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THE ANATOMY AND SYSTEMATIC POSITION OF THE ANTPIPITS *CONOPOPHAGA* AND *CORYTHOPIS*

PETER L. AMES

MUSEUM OF VERTEBRATE ZOOLOGY, UNIVERSITY OF CALIFORNIA,
BERKELEY, CALIFORNIA

MARY A. HEIMERDINGER

CARNEGIE MUSEUM, PITTSBURGH, PENNSYLVANIA

STUART L. WARTER

DEPARTMENT OF BIOLOGY, LONG BEACH STATE COLLEGE,
LONG BEACH, CALIFORNIA

ABSTRACT

The anatomical characters of the passerine family Conopophagidae have been reexamined. The sternum, syrinx, tarsus, antorbital osteology and pterylosis of *Conopophaga* and *Corythopsis* were compared with a broad sample of other suboscines, with particular attention to the Formicariidae and Rhinocryptidae.

Conopophaga was found to lie well within the range of variation of the Formicariidae in the principal characters (sternum and syrinx) used by Forbes in describing the Conopophagidae. The key character was the apparent presence in *Conopophaga* of a four-notched sternum. In nearly all specimens of *Conopophaga*,

however, we found the sternum to have two notches and two large medial fenestrae. The four-notched condition is found in some species of *Grallaria* and *Pittasoma*, both considered to be formicariid. In most of the other characters studied also, *Conopophaga* strongly resembles *Grallaria*.

The genus *Corythopsis* differs from *Conopophaga* and all other furnarioids in the major diagnostic characters examined. In several respects, particularly the pterylosis and syringeal structure, it shows strong affinities with the Tyrannidae.

It is recommended that *Conopophaga* be returned to its former position, near *Grallaria* in the Formicariidae. *Corythopsis* must be moved from the Furnarioidea to the Tyrannoidea; its proper position appears to be in the family Tyrannidae.

RESUMEN

Se han reexaminado los caracteres anatómicos de la familia Conopophagidae (Passeriformes). Se ha hecho una comparación de la osteología del esternón, la siringe, el tarso, y la pterylosis de los géneros *Conopophaga* y *Corythopsis* con abundantes ejemplos de los respectivos huesos de otros suboscines, particularmente de las familias Rhinocryptidae y Formicariidae.

Tomando en cuenta los caracteres principales (esternón y siringe) usados por Forbes para describir la familia Conopophagidae, el género *Conopophaga* cae dentro de la familia Formicariidae. El carácter principal empleado por Forbes fue la aparente presencia de cuatro escotaduras en el esternón. No obstante, en 19 de 20 ejemplares de *Conopophaga* hemos encontrado que el esternón tiene solo dos escotaduras laterales y dos aberturas elípticas en el metasternón. Esternón con cuatro escotaduras se encuentra en unas especies del género formicárido *Pittasoma* como también en algunas especies del género *Grallaria*. En la morfología de la siringe y en la pterylografía, *Conopophaga* y *Grallaria* son muy similares.

El género *Corythopsis* difiere de *Conopophaga* y de todos los demás géneros de Furnarioidea en la mayoría de los caracteres diagnósticos examinados. En varios caracteres y particularmente en la estructura de la siringe *Corythopsis* tiene fuertes afinidades con Tyrannidae.

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CONOPOPHAGA AND CORYTHOPIS

Recomendamos por lo tanto el retorno de *Conopophaga* a su sitio anterior en la familia Formicariidae cerca de *Grallaria*. *Corythopis* debe ser traslado de Furnarioidea a la superfamilia Tyrannoidea. Su adecuado sitio parece estar en la familia Tyrannidae.

INTRODUCTION

The small neotropical family Conopophagidae, the antpipits and gnateaters, as presently understood consists of eleven species of ground-dwelling forest birds, nine in the genus *Conopophaga* Linnaeus and two in the genus *Corythopis* Sundevall (Peters, 1951). Although widely distributed in the northern half of South America, they are shy and little studied. This paper is an effort to clarify the relationships of the two genera through several aspects of their morphology.

Although the first use of the family name Conopophagidae appears to have been by Garrod (1877a), the definition of the family and its separation from the Formicariidae are the work of W. A. Forbes (1881). Years earlier, Müller (1847) had examined the syrinx of *Conopophaga aurita* and had placed the genus near *Thamnophilus* in his "Tracheophonae," a division of the Passeriformes closely approximating the modern superfamilia Furnarioidea (Wetmore, 1960). In the interval between the work of Müller and that of Forbes most authors placed *Conopophaga* and *Corythopis* in the family corresponding to the modern Formicariidae, usually near *Grallaria* and *Chamaeza* (Bonaparte, 1850; Cabanis and Heine, 1859; Burmeister, 1856; Pelzeln, 1871). A few authors placed both genera in the Tyrannidae (Sundevall, 1872; Boucard, 1876).

Forbes stated that the sternum of *Conopophaga lineata* had two pairs of notches in the posterior margin, a condition previously known only in the Rhinocryptidae. He defined the Conopophagidae (1881, p. 438) as "Tracheophonine Passeres, with a holorhinal skull and four-notched sternum, an exaspidean tarsus, and a syrinx with no intrinsic muscles, and with the *sterno-tracheales* not attached to the *processus vocales*." The definition was based on Müller's description of the syrinx of *C. aurita*, a sternum of *C. melanops* examined by Salvin and a specimen of *C. lineata* examined by Forbes himself. The genus *Corythopis*, already thought to

be a close relative of *Conopophaga*, was included in the new family because of certain similarities in external morphology and habitat preference.

Even after the wide acceptance of the family status of the antpipits, a few authors, such as Taczanowski (1884), retained them in the Formicariidae. Since the late nineteenth century, however, the validity of the family Conopophagidae has not been seriously questioned, and in all the standard passerine classifications the Conopophagidae are placed between the Formicariidae and the Rhinocryptidae in the superfamily Furnarioidea. The following classification of the suborder Tyranni by Wetmore (1960) is the most widely accepted and forms the basis for discussion in the present paper:

ORDER PASSERIFORMES

SUBORDER EURYLAIMI	Broadbills
SUBORDER TYRANNI	
SUPERFAMILY FURNARIOIDEA	
FAMILY DENDROCOLAPTIDAE	Woodcreepers
FURNARIIDAE	Ovenbirds
FORMICARIIDAE	Antbirds
CONOPOPHAGIDAE	Antpipits
RHINOCRYPTIDAE	Tapaculos
SUPERFAMILY TYRANNOIDEA	
FAMILY COTINGIDAE	Cotingas
PIPRIDAE	Manakins
TYRANNIDAE	Tyrant Flycatchers
OXYRUNCIDAE	Sharpbill
PHYTOTOMIDAE	Plantcutters
PITTIDAE	Pittas
ACANTHISITTIDAE	New Zealand Wrens
PHILEPITTIDAE	Asities
SUBORDER MENURAE	Lyrebirds and Scrubbirds
SUBORDER PASSERES	Songbirds ("Oscines")

For the purposes of this paper the term "suboscine" refers to members of the suborders Eurylaimi, Tyranni and Menurae, individually or collectively, but we will concern ourselves primarily with the Tyranni. For the general classification within the families of

the Tyranni we follow Peters (1951), Hellmayr (1929), and Cory and Hellmayr (1927).

In the course of separate studies of the syrinx (Ames, 1965), pterylosis (Heimerdinger, 1964), and cranial osteology (Warter, 1965) of passerine birds, we had occasion to reexamine *Conopophaga* and to study *Corythopis* for the first time. Because our initial findings did not support the accepted classification, we undertook a thorough examination of the morphological basis for the family Conopophagidae.

MATERIALS AND ACKNOWLEDGEMENTS

The anatomical characters studied by Forbes, as well as the pterylosis, were studied in nearly all the available specimens of *Conopophaga* and *Corythopis* in the United States and Great Britain. The individuals examined and the characters examined on each are shown in Table 1. The broad scope of our studies permitted the comparison of *Conopophaga* and *Corythopis* with a large and taxonomically diverse series of other passerines. The extent of these comparisons is stated in the sections below pertaining to each of the anatomical characters treated.

We have utilized alcoholic and skeletal specimens from the American Museum of Natural History; British Museum (Natural History); Carnegie Museum; Field Museum of Natural History; Museum of Natural History, University of Kansas; Museum of Zoology, University of Michigan; Museum of Zoology, Louisiana State University; Museum of Comparative Zoology, Harvard University; Peabody Museum of Natural History, Yale University; United States National Museum, and the collection of Dr. Pierce Brodkorb, University of Florida. We are grateful to the authorities in charge of collections in these institutions for permission to utilize their specimens.

We are particularly indebted to Philip S. Humphrey, who collected most of the preserved specimens of *Conopophaga* and *Corythopis* examined in this study. We also extend our appreciation to G. S. Cowles, of the British Museum (Natural History), Miss E. Dobson, of the Royal College of Surgeons of England, and C. W. Benson, of Cambridge University, for their (unfortunately unsuccessful) efforts to locate the specimens of *Conopo-*

phaga discussed by Forbes. Richard L. Zusi, Philip Ashmole and especially Kenneth C. Parkes deserve our thanks for many valuable suggestions regarding the manuscript.

