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## The Classification of the Olive Warbler, *Peucedramus taeniatus*

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### INTRODUCTION

The Olive Warbler, *Peucedramus taeniatus*, has long been classified as a member of the family Parulidae, for it is a "nine-primaried" songbird of the New World, is small, and has a thin bill and a non-tubular tongue. Evidence is developed here, however, to show that it is neither a parulid nor, apparently, a member of any other group belonging to the New World "nine-primaried" Oscines.

Baird knew of the species at the time he revised the classification of North American songbirds (*in* Baird, Cassin, and Lawrence, 1858). He aligned birds in this work generally according to whether they possessed "nine" or 10 primaries, an approach that ever since has influenced the suprageneric taxonomy of the New World Oscines. Yet Baird himself concluded that reduction of the tenth primary may not be an invariable feature even of congeneric species; he consequently allocated "nine-" and 10-primaried species to the genus *Vireo* (*op. cit.*, p. 329). At the same time (*op. cit.*, p. 305) he placed the Olive Warbler (his *Dendroica olivacea*) with the American warblers of the family Parulidae as currently recognized.

A study that I made of the bones and muscles of the avian hyoid (the structure partly controlling the tongue) provided the earliest evidence

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that *Peucedramus* has non-parulid characteristics. The present paper contains an account of this study, which when possible I have limited to a description, and to functional and taxonomic analyses, of hyoidean variations in New World songbirds. The nature of hyoidean variations in other birds is, of course, a related matter, and I remark upon it in several pertinent places. Jaw musculature, a reduced tenth primary, plumage, molt, nest, and eggs may bear on the problem of the classifying of *Peucedramus* and are discussed here, along with certain behavioral traits of *Peucedramus t. arizonae*, the northern race of the Olive Warbler and the only one that occurs in the United States.

#### METHODS OF STUDY

My familiarity with the habits of the Olive Warbler stems chiefly from field work conducted during April, May, June, and July of 1961 on Mt. Lemmon, Santa Catalina Mountains, Arizona. I obtained anatomical data on New World songbirds by comparing dermestid-cleaned hyoids (177 genera, 352 species), and by making complete dissections under an appropriate microscope of the hyoidean musculature of specimens preserved in spirits (115 genera, 188 species). A number of incomplete dissections, involving only the M. hypoglossus posterior, also were made. Eggs and nests were compared in the usual way; in addition cross sections were made of the nests of *Peucedramus*, of the kinglet *Regulus satrapa*, and of various wood warblers of the genus *Dendroica*.

In an attempt to establish the function of hyoidean structures, I (A) constructed mechanical models of the hyoid bones, hyoid muscles, and tongue, (B) watched captive birds feed within the magnifying field of a photo-enlarging lens ( $\times 2-3$ ), and (C) exposed the throat region of living House Sparrows (*Passer domesticus*),<sup>1</sup> an operation that permitted a view of the hyoid horns and associated muscles as the bird moved its tongue forward and backward in the mouth. Even so, I must confess that my knowledge of hyoidean function consists rather more of inferences than of demonstrated facts.

The hyoidean nomenclature used here comes chiefly from Engels (1938). The nomenclature of Humphrey and Parkes (1959) is used in the discussion of molt.

#### ACKNOWLEDGMENTS

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<sup>1</sup> The hyoidean features of *Passer* are very similar to those of the typical Fringillidae.

History and by the loan of specimens from the following individuals and institutions: the American Museum of Natural History; Dr. Paul S. Baldwin; Dr. Robert I. Bowman; California Academy of Sciences; Museum of Zoology, University of Michigan; Museum of Vertebrate Zoology, University of California (Berkeley); and Peabody Museum of Natural History, Yale University. Moreover, donations of very valuable materials were made by Drs. M. Dale Arvey, Mont A. Cazier, Robert W. Dickerman, Joe T. Marshall, Jr., Allan R. Phillips, and Eliot Porter, by Messrs. James T. Bialac, Richard S. Crossin, A. L. Gardner, Patrick J. Gould, Lyndon L. Hargrave, Wallace G. Heath, Jack R. Hensley, Roy Johnson, Seymour H. Levy, Peter Marshall, and William J. Schaldach, and by Miss Ellen Ordway.

I am particularly indebted to Drs. Allan R. Phillips and Joe T. Marshall, Jr., whose contributions of Arizonan and Mexican species formed the basic collection that made my study of the hyoid possible; in addition they gave me the benefit of their great knowledge of Arizonan and Mexican birds.

I wish also to express special gratitude to Drs. Dean Amadon and W. E. Lanyon and Mr. Eugene Eisenmann for their suggestions and help with the manuscript, and to Mr. Patrick J. Gould and Mr. Peter W. Wescott, who accompanied me in the field on several important occasions and shared with me their observations on *Peucedramus*.

## HYOID BONES AND MUSCLES

The hyoid (fig. 1A) is a Y-shaped group of small bones and is saddled between, strung with, and moved by tiny muscles. The ceratobranchialia and epibranchialia, which together constitute the "hyoid horns," embrace the under side of the cranium, while the basihyale and paraglossalia lie in the mouth. Two muscles secure the hyoid to the sides of the mouth. One, the *M. branchiomandibularis*, originates on the anterior medial edge of the mandible and inserts on the epibranchiale (figs. 2A, 3); its contraction pulls the hyoid forward. The second, the *M. stylohyoideus* (figs. 2A, 3), reverses the action of the *M. branchiomandibularis* and helps to pull the hyoid backward. Invariably in New World songbirds the insertion of this muscle is on the basihyale. The point of its origin varies, however, there being the following three kinds of origin in the New World Oscines examined (see table 1):

1. Origin on the posterior dorsal tip of the mandible, a few fibers sometimes attaching superficially to the adjacent *M. depressor mandibulae*. The vast majority of species share this condition (fig. 2A).

2. Origin on the squamosal, the muscle passing across the dorsal surface of the posterior tip of the mandible. This condition has been noted only in a single species, *Coereba flaveola*.

3. Origin on the basitemporal plate of the skull, a condition noted only in *Sitta carolinensis*, *S. pygmaea*, *Chamaea fasciata*, *Regulus calendula*, *R. satrapa*, *Poliophtila caerulea*, and *Peucedramus*.

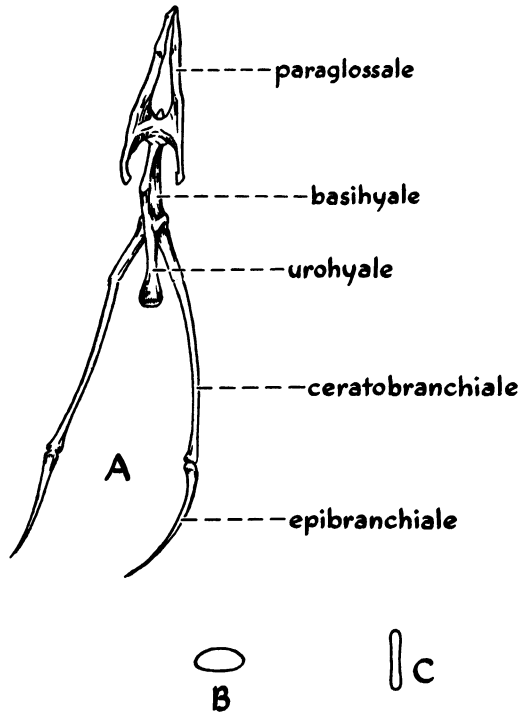


FIG. 1. A. Hyoid of *Saltator*, typical of the Coerebidae, Parulidae, Drepaniidae, Thraupidae, Icteridae, and Fringillidae. B. Cross section of the basihyale in *Peucedramus*. C. Cross section of the basihyale in the Coerebidae, Parulidae, Drepaniidae, Thraupidae, Icteridae, and Fringillidae.

An ability to manipulate the hyoid in some special way presumably is conferred by each of these different arrangements. In cases in which the muscle originates on the mandible, as in wood warblers, it occupies a more lateral position than in those in which it originates on the basitemporal plate, as in kinglets. A wood warbler consequently may be able to draw the hyoid into a more lateral position than a kinglet and in turn shift its tongue sideways (and side to side) better than a kinglet. On the

other hand, the arrangement in kinglets places the muscle in a relatively medial and posterior position; consequently a kinglet may be able to withdraw the hyoid (thus the tongue) deeper into the mouth than a wood warbler. One could set down a number of possible movements that the different origins of the muscle might permit. But such speculation would not alter the fact that at present I cannot demonstrate the functional significance of these alternative origins<sup>1</sup> and that in consequence the taxonomic importance of them remains in doubt.

Mayr (1956) has suggested that, in order to establish the taxonomic significance of the presence or absence of an adaptation, one must know the function of the adaptation and derive from that, if possible, an insight into the selective forces that caused the adaptation to arise or disappear in the evolutionary process. The phylogeny of the adaptation, and thus the systematic importance of its presence or absence, perhaps then can be determined. Bock's (1958) study of the medial brace of the jaw illustrates how one attacks a problem using this approach, an approach that conduces to speculation but has great merit nevertheless, for it compels the taxonomist to study the function of structures and to employ his results in prescribing how easily an adaptation could be evolved or selected out. In a word, it forces the systematist to consider convergence and reversal.

The kinglet-like origin of the *M. stylohyoideus* in *Peucedramus* may be an example of convergence. I cannot show that it is or is not. But I think that probably *Peucedramus* inherited the characteristic from non-parulid ancestors, because the opposite opinion is ill supported by other evidence, some of which arises from further consideration of features in the hyoid.

Any movement of the hyoid, of course, changes the position of the tongue. The tongue is attached to the anterior end of the basihyale and is composed of the two anterior bones of the hyoid (the paraglossalia), plus the tissues investing them. Commonly the hyoid bones are called "tongue bones." But, as I indicate, the paraglossalia alone are the tongue bones. Of all the hyoid bones, they are most directly involved when the tongue undergoes change.

Many hyoidean structures generally escape serious revision in the evolution of new tongue types. Of the bones, the basihyale especially

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<sup>1</sup> The arrangement in *Coereba* is an adaptation correlated with a lengthening of the hyoid horns and the nectar-feeding habit. *Coereba* has quite lengthy hyoid horns. In consequence the muscle that attaches to the posterior tip of the horns, the *M. branchiomandibularis*, has become elongated also, as has the muscle that opposes the *M. branchiomandibularis*, the *M. stylohyoideus*. The origin of this latter muscle has moved posteriorly onto the skull in the process.

