Proceedings of the Indiana Academy of Science
(1988) Volume 98 p. 581-593.

SKELETONS AND THE GENERA OF TANAGERS

J. Dan Webster
Hanover College
Hanover, Indiana 47243

ABSTRACT: There are 248 species of tanagers (Aves, Passeriformes, Thraupinae) arranged in 61 genera and known chiefly from their skins. The author studied 434 skeletons of 191 species of 57 genera, describing the shape or measuring 36 characters on each. Twenty-three characters proved useful in generic discrimination. Presence or absence of a free lacrimal; presence or absence of a manubrium-sternum bridge; shape and size of the interpalatine process; and the tibiotarsus/ulna length ratio were the best discriminants. The phylogeny of the tanagers remains unclear. More specimens must be studied.

INTRODUCTION

The 248 species of tanagers (Passeriformes, Emberizidae, Thraupinae) constitute a large, varied, colorful subfamily of neotropical birds. The last systematist to list all the known genera and species with their characters was Sclater (1886). Ridgway (1902) differentiated all the genera and those species found in North and Central American and the West Indies. Storer discussed the classification (1969) and listed all the forms (1970). Other important contributions were by Wetmore (1914), who described the peculiar stomach of *Euphonia*, and by Beecher (1951), who stated, mainly on the basis of jaw muscles, that several genera of honeycreepers belonged with the tanagers. Lucas (1894) and Bock (1985) differentiated genera of honeycreepers on the basis of tongue structure. Sibley (1970) studied the egg white proteins of 7 genera. Raikow (1978, 1985) devised a classification based mainly on the appendicular myology of 13 genera plus 4 borderline genera. Isler and Isler (1987) utilized the classification of Storer (1970), but their book is important because all the species of tangers are illustrated in color and the distribution, ecology, and behavior are summarized for each species. Sibley and Monroe (1990) listed all the species, classifying them on the basis of Sibley and Ahlquist's DNA work (1986, 1990) on 23 genera.

The classification of tanagers has been based on external anatomy, except for the partial work mentioned above on muscles, tongues, stomachs, and DNA. Skeleton studies have been reported by few workers. Shufeldt (1888) described two genera; Lucas (1894, 1895) mentioned 7 genera besides *Tersina*; Clark (1913) compared 3 genera; Beecher (1953) compared about 5 genera; Tordoff (1954) examined the skulls of 24 genera and figured 6; Berger (1957) examined the pneumatic fossa of the humerus in 15 genera; Bock (1962) of several (number not given) genera; Bock (1960) compared the palatine process of the premaxilla of 21 genera; George (1962) listed 19 genera besides *Tersina* in which he examined the hyoid; Cracraft (1968) mentioned that "most tanagers lacked a lacrimal" (genera unspecified); Lowery and Tallman (1976) in describing *Nephelornis* compared the skeleton with at least 5 genera of tanagers; Bock (1985) described the skulls of

TABLE 1. Genera of tanagers (following Storer, 1970) with the addition of a few species and genera (marked *) differentiated since that time and the subtraction of *Rhodinocichla* and 2 species of *Chlorospingus*.

Genera of Thraupinae	No. of species not examined	No. of species examined	No. of specimens examined
Orchesticus	1		
Schistochlamys		2	5
Neothraupis		1	1
Cypsnagra		1	3
Conothraupis	1	1	2
Lamprospiza		1	2
Cissopis		1	2
Chlorornis		1	4
Compsothraupis	1		
Sericossypha		1	2
Nesospingus		1	3
Chlorospingus	2	7	13
Cnemoscopus		1	2
Hemispingus	2	9	26
*Nephelornis**		1	5
Pyrrhocoma		1	2
Thlypopsis	2	4	9
Hemithraupis	1	2	9
Chrysothlypis	1	1	1
Nemosia	1	1	4
*Microligea**		1	10
*Xenoligea**		1	1
Phaenicophilus		2	5
Calyptophilus	1		
Mitrospingus	1	1	3
Chlorothraupis		3	6
Orthogonys		1	2
Eucometis		1	3
*Granatellus**		3	6
Lanio		4	6
Creurgops		2	2
Heterospingus		1	2
Tachyphonus		8	17
Trichothraupis		1	3
Habia	1	4	10
Piranga	1	8	33
Calochaetes		1	2
Ramphocelus	1	7	14
Spindali		1	2
Thraupis		8	20
Cyanicterus	1		
Buthraupis	5	4	8
Wetmorethraupis		1	2
Anisognathus	1	3	7
Stephanophorus		1	2
Iridosornis	1	4	5
Dubusia		1	2
Delothraupis		1	2

Genera of Thraupinae	No. of species not examined	No. of species examined	No. of specimens examined
Pipraeidea		1	2
Euphonia	7	18	33
Chlorophonia	2	2	6
Chlorochrysa	1	2	4
Tangara	10	38	64
Dacnis	5	4	9
Chlorophanes		1	4
Cyanerpes		4	11
Xenodacnis		1	3
Oreomanes		1	2
Diglossa	8	5	13
*Diglossopis**		3	7
Euneornis		1	6

Diglossa and *Diglossopis*; and Morony (1985) compared *Sericossypha* with 42 other genera. In this paper, the skeletons of all available species are compared.

