

SKELETAL CHARACTERS AND THE GENERA OF WARBLERS

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ABSTRACT. – Skeletons of 98 species of 24 genera of Parulinae were studied. (The other 12 species and 1 genus have not been preserved as skeletons.) Skull, mandible, quadrate, hyoid, humerus, ulna, femur, tibiotarsus, sternum, ribs, and vertebral column were perused; 24 characters proved useful for generic distinctions. Taxonomic suggestions are: Moving *Parula superciliosa* and *P. gutturalis* to *Vermivora*; merging *Parula* with *Dendroica*; moving *Microligea*, *Xenoligea*, and *Granatellus* from Parulinae to Thraupinae; moving *Rhodinocichla* from Thraupinae to Parulinae. The subfamily Parulinae is defined by skeletal characters. Construction of a key to the skeletons of warbler genera resulted in separation of 18 genera.

Studies of warbler systematics have been numerous. However, most of these have utilized only museum skins, or omitted the Middle and South American forms. Very few studies have evaluated genera. Here, using characters of the skeleton only, I attempt to differentiate the warbler genera. Are the genera of warblers, as currently listed, definable entities?

In the first modern revision of the family Mniotiltidae (=Parulidae), Ridgway (1902) recognized 30 genera: *Basileuterus*, *Cardellina*, *Catharopeza*, *Chamaethlypis*, *Certhidea*, *Conirostrum*, *Dendroica*, *Ergaticus*, *Euthlypis*, *Geothlypis*, *Granatellus*, *Helmitheros*, *Hemispingus*, *Icteria*, *Leucopeza*, *Helinaia* (= *Limnothlypis*), *Microligea*, *Mniotilta*, *Myioborus*, *Oporornis*, *Oreothlypis*, *Compsothlypis* (= *Parula*), *Peucedramus*, *Protonotaria*, *Rhodinocichla*, *Seiurus*, *Setophaga*, *Teretistris*, *Helminthophila* (= *Vermivora*), and *Wilsonia*. *Zeledonia* he placed in Turdidae. New genera revived or described since were *Idiotes* (Baird 1865), *Myiothlypis* Todd 1929, *Phaeothlypis* Todd 1929, *Xenoligea* Bond 1967 (erected as a subgenus; raised to full genus by Lowery and Monroe, 1968).

Several of the above genera have been reduced to synonymy or moved to other families. *Certhidia* was removed to Fringillidae (=Emberizinae) by Snodgrass (1903). *Hemispingus* was placed in Thraupinae by Sharpe (1909). *Conirostrum* was variously placed by various authorities in Coerebinae, Thraupinae, and Parulinae. *Oreothlypis* was combined with *Vermivora* by Miller and Griscom (1925). *Chamaethlypis* was combined with *Geothlypis* by Eisenmann (1962). No author since 1929 has recognized *Idiotes* or *Myiothlypis*. Griscom (1957) combined *Limnothlypis* with *Helmitheros*; *Parula*, *Dendroica*, *Peucedramus*, and *Catharopeza* with *Vermivora*; *Myioborus* with *Setophaga*; and *Phaeothlypis* with *Basileuterus*. Griscom's (1957) revision was the only one since 1902 to give diagnoses of all genera recognized. Lowery and Monroe (1968) listed all genera, species, and subspecies with ranges. Kepler and Parkes (1972) in describing *Dendroica angelae* stated that it was conspecific with *Catharopeza bishopi*; they advocated lumping *Catharopeza* with *Dendroica*. Parkes (1961) moved *picta* from *Setophaga* to *Myioborus*, redefined those genera, and (1978) emphasized the characters of *Mniotilta*. George (1962), mainly on the basis of the structure of the basihyoid bone and its muscles, advocated moving *Peucedramus* to Muscicapidae; but Webster (1962) on the basis of external anatomy and osteology stated that it was a parulid. Sibley and Ahlquist (1986) on the basis of DNA, stated that *Peucedramus* was a nine-primaried New World oscine. Several authors questioned the position of *Icteria*, but Sibley and Ahlquist (1982) stated that it was a warbler on the basis of its DNA. *Rhodinocichla* was moved by Clark (1913) to Thraupidae on the basis of skeletal characters, a move which was

followed by Peters (1968=Lowery and Monroe, 1968), G. A. Clark (1974), Raikow (1978), and the A.O.U. (1983). Sibley (1968) moved *Zeledonia* to Parulidae on the basis of egg-white proteins, skeletal, and external characters; Raikow (1978) concurred.

Literature in which particular sets of characters of warbler genera are compared includes: Beecher (1951, 1953), jaw muscles, horny palate, and skull. G. A. Clark (1974, 1981) foot scutes and toe fusion. Avise, Patton, and Aquadro (1980) proteins. Sibley (1968, 1970) egg-white proteins and (with Ahlquist, 1982, 1986, 1990) DNA. Raikow (1978) appendicular myology. Bledsoe (1988) hybrids.

Studies of warbler skeletons have been: Shufeldt (1888) only *Icteria*. Lucas (1894) 3 genera. A. H. Clark (1913) 3 genera. Beecher (1953) skulls of 13 genera. Tordoff (1954) skulls of 12 genera. Bock (1960) palatine process of the premaxilla in 12 genera and (1962) the pneumo-tricipital fossa. Berger (1957) pneumo-tricipital fossa in "a few" genera. Osterhaus (1962) legs of 5 genera. George (1962) hyoid bones of 22 genera. Webster (1962) skulls of 18 genera. Eaton, *et al.* (1962) skeletons of 5 genera. Eaton (*in lit.*, 1965) found that in *Basileuterus* and *Phaeothypis* the dorsal skull windows closed caudally, whereas in all other warbler genera he studied the skull windows closed rostrally. Webster and Goff (1979) vertebral column and ribs of 7 genera. Rising (1988) skeletons of five specimens of *Dendroica*.

In the most recent treatment of the warblers, the A.O.U. (1983) recognized the group as the subfamily Parulinae of the Emberizidae. Twenty-seven genera were listed (exclusion of South America excluded several species but no genera). The species *superciliosa* and *gutturalis*, which had been placed by Ridgway in *Oreothlypis* and by Lowery and Monroe (1968) in *Vermivora*, were moved to *Parula*.

MATERIALS AND METHODS

I examined 339 specimens of 98 species of 24 genera of Parulinae for 40 characters. (The other 12 species and 1 genus don't exist as skeletons in museums; see Table 1.) Examination was under a binocular stereoscopic microscope. Measurements were made with a dial caliper or (for very small bones) with a millimeter scale under a microscope. Not every specimen was studied for all characters because of missing or broken parts. For example, the rib and vertebral characters could be determined only on the 110 best articulated specimens.