TABLE 1  
SHAPE OF BASHYALE, ORIGIN OF M. STYLOHYOIDEUS, AND CONDITION OF M. HYPOGLOSSUS  
POSTERIOR IN THE NEW WORLD SONGBIRDS STUDIED

	Bashyale		Stylohyoideus		Hypoglossus Posterior	
	No. Examined	Shape	No. Examined	Origin	No. Examined	Condition
Alaudidae	2	Cylindrical	1	Mandible	1	A <sup>a</sup>
<i>Eremophila alpestris</i>						
Hirundinidae						
<i>Tachycineta bicolor</i>	2	Cylindrical	—	—	—	—
<i>T. thalassina</i>	2	Cylindrical	—	Mandible	—	—
<i>Progne subis</i>	3	Cylindrical	—	—	—	—
<i>P. chalybea</i>	2	Cylindrical	—	—	—	—
<i>Notiochelidon pileata</i>	1	Cylindrical	—	—	1	B
<i>Stelgidopteryx ruficollis</i>	1	Cylindrical	—	—	—	—
<i>Riparia riparia</i>	4	Cylindrical	—	—	—	—
<i>Hirundo rustica</i>	4	Cylindrical	—	—	—	—
<i>Petrochelidon pyrrhonota</i>	2	Cylindrical	1	Mandible	1	B
<i>P. fulva</i>	2	Cylindrical	—	—	—	—
	1	Cylindrical	—	—	1	B
Corvidae						
<i>Corvus corax</i>	3	Cylindrical	2	Mandible	2	A
<i>Neufriqua columbiana</i>	3	Cylindrical	1	Mandible	2	A
<i>Calocitta formosa</i>	3	Cylindrical	—	—	—	—
<i>Psilorhinus mexicanus</i>	2	Cylindrical	—	—	1	A
<i>Cyanocorax yncas</i>	2	Cylindrical	—	—	—	—
<i>Cissilopha beecheyi</i>	2	Cylindrical	—	—	—	—
<i>Cyanolyca pumilo</i>	2	Cylindrical	—	—	—	—

<sup>a</sup> Symbols: A, no insertion on bashiyale; B, insertion on bashiyale.

TABLE 1—(Continued)

	Basihyale		Stylohyoideus		Hypoglossus Posterior	
	No. Examined	Shape	No. Examined	Origin	No. Examined	Condition
<i>Aphelocoma coerulescens</i>	4	Cylindrical	1	Mandible	1	A
<i>A. ultramarina</i>	5	Cylindrical	2	Mandible	2	A
<i>A. unicolor</i>	1	Cylindrical	—	—	—	—
<i>Cyanocitta stelleri</i>	7	Cylindrical	1	Mandible	1	A
<i>Perisoreus canadensis</i>	2	Cylindrical	1	Mandible	1	A
<i>Pica pica</i>	4	Cylindrical	—	—	—	—
Paridae						
<i>Parus sclateri</i>	6	Cylindrical	2	Mandible	2	A
<i>P. gambeli</i>	4	Cylindrical	1	Mandible	1	A
<i>P. inornatus</i>	3	Cylindrical	1	Mandible	2	A
<i>P. wollweberi</i>	5	Cylindrical	2	Mandible	2	A
<i>Auriparus flaviceps</i>	5	Cylindrical	2	Mandible	2	A
<i>Psaltiriparus minimus</i>	4	Cylindrical	2	Mandible	2	A
Sittidae						
<i>Sitta carolinensis</i>	4	Cylindrical	2	Skull	2	A
<i>S. canadensis</i>	1	Cylindrical	—	—	—	—
<i>S. pygmaea</i>	5	Cylindrical	2	Skull	2	A
Certhiidae						
<i>Certhia familiaris</i>	12	Laterally compressed	3	Mandible	6	B
Chamaeidae						
<i>Chamaea fasciata</i>	2	Cylindrical	1	Skull	1	A
Cinclidae						
<i>Cinclus mexicanus</i>	1	Cylindrical	—	—	—	—
Troglodytidae						
<i>Campylorhynchus brunneicapillus</i>	6	Cylindrical	1	Mandible	1	A

TABLE 1—(Continued)

	Basihyale		Stylohyoideus		Hypoglossus Posterior	
	No. Examined	Shape	No. Examined	Origin	No. Examined	Condition
<i>C. rufinucha</i>	2	Cylindrical	—	—	—	—
<i>C. zonatus</i>	2	Cylindrical	—	—	—	—
<i>Salpinctes mexicanus</i>	5	Cylindrical	—	—	—	—
<i>S. obsoletus</i>	4	Cylindrical	—	—	—	—
<i>Cistothorus platensis</i>	1	Cylindrical	—	—	1	A
<i>Thryomanes bewickii</i>	3	Cylindrical	1	Mandible	1	A
<i>Thryothorus felix</i>	2	Cylindrical	—	—	—	—
<i>T. pleurostictus</i>	3	Cylindrical	—	—	—	—
<i>T. rufalbus</i>	2	Cylindrical	—	—	—	—
<i>T. modestus</i>	3	Cylindrical	—	—	—	—
<i>Trogodytes troglodytes</i>	1	Cylindrical	—	—	—	—
<i>T. aedon</i>	3	Cylindrical	1	Mandible	1	A
<i>Uropsila leucogastra</i>	2	Cylindrical	—	—	—	—
<i>Henicortina leucosticta</i>	2	Cylindrical	—	—	—	—
<i>H. leucophrys</i>	3	Cylindrical	—	—	—	—
Mimidae						
<i>Melanotis caerulescens</i>	4	Cylindrical	—	—	1	A
<i>Mimus polyglottos</i>	6	Cylindrical	1	Mandible	1	A
<i>Oreoscoptes montanus</i>	2	Cylindrical	—	—	—	—
<i>Toxostoma rufum</i>	1	Cylindrical	—	—	—	—
<i>T. bendirei</i>	3	Cylindrical	—	—	—	—
<i>T. curvirostre</i>	6	Cylindrical	1	Mandible	1	A
<i>T. dorsale</i>	4	Cylindrical	1	Mandible	1	A
Turdidae						
<i>Sialia sialis</i>	2	Cylindrical	—	—	—	—



TABLE 1—(Continued)

	Basihyale		Stylohyoideus		Hypoglossus Posterior	
	No. Examined	Shape	No. Examined	Origin	No. Examined	Condition
<i>S. mexicana</i>	3	Cylindrical	—	—	—	—
<i>S. curruoides</i>	3	Cylindrical	—	—	—	—
<i>Myadestes townsendi</i>	3	Cylindrical	1	Mandible	1	A
<i>M. obscurus</i>	2	Cylindrical	—	—	—	—
<i>Phaenais obscura</i>	1	Cylindrical	1	Mandible	1	A
<i>Oenanthe oenanthe</i>	2	Cylindrical	2	Mandible	2	A
<i>Ixoreus naevius</i>	1	Cylindrical	—	—	—	—
<i>Ridgwynia pinicola</i>	1	Cylindrical	—	—	—	—
<i>Catharus aurantirostris</i>	4	Cylindrical	—	—	—	—
<i>C. occidentalis</i>	3	Cylindrical	—	—	—	—
<i>C. dryas</i>	1	Cylindrical	—	—	—	—
<i>Hylocichla minima</i>	2	Cylindrical	2	Mandible	2	A
<i>H. ustulata</i>	1	Cylindrical	—	—	—	—
<i>H. guttata</i>	6	Cylindrical	2	Mandible	2	A
<i>Turdus migratorius</i>	6	Cylindrical	2	Mandible	2	A
<i>T. rufiglorus</i>	2	Cylindrical	—	—	—	—
<i>T. rufo-palliatu</i>	4	Cylindrical	—	—	—	—
<i>T. assimilis</i>	3	Cylindrical	—	—	—	—
<i>T. grayi</i>	5	Cylindrical	—	—	—	—
<i>T. infuscatus</i>	1	Cylindrical	—	—	—	—
Sylviidae						
<i>Poliophtila caerulea</i>	4	Cylindrical	2	Skull	2	A
<i>P. albiloris</i>	2	Cylindrical	—	—	—	—
<i>P. dumicola</i>	2	Cylindrical	2	Skull	2	A
<i>P. nigriceps</i>	5	Cylindrical	—	—	—	—

TABLE 1—(Continued)

	Basihyale		Stylohyoideus		Hypoglossus Posterior	
	No. Examined	Shape	No. Examined	Origin	No. Examined	Condition
<i>Ramphocaelus rufiventris</i>	3	Cylindrical	—	—	1	A
<i>Microbatas cinereiventris</i>	1	Cylindrical	—	—	—	—
<i>Regulus satrapa</i>	5	Cylindrical	3	Skull	3	A
<i>R. catenula</i>	8	Cylindrical	3	Skull	3	A
Motacillidae						
<i>Anthus spinoletta</i>	3	Cylindrical	1	Mandible	1	A
Dulidae						
<i>Dulus dominicus</i>	2	Cylindrical	1	Mandible	1	A
Bombycillidae						
<i>Bombycilla garrulus</i>	3	Cylindrical	1	Mandible	1	A
<i>B. cedrorum</i>	2	Cylindrical	2	Mandible	2	A
Ptilagonatidae						
<i>Ptilogonys cinereus</i>	3	Cylindrical	—	—	—	—
<i>Phanopepla nitens</i>	4	Cylindrical	2	Mandible	2	A
Laniidae						
<i>Lanius ludovicianus</i>	5	Cylindrical	1	Mandible	1	A
Cyclarhidae						
<i>Cyclarhis guianensis</i>	4	Cylindrical	1	Mandible	1	A
Vireolaniidae						
<i>Vireolanius meliophrys</i>	1	Cylindrical	—	—	—	—
<i>Smaragdonanius pulchellus</i>	1	Cylindrical	—	—	—	—
Vireonidae						
<i>Vireo atricapillus</i>	3	Cylindrical	—	—	—	—
<i>V. griseus</i>	2	Cylindrical	—	—	—	—
<i>V. huttoni</i>	10	Cylindrical	3	Mandible	3	A

TABLE 1—(Continued)

	Basihyale		Stylohyoideus		Hypoglossus Posterior	
	No. Examined	Shape	No. Examined	Origin	No. Examined	Condition
<i>V. hypochryseus</i>	2	Cylindrical	1	Mandible	1	A
<i>V. victor</i>	1	Cylindrical	—	—	—	—
<i>V. nanus</i>	2	Cylindrical	—	—	—	—
<i>V. bellii</i>	7	Cylindrical	2	Mandible	2	A
<i>V. solitarius</i>	10	Cylindrical	4	Mandible	4	A
<i>V. olivaceus</i>	6	Cylindrical	4	Mandible	4	A
<i>V. philadelphicus</i>	4	Cylindrical	2	Mandible	2	A
<i>V. gilvus</i>	8	Cylindrical	3	Mandible	3	A
<i>Neochloe brevipennis</i>	1	Cylindrical	—	—	—	—
<i>Hylophilus poicilotis</i>	1	Cylindrical	1	Mandible	1	A
<i>H. decurtatus</i>	4	Cylindrical	2	Mandible	2	A
Coerebidae						
<i>Dioglossa baritula</i>	4	Laterally compressed	1	Mandible	1	B
<i>D. lefresnaya</i>	1	Laterally compressed	—	—	—	—
<i>D. carbonaria</i>	1	Laterally compressed	—	—	—	—
<i>D. albilatera</i>	1	Laterally compressed	—	—	—	—
<i>D. cyanea</i>	1	Laterally compressed	—	—	—	—
<i>Chlorophanes spiza</i>	1	Laterally compressed	—	—	—	—
<i>Cyanerpes cyaneus</i>	5	Laterally compressed	3	Mandible	3	B
<i>C. caeruleus</i>	1	Laterally compressed	—	—	—	—
<i>Dacnis venusta</i>	1	Laterally compressed	—	—	—	—
<i>D. cayana</i>	1	Laterally compressed	—	—	—	—
<i>Coereba flaveola</i>	5	Laterally compressed	1	Mandible	1	B
<i>Atledacnis</i> sp.	1	Laterally compressed	3	Squamosal	3	B
<i>Controstrum bicolor</i>	1	Laterally compressed	1	Mandible	1	B
	2	Laterally compressed	—	—	—	—

TABLE 1—(Continued)

