

THE MANUBRIUM-STERNUM BRIDGE IN SONGBIRDS (OSCINES)

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ABSTRACT. The manubrium-sternum bridge was first described by Shufeldt (1888). In this study, all the Oscine families, most of the subfamilies, and nearly all the species in Parulidae and Thraupinae were surveyed. The structure is well-developed in at least some species within Picathartidae, Sylviidae, Maluridae, Monarchidae, Remizidae, Parulidae, Emberizinae, Cardinalinae, Thraupinae, Tersiniinae, Fringillinae, Carduelinae, and Bubalornithinae. From the erratic systematic distribution of the structure, the manubrium-sternum bridge apparently does not supply phylogenetic information at the family level, although it does at the generic level in some cases.

INTRODUCTION

A bony bridge between the dorsal surface of the manubrium and the coracoid ridge of the sternum was first described by Shufeldt (1888) in the tanager *Piranga ludoviciana*. Clark (1913) noted the structure in *Rhodinocichla rosea* as well as in *Piranga olivacea* and suggested that it was characteristic of tanagers in contrast to other songbirds. Moreno (1984) described a bridge, which she called the spina interna, in 3 species of *Fringilla* and 4 species of *Cisticola*. Morony (1985) described the structure in the tanager *Sericossypha albocristata* as the processus manubrii without reference to the earlier literature. The manubrium-sternum bridge is more generally distributed among the Oscines than earlier authors indicated, but it is not consistent within most species or higher group taxa. To study its distribution, 1375 skeletons representing 331 genera and 628 species were examined (Table 1).

Table 1 and the results presented below follow the classification in Peters (1960-1986) with five exceptions. The classification of the Old World insect eaters follows the more recent Volume 11 rather than earlier volumes. *Coereba* and *Conirostrum* are removed from Parulidae to a separate subfamily Coerebinae of Emberizidae, following the American Ornithologists' Union's check-list (1983). *Zeledonia* is removed from Turdidae to Parulidae, following Sibley (1968) and the American Ornithologists' Union (1983). *Microligea*, *Xenoligea*, and *Granatellus* are removed from Parulidae to Thraupinae, following Webster (1989, in press). A few species and genera described as new since the appropriate volume of Peters was published are added, if their skeletons were examined.

RESULTS

In many tanagers, e.g., *Heterospingus xanthopygius*, the manubrium-sternum bridge is a stout, bony, medial rod extending from the midpoint of the coracoid ridge (= labrum dorsale) of the sternum to the dorsal midpoint of the manubrium (= rostrum sterni) one-third of its length out. In a few specimens of seed eaters, e.g., *Rhodothraupis celaeno* (Emberizidae, Cardinalinae), the bridge is even larger and longer (Figure 1, Rhodot) than in any tanager. The *Rhodothraupis* scale of bridge was characterized as "very large," and the *Heterospingus* scale of bridge was characterized as "large." In many tanagers, e.g., *Tachyphonus luctuosus* (Figure 1, Tach), the bridge is as long as in *Heterospingus*,

Table 1. The distribution of skeletons examined in this study.

Taxon	Number of Genera	Number of Species	Number of Specimens
Alaudidae	1	1	2
Hirundinidae	3	3	3
Motacillidae	2	2	5
Campephagidae	1	1	1
Pycnonotidae	1	1	1
Irenidae	3	3	3
Laniidae	2	2	2
Vangidae	2	2	2
Bombycillidae	3	3	5
Dulidae	1	1	1
Cinclidae	1	2	2
Troglodytidae	3	3	5
Mimidae	4	4	19
Prunellidae	1	2	2
Turdidae	8	10	9
Orthonychidae	1	1	1
Timaliidae	4	4	4
Panuridae	1	1	1
Picathartidae	1	1	1
Poliophtilidae	3	3	4
Sylviidae	24	38	52

Taxon	Number of Genera	Number of Species	Number of Specimens
Muscicapidae	4	8	12
Platysteiridae	2	2	2
Maluridae	1	3	3
Acanthizidae	5	7	7
Monarchidae	10	12	13
Eopsaltridae	3	4	5
Pachycephalidae	2	2	2
Aegithalidae	2	2	2
Remizidae	2	2	3
Paridae	1	1	5
Sittidae	2	3	4
Certhiidae	2	6	18
Rhabdornithidae	1	1	1
Climacteridae	1	1	1
Dicaeidae	2	2	2
Nectariniidae	1	1	1
Zosteropidae	1	1	4
Meliphagidae	5	5	9
Vireonidae	4	7	15
Parulidae	22*	97	326
Emberizinae	49	75	142
Catamblyrhynchinae	1	1	2

