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SPECIES LIMITS OF THE LEAST PYGMY-OWL (*GLAUCIDIUM MINUTISSIMUM*) COMPLEX

STEVE N. G. HOWELL[1] AND MARK B. ROBBINS[2]

ABSTRACT.—The Least Pygmy-Owl (*Glaucidium minutissimum*) complex comprises 10 described taxa that inhabit tropical and subtropical forests. Consistent song differences among taxa in this complex, supported by morphometric, plumage, and habitat data, indicate that, in addition to the recently described *G. hardyi* and *G. parkeri*, four species can be recognized in the Least Pygmy-Owl complex: *G. palmarum* of western Mexico (includes the described subspecies *palmarum, oberholseri,* and *griscomi*); *G. sanchezi* of northeastern Mexico; *G. griseiceps* of southeastern Mexico, Central America, and the Pacific slope of northern South America (includes the described subspecies *griseiceps, rarum,* and *occultum*); and *G. minutissimum* of southeastern Brazil and adjacent Paraguay. *Received 8 Nov. 1993, accepted 9 May 1994.*

The genus *Glaucidium* comprises a number of species of small owls widespread in the Americas, Eurasia, and Africa. Four groups of mainland New World *Glaucidium* are generally recognized: the *G. gnoma* complex (western Canada to Honduras), the *G. brasilianum* complex (southwestern United States to southern South America), the *G. minutissimum* complex (Mexico to South America), and the *G. jardinii* complex (Costa Rica to South America) (Peters 1940, Meyer de Schauensee 1970, A.O.U. 1983, Sibley and Monroe 1990). Although the *G. brasilianum* complex stands out as relatively distinct by virtue of its streaked crown and proportionately longer tail with numerous pale bars, differences between the spotted-crowned *gnoma* and *jardinii* groups and the *minutissimum* group have been confused (e.g., Griscom 1931, König 1991). The *G. minutissimum* (Least Pygmy-Owl) complex comprises the spotted-crowned pygmy-owls of tropical and subtropical forests, distinguished from the *gnoma* and *jardinii* groups of temperate forest habitats by their smaller size and unmarked backs.

TAXONOMIC HISTORY

Until recently, *G. minutissimum* was considered a polytypic species (with eight described subspecies) ranging from both slopes of Mexico to northern Bolivia, Paraguay, and southeastern Brazil (Peters 1940, Meyer de Schauensee 1970, A.O.U. 1983, Parker and Remsen 1987). This traditional taxonomic classification relied heavily on plumage and morphology which, particularly in nightbirds, can be remarkably uniform within genera. The increasing realization that vocalizations are important in unmasking morphologically cryptic species

[1] Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, California 94970.
[2] Dept. of Ornithology, Academy of Natural Sciences, 1900 Benjamin Franklin Parkway, Philadelphia, Pennsylvania 19103. Present address: Division of Ornithology, Museum of Natural History, Univ. of Kansas, Lawrence, Kansas 66045.

was largely responsible for the description of two distinct new species in the *G. minutissimum* complex: *G. hardyi* (Amazonian Pygmy-Owl) (Vielliard 1989) and *G. parkeri* (Subtropical Pygmy-Owl) (Robbins and Howell 1995). König (1991) believed that *G. hardyi* was not part of the *G. minutissimum* complex but is more closely related to the *G. jardinii* complex; he based this on the vocal characters of these taxa. We believe, however, based on plumage pattern, size, biogeography, habitat preferences, and an understanding of the vocal range of all forms involved, that *G. hardyi* is allied to the *G. minutissimum* complex.

Buchanan (1964) clarified much of the confusion that had surrounded the identification and taxonomy of Least Pygmy-Owls in Mexico, in particular pointing out that they do not possess dichromatic plumage commonly associated with other *Glaucidium.* He recognized that Mexican Least Pygmy-Owls were divisible into two natural groups which coincided with biogeographic areas: dark, richly colored birds, ranging from eastern and southern Mexico to South America, and light, dull colored birds in western Mexico. Buchanan (1964) also noted the "contrasting ecological circumstances" of western versus eastern forms and that the two groups might represent separate species. In conclusion, however, he opted for a conservative approach and retained all forms as members of a single species. The A.O.U. (1983) commented that "populations on the Pacific slope of Mexico may constitute a distinct species" and that "Further study of this complex is required to determine relationships."

We have gathered vocal, morphological, and ecological data that dictate a revision of the *G. minutissimum* complex. In addition to the recently described *G. hardyi* and *G. parkeri,* we recognize four species in the Least Pygmy-Owl complex: *G. palmarum* of western Mexico (includes the described subspecies *palmarum, oberholseri,* and *griscomi*); *G. sanchezi* of northeastern Mexico; *G. griseiceps* of southeastern Mexico, Central America, and the Pacific slope of northern South America (includes the described subspecies *griseiceps, rarum,* and *occultum*); and *G. minutissimum* of southeastern Brazil and adjacent Paraguay.

METHODS

We listened to and analyzed tape recordings of a total of 555 songs of 37 individuals from throughout the range of the *minutissimum* complex, with the exception of *G. hardyi,* whose distinctive song was discussed by Vielliard (1989). These included songs of all described taxa: 40 songs of *G. palmarum,* 130 of *G. sanchezi,* 155 of *G. griseiceps,* 160 of *G. parkeri,* and 70 of *G. minutissimum.* Voice showed little or no significant difference among the described races of *palmarum* and *griseiceps,* and we pooled samples of the respective subspecies for between-species analyses. Recordings were analyzed by Howell using a Kay Elemetrics DSP Sonograph, Model 5500. Dominant frequency was determined from a power spectrum (amplitude [dB] plotted against frequency [Hz]). Analysis of variance (ANOVA) was used to test for significance levels in song characters.