	Basihyale		Stylohyoideus		Hypoglossus Posterior	
	No. Examined	Shape	No. Examined	Origin	No. Examined	Condition
Drepanididae						
<i>Loxops virens</i>	1	Laterally compressed	1	Mandible	1	B
<i>L. maculata</i>	2	Laterally compressed	1	Mandible	1	B
<i>Hemignathus wilsoni</i>	1	Laterally compressed	1	Mandible	1	B
<i>Psittirostra bailliei</i>	1	Laterally compressed	1	Mandible	1	B
<i>Himatione sanguinea</i>	1	Laterally compressed	1	Mandible	1	B
<i>Vestiaria coccinea</i>	1	Laterally compressed	1	Mandible	1	B
Parulidae						
<i>Mniotilta varia</i>	4	Laterally compressed	3	Mandible	3	B
<i>Protonotaria citrea</i>	6	Laterally compressed	1	Mandible	1	B
<i>Limothlypis swainsonii</i>	1	Laterally compressed	—	—	—	—
<i>Helmitheros vermivorus</i>	3	Laterally compressed	1	Mandible	1	B
<i>Vermivora chrysoptera</i>	2	Laterally compressed	—	—	—	—
<i>V. celata</i>	12	Laterally compressed	3	Mandible	3	B
<i>V. peregrina</i>	3	Laterally compressed	1	Mandible	1	B
<i>V. ruficapilla</i>	3	Laterally compressed	2	Mandible	2	B
<i>V. virginiae</i>	4	Laterally compressed	3	Mandible	3	B
<i>V. luciae</i>	11	Laterally compressed	5	Mandible	5	B
<i>V. superciliosa</i>	2	Laterally compressed	1	Mandible	1	B
<i>Parula americana</i>	3	Laterally compressed	2	Mandible	2	B
<i>P. pitayumi</i>	2	Laterally compressed	—	—	—	—
<i>Peucedramus taeniatus</i>	14	Cylindrical	9	Mandible	9	A
<i>Dendroica petechia</i>	6	Laterally compressed	2	Mandible	2	—
<i>D. erithaciorides</i>	2	Laterally compressed	—	—	—	—
<i>D. magnolia</i>	8	Laterally compressed	2	Mandible	2	B

TABLE 1—(Continued)

	Basihyale		Stylohyoideus		Hypoglossus Posterior	
	No. Examined	Shape	No. Examined	Origin	No. Examined	Condition
<i>D. tigrina</i>	5	Laterally compressed	1	Mandible	1	B
<i>D. caerulea</i>	2	Laterally compressed	1	Mandible	1	B
<i>D. coronata</i>	2	Laterally compressed	1	Mandible	1	B
<i>D. auduboni</i>	12	Laterally compressed	7	Mandible	7	B
<i>D. nigrescens</i>	12	Laterally compressed	4	Mandible	4	B
<i>D. townsendi</i>	9	Laterally compressed	2	Mandible	2	B
<i>D. vitens</i>	1	Laterally compressed	—	—	—	—
<i>D. chrysoparia</i>	1	Laterally compressed	—	—	—	—
<i>D. occidentalis</i>	6	Laterally compressed	3	Mandible	3	B
<i>D. cerulea</i>	3	Laterally compressed	—	—	—	—
<i>D. fusca</i>	4	Laterally compressed	1	Mandible	1	B
<i>D. dominica</i>	3	Laterally compressed	1	Mandible	1	B
<i>D. gracie</i>	3	Laterally compressed	—	—	—	—
<i>D. pennsylvanica</i>	2	Laterally compressed	—	—	—	—
<i>D. castanea</i>	4	Laterally compressed	1	Mandible	1	B
<i>D. striata</i>	4	Laterally compressed	—	—	—	—
<i>D. pinus</i>	8	Laterally compressed	—	—	—	—
<i>D. kirtlandi</i>	2	Laterally compressed	2	Mandible	2	B
<i>D. discolor</i>	5	Laterally compressed	1	Mandible	1	B
<i>D. palmarum</i>	7	Laterally compressed	2	Mandible	2	B
<i>D. phareta</i>	1	Laterally compressed	1	Mandible	1	B
<i>Catharopeza bishopi</i>	2	Laterally compressed	—	—	—	—
<i>Seiurus aurocapillus</i>	6	Laterally compressed	3	Mandible	3	B
<i>S. motacilla</i>	1	Laterally compressed	1	Mandible	1	B
<i>S. noveboracensis</i>	2	Laterally compressed	1	Mandible	1	B

TABLE 1—(Continued)

	Basihyale		Stylohyoideus		Hypoglossus Posterior	
	No. Examined	Shape	No. Examined	Origin	No. Examined	Condition
<i>Oporornis formosus</i>	5	Laterally compressed	2	Mandible	2	B
<i>O. agilis</i>	3	Laterally compressed	—	—	—	—
<i>O. philadelphia</i>	2	Laterally compressed	—	—	—	—
<i>O. tolmiei</i>	8	Laterally compressed	4	Mandible	4	B
<i>Teretistris fornsi</i>	1	Laterally compressed	—	—	—	—
<i>Microtinea palustris</i>	3	Laterally compressed	1	Mandible	1	B
<i>Geothlypis trichas</i>	5	Laterally compressed	1	Mandible	1	B
<i>G. chapalensis</i>	1	Laterally compressed	—	—	—	—
<i>Chamaethlypis poliocephala</i>	2	Laterally compressed	1	Mandible	1	B
<i>Icteria virens</i>	7	Laterally compressed	2	Mandible	2	B
<i>Granatellus venustus</i>	1	Laterally compressed	—	—	—	—
<i>G. sallaei</i>	2	Laterally compressed	1	Mandible	1	B
<i>Wilsonia citrina</i>	4	Laterally compressed	2	Mandible	2	B
<i>W. pusilla</i>	9	Laterally compressed	3	Mandible	3	B
<i>W. canadensis</i>	5	Laterally compressed	—	—	—	—
<i>Cardellina rubrifrons</i>	5	Laterally compressed	2	Mandible	2	B
<i>Setophaga ruticilla</i>	2	Laterally compressed	2	Mandible	2	B
<i>S. picta</i>	5	Laterally compressed	4	Mandible	4	B
<i>Myioborus</i> sp.	1	Laterally compressed	1	Mandible	1	B
<i>M. miniatus</i>	3	Laterally compressed	—	—	—	—
<i>M. torquatus</i>	1	Laterally compressed	—	—	—	—
<i>M. brunnieps</i>	1	Laterally compressed	—	—	—	—
<i>Euthlypis lachrymosa</i>	3	Laterally compressed	1	Mandible	1	B
<i>Ergaticus ruber</i>	1	Laterally compressed	—	—	—	—
<i>E. versicolor</i>	2	Laterally compressed	2	Mandible	2	B

TABLE 1—(Continued)

	Basihyale		Stylohyoideus		Hypoglossus Posterior	
	No. Examined	Shape	No. Examined	Origin	No. Examined	Condition
<i>Basileuterus leucoblepharus</i>	1	Laterally compressed	1	Mandible	1	B
<i>B. culicivorus</i>	2	Laterally compressed	1	Mandible	1	B
<i>B. melanagenys</i>	3	Laterally compressed	—	—	—	—
<i>B. belli</i>	4	Laterally compressed	1	Mandible	1	B
<i>B. rufifrons</i>	3	Laterally compressed	—	—	—	—
<i>B. delatitri</i>	1	Laterally compressed	—	—	—	—
<i>B. rivularis</i>	1	Laterally compressed	1	Mandible	1	B
Icteridae						
<i>Amblycercus holosericeus</i>	2	Laterally compressed	1	Mandible	2	B
<i>Cassiculus melanicterus</i>	4	Laterally compressed	—	—	—	—
<i>Tangaius aeneus</i>	4	Laterally compressed	1	Mandible	1	B
<i>Molothrus ater</i>	40	Laterally compressed	3	Mandible	3	B
<i>Cassidix mexicanus</i>	22	Laterally compressed	2	Mandible	2	B
<i>Euphagus carolinus</i>	1	Laterally compressed	—	—	—	—
<i>E. cyanocephalus</i>	3	Laterally compressed	—	—	—	—
<i>Dives dives</i>	1	Laterally compressed	—	—	—	—
<i>Icterus galbula</i>	3	Laterally compressed	—	—	—	—
<i>I. bullocki</i>	3	Laterally compressed	—	—	—	—
<i>I. spurius</i>	7	Laterally compressed	—	—	—	—
<i>I. prothemelas</i>	1	Laterally compressed	—	—	—	—
<i>I. parisorum</i>	4	Laterally compressed	1	Mandible	1	B
<i>I. wagleri</i>	3	Laterally compressed	—	—	—	—
<i>I. chrysater</i>	3	Laterally compressed	—	—	—	—
<i>I. gradacauda</i>	2	Laterally compressed	—	—	—	—
<i>I. pectoralis</i>	2	Laterally compressed	—	—	—	—

TABLE 1—(Continued)

	No. Examined	Basihyale	Shape	No. Examined	Stylohyoideus	Origin	Hypoglossus No. Examined	Posterior Condition
<i>I. gularis</i>	2	Laterally compressed	—	—	—	—	—	—
<i>I. cucullatus</i>	5	Laterally compressed	Mandible	2	2	Mandible	2	B
<i>I. pustulatus</i>	6	Laterally compressed	—	—	—	—	—	—
<i>Agelaius phoeniceus</i>	4	Laterally compressed	Mandible	1	1	Mandible	2	B
<i>Xanthocephalus xanthocephalus</i>	5	Laterally compressed	Mandible	1	1	Mandible	1	B
<i>Sturnella magna</i>	4	Laterally compressed	Mandible	1	1	Mandible	1	B
<i>S. magna</i>	9	Laterally compressed	Mandible	1	1	Mandible	1	B
<i>Dolichonyx oryzivorus</i>	4	Laterally compressed	—	—	—	—	—	—
Tersinidae								
<i>Tersina viridis</i>	2	Cylindrical	—	—	—	—	—	—
Catamblyrhynchidae								
<i>Catamblyrhynchus diadema</i>	2	Laterally compressed	—	—	—	—	—	—
Thraupidae								
<i>Chlorophonia occipitalis</i>	2	Laterally compressed	—	—	—	—	—	—
<i>C. cyanea</i>	1	Laterally compressed	Mandible	1	1	Mandible	1	B
<i>Tanagra musica</i>	3	Laterally compressed	—	—	—	—	—	—
<i>T. affinis</i>	2	Laterally compressed	—	—	—	—	—	—
<i>T. lula</i>	2	Laterally compressed	Mandible	2	2	Mandible	2	B
<i>T. gouldi</i>	1	Laterally compressed	—	—	—	—	1	B
<i>Tangara nigrocinata</i>	1	Laterally compressed	—	—	—	—	—	—
<i>T. dowii</i>	1	Laterally compressed	—	—	—	—	—	—
<i>Calospiza cyanoptera</i>	1	Laterally compressed	—	—	—	—	—	—
<i>Compsocoma flavinucha</i>	1	Laterally compressed	—	—	—	—	—	—
<i>Thraupis virens</i>	5	Laterally compressed	—	—	—	—	3	B
<i>T. abbas</i>	3	Laterally compressed	Mandible	1	1	Mandible	1	B



TABLE 1—(Continued)

