



A revised classification of the fluvicoline tyrant flycatchers (Passeriformes, Tyrannidae, Fluvicolinae)

JAN I. OHLSON¹, MARTIN IRESTEDT¹, HENRIQUE BATALHA FILHO², PER G. P. ERICSON¹ & JON FJELDSÅ³

¹Dept of Bioinformatics and Genetics, Swedish Museum of Natural History, Sweden.

²National Inst. of Science and Technology in Interdisciplinary and Transdisciplinary Studies in Ecology and Evolution (INCT IN-TREE), Inst. de Biologia, Univ. Federal da Bahia, Brazil.

³Center for Macroecology, Evolution and Climate and The Natural History Museum of Denmark, University of Copenhagen, Denmark.

Abstract

A new classification is proposed for the subfamily Fluvicolinae in the New World Flycatchers (Tyrannidae), based on the results of a previously published phylogeny including more than 90% of the species. In this classification we propose one new family level name (Ochthoecini) and one new generic name (*Scotomyias*). We also resurrect three genera (*Heteroxolmis*, *Pyrope* and *Nengetus*) and subsume five (*Tumbezia*, *Lathrotriccus*, *Polioxolmis*, *Neoxolmis* and *Myiotheretes*) into other genera to align the classification with the current understanding of phylogenetic relationships in Fluvicolinae.

Key words: Aves, phylogeny, taxonomy, systematics

Introduction

Comprehensive multi-locus phylogenies of the New World flycatchers and their allies (Tyrannoidea), (e.g. Tello *et al.* 2009; Ohlson *et al.* 2013; FjeldsÅ *et al.* 2018) have greatly improved understanding of the deeper evolutionary relationships within this clade. One of the main findings of Ohlson *et al.* (2008) was the old age of the split between the typical tyrant-flycatchers, the flatbills and tody-tyrants and several small old clades. To highlight this, Ohlson *et al.* (2013) favoured dividing the traditional Tyrannidae into several families, with Tyrannidae and Rhynchocyclidae containing the majority of species. Tyrannidae as currently treated (e.g., Dickinson & Christidis 2014) includes just over 300 species divided between the three species-rich subfamilies Elaeniinae, Tyranninae and Fluvicolinae, and the two small subfamilies Hirundineinae and Muscigrallinae.

Phylogenetic studies covering most of the generic diversity in Tyrannidae and its subfamilies have been conducted by Ohlson *et al.* (2008, 2013) and Tello *et al.* (2009). However, many questions remain about relationships within terminal groups, and species-level phylogenetic hypotheses have only been presented for a few clades, e.g. *Muscisaxicola* d'Orbigny & Lafresnaye (Chesser 2000), *Empidonax* Cabanis (Johnson & Cicero 2002) and *Knipolegus* Boie (Hosner & Moyle 2012). The subfamilies in Tyrannidae exhibit strikingly different patterns of morphological and ecological diversity and geographical distribution. A recent near-complete phylogeny (FjeldsÅ *et al.* 2018) has contributed to a much better understanding of the phylogenetic relationships and the biogeographic and ecological patterns in Fluvicolinae. The aim of the present paper is to implement the necessary taxonomic changes, and to update the recommended linear classification, based on the phylogenetic results from FjeldsÅ and colleagues.

The study by FjeldsÅ *et al.* (2018) included samples from 113 of 122 species referred to the subfamily by Dickinson & Christidis (2014). It is lacking data only for *Contopus albogularis* (Berlioz), *C. latirostris* (J. Verreaux) and *C. pallidus* (Gosse); *Fluvicola pica* (Boddaert); *Myiophobus inornatus* Carriker; *Xolmis salinarum* Nores & Yzurietta; and a few species that were included in other molecular studies: *Knipolegus franciscanus* Sneath and *K. nigerrimus* (Vieillot) (Hosner & Moyle 2012); *Muscisaxicola juninensis* Taczanowski and *M. albilora* Lafresnaye

(Chesser 2000); *Guyramemua affine* (Burmeister) (Lopes *et al.* 2018); and species resulting from recently suggested splits in *Pyrocephalus* (Carmi *et al.* 2016). Their study was based on sequence data from six molecular markers: two mtDNA gene regions, cytochrome b (cyt b) and nicotine amide dehydrogenase subunit 2 (ND2); and four nuclear introns: glyceraldehyde dehydrogenase intron 11 (G3P), myoglobin intron 2 (Myo), ornithine decarboxylase introns 6-7 (ODC) and transforming growth factor beta 2 intron 5 (TGFb2).