For morphological analysis we examined 151 specimens (148 assembled at ANSP) of all ten described taxa of the *G. minutissimum* complex, representing virtually all specimens (including the syntypes of *G. minutissimum* and *G. sanchezi* and the holotype of *G. parkeri*) in North American collections (see Robbins and Howell [1995] for a list of specimens examined). In addition, morphometric data from several specimens in foreign institutions (see acknowledgments) and the literature were used in our analysis. Because plumage and morphology showed at best minor differences among the described subspecies of *G. palmarum* and *G. griseiceps,* we pooled samples of the respective subspecies for measurements, which were made by Robbins to the nearest 0.1 mm using dial calipers.

RESULTS

Voice.—The primary songs of the five members of the Least Pygmy-Owl complex discussed below consist of a variable number of hollow,

single-note whistles, or hoots, which are given in bouts that may last for long periods. In addition, *G. palmarum, G. sanchezi, G. griseiceps,* and *G. minutissimum* give a soft, quavering trill that may be repeated up to a few times in succession and which often precedes bouts of hooting; we have not heard a comparable vocalization from *G. parkeri.* The primary song of the sixth species, *G. hardyi,* is a rapid series of short notes run into a quavering roll or trill (Hardy et al. 1990; Frontispiece) and was discussed by Vielliard (1989). This trill is relatively loud and ringing and is not analogous to the soft trills given by other members of the complex; the latter tend to be given by birds in an agitated state, such as when counter-singing or in response to voice playback. The four song characters we examined were frequency (or pitch), duration of notes in a song, duration of intervals between notes in a song (inter-note intervals), and inter-song intervals (Table 1). Frequency, note duration, and inter-note interval were fairly consistent for an individual bird. Inter-song interval was more variable, although some significant inter-specific differences in singing rate were apparent.

The mean dominant frequency varied between 1278 Hz (*parkeri*) and 1483 Hz (*sanchezi*), and within-taxon variation in mean ranged from 92 Hz (*minutissimum*) to 304 Hz (*griseiceps*) (Table 1). The variation in mean for *griseiceps* may seem large, but this species has a large geographic range. Further, Galeotti et al. (1993) showed a variation of 201 Hz (1343–1544 Hz) in the mean fundamental frequency (comparable to the dominant frequency) in ten males in a localized population of the Eurasian Pygmy-Owl (*G. passerinum*). Thus, while song frequency varies among taxa in the *G. minutissimum* complex (e.g., *sanchezi* is significantly higher pitched than all other taxa; $P < 0.05$), frequency may be more important overall for individual than for specific recognition.

The most obvious differences to the human ear among the songs of species in the *G. minutissimum* complex are the different tempos and the varying number and duration of notes which give each species its distinctive song. That both the mean frequency and note duration (0.22–0.29 s; Galeotti et al. 1993) of *G. passerinum* overlap with members of the *G. minutissimum* complex (see above and Table 1) suggests that the number and structure of notes, in combination with the overall tempo, may be the most important taxonomic aspects of *Glaucidium* vocalizations. Further support for the taxonomic value of tempo and number of notes may be found by comparing Example 1 of *G. brasilianum* (Hardy et al. 1990) with *G. palmarum.* The former has short, arched notes of 0.09–0.10 s separated by 0.30 s pauses, and a dominant frequency of 1460 Hz. Other than a steady pacing between the first three notes and more prolonged hooting overall, this bird's song appears spectrographically indistinguish-

TABLE 1

MEAN (±SD) AND RANGE FOR SELECTED SONG CHARACTERS OF THE (*GLAUCIDIUM MINUTISSIMUM*) Complex

	Mean dominant frequency (Hz)	Length of notes (s)	First inter-note interval (s)	Second inter-note interval (s)	Mean inter-song interval (s)
G. palmarum	1416 (±61.1)	0.10 (±0.02)	0.34 (±0.03)	0.31 (±0.03)	4.8 (±1.61)
	(1300–1465[a])	(0.09–0.14[b])	(0.29–0.39[b])	(0.26–0.34[b])	(2.6–5.9[a])
	N = 6/38[c]	N = 6/78[c]	N = 6/13[c]	N = 6/13[c]	N = 6/33[c]
G. sanchezi	1483 (±41.8)	0.26 (±0.03)	0.43 (±0.04)	0.43 (±0.04)	5.2 (±0.73)
	(1390–1540)	(0.21–0.30)	(0.32–0.52)	(0.38–0.47)	(4.3–6.5)
	N = 9/56	N = 9/106	N = 9/45	N = 2/6	N = 9/100
G. griseiceps	1385 (±94.1)	0.14 (±0.04)	0.23 (±0.04)	0.22 (±0.03)	7.3 (±3.70)
	(1232–1536)	(0.09–0.23)	(0.18–0.33)	(0.17–0.29)	(3.2–13.1)
	N = 14/92	N = 13/148	N = 12/28	N = 12/28	N = 12/75
G. parkeri	1278 (±152.2)	0.15 (±0.03)	0.18 (±0.04)	0.26 (±0.06)	2.3 (±0.96)
	(1160–1450)	(0.10–0.22)	(0.10–0.25)	(0.15–0.37)	(1.2–3.0)
	N = 3/52	N = 3/123	N = 3/37	N = 3/37	N = 3/90
G. minutissimum	1358 (±35.7)	0.26 (±0.03)	0.28 (±0.04)	0.26 (±0.01)	7.0 (±2.15)
	(1320–1412)	(0.21–0.32)	(0.22–0.34)	(0.25–0.30)	(3.2–8.2)
	N = 5/44	N = 5/93	N = 5/37	N = 1/11	N = 5/50

[a] Range of individual means.
[b] Range of total number of notes or intervals.
[c] Number of birds/number of notes or intervals.