	No. Examined	Basihyale	Shape	No. Examined	Stylohyoideus	Hypoglossus Posterior	Condition
<i>Spindalis zena</i>	1		Laterally compressed	—	—	—	—
<i>Ramphocelus carbo</i>	1		Laterally compressed	—	—	—	—
<i>R. passerinii</i>	2		Laterally compressed	1	Mandible	1	B
<i>Phlogothraupis sanguinolenta</i>	1		Laterally compressed	—	—	—	—
<i>Piranga rubra</i>	3		Laterally compressed	1	Mandible	1	B
<i>P. flava</i>	5		Laterally compressed	—	—	—	—
<i>P. hepatica</i>	6		Laterally compressed	2	Mandible	2	B
<i>P. leucoptera</i>	6		Laterally compressed	1	Mandible	1	B
<i>P. ludoviciana</i>	5		Laterally compressed	1	Mandible	1	B
<i>P. bidentata</i>	2		Laterally compressed	—	—	—	—
<i>P. erythrocephala</i>	3		Laterally compressed	—	—	—	—
<i>Chlorothraupis carmioli</i>	1		Laterally compressed	—	—	—	—
<i>Habia rubica</i>	4		Laterally compressed	1	Mandible	1	B
<i>H. gutturalis</i>	3		Laterally compressed	1	Mandible	1	B
<i>Lanio aurantius</i>	3		Laterally compressed	1	Mandible	1	B
<i>Eucometis penicillata</i>	1		Laterally compressed	—	—	—	—
<i>Mitrospingus cassinii</i>	1		Laterally compressed	—	—	—	—
<i>Rhodinocichla rosea</i>	3		Laterally compressed	1	Mandible	1	B
<i>Phoenicophilus palmarum</i>	1		Laterally compressed	1	Mandible	1	B
<i>Gypsanagra hirundinacea</i>	1		Laterally compressed	1	Mandible	1	B
<i>Nemosia pileata</i>	1		Laterally compressed	—	—	—	—
<i>Hemithraupis guira</i>	1		Laterally compressed	1	Mandible	1	B
<i>Chlorospingus ophthalmicus</i>	5		Laterally compressed	1	Mandible	1	B
Fringillidae							
Carduelinae							

TABLE 1—(Continued)

	Basihyale		Stylohyoideus		Hypoglossus Posterior	
	No. Examined	Shape	No. Examined	Origin	No. Examined	Condition
<i>Hesperiphona vespertina</i>	2	Laterally compressed	—	—	—	—
<i>H. beillei</i>	1	Laterally compressed	—	—	—	—
<i>Carpodacus cassinii</i>	3	Laterally compressed	1	Mandible	1	B
<i>C. mexicanus</i>	8	Laterally compressed	3	Mandible	3	B
<i>Spinus pinus</i>	3	Laterally compressed	—	—	—	—
<i>S. atriceps</i>	4	Laterally compressed	—	—	1	B
<i>S. notatus</i>	2	Laterally compressed	—	—	—	—
<i>S. tristis</i>	5	Laterally compressed	3	Mandible	3	B
<i>S. psaltria</i>	6	Laterally compressed	3	Mandible	3	B
<i>S. laurencei</i>	5	Laterally compressed	2	Mandible	2	B
<i>Loxia curvirostra</i>	8	Laterally compressed	2	Mandible	3	B
<i>L. leucoptera</i>	2	Laterally compressed	—	—	1	B
<i>Pinicola enucleator</i>	3	Laterally compressed	1	Mandible	1	B
<i>Acanthus flammea</i>	1	Laterally compressed	—	—	—	—
Geospizinae						
<i>Geospiza magnirostris</i>	2	Laterally compressed	1	Mandible	1	B
<i>G. fortis</i>	2	Laterally compressed	—	—	—	—
<i>G. fuliginosa</i>	2	Laterally compressed	1	Mandible	1	B
<i>G. scandens</i>	1	Laterally compressed	—	—	—	—
<i>G. comirostris</i>	1	Laterally compressed	—	—	—	—
<i>Platyspiza crassirostris</i>	1	Laterally compressed	—	—	—	—
<i>Camarhynchus psittacula</i>	2	Laterally compressed	1	Mandible	1	B
<i>C. parulus</i>	2	Laterally compressed	1	Mandible	1	B
<i>Cactospiza pallida</i>	2	Laterally compressed	1	Mandible	1	B
<i>Certhidea olivacea</i>	3	Laterally compressed	1	Mandible	1	B

TABLE 1—(Continued)

	Basihyale		Stylohyoideus		Hypoglossus Posterior	
	No. Examined	Shape	No. Examined	Origin	No. Examined	Condition
Fringillinae						
<i>Saltator atriceps</i>	2	Laterally compressed	1	Mandible	1	B
<i>S. maximus</i>	2	Laterally compressed	1	Mandible	1	B
<i>S. coerulescens</i>	4	Laterally compressed	1	Mandible	1	B
<i>Paroaria</i> sp.	3	Laterally compressed	2	Mandible	2	B
<i>Richmondia cardinalis</i>	16	Laterally compressed	4	Mandible	4	B
<i>Pyrrhuloxia sinuata</i>	12	Laterally compressed	4	Mandible	4	B
<i>Pheucticus chrysophepalus</i>	3	Laterally compressed	—	—	2	B
<i>P. ludovicianus</i>	2	Laterally compressed	—	—	—	—
<i>P. melanocephalus</i>	4	Laterally compressed	1	Mandible	1	B
<i>Guiraca caerulea</i>	4	Laterally compressed	2	Mandible	2	B
<i>Cyanocitta stelleri</i>	3	Laterally compressed	1	Mandible	1	B
<i>Passerina cyanea</i>	2	Laterally compressed	—	—	—	—
<i>P. amoena</i>	5	Laterally compressed	2	Mandible	2	B
<i>P. versicolor</i>	1	Laterally compressed	—	—	—	—
<i>P. rositae</i>	8	Laterally compressed	1	Mandible	1	B
<i>P. citris</i>	1	Laterally compressed	—	—	—	—
<i>P. leclancherii</i>	6	Laterally compressed	—	—	—	—
<i>Sporophila torqueola</i>	3	Laterally compressed	2	Mandible	2	B
<i>S. minuta</i>	2	Laterally compressed	—	—	—	—
<i>Oryzoborus funereus</i>	1	Laterally compressed	—	—	1	B
<i>Volatinia jacarina</i>	6	Laterally compressed	1	Mandible	2	B
<i>Sicalis luteola</i>	1	Laterally compressed	1	Mandible	1	B
<i>Atlapetes albinucha</i>	4	Laterally compressed	1	Mandible	1	B
<i>A. brunnei-nucha</i>	3	Laterally compressed	1	Mandible	1	B

TABLE 1—(Continued)

	Basihyale		Stylohyoideus		Hypoglossus Posterior	
	No. Examined	Shape	No. Examined	Origin	No. Examined	Condition
<i>Arremon aurantirostris</i>	3	Laterally compressed	1	Mandible	2	B
<i>Arremonops rufivirgatus</i>	1	Laterally compressed	—	—	—	—
<i>Chlorura chlorura</i>	7	Laterally compressed	2	Mandible	2	B
<i>Pipilo ocai</i>	2	Laterally compressed	—	—	—	—
<i>P. erythrophthalmus</i>	5	Laterally compressed	1	Mandible	1	B
<i>P. fuscus</i>	7	Laterally compressed	2	Mandible	2	B
<i>P. aberti</i>	5	Laterally compressed	2	Mandible	2	B
<i>Melospiza kienneri</i>	3	Laterally compressed	1	Mandible	1	B
<i>Oriturus superciliosa</i>	4	Laterally compressed	1	Mandible	2	B
<i>Calamospiza melanocorys</i>	6	Laterally compressed	2	Mandible	2	B
<i>Passerculus sandwichensis</i>	5	Laterally compressed	—	—	—	—
<i>Ammodramus saviannorum</i>	6	Laterally compressed	2	Mandible	2	B
<i>A. bairdii</i>	2	Laterally compressed	—	—	—	—
<i>Poocetes gramineus</i>	8	Laterally compressed	3	Mandible	3	B
<i>Xenospiza baileyi</i>	1	Laterally compressed	—	—	—	—
<i>Amnospiza caudacuta</i>	1	Laterally compressed	—	—	1	B
<i>Chondestes grammacus</i>	5	Laterally compressed	3	Mandible	3	B
<i>Aimophila mysticalis</i>	1	Laterally compressed	1	Mandible	1	B
<i>A. humeralis</i>	2	Laterally compressed	—	—	—	—
<i>A. ruficauda</i>	4	Laterally compressed	—	—	—	—
<i>A. carpalis</i>	6	Laterally compressed	2	Mandible	2	B
<i>A. sumichrasti</i>	3	Laterally compressed	1	Mandible	1	B
<i>A. rufescens</i>	3	Laterally compressed	—	—	—	—
<i>A. ruficeps</i>	8	Laterally compressed	2	Mandible	2	B
<i>A. bolteri</i>	3	Laterally compressed	—	—	—	—

TABLE 1—(Continued)

	Basihyale		Stylohyoideus		Hypoglossus Posterior	
	No. Examined	Shape	No. Examined	Origin	No. Examined	Condition
<i>A. castinii</i>	12	Laterally compressed	4	Mandible	4	B
<i>Amphispiza bilineata</i>	7	Laterally compressed	3	Mandible	3	B
<i>A. belli</i>	2	Laterally compressed	—	—	—	—
<i>Junco hyemalis</i>	2	Laterally compressed	1	Mandible	1	B
<i>J. oreganus</i>	3	Laterally compressed	2	Mandible	2	B
<i>J. phaeonotus</i>	9	Laterally compressed	5	Mandible	5	B
<i>Spizella passerina</i>	7	Laterally compressed	4	Mandible	4	B
<i>S. pallida</i>	2	Laterally compressed	—	—	—	—
<i>S. breweri</i>	8	Laterally compressed	3	Mandible	3	B
<i>S. atrogularis</i>	2	Laterally compressed	—	—	1	B
<i>Zonotrichia leucophrys</i>	11	Laterally compressed	3	Mandible	3	B
<i>Z. albicollis</i>	2	Laterally compressed	1	Mandible	1	B
<i>Z. capensis</i>	2	Laterally compressed	—	—	—	—
<i>Passerella iliaca</i>	1	Laterally compressed	—	—	—	—
<i>Melospiza lincolni</i>	6	Laterally compressed	3	Mandible	3	B
<i>M. georgiana</i>	2	Laterally compressed	1	Mandible	1	B
<i>M. melodia</i>	5	Laterally compressed	3	Mandible	3	B
<i>Calcaricus ornatus</i>	6	Laterally compressed	2	Mandible	2	B

