

A distinctive new species of gnatcatcher in the *Polioptila guianensis* complex (Aves: Polioptilidae) from western Amazonian Brazil

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A recent taxonomic revision of the *Polioptila*⁴ *guianensis* (Guianan Gnatcatcher) complex suggested that at least four allopatric species should be recognized in this morphologically and vocally conserved group: *P. guianensis* (Guianan Gnatcatcher), *P. clementsii* (Iquitos Gnatcatcher), *P. facilis* (Rio Negro Gnatcatcher), and *P. paraensis* (Para Gnatcatcher) (Whitney and Álvarez 2005). Based on sight-records of a member of the *P. guianensis* group west of the Rio Madeira, these authors predicted that “an undetected population inhabits most of the region west of the Madeira north of about 7° S, west to Peru; it should be sought especially in forests growing on white sand and extensively weathered clays (both patchily distributed *terra firme* habitats)”. During the intervening years, AW, BMW, and AA have gathered multiple additional recordings of “Guianan Gnatcatchers” from diverse points in the range of the complex (Whittaker *et al.* 2008; Whittaker 2009), and, on 4 and 5 July 2007, AA and AW collected and tape-recorded, respectively, the first two specimens from west of the Rio Madeira, which proved to be phenotypically and genetically distinct from other taxa in the *P. guianensis* complex, justifying recognition of this population as a new species, which we propose to name:

Polioptila attenboroughi

Inambari Gnatcatcher

balança-rabo-do-inambari (Portuguese)



Holotype.— Museu Paraense Emílio Goeldi (MPEG) 63204, skin, adult male; skull 100% ossified; no Bursa of Fabricius; left testis 4 × 3 mm; 6 g; little fat and no molt. Collected (shot) and tape-recorded in a mixed-species canopy flock of insectivores in upland (*terra-firme*) sandy-soil forest by AW on 5 July 2007 at Tupana Lodge, located at km 158 of the BR-319 road in the municipality of Careiro, Amazonas, Brazil (04° 05' 00.2" S; 60° 39' 37.8" W); prepared by AA and Manoel Santa-Brígida under field number TUP 010. Pectoral muscle tissue preserved in approximately 96% alcohol; field number TUP 010. Hologenotype (Chakrabarty 2010) sequences of the mitochondrial gene NADH subunit 2 (1041 bp) deposited in GenBank (accession number KC823272). Tape-recordings of vocalizations archived at the British Library of Natural Sounds under accession number 183249 (available at <http://www.bl.uk/listentonature/main.html>).

Diagnosis: Morphology.— Alphanumeric color designations determined through direct comparison with Smithe (1975). Both vocalizations (loudsongs and multi-note calls) and overall plumage, with males having no black on the head and possessing narrow rectrices with white on the outer three pairs but none on the three central pairs, clearly place *P. attenboroughi* in the *P. guianensis* complex. Adult males (no female specimens are available) of the new taxon are readily distinguished from males of all remaining taxa in the *P. guianensis* complex by decisively darker plumbeous (color # 78) upperparts, chest,

and lower throat, in these respects approaching *P. facilis* and *P. schistaceigula* (Slate-throated Gnatcatcher), further differing from the former by a thin, broken, white eye ring (nearly absent in *P. facilis*), and from the latter by a significantly longer tail with white on the outer feathers, and lack of any white in the head (see Table 1 in SI for a list of specimens examined). From *P. guianensis*, it also differs by a uniform slate throat and breast (instead of having a contrastingly paler whitish throat), and three outermost rectrices with extensive black bases, rather than nearly entirely white. In comparison with recently described *P. clementsii*, it further differs by the greater extent of black bases on outer rectrices (covering approximately 20%, 60%, and 95% of the three outermost rectrices, respectively, in *P. attenboroughi*). From *P. paraensis*, with which the new taxon shares the tail pattern, differentiated only by a much darker slate color of the upperparts, throat, and chest. **Voice.**— The loudsong of *P. attenboroughi* is most similar to that of *P. paraensis* in comprising an evenly paced series of notes at a nearly level frequency, but pace is significantly slower and note shape (and thus, auditory quality) is subtly different. Furthermore, *P. attenboroughi* possesses a distinctive “rasp” series delivered in the context of a complex song that is lacking (or perhaps only very rare?) in *P. paraensis* but shared with *P. schistaceigula* (see *Vocalizations*, below). **Genetic divergence.**— Separated from its sister-species, *P. paraensis*, by approximately 3.9 % sequence divergence, and from the more distantly related *P. schistaceigula* and *P. guianensis*, respectively, by 14.3% and 13.6% sequence divergence