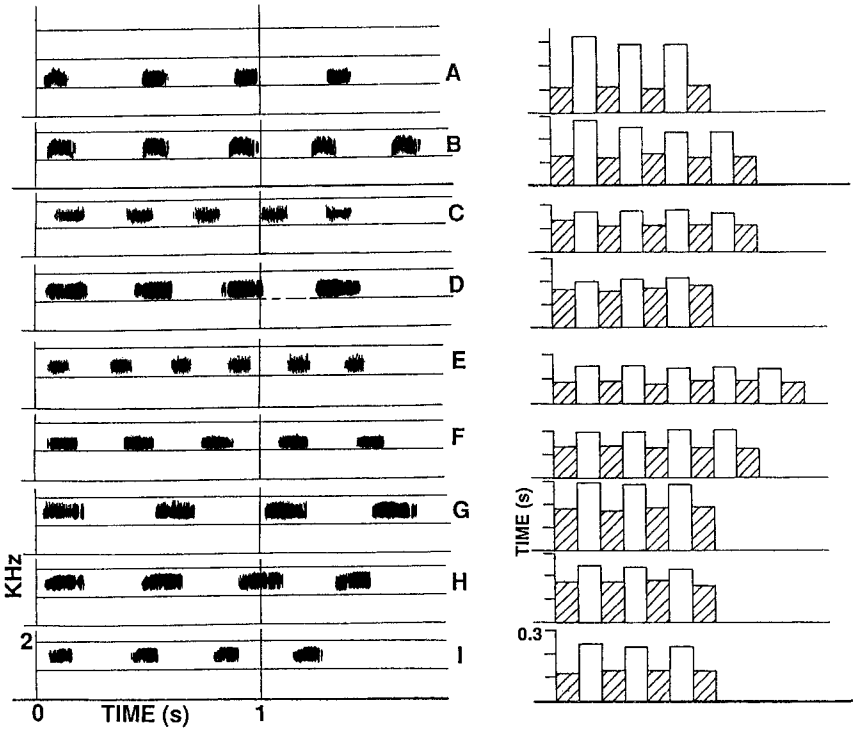

FIG. 1. Spectrograms and histograms of the songs of *Glaucidium palmarum* (A–B) and *G. griseiceps* (C–I) all to the same scale. In histograms, shaded bars represent notes, unshaded bars represent inter-note pauses. In *palmarum,* the short notes are often arched and are separated by relatively long pauses that are 1.9–3.6 × longer than the notes, with the longest pause between the first and second notes. In *griseiceps,* the notes within a song are overall equal in duration and are paced steadily with pauses 1.1–2.0 × the length of the notes. A: *G. p. palmarum.* Microondas La Cumbre, Colima, Mexico. Apr 1988 (Howell). B: *G. p. griscomi.* Cañon de Lobos, Morelos, Mexico. Jun 1991 (Howell). C: *G. g. "occultum".* Uxpanapa, Veracruz, Mexico. Jan 1992 (Howell). D: *G. g. griseiceps.* Gallon Jug, Belize. May 1992 (Whitney). E: *G. g. griseiceps.* Cerro San Gil, Izabal, Guatemala. Feb 1991 (Howell). F: *G. g. "rarum".* Braulio Carillo, Costa Rica. Apr 1982 (Wolf). G: *G. g. "rarum".* Nusagandi, San Blas, Panama. Feb 1987 (Whitney). H, I: *G. g. "rarum?".* Alto Tambo, Esmeraldas, Ecuador, Jul 1990 (Robbins).

able from that of *palmarum* and is thus more similar to it than are other members of the *G. minutissimum* complex.

G. palmarum: songs comprise 2–24 short hoots separated by long pauses (Table 1, Fig. 1A–B). The first inter-note interval is significantly longer than the second ($P < 0.05$), after which the pacing is fairly steady, although intervals between notes often decrease slightly overall throughout

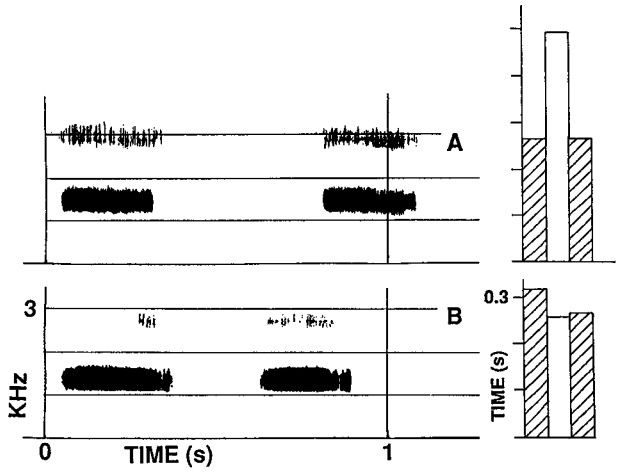

FIG. 2. Spectrograms and histograms (see Fig. 1 for key) of typical songs of *Glaucidium sanchezi* (A) and *G. minutissimum* (B) to same scale. The higher-pitched *sanchezi* has a significantly longer pause between notes, and the second note of *minutissimum* is consistently shorter than the first. A: Rancho del Cielo, Tamaulipas, Jun 1985 (Arvin). B: Floresta Río Doce forest reserve, Espírito Santo, Brazil, Oct 1991 (Whitney).

the song (Fig. 1A–B). The song bouts often begin with two and three-note songs and build up to the commonly given six to 10-note songs; usually when songs reach 6–8 hoots they vary, seemingly randomly, in their number of notes. The first few notes, and sometimes all notes in a song, are arched, contributing to a hollow, wooden to slightly plaintive quality that suggests the Ferruginous Pygmy-Owl (*G. brasilianum*).

Within the *minutissimum* complex, the song of *palmarum* appears closest to *G. griseiceps* from which it is distinguished by its short notes separated by longer intervals (Fig. 1A–B vs 1C–I; Table 1), with the first inter-note interval longest. The difference in tempo between these two species is reflected by the difference between inter-note interval and note duration being significantly greater in *palmarum* than in all populations of *griseiceps* ($P < 0.001$). Also, inter-song interval is significantly shorter in *G. palmarum* than in *G. griseiceps* ($P < 0.05$). *Palmarum* differs from *G. sanchezi* and *G. minutissimum* in its long songs of short notes (Table 1; and compare Figs. 1A–B and 2A–B), and from *G. parkeri* in its longer, steadier-paced songs of short notes, with the first inter-note interval longest, and significantly longer inter-song intervals ($P < 0.05$) (Table 1; compare Figs. 1A–B and Fig. 3).