CRANIAL OSTEOLOGY

In a survey of the cranial osteology of the New World Tyranni, skulls of members of 180 genera of suboscine passerines were examined (Warter, 1965). Attention in the present paper is centered on the character of the lacrymal bone, as it is the most consistent osteological feature separating the Tyrannoidea and Furnarioidea. The only cranial character included by Forbes was the condition of the nares (see below).

In the Furnarioidea free lacrymals were found to be lacking in all 54 non-conopophagid genera examined. In the Formicariidae (fig. 1) the ectethmoid plates are enlarged laterally above the quadratojugal arches, apparently replacing the lacrymals. The lacrymals may actually be wholly fused to normal ectethmoids in this condition, but no evidence of the presence of the former can be found in the adult skull. Partly fused lacrymals are found in the Rhinocryptidae. The remaining two families of the superfamily, the Furnariidae and Dendrocolaptidae, also lack any evidence of free lacrymals and have less developed ectethmoid plates.

In the Tyrannoidea, and in particular in the Tyrannidae (fig. 1), the ectethmoid plates are well developed and the lacrymals, lying alongside, rest upon the quadratojugal arches.

Conopophaga (fig. 1) possesses an antorbital complex like that of the Formicariidae, while *Corythopsis* (fig. 1) has the type found in the Tyrannidae.

Forbes' inclusion of "holorhinal skull" in the definition of the Conopophagidae was a result of the work of Garrod (1877a), who found that among the passerines examined the ovenbirds were unique in the possession of "schizorhinal" nares. Subsequent investigation (von Ihering, 1915; Warter, 1965) has shown that the distinction is not clearcut, as Garrod suggested, for there is considerable variation among ovenbirds and woodcreepers. Since the holorhinal skull is found in all other suboscines, its inclusion in the family description served to separate the Conopophagidae only from the Furnariidae.

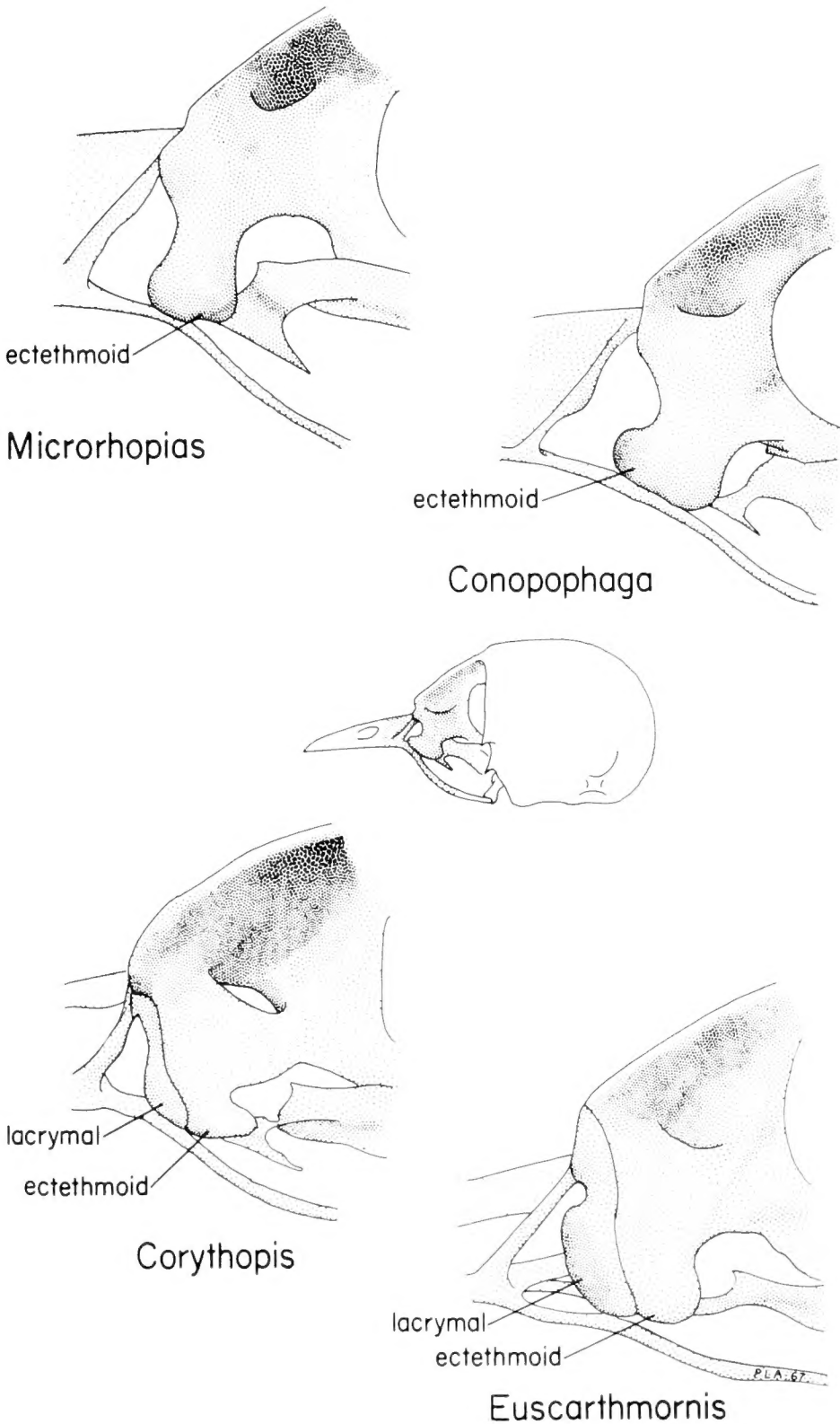


Figure 1. Cranial osteology. The antorbital regions of four suboscine genera: a typical antbird, *Microrhopias quixensis*, $\times 7$; the two genera of antpipits, *Conopophaga lineata*, $\times 6$, and *Corythopis delalandi*, $\times 9$; and a tyrant flycatcher, *Euscarthmornis margaritaceiventer*, $\times 15$. The center figure shows the complete skull of *Conopophaga*, $\times 2$. All figures show an oblique view from the left posterior region.

STERNUM

The configuration of the posterior border of the sternum was studied in twenty specimens of *Conopophaga* and eight of *Corythopsis*. These were compared with 953 specimens of 139 genera, representing all of the families of the suborder Tyranni. We made use both of specimens preserved in alcohol and of dry prepared skeletons. In the alcoholic specimens the notches of the sternum were examined from the inner (dorsal) surface in order to minimize damage to the thoracic area.

A complete discussion of the distribution of the various sternal types in the Tyranni, together with an analysis of the taxonomic value of this character, has been presented in a separate paper (Heimerdinger and Ames, 1967). Sterna were classified by the number of posterior notches and/or fenestrae in the posterior border. It was found that within the Tyranni six types of sternal configuration occur:

- (1) no posterior notches or fenestrae;
- (2) a single pair of lateral fenestrae;
- (3) a single pair of lateral notches;
- (4) a pair of lateral notches plus small metasternal fenestrae;
- (5) a pair of lateral notches plus large metasternal fenestrae;
- (6) two pairs of notches.

The last type is the "four-notched" condition cited by Forbes. The study clearly showed that a particular type of sternal configuration is not necessarily characteristic of a taxonomic group. For instance, an almost complete range of types was found to occur within the superfamily Furnarioidea, and several types may occur within a family or even, occasionally, within a genus or species.

THE STERNUM IN THE SUPERFAMILY FURNARIOIDEA

Of the five furnarioid families, the Dendrocolaptidae exhibit the greatest amount of variability within the family, genus and species. Of 173 specimens in nine genera, the large majority was two-notched (type 3), but types 2, 3, and 4 were sometimes found

in the same species. No specimens were seen with either type 5 or type 6. In general, the woodcreepers tend to have rather solid sterna, one specimen even being devoid of perforations (type 1).

The ovenbirds also have predominately two-notched (type 3) sterna, with a few specimens of the more perforate types. Type 5 sterna were found in five of the 199 specimens examined; they were specimens of: *Xenops rutilans* (one out of two specimens); *Pygarrhichas albogularis* (one out of three); *Sclerurus ruficularis* (one out of one); and *S. guatemalensis* (two out of two).