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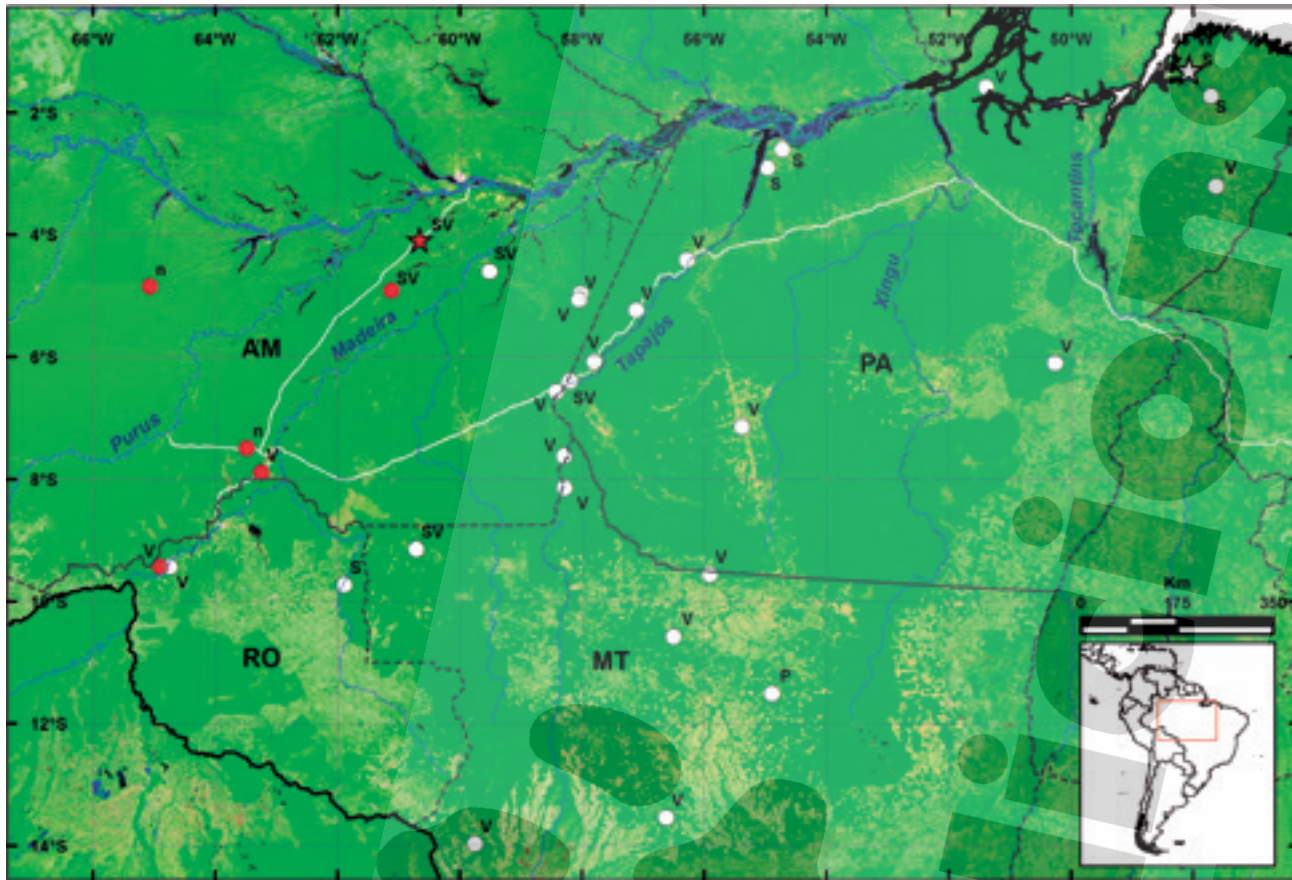