Although the evolutionary relationships of Tyrannidae and its allies have been clarified and corroborated by several independent studies during the last decade, none of the widely used, and regularly updated, checklists (Dickinson & Christidis 2014; Clements *et al.* 2018; Gill & Donsker 2018; Remsen *et al.* 2018) have incorporated this information in a consistent manner. Here we build on the classification proposed in Ohlson *et al.* (2013) for an updated classification of Fluvicolinae. Thus, compared to traditional classifications based on Peters' *Check-list* (Traylor 1979), Fluvicolinae excludes *Onychorhynchus* Fischer, *Myiobius* G. R. Gray and *Terentriacus* Ridgway (now in the separate family Onychorhynchidae), *Myiotriccus* Ridgway, *Hirundinea* d'Orbigny & Lafresnaye, *Pyrhomyias* Cabanis & Heine and *Nephelomyias* Ohlson, Fjeldså & Ericson (now in the separate subfamily Hirundineinae in Tyrannidae, the latter formerly in *Myiophobus* Reichenbach), *Nesotriccus* Townsend (now in Elaeniinae), *Muscigralla* d'Orbigny & Lafresnaye (now in the separate subfamily Muscigrallinae in Tyranninae) and *Machetornis* G. R. Gray (now in Tyranninae). The only additions to the subfamily are *Sublegatus* Sclater & Salvin (formerly in Elaeniinae), and very recently *Guyramemua affine*, which was formerly placed in *Suiriri* d'Orbigny (Lopes *et al.* 2018). With this treatment, Fluvicolinae contains 130 species in 32 genera.

Methods

The phylogenetic trees in Fjeldså *et al.* (2018) are used as our best estimate of the phylogenetic relationships in Fluvicolinae, thus serving as the foundation for our classification. Taxonomic changes are made when needed to define groups that can be identified as monophyletic. To maintain taxonomic stability as far as possible we propose only those changes that follow from groupings receiving strong nodal support, greater than 0.95 posterior probability in the Bayesian analyses.

For the linear classification we use the following principles: tribes, genera and species are arranged in a sequence that follows the phylogeny, starting with the deepest branches, and with the smallest of sister groups first. These principles are recognized in several recent avian classifications (e.g. Clements *et al.* 2018; Gill *et al.* 2018; Remsen *et al.* 2018), although not always followed consistently.

We acknowledge that the delimitation of genera is largely arbitrary, as long as the requirements of monophyly for each named clade are met. Arguments have been made that temporal guidelines should be used in decisions on generic delimitation (e.g. Holt & Jønsson 2014). This would decrease the arbitrariness of generic delimitation, at least to some degree. The result will sometimes be in conflict with generic subdivisions based on phenotypic uniformity, but temporal criteria are easier to define objectively than phenotypic divergence. However, to maintain as much as possible of the traditional classification, we aim to balance these two guidelines in our decisions.

Results and discussion

Taxonomic changes

The phylogeny in Fjeldså *et al.* (2018) clarifies the evolutionary relationships for most species and genera in this radiation. It demonstrates that the chat-tyrant group (*Ochthoeca* Cabanis and its allies) is a monophyletic clade of similar age as the other recognized tribes in Fluvicolinae, and thus in need of a formal name. It also shows that the genera *Myiophobus*, *Xolmis* Boie and probably also *Empidonax* are not monophyletic (see Fjeldså *et al.* 2018; Figs. 1 & 2).

In the case of *Empidonax*, phylogenetic resolution and statistical support for non-monophyly is insufficient for taxonomic changes to be made at this point. There are no known diagnostic morphological features to distinguish between the four *Empidonax* clades, but each of them possesses at least one unique ecological trait that separates them from their congeners (Johnson & Cicero 2002), as follows. *Empidonax virescens* (Vieillot, 1818) is the only species in its clade, and is also the type of the genus. It is unique in inhabiting bottomland forest interior, often near

