script. C. W. Jackson kindly improved our English. We also thank the Corporación Nacional Forestal I Región, DTI (N°3537), and J. Hernández for his valuable field assistance. This study was supported by the BirdLife International/Panamerican Section and the U.S. Fish and Wildlife Service.

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Body Pterylosis of Woodcreepers and Ovenbirds (Dendrocolaptidae and Furnariidae)

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The Dendrocolaptidae and Furnariidae, two groups of Central and South American suboscine passerines, have always been considered closely related. With 52 species, the woodcreepers occur from northern Mexico to central Argentina in forest, forest-edge, and open-woodland habitats, where they nest in holes or cavities. Their body lengths range from 13.5 to 37 cm, and their mass from 12 to 120 g; the plumage is generally dull rufous brown, often streaked or spotted. The most distinctive external features of dendrocolaptids are: usually large, laterally compressed, often decurved bills used as foraging probes on tree trunks; and their rigid, spiny-tipped rectrices used as props against those trunks. Their ecology, behavior, and superficially homogenous morphology reflect the scansorial habits of woodcreepers. The much larger group of ovenbirds (218 species) occurs from central Mexico to Patagonia and the Falkland Islands. The

Furnariidae have radiated into an astonishing diversity of niches, having adapted to arboreal and terrestrial habitats from deep forest to open desert, and from coastal sand dunes and cliffs to above treeline in the Andes. Accordingly, they also are widely variable in external morphology and in the sites and types of their closed nests. Furnariids generally are smaller than dendrocolaptids, ranging from 10 to 28 cm long and with a mass of 9 to 46 g. Their plumage is more varied than that of woodcreepers, but they are still primarily dark brown, olive, or rufous above and lighter below. A few of the treerunners (*Margarornis* "assemblage"; Rudge and Raikow 1992) have somewhat spiny tails.

Morphologically the two groups have similar tracheophone syringes with two pairs of intrinsic syringeal muscles (Ames 1971); their front toes are variously joined at the base (Ridgway 1911, Vaurie 1980); and they have a single pair of notches in the posterior sternum (with a few exceptions and individual variability; Heimerdinger and Ames 1976). DNA-DNA hybridization studies also indicate a close relationship of the two groups (Sibley and Ahlquist 1990). The taxonomic ranking of woodcreepers and ovenbirds has never been settled, with some authors (e.g. Sibley and Ahlquist 1990, Raikow 1994) regarding them as subfamilies of a larger family, Furnariidae. Most traditional classifications, however, have listed them as separate families—the first two (although either family may appear first) of the suborder Tyranni, superfamily Furnarioidea (e.g. Peters 1951, Morony et al. 1975, AOU 1983). The Dendrocolaptidae have been separated from the Furnariidae on the basis of additional syringeal features, particularly the horns on the processi vocales of woodcreepers that are lacking in all ovenbirds except *Geositta*. More traditionally, the separate familial status has rested on the different shapes of the nares—holorhinal (rounded) in dendrocolaptids, pseudoschizorhinal (slitlike) in furnariids—as well as on several characters in the feet and on plumage patterns, especially wing stripes. Feduccia (1973) also found differences in the electrophoretic patterns of their hemoglobin, but as with all the characters used thus far to divide these two groups, there were a few exceptions or intermediate forms. Perhaps it is primarily because no single character has been found that unequivocally separated the woodcreepers and ovenbirds that their taxonomic status is still debated.

Materials and methods.—The technique used has been described previously (Clench 1970, 1985). Skins were removed from 34 specimens freshly collected or preserved in alcohol, pinned flat, dried, and the underside examined under a 10-40× binocular dissecting microscope. The series included 12 specimens of Dendrocolaptidae (11 species, 10 of 13 genera): *Dendrocincla anabatina, D. tyrannina, Deconychura longicauda, Sittasomus griseicapillus, Glyphorhynchus spirurus* (2), *Drymornis bridgesii, Xiphocolaptes major, Dendrocolaptes certhia, Xiphorhynchus guttatus, Lepidocolaptes affinis,* and *Campylorhamphus trochilirostris.* The series of Furnariidae included 22 specimens (21 species, 16 of 34 genera, 3 subfamilies): *Geositta cunicularia, Chilia melanura,* and *Furnarius rufus* in the Furnariinae; *Synallaxis albescens, S. cinnamomea, S. erythrothorax, Certhiaxis cinnamomea, C.* (*Cranioleuca*) *sulfurifera, Phacellodomus rufifrons, Phleocryptes melanops,* and *Anumbius anumbi* in the Synallaxinae; and *Margarornis* (*Premnoplex*) *brunnescens, M. rubiginosus, Lochmias nematura, Pseudoseisura lophotes, Philydor rufus, Automolus leucophthalmus, Sclerurus mexicanus, Xenops* (*Heliobletus*) *contaminatus, X. minutus* (2), and *Pygarrhichas albogularis* in the Philydorinae. The taxonomy employed here is that of Morony et al. (1975), who followed Vaurie (1971) for the Furnariidae. Genera recognized by Peters (1951) but synonymized by Vaurie (1980) are noted above by parentheses.