Of 194 specimens representing 32 genera of Formicariidae, the large majority (171 individuals) had the type of sternum with one pair of lateral notches (type 3). One specimen of *Dysithamnus mentalis* (of 15 examined) had no notches at all, but had a single pair of lateral fenestrae (type 2). Thirteen antbird specimens, representing eight diverse genera, had, in addition to the usual lateral notches, small medial fenestrae (type 4). The only available specimens of *Grallaricula nana* and *Pittasoma michleri* had, respectively, a pair of notches plus large paired medial fenestrae (type 5) and two pairs of notches (type 6). The genus *Grallaria* was found to fall into two categories: nine specimens of six species (*guatemalensis*, *varia*, *haplonota*, *quitensis*, *ruficapilla* and *rufula*) had two-notched sterna (type 3); in *G. perspicillata* one specimen had a pair of notches and large medial fenestrae (type 5) and the other four examined, as well as single individuals of *G. fulviventris* and *ochroleuca*, had four-notched sterna (type 6). It is this four-notched condition that was formerly believed to be restricted to the Rhinocryptidae and Conopophagidae.

The Rhinocryptidae, of which we examined 25 specimens of five genera, were found to be almost uniformly of the type with two pairs of notches (type 6). The exception was one of two specimens of *Pterotochos tarnii* studied, in which the usual two notches were present on the left, but one notch and two fenestrae on the right.

THE STERNUM IN THE SUPERFAMILY TYRANNOIDEA

The sternum in the superfamily Tyrannoidea was found to be more uniform than in the Furnarioidea. The sternal type with a single pair of notches (type 3) predominated in all tyrannoid

families: 334 specimens out of 362. In eighteen specimens, belonging to ten taxonomically diverse genera, one or both notches were closed, i.e. replaced by fenestrae (type 2). In the remaining ten specimens small fenestrae were present in the metasterna (type 4).

THE STERNUM IN *Conopophaga*

Nineteen of the 20 specimens of *Conopophaga* (Table 1) had the sternal type with a pair of notches plus large medial fenestrae (type 5). In the exception, one of 15 specimens of *C. lineata*, there were two notches in the left side of the sternum and a notch and a fenestra in the right side. The specimen of *C. melanops* examined by Salvin (in Forbes, 1881) had a type 6 (four-notched) sternum, as did the specimen of *C. aurita* examined by Forbes. As noted above, our attempts to locate these important specimens were unsuccessful.

From our sample of 20, therefore, it would appear that both Salvin and Forbes had the misfortune to study specimens which were not truly representative of the genus, since the most common condition in *Conopophaga* is one pair of sternal notches with large medial fenestrae (type 5), not two pairs of notches (type 6). It is also possible that there is interspecific variation in predominant sternal type within the genus *Conopophaga*.

THE STERNUM IN *Corythopsis*

All eight specimens of *Corythopsis* had two-notched (type 3) sterna, thus resembling the majority of both superfamilies of the Tyranni.

SUMMARY OF STERNAL EVIDENCE

Heimerdinger and Ames (1967) found that a morphological continuum exists in sternal types from that with no perforations at all (type 1) to that with two pairs of notches (type 6). Within a genus, however, one rarely finds types 4 and 5 sterna. There appear to be two basic classes of sterna: one including types 1 through 4, the other only types 5 and 6. Some functional difference seems to exist between type 4, in which the metasternum is perforated by very small fenestrae, and type 5, in which the fenestrae are large and symmetrical.

TABLE 1: Specimens of *Conopophaga* and *Corythopis* examined, and the characters studied on each.

NUMBER	SKULL	STERNUM	TARSUS	SYRINX	PTERY- LOSIS
<i>Conopophaga lineata</i>					
YPM-2550 Alc. carc.		X		X	
YPM-2551 Alc. carc.		X		X	
YPM-2552 Alc. whole		X	X		
YPM-2553 Alc. whole		X	X	X	X
YPM-2554 Alc. whole		X	X		
YPM-2555 Alc. whole		X	X		
YPM-2556 Alc. whole		X	X	X	X
YPM-2557 Alc. whole		X	X		X
UMMZ-157730 Skeleton	X	X			
UMMZ-157731 Skeleton		X			
UMMZ-158754 Skeleton		X			
AMNH, no number, Alc. whole		X		X	
AMNH, no number, Alc. whole		X			
BM(NH), no number, skeleton		X			
YPM, no number, skeleton		X			
<i>Conopophaga roberti</i>					
USNM (f)-195100 Alc. carc.		X		X	
USNM (f)-195954 Alc. carc.		X		X	
USNM (f)-196021 Alc. carc.		X		X	
<i>Conopophaga melanops</i>					
AMNH (f)-411 Skeleton (trunk)		X			
<i>Conopophaga peruviana</i>					
LSUMZ-42888 Skeleton		X			
<i>Corythopis torquata</i>					
USNM (f)-198562 Alc. carc.		X		X	
USNM (f)-198127 Alc. carc.		X		X	
FMNH-104286 Alc. whole		X		X	X
<i>Corythopis delalandi</i>					
YPM-2558 Alc. whole		X	X	X	X
YPM-2559 Alc. whole		X	X	X	X
YPM-2611 Alc. whole		X	X	X	X
UMMZ-157732 Skeleton	X	X			

Abbreviations: YPM: Yale Peabody Museum; UMMZ: University of Michigan Museum of Zoology; AMNH: American Museum of Natural History; BM(NH): British Museum (Natural History); FMNH: Field Museum of Natural History; LSUMZ: Louisiana State University Museum of Zoology; USNM: United States National Museum; (f): field number; Alc.: Alcoholic; carc.: "carcass," the "body" remaining after preparation of a study skin.

The two-notched (type 3) sternum strongly predominates in all suboscine families except the Conopophagidae and the Rhinocryptidae, in the latter of which it is not found at all. The Formicariidae range in sternal type from 2 to 6, the large majority being type 3, with type 6 limited to a few long-legged ground antbirds. The type 5 sternum may be viewed as a slightly less perforate form of the four-notched type 6. *Conopophaga*, in possessing a less perforate sternum than some members of the genus *Grallaria*, lies within the range of variation of the Formicariidae, even though there are fewer type 5 than type 6 sterna among the antbirds. It also lies within the range of variation of the Furnariidae, but other anatomical features exclude it from that family. The sternum of *Corythopsis*, being of the widespread type 3, is not of great taxonomic significance, except to indicate that this genus may not be as close to *Conopophaga* as was previously supposed.

TARSAL SCUTELLATION

The use of patterns of tarsal scutellation as a taxonomic character is traceable to the work of Sundevall (1872), who studied only a small number of neotropical passerines. The late nineteenth century saw considerable reliance placed upon the condition of the tarsal envelope, but even Ridgway, one of the most consistent users of this character, complained (1907, p. 336), ". . . variations in the tarsal envelope . . . have disappointed me in the hope that they might greatly simplify the classification of the group, for they seem of little value beyond the definition of genera (even sometimes failing here!) or minor supergeneric groups; indeed, it has been found that each of them is more or less variable within what appear to be proper generic limits." More recently, Rand (1959) has discussed the weakness of this character in oscine taxonomy and Warter (1965) has shown it to be unreliable in the Tyrannoidea.

In the present study we examined the tarsi of enough furnarioid specimens to evaluate the statements of Sclater (1890) and Ridgway (1907), but did not attempt an intensive survey. Within each superfamily of the Tyranni nearly all tarsal types are found. For descriptions of the types of tarsal scutellation see Ridgway (1907). Members of the Rhinocryptidae and Formicariidae are

taxaspidean, except for a few that are holaspidean. Among the Tyrannidae the exaspidean pattern is the most common, but a variety of others is also found. Both *Conopophaga* and *Corythopsis* have exaspidean tarsi, but, in view of the general unreliability of this character, we do not feel that much importance should be attached to the patterns of tarsal scutellation at the family level.

SYRINX

The syringes of several conopophagids (see Table 1) were examined as part of a broad study of passerine syringeal anatomy (Ames, 1965) to which the reader is referred for complete details of comparative morphology. A brief summary of the pertinent sections of that work is presented here, insofar as they bear on the taxonomic questions of the present paper.

NOMENCLATURE

For the present purposes, all of the supporting elements of the syrinx may be called "cartilages," although they exhibit degrees of ossification varying from none at all to a considerable amount, as indicated by the uptake of alizarin stain. The terms "tracheal" and "bronchial," "rings" and "semi-rings" were found to be unsuitable in many syringeal configurations. Instead, the elements are designated as members of an anterior "A" series or a posterior "B" series. The two series may be distinguished by cross-sectional shape, consistency, and direction of curvature of the individual elements. The elements in each series are numbered consecutively away from the point where the series meet.

The following adjectives are used to describe the individual elements:

Complete. The element forms a closed circle or ellipse.

Incomplete dorsally (or ventrally). The element forms a closed loop except for a space at the dorsal (or ventral) midline.

Divided. The element consists of two equal halves, separated by a ventral and a dorsal space. Even when widely separated, as in the bronchi, the halves are considered to constitute a single element.

Double. The element consists of two closed coplanar loops, which may be in contact at the midline or separated.

Syringeal muscles are of two types, extrinsic and intrinsic. The former, comprising only *M. tracheolateralis* and *M. sternotrachealis*, originate on a structure not directly related to the syrinx and insert on the syrinx. The intrinsic muscles originate and insert on the syrinx. In the suboscines there are about five distinguishable intrinsic muscles, but no more than two occur in any one species.

