Morphology, vocalizations, and mitochondrial DNA suggest that the Graceful Prinia is two species

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The Graceful Prinia is shown to be comprised of two groups differing in song, in mitochondrial DNA (mtDNA), and subtly in plumage and structure. One group (the southwestern group) occurs from Egypt through Somalia and the Arabian Peninsula, while the other (the northeastern group) occurs from Turkey through northeastern India and Bangladesh. Both groups vary extensively, but the southwestern group is slightly larger but shorter-tailed, with less distinct barring on the uppertail but more distinct dark spots on the undertail, than the northeastern group. The southwestern group sings with clearly separated short phrases, whereas the northeastern group has a continuously reeling song. MtDNA suggests that the two groups diverged ~2.2 million years ago. On the eastern Arabian Peninsula, populations of both groups evidently occur. We suggest that these two groups should be recognized as separate species. We evaluated the utility of new analyses of plumage and structure in this case and found that they add substantial value to integrative analyses determining species limits.

Keywords: integrative taxonomy, mitochondrial DNA, morphology, Prinia gracilis, vocalizations
Prinia gracilis species limits

INTRODUCTION

The Old World “warbler” family Cisticolidae is part of the superfamily Sylvioidea sensu Fregin et al. (2012), which includes a paraphyletic grouping of several Old World “warbler” families (reviews in Alström et al. 2013 and Fjeldså et al. 2020) from which Cisticolidae diverged around 23 million years ago (MYA; Oliveros et al. 2019). Cisticolidae comprises more than 160 species, with a predominantly African and south Asian distribution (Gill et al. 2020). Olsson et al. (2013) proposed, based on a phylogenetic analysis including all genera in this family, that Cisticolidae should be separated into the subfamilies Eremomelininae, Cisticolinae, Priniinae, and Neomixeinae.

Prinias of the genus Prinia are sedentary across Africa and southern Asia to western Indonesia, occurring not only in various open habitats with bushes, tall grass, or reedbeds but also along forest edges and in open forest. All species have rather long, narrow, strongly graduated tails, often with pale and dark subterminal markings, and in most of them the bill and mouth lining become black in breeding males. Several of the species are very similar and more easily separated by song than by appearance. The genus Prinia, the composition of which was modified based on the phylogenetic analysis of Olsson et al. (2013), comprises 23–28 mostly polyporphic species (Dickinson and Christidis 2014, del Hoyo and Collar 2016, Gill et al. 2020). Recent taxonomic revisions have upgraded several subspecies to species status. Based on morphological and vocal characters, the Hill Prinia (Prinia atrogularis) has been suggested to be split into 3 species and the Yellow-bellied Prinia P. flaviventris into 2 species (Rasmussen and Anderton 2005, del Hoyo and Collar 2016). A recent study based on morphology, vocalizations, and mitochondrial and nuclear DNA proposed splitting the Striated Prinia (P. crinigera) into 2 species and the Brown Prinia (P. polychroa) into 3 species (Alström et al. 2020).

The Graceful Prinia (Prinia gracilis) is widespread from Egypt and northeastern Africa through the Middle East to northeastern India (Gill et al. 2020, Ryan 2020; Figure 1); as currently recognized, it is the most widespread prinia and the only member of the genus Prinia to occur in the Western Palearctic (e.g., as defined by Beaman and Madge 1998; Shirihai and Svensson 2018). Twelve subspecies are usually recognized (Mayr and Cottrell 1986, Cramp 1992, Dickinson and Christidis 2014, Clements et al. 2019, Gill et al. 2020, Ryan 2020; Supplemental Material Table S1), some based only on slight morphological differences (e.g., Nicoll 1917, Hartert 1923, Ticehurst and Cheesman 1924, Meyer de Schauensee and Ripley 1953, Watson 1961). Prinia gracilis has an anomalous distribution, as it is the only bird species globally with a range encompassing Egypt through northeastern India, to the exclusion of any other areas. This contrasts with a common avian pattern of species occurrence throughout the Sahara and the Middle East to the northwestern Indian subcontinent, or species pairs in which one is distributed only in North Africa vs. the other from the Arabian Peninsula east to Pakistan or northwest India (summarized in Schweizer et al. 2018). Shirihai and Svensson (2018) divided the 8

RESUMEN

Prinia (Cisticolidae) es una especie residente de áreas abiertas a través de África y Asia e incluye muchas especies políticas cuyos límites específicos no han sido seriamente re-evaluados recientemente. Basados en un análisis taxonómico integral de morfología, canto y ADN mitocondrial (ADNmt), sugerimos que deberían reconocerse dos especies en el complejo de Prinia gracilis. Adicionalmente, nuestros análisis morfológicos muestran la existencia de una forma bien marcada no descripta proveniente del sudeste de Somalia, la cual aquí nombramos con una nueva subspecie. Prinia gracilis es una especie pequeña, parduzca, de cola larga con rayas arriba y partes inferiores pálidas y lisas que se ha sugerido que cae en dos grupos, el grupo nominado del suroeste (desde Egipto hasta Omán) y el grupo lepida del noreste (desde Turquía hasta India). Sin embargo, los caracteres presentados para justificar este agrupamiento son variables y muestran un patrón en mosaico, y si las diferencias genéticas y vocales existen es desconocido. Encontramos diferencias de canto consistentes entre grupos, con el grupo nominado con intervalos de interfase consistentemente más largos, mientras que los miembros del grupo lepida cantan un carrete esencialmente continuo. Un árbol de ADNmt sugiere una profunda división entre los grupos nominado y lepida, con un tiempo de coalescencia de ~ 2.2 millones de años atrás. Los análisis vocales y de ADNmt brindan evidencia de que el taxón carpenteri del noreste de la Península Arábiga pertenece al grupo lepida. Encontramos que, de todos los caracteres morfológicos propuestos, solo las proporciones y el barrado y manchado de la cola distinguen de manera relativamente consistente los dos grupos. Sin embargo, estos caracteres sugieren fuertemente que el este de la Península Arábiga está poblada por taxones de ambos grupos, gracilis y lepida, en diferentes áreas, pero no tenemos datos genéticos y bio-acústicos para corroborar esto. Aunque se necesitan estudios adicionales en las zonas de contacto potenciales, sugerimos que dos especies deberían ser reconocibles en el complejo de P. gracilis, y proponemos la retención del nombre en inglés Graceful Prinia para P. gracilis s.s., mientras que sugerimos que P. lepida sea conocida como Delicate Prinia.

Palabras clave: ADN mitocondrial, morfología, Prinia gracilis, taxonomía integrativa, vocalizaciones

Morfología, vocalizaciones y AND mitocondrial sugieren que Prinia gracilis es dos especies
Western Palearctic subspecies that they recognized into 2 major subspecific groups based on observed morphological differences: the gracilis group in northeastern Africa, the Arabian Peninsula, and the southern Middle East, and the lepida group from Turkey, through Syria, Iraq, and Iran eastwards, and they synonymized 3 of the subspecies (irakensis, carlo, and carpenteri) recognized by recent global checklist authorities (Dickinson and Christidis 2014, Clements et al. 2019, Gill et al. 2020, Ryan 2020). Prinia gracilis sensu lato (henceforth s.l.) occurs in dense, low vegetation, such as scrub, bushes (e.g., Tamarix), and reedbeds, in dry or semi-dry areas, as well as in wetter habitats such as along rivers and lakes and anthropogenic habitats such as wheatfields and gardens (Cramp 1992, Ryan 2020); Shirihai and Svensson (2018) state that the gracilis group inhabits drier habitats than the lepida group.

It is nonmigratory and at least in some areas defends a winter territory (Cramp 1992). Immatures may disperse and the species has been recorded as a vagrant to Cyprus and Crete, but they may breed as early as 2 months of age and the breeding season is prolonged (Cramp 1992).

Morphology has traditionally formed the backbone of knowledge of avian systematics and species limits, and numerous recent studies impacting species limits of birds used extensive morphological analysis in many ways (e.g., Alström et al. 2015, 2016, 2018, 2020, Feo et al. 2015, Fernando et al. 2016, Oswald et al. 2016, Moncrieff et al. 2018, Töpfer 2018, DeRaad et al. 2019, Myers et al. 2019, Palacios et al. 2019, Lima et al. 2020). Ornithologists generally agree on the essential nature of specimens as vouchers; however, much recent work on species limits has involved little if any morphological study. This is due to several factors, among them the tedious, time-consuming nature of morphological analyses; issues with access to sufficient series of each taxon and indirect comparisons; problems in determining homology; dealing with individual, seasonal, sexual, geographic, age-related, and preservational variation; challenges to repeatable quantification of morphological characters; cases that demonstrate a lack of concordance between plumage traits and assortative mating; assumptions that external morphological traits have already been thoroughly studied and are accurately presented in the literature; and perceived low reward.