G. sanchezi: songs comprise 1–3 slow-paced, high-pitched, long hoots with a long pause between them (Table 1; Fig. 2A). Two-note songs

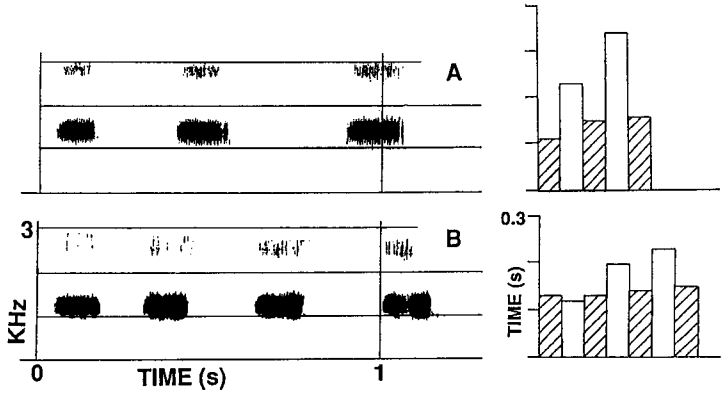

FIG. 3. Spectrograms and histograms (see Fig. 1 for key) of typical songs of *Glaucidium parkeri* to same scale. This species has successively increasing pauses between notes and, to a lesser extent, increasing duration of notes. A: three-note song, 04°37′S, 78°58′W, Prov. Zamora-Chinchipe, Ecuador. July 1992 (Sornoza). B: four-note song, Volcán Sumaco, Prov. Napo, Ecuador. Jan. 1991 (Whitney).

appear commonest, but two and three-note songs may be repeated and alternated, seemingly at random, and single-note songs (apparently unique in this complex) also may be repeated steadily.

The song of *sanchezi* is strikingly different from those of *G. palmarum, G. griseiceps,* and *G. parkeri* by virtue of its long notes and inter-note intervals, and number of notes (Table 1; Figs. 1–3), and it sounds superficially similar to the song of the geographically distant *G. minutissimum.* The song of *sanchezi* is slower-paced, however, because the inter-note interval of *sanchezi* is highly significantly longer than *minutissimum* ($P < 0.001$; Table 1). Thus the inter-note interval of *sanchezi* is 0.03–0.23 s longer ($\bar{x} = 0.15$ s $\pm$ 0.06; N = 21, 2-note songs) than the longest note, vs 0.10 s longer or shorter ($\bar{x} = -0.01$ s $\pm$ 0.06; N = 26, 2-note songs) in *minutissimum.* Also, the second note of a two-note *minutissimum* song is significantly shorter than the first ($P < 0.05$), whereas in *sanchezi* the second note of a two-note song is not significantly different from the first (0.03 s shorter to 0.05 s longer) (Fig. 2). Further differences are the significantly higher frequency of *sanchezi* vs *minutissimum* ($P < 0.001$) and the significantly shorter inter-song interval of *sanchezi* ($P < 0.05$), which helps separate the singing tempo of these two species.

Of interest is the geographic variation apparent between two disjunct populations of *G. sanchezi* that have been tape recorded. Thus, birds at Rancho del Cielo in Tamaulipas give significantly longer notes ($\bar{x} = 0.28$ s $\pm$ 0.01, N = 5 birds) than birds west of El Naranjo in San Luis Potosí

($\bar{x}$ = 0.24 s ± 0.02, N = 4 birds) ($P < 0.001$). In all other respects (noted above), the songs of these populations are similar to one another and differ consistently from all other species in the complex.

G. griseiceps: songs comprise 2–18 hoots of variable duration (Table 1). Like *G. palmarum,* the song bouts of *G. griseiceps* often begin with two and three-note songs and build up to the commonly given six to 10-note songs which then vary, seemingly randomly, in their number of notes. The song has a ringing, slightly bell-like quality, quite different from *palmarum* and would not be mistaken for a Ferruginous Pygmy-Owl. Despite geographic variation (see below), consistent features of the song of *G. griseiceps* are the overall steady pacing between notes, reflected by no significant difference between first and second inter-note intervals (vs shorter in *palmarum,* longer in *parkeri*) and by no significant difference between northern and southern populations in the difference between inter-note interval and note duration (both significantly less than *palmarum*).

This species has the widest latitudinal geographic range and also the greatest variation in the duration of notes among individuals (Fig. 1C–I). Songs of northern individuals average lower-pitched than southern birds, with shorter notes: hoots from southeast Mexico to eastern Guatemala are 0.09–0.19 s long ($\bar{x}$ = 0.11 ± 0.02, N = 6 birds), with a mean dominant frequency of 1339 Hz, while hoots from Costa Rica to northwestern Ecuador are 0.12–0.23 s long ($\bar{x}$ = 0.17 ± 0.03, N = 7 birds), with mean 1428 Hz. Although the note duration of northern populations is significantly shorter than that of southern populations ($P < 0.001$), short and long notes occur in both populations (Fig. 1C–I). There also may be a tendency for northern birds to sing more notes, since we have heard no birds from Costa Rica to northwest Ecuador give more than 12 notes in a song; one recording from Colombia consists simply of six two-note songs which superficially suggest *G. minutissimum* (the notes, however, are much shorter [0.16–0.17 s] and the tempo different than that species). Geographic variation of this degree may be typical in a widespread small owl. For example, for *G. hardyi,* which also has a large geographic range, Vielliard (1989) noted variation in the number of notes (12–36) and in the tempo (10–13 notes/s) which appeared to correlate with distribution; and, for the European Little Owl (*Athene noctua*), Exo (1990) showed that British birds gave higher-pitched and longer calls than birds in Germany. Note also the geographic variation in *G. sanchezi* (above).