Figure 1. Geographic distribution of *Polioptila attenboroughi* and of documented records of *P. paraensis* in Amazonian Brazil. A red star marks the type locality of *P. attenboroughi* at "Tupana Lodge", and letters adjacent to red locality dots provide documentation: S = specimen; V = vocal recording; n = undocumented sight-records. White dots mark documented records of presumed *P. paraensis* (type locality Benevides, Pará, near Belém), including one *P* marking a site documented by a photograph archived on the website www.wikiaves.com.br (WA589871). Black lines mark the boundaries of Brazilian states as indicated by their abbreviations: AM = Amazonas; RO = Roraima; MT = Mato Grosso; PA = Pará. The federal highways BR-319 (linking Manaus and Porto Velho, running north-south) and BR-230 ("Transamazônica" running mostly east-west) are shown in white.

in the mitochondrial gene NADH subunit 2 (see *Phylogenetic relationships*, below).

Distribution.— West of the Madeira and south of the Solimões rivers in the Inambari area of endemism (Silva *et al.* 2005) in Brazil, where presently documented from only a few localities (Whitney and Álvarez 2005, Whittaker *et al.* 2008; Fig. 1).

Description of holotype.— See color illustration. Alphanumeric color designations determined through direct comparison with Smithe (1975). Head, nape, and mantle through uppertail coverts uniform plumbeous (color 78). White eyering, slightly broken at front and back edges. Throat and breast, including some posterior extension to sides, also plumbeous (lightest at the uppermost throat where a few suffused whitish feathers are found). Upper belly and posterior extension to flanks concolor with throat and chest; remaining underparts including undertail coverts white. Primaries and secondaries plumbeous (color 78), outer vanes of primaries finely edged with dark gray, inner vanes narrowly edged whitish. Alula and smaller, overlying feather blackish with thin whitish margin on outer vane; primary coverts same blackish but lacking whitish margins. Underwing coverts white. Tail unworn and distinctly graduated. Three inner pairs entirely blackish. Rectrix No. 4 mostly blackish with a white tip (about 95% blackish); No. 5 mostly blackish (ca. 60%), white towards the tip, mostly on the distal vane. Outer rectrices (pair No. 6) approximately 80% white with approximately basal 20% of proximal vanes blackish. **Soft parts in life:** Iris light brown/creamy; maxilla blackish gray; mandible light gray; tarsi and feet bluish gray. **Standard measurements:** Bill length (culmen from base at skull) 11.9 mm; bill width at anterior edge nares 3.2 mm; bill depth at anterior edge nares 2.5 mm; wing chord 46.7 mm; tail length 51.4 mm; tarsus length 12.5 mm; mass 6 g.

Etymology.— The new taxon is named in honor of Sir David Frederick Attenborough who has long been a mentor to many generations of ornithologists. Sir David has become a worldwide household name with countless magnificent TV natural history programs spanning almost 60 years, which he so passionately presents and narrates. Having had the honor of working with Sir David, one of us (AW) witnessed firsthand his endless passion and appreciation for nature. Sir David is best known for writing and presenting the nine Life Series with the BBC Natural History Unit, which collectively form a comprehensive survey of all life on our planet. He has succeeded like nobody else in cap-

