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A revised classification of the Xolmiini (Aves: Tyrannidae: Fluvicolinae), including a new genus for *Muscisaxicola fluviatilis*

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Abstract.—Recent studies using molecular phylogenetics have provided new insight into the composition of and relationships among species in the avian tribe Xolmiini. Key findings include the paraphyly of *Xolmis*, including the exclusion of *X. dominicanus* from the Xolmiini, and the apparent paraphyly of *Muscisaxicola*. We provide a revised classification of the Xolmiini, including a new genus for *Muscisaxicola fluviatilis*, based on the recent phylogenetic results.

Keywords: *Xolmis*, *Cnemarchus*, tyrant-flycatcher, Tyrannidae, suboscine, systematics

The avian tribe Xolmiini (Tello et al. 2009) is a clade of South American birds found mainly in open country in the southern part of the continent, the Andes, and the northern non-Andean highlands, although a few species inhabit Amazonian or other tropical lowlands. The group includes the genera *Lessonia* Swainson, 1832 (the negritos); *Knipolegus* Boie, 1826 (black-tyrants); *Hymenops* Lesson, 1828 (Spectacled Tyrant); *Satrapa* Strickland, 1844 (Yellow-browed Tyrant); *Muscisaxicola* Orbigny & Lafresnaye, 1837 (ground-tyrants); *Cnemarchus* Ridgway, 1905, *Po-lioxolmis* Lanyon, 1986, and *Myiotheretes* Reichenbach, 1850 (bush-tyrants); *Xolmis* Boie, 1826, and *Neoxolmis* Cory and Hellmayr, 1927 (monjitas); and *Agriornis* Gould, 1839 (shrike-tyrants). Tello et al. (2009) sequenced the nuclear genes RAG-1

and RAG-2 for 13 of the 49 species of the Xolmiini (1–2 species per genus) as part of a genus-level study of the Tyrannides. They determined that this group of genera forms a clade, and they further divided the clade into two subgroups, one consisting of *Lessonia*, *Knipolegus*, and *Hymenops* (termed the *Knipolegus* group), the other of the remaining genera (*Xolmis* group).

Fjeldså et al. (2018) conducted a more comprehensive molecular study of the group, sequencing two mitochondrial genes and four nuclear introns for 43 species of Xolmiini as part of a study of the tyrannid subfamily Fluvicolinae. Broadly speaking, their results supported the monophyly of the group, but *Xolmis dominicanus* was determined to be only distantly related to the Xolmiini, nesting instead within the tribe Fluvicolini (*sensu* Tello et al. 2009). Further, their results suggested that *Muscisaxicola* was sister to

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the rest of the *Xolmiini* (albeit with weak support) and that *Satrapa icterophrys* grouped with the *Knipolegus* group of Tello et al. (2009) rather than with the remainder of their *Xolmis* group (although again with weak support).

As part of a larger phylogenetic project on suboscine birds, Harvey et al. (in review) sequenced loci surrounding 2,389 ultraconserved elements (UCEs) and conserved exons for 48 of the 49 species of *Xolmiini* (all except *Neoxolmis salinarum*; Appendix 1). Detailed methods are described in that study, but, in brief, sequences were assembled using a pipeline based on Phyluce (Faircloth 2016) and two sets of alignments were examined: one with minimal filtering for missing data (T400F), and another with more extensive alignment filtering (HGAPF) using GBLOCKS (Castresana 2000). Phylogenies were estimated using concatenated datasets in ExaML (Kozlov et al. 2015) with 100 bootstrap replicates to evaluate support, and time-calibrated using a penalized likelihood approach (Smith and O'Meara 2012) combined with published fossil records. A summary species-tree method, ASTRAL III (Zhang et al. 2017), was also used, with tips missing from more than 250 loci removed to avert spurious placement.

Harvey et al. (in review) found the *Xolmiini* to form a clade exclusive of *X. dominicanus*, but in their phylogeny, the grouping *Muscisaxicola* + *Satrapa* was sister to the remaining species. Moreover, two genera, *Xolmis* and *Muscisaxicola*, were paraphyletic in their trees. Below we examine the results of Harvey et al. (in review) and prior studies in greater detail. We focus on the primary tree of Harvey et al. (in review), the ExaML T400F tree (Fig. 1, Appendix 2a), but also examine support for key results in the ExaML HGAPF tree (Appendix 2b) and the ASTRAL tree from the T400F alignments (Appendix 2c). We address the paraphyly of *Xolmis* and *Muscisaxicola*, consider the evidence for subsuming *Polioxolmis* into

Cnemarchus, and present a revised classification of the *Xolmiini*.

Xolmis.—*Xolmis* consists of species of open and semi-open country of southern and central South America, but the constituency and classification of the genus have long been unsettled, largely owing to the questionable status of species sometimes placed in *Xolmis* but at other times placed in *Agriornis*, *Neoxolmis*, *Pyrope*, *Myiotheretes*, or *Heteroxolmis*. Cory and Hellmayr (1927) considered *Xolmis* to consist of eight species (Table 1), including one species (*murinus*) now universally included in *Agriornis* (following Vuilleumier in Smith and Vuilleumier 1971), and they described the genus *Neoxolmis* for a closely related species, *rufiventris*, which is still routinely placed in *Neoxolmis*. Recognition of the genus *Pyrope* Cabanis and Heine, 1859, for *pyrope* found favor in regional monographs during a brief time period (e.g., Meyer de Schauensee 1966, Johnson and Goodall 1967, Humphrey et al. 1970), but *Pyrope* has not been recognized by most general references (Table 1). Vuilleumier (in Smith and Vuilleumier 1971), in addition to transferring *murina* to *Agriornis*, expanded *Xolmis* to include six species considered by Cory and Hellmayr (1927) to belong to *Cnemarchus*, *Myiotheretes*, and *Ochthodiaeta*, but this has not been adopted by other references. Traylor (1979) expanded *Neoxolmis* to include *rubetra*; this was adopted by Lanyon (1986) but has also not been followed by others (Table 1). *Heteroxolmis* Lanyon, 1986, was described for *dominicanus*, which differs from other species of *Xolmis* in syringeal and nasal morphology (Lanyon 1986), and this has been followed by some sources. Most recent references have assigned 7–8 species (type species *X. irupero*, *X. velatus*, *X. pyrope*, *X. cinereus*, *X. coronatus*, *X. rubetra*, *X. salinarum*, and sometimes *X. dominicanus*) to *Xolmis* (Table 1).