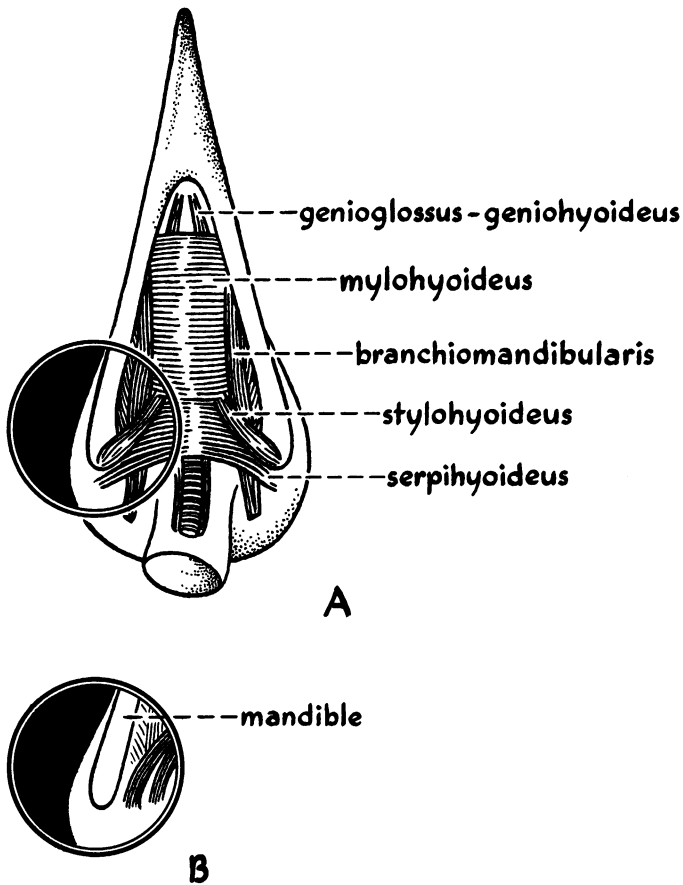


FIG. 2. A. Typical tongue musculature of songbirds, including the Parulidae, superficial dissection, ventral view. Note that the *M. stylohyoideus* originates on the mandible. Redrawn from Engels (1938). B. Origin on the skull of the *M. stylohyoideus* in *Peucedramus*.

seems to maintain an unchanged morphology as species evolve new dietary habits. It has only two fundamental shapes in New World songbirds. Either it is a round, or oval, or block-like bone (fig. 1B), or it is a thin, blade-like bone, the entire structure being laterally compressed (fig. 1C) except the anterior head and in some cases the ventral edge.

If species are segregated according to type of basihyale, a striking fact emerges: the laterally compressed type is restricted, with but one exception, to the Coerebidae, Parulidae, Drepanidae, Thraupidae, Catam-

blyrhynchidae, Icteridae, and Fringillidae (*sensu lato*).<sup>1</sup> The single American 10-primaried species that I have found to possess a laterally compressed basihyale is the Brown Creeper, *Certhia familiaris*. The only species currently classified among the Coerebidae, Parulidae, Drepanididae, Thraupidae, Icteridae, and Fringillidae (*sensu lato*) that, so far as I know,

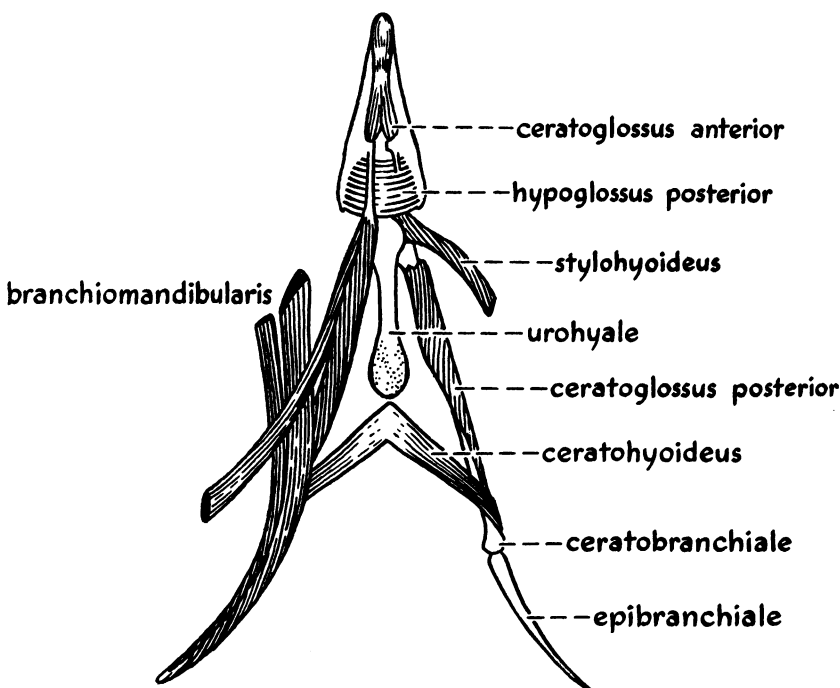


FIG. 3. Tongue musculature of a typical passerine, deep dissection, ventral view. The mylohyoideus and serpihyoideus have been removed. Redrawn from Engels (1938).

possesses the cylindrical type in *Peucedramus*. Table 1 gives the shape of basihyale for each species that I have examined.

The function of the basihyale is to furnish articulating surfaces for the paraglossalia, ceratobranchialia, and urohyale, and to accommodate the insertion of hyoid muscles. In all songbirds that I have examined it is the point of insertion of the *M. stylohyoideus*, the *M. tracheohyoideus*, and

<sup>1</sup> Note the exclusion of the Vireonidae and Tersinidae, two groups that are usually considered as part of the New World assemblage of "nine-primaried" songbirds; but the inclusion of *Rhodinocichla rosea*, a species the allocation of which often has been questioned.

the *M. thyreohyoideus* (fig. 4). Contraction of these muscles withdraws the hyoid. A fourth muscle, the *M. hypoglossus posterior* (fig. 3), inserts on the basihyale in some species, but not in others. It plays no role in withdrawing the hyoid. It is a small transverse muscle that originates on the medial edges of the paraglossalia and has the following different arrangements:

A. The muscle extends as a single, unpaired, uninterrupted band between the paraglossalia, passing beneath a cylindrical basihyale and not inserting on it (fig. 5A); the condition is characteristic of the Alaudidae, Corvidae, Paridae, Sittidae, Chamaeidae, Troglodytidae, Mimidae, Turdidae, Sylvidae, Motacillidae, Bombycillidae, Dulidae, Laniidae, Cyclarhidae, Vireolaniidae, Vireonidae, and *Peucedramus*.<sup>1</sup>

B. The muscle inserts on the ventrolateral faces of a cylindrical basihyale, a few fibers from the posterior margin of the muscle extending freely between the paraglossalia and beneath the basihyale; characteristic of the Hirundinidae only (figs. 5B, 6B).<sup>2</sup>

C. Much of or all the muscle inserts on a laterally compressed basihyale (figs. 5C, 5D, 6C, 6D); characteristic<sup>3</sup> of *Certhia familiaris*, and the Coerebidae, Parulidae, Drepanidae, Thraupidae, Icteridae, and Fringillidae (*sensu lato*).

The condition of the *M. hypoglossus posterior* in each species examined is given in table 1.

It is apparent, I think, that the *M. hypoglossus posterior* cannot function in the same way in all species, though as a general rule the force of its contraction depresses the posterior tips of the paraglossalia, elevating the anterior tips, and raising thereby the tip of the tongue. Contraction of another muscle, the *M. ceratoglossus posterior* (figs. 3, 7), reverses this action. A long slender muscle, it originates on the ceratobranchiale and runs forward, inserting by a lengthy tendon on the ventral side of the paraglossale, in front of the tongue joint (the joint of the paraglossalia-basihyale). A kind of ball-and-socket relationship characterizes the

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<sup>1</sup> This arrangement of the *M. hypoglossus posterior* occurs in all the Suboscines that I have dissected (eight families, 33 genera, 77 species); it appears to be an exclusive characteristic of the Passeriformes. I have not found it, at any rate, in Columbiformes, Psittaciformes, Cuculiformes, Strigiformes, Caprimulgiformes, Apodiformes, Trogoniformes, Coraciiformes, or Piciformes.

<sup>2</sup> In the peculiar African river martin *Pseudochelidon*, the muscle does not insert on the basihyale, though the basihyale is hirundinid (block-like, with flat sides).

<sup>3</sup> Some of the listed species have the entire muscle inserting on the basihyale, while others have only about half of the muscle inserting on that bone. How the two alternatives are distributed between or within families is of interest and will be described in a future paper.



tongue joint, and when the *M. hypoglossus* posterior and the *M. ceratoglossus* posterior alternately contract, the tongue pitches up and down like a teeter-totter (see fig. 7).

One of the three arrangements of the *M. hypoglossus* posterior appears particularly to facilitate teetering of the tongue: that which occurs in *Peucedramus*. This arrangement leaves the muscle free and unified throughout its entire length, none of its fibers inserting on the basihyale, and all of its fibers contributing the force of their contractions toward a single

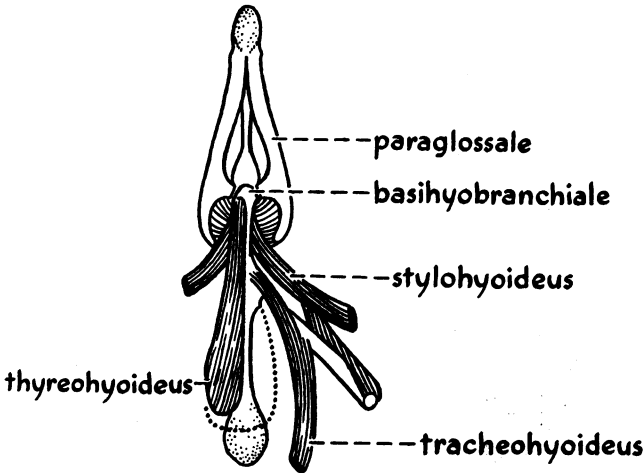


FIG. 4. The tongue musculature of a typical passerine, deep dissection, dorsal view. Basihyobranchiale=basihyale. Redrawn from Engels (1938).

mechanical objective. In consequence, the posterior tips of the paraglossalia are depressed deeply when the muscle contracts, and the anterior tip of the tongue is raised high. Such a tongue movement probably has great value to insectivorous birds, for their spiny prey often is alive and struggling when taken into the mouth. The teetering tongue can pummel an insect, overcome its resistance, and drive it ever deeper into the throat. I have seen nestling *Toxostoma curvirostre*, *T. bendirei*, and other species belabor grasshoppers in just this way with their tongues, and Gardner (1925, p. 7) witnessed the equivalent of it.

But why, if this manner of tongue movement has value to insectivorous species such as *Peucedramus*, do the highly insectivorous wood warblers have an arrangement of the *M. hypoglossus* posterior that cannot fully deliver such movement?

The arrangement in wood warblers must reduce the ability of the

tongue to teeter. About half of the fibers of the muscle insert on the basi-hyale, and contraction of these fibers tends to pull the posterior tips of the paraglossalia inward toward the basihyale, not depressing the tips sufficiently to pull the tongue through a deep arc. The function of the inserted fibers, of course, is not to lessen the ability of the tongue to teeter; they have a valuable function of their own. They secure the paraglossalia to the basihyale, or, in other words, they fasten the tongue securely to the hyoid and give support to the tongue joint. Compared to the situation in

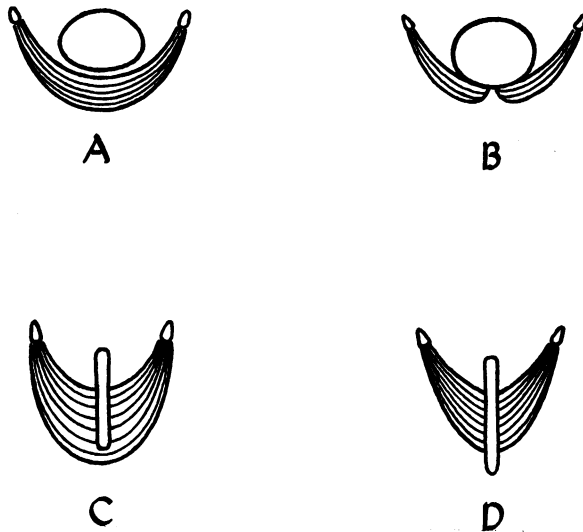


FIG. 5. Diagrammatic cross sections, showing the different arrangements of the M. hypoglossus posterior and basihyale in New World songbirds. A. *Peucedramus*. B. Swallows. C, D. The Parulidae and allied birds.

wood warblers, the tongue joint of *Peucedramus* is weakly supported, and the tongue is flimsily attached to the hyoid. The tongue of *Peucedramus* in consequence is less able to withstand strain than are tongues of wood warblers. Seemingly, then, wood warblers have an adaptation that would permit their tongues to do more strenuous work than the tongue of *Peucedramus*.