THE SYRINX IN THE SUPERFAMILY FURNARIOIDEA

The syringes of members of about half of the 132 genera in this superfamily have been studied to date, representing at least five genera in each of the four larger families. About 50 genera were examined by Müller (1847), two genera (*Grallaria* and *Pteroptochos*) by Garrod (1877b), *Lepidocolaptes* by Rüppell (1933) and *Psilorhamphus* by Plótnick (1958). Ames (1965) described the syringes of 72 genera, about half of which had not been studied by previous authors. A consistent pattern emerges from these studies, from which the following generalizations are drawn.

In all undoubted members of the superfamily the lower trachea is dorsoventrally compressed in the region immediately anterior to the bifurcation (see figs. 2 and 3). In the compressed region the supporting cartilages of the trachea are attenuated or occasionally lacking, forming dorsal and ventral membranous "windows" (*Membranae tracheales*) which led Müller to refer to this type of syrinx as "tracheophone." The *Membranae* vary greatly in antero-posterior length, in the abruptness of the anterior limit, and in the degree of attenuation of the elements crossing them.

At the sides of the "tracheophone" syrinx is a pair of cartilaginous or bony plates or bars called "*Processi vocales*" (Müller, 1847). Their shape is quite uniform within each family, except for a few genera of the *Formicariidae*. In the large majority of members of this family studied (of which *Taraba* and *Dysithamnus* are examples) the *Processi* are small, thin strips of soft cartilage almost entirely hidden by the intrinsic muscles. In a few genera, all strongly terrestrial, (*Formicarius*, *Chamaeza* and *Grallaria*) the *Processi* are large and relatively thick. In the *Rhinocryptidae* the *Processi* are also large, but usually with a narrow "neck" in the middle.

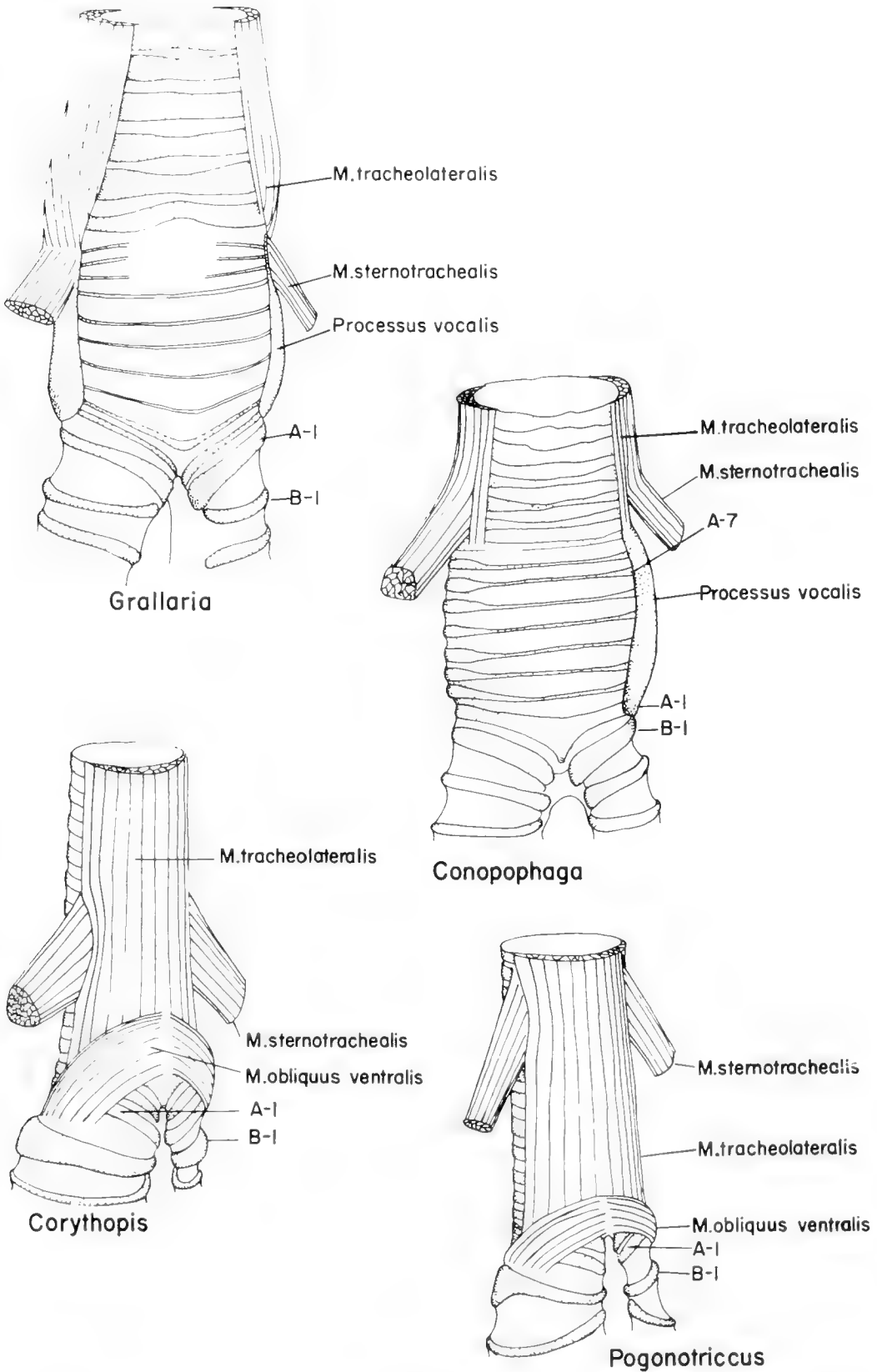
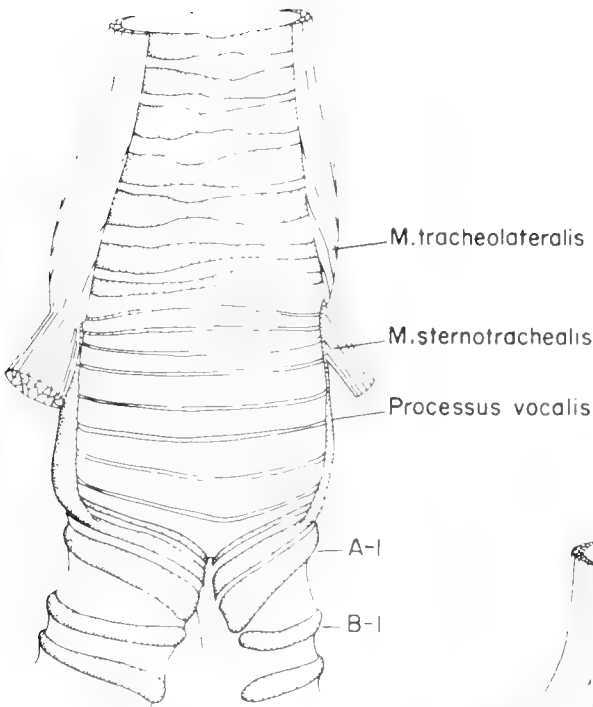
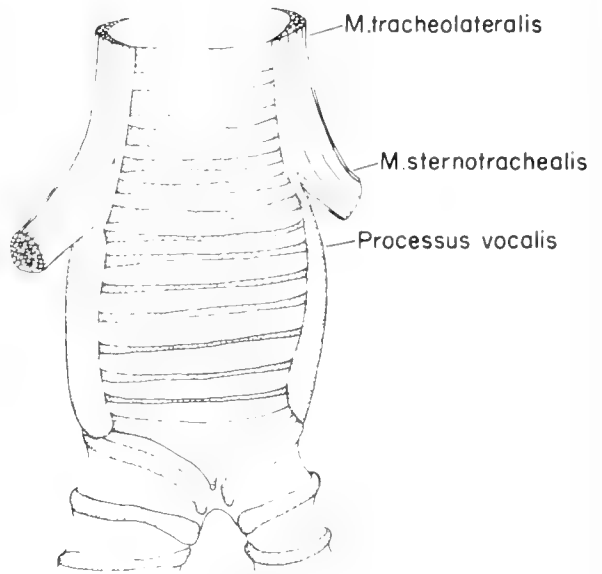


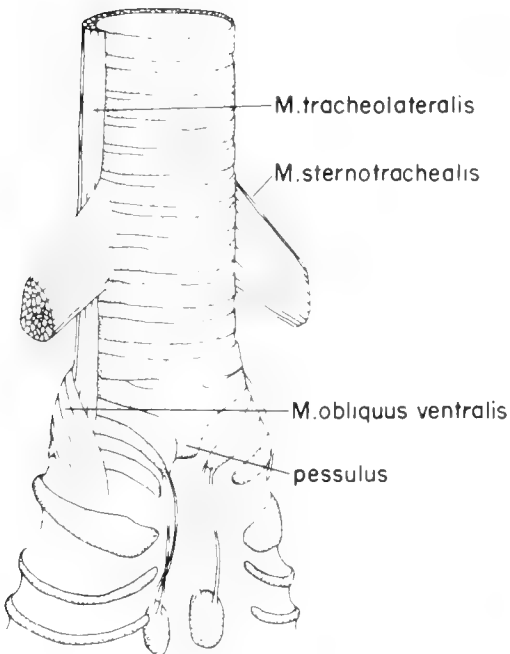
Figure 2. Syrinx of four suboscine genera, ventral view: a terrestrial antbird, *Grallaria ochroleuca*, $\times 6$; the two genera of antpipits, *Conopophaga lineata*, $\times 7$, and *Corythopis delalandi*, $\times 7$; and a tyrant flycatcher, *Pogonotriccus eximius*, $\times 10$.