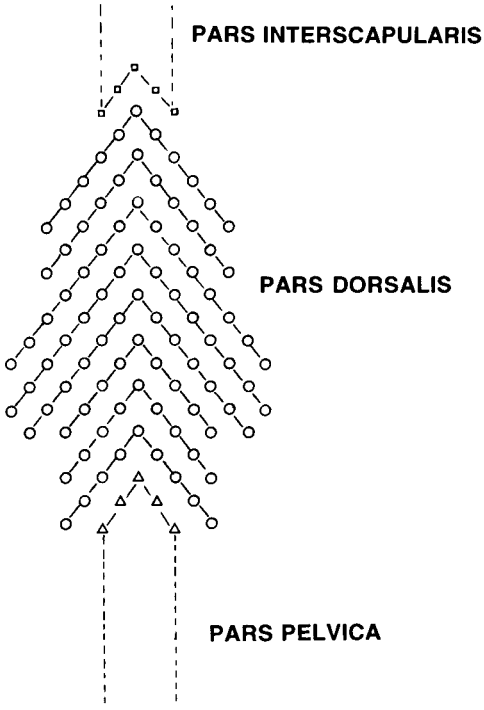
Included in my sample were two specimens of a species in each family in order to check for significant individual variation; none was found. Similarly, two species in the dendrocolaptid genus *Dendrocincla* and two species of the furnariids *Certhiaxis, Margarornis,* and *Xenops* and three of *Synallaxis* were examined for significant intrageneric variation; none was found. The reliability of using a single specimen to establish the pterylographic pattern and relative number of feathers of a genus was confirmed in these families as it has been in other passerines (Clench 1970, 1985, 1992).

Also included in the sample were representatives of the genera that have been found by others to be atypical of their respective families: the woodcreepers *Dendrocincla, Deconychura, Sittasomus,* and *Glyphorhynchus,* and the ovenbirds *Geositta, Automolus, Xenops, Pygarrhichas, Sclerurus,* and two of the ovenbird/treerunner assemblage (*Margarornis, Premnoplex*; Rudge and Raikow 1992).

I studied the pattern of the main body tracts—the pteryla spinalis (spinal tract) that extends down the dorsal surface from the base of the skull to the uropygial gland, and the pteryla ventralis (ventral tract), a paired, mirror-image, wishbone-shaped band of feathers on either side of the breast and abdomen. These tracts have proved to exhibit the most important variation in passerines. Terminology follows that used in Clench (1985). Statistically significant differences in numbers of feathers were determined by the Student's *t*-test.

Results.—In the pteryla spinalis, both families had the general pattern of a solidly feathered rhombic pars dorsalis (i.e. there were no spaces, gaps, or apteria). The partes interscapularis and pelvica were narrow and undistinguished. All specimens had a gap between the posterior border of the pteryla capitalis and the pars interscapularis at the base of the neck; this gap has been present in all the suboscines (Old or New World) that I have studied, but in no oscines.

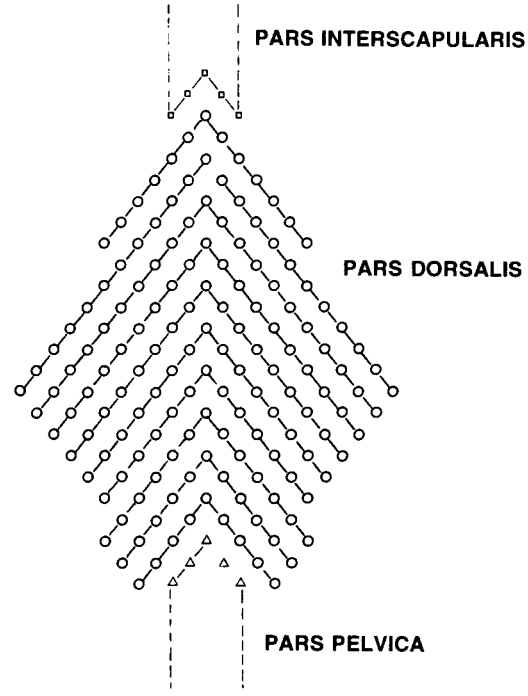
The spinal tract of all the woodcreeper specimens,



Dendrocolaptes certhia

PTERYLA SPINALIS

Fig. 1. Diagrammatic representation of pteryla spinalis of *Dendrocolaptes certhia*. Individual feathers of pars dorsalis indicated by circles, those of last row of pars interscapularis as squares, and first row of pars pelvica as triangles.