Several taxa of prinias show considerable variation, despite the overall drab and relatively featureless plumage of most, and as a group they have received little recent study, although the Western Palearctic subspecies of P. gracilis s.l. have received more study than most (Cramp 1992). Prinias

FIGURE 1. Ranges of the focal taxa, showing locations of sound recordings analyzed (cool-colored circles for gracilis group except black dot for tiny-range natronensis [labeled nat], south and west of white dashed line and warm-colored squares for lepida group, and north and east of white dashed line) and DNA samples (stars in group-specific color). Vocal subgroups are indicated by upper-case letter following subspecies name. Question mark denotes isolated populations of uncertain taxon.
serve as an appropriate group for an evaluation of the value of new morphological analyses, and Rasmussen et al. (2019) recently began to address the questions of whether new morphological study of several widespread prinia taxa (Prinia crinigera, P. polychroma s.l., Prinia flaviventris, P. gracilis, Prinia inornata, and Prinia atrogularis s.l.) with suble yet variable plumage and external structural characters can lead to insights that usefully inform species limits determinations based primarily on genetic and vocal analyses. This preliminary analysis (and, for P. crinigera and P. polychroma, analyses in Alström et al. 2020) showed generally high (75%–100%, but only 50% in P. flaviventris) levels of agreement between estimates of species limits for these taxon groups based on new morphological analyses in comparison to those estimates based on DNA phylogenies and vocalizations.

The anomalous biogeography of P. gracilis, which is unmatched among birds, coupled with the observed variation that has led to its being treated as comprising 2 major subspecific groups (Shirihai and Svensson 2018) strongly suggests that integrative reevaluation of its species limits (Sangster 2018) is required. Although Cramp (1992) stated that there was no information on geographical variation in voice, sonagrams and descriptions therein seem to suggest regional differences in tempo and note spacing of songs. In addition, descriptions of egg color of some southwestern subspecies (whitish to very pale pink) vs. at least one northeastern subspecies (green to pale blue-green; Cramp 1992, Ali and Ripley 1973) are also suggestive of species limits problems.

Here, we examine species limits in the P. gracilis complex, using primarily analyses of song characters and mitochondrial DNA (mtDNA) from across the species’ range and evaluate whether the subtle and variable external morphological characters that typify P. gracilis taxa are adequately known and represented in the literature, and whether morphological analyses can provide new data useful to and congruent with our other sources of information on species limits. In addition, during the course of this study, we found that there is an undescribed subspecies along the southeast coast of Somalia, which we describe herein from specimens.

METHODS

Operational Taxonomic Units and Distributions

For determining our operational taxonomic units for morphological analyses, as a starting point, we followed the subspecific taxonomy and distributional statements of Dickinson and Christidis (2014), Gill et al. (2020), and Ryan (2020), which are all in agreement in recognizing the same 12 subspecies (Supplemental Material Table S1), which we have also mapped as such (Figure 1). However, as we divide the subspecies into 2 major subspecific groups based on our integrative results (see below), we list the subspecies in order from N–S and then W–E, with the SW gracilis group listed first (Supplemental Material Table S1). Several museum specimens were found based on locality of these nonmigratory taxa to be misidentified to subspecies, and these subspecific attributions have been noted and corrected in Supplemental Material Table S2.

Throughout the remainder of this paper, based on our analysis of DNA and vocalizations, we consider the southwestern major subspecific group (deltae, natronensis, gracilis, palaestinae, carlo, ssp. nov., and yemenensis, with hufufae being tentatively assigned to this group), from Egypt east to Israel and Syria, south to Somalia, and east to the Dhofar region of Oman and provisionally the north-central Arabian Peninsula (hufufae), to comprise the gracilis sensu stricto (henceforth s.s.) group. We consider the northeastern major subspecific group (akyildizi, irakensis, lepida, carpenteri, and stevensi), from Turkey and the northeastern Arabian Peninsula region through Iraq to northern India east to Assam and Bangladesh, to comprise the lepida group. This grouping differs from that of Shirihai and Svensson (2018) in that we consider carpenteri valid and to belong in the lepida group based on vocal recordings, with support from morphology (see below).

Unlike most of the species of prinias, P. gracilis s.l. is not to our knowledge frequently visually misidentified, either as specimens or in life. However, it can be confused aurally with other prinias, such as Plain Prinia (Prinia inornata), with which there is minimal geographic overlap except in the Indian Subcontinent. We were thus able to adapt our distributional map (Figure 1) from that in Ryan (2020) and could assume that eBird records (https://eBird.org/species/prin11) are unlikely to include misidentifications of other prinia species complexes that would affect distributions.

Morphological Data Collection and Analyses

Specimens examined. Specimens of all taxa of P. gracilis s.l. were measured and examined for qualitative plumage characters. Those studied were from the American Museum of Natural History (AMNH), New York, USA; Academy of Natural Sciences (ANSP), Philadelphia, USA; Field Museum of Natural History (FMNH), Chicago, USA; Museum of Comparative Zoology (MCZ), Cambridge, Massachusetts, USA; National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C., USA (specimen acronym USNM); the Natural History Museum, Tring, UK (NHMUK, formerly BMNH); University of Michigan Museum of Zoology (UMMZ), Ann Arbor, USA; and Yale Peabody Museum (YPM), New Haven, USA.

Mensural data. Eighteen external morphological characters were measured by P.C.R. as possible for each of 263 museum skin specimens (n provided for each
measurement for each taxon in Supplemental Material Table 3): culmen length from skull base and from distal edge of feathers; bill width and depth from distal edge of nares; unflattened and flattened wing (wing chord and arc, respectively); projection of wingtip beyond longest secondary; shortfalls of outer primaries (distances from each primary 1–5 to wingtip, primaries numbered ascendantly, with primary 10 outermost); tail length (with calipers inserted between middle 2 rectrices); tail graduation (from central rectrix to outermost rectrix in folded tail); maximum central rectrix width (if feathers in good condition); and tarsus and hindclaw lengths. Statistical analyses of mensural data (univariate statistics of mensural characters tested for significance using Bonferroni-adjusted 2-way t-tests with pooled variances and principal component analyses [PCAs] using correlation matrices) were carried out with MyStat (SYSTAT Software, Crane Software International). All raw mensural data are available in Supplemental Material Table S2. Sexes were combined for all analyses due to the small number of reliably sexed specimens available and lack of apparent differences other than the black bill and mouth of breeding adult males. Wing length and bill color characters given in Zduniak and Yosef (2004) as allowing sexing of P. gracilis at Eilat, Israel, are internally inconsistent in that paper and, even if not, would not necessarily apply to other populations. Immatuus are similar to adults and thus were included, but younger juveniles were excluded.

Plumage data. For 147 specimens, scoring using integers of 8 plumage characters of museum skin specimens was done by P.C.R. as follows (see Supplemental Material Figure S1 for reference specimen photos and character state descriptions): upperparts ground color darkness (1 = very pale to 4 = very dark), upperparts grayness (1 = cold gray to 3 = warm brown), mantle streaking contrast (1 = very weak to 5 = very strong), mantle streaking breadth (1 = very narrow to 4 = very broad), flank grayness (1 = cold gray to 3 = warm brown), uppertail barring strength (0 = none to 5 = very strong), number of dark uppertail bars/cm (not used in analyses due to high within-taxon variability), and strength of largest dark subterminal band (1 = very weak to 3 = moderately prominent). In addition, breadth and length (depth) of largest dark subterminal band were measured to the nearest 0.5 mm. For an additional 116 specimens, only 7 of these characters were scored (n for each plumage character scored for each taxon in Supplemental Material Table S4). As noted by Cramp (1992), seasonal variation is minor and feather wear did not appear to be a significant problem for most of the characters scored, with the exceptions of upperparts streaking and the subterminal tail band, which was not scored in highly worn specimens. All plumage scoring data are available in Supplemental Material Table S2, and as with mensural analyses and for the same reasons, sexes and fully grown immatures were pooled. Univariate statistics, Kruskal–Wallis one-way analyses of variance, and PCAs for plumage scores were done on correlation matrices with MyStat. We used Munsell Soil Color Charts (2000) as the color standard for description of a new taxon.