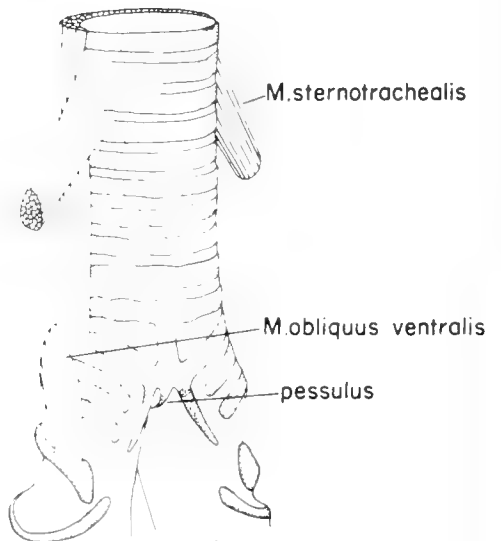
Grallaria



Conopophaga



Corytopis



Pogonotriccus

Figure 3. Syrinx of the same genera, dorsal view.

A characteristic feature of the syrinx in most passerine and non-passerine birds is the pessulus, a bony or cartilaginous rod lying in the midsagittal plane at the juncture of the two internal tympaniform membranes (see below). No unquestioned furnarioid has been found to possess a pessulus, but its absence is not usually considered a diagnostic character of this superfamily.

The syringeal musculature varies among the families of the Furnarioidea. All members of the superfamily have well-developed Mm. tracheolaterales and Mm. sternotracheales. The former originate, as in most, if not all, passerines, on the lateral surfaces of the larynx, extend down the lateral surfaces of the trachea, and insert on the lateral and/or ventral surfaces of the trachea in the syringeal region, or on the anterior ends of the Processi. The Mm. sternotracheales crigrate on the interior surfaces of the coracoid or the costal processes of the sternum or on the fasciae of the intercostal muscles and usually insert on the anterior ends of the Processi. In the "typical" antbirds (those with small Processi) each M. sternotrachealis inserts by two heads, one to the Processus and the other to the dorsolateral surface of the trachea, anterior to the Membranae tracheales.

Intrinsic syringeal musculature takes several basic forms in this superfamily. In the Dendrocolaptidae and Furnariidae there are two pairs of intrinsic muscles. In the "typical" antbirds there is a single pair, originating ventrally, anterior to the Membranae, and inserting on the anterior ends of the Processi. In *Formicarius*, *Chamaeza* and *Grallaria* there are no intrinsic muscles. The syringeal sample includes *G. varia*, a species possessing a two-notched sternum, and two four-notched species, *G. perspicillata* and *G. ochroleuca*. In most tapaculos there is a single pair, originating dorsolaterally and inserting on the ventral surfaces of the anterior ends of the Processi. In *Teledromas*, however, no intrinsic muscles are present.

THE SYRINX IN THE SUPERFAMILY TYRANNOIDEA

The following description of the syrinx in the Tyrannoidea is drawn from Müller (1847), Miskimen (1963), and, principally, Ames (1965 and unpublished notes) and represents the current knowledge of syringeal structure in 23 genera of the Cotingidae,

10 of the Pipridae, 88 of the Tyrannidae, and all seven of the genera which together make up the families Oxyruncidae, Phytotomidae, Pittidae, Philepittidae and Acanthisittidae.

In all members of this superfamily the trachea in the syringeal region is basically cylindrical, lacking the dorsoventral compression which characterizes the syrinx in the Furnarioidea. Frequently there is a partial or complete fusion of the lower A-elements, forming a "drum," which serves as a firm base for muscle operation. This type of syrinx has been termed "haplophone."

The medial surface of each bronchus consists largely of a membranous area usually called the "internal tympaniform membrane." Although rather thick in many places, this membrane usually has a region of extreme thinness, which is believed to be the source of vibrations. Other areas of membrane lie between the supporting elements and are designated with reference to the elements supporting them. Thus, the region between A-1 and A-2 is the "A-1/A-2 membrane."

Near the anterior ends of the internal tympaniform membranes of many tyrannoids are one or more pairs of cartilaginous rods or plates which Miskimen (1963) has named "internal cartilages." They are present in most Tyrannidae, in the Oxyruncidae, and in a few members of the Cotingidae and Pipridae, as these families are presently understood. The internal cartilages vary in shape from straight or slightly curved bars to intricately sculptured plates and in number up to three pairs.

The pessulus is present in most members of this superfamily. Its presence or absence does not appear to be of taxonomic usefulness within the Tyrannoidea, for it may be present in some members of a species and not in others.

The extrinsic muscles are highly variable among members of the Tyrannoidea. In the absence of intrinsic muscles, *M. tracheolateralis* usually inserts on A-1 or B-1, i.e., near the region of bifurcation of the trachea. When one or more intrinsic muscles are present, *M. tracheolateralis* usually inserts anterior to their origin. In many tyrant flycatchers and in members of a few other families this muscle is extremely broad ventrally, the members of the pair being in contact at the ventral midline and covering the ventral half or two-thirds of the trachea. *M. sternotrachealis*, also variable, inserts directly on the lateral surface of the trachea,

on the surface of *M. tracheolateralis*, in continuity with the latter muscle, or by a combination of two or three of these means.

The number of intrinsic muscles varies from none in a few tyrant flycatchers and most cotingas to two pairs in a few flycatchers and one manakin (*Corapipo*). The presence of a pair of oblique ventral muscles, the *Mm. obliqui ventrales* (Ames, 1965), is characteristic of a few cotingas, (*Attila* and similar genera), one manakin (*Ilicura*), the Sharpbill (*Oxyruncus*), and nearly all tyrant flycatchers. This pair of muscles originates on or near the ventral midline of the syrinx and inserts on one or more elements in the region of A-1 and B-1. It is widely believed that the intrinsic muscles throughout the suborder Tyranni attach in the middle of the element of insertion (i.e., midlaterally), and hence the adjective "mesomyodean" and the taxonomic category "Mesomyodi" (Garrod, 1877a; Sclater, 1890; and many others). The term is now obsolete as a taxonomic unit. In actual fact, the region of attachment in the Tyrannoidea is quite variable and terminal insertions are about as frequent as those in the middle of the element. Sometimes the insertion is along the entire length of the element and often part or, rarely, all of the insertion is on the membrane between elements.

THE SYRINX OF *Conopophaga*

The syrinx of *Conopophaga aurita* was described by Müller (1847, p. 40; 1878, p. 32) and that of *C. lineata* by Forbes (1881). Neither description was detailed and only Müller provided an illustration. All eight of our specimens, five of *C. lineata* and three of *C. roberti*, agree with Müller's illustration and text in the basic essentials. The Membranae tracheales extend from A-2 to about A-13, with A-3 through A-9 present as narrow flexible strips separating broader areas of membrane. The shift from the narrow A-9 to the broader anterior elements is gradual, A-10, A-11 and A-12 being intermediate. In this respect *Conopophaga* is similar to *Grallaria*, *Chamaeza* and many rhinocryptids. The Procelli vocales are large, simple, elliptical plates fused posteriorly to A-1 and A-2 and extending anteriorly to the level of A-9 in some individuals and to A-12 in one.

The *Mm. tracheolaterales* are partly continuous with the *Mm.*

sternotracheales, but some fibers at their dorsal and ventral edges insert on the surfaces of A-10, A-11 or A-12. In the individuals with long Processi some fibers of the Mm. tracheolaterales insert on the Processi. The Mm. sternotracheales are very robust. Those fibers not continuous with the Mm. tracheolaterales usually insert on the lateral surfaces of A-10, A-11 or A-12. In one specimen of each of the two species, both individuals with long Processi, the deep fibers of the sternotracheal muscles were attached to the Processi. Forbes' statement (1881, p. 438), that "the *sternotracheales* [are] not attached to the *processus vocales*", must be considered as applying to the majority of specimens of *Conopophaga*, but not to all of them.

No intrinsic muscles have been found in any specimens of *Conopophaga*.