Taxon	Number of Genera	Number of Species	Number of Specimens
Cardinalinae	7	11	33
Thraupinae	58**	193	446
Tersininae	1	1	3
Coerebinae	2	6	17
Drepanididae	3	3	3
Icteridae	19	26	58
Fringillidae	9	15	48
Estrildidae	10	11	11
Ploceidae	13	16	31
Sturnidae	3	3	9
Oriolidae	1	1	1
Dicruridae	1	1	1
Callaeidae	1	1	1
Grallinidae	1	1	1
Artamidae	1	1	1
Cracticidae	1	1	1
Ptilonorhynchidae	2	2	3
Paradisaeidae	1	1	1
Corvidae	4	5	8

* All except *Leucopeza*.

** All except *Orchesticus*, *Compsothraupis*, *Calyptophilus*, and *Cyanicterus*.

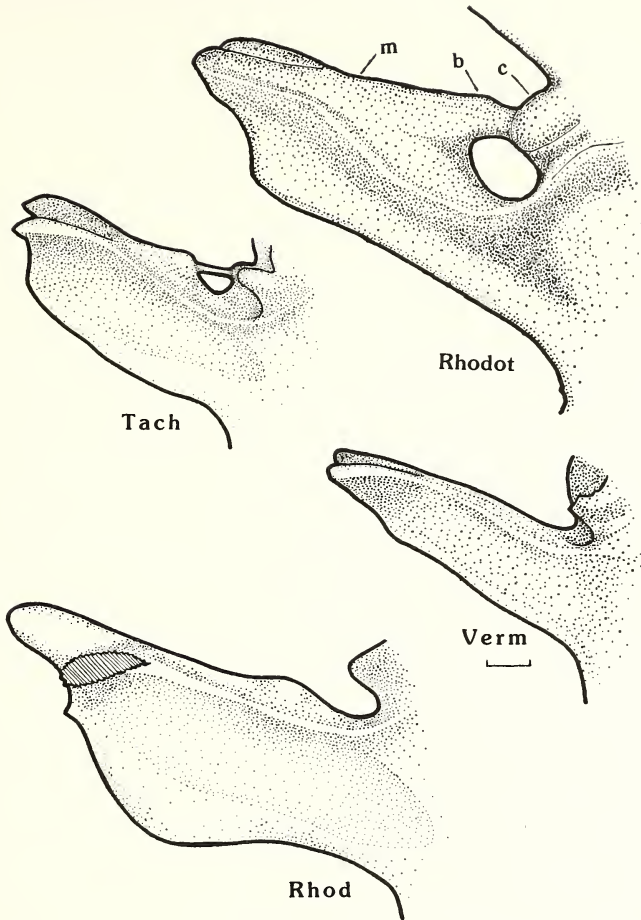


Figure 1. All figures are left lateral views of the rostral end of the sternum drawn with the aid of a camera lucida to the same scale. The scale line, drawn under "Verm[ivora]," is 1 mm. Top left: *Tachyphonus luctuosus*, with a small bridge. Top right: *Rhodothraupis celaeno*, with a very large bridge. Lower left: *Rhodinocichla rosea*, showing a minute bridge with the ligamentous part of the span missing; the left rostral point of the manubrium has been deleted. Lower right: *Vermivora gutturalis*, with no bridge. Labels are: b, manubrium-sternum bridge; c, coracoid ridge; and m, manubrium.

but it is more slender and sometimes the middle quarter of the span is ligamentous. Such a bridge was characterized as "small." In quite a few tanagers and buntings, e.g., *Tangara nigrocincta*, the bridge was characterized as "minute"; in this case, the middle three-fourths of the span is ligamentous (missing in many skeletal preparations), and only the termini are bony (Figure 1, Rhod). When the bridge is distinctly shorter than one-third the length of the manubrium, as it often is in non-tanagers, it is described it as "short."

Table 2. Songbird families and subfamilies in which a manubrium-sternum bridge was observed. In an additional 44 families, no bridge was present; they are listed in Table 1.

