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 Muscicraginiae.

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 (Boddart); Myiophobus inornatus Carriker; Xolmis salinarum Nores & Yzurieta; and a few species that were included in other molecular studies: Knipolegus franciscanus Snethlage and K. nigerrimus (Vieillot) (Hosner & Moyle 2012); Muscisaxicola juninensis Taczanowski and M. albilara Lafresnaye

Accepted by P. Rasmussen: 30 Jan. 2020; published: 2 Mar. 2020

Licensed under a Creative Commons Attribution 4.0 International License http://creativecommons.org/licenses/by/4.0/
(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 Fluvicolineae. Thus, compared to traditional classifications based on Peters’ Check-list (Traylor 1979), Fluvicolineae excludes Onychorhynchus Fischer, Myiobius G. R. Gray and Terenotriccus Ridgway (now in the separate family Onychorrhynchidae), Myiotorchus Ridgway, Hirundinea d’Orbigny & Lafresnaye, Pyrrhomyias Cabanis & Heine and Nephelomyias Ohlson, Fjeldså & Ericson (now in the separate subfamily Hirundineinae in Tyrannidae), the latter formerly in Myiophobus Reichenbach), Nesorotriccus Townsend (now in Elaeniinae), Muscigralla d’Orbigny & Lafresnaye (now in the separate subfamily Muscigrallinae in Tyranninae) and Machetorhynchus. The only additions to the subfamily are Sublegatus Selater & 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 & Jonsson 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 Fluvicolineae, 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. albicularis (P. L. Sclater & Salvin), E. alhorum (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 Cnemoxon 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 Xolminini to Fluvicolinae. 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 closely related. 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: Ochthoea Cabanis, 1847
   Included genera: Ochthoea 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 Ochthoea 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 (Ochthoea, 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 Ochthoea leucophrys (d’Orbigny & Lafrésnaye).
   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 Ochthoea 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.).

   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 *Ochthoea*. 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 *Ochthoea* species. Upperparts dull olive green or brownish, underparts dull olive yellow to dull yellowish white, with smudgy olive flammations 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 *Scotomyias roraimae* replaces each other geographically, we also infer that *S. inornatus* and *S. flavicans* should be included in this genus, although genetic data is lacking for it.

4. Merge *Tumbezia* Chapman, 1925 into *Ochthoea* Cabanis, 1847, *Tumbezia salvini* (Taczanowski) becoming *Ochthoea salvini*. The alternative would be to create a new genus for the clade containing *Ochthoea cinna-momeiventris* (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 euleri* (Cabanis) and *Lathrotriccus griseipectus* (Lawrence) becoming *Aphanotriccus euleri* 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 kittlitzi* 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 preceding 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* (Statius 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)
spodonota* (Berlepsch & Stolzmann)
pulchella (P. L. Sclater & Salvin)
jelskii (Taczanowski)

Colorhamphus Sundevall
parviostris (Gould & G. R. Gray)

Ochthoeeca 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
tittoralis (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)
albicularis (P. L. Sclater & Salvin)
atorum (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* (Linnæus)
*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* Snethlage
*laphotes* F. Boie
*nigerrimus* (Vieillot)
*cyanirostris* (Vieillot)
*cabanisi* Schulz
*signatus* (Taczanowski)
straticeps (d’Orbigny & Lafresnaye)
hudsoni P. L. Sclater
aterrimus Kaup

Cnemarchus Ridgway
erythropygius (P. L. Sclater)
ruftpennis (Taczanowski)

6. 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

7. Nengetus Swainson
   coronatus (Vieillot)
rufiventris (Vieillot)
rubetra (Burmeister)
salinarum (Nares & Yzurieta)
cinereus (Vieillot)
fumigatus (Boissonneau)
fuscorsulcus (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

https://doi.org/10.1016/j.ympev.2016.05.029
https://doi.org/10.1006/mpev.1999.0774


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