THE SYRINX OF *Corythopis*

The syrinx of *Corythopis* (figs. 2 and 3) lacks both of the features associated with the furnarioid syrinx, Membranae tracheales and Processi vocales. The lower trachea is cylindrical. A-1 and A-2 are divided and the remaining A-elements are complete, except in one specimen of *C. torquata*, in which A-3 is divided. A-3 and A-4 are fused, except for short sections in the ventrolateral and dorsolateral regions. A broad, bony pessulus is fused dorsally and ventrally to A-3. B-1 is divided, as are nearly all B-elements in suboscines, and is extremely broad and thick, particularly at the dorsal end. A pair of exceptionally intricate internal cartilages is attached to the dorsal ends of A-2. The shape of these cartilages is highly uniform among the six specimens of *Corythopis* studied. Each cartilage consists of a flattened spongy ball lying in the internal tympaniform membrane at the level of B-4 and connected with A-2 by two slender ribbons of cartilage, also lying in the membrane.

The Mm. tracheolaterales converge ventrally to cover the ventral third of the trachea from about A-20 (variable) to their insertion, which is along a line from A-2 or A-3 laterally to A-6 or A-7 ventrally. The exact position of the insertion appears to be individually variable. The Mm. sternotracheales insert on the lateral surfaces of the trachea, adjacent to the dorsal edges of

the Mm. tracheolaterales. The anteroposterior position is individually variable and sometimes quite asymmetrical.

A single pair of intrinsic muscles, to which the term Mm. obliqui ventrales seems applicable, originates adjacent to the ventral midline on A-3 through A-6 and extends posterolaterally and posterodorsally to insert near the centers of the A-1/B-1 membranes.

SUMMARY OF SYRINGEAL STRUCTURE

The syrinx of *Conopophaga* shows strong similarities to the syringes of an aberrant group of Formicariidae, including *Formicarius*, *Chamaeza* and *Grallaria*, in possessing large Processi vocales and non-bifurcate Mm. sternotracheales, and in lacking intrinsic syringeal muscles. In these respects it also resembles the rhinocryptid genus *Teledromas*, the only tapaculo examined that lacks intrinsic muscles.

Corythopsis possesses several characteristics of the syrinx in which it differs from all of the Furnarioidea and resembles the Tyrannoidea, particularly the Tyrannidae. These are: the lack of Membranae tracheales and Processi vocales; possession of a pessulus; possession of internal cartilages, a feature of the Tyrannidae; and possession of typically tyrannid Mm. obliqui ventrales.

PTERYLOSIS

The study of the pterylosis of the Conopophagidae was part of a much larger investigation into the morphological variation and potential taxonomic utility of pterylosis in passerines (Heimerdinger, 1964). In that study the dorsal and ventral tracts were analyzed on a feather-by-feather basis to determine the geometric pattern formed by the follicles. The method used was a combination of soft x-ray radiographs and microscopic examination of the undersides of flat skins. Variations in feather number and position were analyzed (statistically wherever possible) for significant differences within species, genera, and families of the order Passeriformes. The evaluation of intraspecific variation was based on a sample of 167 House Sparrows (*Passer domesticus*), and verified with other species from a broad spectrum of passerine families. An additional series of 423 specimens, representing 279

genera of 61 families, was examined to determine the range of variation within the order as a whole. Included in this study were 163 specimens of 129 suboscine genera, with representatives of all 13 families in the suborder Tyranni.

It was found that pterylosis is a remarkably constant and conservative anatomical character in passerines. Analysis of the intra-specific data showed that the dorsal and ventral tracts, as delimited, are not subject to significant individual variation, nor are there significant variations correlated with body size, sex, plumage stage, season, or age once an individual has attained the first basic plumage. This means that a single adult specimen is representative of its species. The variable features considered to be taxonomically significant are differences in row patterning and the presence or absence of specific rows or parts of rows. These variations usually characterize well-defined families, superfamilies, and suborders. Only occasionally are such differences seen below the family level.

The results of the broad investigation into passerine pterylosis will be reported in detail in future papers. Only those results which pertain to the comparison between the Conopophagidae and related suboscines will be included here.

In this study the dorsal tract is defined as a single band of feathers in chevron-shaped rows extending down the dorsal midline from the neck to the rump; it has three components, here called the anterior, saddle, and posterior elements (see fig. 4). The saddle element is a widely expanded band of feathers covering the central area of the back from the posterior interscapular region to approximately the level of the acetabulae. The posterior element is narrower than the saddle and extends from the posterior limit of the saddle to the region just anterior to the uropygial gland; it thus covers the lower back and rump. The ventral tract is considered to consist of two bands of feathers (one on each side of the body) which cover the body from the pectoral region to the cloaca; it has two components, here called the flank and main elements. The flank element is a broad band of feathers in chevron-shaped rows, covering the lateral pectoral region. Approximately midway down the trunk this element separates from the narrow medial main element and terminates a few rows posterior to the point of separation.

The variations of primary taxonomic interest in these tracts

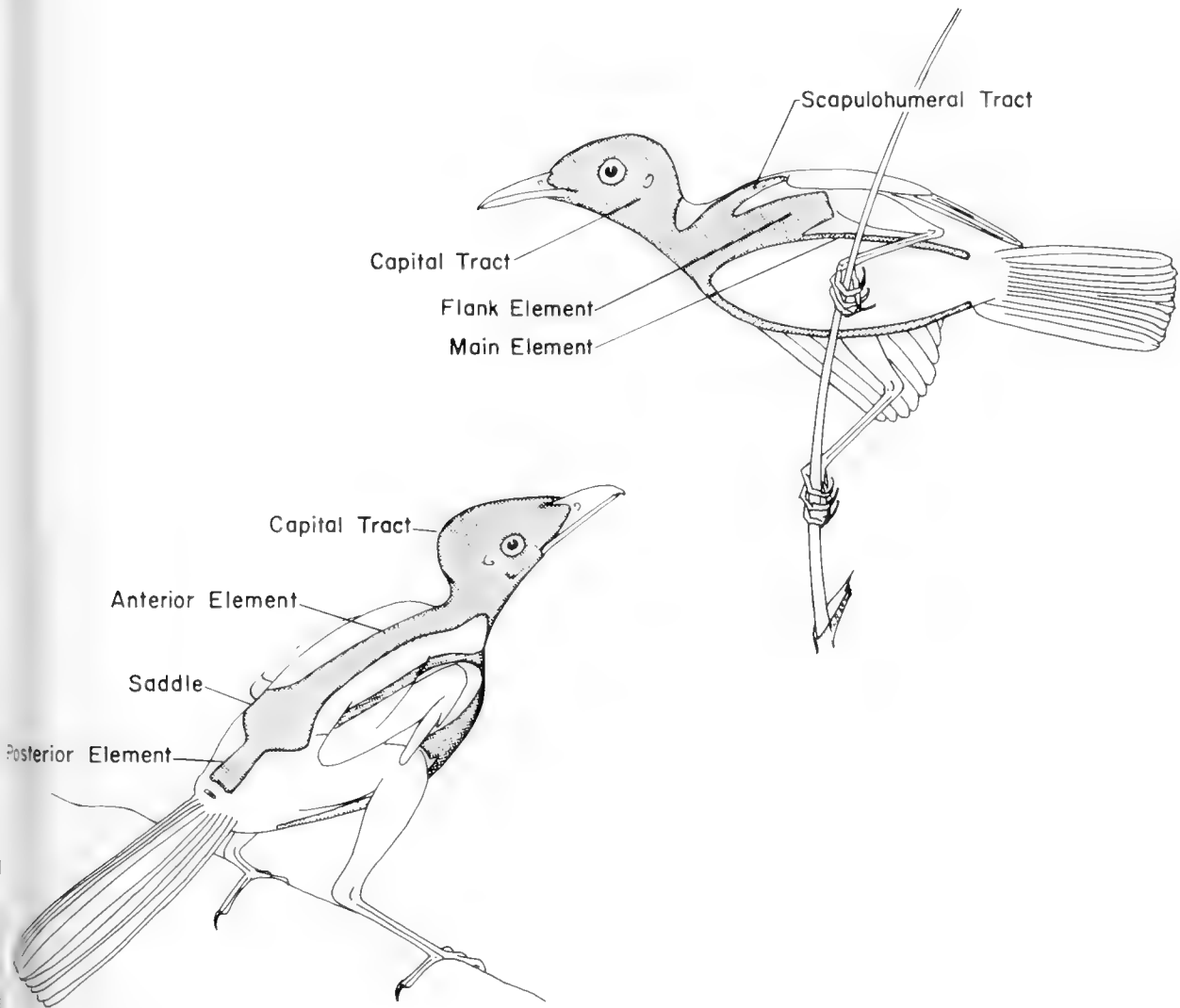


Figure 4. Pterylosis. Positions of body pterylae, shown on a generalized passerine.