Song Analyses

Recordings examined. Sound recordings of songs were obtained from our own collections and from the publicly available sound archives AvoCet (https://avo-cet.integrativebiology.natsci.msu.edu), xeno-canto (www.xeno-canto.org), and Macaulay Library (www.macaulaylibrary.org). For multiple recordings in public libraries collected on the same day at the same location by the same person such that individuals could not be safely identified, one recording was randomly selected for analysis to avoid false repetition. A total of 84 usable recordings, assumed to represent 84 individuals, were analyzed (Supplemental Material Table S5). Other recordings were examined by ear but were not of high enough quality to be quantitatively analyzed. Our own, previously unpublished recordings have been deposited in AvoCet (Supplemental Material Table S5), as have those of others granting permission (Supplemental Material Table S5).

Song data collection. All recordings were resampled at 22.05 kHz and saved as .wav files using Goldwave 5.25 audio processing software (Goldwave, Canada). Sonograms were created in Raven Pro 1.6 (Cornell Lab of Ornithology, Ithaca, New York, USA, Bioacoustics Research Program 2017), with the following settings: Window size = 256 samples, window type = Hann, 3 dB filter bandwidth = 270 Hz, overlap = 50%, size = 2.67 ms, Discrete Fourier Transform size = 256 samples, and spacing = 188 Hz. The contrast was kept fixed at 93, and brightness was adjusted manually for each recording to give a good visual separation between the different song elements and the background noise. The following variables were measured for each phrase (defined as a block of notes that is repeated in series, forming the song) by C.X. and L.Z.: duration, minimum frequency, maximum frequency, bandwidth, peak frequency (the frequency associated with the maximum energy), center frequency (the frequency that divides the selection into 2 frequency intervals of equal energy), aggregate entropy (the disorder in a phrase, with a high value corresponding to a complex frequency variation along the time axis and the lowest value corresponding to a pure tone with no frequency variation along the time axis), and interval (duration from the end of one phrase to the beginning of the next phrase) (Figure 2). In addition, the total number of phrases within a burst of continuous song was counted. In total, 9 variables were generated from the sonograms. The first 5 phrases per song, or all phrases in the song if fewer than 5, were measured. If background noise affected the measuring of a certain phrase, the next or even later phrases were measured instead. The first 5
bursts of song per recording, or all songs in the recording if fewer than 5, were measured. Mean values of phrases were calculated for each burst of song, and mean values of these bursts of song were calculated for each recording. In addition to measurements, the recordings were analyzed by ear.

**Song statistical procedures.** Multivariate analysis of variance (MANOVA) was used to assess the overall differences among taxa, followed by an independent sample t-test for each variable. PCA with varimax rotation was used to compress the original variables into independent principal components (with Eigenvalues larger than 1), and forward stepwise discriminant function analysis (DFA) was used to determine the classification success of our a priori classification. Results from leave-one-out cross validation are reported as percentages of recordings correctly assigned in DFA. In leave-one-out cross validation, each recording was assigned to a taxon based on discriminant functions calculated from all recordings except the one being classified. Statistical analysis was performed using SPSS 21.0 (IBM Corp., Armonk, New York, USA). Data were presented as the mean ± standard deviation. Differences with P values of less than 0.05 were considered significant. Both PCA and DFA were run based on 2 groups (corresponding to the 2 main groups identified; see Results) as well as based on 6 groups corresponding to 6 geographical regions (Figure 1).

**DNA Samples and Analyses.** DNA sample source and sequencing. In total, 14 blood or muscle samples were obtained from 5 localities representing *P. g. palaestinae* (6), *P. g. irakensis* (7), and *P. g. lepida* (1) (Table 1). DNA was extracted using QIA Quick DNEasy Kit (Qiagen Inc., Hilden, Germany), according to the manufacturer’s instructions. We sequenced the mitochondrial cytochrome *b* (cytb) and NADH dehydrogenase 2 (ND2) genes for 14 samples, respectively. Amplification and sequencing followed the protocols described in Olsson et al. (2005).

**Phylogenetic analyses.** Sequences were aligned using the MUSCLE algorithm in Geneious 7.1.9 (Biomatters Ltd.). Phylogenetic analyses were performed by Bayesian inference using BEAST 1.10.4 (Drummond et al. 2012). Model selection was based on the Akaike Information Criterion calculated in jModeltest 2.1.10 (Darriba et al. 2012). The HKY (Hasegawa, Kishino and Yano) model was selected for cytb and the GTR (generalized time reversible) model for ND2. Xml files were generated in the BEAST utility program BEA Uti 1.10.4 and are available in Supplemental Material Table S6. Analyses were run under a strict molecular clock with a normally distributed clock prior with a mean rate of 0.010 and standard deviation 0.001, corresponding to a rate of 2.0% per million years (myr) (cf. Weir and Schluter 2008). Different tree priors were tested in different analyses: a Yule speciation prior with a normal distribution with mean 2.0 and standard deviation 1.0, and a Coalescent Constant Size population prior. The former had a higher marginal likelihood and was, therefore, chosen. Default settings were used for the other priors. Twenty million generations were run, sampled every 1,000 generations. Convergence to the stationary distribution of the single chains was inspected in Tracer 1.7.0 (Rambaut and Drummond 2018) using a minimum threshold for the effective sample size. The joint likelihood and other parameter values reported large effective sample sizes (>1,000). Good mixing of the MCMC and reproducibility were established by multiple runs from independent starting points. Topological convergence was examined by eye. The first 25% of generations were discarded as “burn-in,” well after stationarity of chain likelihood values had been established, and the posterior probabilities were calculated from the remaining samples. Trees were summarized using TreeAnnotator 1.10.4 (included in BEAST package), choosing “Maximum clade credibility tree” and “Mean heights,” and displayed in FigTree 1.4.3 (Rambaut 2002). Ashy Prinia (*Prinia socialis*) and Yellow-bellied Prinia (*P. flaviventris*) were used as outgroups. All sequences have been deposited in GenBank (Table 1).

**RESULTS**

**Morphological Analyses**

**Structure.** Comparison of univariate statistics of measurements (Supplemental Material Table S3) among taxa of the *gracilis* group shows that several taxa differ mensurally primarily in bill and wing length, and that they are otherwise relatively uniform structurally. Most of the taxa of the *lepida* group are also similar structurally, with *carpenteri* being the largest billed and *stevensi* being especially short winged and short tailed (Supplemental Material Table S3). On a PCA (Figure 3A) of external measurements of all taxa, taxa of the *gracilis* group had Factor 1 scores
Prinia gracilis species limits

near or above 0 (except a few gracilis). As Factor 1 is a general size axis contrasting with tail length (Table 2), this reflects the larger overall size but relatively shorter tails of gracilis group members compared with most of the taxa of the lepida group. Four subspecies of the gracilis group (natronensis, SE Somalia ssp. nov. \[n = 1\] in this analysis; see below), yemenensis, and hufufae) have Factor 1 scores near or above 1, reflecting their slightly larger size relative to the other 4 subspecies of this group (deltae, gracilis, palaestinae, and carlo). The taxa of lepida (except carteri) have Factor 1 scores near or below zero, with broad overlap between akyildizi, irakensis, and lepida, and to a lesser extent stevensi, while carteri overlaps broadly in general size with the smaller taxa of the gracilis group (Figure 3A). The positive scores for carteri on Factor 2 reflect their slightly larger bills than other members of the lepida group, whereas the negative scores for stevensi on Factor 2 reflect their shorter wing and tail (Figure 3A, Table 2). The degree of relative structural uniformity within major subspecific groups contrasts with the much stronger between-group morphological differentiation, with almost all characters (except wing shape measurements) being highly statistically significant between the gracilis and lepida groups (Supplemental Material Table S3), and with the near-complete (except for carteri) separation of the 2 groups on Factor 1.

