

SYSTEMATIC AND ECOLOGIC NOTES ON THE OLIVE WARBLER

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SYSTEMATIC POSITION

THE Olive Warbler (*Peucedramus taeniatus*) has been classified by almost everyone for the last 86 years as a monotypic genus, closely related to *Dendroica*. However, Griscom (1957) recommended that *Peucedramus* be merged with *Dendroica* and I (1958) agreed with him. On the contrary, William George (oral communication and papers read orally) and others have recently stated that the Olive Warbler is not a wood warbler (Parulidae) at all, but an Old World warbler of the family Sylviidae, or else a thrush of the family Turdidae. My own study was confined to the skin and skull.

Characters of the skin.—The following eight differential characters listed by Ridgway (1902) or Chapman (1907) are invalid as differentiations from *Dendroica*, because *Peucedramus* does not exceed the variation within the larger genus:

| Character | My observations |
|--|--|
| (1) Bill more slender (subulate) than in <i>Dendroica</i> . | Less slender in <i>Peucedramus</i> than in <i>Dendroica dominica</i> . |
| (2) Bill more rounded than in <i>Dendroica</i> . | Less rounded in <i>Peucedramus taeniatus micrus</i> than in <i>Dendroica dominica</i> . |
| (3) Rectal bristles weak and fewer than in <i>Dendroica</i> . | Same in <i>Peucedramus</i> as in those several species of <i>Dendroica</i> with the longest bristles. |
| (4) White patch in secondaries. | Same in <i>Dendroica coerulescens</i> . |
| (5) Wing-tail difference greater than in <i>Dendroica</i> . | Wing-tail difference in <i>Peucedramus</i> less than that in <i>Dendroica striata</i> . |
| (6) Tarsus one-fourth length of wing; scutellae indistinct or fused. | Same in <i>Peucedramus</i> and in <i>Dendroica</i> . |
| (7) Middle toe with claw shorter than the tarsus; basal phalanx of middle toe united for slightly more than half its length to the outer toe and about half its length to the inner toe. | Same in <i>Peucedramus</i> and in <i>Dendroica</i> . |
| (8) Slight sexual dimorphism in juvenal plumage in <i>Peucedramus</i> , but sexual dimorphism in <i>Dendroica</i> acquired with first winter plumage or never. | No sexual variation distinguishable in 23 specimens in juvenal plumage of <i>Peucedramus</i> . Much foxing and geographic variation; the most important variable, though, is the amount of first winter plumage coming in, and this, of course, is sexually dimorphic. |

The following three differential characters listed by Ridgway (1902) or

Chapman (1907) are valid distinctions from *Dendroica*. To my mind, however, they are not very striking:

| Character | My observation |
|---|---|
| (1) Bill more decurved and notched than in <i>Dendroica</i> . | Very slightly more decurved and notched in <i>Peucedramus</i> than in any <i>Dendroica</i> ; matches <i>Seiurus</i> . |
| (2) Tail distinctly emarginate. | More prominently emarginate in <i>Peucedramus</i> than in any <i>Dendroica</i> . However, three species of conifer-inhabiting <i>Dendroica</i> — <i>pinus</i> , <i>graciae</i> , and <i>discolor</i> —have an emarginate tail. Measured as the difference in length between the longest and shortest rectrices, the figures are: <i>Peucedramus</i> , 5.3 mm average; <i>D. discolor</i> , 3.8; other species of <i>Dendroica</i> , 3.5 to 1.0. |
| (3) Male requires 14 months to acquire adult pattern in <i>Peucedramus</i> ; 3 months in <i>Dendroica</i> . | True in <i>Peucedramus</i> only in the northernmost race; the male adult plumage pattern acquired at about 3 months in many or most individuals of the Central American races. |

One character of the skin is a valid family character. The tenth primary is extremely rudimentary in *Peucedramus*. (A long series of varied age and size examined.) In my opinion this is a more deep-seated taxonomic character than some characters of muscles or bones. If this is correct, *Peucedramus* cannot belong to any family except Parulidae or Thraupidae.