Molecular phylogenies have provided new insights into the systematics of *Xolmis*

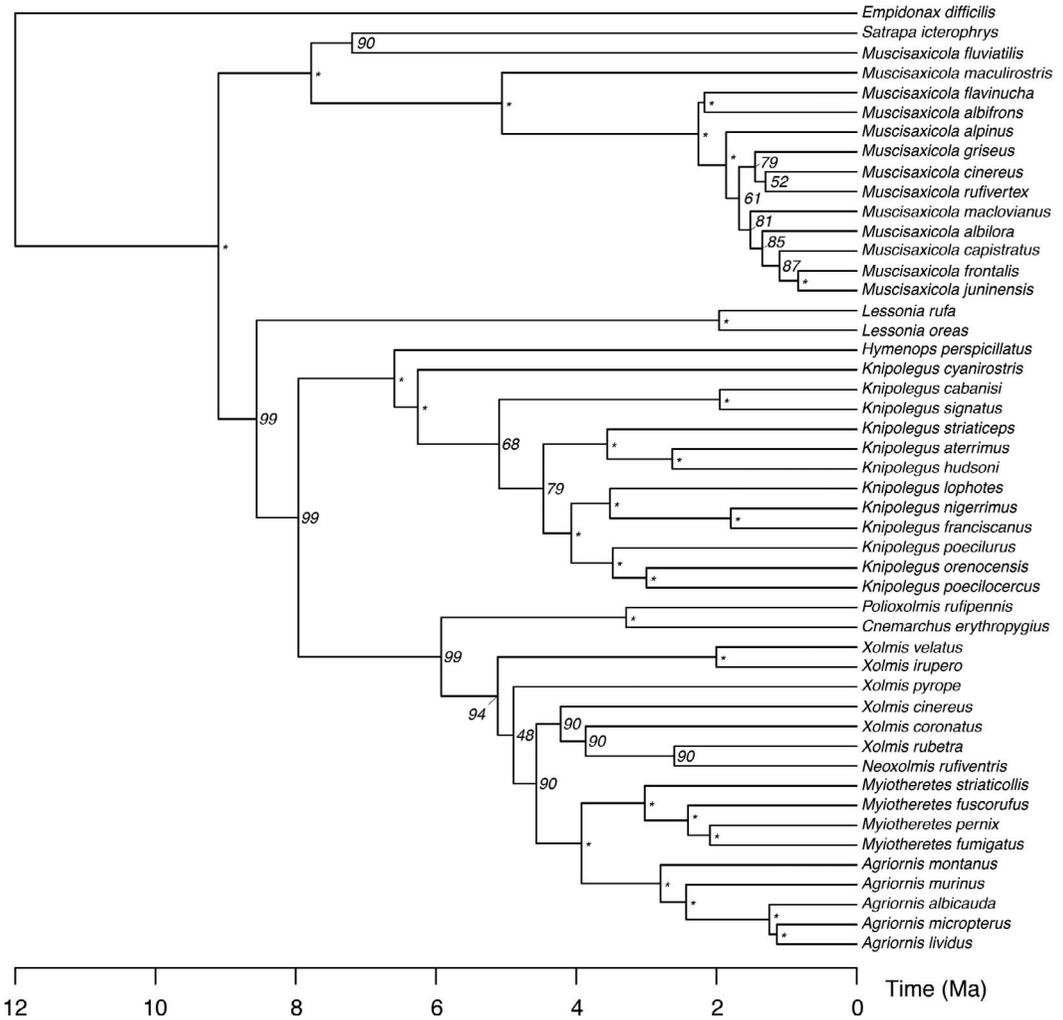


Fig. 1. A phylogeny of the Xolmiini excerpted from the tree of Harvey et al. (in review). This is the ExaML tree from concatenated sequences after minimal filtering for missing data (T400F), dated using TreePL (Smith and O’Meara 2012) and fossil calibrations. Asterisks denote bootstrap support of 100%.

and its close relatives. Tello et al. (2009) sampled only a single species of *Xolmis* (*pyrope*) and placed it as sister to their representatives of *Agriornis*, *Neoxolmis*, and *Myiotheretes*, but Fjeldså et al. (2018) sampled seven species of *Xolmis* (all species except *salinarum*) and determined that *Xolmis* is polyphyletic. As noted above, *X. dominicanus* was found to be only distantly related to the rest of *Xolmis*, instead grouping with *Alectrurus risora* and *Gubernetes yetapa* in the Fluvicolini, another tribe within the subfamily

Fluvicolinae. The other six species occupied two slightly different parts of the Xolmiini. One group, consisting of type species *X. irupero*, *X. velatus*, and *X. pyrope*, was sister to *Agriornis*, *Myiotheretes*, *Neoxolmis rufiventris*, and the remaining species of *Xolmis*; within this group, *X. irupero* was strongly supported as sister to *X. velatus*, and *X. pyrope* was sister to these, although with weak support. *Myiotheretes*, *Neoxolmis rufiventris*, and the remaining species of *Xolmis* formed a four-fold polytomy that was sister to

Table 1.—Selected modern classifications of species of *Xolmis* and possible close relatives.