Plumage. Comparison of univariate statistics for plumage scores (Supplemental Material Table S4) among taxa of the gracilis group shows relative uniformity between populations and variability within populations in most characters, such that few populations differ significantly in single characters. We do not believe that plumage wear has significantly affected the plumage scoring results, but any such impact is likely to create greater within-taxon variance. Table 3 summarizes the characters typifying the 2 major subspecific groups.

| Scientific name | Locality | Sample ID | Tissue | GenBank accession number |
|-----------------|----------|-----------|--------|--------------------------|
| *Prinia gracilis* group | | | | |
| *Prinia gracilis* palaestinae Eilat, Israel | DZUG U0468 Blood | MT774176, MT774190 |
| *Prinia gracilis* palaestinae Eilat, Israel | DZUG U0533 Blood | MT774177, MT774191 |
| *Prinia gracilis* palaestinae Eilat, Israel | DZUG US441 Blood | MT774178, MT774192 |
| *Prinia gracilis* palaestinae Eilat, Israel | DZUG US442 Blood | MT774179, MT774193 |
| *Prinia gracilis* palaestinae Eilat, Israel | DZUG US443 Blood | MT774180, MT774194 |
| *Prinia gracilis* palaestinae Eilat, Israel | DZUG US444 Blood | MT774181, MT774195 |
| *Prinia gracilis* lepida Harike, Punjab, India | DZUG U0461 Blood | JX236402, MT774196 |
| *Prinia gracilis* irakensis Kuwait | VHZ A0733 Blood | MT774183, MT774197 |
| *Prinia gracilis* irakensis Muhafazat Salah ad Din, Iraq | USNM 645824 Muscle | MT774184, MT774198 |
| *Prinia gracilis* irakensis Shush, Khouzestan, Iran | DZUG U5514 Muscle | MT774185, MT774199 |
| *Prinia gracilis* irakensis Shush, Khouzestan, Iran | DZUG U5515 Muscle | MT774186, MT774200 |
| *Prinia gracilis* irakensis Shush, Khouzestan, Iran | DZUG U5516 Muscle | MT774187, MT774201 |
| *Prinia gracilis* irakensis Borazjan, Bushehr, Iran | DZUG U5517 Muscle | MT774188, MT774202 |
| *Prinia gracilis* irakensis Borazjan, Bushehr, Iran | DZUG U5518 Muscle | MT774189, MT774203 |
| *Prinia flaviventris* flaviventris Arunachal Pradesh, India | KJ456420 |
| *Prinia socialis* stewarti Uttarakhand, India | KJ456424 |

Table 2. The degree of relative structural uniformity within major subspecific groups contrasts with the much stronger between-group morphological differentiation, with almost all characters (except wing shape measurements) being highly statistically significant between the gracilis and lepida groups (Supplemental Material Table S3), and with the near-complete (except for carteri) separation of the 2 groups on Factor 1.
In the *lepida* group, Turkish *akyildizi* differs significantly from *irakensis* in darkness and degree of streaking; *carpenteri* differs from *irakensis* and *lepida* in breadth of streaking and dark subterminal tail spots, while *lepida* and *stevensi* differ from each other in several plumage characters (Supplemental Material Table S4). On Factor 1 of a PCA of plumage scores, positive scores reflect mostly stronger mantle streaking and dark subterminal undertail markings, whereas negative scores reflect stronger uppertail barring (Table 2). Nearly all individuals of the *gracilis* group taxa have positive scores on Factor 1 (Figure 3B), with the notable exception of the SE Somalia ssp. nov. (see below). Nearly all the *lepida* taxa, with the strong exception of Turkish *akyildizi*, have negative scores on Factor 1. This reflects the pattern for most taxa of the *gracilis* group to be strongly streaked above but with weak tail barring and large, strongly contrasting subterminal undertail spots, in contrast to most of the taxa of the *lepida* group. On Factor 2, which contrasts larger and more prominent dark subterminal undertail spots against stronger mantle streaking, *akyildizi* is the only taxon with low negative scores, reflecting its exceptionally strong streaking (Figure 4A) but weak tail spots. All 4 specimens of the new Somali subspecies have positive scores on Factor 2, reflecting their weakly streaked upperparts (Figure 3B). Most color and streaking plumage characters tend to be similarly variable between subspecies within the 2 taxon groups, although there are different tendencies in all these characters except upperparts grayness. In contrast, there are marked differences between group means for uppertail barring and size and prominence of dark subterminal tail spots. Most of the taxa of the 2 groups (except the undescribed Somali subspecies and Turkish *akyildizi*) separate out with minimal overlap on Factor 1 of plumage scores (Figure 3B), and *P. g. carpenteri* (Figure 4B) clusters with the *lepida* group. We have examined the type series of *carpenteri* (Figure 4B) and find that, as originally described (Meyer de Schauensee and Ripley 1953), this series fits with the *lepida* group and differs from *hufufae* on the basis of its overall appearance, especially the relatively strongly cross-rayed...
Description of a New Subspecies

Four specimens collected from the seemingly isolated population in Mallable, Somalia (Figure 1), by J. S. Ash in 1979, differ noticeably from other taxa in the western group in their paler color, weaker patterning, and structure. These represent an unnamed taxon presumably best treated as a subspecies of the *Prinia gracilis* group, which we here describe as new:

*Prinia gracilis ashi*, new subspecies

**Holotype.** USNM 571315, male, testes 5 mm, w. [wing-span] 47; wt. 8.5 g; Mallable, Somalia, 2°12’N, 45°37’E, J. S. Ash #355, prep. J. Mwaki, February 16, 1979. Adult. See Figure 5.

**Measurements of holotype (mm).** Culmen from skull, 12.2; wing flattened and straightened, 47.0; tail, 52.9; tarsus, 20.4. See Supplemental Material Table S2 for additional measurements of USNM 571315.

**Paratypes.** USNM 571316, female, ovary UND [undeveloped]; w. 45; wt. 7.9 g; Mallable, Somalia, 2°12’N, 45°37’E, J. S. Ash #355, prep. J. Mwaki, February 16, 1979. Adult. See Figure 5.

USNM 571317, male, testes 4.5 mm; w. 45; wt. 7.2 g; Mallable, Somalia, 2°12’N, 45°37’E, J. S. Ash #355, prep. J. Mwaki, February 16, 1979. Adult. See Figure 5.

USNM 571318, unsexed; wing 43; wt. 6.0 g; Mallable, Somalia, 2°12’N, 45°37’E, J. S. Ash #355, prep. J. Mwaki, February 2, 1979. Adult? See Figure 5.

All 4 specimens of the type series were compared directly with other USNM material of *Prinia gracilis* s.l. (*gracilis* group: *deltae* 13, *gracilis* 1, *palaestinae* 3, *carlo* 1)

| TABLE 2. Summary statistics for results of PCAs of morphological data for the *Prinia gracilis* complex. Variables important on each factor are in **bold** and those especially important in **bold italic.** |
| --- |
| Factor scores | PC1 | PC2 | PC1 | PC2 |
| **External measurements** | | | | |
| Culmen l from skull | 0.84 | -0.06 | 0.57 | 0.54 |
| Bill width from distal nares | 0.78 | -0.19 | 0.68 | 0.56 |
| Bill depth from distal nares | 0.72 | -0.16 | 0.64 | 0.14 |
| Wing l (unflattened) | 0.37 | 0.80 | 0.57 | -0.52 |
| Tail l | -0.35 | 0.80 | - | - |
| Maximum rectrix width | 0.66 | 0.24 | - | - |
| Tarsus l | 0.76 | 0.27 | 0.63 | -0.57 |
| Hind claw l | 0.58 | -0.10 | 0.70 | -0.10 |
| Eigenvalues | 3.42 | 1.48 | 2.29 | 1.22 |
| % total variance explained | 42.77 | 18.49 | 38.14 | 20.38 |
| **Plumage scores** | | | | |
| Mantle streak contrast | 0.41 | -0.80 | 0.78 | 0.12 |
| Mantle streak breadth | 0.59 | -0.57 | 0.83 | 0.36 |
| Uppertail barring strength | -0.66 | 0.02 | -0.55 | -0.26 |
| Subterminal tail band breadth | 0.83 | 0.35 | 0.59 | -0.67 |
| Subterminal tail band length | 0.56 | 0.41 | 0.67 | 0.30 |
| Subterminal tail band strength | 0.78 | 0.21 | 0.66 | -0.51 |
| Eigenvalues | 2.51 | 1.30 | 2.83 | 1.00 |
| % of total variance explained | 41.91 | 21.73 | 47.08 | 16.68 |
**TABLE 3.** Major subspecific groups of *Prinia gracilis* s.l. as constituted herein. Characters are those given in Shirihai and Svensson (S&S; Western Palearctic taxa only), and then as modified by results of the present morphological analyses (the more significant differences in **boldface**), with a summary of the characters best typifying each group. Major subspecific groups as recognized herein not treated separately by Ryan (2020). See Supplementary Material Table S4 for characters of each subspecies as recognized by previous authors and as modified herein.