I studied four more plumage characters, looking especially for similarities between *Peucedramus* and other Oscine groups. These observations reinforce the position that *Peucedramus* belongs in Parulidae, with more distant relationships to Thraupidae and Fringillidae:

| Character | My observation |
|--|--|
| (1) Plumage pattern and color of adult male. | Ochraceous color not matched in other Parulidae except for small markings, but some Thraupidae and Fringillidae come fairly close. Pattern matched closely in several other Parulidae; some tanagers fairly close. |
| (2 and 3) Plumage pattern and color of females and fall immatures. | Outside the Parulidae only the tanagers come close. Amongst the warblers, the similarity of three species of conifer-inhabiting <i>Dendroica</i> (<i>pinus</i> , <i>occidentalis</i> , and <i>townsendi</i>) to <i>Peucedramus</i> is remarkable. In fact, I was unable to pick out immatures of either sex of Olive Warblers from a tray of Hermit Warblers when placed |

(4) Juvenal plumage.

dorsal side up, or from a tray of Townsend Warblers when placed laterally.

The dull olive green of *Peucedramus*, with obscure longitudinal streaks and prominent white wing bars is typical for a warbler and not out of line for a tanager, an icterid, or an emberizine finch. But a streaked juvenal plumage is absent in any Sylviidae and I have found only one Turridae (*Luscinia svecica*) which is streaked. The last is fairly close to the emberizine sparrow-type of juvenal plumage.

Characters of the skull.—Each of the following has been used as a familial characteristic by the recent authority cited (see Fig. 1):

| Character | My observation on <i>Peucedramus</i> with comment |
|--|---|
| (1) Ectethmoid foramen (Beecher, 1953; Brodkorb, 1958). | Double. This puts the genus in either Parulidae or Turridae according to Beecher's classification, and in Parulidae or Turridae according to Brodkorb. |
| (2) Shape of ectethmoid plate and character of lacrimal (Beecher, 1953). | Ectethmoid plate truncate; lacrimal fused. This puts the genus in Sylviidae or Parulidae according to Beecher. |
| (3) Palatine process of premaxilla (Tordoff, 1954; Bock, 1960). | Visible, but mostly fused, in 2 of 5 specimens: completely fused in 3. This indicates Parulidae (Tordoff) or nothing (Bock). |
| (4) Basihyoid (George, in litt.). | Shape of Sylviidae. |
| (5) Maxillo-palatine (Brodkorb, 1958). | Hooked; median part pneumatic, swollen, and bearing an anterior spur. According to the classification of Brodkorb, this <i>Peucedramus</i> shape is probably either sylviid, vireonid, or parulid. According to my observations, vireo maxillo-palatines are very distinct from those of warblers (wider all along their length and very flat). But Parulidae grades into Sylviidae via <i>Dendroica townsendi</i> , which has a small anterior spur, <i>Peucedramus</i> , and <i>Sylvia hortensis</i> . The maxillo-palatine of the last is very similar to that of <i>Peucedramus</i> . |

The following additional skull characters separate Parulidae, including *Peucedramus*, from Sylviidae:

(1) Shape of vomer posteriorly.