The angle of mobility of the cranio-facial hinge was determined on intact skulls. Each skull was soaked in distilled water at room temperature until the ligaments were soft. The upper mandible was then manipulated gently by hand over a protractor, and the maximum gape measured to the nearest 5° mark.

In addition to the species listed in Table 1, I compared 107 skeletons of 33 species of 12 genera (*Granatellus*, *Microligea*, *Xenoligea*, *Hemispingus*, *Thlypopsis*, *Hemithraupis*, *Nephelornis*, *Cyanerpes*, *Euneornis*, *Conirostrum*, *Coereba*, *Certhidea*) which are borderline or of questionable placement. As outgroups I examined for the same 40 characters skeletons of 61 additional genera of Emberizinae, 1 of Catamblyrhynchinae, 8 of Cardinalinae, 48 additional genera of Thraupinae (only 4 genera of Thraupinae were not examined), 1 of Tersininae, 3 of Drepanididae, 19 of Icteridae, 9 of Fringillidae, and 4 of Vireonidae. Also, I compared at least one skeleton from each of the other families and all but 8 (all exclusively Old World) of the subfamilies in the suborder Passeres. For groups other than the warblers I followed the classification in the various volumes of Peters (1960-86). For the warblers, I followed the A.O.U. (1983), but with these discrepancies: (1) South American species were added, following Lowery and Monroe (1968). (2) The species *superciliosa* and *gutturalis* were moved from *Parula* to *Vermivora*.

TABLE 1
WARBLER SKELETONS EXAMINED

Genus	Species Examined	Species not Examined	Number of Specimens Examined
<i>Peucedramus</i>	1		6
<i>Protonotaria</i>	1		8
<i>Vermivora</i>	11		38
<i>Parula</i>	2		8
<i>Dendroica</i>	27	1	82
<i>Mniotilta</i>	1		7
<i>Setophaga</i>	1		7
<i>Catharopeza</i>	1		2
<i>Wilsonia</i>	3		6
<i>Oporornis</i>	4		12
<i>Ergaticus</i>	2		8
<i>Myioborus</i>	6	5	18
<i>Cardellina</i>	1		7
<i>Limnothlypis</i>	1		4
<i>Helmitheros</i>	1		7
<i>Basileuterus</i>	16	5	46
<i>Phaeothlypis</i>	2		7
<i>Zeledonia</i>	1		3
<i>Euthlypis</i>	1		6
<i>Seiurus</i>	3		9
<i>Teretistris</i>	2		3
<i>Leucopeza</i>		1	
<i>Geothlypis</i>	8	1	30
<i>Icteria</i>	1		8
<i>Rhodinocichla</i>	1		7

Anatomic terminology follows Baumel, *et al* (1993) except for a few additional parts in the skull and mandible named by Bock (1960, 1963, 1985). For the palatine process of the maxilla (=maxillopalatine), I have followed Bock (1985) in terming the proximal part the pedicel, but have called the distal part the “club” rather than “terminal plate.” Club is more descriptive of the structure in warblers and most Passeres (Fig. 1), although the structure *is* plate-like and inflated little or not at all in some of the Old World insect eaters. For the pneumo-tricipital (=pneumatic) fossa of the humerus, I have used the term “combined” to refer to the condition found in the 9-primaried New World Oscines (not the unrelated vireos) in which the medial bar is absent, or nearly so, so that the double fossa is combined into one. I believe Bock’s (1962) illustration of *Coccothraustes* as representing the “final stage in the development of the double pneumatic fossa” is too conservative. In most warblers, tanagers, buntings, and blackbirds there is no medial bar at all; the floor of the combined fossa is flat, continuous, and translucent (Fig. 2).

Drawings were made with the aid of a camera lucida. The ruled line is one millimeter in each case; in each figure, except #4, all drawings are made to the same scale.

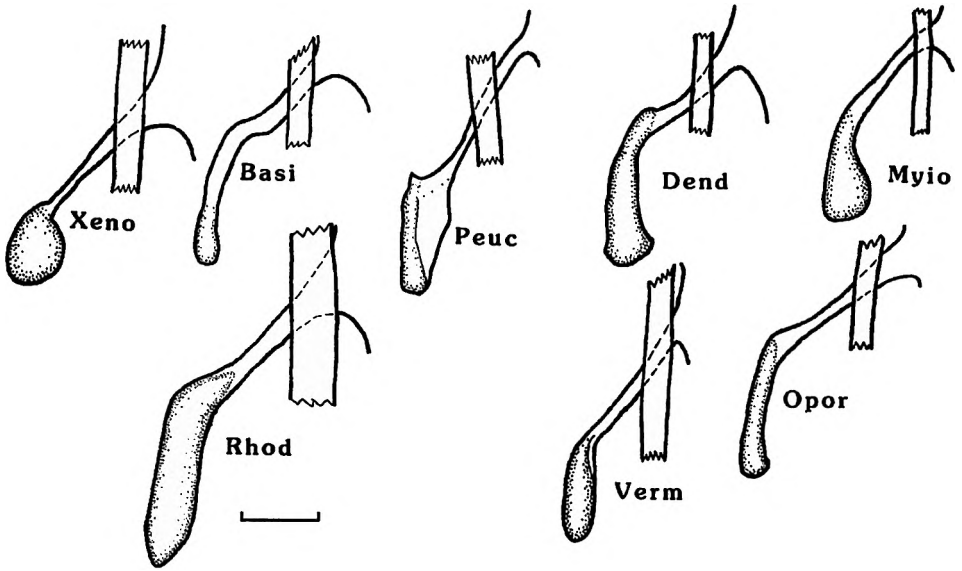


FIG. 1. Left maxillopalatine process of maxilla in ventral view. *Xenoligea montana* (a tanager), *Basileuterus tristriatus*, *Peucedramus taeniatus*, *Dendroica townsendi*, *Myioborus miniatus*, *Rhodinocichla rosea*, *Vermivora superciliosa*, *Oporornis tolmiei*.