MATERIALS AND METHODS

Through the courtesy of 14 museums, 434 tanager skeletons, representing 191 species of 57 of the 61 genera, were studied (see Table 1). In addition, numerous skeletons from a number of possibly related groups were studied (see page 590 for list). On each skeleton, 36 characters were measured with a dial caliper, or their shape was noted using a dissecting microscope. For most mensural characters, a ratio of measurements of 2 different skeletal elements is reported rather than the actual single measurement. All figures were drawn with the aid of a camera lucida. The ruled line is one millimeter in each case.

RESULTS

Twenty-two of the 36 characters proved somewhat useful in generic discrimination; they will be considered in order of clarity or usefulness. The first 7 characters, at least, may separate lines of evolution ("clades") of groups of genera. However, this suggestion is quite tentative. Too few skeletons (none of 4 genera; none of 57 species) were available; several species appeared to have been placed in the wrong genus; perhaps the wrong anatomical features were studied.

(1) The lacrimal was present as a distinct free bone, anterior to the ectethmoid plate, in all specimens of 13 genera (*Schistochlamys, Neothraupis, Cissopis, Chlorornis, Cnemoscopus, Pyrrhocoma, Calochaetes, Anisognathus, Stephanophorus, Iridosornis, Dubusia, Delothraupis,* and *Diglossa*) and in some specimens or species of 12 genera. In all specimens of the other 32 genera, it was either missing or fused with the ectethmoid plate. Usually it was impossible to say whether the lacrimal was missing or fused, but in a few cases, there was an evident suture,