Split wider in Sylviidae and extending farther anteriorly (anterior to interpal-

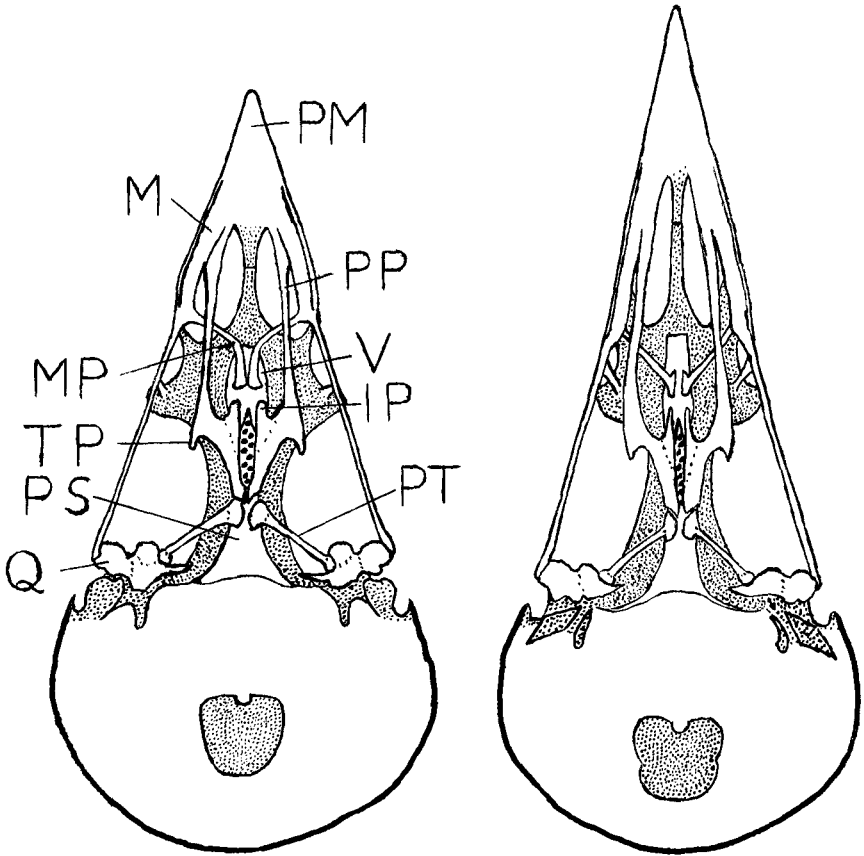


FIG. 1. Ventral view of skulls of two species of warblers drawn to the same scale. Left, *Dendroica auduboni*; right, *Peucedramus taeniatus*. The more dorsal structures are in fine stipple; the anterior part of the parasphenoid (parasphenoidal rostrum) is in coarse stipple. Key: PT—Pterygoid. IP—Interpalatine process. V—Vomer (prevomers). PP—Prepalatine bar. PM—Premaxilla. M—Maxilla. MP—Maxillopalatine. TP—Transpalatine process. PS—Parasphenoid. Q—Quadrate.

tine process and end of parasphenoid); split narrower in Parulidae and extending not so far (rarely beyond the midpoint of the interpalatine process and not so far as the tip of the parasphenoid).

Absent, or else wide from whole width of palatine shelf in Sylviidae; always present but relatively narrow and from lateral edge, only, of palatine in Parulidae.

Narrower in Sylviidae; broader in Parulidae.

(2) Transpalatine process.

(3) Posterior palatine bone.

In the following skull characters the various warblers differ among themselves:

- | | |
|--|---|
| (1) Shape of interpalatine process. | <i>Peucedramus</i> long and rod-like, near <i>Chamaethlypis</i> and <i>Icteria</i> . |
| (2) Shape of transpalatine process. | <i>Peucedramus</i> long and rounded, near <i>Vermivora</i> , and <i>Dendroica</i> . |
| (3) Thickness of lateral process of nasal in lateral view. | <i>Peucedramus</i> broad and heavy, near <i>Icteria</i> , <i>Chamaethlypis</i> , and <i>Oporornis</i> . |
| (4) Naso-frontal hinge. | But slightly developed in <i>Peucedramus</i> , near <i>Seiurus</i> . |
| (5) General shape of skull in dorsal or ventral view. | Long and slender in <i>Peucedramus</i> , nearest <i>Dendroica</i> . |

Characters of the skull, then, mostly indicate that *Peucedramus* is a legitimate genus of wood warblers, with affinities to *Dendroica*, *Icteria*, and *Chamaethlypis*. However, the hyoid apparatus is divergent in character. Characters of the skin, on the other hand, indicate that generic separation of *Peucedramus* from *Dendroica* is unwarranted. Studies of the rest of the skeleton, the other anatomical systems, and especially of behavior, are needed before the classification of the Olive Warbler can be regarded as settled.

GEOGRAPHIC VARIATION

The races of the Olive Warbler were revised by Miller and Griscom (1925) and, recently, by me (1958). The present notes constitute only a revision of my earlier paper, based on a restudy of much of the same material, plus 151 additional specimens. Of the last, most were in fresh plumage, including 49 which I collected in Mexico.

Variation in wing length can now be analyzed statistically (Table 1). Two observations are pertinent: (1) Bermann's Rule is applicable, despite the facts that there is little or no migration and that the climates inhabited in the various areas are not strikingly varied. (2) The only significant breaks occur between *giraudi* and *taeniatus* and between *taeniatus* and *micrus*.

Variation in tail length (Table 2) shows only one significant point—the short tail of the southernmost race, *micrus*.