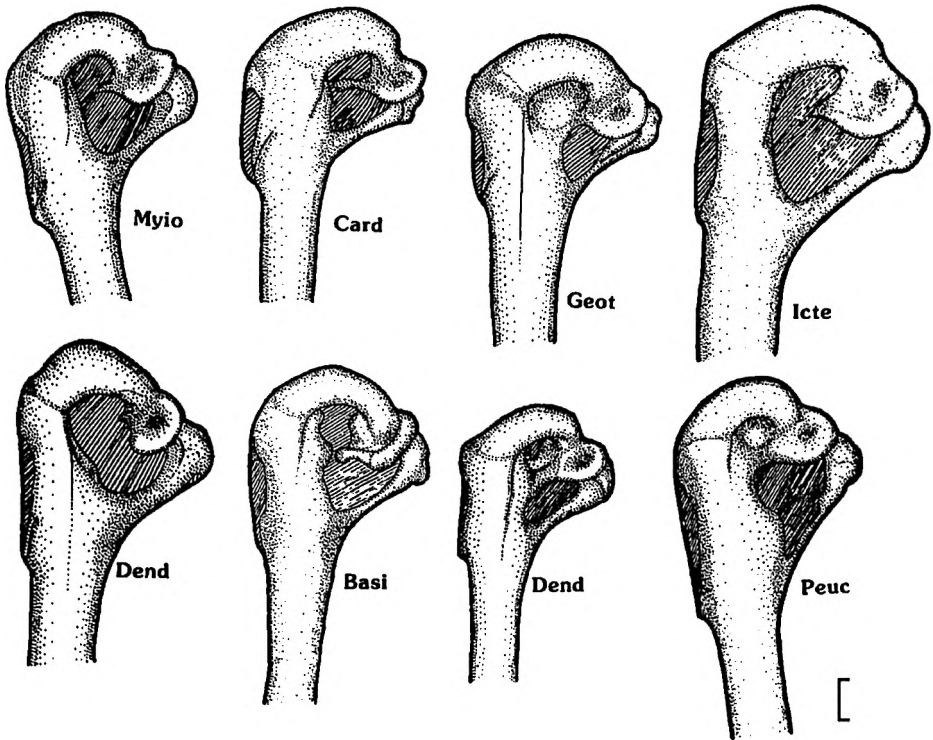


FIG. 2. Pneumo-tricipital fossa of left humerus in ventral view; striated areas are translucent. *Myioborus ornatus*, *Cardellina rubrifrons*, *Geothlypis poliocephala*, *Icteria virens*, *Dendroica coronata*, *Basileuterus tristriatus*, *Dendroica vitellina*, *Peucedramus taeniatus*. Notice that the medial bar is incomplete or absent in all but *Geothlypis* and *Dendroica vitellina*.

RESULTS

The first 27 characters are listed in the order, approximately, of their usefulness in making generic distinctions.

(a) In most genera there were no bones in the nose; in *Helmitheros* there were nasal conchs; in *Rhodinocichla* (Fig. 3) there was a nasal septum; also a very incomplete nasal septum was found erratically in *Dendroica* (1 of 78 specimens), and *Setophaga* (1 of 7).

(b) Length of skull (measured from the caudal corner of the external nare) was the only absolute size measure used. Only *Basileuterus coronatus*, *Icteria*, *Zeledonia*, and *Rhodinocichla* exceeded 20.8 mm; only *Vermivora bachmani* and *Parula americana* were less than 16.

(c) The interpalatine process (Fig. 3) was in most specimens shaped like a knife blade, with the thick edge medial. In a few specimens each of *Peucedramus*, *Geothlypis*, *Icteria*, and *Rhodinocichla* it was nearly round in cross section. It was shortest (1.5 as long as wide) in *Dendroica vitellina*, *Oporornis tolmiei*, *Limnothlypis*, and *Basileuterus rufifrons* and longest (5 as long as wide) in *Peucedramus*.

(d) The transpalatine process (Fig. 3) was recorded as the ratio of length/width at base. It was shortest (.8) in *Setophaga* and some species of *Vermivora*. It was longest (2.5-3.5) in *Zeledonia*, *Euthlypis*, *Icteria*, and two species of *Dendroica*.

(e) The lateral margin of the caudolateral plate of the palatine caudally, but rostral to the transpalatine process (Fig. 3), was concave or straight (as in most tanagers) in *Euthlypis*, but in 23 genera it was convex. In *Protonotaria* (2 specimens), *Wilsonia* (1), *Myioborus* (1), and *Teretistris* (1) a few exceptional specimens were straight.

(f) Premaxilla length/width ratio (obviously not very different from bill shape) varied from a minimum of 1.7 in *Cardellina* and *Myioborus ornatus* to 3.4 in *Limnothlypis*.

(g) The retroarticular process of the mandible was measured as the ratio of length to width at base (Fig. 4). It was shortest (.9-1) in *Dendroica palmarum* and *Peucedramus* and longest (3.0) in *Vermivora bachmani* and *V. superciliosa*. Outside *Vermivora*, only *Geothlypis flavovelata* reached 2.0. Within *Vermivora*, the length was 3.0 in *bachmani* and *superciliosa*, 2.4-2.7 in *chrysoptera*, *pinus*, *peregrina*, *celata*, *ruficapilla*, and *gutturalis*, 2.0 in *luciae*, but 1.6 with the lateral surface slanting laterally ventrally (rather than vertical or slanting medially) in *virginiae* and *crissalis*.

(h) The zygomatic process of the squamosal was measured as the ratio of length to width at base (Fig. 5). It was shortest (.9) in *Teretistris*, and longest in *Peucedramus* (2.6) and *Vermivora bachmani* (4).

(i) Supraorbital ratio was calculated as width of cranium/supraorbital width. It was highest in *Basileuterus belli* (6.8) and lowest (3.2) in *Rhodinocichla* and *Vermivora chrysoptera*.

(j) Shape of the rostral basibranchial (=basihyoid) was a useful generic distinction (Fig. 6). In *Peucedramus* it was round in cross section at the midpoint (cf. George, 1963); in other specimens and genera it was compressed (2-3 times as high as wide).

(k) The pneumo-tricipital fossa of the humerus was always of the combined type, but with variations (Fig. 2). In most specimens the bottom of the fossa was translucent and continuous between dorsal and ventral parts. In *Peucedramus*,

FIG. 3. Ventral view of palate, showing nasal septum, palatine, interpalatine process, transpalatine process, and maxillopalatine process of the maxilla. *Dendroica townsendi*, *Rhodinocichla rosea*, *Basileuterus culicivorus*.