(within the New World families of the Tyranni) are: in the saddle, the presence or absence of an apterium (an area lacking contour feathers), full or partial (extending either down the entire midline length, or found just in the posteriormost part of the saddle); in the posterior element, the width, strength, and regularity of row arrangement; and in the flank element, the configuration of the posterior margin. This last-named character is determined by differing relative lengths of the two sides of the chevron-shaped rows in that area (see fig. 6); these differences may seem minor at first glance, but they have proved to be absolutely consistent within the various families of suboscines.

THE PTERYLOSIS OF THE FURNARIOIDEA

Within the Furnarioidea, all the families are pterylographically distinct from one another; their various tract types or combinations of tract types are unique, either among the New World suboscines, or within the entire order Passeriformes. The Dendrocolaptidae have a type of ventral tract which is found in no other family of passerines. The Furnariidae have a solidly feathered saddle, strong and narrow posterior element, and oblique margin to the flank; this combination does not occur anywhere else in New World suboscines, but is seen in the majority of oscines. The Rhinocryptidae have a type of ventral tract unique within passerines; the one exception to this is *Melanopareia maranonicus* whose pterylosis is very similar to several genera of Formicariidae, and which will be discussed in a future paper.

The Formicariidae (45 specimens of 31 genera examined) vary considerably more than do other suboscine families. Most of the genera (28) have solidly feathered saddles, and the posterior elements are either reduced to a few small irregularly arranged feathers, or are completely absent. The three remaining genera, *Formicarius*, *Chamaeza*, and *Grallaria*, differ strongly from the family type and from each other. *Formicarius* (four specimens of three species examined) is the only New World suboscine genus studied with a *partial* apterium in the saddle. It also differs from the "typical" antbirds by having a broad and heavily feathered posterior element. *Chamaeza* (two specimens of *C. campanisona*) is exceptionally heavily feathered throughout the entire length of the dorsal tract; the tract is very broad, and there is no apterium in the saddle. *Grallaria* (one specimen each of *G. rufula* and *G. guatemalensis*) also has a solidly feathered saddle and posterior element, but there is a weakness (small feathers, widely spaced) in the posterior element at its junction with the saddle. This weakness is unique among the genera of antbirds available for study. In view of the dichotomy of sternal types within the genus *Grallaria*, there is a particular need for a thorough study of the pterylosis of this genus, as well as of *Grallaricula* and *Pittasoma*. At present, *Grallaria* is extremely poorly represented in alcohol collections, and the other two genera are totally lacking.

All of the antbird genera studied have the same type of ventral

tract: an oblique posterior margin of the flank element, which is also found in ovenbirds and the majority of oscines.

THE PTERYLOSIS OF THE TYRANNOIDEA

The New World families of this group, the Cotingidae, Pipridae, Tyrannidae, Oxyruncidae, and Phytotomidae, all have very similar pteryloses; there are few familial differences of the magnitude seen in the Furnarioidea. With the possible exception of two aberrant cotingid genera, all New World tyrannoideans have the same type of saddle, with an apterium extending down the dorsal midline for the full length of the element. This apterium is formed by the absence of the central feather or feathers of each saddle row. In many species only the single central feather is missing in some or all the rows, giving the superficial appearance of a solidly feathered saddle or one with a short apterium in the posterior end. This has led to descriptions of partial apteria in several genera of tyrannoideans, e.g., Nitzsch (1867), Beebe *et al.* (1917), Johnson (1963), etc. Close, feather-by-feather analysis of the rows, however, reveals the long narrow apterium.

Differences in the width of the apterium are particularly striking in certain genera of tyrant flycatchers. The tyrannid sample in this study consisted of 38 specimens of 32 genera, and included representatives of all seven subfamilies of Cory and Hellmayr (1927). *Euscarthmornis*, *Pogonotriccus*, *Phylloscartes*, and other related genera in the "Euscarthminae" have very narrow apteria, as do *Leptopogon* and *Serpophaga*. All other tyrannids and the rest of the New World Tyrannoidea examined have medium to wide apteria.

The posterior elements of most of this superfamily are also very similar: moderately to heavily feathered, with evenly and regularly arranged rows of feathers. The exceptions to this type are found in several flycatcher genera: *Rhynchocyclus*, *Oncostoma*, *Euscarthmornis*, *Myiornis*, *Hemitriccus*, *Pogonotriccus*, *Phylloscartes*, and other related forms, which have relatively weak and poorly organized posterior elements.

The ventral tract in four of the five New World tyrannoidean families is distinguished by a truncated posterior margin of the flank element, a type that is found in no other passerines. The

fifth family, Phytotomidae, has an oblique margin to the flank similar to that in Formicariidae, Furnariidae, and most oscines.

THE PTERYLOSIS OF *Conopophaga*

The dorsal tract of *Conopophaga* is very similar to that of *Grallaria* in the number, length, and strength of rows, and in a rather distinct configuration of the saddle (which is unlike that of any other formicariid genus). In the ventral tract, *Conopophaga* has the same type of oblique flank margin as the Furnariidae, Formicariidae, and most oscines (see figs. 5 and 6).

THE PTERYLOSIS OF *Corythopsis*

The saddle of *Corythopsis* has the full apterium associated with the Tyrannoidea. The apterium is very narrow, and most closely resembles that seen in certain genera of the Tyrannidae: *Euscarthmornis*, *Pogonotriccus*, etc. The posterior element of *Corythopsis* also has a comparative weakness similar to that found in many of the same genera of the "Euscarthminae." The ventral tract has the truncated flank margin restricted to the major families of the Tyrannoidea (see figs. 5 and 6).

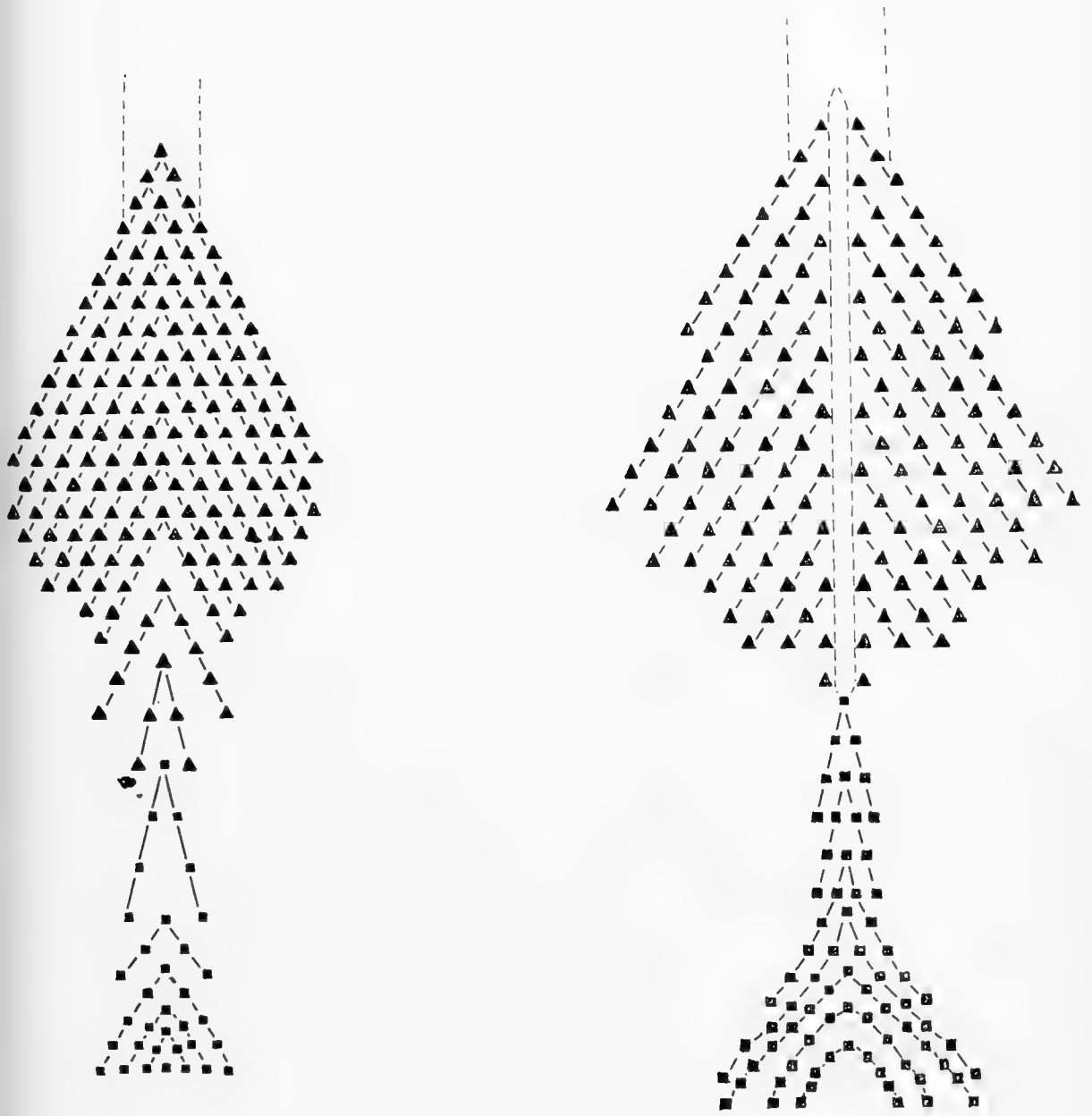
SUMMARY OF PTERYLOGRAPHIC EVIDENCE

The combination of dorsal and ventral feather tract types seen in *Conopophaga* is distinct; the only other New World suboscine genus examined that shows the same combination is *Grallaria*. *Corythopsis* is markedly different from *Conopophaga* and all other furnarioideans in its pterylosis, but agrees well in tract types with the cotinga-manakin-flycatcher-sharpbill complex of the Tyrannoidea. In details of apterium width and posterior element strength it shows its closest similarities to several genera in the Tyrannidae: *Euscarthmornis*, *Pogonotriccus*, *Phylloscartes*, and several similar genera.