| Character                          | gracilis group                                                                 | lepida group                                                                 |
|-----------------------------------|-------------------------------------------------------------------------------|----------------------------------------------------------------------------|
| Structure (S&S)                   | “Larger size”                                                                 | “Small with relatively longer tail (and bill and tarsus shorter)”          |
| Structure (this study)            | Longer, broader, and deeper **bill; shorter** broader **tail; longer** **tarsus** and hindclaw | **Shorter**, narrower, shallower **bill; longer** but narrower **tail; shorter tarsus** and hindclaw |
| Darkness (S&S)                    | “Paler uppperparts”                                                           | “Generally darker brown uppperparts”                                      |
| Darkness (this study)             | No difference                                                                 | No difference                                                              |
| Streaking (S&S)                   | “Finer streaks and obscure body-sides streaking”                             | “Broader, ill-defined streaks and rather obvious breast-side markings”    |
| Streaking (this study)            | Slight tendency for heavier streaking but weakest-streaked taxon in this group (ssp. nov.) | Slight tendency for weaker streaking but strongest-streaked taxon in this group (*akyildizi*) |
| Flanks, etc. color (S&S)          | Not mentioned                                                                 | Obvious breast-side markings only holds for *akyildizi*                   |
| Flanks, etc. color (this study)   | Slight tendency toward **grayness**                                           | Not mentioned                                                             |
| Uppertail barring (S&S)           | Not mentioned                                                                 | Slight tendency toward **warmness**                                       |
| Uppertail barring (this study)    | **Weak** except in ssp. nov.                                                 | Not mentioned                                                             |
| Subterminal tail band (S&S)       | “Strongly developed”                                                          | More **prominent**                                                        |
| Subterminal tail band (this study) | **Large and prominent**, duller in ssp. nov.                                 | “Poorly developed;” “narrower and fainter”                                |
| Summary of useful major subspecies-group characters | Larger size with relatively shorter, broader tail; upptail barring scarcely visible but undertail subterminal dark spots large and strong | Smaller size with longer thinner tail, more obvious upptail barring and smaller, and weaker undertail subterminal dark spots |
Description of holotype. Crown and upper mantle base color, between light gray and gray, 5YR 6/1–7/1; short, narrow streaks at mid-point (darkest point), dark reddish
brown, 5YR 3/2, paling at either end to dark reddish gray, 5YR 4/2; streaks especially short, numerous, and crisp on forehead, but especially pale and washed out on nape, and longer and dark for more of their length on upper mantle; base color of upper mantle grades to pinkish gray, 7.5YR 6/2 on lower mantle and rump, where streaks vague and paler, dark brown 7.5YR 4/2; base upper tail-coverts slightly paler; pinkish gray 7.5YR 7/2. Lores vaguely whitish, but no pale eyestripe evident on either side of face; crown color grades smoothly into whitish sides of face, including subocular and auricular regions; underparts from chin to undertail coverts pure unmarked white, but sides of neck, breast, and flanks have scattered small patches tinged very pale brown, 7.5YR 8/3, and sides of breast slightly grayer, white 7.5YR 8/1. Wing feathers mainly brown to dark brown, 7.5YR 4/2–5.2, with a few vaguely darker intrusions and broad pale pinkish gray 7.5YR 7/2 on outer web of innermost tertial, other tertials and secondaries edged less distinctly but darker,

**FIGURE 5.** Type series of *Prinia gracilis ashi*, ssp. nov., in dorsal (A), lateral (B), and ventral views (C), from left to right in each group, USNM 571315 (holotype), USNM 571316 (paratype), USNM 571317 (paratype), and USNM 571318 (paratype). (D) Comparison of the type of *P. gracilis* “anguste” (USNM 587495; synonym of *hufu*) with 2 specimens of *P. g. ashi* (USNM 571316 and USNM 171318) and a recently collected specimen of *P. g. carlo* from Djibouti (USNM 647827).
light brown 7.5YR 6/4, with distal tips white 7.5YR 8/1, to 2 mm wide on either side of shaft but interrupted by darker shaft streak, dark brown 7.5YR 4/2, which nearly reaches feather tip. Uppertail surface, older feathers base color brown, 7.5YR 5/2–6/2, growing central rectrix base color dark brown, 7.5YR 4/2; barring on older feathers dark brown, 7.5YR 4/2, on growing feather dark gray, 7.5YR 4/1; dark subterminal band dark brown, 7.5YR 3/2, broad but only vaguely demarcated on proximal end; terminal band white, 7.5YR 8/1, c. 1 mm long at widest point on growing central rectrix, purer white, and up to 2 mm long on other rectrices. Undertail surface light gray, 7.5YR 7/2, vaguely barred light brownish gray 7.5 6/2, the palest subterminal bands (outermost and innermost rectrices) 7.5YR 5/3, and the darkest 7.5YR 4/2. Soft parts described from dried skin: Culmen blackish-brown, paler near base; mandible mid-brown, gonydeal ridge, and proximal 2/3 pale flesh; tarsi and toes pale, claws distally dark horn.

**Distribution.** *Prinia gracilis ashi* is known only from the eastern coast of Somalia from about 2° to 3° 30′N, in the narrow belt of coastal saltbush *Atriplex* (Ash 1982), “primarily in shrubby halophytic vegetation” (Ash and Miskell 1998). Despite considerable searching, Ash (1982) found it only in 6 sites in that area and stated that, in the 200-km stretch of coastline northeast of Mogadishu where he had found it, there are few sites with suitable habitat. Between the known range of *P. g. carlo* and *P. g. ashi*, there are extensive areas of coastline with inhospitable sea-cliffs and sand dunes (Ash 1982). Nevertheless, Ash (1982) and Ash and Miskell (1998) considered it likely to occur wherever there is suitable coastal vegetation north of about Mogadishu.

**Etymology.** We are pleased to name this new subspecies after the late John Sidney Ash (1925–2014), the collector of the type series, who made many important ornithological discoveries during his years of field work in Somalia,
Ethiopia, and elsewhere (Ash 1982, 1983; Ash and Miskell 1983, 1998).

Variation. Two paratypes (USNM 571316 and 571317; Figure 5) are slightly paler and warmer-toned above (base color light brownish gray, 10YR 6/2), with slightly paler brown streaking above than the holotype, while the third paratype (USNM 571318) is palest of all (base color light gray 10YR 7/2). The paratypes show that the rufescent edgings to outer webs of tertials and secondaries wear to whitish. Two paratypes (USNM 571316 and 571317) have large, obvious white loral patches that extend to form partial white eye rings that are incomplete caudally. Compared with the holotype, the breast sides are slightly whiter on USNM 571317 and slightly grayer on USNM 571318. The female and unsexed paratypes (USNM 57136 and 57138, respectively) have the mandibles nearly entirely pale.

Remarks. Ash (1982) remarked upon the major range discontinuity of the south coastal Somali population but stated that his specimens from there did not differ from 2 fresh May specimens from Zeila from northwestern Somalia. Ash and Miskell (1983, 1998), Ash and Atkins (2009), and Redman et al. (2009) thus listed this population as P. g. carlo, although according to Cramp (1992) the subspecies is unknown. At the time of their accession to the National Museum of Natural History, there were probably no specimens of carlo in the NMNH collection for comparison and the lone specimen there now (USNM 647827) is considerably darker overall (Figure 5D). We have studied a series of 7 Zeila (Zaila) specimens at NMUK, the only ones from this locality of which we are aware (Supplemental Material Table S2; vertnet.org), which includes one May 21, 1895, specimen (NMUK 1896.2.18.3) and one April 9 specimen (NMUK 1902/1/20/121). It is, therefore, likely that Ash compared his February Mallable specimens with the May and possibly April bird at the NMUK, but he did not indicate which characters he examined, and it is not clear why he would not have also compared them with the other specimens, which are from November and December. Several plumage scores for the Mallable birds differ, mostly with minimal overlap, from the series of 7 from Zeila, which are also generally slightly smaller though small sample sizes preclude statistical comparisons.