small streams. The second clade [*E. flaviventris* (W. M. Baird & S. F. Baird), *E. flavescens* Lawrence, *E. difficilis* (S. F. Baird) and *E. occidentalis* Nelson] differs from other *Empidonax* species by placing a mossy nest on a ledge or in a crevice, instead of placing a nest of plant fibers in a branch fork. The third clade, which consists of *E. albigularis* (P. L. Sclater & Salvin), *E. alnorum* (Brewster) and *E. traillii* (Audubon), differs from other *Empidonax* species by breeding in damp, often semi-open habitats like moist thickets and bog margins, in contrast to the generally dry to mesic woodland or forest edge habitat of other species. The fourth clade [*Empidonax atriceps* Salvin, *E. fulvifrons* (Giraud Jr.), *E. minimus* (W. M. Baird & S. F. Baird), *E. wrightii* S. F. Baird, *E. hammondii* (Xántus), *E. affinis* (Swainson) and *E. oberholseri* A. R. Phillips] differs from other *Empidonax* clades by having unmarked eggs. If a division of *Empidonax* into several genera is shown to be necessary, the name *Empidonax* is applicable to the clade containing *E. virescens*, whereas the name *Cnemonax* Brodkorb, 1936 (type species *Empidonax atriceps*) is available for a clade containing *E. atriceps* (clade 4 in this work). Any further new genera would need new names.

To adjust the classification of Fluvicolinae to these and other findings, we recommend changes as follows below.

1. Recognize *Heteroxolmis* Lanyon, 1986 (type = *Tyrannus dominicanus* (Vieillot) for *Xolmis dominicanus* and remove it from Xolmini to Fluvicolini. The distinctiveness of *dominicanus* from other *Xolmis* species was recognized by Lanyon (1986) based on morphological characters of the nasal capsule and syrinx, but he regarded the two genera as close relatives. Among the character states that motivated a separation from *Xolmis* is a fully ossified nasal capsule, including alinasal walls and turbinals, which is also found in *Alectrurus* Vieillot, *Gubernetes* Such, *Fluvicola* Swainson and *Arundinicola* d'Orbigny (Lanyon 1986). As the gender of *Heteroxolmis* is feminine (see Lanyon 1986, fig. 24), the name of the species becomes *Heteroxolmis dominicana*.

2. Ochthoecini, Ohlson, Irestedt, Batalha Filho, Ericson and Fjeldså, new family group name

Type genus: *Ochthoeca* Cabanis, 1847

Included genera: *Ochthoeca* Cabanis, *Myiophobus* Reichenbach, *Colorhamphus* Sundevall, *Silvicultrix* Lanyon, and *Scotomyias*, Ohlson, Irestedt, Batalha Filho, Ericson and Fjeldså.

Diagnosis: A morphologically homogeneous group, which is well-supported in all published phylogenetic studies. There are no known internal anatomical characters that define the clade. Morphologically and behaviorally the group is well-defined as sexually monomorphic flycatchers with a compact body shape, generally upright posture with protruding breast when perched, and moderately long tails, moderately long tarsi, and a triangular, moderately compressed and broad-based bill with rictal bristles extending slightly beyond the middle of the bill. Plumage colouration and patterns generally simple. In general, colouration includes dark olive, earthy brownish or sooty upperparts and underparts varying from sooty grey to rufous, pale grey, dull yellowish or bright yellow depending on the species. Some species have a rufous breast band; streaking on the chest occurs only in *Myiophobus*. *Myiophobus* and *Ochthoeca salvini* have distinctive pale wing bars, otherwise wing patterns are usually subdued, mostly in the form of dull cinnamon or buff wing bars. Distinctive markings include bright white, yellow, or rufous bands across forehead and eyebrow (*Ochthoeca*, *Silvicultrix*) and bright yellow or orange coronal patches (*Myiophobus*, *Scotomyias*).

Cladistic definition: All descendants of the most recent common ancestor of *Myiophobus fasciatus* (Statius Müller) and *Ochthoeca leucophrys* (d'Orbigny & Lafresnaye).

Habitat and distribution: *Myiophobus* has a wide distribution in scrubby habitats in tropical lowlands of South America; the remainder of the genera are largely restricted to the Andes, with one species in the Tumbesian lowlands, one species in the tepuis and one species in the austral *Nothofagus* forest. Most species occur in humid forest undergrowth and edges, but one clade in *Ochthoeca* favours drier habitats. All species forage by short sallies to air or vegetation, usually from a low perch.

The name Ochthoecini appears in Fjeldså (2012) but there it does not fulfill requirements for new family group names in the ICZN (e.g. articles 13.1 and 16.1: no description or diagnosis, no explicit intent to establish it as a new name etc.).

3. *Scotomyias*, Ohlson, Irestedt, Batalha Filho, Ericson & Fjeldså, new genus

Type species: *Myiobius flavicans* P. L. Sclater, currently recognized as *Myiophobus flavicans*.

Included species: *Scotomyias flavicans*, *Scotomyias inornatus* (Carriker), *Scotomyias phoenicomitra* (Taczanowski & Berlepsch) and *Scotomyias roraimae* (Salvin & Godman). These species are all currently recognized as members of *Myiophobus*.