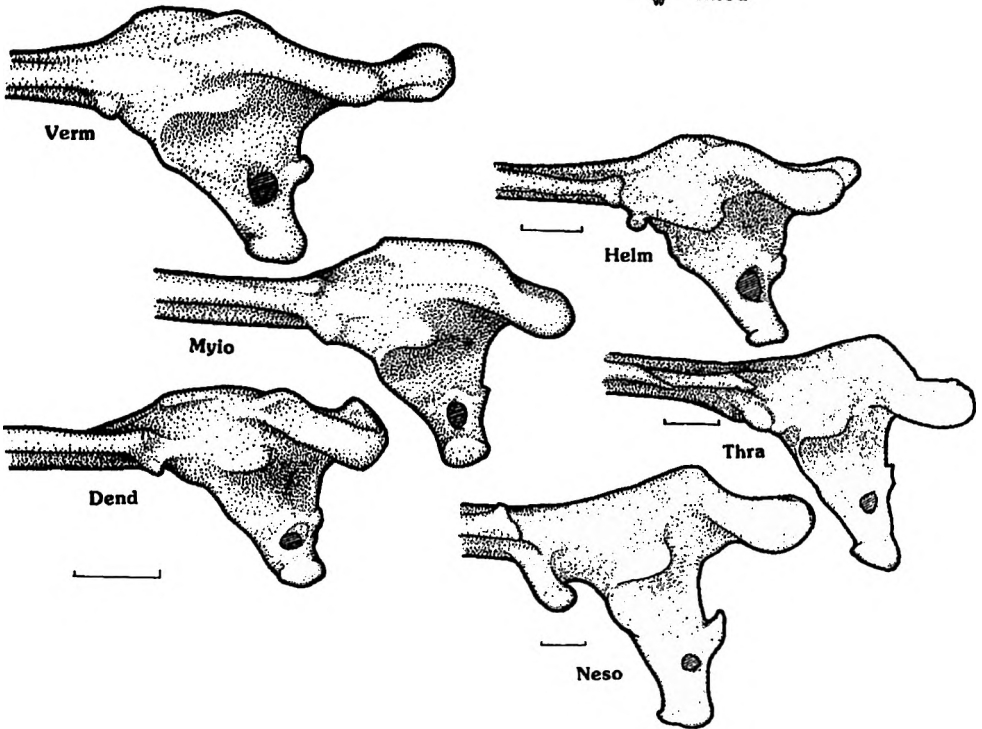
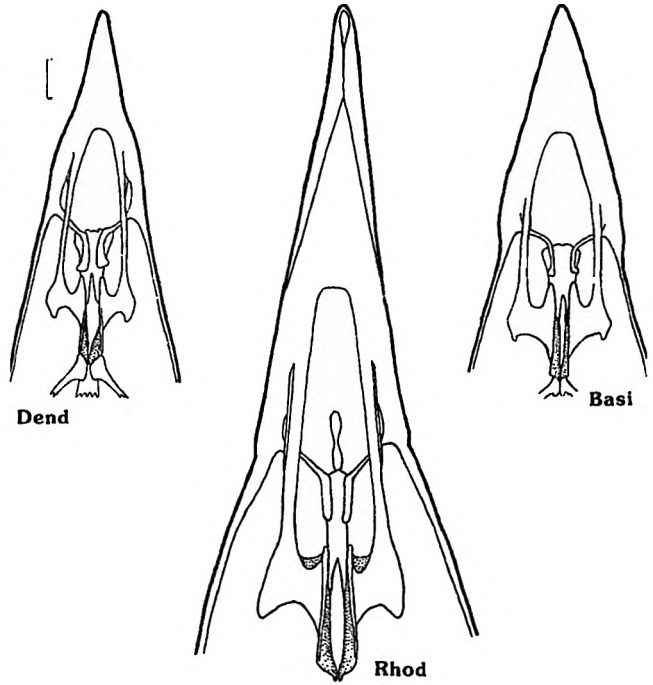


FIG. 4. Articular region of mandible in dorsal view, showing retroarticular process, process 7b, and pseudotemporal process. *Vermivora gutturalis*, *Helmitheros vermivorus*, *Myioborus picta*, *Thraupis abbas* (a tanager), *Dendroica palmarum*, *Nesospingus speculiferus* (a tanager). The 3 left-hand drawings are to one scale, that of *Dendroica*; each of the others has its own scale.

Zeledonia, and one specimen each of *Seiurus*, *Geothlypis*, and *Icteria*. the dorsal fossa had an opaque bottom, was somewhat shallower than the ventral fossa, and had a step-down (not a ridge) marking the division between the two fossae. In one specimen of *Vermivora*, 4 of *Dendroica*, one of *Basileuterus*, and 2 of *Phaeothlypis* there was a medial bar, a low, rounded ridge extending clear across the bottom of the fossa from the shank of the dorsal fossa to the distal wall and separating two areas of translucence. In *Icteria* and *Rhodinocichla* the fossa was somewhat longer than in other genera, extending further distally.

(l) A manubrium-sternum bridge (Fig. 7) was erratic. In those specimens of *Dendroica*, *Catharopeza*, *Basileuterus*, and *Geothlypis* where it occurred, it was shorter than the bridges of tanagers such as *Chlorophanes* and *Sericossypha* (cf. Webster, 1993). It was present and bony throughout in *Dendroica pharetra*, *Catharopeza*, *Geothlypis nelsoni*, and one specimen of *Rhodinocichla*; it was very slender, with the middle part ligamentous or missing in *Basileuterus signatus* and some specimens of *Dendroica pinus*, *D. graciae*, and *D. adelaidae* as well as the other 3 specimens of *Rhodinocichla*.

(m) Ratio of the lengths of tibiotarsus/ulna was one of the most consistent characters within species and genera. It varied from 1.3 in *Peucedramus*, *Protonotaria*, *Limnothlypis*, *Helmitheros*, *Mniotilta*, *Cardellina*, *Rhodinocichla*, and a few species of *Dendroica* to 1.9 in *Geothlypis nelsoni* and 2.2 in *Zeledonia*, which has decidedly large legs and small wings for a warbler.

(n) Another measure of relative leg to wing size used was ratio of the lengths of tibiotarsus/humerus. The low extreme of 1.4 was in *Catharopeza*; the high of 2.3 was in *Zeledonia*.

(o) Ratio of the lengths of tibiotarsus/femur was rather uniform except that *Rhodinocichla* was low at 1.5 and *Geothlypis rostrata* high at 2.5.

(p) Ratio of the lengths of ulna/humerus again brought out the unique character of *Zeledonia* as lowest at 1.0; *Dendroica vitellina* was the highest at 1.4.