Color variation, based only on fresh-plumaged specimens, clearly differentiates five subspecies. The following synopsis includes only an abbreviated color diagnosis of each race, plus conclusions new or different from those in my earlier (1958) report.

Peucedramus taeniatus arizonae (Miller and Griscom). Paler, grayer, and less green than all other races; adult males also duller ochraceous anteriorly than all other races; females and immature males also yellower, less orangish anteriorly and browner dorsally than all other races.

P. t. jaliscensis (Miller and Griscom). Paler generally than the three succeeding

TABLE I
MEASUREMENTS IN MILLIMETERS OF THE WING OF MALE OLIVE WARBLERS IN ADULT
PLUMAGE

| Subspecies | Sample size | Population | Range | Mean | Standard deviation | Coefficient of variability |
|--------------------|-------------|--|-------|-------|--------------------|----------------------------|
| <i>arizonae</i> | 51 | Arizona, New Mexico | 75-80 | 77.53 | 1.46 | 1.88 |
| | 7 | Northwestern Coahuila | 76-81 | 78.29 | — | — |
| | 29 | Northwestern Chihuahua | 74-78 | 75.93 | 1.18 | 1.56 |
| <i>jaliscensis</i> | 15 | Durango, Zacatecas, southwestern Chihuahua | 73-80 | 76.60 | 1.71 | 2.23 |
| | 13 | Sierra Madre Oriental, in San Luis Potosi, Nuevo Leon, Tamaulipas | 73-79 | 76.08 | 1.58 | 2.07 |
| | 4 | Sierra de Tamaulipas | 69-75 | 73.00 | — | — |
| | 8 | Nayarit, western Jalisco | 75-79 | 77.00 | 1.51 | 1.97 |
| <i>giraudi</i> | 51 | Vera Cruz, Est. de México, Morelos, Dist. Federal, Michoacan, north-central Jalisco | 73-79 | 76.33 | 1.63 | 2.14 |
| <i>taeniatus</i> | 11 | Oaxaca, Guerrero | 68-75 | 72.27 | 1.91 | 2.65 |
| | 6 | Chiapas | 71-76 | 73.50 | — | — |
| <i>micrus</i> | 8 | Honduras, El Salvador | 66-71 | 68.50 | 1.50 | 2.19 |

rices; less green dorsally and especially on the edgings of the remiges, rectrices, and scapulars than *giraudi*; females and immature males also duller, less orangish anteriorly than the three succeeding races; anterior ochraceous of adult males paler than *giraudi*, duller than *taeniatus* and *micrus*.

P. t. giraudi Zimmer. Greener than all other races; also paler dorsally than *taeniatus* and *micrus*; anterior ochraceous of adult males duller and darker than *taeniatus* and *micrus*; females and immature males less orangish anteriorly than *taeniatus* and *micrus*.

P. t. taeniatus (du Bus). Greener and browner, more olivaceous, dorsally and ventrally than *micrus*; anterior ochraceous of adult males also darker and duller than *micrus*.

P. t. micrus (Miller and Griscom). Generally more blackish, less green, than all other races; females and immature males more orangish anteriorly than all other races; anterior ochraceous of adult males paler, brighter and more orange than in all other races (slightly on the Tawny side of Orange); rump of adult males blackish or leaden gray, concolor with the back, rather than more or less greenish as in all other races.

Neither Miller and Griscom (1925) nor I (1958) gave a correct color diagnosis of *micrus*, for lack of fresh-plumaged material. The bill of *micrus* is smaller and wider than in the more northern races, as both revisions noted.

In summary, the five races of the Olive Warbler recognized by previous revisers are upheld. Of these, the race *jaliscensis* is the weakest; it is distinguishable about 90 per cent from 90 per cent of all specimens or 95 per cent from 95 per cent for adults in fresh plumage. The race *micrus* is the most distinct—100 per cent from 100 per cent in the sample examined.