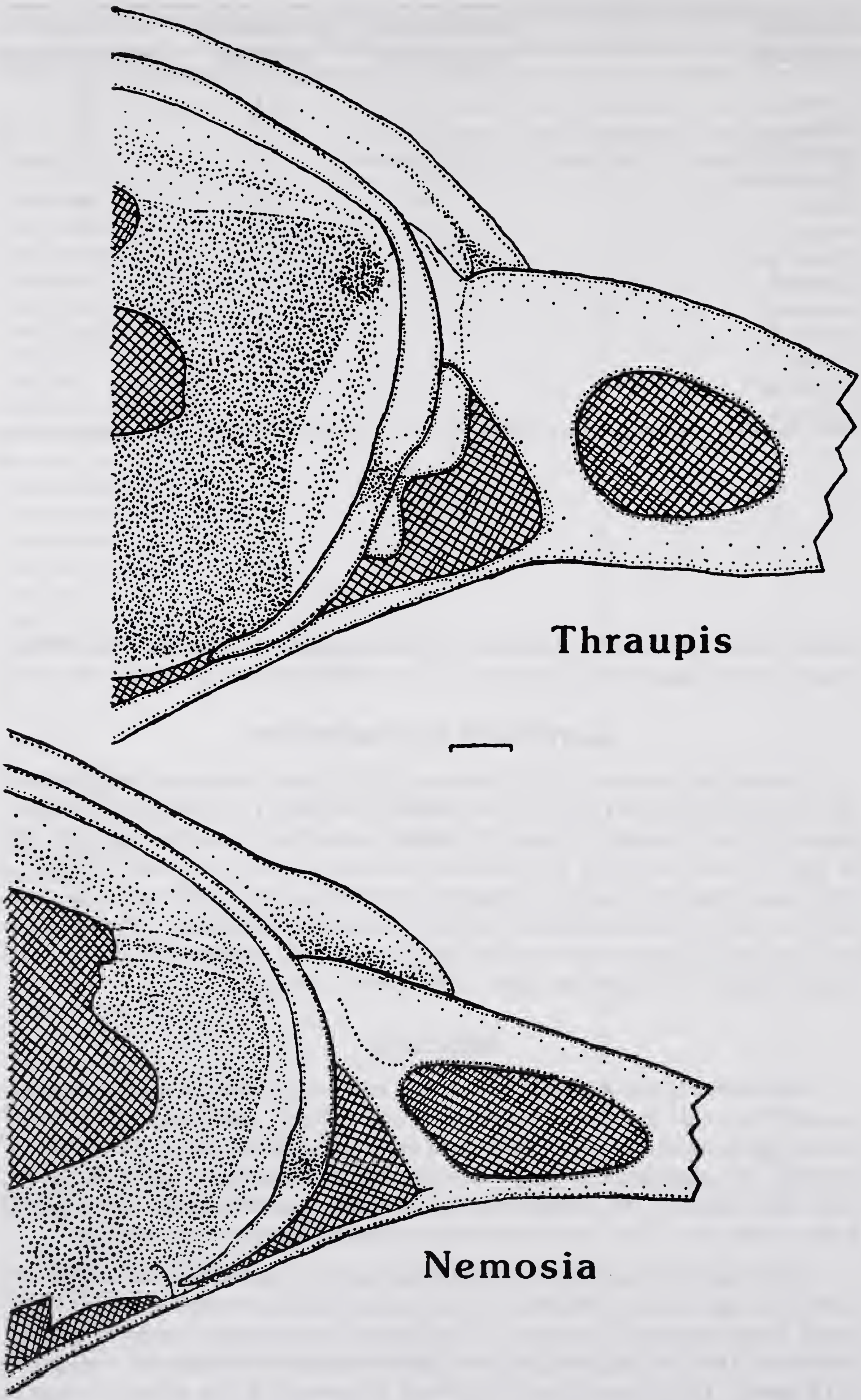

FIGURE 1. Lateral views of skulls of *Thraupis sayaca* and *Nemosia pileata*, drawn to the same scale. There is a free lacrimal in *Thraupis*.

FIGURE 2. Lateral views of anterior part of sternum of *Piranga bidentata* and *Hemispingus superciliaris*, drawn to the same scale. There is a large manubrium-sternum bridge in *Piranga*.