Species epithet	Cory and Hellmayr (1927)	Vuilleumier <i>in</i> Smith and Vuilleumier (1971)	Traylor (1979)	Lanyon (1986)	Ridgely and Tudor (1994)*	Remsen et al. (2019)**	Ohlson et al. (2020)	this paper
<i>velatus</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>
<i>irupero</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>
<i>pyrope</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Pyrope</i>	<i>Pyrope</i>
<i>cineurus</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Nengetus</i>	<i>Nengetus</i>
<i>coronatus</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Nengetus</i>	<i>Nengetus</i>
<i>rubetra</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Neoxolmis</i>	<i>Neoxolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Nengetus</i>	<i>Nengetus</i>
<i>salinarum</i> ***								
<i>rufiventris</i>	<i>Neoxolmis</i>	<i>Neoxolmis</i>	<i>Neoxolmis</i>	<i>Neoxolmis</i>	<i>Neoxolmis</i>	<i>Neoxolmis</i>	<i>Nengetus</i>	<i>Nengetus</i>
<i>nurinus</i>	<i>Xolmis</i>	<i>Agriornis</i>	<i>Agriornis</i>	<i>Agriornis</i>	<i>Agriornis</i>	<i>Agriornis</i>	<i>Agriornis</i>	<i>Agriornis</i>
<i>dominicanus</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Xolmis</i>	<i>Heteroxolmis</i>	<i>Heteroxolmis</i>	<i>Xolmis</i>	<i>Heteroxolmis</i>	<i>Heteroxolmis</i>
<i>rufipennis</i>	<i>Cnemarchus</i>	<i>Xolmis</i>	<i>Myiotheretes</i>	<i>Polioxolmis</i>	<i>Polioxolmis</i>	<i>Polioxolmis</i>	<i>Cnemarchus</i>	<i>Cnemarchus</i>
<i>erythropygius</i>	<i>Cnemarchus</i>	<i>Xolmis</i>	<i>Myiotheretes</i>	<i>Cnemarchus</i>	<i>Cnemarchus</i>	<i>Cnemarchus</i>	<i>Cnemarchus</i>	<i>Cnemarchus</i>
<i>striaticollis</i>	<i>Myiotheretes</i>	<i>Xolmis</i>	<i>Myiotheretes</i>	<i>Myiotheretes</i>	<i>Myiotheretes</i>	<i>Myiotheretes</i>	<i>Nengetus</i>	<i>Myiotheretes</i>
<i>pernix</i>	<i>Ochthodiaeta</i>	<i>Xolmis</i>	<i>Myiotheretes</i>	<i>Myiotheretes</i>	<i>Myiotheretes</i>	<i>Myiotheretes</i>	<i>Nengetus</i>	<i>Myiotheretes</i>
<i>fumigatus</i>	<i>Ochthodiaeta</i>	<i>Xolmis</i>	<i>Myiotheretes</i>	<i>Myiotheretes</i>	<i>Myiotheretes</i>	<i>Myiotheretes</i>	<i>Nengetus</i>	<i>Myiotheretes</i>
<i>fuscorufus</i>	<i>Ochthodiaeta</i>	<i>Xolmis</i>	<i>Myiotheretes</i>	<i>Myiotheretes</i>	<i>Myiotheretes</i>	<i>Myiotheretes</i>	<i>Nengetus</i>	<i>Myiotheretes</i>

* same classification used by Gill and Donsker (2019).

** same classification used by Dickinson and Christidis (2014), Clements et al. (2019), and del Hoyo et al. (2019).

*** *Neoxolmis salinarum* was described as separate from *rubetra* by Nares and Yzurietia (1979).

Agriornis: all species of *Myiotheretes* formed one part of this polytomy, *Neoxolmis* + *X. rubetra* another part, and *X. cinereus* and *X. coronatus* the third and fourth parts, respectively. Ohlson et al. (2020) proposed a new classification based on the phylogenetic results of Fjeldså et al. (2018). Changes included the restriction of *Xolmis* to *irupero* and *velatus*; the resurrection of *Pyrope* for *pyrope*; the resurrection of *Nengetus* Swainson, 1827, for *cinereus*, *coronatus*, *rubetra*, *salinarum*, *rufiventris*, and the four species of *Myiotheretes*; and the subsuming of *Polioxomis* into *Cnemarchus* (Table 1).

The primary phylogeny of Harvey et al. (in review) supported the placement of *X. dominicanus* outside of the Xolmiini (as in Fjeldså et al. 2018) and as sister to *Alectrurus* (Appendix 2a), which necessitates the transfer of this species to *Heteroxolmis*. The remaining species of *Xolmis*, however, did not form a polyphyletic group, but instead formed a paraphyletic grade (along with *N. rufiventris*) basal to sister taxa *Myiotheretes* and *Agriornis* (Fig. 1). *Xolmis rubetra*, *X. coronatus*, and *X. cinereus*, together with *N. rufiventris* (which was sister to *X. rubetra*), formed a clade that was sister to *Myiotheretes* + *Agriornis*, and *X. pyrope* and *X. velatus* + *X. irupero* were successive sisters to this clade (i.e., *Myiotheretes*, *Agriornis*, *N. rufiventris*, and the other three species of *Xolmis*). Most nodes in this part of the tree received strong bootstrap support (90–100%), but the node uniting *pyrope* with its sister group was weakly supported (48%). The tree based on heavily filtered alignments (HGAPF) contained similar relationships to the primary (T400F) tree, but placed the divergence leading to *X. pyrope* deeper than that leading to *X. velatus* + *X. irupero* (Appendix 2b). Again, the relationship between *X. velatus* + *X. irupero* and its sister group was weakly supported (63% bootstrap). The T400F Astral tree (Appendix 2c) supported the primary T400F tree in this part of the

topology but with a weak local posterior probability (0.67). Astral relationships deeper in the clade may have been spuriously driven by high levels of missing data in the samples of *A. lividus* (missing from 226 loci), *M. striaticollis* (224 loci), and *M. pernix* (138 loci). Despite uncertainty in the relative timing of the divergences involving the branches leading to *X. pyrope* and *X. velatus* + *X. irupero*, the paraphyly of *Xolmis* is unambiguous.

Lack of a monophyletic *Xolmis* necessitates a change in the classification of this section of the Xolmiini, and the sister relationship of *Agriornis* and *Myiotheretes* precludes adoption of the classification of Ohlson et al. (2020), who retained *Agriornis* while subsuming *Myiotheretes* into *Nengetus*. One option would be to merge all species of *Xolmis*, *Neoxolmis*, *Myiotheretes*, and *Agriornis* into a single genus, for which *Xolmis* has priority. The depth of the node uniting these genera is roughly the same as those uniting *Knipolegus* and *Muscisaxicola* (excluding *M. fluviatilis* – see below). However, *Knipolegus* and *Muscisaxicola* are extremely conservative genera phenotypically, whereas *Xolmis*, *Neoxolmis*, *Myiotheretes*, and *Agriornis* encompass a much wider range of phenotypic variation, reducing the appeal of this option. Another option, in sharp contrast to the previous alternative, would be to retain *Agriornis* and *Myiotheretes* and apportion the species currently in *Xolmis* and *Neoxolmis* into five genera: *Xolmis* for *irupero* and *velatus*; *Pyrope* for *pyrope*; *Nengetus* for *cinereus*; a new genus for *coronatus*; and *Neoxolmis* for *rufiventris*, *rubetra*, and *salinarum*. This would result in three monotypic genera and two others containing two and three species, respectively, which seems excessively split considering that these species have generally been placed in two genera, and all but one generally in the single genus *Xolmis*. A third option would be to retain *Agriornis* and *Myiotheretes*, either as separate genera or as a single genus (*Agriornis*), but to limit

the division of *Xolmis* to the minimum required by the principle of monophyly of genera. This would result in the division of *Xolmis* into three genera: *Xolmis* for *irupero* and *velatus*, *Pyrope* for *pyrope*, and *Nengetus* for *rufiventris*, *rubetra*, *salinarum*, *coronatus*, and *cinereus*. Except for their subsuming of *Myiotheretes* into *Nengetus*, this is the classification adopted by Ohlson et al. (2020). We recommend the five-genus version of the third option above, which splits *Xolmis* into three genera while retaining *Agriornis* and *Myiotheretes* as separate genera. This option would also result in the least disruption to the current classification, thereby promoting taxonomic stability.