Although P. g. ashi resembles the palest individuals of P. g. lepida in color and strength of streaking, and most of the taxa in this group in uppertain barrining, we consider it unlikely to belong in this species group because of its particularly large bill, relatively short broad tail, and large (though not strongly contrasting) subterminal tail spots, as well as on biogeography.

Vocal Analyses

Overall patterns. Two main song groups are discernible based on the appearance of sonograms and auditory impression: (1) a southwestern group from Israel, Egypt, west Saudi Arabia, Djibouti, Yemen, and south Oman (corresponding to the gracilis group with the exclusion of part of the northeastern Arabian Peninsula) and (2) a northeastern group from Turkey, Iraq, Kuwait, Iran, NE Saudi Arabia, UAE, north Oman, Afghanistan, Pakistan, India, Nepal, and Bangladesh (conforming to the lepida group, except that it also includes birds from part of the northeastern Arabian Peninsula; Figure 1). The main difference between these groups is that the southwestern group has considerably longer intervals between the phrases, thereby producing a song with short units delivered at a slower tempo, whereas the northeastern group has very short silent intervals between the song units (phrases), rendering the song a continuous grating reel (Figures 7 and 8, Table 4).

The songs of birds from Israel and northern Egypt (Figure 7A–H, Supplemental Material Table S5) consist of a monotonous repetition of short (0.22–0.36 s; mean 0.28 s; ± 0.04 SD) phrases that are separated by well-marked silent intervals (0.04–0.16 s; mean 0.09 s; ± 0.02 SD); in our sample, a mean of 2.00–17.50 (mean 7.47; ± 4.70 SD) phrases was given within a burst of song. The phrases are built up of a buzzing trill followed by a “warble” of a few notes at alternating pitch; one of these notes is usually an upward-pointing “spike.” Occasionally, there are 2 trills at different frequency, separated by 1 or 2 notes (Figure 7A and E). Songs of birds from the southern part of the Arabian Peninsula (west Saudi Arabia, Yemen, and south Oman) are basically similar to Israel and Egypt, although our sample is small (n = 4; Figure 7I–K, Supplemental Material Table S5). Our small song sample from Djibouti (n = 2 individuals, 3 phrase types; Figure 7L, Supplemental Material Table S5) is reminiscent of those from Israel, Egypt, Saudi Arabia, Yemen, and south Oman but more complex.

The songs of birds from the Indian Subcontinent (Pakistan, India, and Bangladesh) (Figure 7U–Y, Supplemental Material Table S5) are made up of a short buzzing and clicking phrase that is monotonously and rapidly repeated, often for lengthy periods without interruption (in our sample up to 7.2 s). The phrases are short (0.18–0.27 s; mean 0.22 s; ± 0.02 SD) and are separated by extremely brief silent intervals (0.01–0.04 s; mean 0.02 s; ± 0.01 SD). They begin with a fast series of very thin elements that form a buzzing trill and end with a “warble” consisting of a variable number of notes at alternating pitch; the trill and “warble” parts are of approximately equal duration. A mean of 2.40–22.50 (mean 9.49; ± 5.11 SD) phrases was recorded in a single burst of song, but one and the same bird was only noted to sing with a single phrase type except in a few cases, where a male was noted to switch from one to a second phrase type after some time (never in the same burst of song).
Birds from Iran and the northeastern part of the Arabian Peninsula (UAE and north Oman) (Figure 7P–T, Supplemental Material Table S5) have basically similar songs to those from Pakistan, India, and Bangladesh, although the buzzing trill tends to be proportionately longer and more distinct and the “warble” proportionately shorter. The songs of Turkish birds (Figure 7M–O, Supplemental Material Table S5) have a proportionately even longer buzzing trill and shorter and simpler warble.

**Statistical analyses of song.** Univariate comparisons between the 2 main groups identified above are significantly different (MANOVA: Pillai’s Trace = 0.87, $F_{8,75} = 61.82$, $P < 0.001$; Table 4). Specifically, the northeastern (lepidina) group has on average shorter duration of the phrases and,
especially, shorter intervals between the phrases compared with the southwestern (gracilis) group (only 4 recordings overlapping marginally between the 2 groups in interval between phrases), and on average a larger number of phrases per song bout. The Peak Frequency averages lower and the Aggregate Entropy higher in the northeastern group than in the southwestern group, although audibly it matches the southwestern group rather than the northeastern group.

The DFA correctly classified 100% of the recordings to either of the 2 major subspecific groups (Table 6). However, the subgroups within these groups based on broad geographical distributions which may include more than one described subspecies (Figure 1) [A] Israel and north Egypt (deltae); [B] south Arabian Peninsula (yemenensis) and Djibouti (carlo); [C] Turkey (akyildizi); [D] Iran (irakensis); [E] eastern Arabian Peninsula (carpenteri); and [F] Indian Subcontinent (lepida, stevensi) were poorly differentiated. Subgroups A, B, and C had the highest classification correctness, 71.4%, 65.5%, and 66.7%, respectively (Table 7). The discrepancy between the classifications based on 2 and 6 groups is likely due to the small samples in the 6-group comparison. According to Williams and Titus (1988), sample sizes in each group should be at least 3 times larger than the number of variables used in the DFA. As we used 9 variables, at least 27 recordings would be required for each group, which was the case for only one group.

**DNA Analyses**

The tree based on the mitochondrial cyt b and ND2 genes (Figure 9) recovered 2 clades with posterior probability 1.00, one comprising the samples from Israel (gracilis group), and the other one comprising the samples from India, Iran, Iraq, and Kuwait (belonging to the lepida group). The split between these 2 clades was estimated at 2.2 MYA (95% highest posterior distribution 1.6–2.9 myr). In contrast, the variation within these 2 groups was very minor.

### DISCUSSION

#### Taxonomy

Our analyses integrating morphometrics, plumage, song, mtDNA, and geographical distributions congruently

| Variables                  | Southwestern group A, B (mean ± SD) | Northeastern group C–F (mean ± SD) | t<sub>82</sub> | P     |
|----------------------------|------------------------------------|-----------------------------------|---------------|-------|
| Duration (s)               | 0.28 ± 0.03                        | 0.22 ± 0.03                       | -9.12         | <0.001|
| Minimum frequency (kHz)    | 3.06 ± 0.42                        | 3.19 ± 0.43                       | 1.35          | 0.179 |
| Maximum frequency (kHz)    | 7.41 ± 0.77                        | 7.59 ± 0.58                       | 1.22          | 0.226 |
| Bandwidth (kHz)            | 4.35 ± 1.00                        | 4.41 ± 0.81                       | 0.27          | 0.791 |
| **Peak frequency** (kHz)   | **5.17 ± 0.55**                     | **4.79 ± 0.59**                   | **-3.05**     | **0.003**|
| Center frequency (kHz)     | 5.14 ± 0.41                        | 5.05 ± 0.44                       | -0.99         | 0.325 |
| Aggregate Entropy          | 4.35 ± 0.36                        | 4.64 ± 0.42                       | 3.23          | 0.002 |
| Interval (s)               | 0.09 ± 0.02                        | 0.02 ± 0.01                       | -17.76        | <0.001|
| Number of Phrases per song bout | 7.22 ± 4.44                    | 13.06 ± 7.29                      | 4.21          | <0.001|

**FIGURE 8.** Songs from 2 groups can be separated by PC2 and PC3. Color-coded by taxon as for Figure 1, with members of the gracilis group coded by cool-colored circles and members of the lepida group by warm-colored squares.