Automolus leucophthalmus

PTERYLA SPINALIS

Fig. 2. Diagrammatic representation of pteryla spinalis of *Automolus leucophthalmus*. Conventions as in Figure 1.

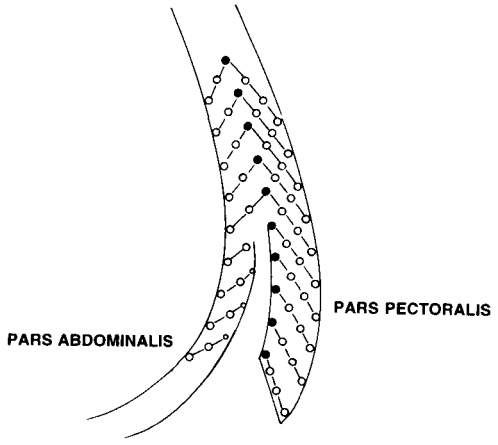
exemplified by *Dendrocolaptes certhia* (Fig. 1), was relatively narrow and comparatively sparsely feathered for passerines of this large body size. The mean number of feathers in the pars dorsalis (the tract's rhombic-shaped central portion) was 100.7 ± SE of 3.8 (range 92–112) in eight rows. There were 92 feathers in the pars dorsalis of *Dendrocolaptes certhia*, which has a mass of about 80 g.

In contrast, all the generally smaller furnariids studied had a significantly more heavily feathered pars dorsalis, with a mean of 143.0 ± 5.9 feathers in 8 to 10 rows ($P < 0.001$). *Automolus leucophthalmus* (Fig. 2) was typical in pattern. The family sample ranged from 128 to 164 feathers in the pars dorsalis, except for 112 in the tiny species *Xenops minutus* (body mass of only 9 g).

In the pteryla ventralis, the two groups had the same difference in degree of feathering, but there was an even more striking difference in pattern. In the flank region where the two parts of the tract divide, woodcreepers showed a simple splitting of the more anterior chevron-shaped rows at the central feather and a continuation of the pars pectoralis as single-armed lateral rows (e.g. *Dendrocolaptes certhia*; Fig. 3). In my experience, this pattern is unique within the Passeriformes, and all the woodcreepers examined had it—with no exceptions or intermediate conditions.

In contrast, the pars pectoralis in the Furnariidae (e.g. *Automolus leucophthalmus*; Fig. 4) was formed by two-armed chevron-shaped rows and ended in an oblique border with the lateral arms shorter than the medial. Without exception, all ovenbirds examined had this pattern, which is also seen in other New World suboscines such as members of the Formicariidae, and in all oscines.

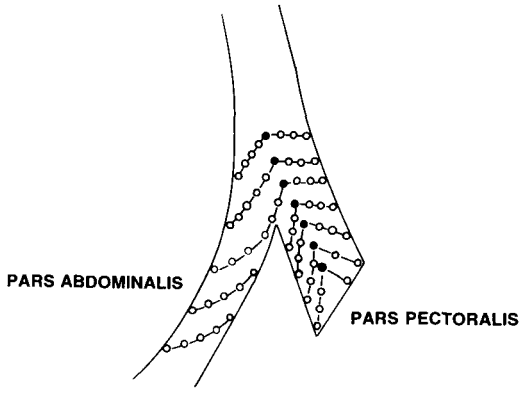
Discussion.—Before my study, the pterylosis of the Dendrocolaptidae and Furnariidae was almost unknown. In the only previous description of the pterylography of these families, Nitzsch (1867) did not analyze the tracts in detail, but noted that *Dendrocolaptes* had an elongated rounded rhombic pars dorsalis, and the posterior end of the flank was widely separated from the pars abdominalis. He also studied four genera of ovenbirds—"*Synallaxis*" (=*Leptasthenura*) *setaria*, *Ochetorhynchus* (=*Upucerthia*) *ruficaudus*, "*Opetiorhynchus rupestris*" (=*Cinclodes patagonicus*), and



Dendrocolaptes certhia

PTERYLA VENTRALIS

Fig. 3. Diagrammatic representation of left flank region of pteryla ventralis of *Dendrocolaptes certhia*. Central row feathers indicated as ●.



Automolus leucophthalmus

PTERYLA VENTRALIS

Fig. 4. Diagrammatic representation of left flank region of pteryla ventralis of *Automolus leucophthalmus*. Central row feathers indicated as ●.

several species of *Furnarius*, including *F. rufus* and *F. figulus*. He noted correctly that they had a solid rhombic pars dorsalis and typically passerine pterylosis.