Taxon	Bridge occurrence	Bridge type if present
Irenidae	Occasional	Minute
Mimidae	Occasional	Minute
Picathartidae	Present	Small
Sylviidae	Frequent	Ridge; large, small or minute
Maluridae	Frequent	Large
Monarchidae	Occasional	Ridge; large
Remizidae	Frequent	Ridge; large
Meliphagidae	Occasional	Minute
Parulidae	Rare	Small or minute
Emberizidae, Emberizinae rarely	Erratic	Large, small, or minute; a ridge
Emberizidae, Cardinalinae	Erratic	Very large, small, or minute
Emberizidae, Thraupinae	Frequent	Large, small, or minute
Emberizidae, Tersininae	Present	Large, small, or minute
Emberizidae, Coerebinae	Occasional	Minute
Icteridae	Rare	Minute
Fringillidae, Fringillinae	Present	Very large, large, or minute
Fringillidae, Carduelinae	Rare	Small or minute
Ploceidae, Bubalornithinae	Present	Very large
Ploceidae, Passerinae	Occasional	Minute
Corvidae	Occasional	Minute

The bridge was missing in all the specimens examined from those 44 families and all those genera not discussed below. Table 2 summarizes this data.

In Irenidae, a minute bridge was present in *Irena puella* but not in *Chloropis aurifrons* or *Aegithina typhia*. In Mimidae, a minute bridge was present in 1 of the 5 specimens of *Toxostoma rufa*. In Picathartidae, the single specimen of *Picathartes oreas* had a small, short bridge. In Sylviidae, there was great variation, but the structure, when present, was really a ridge rather than a bridge, because there was a thin, median keel of attachment to the manubrium from the dorsal rod. The ridge was absent in *Bradypterus*, *Melocichla*, *Megalurus*, *Hippolais*, *Chloropeta similis*, *Urolais*, *Apalis*, *Phyllolais*, *Eremomela pusilla*, *Hyliota*, *Phylloscopus*, and *Sylvia*. A large, short ridge was present in *Bathmocercus cerviniventris*, *Nesillas typica*, *Cisticola chubbi*, *C. chiniana*, *C. natalensis*, *Camaroptera brachyura*, *Eremomela scotops*, *Sylvietta brachyura*, and *Hypergerus lepidus*. A small, short ridge was present in *Acrocephalus schoenobaenus*, *Chloropeta natalensis*, *Orthotomus atrogularis*, and *Macrosphenus concolor*. Of 2 specimens of *Acrocephalus scirpaceus*, one had a small, short ridge, and the other had a minute, short ridge. Of 2 specimens of *Prinia subflava*, one had a large, short ridge, and the other had a small, short ridge. In the single specimen of *Prinia leucopogon*, the apparent corresponding structure was abbreviated into an almost vertical column supporting the coracoid ridge. In *Regulus*, the ridge was absent in 5 specimens each of *R. satrapus* and *R. calendula*, but in the one *R. ignicapillus* specimen, a column appeared caudally as in *Prinia leucopogon*.

In Maluridae, there was no bridge in *Malurus alboscapulatus*, but in a single specimen each of *M. cyaneus* and *M. coronatus*, there was a large, short bridge. In Monarchidae, there was a large, short ridge (as in Sylviidae) in the single specimen of *Philentoma pyrrhopterum* examined, and in the one *Terpsiphone viridus* specimen examined, there was a caudal, almost vertical column as in *Prinia leucopogon*.

In Remizidae, there was no bridge in *Auriparus*, but in *Remiz*, a large, short ridge (as in Sylviidae) was present. In Meliphagidae, there was no bridge in 4 genera, but a single specimen of *Promerops* had a minute bridge. In Parulidae, the bridge was absent in 17 genera but present in at least one specimen in each of 5 other genera. Within *Dendroica* (all 27 species examined), the bridge was absent in 22 species. It was small and short in all 4 specimens of *D. pharetra*; minute and short in 2 of 7 specimens of *D. plumbea* (absent in 5); minute and short in 1 of 3 specimens of *D. pinus* (absent in 2); minute and short in 1 of 5 specimens of *D. graciae* (absent in 4); and minute and short in 1 of 3 specimens of *D. adelaidae*. The bridge was small and short in both specimens of *Catharopeza bishopi*. Within *Seiurus* (all 3 species examined), the bridge was absent in all 6 specimens of 2 species and in 2 of 3 specimens of *S. noveboracensis*, but in one Ovenbird, there was a short, minute bridge. Within *Geothlypis* (12 species examined — all except *G. beldingi*), the bridge was absent in 9 species (including the 4 usually referred to *Oporornis*). The bridge was small and short in the single specimen of *G. nelsoni*; minute and short in 1 of 12 specimens of *G. trichas* (absent in 11); and small and short in 1 of 2 specimens of *G. speciosa* (absent in one). Within *Basileuterus*, the bridge was absent in 15 species but short and minute in both specimens of *B. signatus*.