Diagnosis: Small (11–13.5 cm body length), compact chat-tyrants with subdued colours but proportions similar to those of close relatives *Silvicultrix* W. Lanyon and *Ochthoeca*. All species have an orange or yellow semi-concealed coronal stripe (males only), but lack the prominent bright eyebrow stripe typical of all *Silvicultrix* and *Ochthoeca* species. Upperparts dull olive green or brownish, underparts dull olive yellow to dull yellowish white, with smudgy olive flammulations on chest and body sides. Wings and tail have varying degrees of diffusely demarcated cinnamon or buffy edges to secondary coverts and fringes of the remiges, forming distinctive wing-bars only in *M. roraimae*. These markings extend along the whole length of the feathers, with no contrasting black area at the base of the secondaries in the closed wing, as seen in *Nephelomyias* and *Myiophobus*. Iris always dark, legs dark grey or blackish, upper mandible blackish, lower mandible usually dull orange to flesh-coloured. There are no known synapomorphies in internal anatomy for this group.

Cladistic definition: All descendants of the most recent common ancestor of *Scotomyias flavicans* and *S. roraimae*.

Habitat and distribution: All species inhabit understorey and thickets in humid forest in the Andes and the Guiana Highlands, mainly in the lower montane forest, up to 2700 m. Generally rather quiet and sluggish and normally found in pairs or family groups. Usually forage independently and do not follow mixed feeding parties; forage with short aerial sallies from a low perch.

Etymology: Gr. σκοτος *skotos* darkness, gloom; Mod. L. *myias* flycatcher. Refers to the dark and shadowy forest interior habitat of all species in the genus, a habitat in which few other members of Fluvicolinae are found. The name is masculine in gender.

Comments: These species form a strongly supported clade sister to *Silvicultrix* (Fjeldså *et al.* 2018). In view of the close similarity both in plumage and syringeal characters (Lanyon 1986) and the fact that *S. inornatus* and *S. flavicans* replace each other geographically, we also infer that *S. inornatus* should be included in this genus, although genetic data is lacking for it.

4. Merge *Tumbezia* Chapman, 1925 into *Ochthoeca* Cabanis, 1847, *Tumbezia salvini* (Taczanowski) becoming *Ochthoeca salvini*. The alternative would be to create a new genus for the clade containing *Ochthoeca cinnamomeiventris* (Lafresnaye) and *O. thoracica* (Taczanowski), which in our opinion would be an unnecessary splitting of a morphologically and ecologically homogenous clade.
5. Merge *Lathrotriccus* W. E. Lanyon & S. M. Lanyon, 1986 into *Aphanotriccus* Ridgway, 1905, *Lathrotriccus eulerei* (Cabanis) and *Lathrotriccus griseipectus* (Lawrence) becoming *Aphanotriccus eulerei* and *Aphanotriccus griseipectus*. The two clades are reciprocally monophyletic, but the estimated divergence date between them (ca. 2.5 Mya) is comparable to within-genus divergence times in well-established genera in Tyrannidae, and there are no significant behavioural or morphological differences between the two.
6. Merge *Polioxolmis* W. E. Lanyon, 1986, into *Cnemarchus* Ridgway, 1905, *Polioxolmis rufipennis* (Taczanowski) becoming *Cnemarchus rufipennis*. The estimated divergence date between them (ca. 4.5 Mya) is comparable to within-genus divergence times in well-established genera in Tyrannidae, and differences in morphology and behaviour between the two are not significant.
7. Recognize *Pyrope* Cabanis & Heine, 1859 [type *Pyrope kittlitzii* Cabanis & Heine, currently *Xolmis pyrope* (Kittlitz, 1830)] for *Xolmis pyrope*.
8. Recognize *Nengetus* Swainson, 1827 [type *Tyrannus nengeta* Swainson, currently known as *Xolmis cinereus* (Vieillot)] for *Xolmis cinereus*, *X. coronatus* (Vieillot), *X. rubetra* (Burmeister), *X. salinarum*, *Neoxolmis rufiventris* (Vieillot), sole species in *Neoxolmis* (Hellmayr, 1927), and all four species currently placed in the genus *Myiotheretes* (Reichenbach, 1850). This creates a genus with broad morphological and behavioural variation from terrestrial, long-legged species like *N. rufiventris* to the arboreal, short-legged species formerly in *Myiotheretes*. However, apart from the differences in tarsal length, as an adaptation to an arboreal

foraging strategy, morphological differences are not strong. An alternative arrangement would have been to retain *Myiotheretes*, move *X. rubetra* and *X. salinarum* to *Neoxolmis*, erect a new genus for *X. coronatus* and reserve the name *Nengetus* for *X. cinereus*. However, the unresolved phylogenetic positions of *N. cinereus* and *N. coronatus* within this clade argue against placing them in monophyletic genera. *Nengetus* is male in gender, so no suffix changes are needed in the species epithets of any of its included species.