Feduccia (1973) considered *Dendrocincla, Deconychura, Sittasomus*, and *Glyphorhynchus* to be an "intermediate" group of woodcreepers, with a mosaic of ovenbirdlike characters, particularly in the wing stripe and in skull, hindlimb, and sternal characters. *Glyphorhynchus* also showed a hemoglobin pattern identical to that of ovenbirds. Sibley and Ahlquist (1990) studied three of the four genera in question (*Dendrocincla, Sittasomus*, and *Glyphorhynchus*) along with five others and concluded a close relationship within the woodcreepers, and between that group and the ovenbirds. Raikow (1994) found the woodcreepers as a whole to be monophyletic.

The pterylographic pattern of the four intermediate genera was perfectly uniform and typical of the other dendrocolaptids examined. In all respects the feather counts were also identical or very similar. For example, the two smaller species, *Sittasomus griseicapillus* and *Glyphorhynchus spirurus*, had 92 and 96 feathers, respectively, in the pteryla spinalis, pars dorsalis. *Dendrocincla anabatina, D. tyrannina*, and *Deconychura longicauda* had 112, 112, and 100, respectively (family $\bar{x} = 100.7 \pm 3.8$).

Ames (1971) found that *Geositta*, an otherwise typical furnariid, had large horns on the processi vocales of the syrinx, typical of dendrocolaptids. In his discussion of the anomaly, Feduccia (1973:47) noted "it is difficult to understand what similar function would be demanded of this lark-like open country bird, that would be similar to the deep-forest inhabiting woodhewers." *Geositta* has remained a member of the ovenbirds in all recent classifications, and its pterylosis agrees with this designation. The syringeal oddity remains to be explained.

Based primarily on comparative osteology, Feduccia (1973) proposed that the species in the *Margarornis* assemblage, despite their scansorial habits and making some use of the tail as a prop against tree trunks, were not dendrocolaptids (contra Sclater 1890) and should be retained in the Furnariidae. Depending on which taxonomist one follows, this assemblage has six or eight species in four genera; Vaurie (1971, 1980) included them all in *Margarornis*. For his study, Feduccia (1973) had specimens of *Margarornis rubiginosus* and *Premnoplex brunnescens*, but not of *Premnornis* (*guttuligera*) or *Roraimia* (*adusta*). With material of all four genera, and emphasizing myological characters of the fore- and hindlimbs, Rudge and Raikow (1992) concluded that the treerunners were a monophyletic group of ovenbirds. The pterylosis also supports *Margarornis* as a furnariid.

Feduccia (1973) noted that *Automolus* was another intermediate form, similar to *Dendrocincla* and related woodcreepers. In addition, he remarked that *Xenops* was similar to dendrocolaptids in its tibiotarsus and recommended that the scansorial genus *Pygarrhichas*, which Sclater (1890) had considered a woodcreeper, be retained in the Furnariidae. The pterylosis of all three is in perfect agreement with the other ovenbirds I examined.

In summary, the body pterylosis of the Dendrocolaptidae and Furnariidae is entirely consistent within their respective groups. Most importantly, the Dendrocolaptidae have a unique configuration in the ventral tract that distinguishes them from all other *Passerines*. In contrast, the ventral pattern of the Fur-

nariidae is similar to that seen in other New World suboscines and all oscines. Woodcreeper and ovenbird genera that have intermediate or conflicting aspects in other morphological characters show a clear pterylographic pattern that can be used to place any of the genera studied in one group or the other. Pterylosis always has proved in my other studies of passerines to be an evolutionarily conservative character (Clench 1970, 1985). Therefore, because there is a striking pattern difference in the ventral tract and relatively strong differences in the degree of feathering, and because a body of other morphological data supports the traditional separation of the two groups, I suggest that they should continue to be regarded as separate families.

Acknowledgments.—Kenneth C. Parkes, Philip S. Humphrey, and I collected some of the specimens specifically for this study; the specimens are now part of the alcohol-preserved or flatskin material at Carnegie Museum of Natural History or Peabody Museum of Natural History, Yale University. The majority of specimens came from alcohol collections at: Carnegie Museum of Natural History; Peabody Museum of Natural History, Yale University; and the National Museum of Natural History, Smithsonian Institution. I sincerely thank all the curatorial friends who provided material for this very long-term study.

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Conservation Commentary: Ornithology and the National Biological Survey

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Secretary of the Interior of the United States, Bruce Babbitt, created the National Biological Survey (since renamed National Biological Service; hereafter NBS) by secretarial order on 29 September 1993. In creating the new bureau, the Secretary consolidated the research, survey, and monitoring functions of seven Department of Interior bureaus, including the Fish and Wildlife Service, National Park Service, and Bureau of Land Management. The NBS mission is to work with others to provide the scientific understand-

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