by Dickinson *et al.* (2011: table 21), and we accept that date as correct.

Etymology. This feminine name is a combination of *Leptotila* and *Geotrygon*, to reflect concepts of the present and past relationship of the type and only species by emphasizing its phylogenetic association with *Leptotila* and its *Geotrygon*-like form and habits.

A clade of six mainly montane species generally allotted to *Geotrygon* was recovered (Johnson and Weckstein 2011; Fig. 1) as sister to a clade containing all species of *Zenaida*. No generic name is currently available for this group, for which we propose:

***Zentrygon*, new genus**

Type species. *Geotrygon costaricensis* Lawrence, 1868.

Diagnosis. Differs from *Zenaida*, to which it is phylogenetically most closely related, in having the tail short and square or rounded rather than long and graduated, relatively shorter than the wing, and the wing rounded rather than pointed, with the inner vane of the outer primary not emarginated.

Included species. In addition to the type species this genus contains the species originally described as *Geotrygon lawrencii* Salvin, 1874; *Geotrygon albifacies* Sclater, 1858; *Columba frenata* Tschudi, 1843; *Geotrygon goldmani* Nelson, 1912; and *Geotrygon chiriquensis* Sclater, 1856. All were sampled by Johnson and Weckstein (2011) and are placed in the same clade in the present study. In addition, we tentatively include the species *Geotrygon carrikeri* Wetmore, 1941, once considered a subspecies of *lawrencii*, and *G. linearis* (Prévost, 1843), treated as forming a superspecies with *frenata* by Godwin (1967, 1983) and Gibbs *et al.* (2001).

Comments. Delimitation of this genus is based on the phylogeny shown in Fig. 1. All the included species have long been considered to be part of the genus *Geotrygon* (or *Oreopelia*), and all share with the species remaining in that genus the morphological and behavioral characteristics brought to mind by the term “ground-dove.” As classifications are more frequently being based on DNA sequence data, it is becoming increasingly difficult to provide meaningful diagnoses based on morphological characters for taxa above the species level. For example, we cannot find characters that diagnose all members of *Zentrygon* from *Geotrygon* *sensu stricto*.

Etymology. This feminine name is formed from *Zenaida* and *Geotrygon*, to reflect the phylogenetic relationship with the former genus and the general form and habits long associated with quail-doves.