See above and under *G. palmarum* for a discussion of the song differences between it and *griseiceps.* The long series of relatively short notes with short inter-note intervals readily distinguish *griseiceps* from *G. sanchezi* and *G. minutissimum* (Table 1; Figs. 1–2). Note that populations of

griseiceps geographically nearest *sanchezi* have fast-paced, multiple-noted songs ($\bar{x}$ = 7 notes/song in Veracruz and Chiapas, Mexico) quite different from the higher pitched, slow-paced, one to three-note song of *G. sanchezi* (Fig. 1C vs Fig. 2A). Southern populations of *griseiceps* (eastern Panama/adjacent Colombia and northwestern Ecuador) have higher pitched and slower-paced songs in contrast to the lower pitched, faster-paced song of *parkeri* (Fig. 1G–I vs Fig. 3).

G. parkeri: songs comprise 2–4 relatively short, low-pitched hoots, and are characterized by a distinct, consistently increasing length of inter-note interval (Fig. 3; Table 1). Thus the second pause of a three-note song is significantly longer than the first (Table 1; $P < 0.01$), the effect to the human ear being that of slowing down or a hesitation before the last note of the song, e.g., "*hu hu, hu*". Although masked in Table 1, which combines all notes in songs to give a mean, the duration of notes also increases overall, with the last note of a song 0.01–0.10 s longer than the first ($\bar{x}$ = 0.04 s ± 0.02, N = 28 songs) ($P < 0.001$). Another distinctive feature of this species' song is the inter-song intervals are significantly shorter than in all other species in this complex (Table 1; $P < 0.05$).

The song of *parkeri* differs from *G. palmarum* and *G. griseiceps* by having fewer notes and from *G. sanchezi* and *G. minutissimum* in its short notes. It differs from all other taxa in this complex in tempo, in particular the increasing length of inter-note intervals, and in the very short inter-song interval.

G. minutissimum: the song of this species typically consists of two, low-pitched, long hoots separated by a pause about equal to the duration of the notes (Table 1; Fig. 2B). Three and four-noted songs have been recorded rarely (Sick 1993; D. Stotz, pers. comm.; B. Whitney, tape recording) and have long notes and pauses similar to two-note songs. The song of *minutissimum* is obviously different from that of all other species except *G. sanchezi* (Table 1; Figs. 1–3); distinctions between these two taxa are discussed under the latter.

Morphology.—When viewing specimens in series, three groups stand out immediately by virtue of their plumage coloration: the pale west Mexican birds (*G. palmarum*); the dark, reddish-brown birds from eastern Mexico to Brazil (*G. sanchezi, G. griseiceps, G. hardyi, G. minutissimum*); and the dark, gray-brown birds, with distinct white spots on their scapulars and wings, from the east slope of the Andes (*G. parkeri*). No sexual dimorphism in plumage is apparent in any of the taxa except *sanchezi,* in which females are redder than males.

Although birds from west Mexico have been labeled as three different subspecies (*palmarum, oberholseri,* and *griscomi*), when viewing series of all three in comparably fresh plumage, the only noticeable difference

is the more finely spotted, or flecked, head of specimens from southern Oaxaca, compared with birds from elsewhere in the range of *G. palmarum.* Binford (1989) also noted this character and suggested these birds may represent an undescribed subspecies. Moore (in Friedmann et al. 1950) questioned the validity of *oberholseri.* Our analysis supports Moore, and we propose that *oberholseri* be synonymized with *palmarum.* The subspecies *griscomi,* however, of the interior Río Balsas drainage, may be distinguishable from other west Mexican birds by its average greater size (Moore 1947), although larger series are desirable to evaluate fully the characters of this form.

Our sample, although larger than those used to describe the three subspecies of *G. griseiceps,* is insufficient to show significant mensural or plumage differences that correlate consistently with these subspecies. Although birds from Mexico through Honduras (*occultum* and *griseiceps*) average shorter-tailed than birds from Costa Rica and Panama (*rarum*), there is overlap in this character. Similarly, some birds from southeast Mexico have heavily spotted heads like birds from southern Central America. We propose that *G. griseiceps* can be considered monotypic until larger series of adult specimens in comparably fresh plumage are available to evaluate critically geographic variation.

On the whole, mensural differences are slight among the taxa in this complex. Although some differences are apparent, it is not clear what biological significance, if any, they may have. Male *G. palmarum* have significantly shorter wings than males of all other species ($P < 0.001$; Table 2) and have significantly longer tails than males of all other species except *G. sanchezi* (Table 2). The wing/tail ratio is least in the two northern species, *G. palmarum* and *G. sanchezi* (1.6) and greatest in *G. hardyi* and *G. parkeri* (1.9) of South America. Thus the two subtropical taxa (*sanchezi* and *parkeri*) are at opposite ends of this scale.

For the two species represented by adequate sample sizes for both males and females, *G. palmarum* and *G. sanchezi,* the sexes differ significantly in wing length, and *palmarum* females also have longer tails than males (Table 2; *t*-test, two-tailed, $P < 0.001$).

Plumage within the genus *Glaucidium* is, on the whole, remarkably uniform. For example, based solely on plumage coloration and pattern, *G. hardyi* was not recognized as a taxon separate from *minutissimum* until its distinctive voice was recorded. Nonetheless, the six species in the *G. minutissimum* complex show consistent plumage differences from one another and are illustrated in the Frontispiece which should be consulted for interpretation of colors used in the following descriptions. The number of tail bars noted below includes the distal bar which is near or at the tip

TABLE 2

MEAN (±SD) FOR SELECTED MEASUREMENTS (IN MM) OF THE *GLAUCIDIUM MINUTISSIMUM* Complex

	Wing (chord)		Tail (central rectrix)		Mass
	Male	Female	Male	Female	Males only
G. palmarum[a]	82.9 (±1.9) N = 79	85.9 (±1.8) N = 17)	52.5 (±1.6) N = 74	54.5 (±1.2) N = 16	44.9 (±2.5) N = 19
G. sanchezi	87.3 (±1.4) N = 6	91.0 (±2.4) N = 5	52.7 (±2.8) N = 5	55.0 (±0.5) N = 4	53.5 (±2.1) N = 2
G. griseiceps[b]	87.2 (±2.7) N = 10		47.8 (±1.8) N = 10		50.6 (±1.1) N = 3
G. parkeri	93.2 (±3.9) N = 3		50.0 (±3.4) N = 3		61.6 (±2.5) N = 3
G. hardyi	92.2 (±1.6) N = 7		46.8 (±1.8) N = 7		55.1 (±3.3) N = 4
G. minutissimum	86.4 (±3.9) N = 6		49.7 (±4.2) N = 6		

[a] Includes *oberholseri* and *griscomi*.
[b] Includes *occultum* and *rarum*.

of the rectrices and can be absent if the tail tip is extremely worn. In life, the basal 1–2 tail bars are covered by the crissum and uppertail coverts.