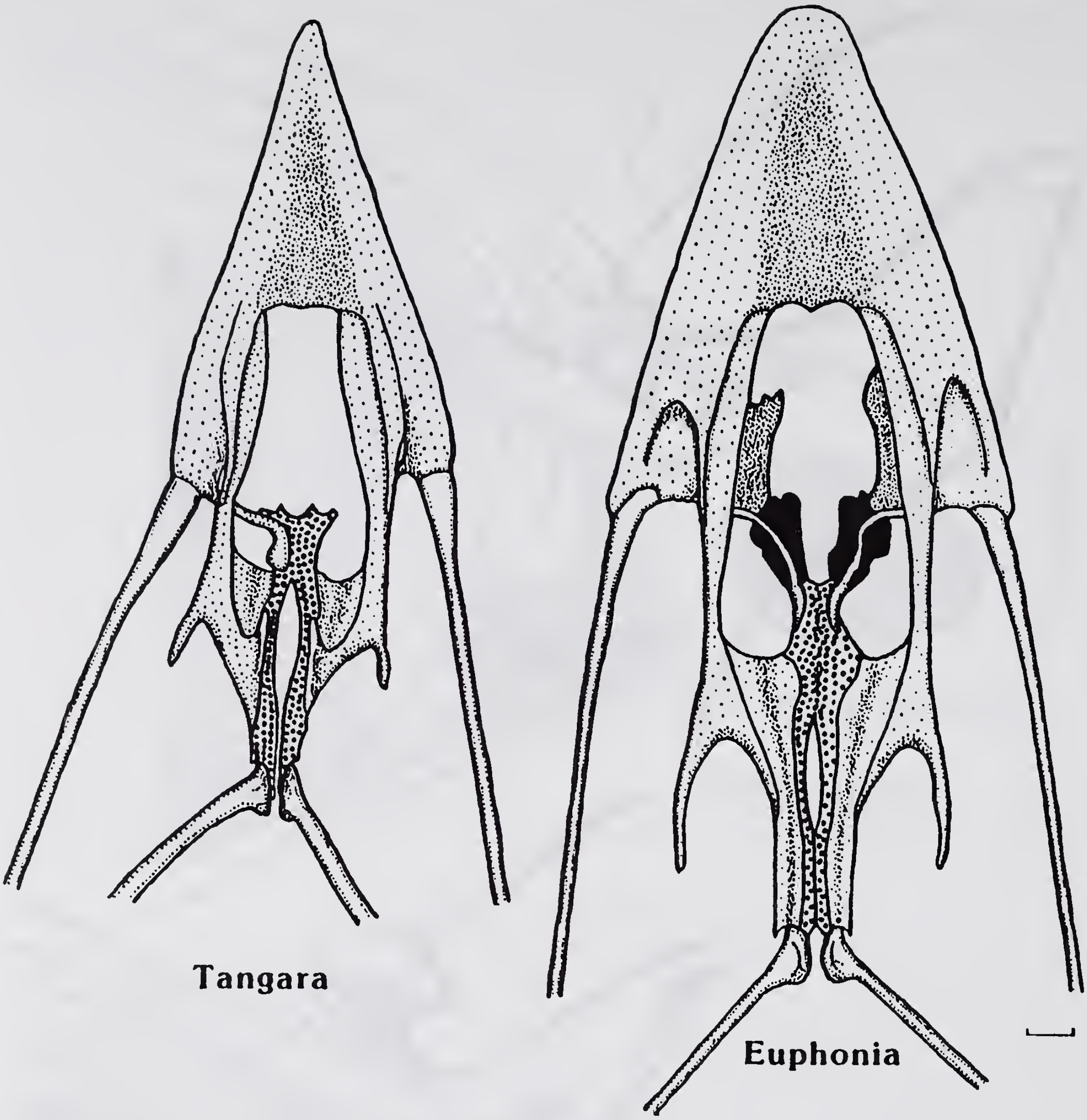

FIGURE 3. Ventral views of palates of *Euphonia chalybea* and *Tangara punctata*, drawn to the same scale, vomers coarsely stippled. In *Euphonia*, the interpalatine process is lacking; the palatine process of the premaxilla is small but evident; the lateral margin of the palatine posteriorly is concave; the transpalatine process is 4 times as long as wide; and the bony nasal capsules are drawn black. In *Tangara*, the interpalatine process is moderate; the palatine process of the premaxilla is small but evident; the lateral margin of the palatine posteriorly is concave; the transpalatine process is 6 times as as long as wide; the left maxillopalatine is broken off; and the nasal capsules are not bony.

indicating fusion. When present, the bone was nearly always pneumatic; in some species, it was larger than the one drawn (Figure 1, upper drawing) and in others smaller.

(2) The interpalatine process of the palatine was very small or missing entirely in all specimens of 7 genera (*Chlorornis, Calochaetes, Buthraupis, Iridosornis, Dubusia, Pipraeidia,* and *Cyanerpes*) and in some species or specimens of 14 more, but it was always long or of moderate size in 36 genera (Figure 2).