Muscisaxicola.—*Muscisaxicola* is a genus of ground-dwelling tyrant-flycatchers endemic to South America. Twelve of the 13 species are typically found in open habitats of the high Andes and Patagonia, but the thirteenth species, *M. fluviatilis*, occurs in the lowlands of Amazonia, where it is found on sandbars along watercourses. A complete phylogeny of the genus based on two mitochondrial genes showed that most species of *Muscisaxicola* form a tight, distinct, well-supported clade, termed the “typical clade” (Chesser 2000). However, two species, *M. fluviatilis* and *M. maculirostris*, were found to be rather distantly related to the other species and of somewhat uncertain affinities, although *M. maculirostris* was a weakly supported sister to the typical clade in all analyses. Relationships of *M. fluviatilis* were especially poorly resolved, and in some analyses it was sister to one of the outgroup species rather than to the other species of *Muscisaxicola*.

Fjeldså et al. (2018) sampled *M. maculirostris*, *M. fluviatilis*, and nine of the 11 typical species of *Muscisaxicola* in their study of the Fluvicolinae. As in Chesser (2000), all typical species formed a tight, well-supported clade. *Muscisaxicola maculirostris* was strongly supported as sister to this clade. However, *M.*

fluviatilis was only distantly related to the other species. It was sister to the rest of *Muscisaxicola*, but this sister relationship received poor support (ca. 0.60 posterior probability).

Harvey et al. (in review) sequenced all species of *Muscisaxicola* in their genomic study of suboscine birds. They found that the 11 typical species of *Muscisaxicola* formed a well-supported clade and that *M. maculirostris* was sister to this clade, confirming previous results. However, *M. fluviatilis*, rather than grouping loosely with the other species of *Muscisaxicola*, was sister to *Satrapa icterophrys* (Fig. 1). The latter species had not been included in Chesser (2000) but was included in Fjeldså et al. (2018), where its relationships were unresolved. Bootstrap support for the *M. fluviatilis*-*Satrapa* sister relationship was strong if not overwhelming (90%). In the tree based on heavily filtered alignments (HGAPF), the support for this relationship was 79% (Appendix 2b). *Satrapa* was not present in the T400F Astral tree as it lacked data from 445 loci, but *M. fluviatilis* was sister to a long branch subtending the remainder of *Muscisaxicola* (Appendix 2c).

Based on the molecular results of Chesser (2000), Fjeldså et al. (2018), and Harvey et al. (in review), it seems clear that *M. fluviatilis* is only distantly related to true *Muscisaxicola*. It is also distinct, both genetically and morphologically, from its apparent sister species *S. icterophrys*. The depth of the node uniting *M. fluviatilis* and *S. icterophrys*, estimated at ca. 7 mya, is much deeper than the node uniting all other species of *Muscisaxicola*, and it is also deeper than the nodes uniting all other genera in the Xolmiini (Fig. 1). Moreover, the habitat, behavior, and predominantly yellow and olive plumage of *S. icterophrys* are unlike that of any species of *Muscisaxicola*, including *M. fluviatilis*, making transfer of *fluviatilis* to *Satrapa* untenable. Therefore, we describe a new genus for *M. fluviatilis* below.

Syrtidicola genus nov. Chesser, Harvey,
Brumfield, and Derryberry

Type species.—*Muscisaxicola fluviatilis*
Sclater and Salvin, 1866.

Included species.—*Syrtidicola fluviatilis*
(Sclater and Salvin, 1866) comb. nov.,
Little Ground-Tyrant.

Diagnosis, morphology.—Small passerine birds, typically 13–14 cm, 12–15 g. Plumage grayish-brown above, off-white below, slightly darker on breast. Wings brown, edged rufous; tail blackish; indistinct buffy superciliary; thin black bill. Distinguished from the very similar *Muscisaxicola maculirostris* (14–15 cm, 12.5–16.5 g) by reduced superciliary, proportionately shorter tail, and slightly smaller average size. Distinguished from all other former congeners in *Muscisaxicola* by notably smaller size: shorter overall length (13–14 vs. 15–21.5 cm); shorter wing, tail, and bill lengths; and smaller body mass (12–15 vs. 17–62 g). Probable phylogenetic sister species *Satrapa icterophrys* easily distinguished from *S. fluviatilis* by its bright yellow breast and superciliary and dark olive back.

Etymology.—The generic name, from the stem of the genitive *syrtidos* (sandbar or sandbank) Latinized from Greek and the Latin *cola* (dweller), when combined with the species name *fluviatilis* (riverine), indicates that this species inhabits sandbars along rivers. The name is masculine in gender.

Molecular analyses.—Genomic analyses of all species of tyrant-flycatcher suggested that *Syrtidicola* is sister to *Satrapa icterophrys*, and that, together, these two genera are sister to *Muscisaxicola*. For detailed methods see Harvey et al. (in review).

Registration.—This name has been registered in ZooBank with registration number urn:lsid:zoobank.org:act:5F57D603-8C98-4F5F-8976-8FA375D9BAC1.

Cnemarchus and Polioxolmis.—*Cnemarchus erythropygius* and *Polioxolmis rufipennis* are sisters in the Harvey et al. (in review) phylogeny, but the depth of the node uniting them suggests, based solely on the phylogenetic data, that they could either continue to be placed in separate monotypic genera or that *Polioxolmis* could be subsumed into *Cnemarchus* (Fig. 1). The depth of this node is similar in the trees based on both minimally (T400F) and heavily (HGAPF) filtered datasets (Appendix 2b; *Cnemarchus* was missing from the T400F Astral tree). Some phenotypic similarities also suggest a single genus as a valid option, although the two species differ in plumage, morphometrics, and proportions. Both species occupy montane scrub and low woodland in the high Andes, *C. erythropygius* from Colombia south to Bolivia and *P. rufipennis* from Peru south to Chile and Argentina, and both typically forage by dropping to the ground from a perch. Both species are rather strikingly plumaged for the Tyrannidae although in quite different ways. The plumage of *P. rufipennis*, when perched, is a rather uniform gray, but in flight it has conspicuous rufous wing and tail patches. *Cnemarchus erythropygius*, a slightly larger species, is among the most colorful of tyrant-flycatchers, its plumage highlighted by its rufous belly, tail patches, and underwing coverts; its whitish crown; and its conspicuous white wing patches.