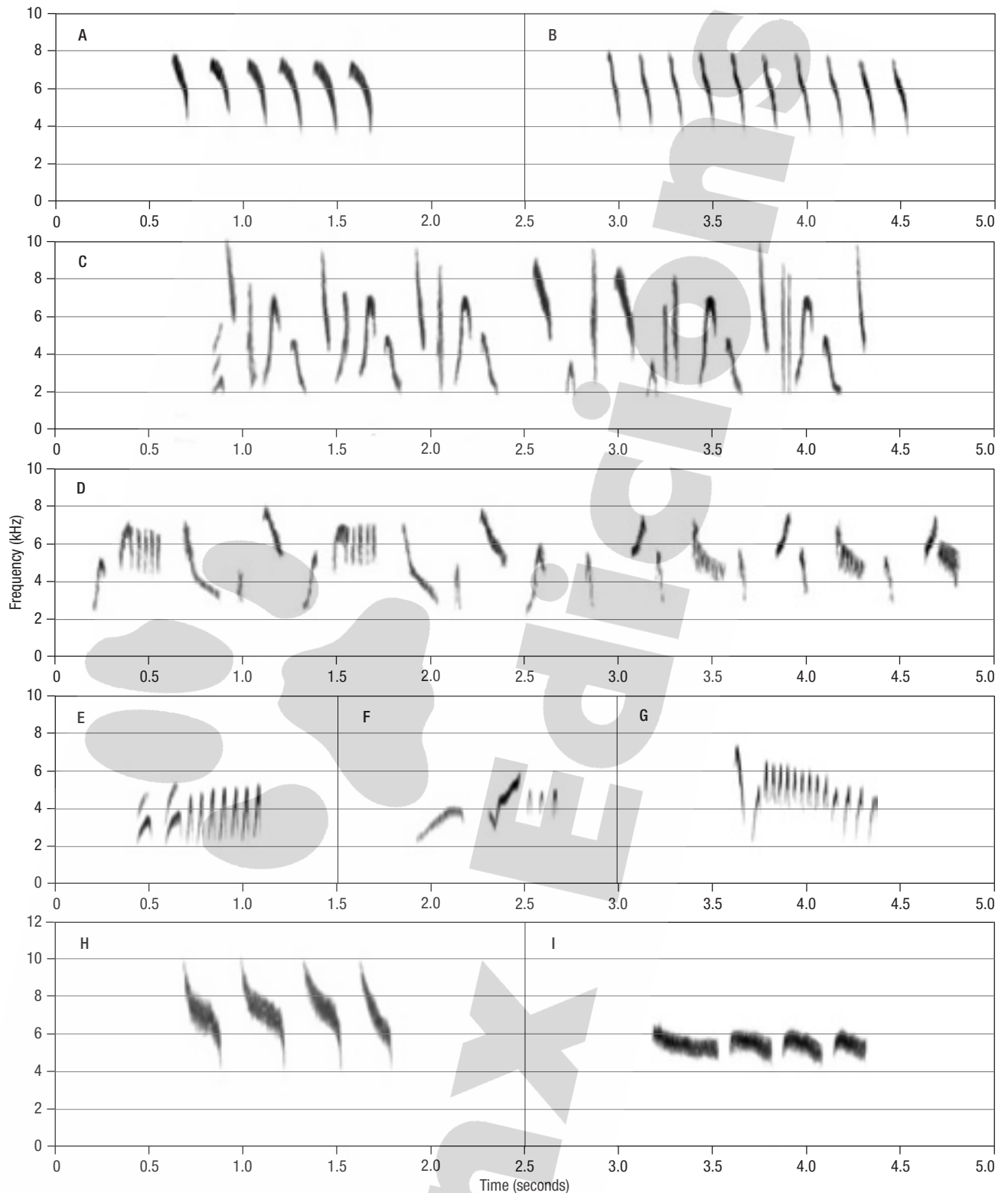
tivating countless millions of television spectators worldwide, enabling them to appreciate and enjoy nature for the first time, and clearly highlighting the major perils facing our magnificent planet earth and its wildlife. Sir David has done an outstanding job documenting important current topics such as global warming and the alarming numbers of species that humans are driving towards extinction, and confirming the essential need for us to do a much better job of conserving our planet's precious nature for future generations to enjoy.

The English and Portuguese names reference the center of endemism to which *Polioptila attenboroughi* is restricted.