New linear classification

Current classifications in various checklists, are inconsistent with respect to how well classification follows phylogeny. The following is our phylogeny-based recommendation for a linear classification of Fluvicolinae. Numbers refer to the foregoing section, see also Fig. 1. Species marked with an asterisk were not sampled in the phylogeny on which this classification is based.

FAMILY Tyrannidae Vigors

SUBFAMILY Fluvicolinae Swainson

TRIBE Fluvicolini Swainson

Guyramemua Lopes, Chaves, Aquino, Silveira & Santos

*affine** Burmeister

Sublegatus Sclater & Salvin

modestus (Wied)

arenarum (Salvin)

obscurior Todd

Colonia J. E. Gray

colonus (Vieillot)

Arundinicola d'Orbigny

leucocephala (Linnaeus)

Fluvicola Swainson

nengeta (Linnaeus)

albiventer (Spix)

*pica** (Boddaert)

Pyrocephalus Gould

rubinus (Boddaert)

*obscurus** Gould

*nanus** Gould

*dubius** Gould & G. R. Gray

Muscipipra Lesson

vetula (M. H. K. Lichtenstein)

Gubernetes Such

yetapa (Vieillot)

1. *Heteroxolmis* W. E. Lanyon

dominicana (Vieillot)

Alectrurus Vieillot

*tricolor** (Vieillot)

risora (Vieillot)

2. **TRIBE Ochthoecini Ohlson, Irestedt, Batalha Filho, Ericson & Fjeldså, this paper**

Myiophobus Reichenbach

cryptoxanthus (P. L. Sclater)

fasciatus (Stadius Müller)

3. *Scotomyias* Ohlson, Irestedt, Batalha Filho, Ericson & Fjeldså, this paper

flavicans (P. L. Sclater)

phoenicomitra (Taczanowski & Berlepsch)

roraimae (Salvin & Godman)

*inornatus** (Carriker)

Silvicultrix W. E. Lanyon

diadema (Hartlaub)

frontalis (Lafresnaye)

*spodionota** (Berlepsch & Stolzmann)

pulchella (P. L. Sclater & Salvin)

jelskii (Taczanowski)

Colorhamphus Sundevall

parvirostris (Gould & G. R. Gray)

Ochthoeca Cabanis

cinnamomeiventris (Lafresnaye)

thoracica Taczanowski

*nigrita** P. L. Sclater & Salvin

4. *salvini* (Taczanowski)

fumicolor P. L. Sclater

rufipectoralis (d'Orbigny & Lafresnaye)

piurae Chapman

oenanthoides (d'Orbigny & Lafresnaye)

leucophrys (d'Orbigny & Lafresnaye)

TRIBE Contopini Fitzpatrick

Ochthornis P L Sclater

littoralis (Pelzeln)

Cnemotriccus Hellmayr

fuscatus (Wied)

5. *Aphanotriccus* Ridgway

euleri (Cabanis)

griseipectus (Lawrence)

capitalis (Salvin)

audax (Nelson)

Xenotriccus Dwight & Griscom

callizonus Dwight & Griscom

mexicanus (J. T. Zimmer)

Sayornis Bonaparte

saya (Bonaparte)

phoebe (Latham)

nigricans (Swainson)

Empidonax Cabanis

virescens (Vieillot)

flaviventris (W. M. Baird & S. F. Baird)

flavescens (Lawrence)

difficilis (S. F. Baird)

occidentalis (Nelson)

albigularis (P. L. Sclater & Salvin)

alnorum (Brewster)

traillii (Audubon)

atriceps (Salvin)

fulvifrons (Giraud Jr.)

wrightii (S. F. Baird)

minimus (W. M. Baird & S. F. Baird)

hammondii (Xantus)

affinis (Swainson)

oberholseri (A. R. Phillips)
Mitrephanes Coues
phaeocercus (P. L. Sclater)
olivaceus Berlepsch & Stolzmann
Contopus Cabanis
cooperi (Nuttall)
ochraceus P. L. Sclater & Salvin
fumigatus d'Orbigny & Lafresnaye
lugubris Lawrence
pertinax Cabanis & Heine
virens (Linnaeus)
caribaeus (d'Orbigny)
hispaniolensis (H. Bryant)
*pallidus** (Gosse)
*latirostris** (J. Verreaux)
nigrescens (P. L. Sclater & Salvin)
cinereus (Spix)
sordidulus P. L. Sclater
*punensis** Lawrence
*albogularis** Berlioz