I think, however, that new stress placed on the tongue could lead to the rapid rise of this adaptation. The stress might ensue, for example, as a bird evolves a longer tongue. My data show that the paraglossalia of birds of equal size are always longest in the longer-tongued species. My data also show that the posterior tips of the paraglossalia are always about

the same length, regardless of the over-all length of the paraglossalia. I conclude that the anterior tips of the paraglossalia increase in length as the tissues of the tongue elongate. Now, a lengthening of the paraglossalia would add new and unbalanced weight to that part of the tongue that extends forward beyond the tongue joint. The added weight inevitably would place a strain on the joint and could precipitate the selective process by which the *M. hypoglossus posterior* becomes inserted on the basihyale. I accordingly conclude that the presence or absence of this adaptation may have little suprageneric significance.

An associated adaptation, the laterally compressed basihyale, appears, however, to have considerable suprageneric significance. It clearly does not arise in ready response to the vicissitudes of the *M. hypoglossus posterior*. In both swallows and wood warblers, the *M. hypoglossus posterior* inserts heavily on the basihyale, yet the basihyale of a wood warbler differs from that of a swallow, the former being a laterally compressed bone and the latter a block-like bone with flattened lateral surfaces. The difference between the shape of the bones seems not attributable to a difference in the relationship of the muscle to the bone during the early growth and development of the birds. The basihyalia of nestling Barn Swallows (*Hirundo rustica*) and nestling Painted Redstarts (*Setophaga picta*) are similar blocks of cartilage, equally invested by the *M. hypoglossus posterior*. As the nestlings develop into fledglings, the basihyale of *Setophaga* becomes laterally compressed, while that of *Hirundo* does not.

The basihyale of nestling *Peucedramus*, incidentally, has about the same shape as that of nestling *Hirundo* and that of *Setophaga*, but the *M. hypoglossus posterior* simply extends beneath the basihyale, as it does in adults.

I suspect that the laterally compressed basihyale arises in response to selection directed toward the securing of the tongue to the hyoid with maximum firmness. Its flat vertical sides afford ideal surfaces for the effective massing of muscle, and, when gripped between muscle, a laterally compressed bone is held as a thin flat board in the jaws of a vise. It is less apt to yield to strain, and to be rotated out of its articulations, than is a cylindrical bone. Only swallows have the *M. hypoglossus posterior* inserted on a cylindrical basihyale, which is an adequate arrangement for birds of their habits. The tongue joint of a swallow probably needs to withstand only the special strain caused by gusts of air striking into the open mouth as a bird engulfs insects in flight. But the tongue joint of certain other birds must withstand relatively great strain.

Consider, for example, the strain to which the joint seemingly is subjected in *Cyanerpes cyaneus*. *Cyanerpes* is a small bird, yet it has a very long tongue. Within the tongue it has paraglossalia measuring about 8.0 mm.

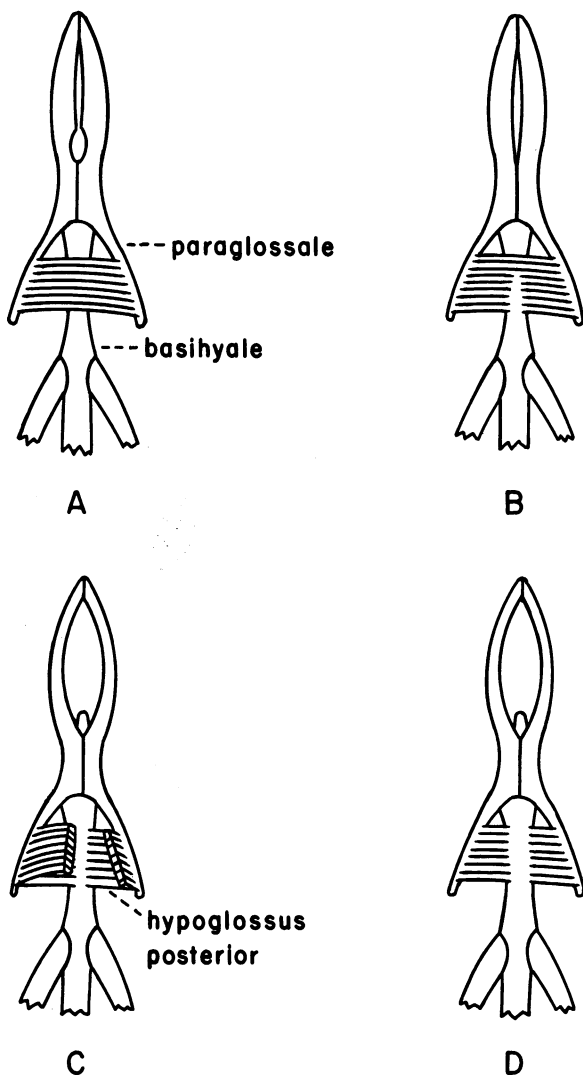


FIG. 6. Ventral views of the different arrangements of the *M. hypoglossus posterior* in New World songbirds. A. *Peucedramus*. B. Swallows. C, D. The Parulidae and allied birds.

in total length (the paraglossalia of *Dendroica*-sized wood warblers are about 5.0 to 5.5 mm.). Only about 1.0 mm. of the total 8.0 mm. lies behind the tongue joint; the other 7.0 mm. extends forward beyond the tongue joint. Thus nearly the entire weight of the tongue (a relatively

“heavy tongue”) occurs beyond the tongue joint (the fulcrum). The strain placed on the joint by the resulting leverage is at least potentially terrific. Support given to the joint by the *M. hypoglossus posterior* would reduce the strain, but, in order to furnish the needed support, the muscle must have a strong attachment to the basihyale. The laterally compressed basihyale provides the surfaces for effecting a very sturdy attachment.

Another source of strain on the tongue joint is the tongue movements, especially those that are made beyond the tip of the bill. *Cyanerpes* uses its semitubular tongue to probe into nectar far beyond the tip of the bill.

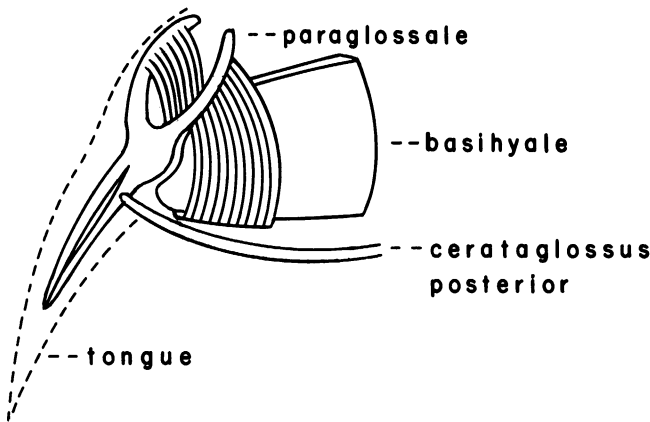


FIG. 7. Oblique dorsal view of the arrangement of the *M. hypoglossus posterior*, basihyale, and paraglossalia. When the muscle contracts, the posterior tips of the paraglossalia are depressed, raising the anterior tips. Contraction of the *M. ceratoglossus posterior* reverses this action.

The tongue receives little if any ventral support from the mandible under these circumstances; it is like a straw in a milkshake. Strain at the tongue joint must therefore increase, heightening the need for support of the joint. Because the *M. hypoglossus posterior* is responsible at one and the same time for lifting the weight of the tongue and for strengthening the tongue joint, it should and does have a strong attachment to the basihyale.

I doubt that the advent of the laterally compressed basihyale into the New World “nine-primaried” Oscines could have occurred by way of any living genus of wood warblers, unless one includes such genera as *Coereba* in the family, as Beecher (1951) has done. The traditional Parulidae seem not to require stout attachment of the tongue to the hyoid, for they are “light-tongued” species. It is easier to believe that they inherited

the adaptations from "long-tongued" ancestors which did require it—from birds like the present Coerebidae, or perhaps even from an insectivorous species with a long, probing tongue that demanded stout attachment to the hyoid, a bird with habits like those of *Certhia*.

It is interesting to note that in woodpeckers (Picidae) the problem of strengthening the tongue joint has been solved through the fusion of the paraglossalia to the basihyale, which has thus eliminated the tongue joint altogether. The hummingbirds (Trochilidae) solved the problem in essentially the same way as the Coerebidae, as doubtless have other nectar-feeding birds with which I am not yet familiar. I should point out that not a long bill, nor a long tongue, nor the nectar-feeding habit is a guarantee that a species will have a laterally compressed basihyale. Woodcreepers (Dendrocolaptidae) and thrashers (Mimidae) have long bills and somewhat elongated tongues, and the vireonid genus *Hylophilus* has the nectar-feeding habit, but none of these species that I have examined has a laterally compressed basihyale.<sup>1</sup>

The presence or absence of the laterally compressed basihyale does not furnish undoubted evidence of interfamilial relationships. The fact that *Certhia* has the feature does not mean that *Certhia* is closely related to the New World "nine-primaried" Oscines. It could mean this, but probably it means only that convergence has taken place. Yet I would argue that birds with laterally compressed basihyalia are supragenerically distinct from species that have cylindrical basihyalia. The hypothesis achieves a certain validity in view of the apparent significance of the laterally compressed basihyale in the Coerebidae, Parulidae, Drepanididae, Thraupidae, Icteridae, and Fringillidae. Having once arisen in the New World, "nine-primaried" Oscines, the feature has endured, even in wood warblers. This may be explained by an important fact that I have not mentioned, namely, that the advent of the laterally compressed basihyale led to a significant change in the morphology, and therefore to a change in the mechanical aptitude, of the *M. hypoglossus* posterior.

In *Peucedramus* the hypoglossus posterior is an unpaired transverse band (a single unit of contractile fibers) that simply passes beneath a cylindrical basihyale. But in wood warblers the muscle is not a single unit; the basihyale bisects the dorsal fibers of it, which divides the muscle into three units: the two units of dorsal fibers that attach to the opposite sides of the

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<sup>1</sup> In furnariids and phytotomids, the posterior one-half of the basihyale (where the *M. tracheohyoideus* and *M. thyreohyoideus* insert) is laterally compressed. I expect soon to report on hyoidean variation in the Suboscines, so report here only that the basihyalia of the Furnariidae and Phytotomidae provide evidence that the laterally compressed basihyale has a complex evolution.

basihyale, and the single ventral unit that extends beneath the basihyale. Each of these units comprises a potentially independent battery of contractile fibers. If the potential for independent contraction of the batteries has been realized, the tongue of a wood warbler can be tilted into angular positions. For example, if the dorsal fibers on one side of the basihyale contracted in conjunction with the adjacent *M. ceratoglossus* posterior, one side of the tongue would be depressed, raising the other side; the tongue consequently could be rocked from side to side, like a canoe. Such a movement might well compensate a parulid for the reduction of the ability to teeter its tongue; the latter movement, moreover, might still to some extent be made by a parulid, owing to the ventral battery of fibers. Independent contraction of this battery would tend, of course, to raise the tip of the tongue.