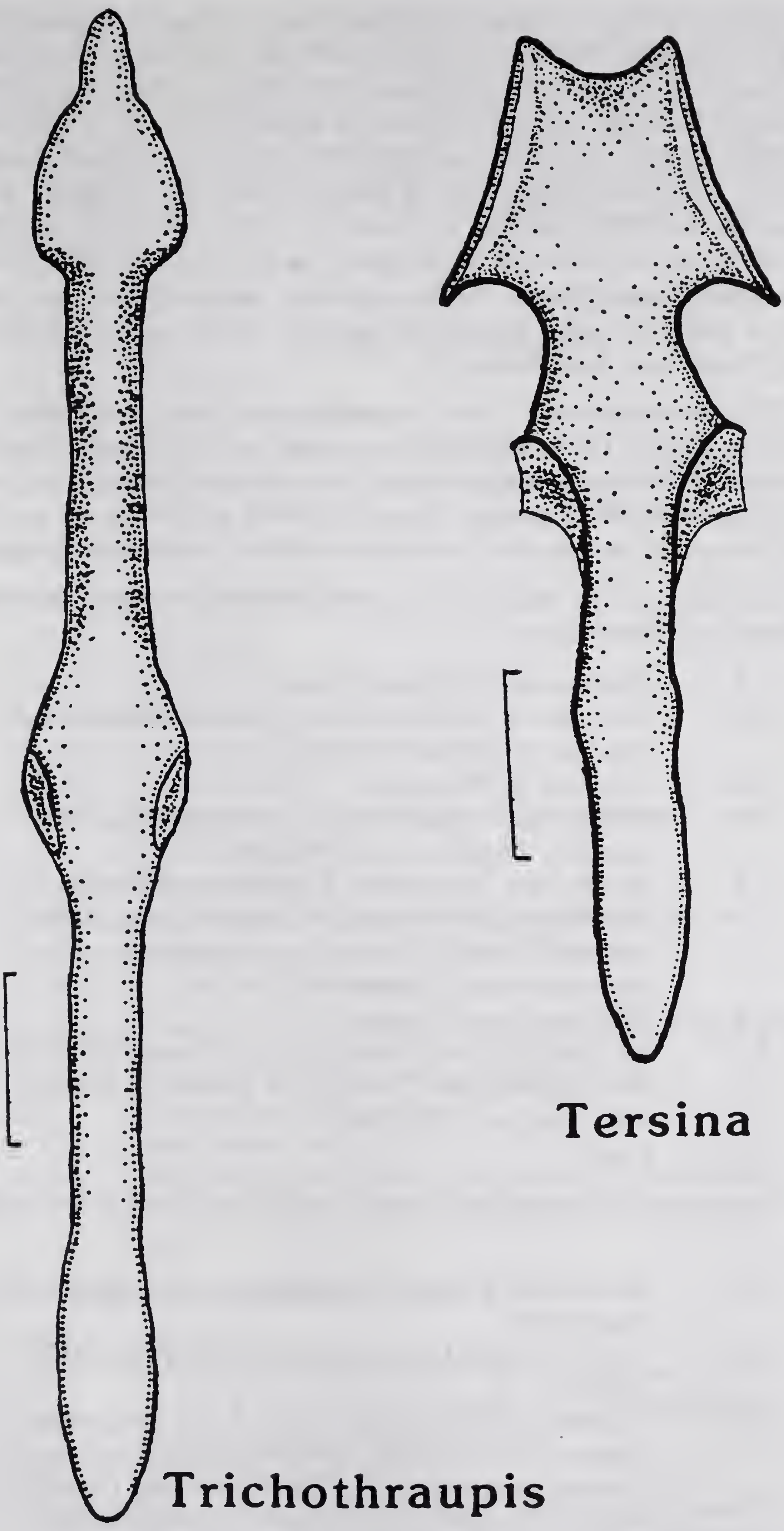

FIGURE 4. Ventral views of basihyoid and basibranchial of *Trichothraupis melanops* and *Tersina viridis*.

(3) The manubrium-sternum bridge was always present in 5 genera (*Conothraupis, Heterospingus, Habia, Cyanerpes,* and *Chlorophanes*) and was present in some specimens of 7 genera (*Sericossypha, Hemithraupis, Nemosia, Nephelornis, Tachyphonus, Piranga,* and *Xenodacnis*); in these 12 genera, it was always or usually large. In 15 more genera, the manubrium-sternum bridge was sometimes present as a very small structure; in 30 genera, it was always absent (Figure 3). The structure was first described by Shufeldt (1888) and emphasized by Clark (1913). It is neither universal in the tanagers, as suggested by Clark, nor unique to *Sericossypha* (*contra* Morony, 1985). As noted elsewhere (Webster, 1993), the structure is largest in some finches and cardinals of the genera *Rhodothraupis, Fringilla, Bubalornis,* and *Dinemellia.*

(4) The palatine process of the premaxilla was large or moderate (Tordoff, 1954, classes P1 and P2) in all specimens examined of 7 genera (*Neothraupis, Conothraupis, Chlorothraupis, Creurgops, Heterospingus, Piranga,* and *Euneornis*) and some specimens of 16 genera. It was small but evident in all specimens of the other 34 genera, except for a very few in which it was absent (Figure 2).

(5) Calculation of the mean of the ratio of tibiotarsus length/ulna length for each species gave these figures:

2.1 -	*Hemispingus rufosuperciliosus.*
1.9 -	*Nephelornis* and *Xenodacnis*; 1 species of *Habia*; and 1 species of *Diglossa.*
1.8 -	1 species of *Thlypopsis.*
1.7 -	*Dubusia* and 1 species each of *Chlorospingus, Hemispingus, Thlypopsis,* and *Diglossa.*
1.6 -	*Pyrrhocoma, Microligea, Xenoliga,* and *Delothraupis;* 3 species of *Hemispingus;* 2 species each of *Chlorospingus* and *Diglossa;* and 1 species each of *Iridosornis* and *Thlypopsis.*
1.5-1.2 -	Most species and genera.
1.1 -	*Sericossypha* and *Wetmorethraupis*; 3 species each of *Tachyphonus* and *Thraupis*; 2 species of *Piranga*; and 1 species of *Tangara.*
1.0-.9 -	*Lanio.*

(6) The mean of the ratio of tibiotarsus length/femur length for each species was:

2.0 -	*Xenodacnis*; 2 species of *Diglossa*; and 1 species of *Diglossopis.*
1.9 -	2 species each of *Diglossa* and *Hemispingus*; and *Diglossopis.*
1.9 -	*Pyrrhocoma, Thlypopsis, Nephelornis, Microligea, Granatellus, Spindalis,* and *Oreomanes*; 4 species of *Hemispingus*; 2 species of *Iridosornis*; and 1 species each of *Chlorospingus, Diglossa,* and *Diglossopis.*
1.7-1.5 -	Most species and genera.

(7) The ectethmoid foramen was always single in 18 genera (*Neothraupis, Conothraupis, Lamprospiza, Cissopis, Chlorornis, Nesospingus, Chlorothraupis, Eucometis, Granatellus, Trichothraupis, Habia, Piranga, Orthogonys, Stephenophorus, Dubusia, Delothraupis, Pipraeidea,* and *Oreomanes*) and always double in 6 (*Sericossypha, Phaenicophilus, Xenoligea, Mitrospingus, Heterospingus,* and *Euneornis*). It was mixed (either single, double and pinched; or single and pinched; or double and pinched; or double and single; or always pinched) in various specimens of 33 genera.