**FIGURE 9.** Songs from 2 groups can be separated by PC2 and PC3. Color-coded by taxon as for Figure 1, with members of the gracilis group coded by cool-colored circles and members of the lepida group by warm-colored squares.
We identified 2 major subspecific groups: (1) a southwestern group comprising birds from Egypt, Israel, west and probably north-central Arabian Peninsula, Yemen, south Oman, Djibouti, and Somalia (P. g. deltae, P. g. natronensis, P. g. gracilis, P. g. palaestinae, P. g. carlo, P. g. ashi (ssp. nov.), P. g. yemenensis, and tentatively P. g. hufufae) and (2) a northeastern group comprising birds from Turkey, Kuwait, Iraq, UAE and northern Oman (northeastern Arabian Peninsula), Iran, Afghanistan, Pakistan, India, Nepal, and Bangladesh (P. g. akyildizi, P. g. irakensis, P. g. carpenteri, P. g. lepida, and P. g. stevensi). As has already been noted above, Shirihai and Svensson (2018) referred to the first group as the gracilis group and the second as the lepida group, although they synonymized carpenteri (of the lepida group but more similar in size to the gracilis group) with hufufae (which they placed in the gracilis group; see below). This also accords with the subspecific distribution of tail characters summarized, though not accorded major subspecific group significance, in Cramp (1992).

We suggest that under the General Lineage Concept (de Queiroz 1998, 2007) these major subspecific groups are best treated as 2 separate species, P. gracilis and P. lepida, respectively (by priority, see Supplemental Material Table S1), as there is strong evidence that they represent independent lineages. More comprehensive sampling, especially from Syria and the Arabian Peninsula, including genetic evidence from these areas, is required to confirm the membership of hufufae within the gracilis group and carpenteri within the lepida group and also to evaluate levels of gene flow to allow the assessment of taxonomic rank under the Biological Species Concept (Mayr 1963). If split, we suggest that P. gracilis s.s. should retain the English name Graceful Prinia, because of its scientific name as well as its broad familiarity in the Western Palearctic (although it has been noted to be a rather ungraceful species; Cramp 1992). As there is no widely familiar or apt alternative English name for P. lepida, we suggest adapting Blyth’s (1844) apparent meaning of the scientific epithet, as evidenced by his description of it as a “delicate little species,” and naming it Delicate Prinia, which emphasizes the structural differences between this prinia and Graceful Prinia, as well as from most other prinia species.

Our recommendations regarding recognition of subspecies are summarized in Supplemental Material Table S1. We agree with Shirihai and Svensson (2018) regarding the synonymy of P. g. carlo in P. g. gracilis. We further

### Table 5

Summary statistics for results of PCA of song measurements. The most important variables for discrimination between the 2 main groups are in bold.

| Variables                  | PC1  | PC2  | PC3  |
|----------------------------|------|------|------|
| Duration (s)               | 0.08 | -0.03| **0.76** |
| Minimum frequency (Hz)     | -0.75| 0.39 | -0.27|
| Maximum frequency (Hz)     | 0.84 | 0.37 | -0.12|
| Bandwidth (Hz)             | 0.99 | 0.09 | 0.04 |
| Peak frequency (Hz)        | -0.06| 0.83 | 0.35 |
| Center frequency (Hz)      | 0.04 | 0.96 | 0.09 |
| Aggregate Entropy          | 0.26 | 0.54 | -0.33|
| Interval (s)               | -0.16| 0.07 | **0.90**|
| Number of Phrases          | -0.15| -0.12| **-0.65**|
| Eigenvalue                 | 2.36 | 2.21 | 2.14 |
| Variance explained (%)     | 26.20| 24.52| 23.83|

### Table 6

Predicted group membership of 2 main groups (subgroups indicated by capital letters) based on song variables in forward stepwise DFA; 100% of the recordings were correctly assigned.

| Group membership | Southwestern (A, B) | Northeastern (C–F) |
|------------------|---------------------|---------------------|
| Northeastern     | 0                   | 49                  |
| Southwestern     | 35                  | 0                   |

### Table 7

Predicted group membership of 6 geographical groups based on song variables in forward stepwise DFA; 46.4% of the recordings were correctly assigned.

| Group membership                        | Israel, Northern Egypt (A) | South Arabian Peninsula and Djibouti (B) | Turkey (C) | Iran (D) | Northeast Arabian Peninsula (E) | Indian subcontinent (F) |
|-----------------------------------------|-----------------------------|------------------------------------------|------------|----------|---------------------------------|------------------------|
| Israel, Northern Egypt (A)              | 19                          | 8                                        | 2          | 0        | 0                               | 0                      |
| Southern Arabian Peninsula and Djibouti (B) | 2                          | 4                                        | 0          | 0        | 0                               | 0                      |
| Turkey (C)                              | 0                           | 0                                        | 5          | 1        | 0                               | 1                      |
| Iran (D)                                | 0                           | 0                                        | 2          | 8        | 2                               | 1                      |
| Northeast Arabian Peninsula (E)         | 0                           | 0                                        | 0          | 2        | 1                               | 4                      |
| Indian subcontinent (F)                 | 0                           | 0                                        | 6          | 5        | 9                               | 2                      |
agree with these authors that \textit{P. l. irakensis} should be synonymized with \textit{lepida}. However, contra Shirihai and Svensson (2018), we consider that \textit{carpenteri} belongs to the \textit{P. lepida} group and should not be synonymized with \textit{P. g. hufufae}, which we agree with these authors is probably a member of the \textit{gracilis} group. Shirihai and Svensson (2018) stated that \textit{P. g. carpenteri} has “been separated on account of being darker and bolder streaked above [than \textit{hufufae}], but if anything the opposite is true” (Shirihai and Svensson 2018). However, \textit{carpenteri} was originally described as being more distinctly streaked than \textit{hufufae} (not as being darker; Meyer de Schauensee and Ripley 1953), and, according to our scoring, \textit{hufufae} averages significantly more contrasting and broadly streaked, while the 2 taxa are not significantly different in upperparts darkness (Supplemental Material Table S4). Instead, \textit{carpenteri} was described as being darker than \textit{irakensis} and \textit{lepida} (Meyer de Schauensee and Ripley 1953), among other stated differences, including the \textit{lepida}-type tail pattern of \textit{carpenteri}. In any case, the variability that led Shirihai and Svensson (2018) to lump \textit{carpenteri} into \textit{hufufae}, coupled with the relatively short distances and patchwork taxon distribution as reflected by the specimen record (Figure 1) coupled with an apparent lack of major modern range discontinuity (https://ebird.org/species/grapri1), suggests that there may be a zone of secondary contact between the \textit{gracilis} and \textit{lepida} groups somewhere along the northeastern Arabian Peninsula coast. However, the type series of \textit{P. g. carpenteri} from farther south in the United Arab Emirates and north Oman area of the Arabian Peninsula shows relative uniformity (Figure 5B) in plumage but some structural intermediacy between the \textit{gracilis} and \textit{lepida} groups, mainly in their relatively longer bill and wing than other members of the \textit{lepida} group. Further study, especially of DNA and vocalizations, is needed to corroborate our tentative morphology-based assignment of \textit{hufufae} to the \textit{gracilis} group and our assignment of \textit{carpenteri} to the \textit{lepida} group.

While it is widely acknowledged that oscine passerines are song learners, the degree to which geographical differentiation in song in oscines is due to genetic or cultural evolution is contentious and unknown. Whether differences in oscine song characteristics represent dialects or can be used in integrative taxonomy is still a point of disagreement, and caution is essential, particularly in those species that have wide repertoires and

![Figure 9](https://academic.oup.com/auk/article/138/2/ukab014/6255519)

**Figure 9.** Tree based on mitochondrial cytb and ND2. Blue bars at nodes represent 95% highest posterior density; asterisks indicate posterior probability of 1.00.
especially where mimicry is involved. For these reasons, it is important to analyze multiple individuals from as large a part of the distribution as possible. However, it seems clear that most of the oscines have at least partially innate songs, the details of which can be modified through learning. Songs of kinglets (Reguliidae), treecreepers (Certhiidae), and leaf warblers (Phylloscopidae) have been shown to carry phylogenetic signal (Tietze et al. 2015, Päckert 2018). In other oscine taxa, we have found song variation to be broadly congruent with species limits as determined on the basis of morphology and DNA (e.g., Alström et al. 2015, 2016, 2018, 2020, 2021). In the Cisticolidae, to which prinias belong, each species tends to have distinctive song that varies little (Ryan et al. 2006). Indeed, the bewildering variety of African cisticola species are often most reliably identified by song, so much so that the English names of several reflect their distinctive songs (e.g., Ryan et al. 2006). In the sole prinia species complex for which we are aware of an integrative taxonomic analysis, the Prinia cinigera and P. polychroa species group (Alström et al. 2020), we found similar levels of vocal differentiation and congruence with other datasets to that of P. gracilis s.l. Thus, while without captive-rearing experiments we cannot prove that the song variation in P. gracilis s.l. is genetically determined, we can show that, as with these and many other oscine taxa, it is strongly correlated with lineage divergence and thus is useful in determining species limits.