TRIBE Xolmini Tello, Moyle, Marchese & Cracraft

Satrapa Strickland
icterophrys (Vieillot)
Lessonia Swainson
rufa (J. F. Gmelin)
oreas (P. L. Sclater & Salvin)
Muscisaxicola d'Orbigny & Lafresnaye
fluviatilis P. L. Sclater & Salvin
maculirostris d'Orbigny & Lafresnaye
alpinus (Jardine)
*albilora** Lafresnaye
maclovianus (Garnot)
frontalis (Burmeister)
capistratus (Burmeister)
griseus Taczanowski
*juninensis** Taczanowski
cinereus Philippi & Landbeck
rufivertex d'Orbigny & Lafresnaye
flavinucha Lafresnaye
albifrons (Tschudi)
Hymenops Lesson
perspicillatus (J. F. Gmelin)
Knipolegus F. Boie
orenocensis Berlepsch
poecilocercus (Pelzeln)
poecilurus (P. L. Sclater)
*franciscanus** Sneath
lophotes F. Boie
*nigerrimus** (Vieillot)
cyanirostris (Vieillot)
cabanisi Schulz
signatus (Taczanowski)

- straticeps* (d'Orbigny & Lafresnaye)
hudsoni P. L. Sclater
aterrimus Kaup
Cnemarchus Ridgway
erythrogygius (P. L. Sclater)
6. *rufipennis* (Taczanowski)
7. *Pyrope* Cabanis & Heine
pyrope (Kittlitz)
Xolmis F. Boie
irupero (Vieillot)
velatus (M. H. K. Lichtenstein)
Agriornis Gould
murinus (d'Orbigny & Lafresnaye)
montanus (d'Orbigny & Lafresnaye)
albicauda (Philippi & Landbeck)
lividus (Kittlitz)
micropterus Gould
8. *Nengetus* Swainson
coronatus (Vieillot)
rufiventris (Vieillot)
rubetra (Burmeister)
salinarum (Nores & Yzurieta)
cinereus (Vieillot)
fumigatus (Boissonneau)
fuscorufus (P. L. Sclater & Salvin)
striaticollis (P. L. Sclater)
pernix (Bangs)

Acknowledgments

Terry Chesser, Pamela Rasmussen and one anonymous reviewer are thanked for valuable comments on an earlier version of the manuscript.

References

- Brodkorb, P. (1936) A new genus for *Empidonax atriceps* Salvin. *Occasional Papers of the Museum of Zoology, University of Michigan*, 331, 1–4.
Cabanis, J. (1847) Ornithologische Notizen. *Archiv für Naturgeschichte*, 13 (1), 186–352.
Cabanis, J. & Heine, F. (1859) Verzeichniss der ornithologischen Sammlung des Oberamtmann Ferdinand Heine, auf Gut St. Burchard vor Halberstadt. *Museum Heineanum*, 2, 1–76.
Carmi, O., Witt, C.C., Jaramillo, A. & Dumbacher, J.P. (2016) Phylogeography of the Vermillion Flycatcher species complex: multiple speciation events, shifts in migratory behavior, and an apparent extinction of a Galápagos-endemic bird species. *Molecular Phylogenetics and Evolution*, 102, 152–173.
<https://doi.org/10.1016/j.ympev.2016.05.029>
Chapman, F.M. (1925) Descriptions of one new genus and species of birds from Peru and Ecuador. *American Museum Novitates*, 205, 1–12.
Chesser, R.T. (2000) Evolution in the high Andes: the phylogenetics of *Muscisaxicola* ground-tyrants. *Molecular Phylogenetics and Evolution*, 15, 369–380.
<https://doi.org/10.1006/mpev.1999.0774>
Clements, J.F., Schulenberg, T.S., Iliff, M.J., Roberson, D., Fredericks, T.A., Sullivan, B.L. & Wood, C.L. (2018) The eBird/Clements Checklist of Birds of the World. Version 2018. Available from: <http://www.birds.cornell.edu/clementschecklist/download/> (accessed 14 April 2019)
Dickinson, E.C. & Christidis, L. (2014) *The Howard and Moore Complete Checklist of the Birds of the World. 4th Edition. Vol.*