TABLE 2
MEASUREMENTS IN MILLIMETERS OF THE TAIL OF MALE OLIVE WARBLERS IN ADULT
PLUMAGE

| Subspecies | Sample size | Population | Range | Mean | Standard deviation | Coefficient of variability |
|--------------------|-------------|--|-------|-------|--------------------|----------------------------|
| <i>arizonae</i> | 51 | Arizona, New Mexico | 47-54 | 50.45 | 1.81 | 3.59 |
| | 7 | Northwestern Coahuila | 49-54 | 51.86 | — | — |
| | 29 | Northwestern Chihuahua | 48-53 | 50.07 | 1.37 | 2.74 |
| <i>jaliscensis</i> | 14 | Durango, Zacatecas, southwestern Chihuahua | 46-54 | 50.29 | 2.08 | 4.14 |
| | 13 | Sierra Madre Oriental in San Luis Potosi, Nuevo Leon, Tamaulipas | 46-54 | 50.23 | 2.08 | 4.14 |
| | 4 | Sierra de Tamaulipas | 46-50 | 47.75 | — | — |
| | 8 | Nayarit, western Jalisco | 46-52 | 49.12 | — | — |
| <i>giraudi</i> | 49 | Vera Cruz, Est. de México, Morelos, Dist. Federal, Michoacan, north-central Jalisco | 47-54 | 50.43 | 1.89 | 3.78 |
| <i>taeniatus</i> | 16 | Oaxaca, Guerrero, Chiapas | 47-54 | 49.19 | 1.74 | 3.53 |
| <i>micrus</i> | 8 | Honduras, El Salvador | 53-51 | 46.25 | — | — |

Two populations, those of the Sierra de Tamaulipas and of the state of Chiapas plus Guatemala, show enough differentiation to be mentioned as "almost" subspecies. The latter was once named "*aurantiacus*" by Ridgway (1896).

Additional specimens examined.—These skins were studied, in addition to those listed in my previous report: *P. t. arizonae*—Southeastern Arizona, 5; northwestern Coahuila, 1; Northern Chihuahua, 22. *P. t. jaliscensis*—Southern Coahuila, 1; Nuevo Leon, 11; San Luis Potosi, 20; Durango, 6; Zacatecas, 1; Nayarit, 1; Jalisco, 3. *P. t. giraudi*—Michoacan, 15; estado de México, 29; Distrito Federal, 5; Morelos, 6; Vera Cruz, 2. *P. t. taeniatus*—Oaxaca, 10; Chiapas, 2; Guatemala, 1. *P. t. micrus*—El Salvador, 2; Honduras, 8.

ECOLOGICAL REMARKS

The Olive Warbler inhabits pine forests from southeastern Arizona to Nicaragua. In several parts of the range (for instance, Zacatecas) the more arid fasciations of the pine forest are inhabited, but in other areas (for instance, Oaxaca) only humid, high elevation pine forests are utilized.

The ranges of the Olive Warbler and of Grace's Warbler (*Dendroica graciae*) make an interesting ecological and geographical comparison. The two species appear to occupy very similar ecological niches. Grace's Warbler, too, inhabits pine forests from the southwestern United States to Nicaragua. (See range maps, Webster, 1958 and 1961.)

Comparing the ranges of the two species, I note these differences: (1) The

only large area inhabited by Grace's Warbler but not by the Olive Warbler is in the United States—northern Arizona, northern and eastern New Mexico, and the southern edges of Utah and Colorado. (2) The only large area inhabited by the Olive but not by Grace's is eastern Mexico—from isolated peaks in Coahuila south through the Sierra Madre Oriental and the eastern part of the Trans Volcanic Range to eastern Oaxaca. (3) In Arizona, Durango, and Jalisco the two species are coresident in some pine forests, but the Olive extends to considerably higher elevations. (4) In Central America and north along the Pacific Coast to southern Sinaloa Grace's Warbler inhabits low and middle elevation pine forests, whereas the Olive Warbler is found in high elevation pines.

On neither Grace's nor the Olive Warbler have detailed behavior studies been reported. Foraging behavior is similar, although Grace's abandons foliage gleaning a little more often to fly out for a flying insect, and tends to forage farther out on the tips of the branches. (The Olive is about one-fifth again the larger.) In fall and winter the Olive is usually in flocks of 4 to 15 birds, whereas Grace's is ordinarily single or in pairs.

Grace's Warbler is apparently dependent on a nearby source of surface water, for I have never found one more than a few hundred yards from a permanent stream. On the other hand, the Olive Warbler, in Nuevo Leon, Durango, and Zacatecas, at any rate, is often found miles from any surface water—especially in June, before the rains have soaked the soil and started the creeks.

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