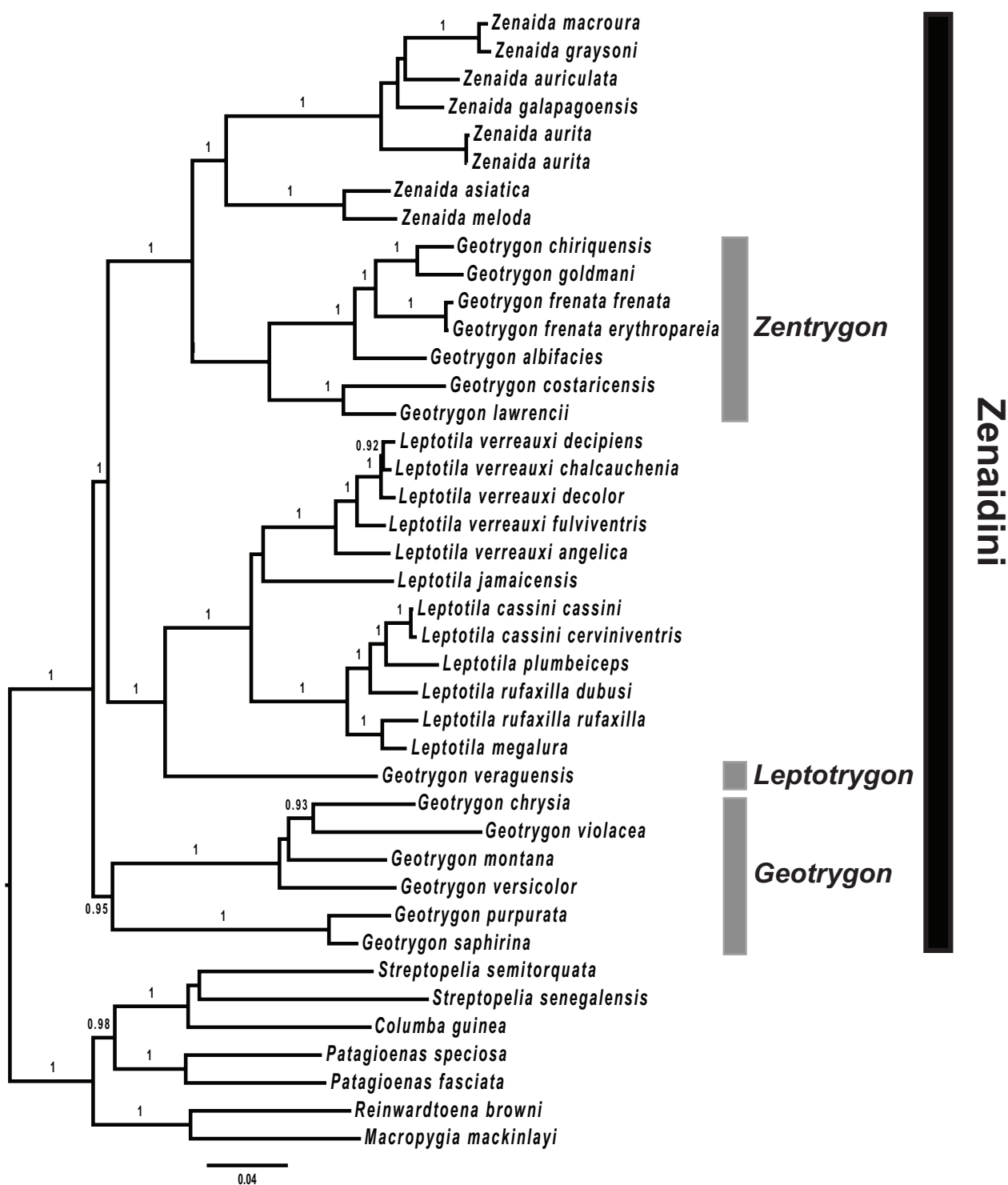


FIGURE 1. Phylogeny resulting from partitioned Bayesian analysis of combined mitochondrial cytochrome-b, COI, and ND2, and nuclear beta fibrinogen intron 7 sequences for *Geotrygon*, *Leptotila*, and *Zenaida* plus outgroups. Sequences are from Johnson and Weckstein (2011) except for those for *G. versicolor* and *G. chrysia*, which are newly obtained for COI, ND2, and beta fibrinogen intron 7 only. Numbers on nodes indicate Bayesian posterior probabilities; only posterior probabilities greater than 0.90 are shown. Names reflect prior taxonomic classification, with the monophyletic focal group Zenaidini and the proposed novel classification indicated with side bars.

Taxonomic recommendations

The genera of doves treated herein form a well-supported phylogenetic group (see Johnson and Weckstein 2011), and share many features of morphology and plumage. We propose that they be recognized as a tribe Zenaidini and suggest the following sequential listing of species, based on Fig. 1 and using the following conventions: (1) the branch with the fewest genera is listed first at each node of the phylogeny; (2) within a genus, the branch with the fewest species at each node is listed first; and (3) for terminal species pairs, the northwestern-most is listed first. Species not included in Fig. 1 and thus placed using traditional views of relationships (mainly from Baptista *et al.* 1997) are marked with an asterisk (*).

Tribe Zenaidini

Genus *Geotrygon*

Geotrygon purpurata
Geotrygon saphirina
Geotrygon versicolor
Geotrygon montana
Geotrygon violacea
Geotrygon caniceps *
*Geotrygon leucometopia**
Geotrygon chrysis
*Geotrygon mystacea**

Genus *Leptotrygon*

Leptotrygon veraguensis

Genus *Leptotila*

Leptotila verreauxi
Leptotila jamaicensis
Leptotila cassini
Leptotila conoveri *
Leptotila ochraceiventris *
Leptotila plumbeiceps (incl. *battyi**, treated as a species by Gibbs *et al.* (2001) and Dickinson (2003))
Leptotila rufaxilla
Leptotila wellsi *
Leptotila pallida *
Leptotila megalura

Genus *Zentrygon*

Zentrygon carrikeri *
Zentrygon costaricensis
Zentrygon lawrencii
Zentrygon albifacies
Zentrygon frenata
*Zentrygon linearis**
Zentrygon chiriquensis
Zentrygon goldmani

Genus *Zenaida*

Zenaida asiatica
Zenaida meloda
Zenaida aurita
Zenaida galapagoensis
Zenaida auriculata
Zenaida macroura
Zenaida graysoni