(q) Ratio of ulna length/femur length varied from .9 in *Zeledonia* to 1.5 in *Peucedramus*, *Dendroica graciae*, *D. coronata*, and *Geothlypis rostrata*.

(r) The maxillopalatine process of the maxilla (Fig. 1) was fairly consistent in the warblers--a slender pedicel and a slightly expanded pneumatic club of moderate length. In some specimens the angle between pedicel and club was abrupt; in others it was a slow curve. In *Icteria*, most specimens of *Cardellina*, and 3 specimens of *Myioborus* the club was short and fat, more expanded. A rostral spur at the pedicel-club junction was present in *Peucedramus* and 5 species plus some specimens of 4 more species of *Dendroica*.

(s) The orbitonasal (=ectethmoid) foramina were usually double (Fig. 8; cf. Beecher, 1953). They were touching, or pinched, in a few individuals of 6 genera. In one specimen each of *Dendroica pityophila* and *Icteria* there was a single foramen. In most specimens of *Peucedramus*, *Phaeothlypis*, and *Zeledonia* the lateral orbitonasal foramen was on the rim of the orbit rather than inside the orbit; and this variant also occurred in one specimen of *Seiurus motacilla* and several specimens of 2 species of *Basileuterus*.

(t) The orbital process of the quadrate (Fig. 9) was measured as to whether shorter than the rest of the quadrate, equal in length to the rest of the quadrate, or longer than the rest of the quadrate. In each length group, each specimen was categorized as tapering slightly, moderately, or distinctly. Variability was too great to make this a neat generic distinction. The long, only slightly tapering type, found in most tanagers and other nine-primaried song birds, was seen only in a few specimens of *Icteria* and *Rhodinocichla*.

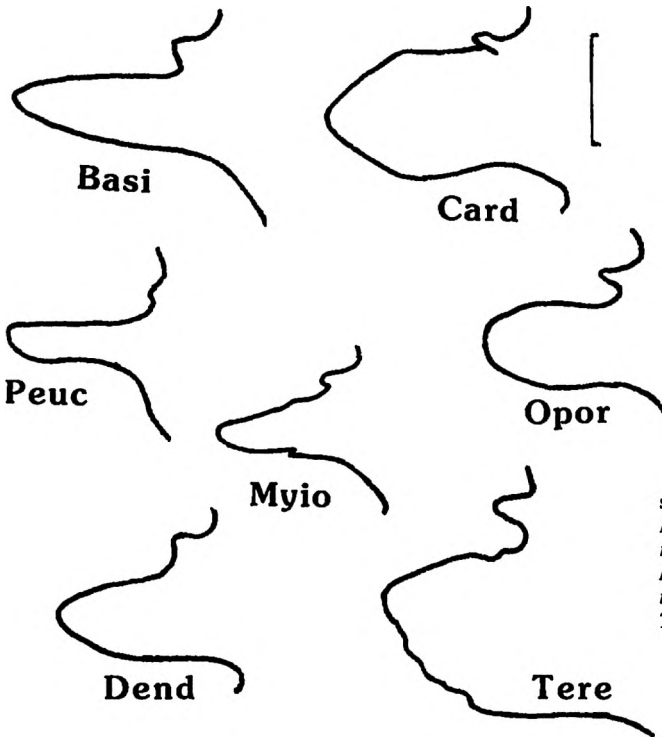


FIG. 5. Zygomatic process of squamosal showing proportions. *Basileuterus coronatus*, *Cardellina rubrifrons*, *Peucedramus taeniatus*, *Myioborus ornatus*, *Oporornis tolmiei*, *Dendroica kirtlandii*, *Teretistris fornsi*.

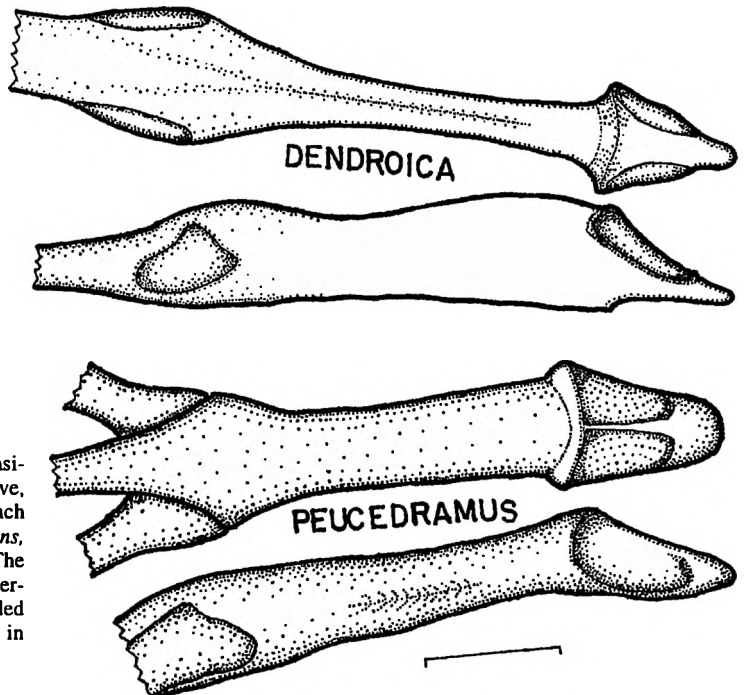


FIG. 6. Rostral basi-branchial; dorsal view above, lateral view below in each case. *Dendroica coerulescens*, *Peucedramus taeniatus*. The proximal part of the ceratobranchial has been included in *Peucedramus*, but not in *Dendroica*.

(u) The angle of mobility of the cranio-facial hinge was fairly consistent within each species (for instance, *Basileuterus luteoviridis* N16, M23°, R20-30°), but varied radically within each of the genera *Dendroica* and *Basileuterus*. Range in the warblers was from 5° in *Seiurus aurocapillus* to 45° in *Basileuterus culicivorus*.

(v) Ratio of the lengths of humerus/femur was calculated; it gave poorer generic separation than the 5 long bone ratios discussed above.

(w) The pseudotemporal process, on the medial side of the mandible (Fig. 4), was in most cases small and round. It was smallest (.3 as high as wide) in *Peucedramus*, *Parula*, and some species of *Dendroica*; longest (1.8 times as high as wide) in *Rhodinocichla*; of moderate height but ridge-shaped in *Icteria*, most specimens of *Protonotaria*, and single specimens each of *Seiurus aurocapillus* and *Geothlypis poliocephala*.