(8) The ratio of braincase width/supraorbital width for each species was:

7.0-6.3 - *Cypsnagra* and 3 species of *Thlypopsis.*
6.1 - *Nephelornis.*
5.9-3.1 - Most species and genera.
3.0-2.6 - *Cissopis* and *Sericossypha*; 2 species of *Chlorothraupis*; 3 species of *Piranga*; 2 species each of *Rhamphocelus* and *Lanio*; and 1 species of *Thraupis.*
2.1 - 1 species of *Piranga.*

(9) Premaxillary length/width was:

3.7-2.9 - *Cyanerpes.*
3.4 - *Oreomanes.*
3.1-2.2 - *Diglossa.*
2.7-2.6 - 2 species of *Diglossopis.*
2.5-2.2 - *Phaenicophilus.*
2.2-2.1 - *Sericossypha, Microligea,* and *Chlorophanes*; 2 species of *Thlypopsis.*
2.0-1.3 - Most species and genera.
1.2-1.1 - *Stephanophorus*; 3 species of *Tangara*; 2 species of *Anisognathus*; and 1 species of *Thraupis.*
1.2-0.9 - 12 species of *Euphonia.*

(10) Skull length was the only absolute size (mm) measure used. It was:

31-29 – *Sericossypha* and 3 species of *Buthraupis.*
28 - *Cissophis* and *Chlorornis.*
27-18 - Most species and genera.
17-16 - *Chrysothlypis*; 4 species of *Euphonia*; and 1 species each of *Tangara, Dacnis, Hemithraupis,* and *Diglossa.*

(11) Tarsometatarsus length/femur length was:

1.6-1.4 - *Diglossa*
1.4 – *Pyrrhocoma, Nephelornis, Microligea,* and *Oreomanes*; 2 species each of *Diglossopis* and *Hemispingus*; and 1 species of *Thlypopsis.*
1.3-1.1 - Most species and genera.
1.0 - *Calochaetes, Wetmorethraupis;* 5 species of *Thraupis*; 4 species each of *Piranga* and *Tangara*; 3 species each of *Euphonia* and *Lanio*; 2 species of *Rhamphocelus*; and 1 species of *Chlorophonia.*
0.9 - *Sericossypha.*

(12-23) Ratio of tarsometatarsus length/width separated 10 genera and parts of 14 genera from the rest. Length of the transpalatine process separated 13 genera and parts of 13 more from the rest. Length of the retroarticular process of the mandible separated 1 genus (*Oreomanes*) and parts of 3 others from the rest. Shape of the orbital process of the quadrate separated 1 genus (*Oreomanes*) and parts of 13 genera from the rest. Length of the pseudotemporal process of the mandible separated 10 genera and parts of 12 others from the rest. Shape of the lateral margin of the palatine posteriorly separated 1 genus (*Neothraupis*) and parts of 20 more from the rest. Ratio of tibiotarsus length/humerus length separated 11 genera and parts of 10 from the rest. Ratio of tibiotarsus length/ tarsometatarsus length separated 8 genera and parts of 11 from the rest. Shape of the squamosal (= suprameatic) process separated 4 genera and parts of 8 genera from the rest. Ratio of ulna length/humerus length separated 2 genera and parts of 7 others from the rest. Shape of the pneumatic fossa of the humerus separated one genus (*Sericossypha*) from the rest. Shape of the maxillopalatine separated 20 genera from the rest.

(24-36) These characters were observed or measured on each specimen but were much too uniform for generic discriminants: fronto-nasal hinge mobility, basihyoid-basibranchial shape, angle of internal tuberosity of humerus with shaft, ratio of ulna length/femur length, ratio of humerus length/femur length, shape of the internal process of the mandible, relative digit (= trochlear) lengths of metatarsus, and distal bend of tarsometatarsus. These characters were observed but were too variable within each species or each genus to be generic discriminants: shape of ectethmoid plate margin, internasal septum and nasal capsules (apparently defective specimens were too common, but bony nasal capsules were usually present—present in all or most specimens in 16 of the 18 species—in *Euphonia*, as shown in Figure 3, and only 5 other genera; more and better specimens will probably demonstrate this to be a valid generic character), shape of lateral process of nasal, shape of anterior end of vomer, and process 7b of mandible. Also, 11 more characters, mostly of the vertebrae and ribs, were rcorded on most of 59 specimens of 48 species of tanagers in earlier years in connection with my studies of warbler skeletons (Webster and Goff, 1979; Webster, in prep.). None provided useful information for generic classification.

In the pages above, neither the question of the boundary of the subfamily Thraupinae nor its relationship to other groups was addressed; the author has instead, simply considered the genera and species as listed by Storer (1970), added the new species and two genera described since, plus 3 genera the author had transferred from Parulinae in an earlier paper (Webster, in prep.). Also, the author removed one genus (*Rhodinocichla*) to Parulinae, following Ridgway (1902) but *contra* Storer (1970). The skeletons of *Rhodinocichla* and other borderline or recently questioned genera (*Conirostrum, Coereba, Tersina, Catamblyrhynchus, Rhodospingus, Coryphospingus,* and *Paroaria*) were compared as well as 24 (all but one) of the genera of Parulinae, 49 of the genera of Emberizinae, 19 of Icterinae, and 7 of Cardinalinae. The 7 skeletons of *Rhodinochinhla rosea* examined fit better with the warblers (Parulinae) than with the tanagers (Thraupinae) on each of the subfamily characters mentioned below.