REMARKS

Type series.— Paratypes of *P. attenboroughi* are the following two specimens: MPEG 63203: skin, adult male, left testis 6×4 mm, no molt, collected (shot) in the canopy of upland (*terra firme*) sandy-soil forest by AA on 4 July 2007 at the type locality and prepared by AA and Manoel Santa-Brigida under field number TUP 003. Tissue samples deposited at MPEG under field number TUP 003. Mitochondrial gene NADH subunit 2 sequences deposited in GenBank (KC823273). Recordings of vocalizations archived at British Library of Natural Sounds under accession number 183249 (available at <http://www.bl.uk/listentonature/main.html>). INPA 2233: skin, adult male, left testis 6×5 mm, trace molt, no Bursa, skull 100% ossified, collected (shot) in the canopy of upland (*terra firme*) forest by Mario Cohn-Haft on 18 July 2007 at "Campo da Catuquirá", ca. 240 km south of Manaus, Amazonas, Brazil ($04^{\circ} 55' S$; $61^{\circ} 07' W$) and ca. 100 km to the southeast of the type locality in the Madeira-Purus interfluvium; specimen prepared by Mario Cohn-Haft and Ingrid Macedo under field number MCH 665. Tissue samples deposited at INPA under number A-1397; not sequenced. Recordings of vocalizations archived at the Macaulay Library of Natural Sounds under accession number 169991. **Variation in the type series:** The type series includes three specimens, all males. The only apparent slight variation pertains to the iris color, which is recorded as light-brown/creamy in the holotype, light orange-brown in MPEG 63203, and dark brown in INPA 2233. Whether this represents a true type of variation or just

Figure 2. Spectrograms of characteristic vocalizations of *Polioptila attenboroughi* for comparison with homologous vocalizations of selected members of the *Polioptila schistaceigula* complex, and of other taxa presented at the same spectrogram scales by Whitney and Alvarez (2005). A) *P. attenboroughi* loudsong (Amazonas, ca. 50 km south Humaitá; 17 December 2011, Whitney recording BMW-15034); B) *P. paraensis* loudsong (Pará, ca. 53 km west Jacareacanga; 14 July 2008, Whitney recording BMW-4621). This is the same locality from which the tissue sample representing *P. paraensis* used in this study was collected. The sample of loudsongs measured in the vocal analysis, from nearer the type locality of *P. paraensis*, was considerably faster-paced (see data in SI, and spectrogram C in figure 3 of Whitney and Álvarez 2005); C) *P. attenboroughi* complex song (Amazonas, ca. 50 km south Humaitá; 19 December 2010, Whitney recording BMW-11956); D) *P. schistaceigula* (Panamá; Darién, near Cana; 4 January 1993, Whitney recording ML-161468); E) *P. attenboroughi* multi-note call (same recording as A, above); F) *P. schistaceigula* multi-note call (same recording as D, above). Multi-note calls may comprise more notes than this example; G) *P. guianensis* multi-note call (Amazonas, ca. 60 km north Manaus, INPA tower; 13 September 2010, Whitney recording BMW-10821); H) *P. attenboroughi* multi-note rasp (same recording as C, above); and I) *P. schistaceigula* multi-note rasp (same recording as D and F, above).

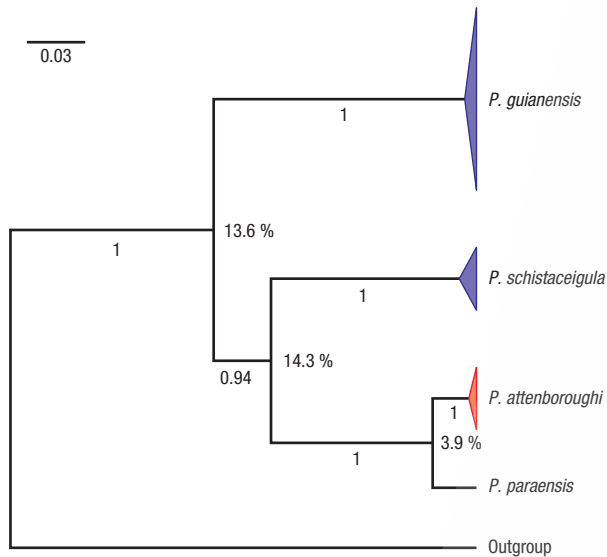


subjectively distinct transcriptions of iris colors cannot be properly assessed at this time given such a small series of specimens. Nevertheless, widely distinct iris colors have also been recorded within series of specimens of other taxa in the *P. guianensis* complex (Whitney and Álvarez 2005; see also Table 1 in SI for a list of specimens examined), suggesting that at least some individual variation is involved.