(x) The shape and size of process 7b, on the lateral surface of the mandible (Fig. 4) were consistent in some species and genera, but varied in others. The smallest, most inconspicuous type of process was consistent in *Mniotilta Cardellina*, *Icteria*, and *Rhodinocichla*, and also found in some species or specimens of *Protonotaria*, *Dendroica*, *Wilsonia*, *Basileuterus*, *Phaeothlypis*, *Ergaticus*, and *Teretistris*. The largest type of process was consistent in *Limnithlypis* and *Zeledonia* and also found in some species or specimens of *Helmitheros*, *Oporornis*, *Basileuterus*, *Myioborus*, and *Geothlypis*.

(y) The shape of the lateral margin of the ectethmoid bone (truncate vs. winged as described by Beecher, 1953) varied from truncate in several genera (Fig. 8) to winged in most specimens of *Icteria* and *Rhodinocichla*. *Dendroica*, *Seiurus*, and *Geothlypis* each included specimens I classified as truncate, near truncate, and almost winged.

(z) The presence or absence of a free prefrontal bone (=lacrimal) was not a useful discriminant of warbler genera. It was present as a small, thin, not pneumatic free bone in 2 specimens of *Peucedramus*, but absent in all other specimens.

(aa) No pattern of generic distinction emerged when data on the palatine process of the premaxilla (cf. Tordoff, 1954; Bock, 1960) were recorded on the warblers using the 4 classes described by Tordoff. Only a single specimen of *Catharopeza* belonged to class 2--"palatine process of the premaxilla adjacent to but not closely fused with prepalatine bar for most of its length." The other 338 specimens were about half class 3 and half class 4, with the process partly or completely fused. Some characters proved worthless for generic distinction. The shape of the maxillary process of the nasal and the shape of the rostral end of the vomer were too variable within each species. The degree of overhang of the supraorbital ridge and the shape of the medial process of the mandible were too uniform within the warblers. There was (Webster and Goff, 1979) less often a free rib on vertebra #13 in *Vermivora* than in other genera (27%, N=15 in *Vermivora*, 39-81%, N=95 in other genera). Similarly, there were less often 2 instead of one free thoracodorsal ribs in *Dendroica* (7%, N=28 in *Dendroica*; 20-43%, N=82 in other genera). Number of free ribs, number of ribs articulating with the sternum, number of ribs with uncinat processes, position of first vertebra of synsacrum, number of vertebrae in synsacrum, number of free caudal vertebrae, and position and number of vertebral hypapophyses all were observed on the 110 articulated warbler skeletons. None provided useful taxonomic information.

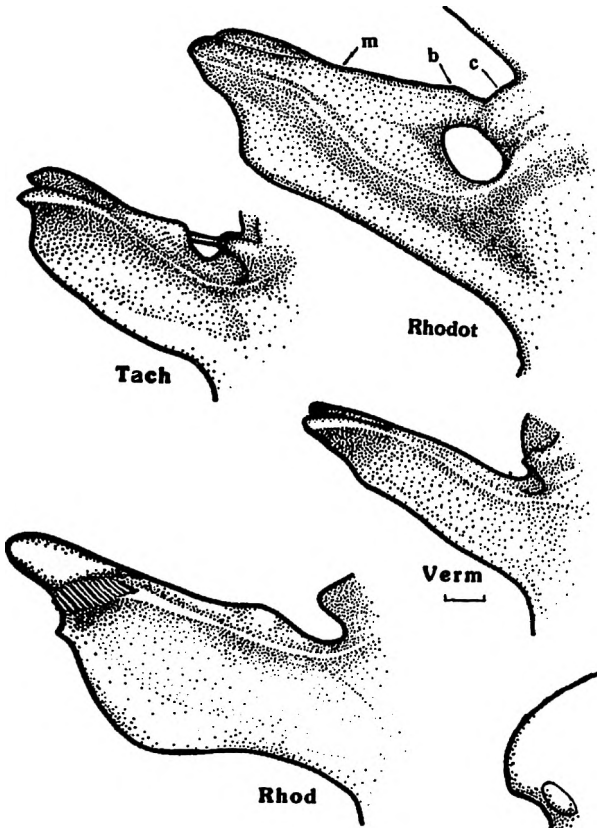


FIG. 7. Manubrium-sternum bridge in lateral view. Top right *Rhodotrappis celaeno* (a cardinal, bridge very large). Top left *Tachyphonus luctuosus* (a tanager, bridge small). Lower right *Vermivora gutturalis* (no bridge). Lower left *Rhodinocichla rosea* (bridge minute with middle part missing because ligamentous). Labels: m, manubrium; b, manubrium-sternum bridge; c, coracoid ridge.