An evaluation of the variation in egg color within the major groups would be of interest, as differences have been noted between taxa representing the 2 putative species. According to Cramp (1992), clutches from North Africa and Israel (i.e. part of the gracilis group) have a whitish to very pale pink background, while those from Iraq (i.e. part of the lepida group) have a green to pale blue-green background, but no sample size was presented. Ali and Ripley (1973) cited Baker for information that lepida has pale greenish eggs, but localities were not presented. Whether these putative differences characterize the eggs of the 2 major subspecific groups is unknown. Further, a possible difference in the presence of bill-snapping behavior in the northeastern group vs. absence in the southwestern group mentioned in Ali and Ripley (1973) requires investigation.

Usefulness of Morphological Data
The morphological results corroborate and thus strengthen the pattern shown by mtDNA and vocalization analyses that suggest 2 species groups within P. gracilis s.l. The discrepancies noted above with respect to the synonymy of carpenteri with hufufae (Shirihai and Svensson 2018), coupled with those tabulated in Table 3 and Supplemental Material Table S1 between previous morphological assessments of subspecific and species group characteristics and our assessment, show clearly that knowledge of the morphological variation of taxa of the P. gracilis s.l. complex has remained inadequate and unsettled up to the present. This has a significant impact on the species-group attribution of the 2 subspecies hufufae and carpenteri when P. gracilis is considered to comprise 2 species. It thus not only affects data on distribution and identification but also potentially compromises future studies on species limits, ecology, and biogeography, thus showing that new morphological studies such as ours can indeed add value in enabling such clarification or at least highlighting areas where more work is needed. Further contributions of these morphological analyses to this integrative analysis of species limits include the clarification of identification criteria that may not only aid in further establishing distributional limits but may also help in future efforts to understand the nature of any contact zones.

The results of the study of subspecific variation show apparently parallel evolution in darkness and degree of streaking between taxa of both species-groups. Most of the gracilis taxa are darker and more heavily streaked than most of the lepida taxa, although the palest, least streaked P. gracilis s.l. taxon (the new Somali subspecies P. g. ashi) is presumably a member of the gracilis group and the darkest, most heavily streaked taxon (Turkish akylidizi) is clearly a member of the lepida group based on song and structure and thus both appear to be outliers on plumage within their taxon group. These traits might be found upon further study to be related to substrate-matching and subject to strong selective pressure, melanin deposition being affected by degree of gene expression (e.g., melanin variation in juncos Junco; Abolins-Abols et al. 2018) rather than presence/absence of mutations (e.g., dark morph of Bananaquit, Coereba flaveola; Theron et al. 2001). In addition, previous analyses of morphological variation within the complex were presumably based on study of much smaller series than are available now and summarized measurements taken by different workers (e.g., Cramp 1992), and variation can now much more readily be quantified morphometrically. Furthermore, without the morphological analyses covering all known taxa in the complex, we would not have been able to recognize and establish that there is a previously undescribed subspecies in southeastern Somalia. In summary, with respect to whether new morphological analyses are valuable to determination of species limits and thus worth the additional effort, we consider that our study of the P. gracilis complex adds to the evidence that indeed they are, for several reasons.

The P. gracilis complex provides a more straightforward case study than do many others, as only 2 main groups have been identified, they are nonmigratory, they are not seasonally or sexually highly variable, there are typical (though
subtle and variable) morphological characteristics that define each group, and known nomenclatural problems are lacking, among other factors. Other complexes may involve more complicating factors, such as the case of presumptive sympathy in Yunnan, China, between Prinia crinigera and P. polychroa, which led to their long-standing treatment as 2 species (Alström et al. 2020). Alström et al. (2020) found, based largely on morphology (subsequently verified genetically), that the sympathy actually involves what were until now considered 2 forms of P. crinigera, which were shown to be non-sister taxa that differ vocally, and that P. polychroa was uninolved in the sympathy and does not even occur in China (Alström et al. 2020). In another example, field observations of major differences in song between alpine- and montane forest-breeding Plain-backed Thrushes (Zoothera mollissima) in the same area of the eastern Himalayas led to the finding that these were unrecognized sympatric reciprocally monophyletic units, and morphological study showed numerous structural and plumage differences that had remained unrecognized even though series of both taxa had resided in the same museum trays for over 150 years (Alström et al. 2016).

**Biogeography and Conservation**

The P. gracilis s.l. complex provides an anomalous biogeographic case, one not similar to that of any other bird species. Most other widespread birds of these areas also occur much farther west in North Africa, farther north into Central Asia, or only east to the northwestern Indian Subcontinent. The most similar distribution among birds is that of the Clamorous Reed Warbler Acrocephalus stentoreus, not surprisingly another wetland edge species. As currently recognized, the Clamorous Reed Warbler not only occurs from Egypt through the wetlands of the Persian Gulf coast, northern India, but also breeds in much of Central Asia, south India and Sri Lanka, and southern China. However, we note that A. stentoreus is also comprised of 2 species groups (Rasmussen and Anderton 2005, del Hoyo and Collar 2016), one in Egypt and the Levant, and the other through the rest of its range in 3 oddly disjunct subspecies that might be better treated as separate species.

However, even if split into 2 species, P. gracilis s.s. and P. lepida, as we suggest here, few avian species share similar ranges with either of the component species. Not surprisingly, given its essential restriction to riverbank sandbars and coastal dunes, the bird species with the most similar distribution to lepida is the Sand Lark (Alaudala raytal), with the riverine grassland-inhabiting White-tailed Stonechat (Saxicola leucurus) also being somewhat similar, but the western range limits of both are shifted somewhat eastward, from Iran and Pakistan, respectively, and both inhabit central Myanmar, unlike P. lepida. The only avian species as currently recognized that has a distribution very similar to that of P. gracilis s.s is Nile Valley Sunbird (Hedydipna metallica) (when split from Pygmy Sunbird [H. platura]).

The mosaic distribution of subspecies of P. gracilis and P. lepida, if recognized as specifically distinct, with hufufae putatively of the gracilis group interspersed between irakensis and carpenteri of the lepida group along the eastern side of the Arabian Peninsula, is not surprising given what is known about the biogeography of other taxa, particularly reptiles and amphibians (Portik and Papenfuss 2015 and references therein). Arabian toad taxa show a complex evolutionary history, with some derived from African ancestors, while others have Eurasian or South Asian origins (Portik and Papenfuss 2015). The presence of P. gracilis hufufae along the northeastern side of the Arabian Peninsula can be readily explained by its apparently fairly good dispersal capabilities, as it occurs mostly around often widely spaced waterbodies in desert regions, and there are several isolated populations even in the central Arabian Peninsula (not mapped in Figure 1). The presence of P. lepida carpenteri of presumably South Asian origin, just to the south of the range of hufufae, on the other hand, is easily explained given the short distance across the Persian Gulf from Iran at the Musandam Peninsula, especially during periods of glacial maxima, when the gulf was much reduced (Lambeck 1996).

Both groups, which we suggest should be treated as 2 polytypic species, are generally common in appropriate habitat and have broader habitat tolerances than many other wetland edge species and are indeed able to colonize new areas (Cramp 1992, Zduniak and Yosef 2004). Apart from the potential risk of extirpation of the very localized subspecies P. g. natromenis of the Wadi El Natrun area, which is under considerable anthropogenic pressure from many causes (Baha el Din 2011), neither of the putative daughter species P. gracilis s.s or P. lepida are likely to face severe threats in the near future.

**SUPPLEMENTAL MATERIAL**

Supplementary material is available at The Auk: Ornithological Advances online.

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**Authors contributions:** P.A. conceived the study, collected field data, analyzed molecular data and some sound data, and co-wrote the text (mainly Introduction, vocalizations, DNA sections, and Discussion); P.C.R. collected and analyzed morphological data, uploaded recordings to AVoCet, and co-wrote the text (mainly Abstract, Introduction, morphology including the description of a new subspecies, and Discussion); C.X., L.Z., C.L., and J.M. analyzed sound data, and co-wrote text on vocalizations; A.S. contributed DNA samples; and U.O. took part in the planning of the study and carried out the lab work. All authors read and agreed on the final text.

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