2. Aves Press, Eastbourne, 752 pp.

- Fjelds , J. (2012) Diversification of the Neotropical avifauna: disentangling the geographical patterns of persisting ancient taxa and phylogenetic expansions. *Ornitologia Neotropical*, 23, 13–27.
- Fjelds , J., Ohlson, J.I., Batalha Filho, H., Ericson, P.G.P. & Irestedt, M. (2018) Rapid expansion and diversification into new niche space by fluvicoline flycatchers. *Journal of Avian Biology*, 49 (3), jav-01661.
<https://doi.org/10.1111/jav.01661>
- Gill, F. & Donsker, D. (Eds.) (2018) IOC World Bird List. Version 8.1. Available from: <https://www.worldbirdnames.org/ioc-lists/master-list-2/> (accessed 12 January 2020)
<https://doi.org/10.14344/IOC.ML.8.1>
- Hellmayr, C.E. (1927) Catalogue of birds of the Americas and the adjacent islands, part 5. *Publications of the Field Museum of Natural History*, Zoological Series, 13 (5), 1–517.
- Holt, B.G. & J nsson, K. (2014) Reconciling hierarchical taxonomy with molecular phylogenies. *Systematic Biology*, 63, 1010–1017.
<https://doi.org/10.1093/sysbio/syu061>
- Hosner, P.A. & Moyle, R.G. (2012) A molecular phylogeny of black-tyrants (Tyrannidae: *Knipolegus*) reveals strong geographic patterns and homoplasy in plumage and display behavior. *Auk*, 129, 156–167.
<https://doi.org/10.1525/auk.2012.11101>
- Johnson, N.K. & Cicero, C. (2002) The role of ecological diversification in sibling speciation of *Empidonax* flycatchers (Tyrannidae): multigene evidence from mtDNA. *Molecular Ecology*, 11, 2065–2081.
<https://doi.org/10.1046/j.1365-294X.2002.01588.x>
- Kittlitz, F.H. (1830)  ber Einige V gel von Chili. *Memoires de l'Acad mie Imperiale des Sciences*, 1, 173–194.
- Lanyon, W.E. (1986) A phylogeny of the thirty-three genera in the *Empidonax* assemblage of tyrant flycatchers. *American Museum Novitates*, 2846, 1–64.
- Lanyon, W.E. & Lanyon, S.M. (1986) Generic status of Euler's Flycatcher: A morphological and biochemical study. *Auk*, 103, 341–350.
<https://doi.org/10.1093/auk/103.2.341>
- Lopes, L.E., Chaves, A.V., de Aquino, M.M., Silveira, L.F. & dos Santos, F.R. (2018) The striking polyphyly of *Suiriri*: Convergent evolution and social mimicry in two cryptic Neotropical birds. *Journal of Zoological Systematics and Evolutionary Research*, 56, 270–279.
<https://doi.org/10.1111/jzs.12200>
- Ohlson, J.I., Fjelds , J. & Ericson, P.G.P. (2008) Tyrant flycatchers coming out in the open: phylogeny and ecological radiation of Tyrannidae (Aves, Passeriformes). *Zoologica Scripta*, 37, 315–335.
<https://doi.org/10.1111/j.1463-6409.2008.00325.x>
- Ohlson, J.I., Irestedt, M., Ericson, P.G.P. & Fjelds , J. (2013) Phylogeny and classification of the New World suboscines (Aves, Passeriformes). *Zootaxa*, 3613 (1), 1–35.
<https://doi.org/10.11646/zootaxa.3613.1.1>
- Reichenbach, H.G.L. (1850) *Avium Systemae Naturale*, Expedition der vollst ndigsten naturgeschichte, Dresden und Leipzig, 36 pp. [pp. 52–87]
- Remsen Jr., J.V., Areta, J.I., Cadena, C.D., Claramunt, S., Jaramillo, A., Pacheco, J.F., Robbins, M.B., Stiles, F.G., Stotz, D.F. & Zimmer, K.J. (2019) *A Classification of the Bird Species of South America*. *American Ornithological Society*. Available from: <http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm> (accessed 2 October 2019)
- Ridgway R. (1905) Descriptions of some new genera of Tyrannidae, Pipridae, and Cotingidae. *Proceedings of the Biological Society of Washington*, 18, 207–210.
- Swainson, W. (1827) On several groups and forms in ornithology, not hitherto defined. *The Zoological Journal*, 3, 158–175.
- Tello, J.G., Moyle, R.G., Marchese, D.J. & Cracraft, J. (2009) Phylogeny and phylogenetic classification of the tyrant flycatchers, cotingas, manakins, and their allies (Aves: Tyrannides). *Cladistics*, 25, 1–39.
<https://doi.org/10.1111/j.1096-0031.2009.00254.x>
- Traylor, Jr.M.A. (1979) Tyrannidae. In: Traylor, Jr. M.A. (Ed.), *Peters' Check-list of the Birds of the World. Vol. 8*. Museum of Comparative Zoology, Cambridge, Massachusetts, pp. 1–365.