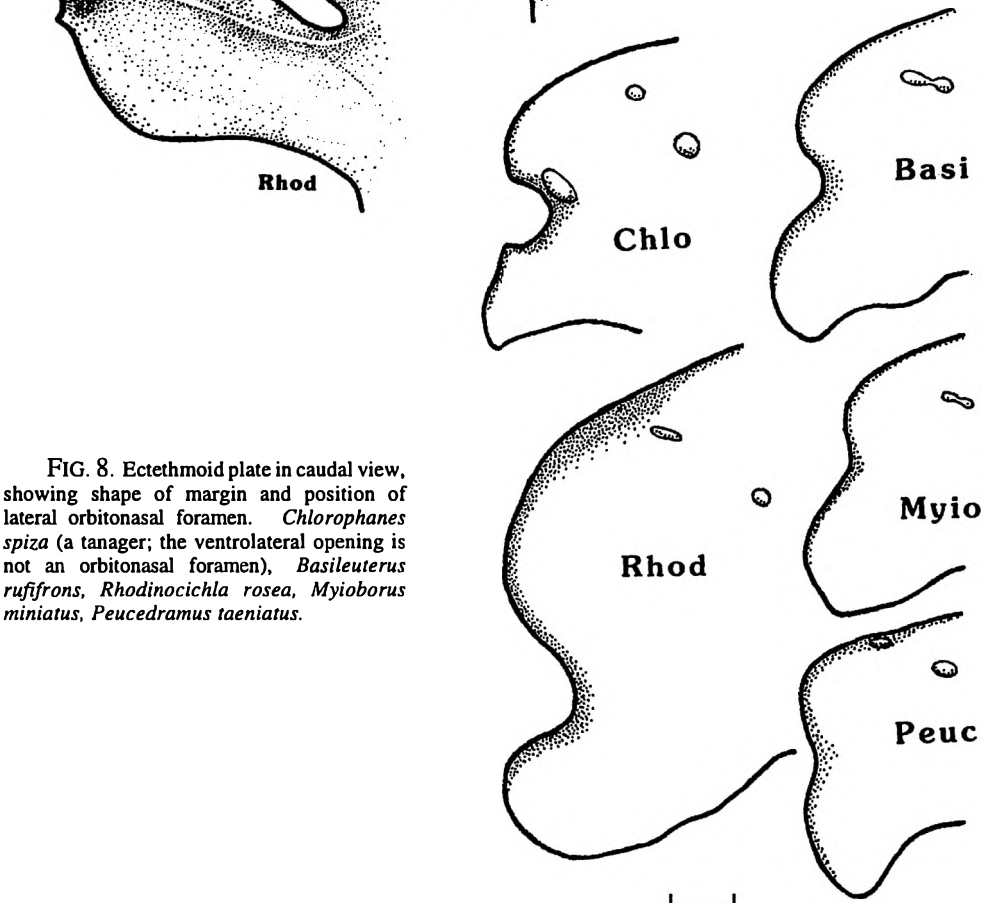


FIG. 8. Ectethmoid plate in caudal view, showing shape of margin and position of lateral orbitonasal foramen. *Chlorophanes spiza* (a tanager; the ventrolateral opening is not an orbitonasal foramen), *Basileuterus rufifrons*, *Rhodinocichla rosea*, *Myioborus miniatus*, *Peucedramus taeniatus*.

KEY TO GENERA
(Measurements in mm.)

- A. Rostral basibranchial round in cross-section at middle *Peucedramus*
 AA. Rostral basibranchial compressed at middle B
 B. Length of skull 21.8 or more C
 BB. Length of skull 21.1 or less E
 C. Lengths of tibiotarsus/ulna 2.2; lengths of tibiotarsus/humerus 2.3; process 7b of mandible large *Zeledonia*
 CC. Lengths of tibiotarsus/ulna 1.6 or less; lengths of tibiotarsus/humerus 1.9 or less; process 7b of mandible small D
 D. Length of skull over 26; nasal septum present *Rhodinocichla*
 DD. Length of skull less than 24; nasal septum absent *Icteria*
 E. Palatine with lateral margin caudally straight or concave and transpalatine process more than 3 times as long as wide *Euthlypis*
 EE. Palatine with lateral margin caudally convex and transpalatine process less than 2.6 times as long as wide. In rare exceptions, palatine margin convex but transpalatine process as much as 3.5 times as long as wide, or palatine margin straight but transpalatine process less than 2.2 times as long as wide F
 F. Premaxilla 3.4 times as long as wide *Limnothlypis*
 FF. Premaxilla not more than 2.8 times as long as wide G
 G. Zygomatic process of squamosal wider than long *Teretistris*
 GG. Zygomatic process of squamosal longer than wide (1.2 to 2.5 times as long as wide) H
 H. Premaxilla 1.7 times as long as wide; interpalatine process 4.2 times as long as wide *Cardellina*
 HH. Premaxilla more slender (1.8 or more times as long as wide) or if 1.7 times as long as wide, then interpalatine process shorter (less than 2.5 times as long as wide) I
 I. Lengths tibiotarsus/ulna 1.6 or more K
 II. Lengths tibiotarsus/ulna 1.5 or less J
 J. Nasal conchs partly bony, attached to vomer; premaxilla slender, 2.4 times as long as wide; lengths tibiotarsus/femur 1.7 *Helmitheros*
 JJ. Nasal conchs not bony; premaxilla rarely as slender as 2.4 (one species in each of *Vermivora* and *Dendroica*); Lengths tibiotarsus/femur 1.8 or more L
 K. Lengths of ulna/humerus 1.1 or, if 1.2, then palatine process of maxilla pedicel-club angle abrupt *Geothlypis*
 KK. Lengths of ulna/humerus 1.2 or more; palatine process of maxilla pedicel-club angle a gradual curve *Basileuterus*
 L. Length of skull 20.0 or more M
 LL. Length of skull 19.3 or less N
 M. Lengths of tibiotarsus/humerus 1.4 *Catharopeza*
 MM. Lengths of tibiotarsus/humerus 1.7 *Seiurus*
 N. Transpalatine process .8 times as long as wide; skull 17.2 long *Setophaga*
 NN. Transpalatine process as long as wide or longer, or, if shorter (*Vermivora crissalis* and *gutturalis*), then skull 16.4 long or less O
 O. Lengths of ulna/femur 1.3 or more, or if 1.2 (*Dendroica petechia* and *D. cerulea*), then skull only 17.2-18.0 long Q
 OO. Lengths ulna/femur 1.2 or less and skull 18.4 long or more P
 P. Lateral orbitonasal foramen on rim of orbit; premaxilla 2.0 times as long as wide *Phaeothlypis*

- PP. Lateral orbitonasal foramen inside orbit; premaxilla 2.1 or more times as long as wide *Oporornis*
- Q. Retroarticular process of mandible 2 or more times as long as wide
 *Vermivora* (but excluding *V. virginiae* and *crissalis*)
- QQ. Retroarticular process of mandible 1.6 or less times as long as wide R
- R. Supraorbital ratio 3.8 or less; length of skull 19.1 *Protonotaria*
- RR. Supraorbital ratio 4.1 or more; length of skull 18.5 or less (except *Dendroica pinus* 19.2) *Parula*, *Mniotilta*, *Dendroica*, *Wilsonia*, *Ergaticus*, *Myioborus*, and 2 species of *Vermivora* (*V. virginiae* and *crissalis*)