In Emberizinae (Emberizidae), the bridge was missing in 37 genera but was present to some degree in 12 genera. In *Ammodramus*, there was a large, short bridge in one specimen of *A. maritimus* and a minute, short bridge in the other specimen; there was a minute, short bridge in 1 of the 2 specimens of *A. sandwichensis*; and the bridge was absent in both specimens of *A. savannarum*. In *Aimophila*, the bridge was absent in 18

specimens of 8 species, but minute and short in 1 of 2 specimens of *A. aestivalis*. In *Oriturus*, *Sporophila*, and *Pselliophorus*, there was a condition as in *Prinia leucopogon* (see above) — a large vertical column or post extending from the caudal end of the manubrium to the dorsal midpoint of the coracoid ridge. In *Melanospiza*, there was a small, short bridge in one specimen but none in another. In *Piezorhina* and *Geospiza*, there was a small, short bridge. Of the 4 specimens of *Certhidea*, one had a large, short ridge (i.e., with a keel of attachment to the manubrium), one a small, short bridge, one a minute, short bridge, and one no bridge. In *Arremonops*, the single specimen had a small, short ridge (i.e., with a keel of attachment to the manubrium). In *Saltatricula*, *Coryphospingus*, and *Paroaria*, there was a minute bridge in each case.

In Cardinalinae, the bridge was absent in *Spiza*, *Pheucticus*, *Saltator*, and *Passerina*. In *Cardinalis cardinalis*, there was a minute bridge in 6 but none in 4 other specimens. In *C. sinuatus*, the single specimen had a small bridge. In *Caryothraustes*, all 3 specimens had a minute bridge. In *Rhodothraupis*, the single specimen had a very large bridge.

In Thraupinae (Emberizidae), the bridge was erratic in occurrence. In 28 genera, the bridge was absent, but in 30 genera, it was present in at least some of the specimens. In *Heterospingus*, it was large in the 2 specimens examined. In *Chlorophanes*, it was large in 2, small in 2, and minute in one. In *Habia*, 10 specimens (including 4 species; all except *H. cristata*) all had the bridge, but it varied from large to minute. In *Cyanerpes*, 11 specimens (including all 4 species) all had the bridge, and it was either small or minute. In *Conothraupis speculigera*, both specimens had a minute bridge. In *Sericossypha albocristata*, one (the specimen discussed by Morony, 1985) had a large bridge, but one had none. In *Hemithraupis* (both species), all 5 specimens of *H. guira* had the bridge, though it varied from large to minute; 4 specimens of *H. flavicollis* included 2 with a small bridge, one with a minute bridge, and one with none. In *Nephelornis oneilli*, one had a large bridge, but 4 had none. In *Rhodinocichla rosea*, 2 of the 7 specimens had a small bridge, 4 had a minute bridge, and one had none. In *Nemosia pileata*, the bridge was small in one specimen but missing in 3. In *Tachyphonus* (all 8 species examined), the bridge was either small or minute in 11 specimens (total for *T. rufiventer*, *T. luctuosus*, *T. coronatus*, and *T. phoeniceus*) but absent in 6 specimens (total for *T. cristatus*, *T. surinamus*, and *T. delatrii*). In *Piranga* (8 of the 9 species examined), the bridge was absent in all 4 specimens of *P. leucoptera*, both specimens of *P. erythrocephala*, and 2 of 9 specimens of *P. rubra*. It was present but varying from large to small to minute in all 3 specimens of *P. bidentata*, both specimens of *P. flava*, 7 of the 9 specimens of *P. rubra*, all 3 specimens of *P. roseogularis*, all 5 specimens of *P. olivacea*, and all 5 specimens of *P. ludovicianus*. In *Xenodacnis parina*, one specimen had a small, short bridge, but 2 others had none. In the genera *Schistochlamys*, *Lamprospiza*, *Nesospingues*, *Hemispingus*, *Phoenicophilus*, *Microligea*, *Chlorothraupis*, *Eucometis*, *Trichothraupis*, *Rhamphocelis*, *Iridosornis*, *Delothraupis*, *Chlorochrysa*, *Tangara*, *Oreomanes*, *Diglossa*, and *Euneornis*, the bridge was usually missing, but in a few scattered specimens, it was present but minute.