In the DNA classification of Sibley and Ahlquist (1986, 1990), the tribe Thraupini includes the tanagers, all of the borderline genera mentioned above, and many of the genera usually (Paynter, 1970) assigned to Emberizinae. Especially at the level of tribes and genera, it is unwise to base a new classification on only one type of evidence, when the authors have examined only 38% of the genera of tanagers and 32% of the genera of emberizines. Raikow's (1978, 1985) classification is based on evidence from even fewer genera. The average linkage clustering tree showing DNA relationships within the tanagers as presented by Sibley and Ahlquist (1990, p. 870) was compared closely with this skeletal data, as were their various melting curves and their Fitch tree. Correlation was virtually absent with the 11 skeletal characters which ranked highest for generic distinctions (above). Correlation of Sibley and Ahlquist's data with the classification of Storer (1970), based principally on plumage and other external anatomy, was also very poor.

The unique anatomy of the swallow tanager (*Tersina viridis*) is worth emphasis. Figure 4, right drawing, shows the basihyoid + basibranchial in contrast with that of a typical tanager. In *Tersina*, not only is the basihyoid short and stout; it is round in cross-section medially, and the anterior end is almost T-shaped rather than sagittate. The shape of the basihyoid as shown in *Trichothraupis* (left drawing) is similar to that in all other 9-primaried new world oscines except for *Tersina* and *Peucedramus* (George, 1962; Webster, in prep.). *Peucedramus*, the olive warbler, has a hyoid which is less aberrant than that of *Tersina*, for the anterior end is almost normal, and only the median part is peculiar—round in cross-section rather than compressed. In *Tersina*, the entire posterior palatine shelf is missing, including the transpalatine process (Lucas, 1895; Tordoff, 1954). The ratio of braincase width/supraorbital width (2.4) is less than in all but one species of tanager. The pseudotemporal process of the mandible is smaller than in any tanager—indeed missing entirely in 2 specimens. The tibiotarsus/tarsometatarsus ratio is higher than in any tanager. In other features studied, *Tersina* fitted within the variation found in tanagers.

A definition of the subfamily Thraupinae (genera as listed in Table 1) on the basis of mostly skeletal characters is: insectivorous, nectarivorous, or frugivorous (or a combination of those) 9-primaried new world oscines; skeleton lightly or moderately built; premaxilla (or bill) moderately stout or slender; maxillopalatine club pneumatic and usually fat; palatine process of the premaxillary evident and sometimes prominent; lateral margin of palatine posteriorly almost always straight or concave; transpalatine process slender, usually more than 3 times as long as wide; orbital process of quadrate nearly always longer than rest of quadrate and usually with little taper; basihyoid compressed medially and sagittate anteriorly; pneumatic fossa of humerus usually of combined type, although often with a slight medial bar or step-down, or rarely double with a prominent medial bar; and internal tuberosity of head of humerus making an angle of 55-70° with shaft, usually 60° or more.

DISCUSSION

Any good classification is based on a wide variety of data. Therefore, the skeletal features described here are inadequate for a rigorous systematic revision of the tanagers. However, new data presented here may help to resolve some problems. Several species may have been placed in the wrong genera in *Hemithraupis, Hemispingus, Thraupis, Buthraupis, and Tangara,* because these genera show such great variability in the skeleton. On the other hand, almost no skeletal differences were found between *Euphonia* and *Chlorophonia,* between *Delothraupis* and *Dubusia,* and between *Tachyphonus* and *Trichothraupis*. Perhaps, these pairs of genera, in each case already placed side-by-side by Storer (1970), should be united. The very distinct skeletal features of *Tersina* confirm the traditional placement of that species in a separate subfamily or family.

ACKNOWLEDGMENTS

The author wishes to thank the curators of these museums for allowing me to examine specimens under their care: American Museum of Natural History, British Museum (Natural History), California Academy of Sciences, Museum of Vertebrate Zoology of the University of California, Carnegie Museum, Field Museum of Natural History, Florida State Museum at the University of Florida, University of Kansas Museum of Natural History, Louisiana State University Museum of Zoology, University of Michigan Museum of Zoology, Royal Ontario Museum, United States National Museum of Natural History, and Peabody Museum of Natural History of Yale University. Allan R. Phillips loaned me specimens from his personal collection. Hanover College helped me with a grant toward my expenses. Daryl Karns was a helpful critic of the manuscript.