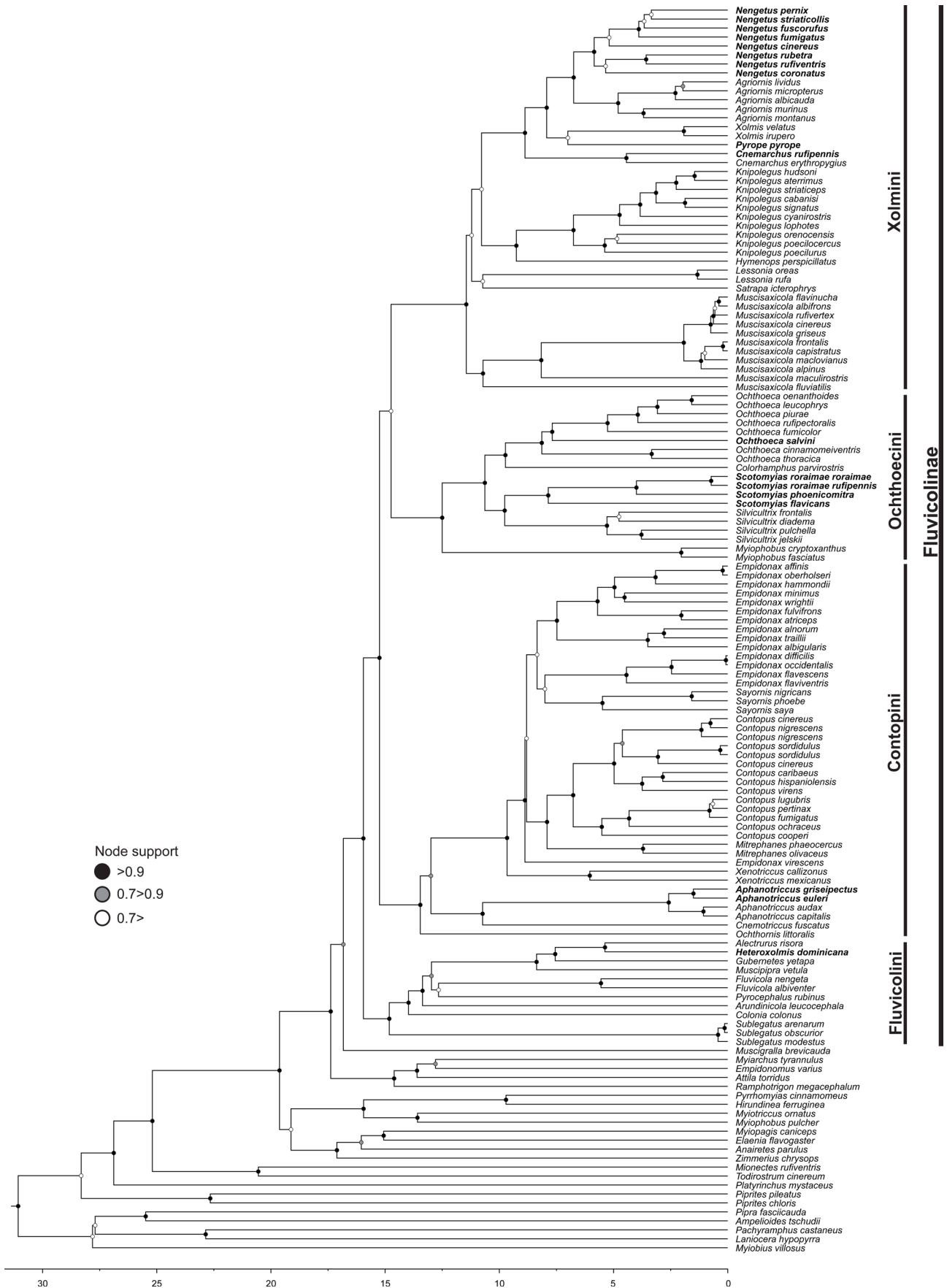


FIGURE 1. Chronogram with Bayesian posterior probabilities. Taxa in bold are affected by taxonomic changes proposed in this paper.