Ecology and behavior.— *Polioptila attenboroughi*, like other members of the *P. guianensis* complex, forages alone or in pairs in the canopy of upland (*terra firme*) sandy-soil forest, apparently exclusively in association with mixed-species canopy flocks. While foraging, it usually gleans prey off the surface of leaves and twigs, mainly in dense terminal branches, while in fast motion and with its tail cocked and flicked laterally, and rec-

trices sometimes spread. It can also chase flushed prey into the air by "jumping" and flying short distances, quickly returning to tree branches. So far, apparently no records outside tall, upland sandy-soil forest exist, so the species seems tied to this patchily distributed habitat in western Amazonia. Due to its weak, high-pitched voice, and overall low density, it is easily overlooked. The nest and eggs remain unknown.

Vocalizations.— Figure 2 enables comparison of characteristic vocalizations of *Polioptila attenboroughi* with pertinent, homologous vocalizations of other members of the overall *P. schistaceigula* complex, complementing data and spectrograms presented at equivalent scales by Whitney and Álvarez (2005; their figure 3). Typical vocalizations of these taxa, including those used to make the spectrograms in Figure 2, are available



for listening on the IBC website. As expected, among comparisons of all taxa, the loudsong of *P. attenboroughi* ($n = 4$) most resembles that of its sister-species, *P. paraensis*, but an attentive listener will discern distinctions in pace (number of notes per second, perceptibly slower in *P. attenboroughi* $P < .001$; data in SI) and auditory quality, an attribute determined by the shapes of the individual notes in the vocalizations but difficult to quantify. A complex song featuring repetitions of multi-syllabic phrases sometimes interspersed with short calls, rasps, or a few normal loudsongs has been recorded twice within our small sample of recordings of *P. attenboroughi*, and the few available recordings of *P. schistaceigula* (BMW and parts of some recordings archived on www.xeno-canto.org) show clear similarity to these (compare Figs. 2C and 2D). Whitney and Álvarez (2005) described a similar vocalization of *P. clementsi* heard once by BMW but not tape-recorded. In more than twenty encounters with vocalizing *P. paraensis* from across the range of that taxon, BMW has never heard any vocalization reminiscent of this complex song. This is not to assert that *P. paraensis* and apparently closely related populations south of the Amazon and east of the Madeira do not possess a homologous vocalization, but if it does exist, it must be a rarely used part of the repertoire. The vocalization most congruent with genetic data indicating shared evolutionary history among members of the *P. schistaceigula* complex (see *Phylogenetic relationships*, below) is the multi-note call, the only vocalization delivered by all members in clearly recognizable (to human beings) pattern and auditory quality.

Phylogenetic relationships and taxonomy.— DNA sequence data for the mitochondrial gene NADH subunit 2 (ND2, 1041 base pairs) were obtained for 7 individuals of the *P. guianensis* complex, including all taxa but *P. clementsi* and *P. facilis*. A preliminary multi-locus molecular phylogeny of the family Polioptilidae indicated that all taxa of the *P. guianensis* complex sequenced and *P. schistaceigula* are monophyletic and sister to all remaining *Polioptila* species (Klicka *et al.*, unpub. data). Hence, in addition to taxa of the *P. guianensis* complex, *P. schistaceigula* and *P. plumbea* (outgroup) were also included in the molecular analysis discussed herein (see Table 2 in SI for a list of specimens sequenced). A maximum clade credibility tree using Bayesian inference recovered a paraphyletic *P. guianensis* complex with respect to *P. schistaceigula*, with the latter species being closer to *P. attenboroughi* and *P. paraensis*, which grouped as sister taxa with maximum statistical support (Fig. 3). Unfortunately, no sequences of *P. clementsi* and *P. facilis* were available, so their phylogenetic position and genetic distinctiveness with respect to *P. attenboroughi* and other taxa in the *P. guianensis* complex could not be assessed. Despite this sampling limitation, most morphological characters (i.e., white/black proportion on rectrices, eye-ring pattern, bill and tail lengths) and vocal attributes point to a closer relationship be-

tween *P. attenboroughi* and *P. paraensis*, in congruence with the molecular data.