## COMPARISON OF *PEUCEDRAMUS* WITH THE PARULIDAE

*Peucedramus* supposedly is a wood warbler. If it is a true wood warbler, its characteristics should fit reasonably well into the patterns of structural and behavioral variability that distinguish the Parulidae. Therefore a point by point comparison of *Peucedramus* with its supposed relatives is in order.

### HYOIDEAN STRUCTURES

As mentioned above, the arrangement of the *M. hypoglossus* posterior, the shape of the basihyale, and the origin of the *M. stylohyoideus* in *Peucedramus* are non-parulid. *Peucedramus* has the hyoidean features of *Regulus* and *Polioptila*, birds that are placed in the Sylviidae by many, and of the following Old World birds generally placed in or near the Sylviidae: *Hylia prasina*, *Sericornis gutturalis*,<sup>1</sup> *Phylloscopus subaffinis*, *Seiurus poliogenys*, *Cisticola juncidis*, *C. dambo*, *C. exilis*, and *C. chiniana*. However, many Old World Sylviidae<sup>2</sup> have the origin of the *M. stylohyoideus* on the mandible instead of on the basitemporal plate; thus they differ from the above species.

<sup>1</sup> *Sericornis* is placed in the subfamily Malurinae of the Muscicapidae by Mayr and Amadon (1951). In the other Malurinae that I have dissected the *M. stylohyoideus* originates on the mandible; these species are: *Todopsis wallacii*, *T. cyanocephala*, *Malurus assimilis*, *M. melanocephalus*, *Epthianura tricolor*, *Acanthiza* sp., *Gerygone palpebrosa*, *G. flavolateralis*, and *G. gutturalis*.

<sup>2</sup> *Bradypterus cinnamomeus*, *Dromocercus seebohmi*, *Calamonistes cinereus*, *Megalurus palustris*, *Acrocephalus arundinaceus*, *A. aequinoctialis*, *A. cafer*, *Calamocichla newtoni*, *Abroscopus superciliosus*, *Cameroptera brevicaudata*, *Eremomela scotops*, *Prinia* sp., and *Thamnornis chloropetoides*.

In *Ramphocaenus rufiventris* and *Microbates cinereiventris*, New World birds currently classified in the Sylviidae, the basihyale is cylindrical as in *Peucedramus*. I have not yet had an opportunity to examine the M. stylohyoideus of these species, or of the following Old World Sylviidae, each of which has a cylindrical basihyale and is therefore like *Peucedramus* so far as known: *Cettia cetti*, *Phylloscopus bonellii*, *Regulus ignicapillus*, *R. regulus*, *Sylvia curruca*, and *S. hortensis*.

#### JAW MUSCLES

The Olive Warbler lacks the pinnate jaw muscles which are typical of the New World "nine-primaried" Oscines. Dr. William Beecher, into whose hands I placed a specimen of *Peucedramus* in March, 1960, furnished the following opinion (*in litt.*) of the jaw muscle pattern of the Olive Warbler: "M6 . . . is bifid and parallel, while it is trifid and pinnate in the 25 species of Parulids I have dissected. Also, M7B is parallel in *Peucedramus*, and it is always pinnate in Parulidae." "M6" is Beecher's M. pseudotemporalis superficialis, and "M7B" is his M. adductor mandibulae externus medialis (Beecher, 1953).

Mayr (1955), Bock (1960), and others discount Beecher's (1953) phylogenetic interpretations of the jaw-muscle patterns of the Oscines. They argue, correctly I think, that he failed to take fully into account possible evolutionary reversals and convergence. Nevertheless it may be taxonomically significant that the jaw-muscle pattern of *Peucedramus* differs widely from that of its supposed familial kin. Beecher's illustration (1953, p. 277) of the jaw muscles of *Phylloscopus borealis* (Sylviidae) represents quite exactly the jaw muscles of *Peucedramus*. To my knowledge, no other supposed New World, "nine-primaried" oscine of whatever family has the jaw-muscle pattern of a sylviid.

#### TENTH PRIMARY

Mayr and Amadon (1951, pp. 14–15) rendered their opinion of the significance of the reduced tenth primary as follows: "The classification of Stejneger, followed in considerable measure by that of Wetmore, places much weight on the relative reduction of the tenth (outer) primary. This trend toward specialization is of some importance, especially since all, or almost all, of the Suboscines have a long tenth primary, longer than in any oscine. On the other hand, reduction of the tenth primary is certainly subject to reversal and is a highly adaptive, plastic, and polyphyletic character. For example, the genus *Urocynchramus* of the fringilline finches has a relatively long tenth primary, though all other finches lack one. Other families in which the tenth primary may be present or absent



from genus to genus are the Bombycillidae (*sensu lato*), Dicaedidae, and Sturnidae. The seemingly primitive Alaudidae have the tenth primary quite reduced or even vestigial in a few genera. Some highly specialized families, such as the Nectariniidae, have a moderately developed tenth primary."

The length of the tenth primary varies considerably within the Parulidae. This variation is best expressed by a ratio which compares the length of the primary to the length of its overlying covert. Such ratios quickly reveal that the covert is longer than the primary in nearly all wood warblers, but, at least in some unworn specimens of *Vermivora superciliosa*, the primary may be as much as 1 mm. longer than, and extend beyond the tip of, the covert, where it can be seen in study skins quite easily.

Ridgway (1901, p. 21) attempted to distinguish between the reduced tenth of certain vireos and that of the rest of the New World "nine-primaried" Oscines. The former he called a "*visible rudimentary primary*"; the latter he termed "still more rudimentary and *entirely concealed*." He went on to say: "In so-called ten-primaried birds in which the tenth primary is rudimentary it consists of a minute, narrow, and pointed quill, less than half as long as the primary coverts, lying upon the inner side of the basal portion of the outer web of the outermost large primary, whereas in all so-called nine-primaried Oscines it is still more minute and lies upon the *outer* side of the wing next to the outermost primary covert."

This appears to state that in such birds as *Vireo flavifrons* the reduced tenth and its covert are differently arranged from those in, for example, *Vermivora superciliosa*. A comparison of alcoholic specimens under a dissecting microscope reveals that no such difference exists. The primary and covert in *Vermivora superciliosa* occupy precisely the same positions on digit II and have the same relationship to each other as in *Vireo flavifrons*. Moreover, the primary in *Vermivora superciliosa* may be just as long as in *Vireo flavifrons* (8.0 mm.).

The reduced tenth primary in *Peucedramus* is completely concealed by its covert, which constitutes the chief morphological argument for classifying the species as a wood warbler, but I think the argument should not be taken too seriously. *Peucedramus* has a relatively long, pointed wing; reduction of the tenth primary seems often to have occurred in conjunction with just such a wing (the Alaudidae in part, the Hirundinidae, and the Motacillidae).

#### PLUMAGE

The same or very nearly the same ochraceous coloration of head and

breast of the fully adult male Olive Warbler occurs also in the dress of the wood warblers *Parula americana*, *P. pitiayumi*, *Euthlypis*, *Granatellus*, and *Dendroica petechia*, but not in other wood warblers. The same color occurs in numerous non-parulids, including Neotropical gnatwrens currently classified as sylviids (*Ramphocaenus rufiventris* and *Microbates cinereiventris*). Shades of what probably represent the pigment basic to ochraceous appear in the plumage of songbirds the world over.

*Peucedramus* has two wing bars. Among United States warblers, the birds of nine genera lack wing bars. In the genus *Vermivora*, several species have two wing bars, while others have none. The birds of the genus *Dendroica* generally all possess two wing bars, but *D. caerulescens* has only one. The presence or absence of wing bars, then, seems to be a poor generic indicator even within the Parulidae, and it is surely, like coloration, of no value in the establishment of familial relationships. The same can be said of one other notable feature of the plumage in *Peucedramus*—the white tail patch that is also present in *Dendroica*. One must admit, nevertheless, that *Peucedramus* displays the general plumage pattern of a possible *Dendroica*, and both Griscom (in Griscom and Sprunt, 1957, p. 349) and Webster (1958) have suggested merging the genus with *Dendroica*. The plain fact is that *Peucedramus* combines in its plumage a number of parulid features, none of which in itself furnishes a dependable clue to what family the bird belongs. Such convergence is startling, yet is commonplace among passerines.

#### MOLT

The succession of plumage in males of *Peucedramus* is puzzling. Males of the northern race, *arizonae*, do not acquire their definitive plumage until the second prebasic molt, having remained in first basic plumage through a year or more; they mate in this dress. According to Webster (1958), a proportion of the males of the other races acquire the definitive plumage at the first prebasic molt. His data show that this proportion may be 100 per cent in the races *taeniatus*, *aurantiacus*, and *micrus*. Thus the molt of the male Olive Warbler appears to vary geographically, a trait that is not, so far as I know, typical of wood warblers or any other passerine family, but is known in such birds as *Lalage sueurii* (Camphephagidae), some *Cisticola* (Sylviidae), and others (see Mayr, 1942, pp. 50–52).

However, a specimen of the extreme southern race, *micrus*, from Nicaragua (A.M.N.H. No. 328067) demonstrates that at least some males of that population acquire the definitive plumage not sooner than the second prebasic molt. The bird was collected at Tigre, July 4, 1937; its primaries and rectrices are badly worn, a condition not to be expected in

July of recently fledged *Peucedramus*. The specimen is molting and displays a profusion of ochraceous feathers emerging through the yellow feathers of the throat, chest, and head.

#### NEST

Of *Peucedramus*, as of many passerines, the female alone builds the nest. Her materials are wire-like rootlets which she gathers on the ground, and, in Arizona populations at least, white soft plant fibers which she peels from the under surface of living leaves of the silver-leaved oak (*Quercus hypoleucoides*). With the rootlets she erects a spare circular framework on a crotch among needles in the terminal spray of a fir or pine branch, using spider web to lash and tape the rootlets to one another and to the crotch. The white plant fibers she piles along the inner wall of the framework, until the rootlets become the springs for a white, soft, thick mattress; a few rootlets are used to line the bottom of the nest. The outside of the nest, meanwhile, she has decorated ornately with the delicate reddish brown bracts of needles of yellow pine (*Pinus ponderosa*), sometimes adding lichens.

The same materials and design went into the construction of the eight nests that I have examined. Each is shaped like a sugar bowl and has a contracted rim.

One will wonder at the evolutionary pathway that led *Peucedramus* to the silvery under side of the leaf of the silver-leaved oak. This fibrous layer is difficult to remove. It will not, for example, rub off when abraded by the human finger. Apparently *Peucedramus* has developed a technique for prying beneath the layer with her bill and for stripping it off swiftly. Patrick J. Gould once observed a bird enter a silver-leaved oak and several minutes later carry off a great mouthful of the material.