DISCUSSION AND CONCLUSIONS

Conopophaga

Forbes based his separation of the Conopophagidae from the Formicariidae on two anatomical characters, the sternum and the syrinx, each of which had previously been examined in only a few



Conopophaga

Corythopis

Figure 5. Pterylosis, dorsal region: saddle and posterior elements of *Conopophaga lineata* and *Corythopis delalandi*.

antbirds and tapaculos. In the nineteenth century, morphological uniformity of major structures was assumed to exist at least up to the generic level and usually to the family level. It is unfortunate that both of the anatomical characters emphasized by Forbes have

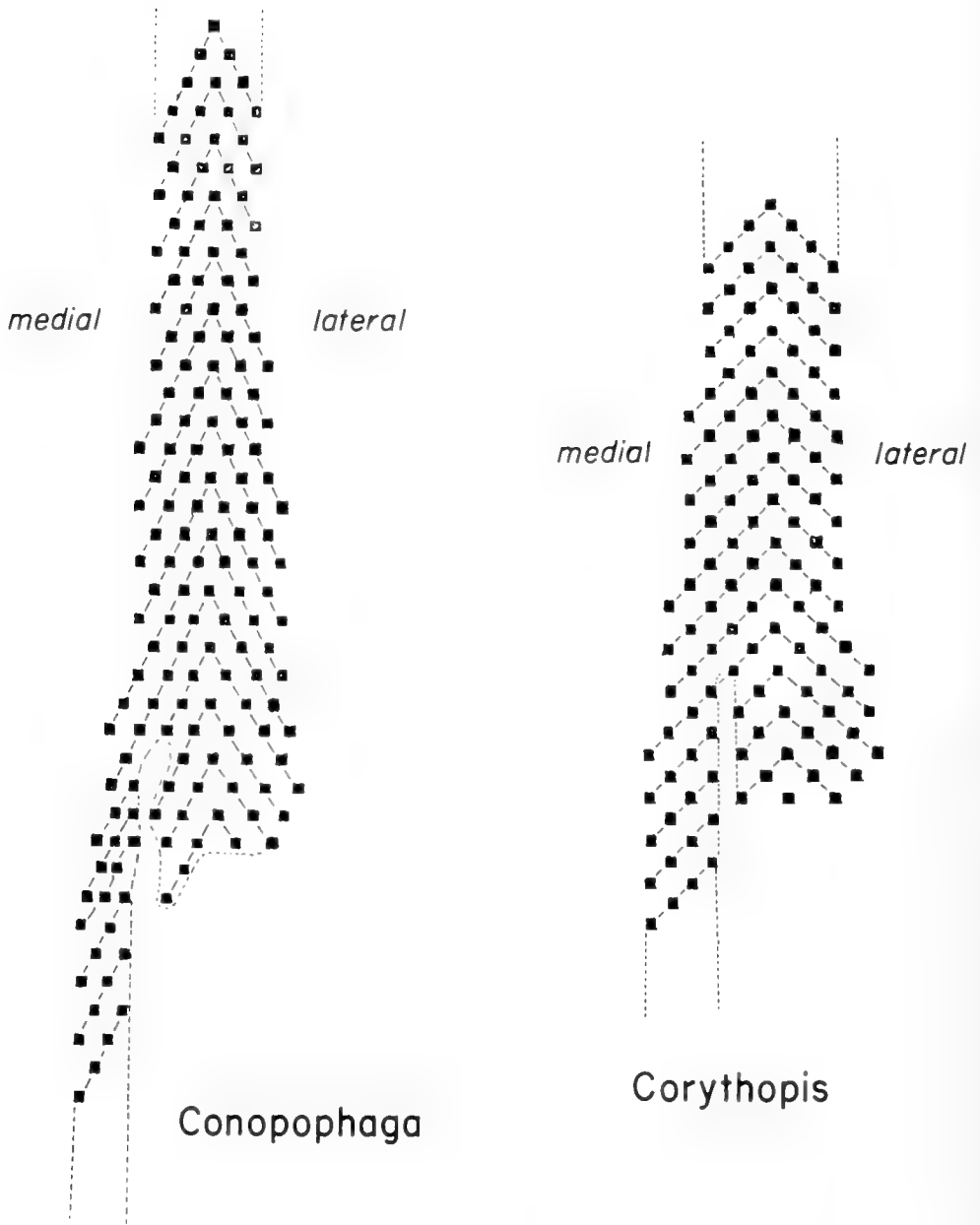


Figure 6. Pterylosis, ventral region: ventral tracts of *Conopophaga lineata* and *Corythopsis delalandi*.

now been found to be individually variable in the details that he believed to be important.

The morphological features discussed in the present report are summarized in Table 2. In all but one of the characters used to define the Conopophagidae, *Conopophaga* lies well within the range of variation of the Formicariidae, as that family is presently understood. In the excepted character, tarsal scutellation, *Conopo-*

TABLE 2: Summary of taxonomic characters: *Conopophaga* and *Corythopis* compared with Rhinocryptidae, Formicariidae, and Tyrannidae.

CHARACTER	RHINOCRYPTIDAE	FORMICARIIDAE	<i>Conopophaga</i>	<i>Corythopis</i>	TYRANNIDAE
Lacrimal bones	partly fused to ectethmoid	lacking	lacking	present	present
Sternal type ²	5, 6	3, 5, 6	5, 6	3	2, 3, 4
Tarsus ³	taxaspidean	holaspidean	exaspidean	exaspidean	exaspidean
Syrinx					
Type	tracheophone	tracheophone	tracheophone	haploophone	haploophone
No. pr. intr. muscles	none or one	none	none	one (oblique)	none to two (usually oblique)
Pterylosis					
Apterium in saddle	absent	absent	absent	present	present
Flank margin	unseparated	oblique	oblique	truncated	truncated

¹ Includes only *Grallaricula*, *Pittasoma* and *Grallaria*; *Formicarius* and *Chamaeza* are omitted due to their anatomical peculiarities.

² Where more than one sternal type is found, the dominant type is indicated in bold-faced numbers.

³ Predominant type in group; most families are highly variable.

phaga is unlike both the antbirds and the tapaculos, but is like some tyrannids. The skull of *Conopophaga* is far more formicariid than rhinocryptid. Its sternum suggests close affinities with *Pittasoma*, *Grallaricula* and *Grallaria*; its syrinx and pterylosis are like those of *Grallaria*—alcoholic specimens of *Pittasoma* and *Grallaricula* are not available. Two other genera of long-legged antbirds, *Formicarius* and *Chamaeza*, which *Conopophaga* resembles in its syringeal structure, are strongly atypical of the family in the sternum and pterylosis.

The separation of *Conopophaga* from the antbirds, therefore, is not supported by the results of our study. In the light of all presently available evidence, we feel it advisable to follow the conservative course and return *Conopophaga* to the Formicariidae, placing it in the neighborhood of *Grallaricula* and *Grallaria*.

Corythopsis

Corythopsis differs strongly from *Conopophaga* and from all other members of the Furnarioidea in most of the morphological characters studied. Three of these characters are diagnostic of the superfamily: the syrinx, antorbital osteology, and dorsal pterylosis. Of the three, only the syrinx has been used in the past as a definitive superfamily character, but it alone is sufficient for removal of *Corythopsis* from the Furnarioidea, as the superfamily is currently understood. The presence of free lacrymal bones and of a full apterium in the dorsal saddle strongly support the transfer of *Corythopsis* to the Tyrannoidea. The evidence at hand suggests that, within this superfamily, the affinities of *Corythopsis* lie with the Tyrannidae; the syrinx, pterylosis and external appearance of members of the genus are far more typical of the tyrant flycatchers than of any other family.

Some taxonomists may be reluctant to include *Corythopsis* in the Tyrannidae, but we can find no grounds for excluding it from this already diverse family. The precise relationships of *Corythopsis* within the family cannot be determined from the anatomical characters discussed in this paper. We hope that other students of tyrannid systematics will be encouraged to investigate further taxonomic characters of *Corythopsis*.

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