The uncorrected p genetic distance between *P. attenboroughi* and *P. paraensis* (3.9%; Fig. 3) is nearly identical to that reported for a pair of parapatric sister-species of *Polioptila* in North America (4% for *P. californica* and *P. melanura*), and also based on the same gene (Zink and Blackwell 1998). It is important to note, however, that our single sample of *P. paraensis* was collected more than 1200 km southwest of the type locality of the taxon, and, more importantly, across the Xingu and Tapajós rivers. Our vocal analysis (above) supported by more superficial comparisons among a larger sample of recordings from across the range of *P. paraensis* showed (BMW, *pers. obs.*) that toptypical loudsongs are about 20% faster than those typical of the Madeira-Tapajós interfluvium (compare spectrograms, Fig. 2B with figure 3C of Whitney and Álvarez 2005, and listen to the recordings on the IBC website). For these reasons, it is unlikely that the 3.9% mtDNA divergence we recovered is representative of the genetic distance between *P. attenboroughi* and toptypical *P. paraensis*; we suspect it is significantly underestimated, which further reinforces a separate species status for *P. attenboroughi*. Furthermore, the paraphyly of the *P. guianensis* complex added to the surprisingly high genetic distance (13.6%) separating *P. guianensis* from the clade uniting *P. schistaceigula*, *P. attenboroughi* and *P. paraensis*, supports the taxonomic arrangement suggested by Whitney and Álvarez (2005), whereby all named taxa and perhaps other populations of the *P. guianensis* complex are best treated as separate species (see suggested common names therein). It also provides the basis for treating both the *P. guianensis* complex and *P. schistaceigula* as a single radiation of allopatric and parapatric taxa, properly called the *P. schistaceigula* complex due to nomenclatural priority.

Conservation.— *Polioptila attenboroughi* is a low density species throughout most of its range, and probably has an extensive but patchily distributed population endemic to the Inambari center of endemism in western Amazonia. Of particular concern is the recent advancement of soybean plantations and general infrastructure along the BR-319 highway linking Manaus to Porto Velho in Brazil, which bisects the Purus-Madeira interfluvium, apparently the main stronghold of the species. If the advancement of agro-business and infrastructure development at the core of *P. attenboroughi*'s range becomes more widespread, as it seems likely to do if and when this highway is improved, it could imperil this and many other endemic *terra-firme* species of the Inambari region in the long run.

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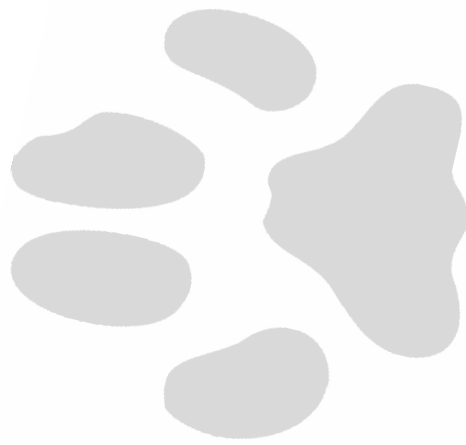
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Figure 3. Phylogenetic relationships within the *Polioptila schistaceigula/guianensis* complex recovered by Bayesian analysis based on 1041 bp of ND2 sequences. Numbers refer to posterior probabilities values and genetic distances (% of average uncorrected p sequence divergence) between sister groups associated with the labeled nodes (see Table 2 in SI for detailed information). Note the paraphyly of taxa formerly grouped as subspecies of *P. guianensis* (*guianensis* and *paraensis*) and the new taxon *P. attenboroughi* described herein. High statistical support values (i.e., 1) and sequence divergence levels associated with nodes grouping *Polioptila attenboroughi*, *P. guianensis*, *P. paraensis*, and *P. schistaceigula* are, in concert with documented levels of phenotypic differentiation, consistent with their ranking as species-level taxa.

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