G. palmarum: crown and nape grayish tawny-brown, with extensive whitish to pale buff spotting, and slightly grayer than tawny olive-brown back. Bars on the closed wings are formed by pale cinnamon to buffy-white spots on the outer webs of the primaries and secondaries. Tail with six or seven white to buffy-white bars. Sides of chest and streaking on underparts cinnamon-brown to dark cinnamon-brown.

Palmarum is paler overall than *G. sanchezi,* its head being less contrastingly gray than male and less rich brown than female *sanchezi* with, on average, more extensive pale head spots; the chest sides and underpart streaks are paler, cinnamon-brown. From *G. griseiceps* and *G. minutissimum, palmarum* differs in the same respects as it does from *sanchezi,* except that the extent of pale head spotting is similar in all three and the tail of *palmarum* has six or seven pale bars. From *G. hardyi, palmarum* differs in its overall paler plumage, less contrasting gray head, and in six or seven pale tail bars. From *G. parkeri, palmarum* is told by its paler coloration, lack of bold white spots on the scapulars and wings, and in six or seven pale tail bars.

G. sanchezi: this species is unique in the Least Pygmy-Owl complex in that the sexes are dichromatic. The male has a gray-brown crown and

nape with fine pale buff to whitish spots on the forecrown; the nape contrasts slightly with the grayish olive-brown back. Bars on the closed wings are formed by pale cinnamon to pale buff spots on the outer webs of the primaries and secondaries. The chest sides and underpart streaks are dark olivaceous tawny-brown, and the tail has six whitish bars. The female has the crown, nape, and upperparts washed with cinnamon and dorsally is overall fairly uniform and distinctly redder than the male. The forecrown is finely spotted with pale buffy-cinnamon. The chest sides and underpart streaks are dark rufous-brown, and the six pale tail bars are tinged buff to pale cinnamon. In two of six males and one of four females the pale head spots extend back laterally to the nape.

Male *sanchezi* differ from *G. griseiceps* and *G. minutissimum* by their more olivaceous, less rufous upperparts and underpart streaks and from *minutissimum* by their grayer head. Female *sanchezi* differ from *griseiceps* by the cinnamon-brown cast to their head. Both sexes of *sanchezi* also differ from *griseiceps* and *minutissimum* in their six pale tail bars and, on average, less extensive pale spotting on the head. From *G. hardyi, sanchezi* differs in its six pale tail bars, less contrasting gray head, slightly paler and more olivaceous upperparts, and, on average, less extensive pale crown spotting. Some *hardyi* and male *sanchezi,* however, are extremely similar in overall coloration. From *G. parkeri, sanchezi* differs in its six pale tail bars and paler and redder plumage that lacks bold white spots on the scapulars and wings. See under *G. palmarum* for differences between it and *sanchezi.*

G. griseiceps: crown, nape, and upperparts rich olivaceous-brown to rufous-brown with a grayer wash to the head and whitish to buffy-white spotting on the crown and nape. Bars on the closed wings are formed by pale cinnamon spots on the outer webs of the primaries and secondaries. Tail with five white to buffy-white bars. Chest sides and underpart streaks rufous-brown.

From *G. minutissimum, griseiceps* differs in its grayer head, darker and redder chest and underpart streaking but less rufescent back. From *G. hardyi, griseiceps* differs in its less contrasting gray head, and redder upperparts and chest and underpart streaking. From *G. parkeri, griseiceps* differs in its paler and redder plumage that lacks bold white spots on the scapulars and wings. See under *G. palmarum* and *G. sanchezi* for differences between those species and *griseiceps.*

G. minutissimum: crown and nape dusky cinnamon-brown with whitish to buffy-white spots extending back to the nape; back rufous-brown. Bars on the closed wings are formed by pale cinnamon spots on the outer webs of the primaries and secondaries. Tail with five white to buffy-white bars. Chest sides and underpart streaks rufous-brown to dark cinnamon-brown.

From *G. hardyi, minutissimum* differs in its redder crown, upperparts, chest sides, and underpart streaks. From *G. parkeri, minutissimum* differs in paler and redder plumage that lacks bold white spots on the scapulars and wings. See under *G. palmarum, G. sanchezi,* and *G. griseiceps* for differences between those species and *minutissimum.*

G. hardyi: crown and nape brownish-gray with extensive white spotting, contrasting slightly with dark gray-brown back. Bars on the closed wings are formed by pale cinnamon spots on the outer webs of the primaries and secondaries. The tail has five whitish bars. The chest sides and underpart streaks are dusky cinnamon-brown to brown. From *G. parkeri, hardyi* differs in its redder plumage that lacks bold white spots on the scapulars and wings. See other taxa for differences between them and *hardyi.*

G. parkeri: a distinctive species characterized by its dark gray-brown to brown crown, nape, and upperparts with extensive whitish head spotting, bold white spots on the scapulars, and contrasting white spots and bars on the wings; its tail has five white bars (Robbins and Howell 1995). See other taxa for differences between them and *parkeri.*

Distribution and habitat.—The six species in the *G. minutissimum* complex have allopatric distributions (see Frontispiece). With the exception of *palmarum,* all Least Pygmy-Owls inhabit the upperstory of tall, humid forest, helping explain why they are often overlooked and why so few specimens exist of the Central and South American species.