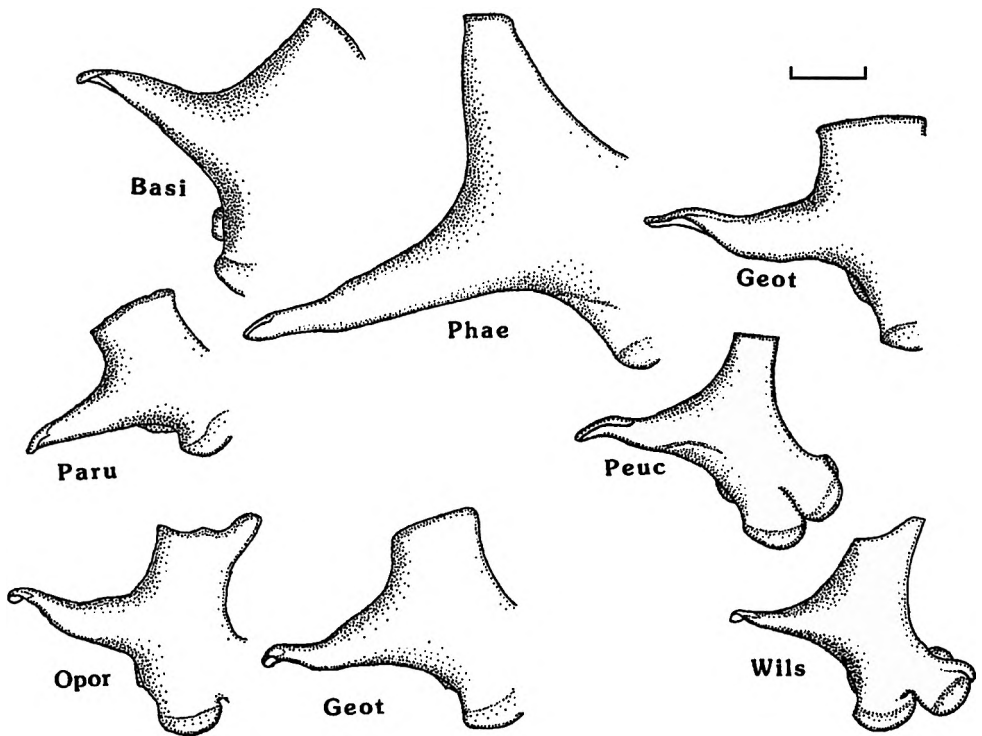


FIG. 9. Orbital process of left quadrate in latero-dorsal view. *Basileuterus coronatus*, *Phaenicophilus palmarum* (a tanager), *Geothlypis poliocephala*, *Parula pitiayumi*, *Peucedramus taeniatus*, *Oporornis tolmiei*, *Geothlypis aequinoctialis*, *Wilsonia pusilla*.

SYSTEMATIC RELATIONSHIPS OF WARBLERS AS A UNIT

If the Parulinae are delimited as the 24 examined genera listed in Table 1, the subfamily may be defined: Lightly built, slender, insectivorous 9-primaried New World Oscines; Emberizidae. Lateral margin of caudolateral plate of the palatine convex; transpalatine process blunt, never more than 3.5 times as long as wide and usually less than twice as long as wide; orbital process of quadrate shorter than or equal in length to rest of quadrate; club of the palatine process of the maxilla pneumatic but slender; pneumotricipital fossa of humerus of combined type and usually with no medial bar or step-down; ventral tuberculum of head of humerus making an angle of 40-55° with shaft, although a few individuals reach 60°; prefrontal bone absent or fused; orbitonasal foramina double; manubrium-sternum bridge absent or small; premaxilla usually slender; palatine process

of the premaxilla fused with the rostral part of the palatine bar for its entire length, and the suture not evident in about half the individuals. No individual specimen of the subfamily is exceptional in more than 2 of the preceding skeletal characters, and no species in more than one.

This characterization of Parulinae excludes *Microligea*, *Xenoligea*, and *Granatellus* of those listed by the A.O.U. (1983); it includes *Rhodinocichla* from the Thraupinae. *Microligea*, *Xenoligea*, and *Granatellus* all have the lateral margin of the caudolateral plate of the palatine straight or concave and the transpalatine process 2.4 to 5.5 times as long as wide. *Granatellus* (always) and *Microligea* (usually) have a single orbitonasal foramen. *Microligea* has 5 additional exceptions to the above list of characters, and *Xenoligea* has 3. *Rhodinocichla* has no exceptions.

CONCLUSIONS

Altogether the data on skeletons show that of the 24 genera recognized in Parulinae, 9 are especially distinctive in skeletal anatomy: *Peucedramus*, *Catharopeza*, *Cardellina*, *Limnothlypis*, *Helmitheros*, *Zeledonia*, *Euthlypis*, *Icteria*, and *Rhodinocichla*, each with one species. Two genera, *Dendroica* and *Geothlypis*, are more heterogenous than the rest in skeletal anatomy. The other 13 are less distinctive than the former 9 but less heterogenous than the latter 2. In answer to the question raised at the beginning of this paper, 18 of the 24 genera considered are definable entities and 6 aren't, on the basis of the skeleton.

A few points are in order about recent generic arrangements of the warblers in the light of skeletal anatomy. All except the sixth point have been adopted elsewhere in this paper:

- (1) *Zeledonia* belongs to the subfamily, but is one of the most distinct genera.
- (2) *Oporornis* is as distinct as most genera, and not particularly close to *Geothlypis*.
- (3) Lumping of *Catharopeza* with *Dendroica* is not supported; it would make the most varied genus even more varied. Conversely, the suggestion by Kepler and Parkes (1972) that *Dendroica plumbea*, *D. angelae*, *D. pharetra*, and *Catharopeza bishopi* constitute a West Indian superspecies is weakly supported by one piece of evidence from the skeletons. The manubrium-sternum bridge, uncommon in warblers, was found in some specimens of *plumbea* and all of *pharetra* and *bishopi*; though absent in *angelae*.
- (4) *Parula superciliosa* and *P. gutturalis* belong in *Vermivora* on the basis of their long retroarticular processes.
- (5) The lumping of *Chamaethlypis* with *Geothlypis* is supported.
- (6) Lumping of *Parula* and 2 of the species of *Vermivora* (*crissalis* and *virginiae*) with *Dendroica* is justified by lack of skeletal distinction. Several authors in recent decades have pointed out the lack of distinction of these genera in non-skeletal characters. The result of such lumping would leave the combined genus no more varied in skeletal anatomy than it is at present. The genera *Mniotilta*, *Wilsonia*, *Ergaticus*, and *Myioborus*, also, are indistinguishable from *Dendroica* on the basis of the skeleton. However, in these cases, characters of external anatomy are adequate for generic distinction (Ridgway, 1902; Griscom, 1957; Parkes, 1961, 1978).
- (7) The systematic position of *Peucedramus* remains moot. George (1962) placed it in Muscicapidae; Raikow (1978) and Phillips (1991) in Sylviidae; Webster (1962) in Parulidae; A.O.U. (1983) in Parulinae; Sibley and Monroe (1990) in a

subfamily Peucedraminae separate from all other 9-primaried New World oscines. The majority of skeletal (above) and external anatomic features (Webster 1962) place it with Parulinae.

I omit hypotheses of evolutionary relationships, which should include non-skeletal character sets. For the present, I suggest the linear order of genera adopted in Table 1.

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