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Literature cited

- American Ornithologists' Union (1998) *Check-list of North American Birds*, 7th edition. American Ornithologists' Union, Washington, D.C., 829 pp.
- Banks, R.C., Cicero, C., Dunn, J.L., Kratter, A.W., Rasmussen, P.C., Remsen, J.V., Jr., Rising, J. D. & Stotz, D.F. (2004) Forty-fifth supplement to the American Ornithologists' Union *Check-list of North American Birds*. *Auk*, 121, 985–995.
- Baptista, L.F., Trail, P.W. & Horblit, H.M. (1997) Family Columbidae (pigeons and doves). In: Hoyo, J. del, *et al.* (Eds.), *Handbook of the Birds of the World, Vol. 4. Sandgrouse to cuckoos*. Lynx Edicions, Barcelona. pp. 60–243.
- Deignan, H.G. (1961) Type specimens of birds in the United States National Museum. *Bulletin U.S. National Museum*, 221, 1–718.
- Dickinson, E.C. (Ed.) (2003) *The Howard and Moore Complete Checklist of the Birds of the World. 3rd edition*. Princeton University Press, Princeton, New Jersey, 1039 pp.
- Dickinson, E.C., Overstreet, L.K., Dowsett, R.J. & Bruce, M.D. (Eds.) (2011) *Priority! The Dating of Scientific Names in Ornithology*. Aves Press, Northampton, UK, 319 pp. + CD-ROM.
- Garrido, O.H., Kirwan, G.M. & Capper, D.R. (2002) Species limits within Grey-headed Quail-Dove *Geotrygon caniceps* and implications for the conservation of a globally threatened species. *Bird Conservation International*, 12, 169–187.
<http://dx.doi.org/10.1017/S0959270902002101>
- Gibbs, D., Barnes, E. & Cox, J. (2001) *Pigeons and Doves. A Guide to the Pigeons and Doves of the World*. Yale University Press, New Haven, Connecticut, 615 pp.
- Gill, F.B. & Wright, M. (2006) *Birds of the World: Recommended English Names*. Princeton University Press, Princeton, New Jersey, 259 pp.
- Goodwin, D. (1958) Remarks on the taxonomy of some American doves. *Auk*, 75, 330–334.
<http://dx.doi.org/10.2307/4081978>
- Goodwin, D. (1967) *Pigeons and Doves of the World*. British Museum (Natural History), London, 446 pp.
- Goodwin, D. (1983) *Pigeons and Doves of the World*, 3rd edition, Cornell University Press, Ithaca, New York, 363 pp.
- Hellmayr, C.E. & Conover, B. (1942) *Catalogue of birds of the Americas*. Field Mus. Nat. Hist. Publ., Zool. Ser., 13, pt. 1, no. 1.
- Johnson, K.P. & Weckstein, J.D. (2011) The Central American land bridge as an engine of diversification in New World doves. *Journal of Biogeography* 38, 1069–1076.
<http://dx.doi.org/10.1111/j.1365-2699.2011.02501.x>
- Lanfear, R.B., Calcott, S.Y., Ho, W. & Guindon, S. (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analysis. *Molecular Biology and Evolution*, 29, 1695–1701.
<http://dx.doi.org/10.1093/molbev/mss020>
- Lawrence, G.N. (1866) Characters of seven new species of birds from Central and South America, with a note on *Thaumatia chionurus* Gould. *Annals of the Lyceum of Natural History of New York*, 8, 341–350.
<http://dx.doi.org/10.1111/j.1749-6632.1867.tb00322.x>
- Lawrence, G.N. (1868) A catalogue of the birds found in Costa Rica. *Annals of the Lyceum of Natural History of New York*, 9, 86–149.
<http://dx.doi.org/10.1111/j.1749-6632.1870.tb00177.x>
- Peters, J.L. (1937) *Check-list of Birds of the World, Vol. 3*. Harvard University Press, Cambridge, Massachusetts, 311 pp.
- Remsen, J.V., Jr., Cadena, C.D., Jaramillo, A., Nores, M., Pacheco, J.F., Pérez-Emán, J., Robbins, M.B., Stiles, F.G., Stotz, D.F. & Zimmer, K.J. (2012) A classification of the bird species of South America. American Ornithologists' Union. Available from: <http://www.museum.lsu.edu/~Remsen/SACCBaseline.html> (Accessed 13 May 2013)
- Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3. Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574.
<http://dx.doi.org/10.1093/bioinformatics/btg180>
- Wetmore, A. (1968) *The Birds of the Republic of Panamá, Vol. 2*. Smithsonian Miscellaneous Collections, Vol. 150., pt. 2., 605 pp.