G. palmarum: endemic to western Mexico where it occupies a range of habitats, in arid to semihumid conditions, from near sea level to 1500 m elevation (Buchanan 1964, Howell, pers. obs.). It occurs on the Pacific Slope from central Sonora (foothills east of Hermosillo; Howell and S. Webb, pers. obs.) to central Oaxaca (foothills inland of Puerto Angel; Howell and P. Pyle, pers. obs.) and also in the Balsas drainage of southern Morelos (Friedmann et al. 1950, Fig. 1B) and northern Guerrero (Friedmann et al. 1950). There is no indication that the ranges of *G. palmarum* and *G. griseiceps* approach one another in the Isthmus of Tehuantepec since they occupy different habitats (arid thorn forest vs humid rain forest); their allopatric ranges are typical of numerous Pacific and Atlantic slope forms in this region, e.g., *Chlorostilbon auriceps, Tityra semifasciata griseiceps,* and *Cyanocompsa parellina indigotica* on the Pacific slope vs *C. canivetii, T. s. personata,* and *C. p. parellina* on the Atlantic slope (Miller et al. 1957, Binford 1989, Howell 1993).

In much of its range, *palmarum* occurs in tropical deciduous forest (thorn forest), usually in foothills, whereas *G. brasilianum* is common in lowlands. These two species do occur sympatrically, however, and their exact ecological differences have yet to be determined. *Palmarum* occurs

from thorn forest through semideciduous forest up into dry oak woodland and, less often, dry pine-oak woodland where it can occur sympatrically with the highland species *G. gnoma* (Schaldach 1963). In much of western Mexico, *palmarum* is, at least locally, fairly common to common (considered "very common" by Binford [1989]). In southern Nayarit and Colima, the highest density of *palmarum* occurs in barrancas at the upper edge of the tropical deciduous forest (Schaldach 1963, Howell, pers. obs.). It also has been noted from "palm forest on a low ridge near the sea" (Nelson 1901) and from "swamp forests" (Binford 1989).

G. sanchezi: endemic to northeastern Mexico where it occurs locally in southern Tamaulipas and eastern San Luis Potosí. It inhabits subtropical, humid evergreen and semideciduous forest from 900 to 2100 m elevation (Lowery and Newman 1949, Webster 1974, J. Arvin, pers. comm., Howell, pers. obs.). Unlike *palmarum* in western Mexico, *sanchezi* appears to be locally fairly common to uncommon (Arvin, pers. comm., Howell, pers. obs.).

G. griseiceps: occurs from northern Oaxaca (Binford 1989; Howell, tape recording) and southeastern Veracruz (Fig. 1C) south on the Atlantic Slope of Mexico and Central America to northwestern Colombia (A.O.U. 1983, Sibley and Monroe 1990). There also is one record from 1300 m elevation on the Pacific Slope of Guatemala (B. Whitney, tape recording). The first records of this species south of the Panamanian/Colombian border (Hilty and Brown 1986) were of two pairs seen and recorded (LNS 63147, 63168, 63174, 63424–5; Fig. 1H–I) in mid-July 1990, north–northwest of Alto Tambo, Prov. Esmeraldas, Ecuador (00°57′N, 78°33′W), by Robbins during the course of ANSP inventory work. Even after voice playback, both pairs remained over 35 m up in the subcanopy of pristine, wet evergreen hill forest at ca 350 m elevation. *Griseiceps* inhabits tropical humid evergreen forest (rain forest) and forest edge from near sea level to 1300 m elevation. It is uncommon to locally fairly common (Stiles and Skutch 1989, Howell, pers. obs.) and has been considered "rare to locally uncommon" (Ridgely and Gwynne 1989).

G. parkeri: known from 1450–1975 m elevation on outlying ridges of the east slope of the Andes of Ecuador and Peru, and it may well occur also in southeastern Colombia (Robbins and Howell 1995). It occurs in subtropical evergreen forest and, while apparently not particularly uncommon, like other humid forest forms of the Least Pygmy-Owl complex, it may be overlooked easily.

G. hardyi: this species is generally considered uncommon and inhabits the upperstory of humid evergreen forest (rain forest), specifically tall terra firma, transitional, and varzea forest, over much of Amazonian South America, being unknown above 350 m elevation (Vielliard 1989, Parker

1982, Parker and Remsen 1987). It is unrecorded from Colombia, Ecuador, and north of the Río Amazonas and west of the Río Ucayali drainage in Peru. In addition to the records listed by Vielliard (1989), König (1991), and specimen localities listed by Robbins and Howell (1995), T. Parker (pers. comm.) recorded this species as far north and west in Peru as the right (east) bank of the Río Ucayali, southeast of Pucallpa, Depto. Ucayali. *G. hardyi* is further known from several localities in southeastern Peru (Parker 1982, pers. comm.) and northern Bolivia (Parker and Remsen 1987, Remsen and Traylor 1989). Parker (pers. comm.) also found the species in Brazil on the west bank of the Río Tapajós at Itaitus, Pará, and south of Alta Floresta, Río Teles Pires, Mato Grosso. The specimen record by M. Cohn-Haft (pers. comm.) at ca 80 km north of Manaus, Amazonas, Brazil, is the westernmost site this species has been found north of the Río Amazonas.

G. minutissimum: with the realization that the Amazonian lowlands are occupied by *G. hardyi,* the range of true *minutissimum* appears to be restricted to southeastern Brazil and adjacent Paraguay (Vielliard 1989). This species occurs in tropical humid evergreen forest (rain forest) and edge from sea level to 1000 m elevation and seems intolerant of secondary forests (D. Stotz, pers. comm.). It is uncommon to locally fairly common, and in southeast Brazil it appears commonest at foothill elevations of 500–800 m (Stotz, pers. comm.).