Generic placement of the two species has varied. *Polioxolmis rufipennis* (Taczanowski, 1874) was originally described in *Muscisaxicola* and *C. erythropygius* (Sclater, 1853) in *Taenioptera* (= *Xolmis*), but *erythropygius* has been placed regularly in *Myiotheretes* (e.g., Sclater 1888, Meyer de Schauensee 1966, Traylor 1979) and *rufipennis* occasionally so (e.g., Traylor 1979). Ridgway (1905) noted the distinctiveness of *erythropygius* from *Myiotheretes* and described the genus *Cnemarchus* for it based on its much smaller bill, relatively longer tarsus, lack of primary emargina-

tion, proportionately longer tail, rufous rump, and lack of rufous coloration in its wings. Cory and Hellmayr (1927) recognized *Cnemarchus* and included *rufipennis* in the genus in addition to *erythrogygius*, considering *rufipennis* closer to *Cnemarchus* than to any other genus, despite its “somewhat longer second primary and much more elongated bill” (p. 39). They were the first to treat the two species as an exclusive group. The two species were later paired as a species group in Vuilleumier’s (in Smith and Vuilleumier 1971) greatly expanded genus *Xolmis*, separated from other species by the combination of “relatively narrower bill, relatively longer tarsus, and longer claw of hallux” (p. 195). Nevertheless, Vuilleumier did not consider the two species to be particularly closely related.

Lanyon (1986) found that *erythrogygius*, *rufipennis*, and the four species of *Myiotheretes* (*striaticollis*, *pernix*, *fumigatus*, *fuscorufus*) formed a clade within his larger *Muscisaxicola* group, but found three unique characters in each of *erythrogygius* and *rufipennis* and could not determine relationships among *erythrogygius*, *rufipennis*, and the four species of *Myiotheretes*, which together formed a trichotomy in his phylogenetic tree. This persuaded him to recognize *Myiotheretes* for the four species and *Cnemarchus* for *erythrogygius*, and to describe the new genus *Polioxolmis* for *rufipennis*, based on its strongly differentiated syrinx. Most recent references have recognized *Polioxolmis*, although Ohlson et al. (2020) subsumed *Polioxolmis* into *Cnemarchus* (Table 1).

In the Harvey et al. (in review) phylogeny (Fig. 1), the depth of the node uniting *erythrogygius* and *rufipennis* is shallower (at approx. 3.75 mya) than the depth of the nodes uniting species of most larger genera of Xolmiini, including *Muscisaxicola* (whether excluding or including *fluviatilis*), *Knipolegus*, and *Neoxolmis* (as redefined above), which range from approx. 4.5–7 mya, as well as several internal nodes

within these genera. However, the depth of the node uniting *erythrogygius* and *rufipennis* is deeper than the depth of the nodes uniting species of *Agriornis* and species of *Myiotheretes*, respectively (each ca. 3.5 mya), although it is slightly shallower than that for the node uniting *Agriornis* with *Myiotheretes* (4 mya). Thus, as with the morphology, a case can be made either for placing *erythrogygius* and *rufipennis* in a single genus or placing them in two monotypic genera. We recommend following the lead of Cory and Hellmayr (1927) and placing both species in *Cnemarchus*. Congeneric status emphasizes their similarities in habitat, range, behavior, bill width, and certain aspects of plumage (e.g., rufous tail patches), as well as their phylogenetic relationship as sister species.

Revised classification of the Xolmiini.—The following classification adopts the recommendations above and follows standard procedures for converting phylogenies into linear sequences (e.g., Remsen et al. 2019). Type species of polytypic genera are designated with an asterisk. *Neoxolmis salinarum*, not sequenced by Harvey et al. (in review), is placed to follow its obvious sister species *N. rubetra*.

Satrapa
icterophrys
Syrtdicola
fluviatilis
Muscisaxicola
maculirostris
albifrons
flavinucha
alpinus
griseus
*rufivertex**
cinereus
maclovianus
albilora
capistratus
juninensis
frontalis
Lessonia

oreas
*rufa**
Hymenops
perspicillatus
Knipolegus
*cyanostris**
signatus
cabanisi
striaticeps
aterrimus
hudsoni
poecilurus
orenocensis
poecilocercus
lophotes
franciscanus
nigerrimus
Cnemarchus
*erythropygius**
rufipennis
Xolmis
velatus
*irupero**
Pyrope
pyrope
Nengetus
*cinereus**
coronatus
rubetra
salinarum
rufiventris
Myiotheretes
*striaticollis**
fuscorufus
pernix
fumigatus
Agriornis
montanus
murinus
albicauda
*micropterus**
lividus

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Literature Cited

- Castresana, J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* 17:540–552.
- Chesser, R. T. 2000. Evolution in the high Andes: the phylogenetics of *Muscisaxicola* ground-tyrants. *Molecular Phylogenetics and Evolution* 15:369–380.
- Cory, C. B., & C. E. Hellmayr. 1927. Catalogue of birds of the Americas and the adjacent islands, Part V, Tyrannidae. Field Museum of Natural History, Zoological Series, Vol. 13.
- del Hoyo, J., A. Elliott, J. Sargatal, D. A. Christie, & G. Kirwan (eds.). 2019. Handbook of the birds of the world alive. Lynx Edicions, Barcelona. (retrieved from <http://www.hbw.com/> on 10 October 2019)
- Dickinson, E.C., & Christidis, L. (eds.) 2014. The Howard and Moore complete checklist of the birds of the world, 4th Edition, Vol. 2: Passerines. Aves Press, Eastbourne, U.K.
- Faircloth, B.C. 2016. PHYLUCE is a software package for the analysis of conserved genomic loci. *Bioinformatics* 32:786–788.
- Fjeldså, J., J. I. Ohlson, H. Batalha-Filho, P. G. P. Ericson, & M. Irestedt. 2018. Rapid expansion and diversification into new niche space by fluvicoline flycatchers. *Journal of Avian Biology* 2018: e01661.
- Gill, F. B., and D. Donsker (eds.). 2019. IOC World Bird List (v9.2). doi : 10.14344/IOC.ML.9.2. (last accessed on 10 October 2019)
- Harvey, M. G., G. A. Bravo, S. Claramunt, A. M. Cuervo, G. E. Derryberry, J. Battilana, G. F. Seeholzer, J. S. McKay, B. C. O’Meara, B. C. Faircloth, S. V. Edwards, J. Pérez-Emán, R. G. Moyle, F. H. Sheldon, A. Aleixo, B. T. Smith, R. T. Chesser, L. F. Silveira, J. Cracraft, R. T. Brumfield, & E. P. Derryberry.