None of the nests of wood warblers examined by me (17 genera, 58 species) resembles those of *Peucedramus*. But the two nests of the Golden-crowned Kinglet (*Regulus satrapa*) that I have studied seem expressive of an architectural heritage that could have stemmed from the same source as that of *Peucedramus*. They are sugar-bowl-shaped, have a contracted rim, and are lined on the extreme bottom with rootlets (and shredded bark). The rest of the cup is lined with feathers, however, each feather being directed so that its shaft spears into the walls. Green moss instead of silvery fibers form the nest body, and the outer decorations are lichens, liverwort, and little twigs, not pine bracts. Yet, like the nests of *Peucedramus*, they are composed of small chunks of compressible material mashed into a spongy quilt. Wood warblers make their nests by winding strips of hard material into layered baskets or by bending large masses

of material into cups. When and if they decorate the outside of the nest, they use comparatively gross materials in a rather slapdash style.

#### EGGS

According to Brandt (1951, p. 563), the veteran collector F. C. Willard once said to him, "The Olive Warbler should be called the Black-egged Warbler." The eggs of *Peucedramus* are very much darker than those of wood warblers (18 genera, 60 species examined), being grayish green and quite heavily spotted and splotched with olive and brown. They are much like the darkest examples of the gnatcatchers, *Poliophtila*.

#### WINTER DISTRIBUTION

*Peucedramus* occupies cold coniferous forest throughout at least some winters in the Santa Catalina Mountains, Arizona, though perhaps only in very small numbers. I have three times encountered and collected solitary wintering males there when snow covered the ground: December 31, 1955, at Summerhaven, and December 27, 1956, and March 10, 1959, on the ridge above Bear Wallow. Each specimen was an ochraceous-headed male.

As far as I am able to determine, breeding parulids of the mountaintops north of Mexico do not remain at, or near, their northernmost range limits in winter. The Yellow-throated Warbler (*Dendroica dominica*), however, is apparently a permanent resident in Florida, as is the Pine Warbler (*Dendroica pinus*). In Mexico both species of *Ergaticus* permanently occupy higher mountain forests. Furthermore, the Myrtle Warbler (*Dendroica coronata*) occurs in southern Massachusetts and southward in winter "amid ice and snow and sometimes zero temperatures" (Brandt, 1951, p. 252).

#### CALL NOTES AND SONG

The call note of *Peucedramus* is a silvery descending whistle, reminiscent of the "phew" call of the Western Bluebird (*Sialia mexicana*). Scott (1885, p. 173) wrote of it as follows: "A call note so like that of their associates (Western Bluebirds) as to be almost identical. It seemed to me only a clearer whistle of more silvery tone."

I know of no wood warbler with a call note that resembles it.

Sometimes *Peucedramus* emits a "chupp" note that seems exactly like the flight call of *Sialia mexicana*. I have heard it delivered but a few times, and only when birds were moving in flocks through the treetops during the spring migration.

The song of *Peucedramus* is, as Peterson (1961, p. 251) aptly describes it, a "ringing chant; several variations: *tiddle tiddle tiddle ter* or *peter peter peter . . .*" Oddly enough, males wintering over in the Santa Catalinas deliver this song while foraging through the trees, a fact called to my attention by Dr. Allan R. Phillips. Though the Olive Warbler does not begin nesting until late April, I have heard singing males on December 31, 1955, December 27, 1956, and March 10, 1959.

The song evidently is given by females as well as by males in the breeding season. On April 29, 1961, Patrick J. Gould, Peter W. Wescott, and I observed a bird in plumage of female type which chanted loudly several times. It was carrying plant material in its mouth and hopping through pine branches toward a nest that we had located earlier the same morning. The bird went toward the nest and disappeared among the needles at the nest site. When it emerged moments later and flew off, it carried nothing in its bill. We concluded that the bird in question was engaged in nest construction, and, since only females build, we additionally concluded that they sing.

Subsequent observations of other supposed females seemed to confirm this idea. But because males in first basic plumage closely resemble females, and because none of the supposed females that sang was collected and sexed, I am not prepared to state as fact that female Olive Warblers sing.

Female song has been reported for *Basileuterus fulvicauda* (Skutch, 1954, p. 348) but apparently for few if any other parulids. It is not an uncommon trait of certain sylviids, wrens, cardueline finches, and others (see Nice, 1943, pp. 127–132; Van Tyne and Berger, 1959, pp. 139–141).

#### NEST SANITATION

Nests of *Peucedramus* in which young have been successfully reared are found to be soiled with excrement (three specimens), as are the needles immediately adjacent to the nests. The soiling seems to occur during the final days that the young spend in or about the nest. The great majority of droppings are deposited on the nest rim and sides, almost none in the cup.

Nest soiling is a known trait of many estrildine and cardueline finches, but of extremely few other passerine species. I have not discovered any report of the trait in wood warblers. My own observations indicate that it probably does not occur in *Vermivora*, *Dendroica*, *Oporornis*, *Icteria*, *Wilsonia*, and *Cardellina*, or in the Vireonidae.

Many scattered data on nest sanitation in Old World birds have been brought together and reviewed by Blair and Tucker (1941), and by

Tucker (1941). These accounts, though inconclusive for most species, leave little doubt that nest soiling is unrecorded for the Sittidae, Certhiidae, Turdidae, and Sylviidae.

### TAXONOMIC POSITION OF *PEUCEDRAMUS*

The definite assignment of *Peucedramus* to one family or another is impossible at present. The data presented here indicate that the bird belongs neither to the Parulidae nor to related "nine-primaried" groups, but none of the data reveals beyond doubt the true affinities of the bird. The Olive Warbler, to be sure, has the hyoidean features of *Regulus*, *Poliophtila*, *Cisticola*, and *Phylloscopus*, but I have yet to dissect *Ramphocaenus*, *Microbates*, or many Old World Sylviidae. The nature of hyoidean variation in these birds, and in Old World songbirds generally, must be learned before hyoidean characteristics can be employed with confidence to help in our classifying the Olive Warbler as to family. The sylviid-like jaw muscles, the kinglet-like nest, and the *Sialia*-like call note of *Peucedramus* are interesting clues to but not proof of familial relationships. I have given careful consideration to the possibility that the bird might be an aberrant vireo, for vireos have cylindrical basihyalia, and several species have "nine" primaries. However, the pinnate jaw muscles of the vireonids (see Beecher, 1953, p. 305), and the mandibular origin of M. stylohyoideus, are characteristics not shared by *Peucedramus*.

The mainly Middle American distribution of *Peucedramus* suggests that the species may have arisen from a Neotropical form, though its confinement to montane coniferous forest could be interpreted as a relic pattern implying Old World or at least boreal derivation.

Perhaps the avifaunas of South or Central America contain a species or several species with hyoidean and other anatomical features that resemble those of *Peucedramus*. Such a bird, or birds, may be included among the New World "nine-primaried" Oscines, for many tanagers and certain honeycreepers have never been dissected and are very little known. *Poliophtila*, of course, occurs in the neotropics (as do *Ramphocaenus* and *Microbates*), and it is of special interest to note that *Peucedramus* and *Regulus satrapa* (which has a relatively short tenth primary) have overlapping breeding ranges in the coniferous forests of southern Arizona, Mexico, and Guatemala, and that they build somewhat similar nests. To turn the golden crown of male *R. satrapa*<sup>1</sup> into the ochraceous head of male *Peu-*

<sup>1</sup> Males of the Madeira Island race of the Firecrest, *Regulus ignicapillus madeirensis*, strongly resemble male *Peucedramus t. micrus* in crown color and in the shape and the size of the bill; moreover, the feathers of the sides of the neck in this kinglet are ochraceous.

*cedramus*, of course, requires the liberal use of imagination, but other external features of this kinglet occur naturally in male and female *Peucedramus*: double wing bars, the same yellow-green color in the wings, and the dark patch in front of the eye (which could be expanded easily to the proportions of the patch in *Peucedramus*, by the drawing of the black crown feathers downward over the white superciliary stripe). Some specimens of *R. satrapa* even show a strong trace of white in the tail. The genus *Regulus*, however, is surely Palearctic in origin.

Beecher (*in litt.*) thinks *Peucedramus* may be an Old World chat (Saxicolinae): "The muscle patterns of the Sylviidae and Saxicolinae (Turdidae) are extremely close. *Peucedramus* is actually closer to Saxicolinae (it is identical with Saxicolinae) than to Sylviidae but, as mentioned in my phylogeny paper (p. 276), I had to resort to another character to separate these two groups beyond doubt. The ectethmoid foramen in Sylviidae is single, but in Saxicolinae double—the second opening being on the very edge of the orbit. *Peucedramus* has it as in Saxicolinae. The tongue, too, seems like that of a chat. However, this would be somewhat specialized Old World chat, different from typical species, as may be judged by the fact that it has 9 primaries. But the 10th primary in the Old World warblers and chats is very small."

I do not agree with Beecher's opinion. The *M. stylohyoideus* of thrushes, and of the single saxicoline that I have dissected, the Wheatear (*Oenanthe*), originates on the mandible, not on the basitemporal plate as in *Peucedramus*. Also, *Peucedramus* (and sylviids) have unspotted young; the young of thrushes (including chats) are spotted. The Saxicolinae, moreover, are mainly ground dwellers and boreal where they appear on the fringes of the New World, while *Peucedramus* is arboreal and mainly Middle American.

It may seem impractical to remove the genus from the Parulidae since it cannot yet definitely be assigned elsewhere, but in my opinion it would be misleading to retain it in the Parulidae, where it clearly does not belong. My conclusion, accordingly, is that *Peucedramus* is best allocated at present to the Muscicapidae (*sensu lato*) and assigned to an uncertain position within or near the subfamily Sylviinae.

## SUMMARY

New World songbirds display various conditions in the shape of the basihyale bone of the hyoid, in the manner of insertion of the *M. hypoglossus* posterior, and in the point of origin of the *M. stylohyoideus*. Table 1 provides a summary which denotes the variations in the basihyale

for 177 genera and 352 species, and those in the hyoidean myology for 115 genera and 188 species.

The hyoidean variations have a consistent distribution within families, but one supposed member of the Parulidae, *Peucedramus taeniatus*, displays none of those of its supposed familial kin. It has, instead, those of some Sylviidae, and of *Sitta* and *Chamaea*.

In *Peucedramus* the basihyale is cylindrical, the M. hypoglossus posterior does not insert on it, and the M. stylohyoideus takes its origin from the basitemporal plate of the skull. In the Parulidae the basihyale is laterally compressed, the M. hypoglossus posterior inserts on it, and the M. stylohyoideus originates on the posterior tip of the mandible.

Functional analyses suggest that, on the whole, the contrasting hyoidean features of *Peucedramus* and wood warblers are such as to preclude the assignment of the species to the same family.

*Peucedramus* has a jaw-muscle pattern like that of *Phylloscopus borealis* (Sylviidae), builds a nest reminiscent of that of *Regulus satrapa* (Sylviidae), and utters call notes quite like those of *Sialia mexicana* (Turdidae). The young soil the nest.

Almost the only important characteristics that *Peucedramus* shares with the Parulidae are a reduced tenth primary (a polyphyletic feature in songbirds) and an exclusively American distribution.

The Olive Warbler is misplaced in the Parulidae and does not belong elsewhere in the New World "nine-primaried" Oscines. Though present evidence seems not sufficient for one to classify the bird with certainty, it should be removed from the Parulidae and assigned tentatively to the Musciapidae (*sensu lato*).

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