Conclusions.—The differences in song among members of the *G. minutissimum* complex are comparable to or greater than other species-level song differences within genera of small owls such as *Glaucidium* (e.g., *G. brasilianum* and *G. palmarum*), *Otus* (e.g., *O. kennicottii, O. seductus,* and *O. cooperi*; A.O.U. 1983, Hardy et al. 1990), and *Aegolius* (e.g., *A. acadicus* and *A. ridgwayi*; A.O.U. 1983, Hardy et al. 1990). Further, no song types of any one species in the *minutissimum* complex have been heard in populations of the other five species. These vocal dissimilarities are supported by differences in structure, plumage, and habitat. In addition, the six species of the *minutissimum* complex are allopatric. Criteria for both biological and phylogenetic species concepts appear to be met, and thus we propose the following revision. Suggested English names reflect the distributions of the four forms that we have elevated to species rank.

Glaucidium palmarum Colima Pygmy-Owl

Glaucidium palmarum Nelson 1901, Auk 18, p. 46.

Type specimen.—USNM No. 155955, adult female. Collected 5 April 1897 by E. W. Nelson and E. A. Goldman.

Type locality.—Arroyo de Juan Sanchez, Territory of Tepic, Mexico.

Measurements of type.—Wing 87 mm; tail 56 mm.

Geographic range.—Endemic to western Mexico from Sonora to Oaxaca (sea level–1500 m).

Characters.—Relatively long-tailed and short-winged. Plumage distinctive: relatively pale, grayish tawny-brown overall, with 6–7 pale tail bars. Song: 2–24 short notes separated by long pauses, the longest pause between the first and second notes.

Specimens examined.—102 skins, six tape recordings (listed by Robbins and Howell 1995).

Glaucidium sanchezi Tamaulipas Pygmy-Owl

Glaucidium minutissimum sanchezi Lowery and Newman 1949, Occas. Papers LSUMZ, 22, pp. 1–4.

Type specimen. LSUMZ No. 11002, adult male. Collected 14 May 1947 by R. J. Newman.

Type locality.—Llano de Garzas, near Cerro Coneja, San Luis Potosí, Mexico.

Measurements of type.—Wing 90.1 mm; tail 57 mm.

Geographic range.—Endemic to NE Mexico in SW Tamaulipas and E San Luis Potosí (900–2100 m).

Characters.—Relatively long-tailed. From *G. palmarum* by darker plumage (cinnamon-brown overall). From other forms by six pale tail bars and reduced and finer pale flecks on crown. Sexes dimorphic (female redder). Song: 1–3 high-pitched, long notes separated by long pauses.

Specimens examined.—13 skins, nine tape recordings (listed by Robbins and Howell 1995).

Glaucidium griseiceps Central American Pygmy-Owl

Glaucidium griseiceps Sharpe 1875, Ibis 1875, p. 41.

Type specimen.—Lectotype: British Museum No. 75.6.14.45, "Ex. coll. Bouvier", unsexed, undated.

Type locality.—Veragua (Panama) and Chisec and Choctum (Guatemala); restricted to tropical lowlands (Coban) of Alta Vera Paz, Guatemala, by Griscom (1931).

Measurements of type.—Wing 87 mm; tail 52 mm.

Geographic range.—SE Mexico to NW South America (sea level–1300 m).

Characters.—Relatively short-tailed. Plumage relatively dark, rufous-brown overall with five pale tail bars. Plumage redder overall than *G.*

parkeri or *G. hardyi,* crown grayer than *G. minutissimum.* Song: 2–18 steadily paced notes of approximately equal duration.

Specimens examined.—13 skins, 14 tape recordings (listed by Robbins and Howell 1995).

Glaucidium parkeri Subtropical Pygmy-Owl

Glaucidium parkeri Robbins and Howell 1995, Wilson Bull. 107, pp. 1–6.

Type specimen. ANSP No. 185160, adult male. Collected 22 July 1992 by F. Sornoza M.

Type locality.—Ecuador: Prov. Zamora-Chinchipe; Panguri, ca 12 km NE San Francisco del Vergel, 04°37′S, 78°58′W.

Measurements of type.—Wing 91.8 mm; tail 48.5 mm.

Geographic range.—E slope of Andes in Ecuador and Peru (1450–1975 m).

Characters.—Relatively long-winged. Plumage distinctive: relatively dark gray-brown overall with bold white spots on crown, nape, and wing coverts; five pale tail bars. Song: two–four notes with increasing length of pause between notes; short inter-song interval.

Specimens examined.—three skins, four tape recordings (listed by Robbins and Howell 1995).

Glaucidium hardyi Amazonian Pygmy-Owl

Glaucidium hardyi Vielliard 1989, Revta. Bras. Zool., 6, pp. 685–693.

Type specimen.—ZUEC (Universidade Estadual de Campinas, Brazil) No. 1194, male. Collected 16 April 1983 by J. Vielliard.

Type locality.—20 km SW Presidente Medici Rondônia, Brazil.

Measurements of type.—Wing 94 mm; tail 52 mm.

Geographic range.—Amazonian South America (sea level–350 m).

Characters.—Relatively long-winged. Plumage relatively dark, grayish rufous-brown with five pale tail bars. Head and upperparts grayer than *G. griseiceps* and *G. minutissimum.* Song: 12–36 notes given in rapid trill.

Specimens examined.—seven (listed by Robbins and Howell 1995).

Glaucidium minutissimum Brazilian Pygmy-Owl

Strix pumila Temminck 1821, Pl. col., livr. 7, pl. 39.
Strix minutissima (Wied) 1830, Beitr. Naturg. Bras., 3, pt. 1, p. 242.

Type specimen.—Syntypes: AMNH No. 6345 (male), 6345 bis (female), undated.

Type locality.—Interior state of Bahia, Brazil.

Measurements of syntypes.—Wing 87.7, 90.8 mm; tail 50.3, 50.6 mm.

Geographic range.—SE Brazil and adjacent Paraguay.

Characters.—Relatively short-winged. Plumage relatively dark, rufous-brown overall with five pale tail bars. Crown redder than *G. griseiceps* or *G. hardyi.* Song: two–four long notes separated by shorter pauses than *G. sanchezi.*

Specimens examined.—13 skins, five tape recordings (listed by Robbins and Howell 1995).

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