- in review*. The evolution of a tropical biodiversity hotspot. *Science*
- Humphrey, P. S., D. Bridge, P. W. Reynolds, & R. T. Peterson. 1970. *Birds of Isla Grande (Tierra del Fuego)*. Smithsonian Institution, Washington.
- Johnson, A. W., & J. D. Goodall. 1967. *The birds of Chile and adjacent regions of Argentina, Bolivia, and Peru, Vol. II. Platt Establecimientos Gráficos, Buenos Aires.*
- Kozlov, A. M., A. J. Aberer, & A. Stamatakis. 2015. ExaML version 3: a tool for phylogenomic analysis on supercomputers. *Bioinformatics* 31:2577–2579.
- Lanyon, W. E. 1986. A phylogeny of the thirty-three genera in the *Empidonax* assemblage of tyrant flycatchers. *American Museum Novitates* 2846:1–64.
- Meyer de Schauensee, R. 1966. *The species of birds of South America and their distribution*. Academy of Natural Sciences of Philadelphia.
- Nores, M., & D. Yzurieta. 1979. Una nueva especie y dos nuevas subespecies de Aves (Passeriformes). *Academia Nacional de Ciencias Miscelánea* No. 61.
- Ohlson, J. I., M. Irestedt, H. B. Filho, P. G. P. Ericson, and J. Fjeldså. 2020. A revised classification of the fluvicoline tyrant flycatchers (Passeriformes, Tyrannidae, Fluvicolinae). *Zootaxa* 4747:167–176.
- Remsen, J. V., Jr., J. I. Areta, E. Bonaccorso, S. Claramunt, A. Jaramillo, J. F. Pacheco, C. Ribas, M. B. Robbins, F. G. Stiles, D. F. Stotz, & K. J. Zimmer. 2019. *A classification of the bird species of South America*. American Ornithological Society. <http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm>
- Ridgely, R. S., & G. Tudor. 1994. *The birds of South America, Vol. 2: the suboscine passerines*. University of Texas Press, Austin, Texas, 814 pp.
- Ridgway, R. 1905. Descriptions of some new genera of Tyrannidae, Pipridae, and Cotingidae. *Proceedings of the Biological Society of Washington* 18:207–210.
- Slater, P. L. 1888. *Catalogue of the birds in the British Museum (Natural History), Vol. 14.*
- Smith, S. A., & B. C. O'Meara. 2012. treePL: Divergence time estimation using penalized likelihood for large phylogenies. *Bioinformatics* 28:2689–2690.
- Smith, W. J., & F. Vuilleumier. 1971. Evolutionary relationships of some South American ground tyrants. *Bulletin of the Museum of Comparative Zoology* 141:179–268.
- Tello, J. G., R. G. Moyle, D. J. Marchese, & J. Cracraft. 2009. Phylogeny and phylogenetic classification of the tyrant flycatchers, cotingas, manakins, and their allies (Aves: Tyrannidae). *Cladistics* 25:429–467.
- Traylor, M. A., Jr. 1979. Subfamily Fluvicolinae. Pp. 112–186 *in* M. A. Traylor Jr., ed., *Peters' Check-list of the Birds of the World, Vol. VIII*. Museum of Comparative Zoology, Cambridge, Massachusetts, 365 pp.
- Zhang, C., E. Sayyari, & S. Mirarab. 2017. "ASTRAL-III: increased scalability and impacts of contracting low support branches" *in* *Comparative Genomics. RECOMB-CG 2017. Lecture Notes in Computer Science*. J. Meidanis, L. Nakleh, Eds. (Springer), vol 10562.

Appendix 1.—Species identification, tissue and voucher information, and geographical locality data for genetic samples used in this study.

Species	Tissue Source	Tissue Number	Voucher Source	Voucher Number	Locality
<i>Satrapa icterophrys</i>	KU	9896	KU	96944	ARGENTINA: Jujuy, 2 km E Ocloyas
<i>Muscisaxicola fluviatilis</i>	LSUMZ	1188	LSUMZ	101487	BOLIVIA: La Paz, Río Beni, 20 km by river N Puerto Linares
<i>Muscisaxicola maculirostris</i>	LSUMZ	103850	LSUMZ	114267	PERU: Arequipa, Cerro Coscantire, ca 5 Km E Chala
<i>Muscisaxicola flavimucha</i>	AMNH	12184	AMNH	24336 (skel)	CHILE: Region Metropolitana, Cordillera, 15 km ENE Embalse El Yeso
<i>Muscisaxicola albifrons</i>	LSUMZ	22576	LSUMZ	163132	BOLIVIA: La Paz, Prov. Murillo, Zongo Valley, 7 km by road N summit
<i>Muscisaxicola alpinus</i>	LSUMZ	30037	MECN	FS1917	ECUADOR: Carehi, Tufino
<i>Muscisaxicola griseus</i>	KU	17552	KU	113906	PERU: Junin, above Toldopampa
<i>Muscisaxicola cinereus</i>	AMNH	12179	AMNH	24329 (skel)	CHILE: Region Metropolitana, Cordillera, 2 km ENE Embalse El Yeso
<i>Muscisaxicola rufivertex</i>	LSUMZ	7728	LSUMZ	119203	PERU: Arequipa, ca. 37 road km E Arequipa
<i>Muscisaxicola maclovianus</i>	KU	11679	KU	98363	ARGENTINA: Río Negro, NW El Bolson, Cerro Perito Moreno
<i>Muscisaxicola albiflora</i>	AMNH	12171	AMNH	24333 (skel)	CHILE: Region Metropolitana, Cordillera, 2 km ENE Embalse El Yeso
<i>Muscisaxicola capistratus</i>	AMNH	12128	AMNH	23973	ARGENTINA: Río Negro, Norquino, ca. 5 km E Manuel Choique on Ruta Provincial 6
<i>Muscisaxicola frontalis</i>	AMNH	12167	AMNH	24331 (skel)	CHILE: Region Metropolitana, Cordillera, 2 km ENE Embalse El Yeso
<i>Muscisaxicola juninensis</i>	LSUMZ	1203	LSUMZ	101479	BOLIVIA: La Paz, 4.5 km by road W hydroelectric dam on Zongo Valley road
<i>Lessonia rufa</i>	AMNH	9938	AMNH	23964	ARGENTINA: Río Negro, Bariloche, El Boquete, 700 m.
<i>Lessonia oreas</i>	LSUMZ	61378	LSUMZ	181854	PERU: Huancavelica, 15 km SW Huanchacolpa
<i>Hymenops perspicillatus</i>	USNM	14701	USNM	630410	URUGUAY: Soriano, Cardona, ca 9 km N, at Estancia Santa Emilia
<i>Knipolegus cyanirostris</i>	USNM	14744	USNM	630514	URUGUAY: Tacuarembó, Tacuarembó, ca 45 km N, at Cuchilla Laureles, Estancia La Furiosa
<i>Knipolegus cabanisi</i>	KU	9690	KU	96853	ARGENTINA: Jujuy, E slope Sierra Santa Barbara
<i>Knipolegus signatus</i>	LSUMZ	44150	LSUMZ	174119	PERU: San Martín, ca. 22 km ENE Florida
<i>Knipolegus striaticeps</i>	LSUMZ	38892	LSUMZ	171372	BOLIVIA: Santa Cruz, Prov. Cordillera, 38 km E Abapó
<i>Knipolegus aterrimus</i>	LSUMZ	6578	LSUMZ	124318	BOLIVIA: Santa Cruz, Caballero, 2.5 km N Tambo, Río San Isidro (Río Pulquina) Valley
<i>Knipolegus hudsoni</i>	LSUMZ	18865	LSUMZ	153924	BOLIVIA: Santa Cruz, Cordillera, Estancia Perforación, ca. 130 km E Charagua
<i>Knipolegus lophotes</i>	USNM	14741	USNM	630417	URUGUAY: Tacuarembó, Tacuarembó, ca. 46 km N, at Cuchilla Laureles, Estancia La Furiosa