LITERATURE CITED

Beecher, W.J. 1951. Convergence in the Coerebidae. Wilson Bull. 63: 274-287.

__________. 1953. A phylogeny of the Oscines. Auk 70: 270-333.

Berger, A.J. 1957. On the anatomy and relationships of *Fregilupus varius*, an extinct starling from the Mascarene Islands. Bull. Amer. Mus. Natur. Hist. 113: 225-272.

Bock, W.J. 1960. The palatine process of the premaxilla in the Passeres. Bull. Mus. Comp. Zool. 122: 361-488.

__________. 1962. The pneumatic fossa of the humerus in the Passeres. Auk 79: 425-443.

__________. 1985. Is *Diglossa* (?Thraupinae) monphyletic? *In:* P.A. Buckley, *et al.* (Eds.), *Neotropical Ornithology*, pp. 319-332, Ornithol. Monog. 36: 1-1041.

Clark, H.L. 1913. Notes on the Panama thrush-warbler. Auk 30: 11-15.

Cracraft, J. 1968. The lacrimal-ectethmoid bone complex in birds: A single character analysis. Amer. Midl. Natur. 80: 316-359.

George, W.G. 1962. The classification of the olive warbler, *Peucedramus taeniatus*. Amer. Mus. Nov. 2103: 1-41.

Isler, M.L. and P.R. Isler. 1987. The tanagers: Natural history, distribution, and identification. Smithsonian Inst. Press, Washington, 404 pp.

Lowery, G.H., Jr. and D.A. Tallman. 1976. A new genus and species of nine-primaried oscine of uncertain affinities from Peru. Auk 93: 415-428.

Lucas, F.A. 1894. Notes on the anatomy and affinities of the Coerebidae and other American birds. Proc. U.S. Nat. Mus. 17: 299-312.

__________. 1895. Osteological and pterylographical characters of the Procniatidae. Proc. U.S. Nat. Mus. 18: 505-507.

Morony, J.J., Jr. 1985. Systematic relations of *Sericossypha albocristata* (Thraupinae). *In:* P.A. Buckley, *et al.* (Eds.), *Neotropical Ornithology*, pp. 383-389, Ornithol. Monog. 36: 1-1041.

Paynter, R.A., Jr. 1970. Subfamilies Emberizinae, Catamblyrhynchinae, and Cardinalinae. *In:* J.L. Peters, *et al., Check-list of Birds of the World, 13*, pp. 1-245, Mus. Comp. Zool., Cambridge, 443 pp.

Raikow, R.J. 1978. Appendicular myology and relationships of the new world nine-primaried oscines (Aves: Passeriformes). Bull. Carnegie Mus. Natur. Hist. 7: 1-43.

__________. 1985. Problems in avian classification. *In:* R.F. Johnston (Ed.), *Current Ornithology, 2*, pp. 187-212, Plenum, New York, 364 pp.

Ridgway, R.L. 1902. Birds of North and Middle America. Bull. U.S. Nat. Mus. 50 (II): 1-834.

Sclater, P.L. 1886. Catalogue of the birds in the British Museum, 2. British Mus., London, 431 pp.

Sibley, C.G. 1970. A comparative study of the egg-white proteins of passerine birds. Bull. Peabody Mus. Natur. Hist. Yale Univ. 32: 1-131.

__________ and J.E. Ahlquist. 1986. The phylogeny and classification of the passerine birds, based on comparison of the genetic material. *In:* V.D. Ilyichev and V.M. Gavrilov (Eds.), *Proceedings of the 18th International Ornithological Congress, Vol. 1*, pp. 83-121, Nauka Publ., Moscow, 576 pp.

__________ and __________. 1990. Phylogency and classification of birds; A study in molecular evolution. Yale Univ. Press, New Haven, 976 pp.

__________ and B.L. Monroe, Jr. 1990. Distribution and taxonomy of birds of the world. Yale Univ. Press, New Haven, 1111 pp.

Storer, R.W. 1969. What is a tanager? Living Bird 8: 127-136.

__________. 1970. Subfamilies Thraupinae and Tersininae. *In:* J.L. Peters, *et al., Check-list of Birds of the World, 13*, pp. 246-409, Mus. Comp. Zool., Cambridge, 443 pp.

Tordoff, H.B. 1954. A systematic study of the avian family Fringillidae based on the structure of the skull. Misc. Pub. Mus. Zool. Univ. Michigan 81: 1-42.

Webster, J.D. in prep. Skeletal characters and the genera of warblers.

__________. 1993. The manubrium-sternum bridge in Oscines. Proc. Indiana Acad. Sci. 101: 299-308.

__________ and S.G. Goff. 1979. Variation in the vertebral column and ribs of song birds. Proc. Indiana Acad. Sci. 87: 450-459.

Wetmore, A. 1914. The development of the stomach in the Euphonias. Auk 31: 458-461.