In Tersininae (Emberizidae), the bridge in 3 specimens of *Tersina viridis* varied in size from large to minute. In Coerebinae, the bridge was minute in 2 of 7 specimens of *Coereba flaveola* but absent in 10 specimens of 5 species of *Conirostrum* and the other 5 *Coereba*. In Icteridae, the bridge was absent in all genera except in 1 of 2 specimens each of 3 species of *Cacicus*, in which it was minute.

In Fringillinae (Fringillidae), the bridge was always present; it was very large or large in 10 specimens of *Fringilla coelebs* and in one specimen of *F. teydea*, but it was

minute in 3 specimens of *F. montifringilla* (also described by Moreno, 1984). In Carduelinae, it was absent except in 1 of 3 specimens of *Serinus*, where it was small, and in 1 of 2 specimens of *Carduelis flammea*, where it was minute. In Ploceidae, the bridge was very large in one specimen each of *Bubalornis* and *Dinemellia* but absent in *Passer montanus*, *Petronia*, *Montifringilla*, *Sporopipes*, *Amblyospiza*, *Ploceus*, *Malimbus*, *Quelea*, *Foudia*, *Euplectes*, and *Vidua paradisaea*. In *Passer domesticus*, it was minute in 7 specimens and absent in 2; in *Vidua chalybeata*, it was minute in a single specimen. In Corvidae, a minute bridge was present in 1 of 3 specimens of *Cyanocitta cristata*.

DISCUSSION

These data constitute a single character study (*sensu* Bock, 1960), especially when combined with the data provided by Moreno (1984). The erratic occurrence of the manubrium-sternum bridge leads to the conclusion that its presence or absence tells us little or nothing about the evolution of major passerine groups (= families). On the other hand, within those groups (Parulidae and Thraupinae) which were studied rather completely, the pattern of occurrence and size of the structure suggests some possible generic and specific relationships. For example, among the New World warblers, the bridge is generally absent or minute and rare. But in *Catharopeza bishopi* of St. Vincent and *Dendroica pharetra* of Jamaica, the bridge was present and small in all specimens examined. *Dendroica plumbea* from the Lesser Antilles and *D. adelaidae* from St. Lucia were among the very few other parulids in which a minute bridge occurred in even a minority of specimens. A single specimen of *D. angelae* from Puerto Rico (borrowed from Louisiana State University) lacked the bridge. Kepler and Parkes (1972) suggested that *Catharopeza bishopi*, *D. pharetra*, *D. plumbea*, and *D. angelae* constituted a West Indian superspecies on the basis of distribution and external anatomical features. The distribution and size of the manubrium-sternum bridge support Kepler and Parkes' suggestion of relationships among *C. bishopi*, *D. pharetra*, and *D. plumbea*, but neither support nor deny the relationship of these species to *D. angelae*. Other systematic relationships are suggested within families wherein sampling was inadequate. Within Sylviidae, the distribution and size of the ridge suggest a very different sequence of genera than that adopted by Mayr and Cottrell (Peters, 1986, Vol. 11). The peculiar "ridge, not bridge" structure was observed almost exclusively in Sylviidae and Monarchidae, which suggests phylogenetic relationship, yet was uncomfortably erratic in occurrence. Within Emberizinae and Cardinalinae, the erratic distribution of the bridge calls for further study. Within Fringillidae, the consistent presence of the bridge in *Fringilla*, but not the other genera, lends weight to the separation of a subfamily Fringillinae from Carduelinae (cf. Moreno, 1984). Within Ploceidae, the very large bridge in *Bubalornis* and *Dinemellia*, along with its absence or minute presence in other genera, lends weight to the separation of a subfamily Bubalornithinae.

The function of the manubrium-sternum bridge is unknown, although it must strengthen the manubrium dorsally. Perhaps the bridge provides extra bracing in species with unusually far rostral extension of the supracoracoideus muscle.

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