Appendix 1.—Continued.

Species	Tissue Source	Tissue Number	Voucher Source	Voucher Number	Locality
<i>Knipolegus nigerrimus</i>	MPEG	DZ-5162	DZUFMG	5162	BRAZIL: Minas Gerais, Alto da Pedra Menina, distrito Pedra Menina, Rio Vermelho
<i>Knipolegus franciscanus</i>	MZUSP	82727	MZUSP	82727	BRAZIL: Minas Gerais, Itacarambi
<i>Knipolegus poecilurus</i>	USNM	10607	USNM	625232	GUYANA: North Side Acari Mountains
<i>Knipolegus orenocensis</i>	LSUMZ	3178	LSUMZ	110630	PERU: Loreto, Isla Ronco, Río Napo opposite Libertad, 80 km N Iquitos
<i>Knipolegus poecilocercus</i>	AMNH	14176	MPEG	59626	BRAZIL: Amazonas, Estrada Manacapuru, Novo Airao
<i>Polioxolmis rufipennis</i>	KU	19488	KU	113489	PERU: Ayacucho, 3 km S Lirriopata
<i>Cnemarchus erythropygius</i>	LSUMZ	30022	LSUMZ	162118	ECUADOR: Carehi, ca. 6 km W Tuffiño
<i>Xolmis velatus</i>	LSUMZ	38195	LSUMZ	169244	BOLIVIA: Santa Cruz, Estancia Cambaras, 38 km SWW San Matias
<i>Xolmis irupero</i>	USNM	14801	USNM	630525	URUGUAY: Colonia, Carmelo, 11.3 km NNE
<i>Xolmis pyrope</i>	AMNH	12144	AMNH	24313 (skel)	CHILE: Region Metropolitana, Chacabuco, ca. 4 km SSW by road from peak of Cerro de El Roble
<i>Xolmis cinereus</i>	USNM	14699	USNM	630409	URUGUAY: Soriano, Cardona, ca. 9 km N, at Estancia Santa Emilia
<i>Xolmis coronatus</i>	KU	11859	KU	98464	ARGENTINA: Río Negro, WSW San Antonio Oeste
<i>Xolmis rubetra</i>	KU	11946	KU	98463	ARGENTINA: Río Negro, WSW San Antonio Oeste
<i>Neoxolmis rufiventris</i>	LSUMZ	77413 (toepad)	LSUMZ	70016	ARGENTINA: Chubut, Chubut
<i>Myiotheretes striaticollis</i>	LSUMZ	38280	LSUMZ	169199	BOLIVIA: Santa Cruz, La Pajcha, 28 km S Samaipata
<i>Myiotheretes fusciorufus</i>	LSUMZ	1837	LSUMZ	106178	PERU: Pasco, Santa Cruz, ca 9 km SSE Oxapampa
<i>Myiotheretes pernix</i>	USNM	387496 (toepad)	USNM	387496	COLOMBIA: Magdalena, Siminchucua, Sierra Nevada de Santa Marta
<i>Myiotheretes fumigatus</i>	IAYH-CT	11345	ICN	36813	COLOMBIA: Cesar, Manaure, Sabana Rubia, Casa 7e Vidrio
<i>Agriornis montanus</i>	LSUMZ	7610	LSUMZ	124280	BOLIVIA: Oruro, Prov. Sajama, 10 km by road E Sajama
<i>Agriornis murinus</i>	KU	11848	KU	98461	ARGENTINA: Río Negro, WSW San Antonio Oeste
<i>Agriornis albicauda</i>	LSUMZ	72330	CORBIDI	GFS226	PERU: Lima, Río Shuncha, 8 km E Laraos
<i>Agriornis micropterus</i>	AMNH	13502	AMNH	27767	ARGENTINA: Río Negro, Picaniqueu, near Neneo Ruca
<i>Agriornis lividus</i>	YPM	83046 (toepad)	YPM	83046	ARGENTINA: Río Negro, El Bolson
<i>Empidonax difficilis</i>	AMNH	15581	AMNH	28484 (skel)	USA: Washington, Thurston County, Yelm
<i>Phelesia inornata</i>	ICN	38372 (toepad)	ICN	38372	COLOMBIA: Arauca, Municipio Arauca
<i>Suiriri affinis</i>	MZUSP	79714	MZUSP	79714	BRAZIL: Tocantins, ESEC Serra Geral de Tocantins
<i>Sublegatus modestus</i>	LSUMZ	15283	LSUMZ	150869	BOLIVIA: Santa Cruz, Velasco, PreParque Nacional
<i>Sublegatus arenarum</i>	FMNH	394498	FMNH	394498	TRINIDAD & TOBAGO: Trinidad, Chacachacare
<i>Sublegatus obscurior</i>	USNM	11764	USNM	625645	GUYANA: Upper Essequibo River, Konashen
<i>Colonia colonus</i>	KU	3731	KU	91436	PARAGUAY: Itapúa, San Rafael National Park, San Pedro Mi

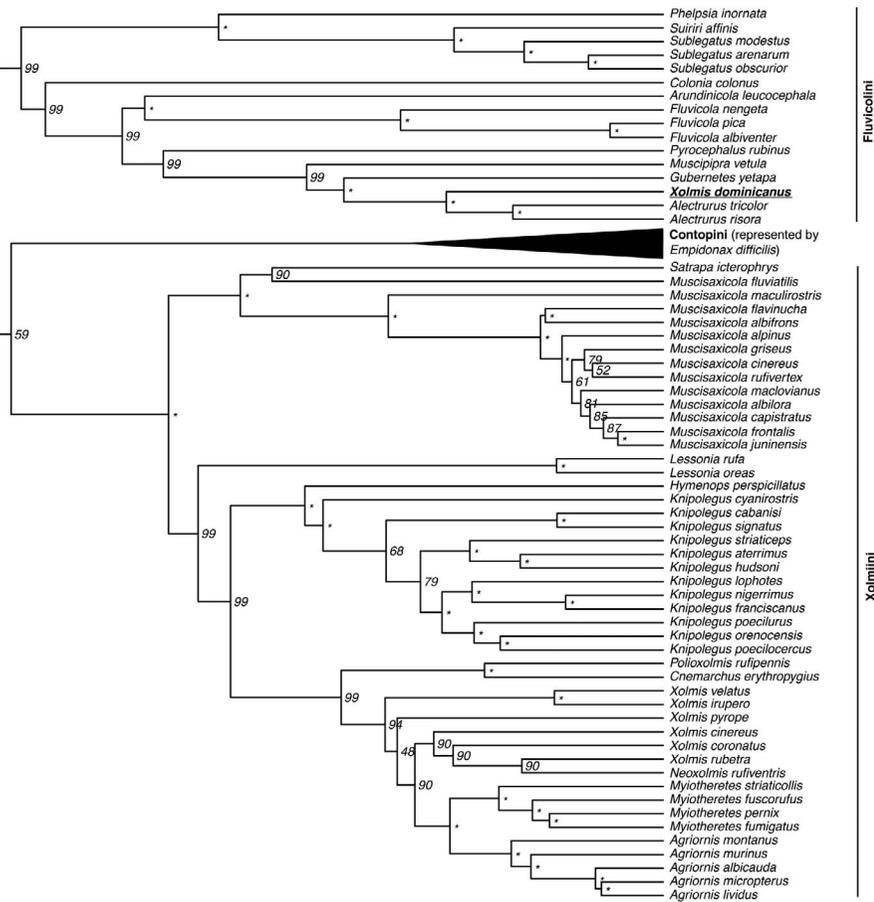
Appendix 1.—Continued.

Species	Tissue Source	Tissue Number	Voucher Source	Voucher Number	Locality
<i>Arundinicola leucocephala</i>	LSUMZ	38036	LSUMZ	169058	BOLIVIA: Santa Cruz, Estancia Cambaras, 38 km SWW San Matias
<i>Fluvicola nengeta</i>	MPEG	CPE-050	MPEG	70474	BRAZIL: Alagoas, Ibatiguara, Usina Serra Grande, Engenho Coimbra
<i>Fluvicola pica</i>	USNM	14542	USNM	627560	GUYANA: Almond Beach, near Mouth of Waimi River
<i>Fluvicola albiventer</i>	LSUMZ	38135	LSUMZ	169060	BOLIVIA: Santa Cruz, Estancia Cambaras, 38 km SWW San Matias
<i>Pyrocephalus rubinus</i>	LSUMZ	37157	LSUMZ	165133	USA: Texas, ca. 12 1/2 mi N Brackettville
<i>Muscipira vetula</i>	AMNH	315092 (toepad)	AMNH	315092	BRAZIL: Palmital (São Francisco)
<i>Gubernetes yetapa</i>	KU	95	KU	88378	PARAGUAY: Concepción, San Luis National Park
<i>Xolmis dominicanus</i>	USNM	14897	USNM	630166	URUGUAY: Rocha, Rocha, 8.8 km NE, at Arroyo de las Conchas
<i>Alectrurus tricolor</i>	KU	3596	KU	91404	PARAGUAY: Itapúa, San Rafael National Park, San Pedro Mi
<i>Alectrurus risora</i>	KU	3430	KU	90263	PARAGUAY: Misiones, San Juan Bautista, 20 km SW

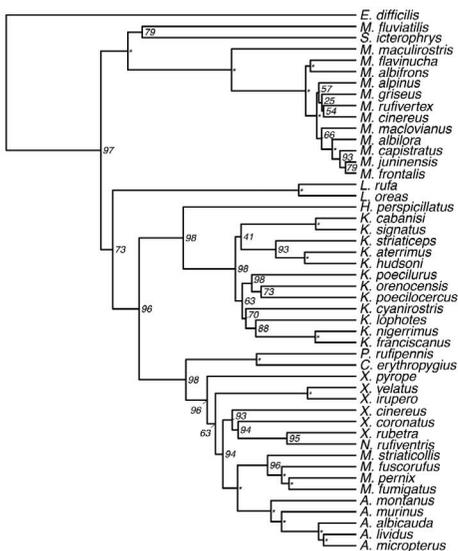
Appendix 2.

Additional phylogenies of the Xolmiini excerpted from those of Harvey et al. (in review). (A) The same ExaML T400F tree from Figure 1, with *Fluvicolini* added and a single representative of *Contopini* included. (B) An ExaML tree of concatenated sequences after heavy filtering for missing data (HGAPF). (C) A coalescent-based species tree estimated using ASTRAL-III with minimally filtered sequences (T400F), after removing individuals missing from more than 250 gene trees. ASTRAL does not estimate terminal branch lengths, so these were assigned the median length of the internal branches for visualization purposes. Values at nodes indicate bootstrap support for ExaML trees and local posterior probabilities for the ASTRAL tree. In all trees, asterisks denote complete support (bootstrap support = 100% or posterior probability = 1.0).

A



B



C

