

## Body Pterylosis of *Atrichornis*, *Menura*, the 'Corvid Assemblage' and Other Possibly Related Passerines (Aves: Passeriformes)

MARY HEIMERDINGER CLENCH

Carnegie Museum of Natural History, Pittsburgh, Pennsylvania and Florida State Museum,  
University of Florida, Gainesville, Florida, U.S.A.\*

**ABSTRACT.** In a study of the body pterylosis of *Atrichornis clamosus* and *Menura novaehollandiae*, the dorsal and ventral feather tracts of these taxonomic enigmas are compared with the pterylae of 96 other passerine genera in an effort to discover relationships. I conclude that scrub-birds and lyrebirds are each other's closest relatives but that the degree of similarity is such that they should remain separated taxonomically, at least in different families. Their next closest relationships lie with the Paradisaeidae-Ptilonorhynchidae-Callaeidae complex; the degree of similarity is not strong, but it is stronger than it is to any other passerine group.

Other major conclusions of this study are that: 1) the so-called 'corvid assemblage' is not a natural group; 2) *Astrapia* is a core member of the Paradisaeidae-Ptilonorhynchidae group, with its pattern lying between the normal patterns for paradisaeine and cnemophiline birds-of-paradise and reminiscent of that of bowerbirds; 3) *Platylophus* is not a corvid and *Podoces*, *Pseudopodoces*, and *Ptilostomus* are probably not, either; and 4) *Grallina* shows no pterylographic relationship to *Struthidea* and *Corcorax*.

CLENCH, MARY HEIMERDINGER, 1985. Body pterylosis of *Atrichornis*, *Menura*, the 'corvid assemblage' and other possibly related passerines (Aves: Passeriformes). Records of the Australian Museum 37(3): 115-142.

**KEYWORDS:** Atrichornithidae, Corvidae, Menuridae, Paradisaeidae, Ptilonorhynchidae, Grallinidae, Artamidae, Callaeidae, Cracticidae, Oriolidae, Dicruridae, Sturnidae, Laniidae, pterylosis, relationships.

Results of my initial study of the body pterylosis of the Passeriformes (Heimerdinger, 1964) strongly suggested that study of this character system in the 'corvid assemblage' could help to determine relationships therein. In contrast to many oscines, the crows and jays and some of the other groups commonly considered to be related to them, seemed to show distinctive features in their pterylosis—either dorsal or ventral or both. Since the initial study, I gradually have acquired a broad sample of specimens of most of the genera involved. As I reported at the XVIth International Ornithological Congress in Canberra (Clench, 1975, incorporated in the present study), I consider the *Menurae* to be related to this assemblage, and hence have delayed publication until an adequate specimen of *Atrichornis* was available to complete the series.

In the following report I have included descriptions and discussion of not only *Atrichornis* and *Menura* and those families often regarded as part of the corvid assemblage (Corvidae, Sturnidae, Paradisaeidae,

Ptilonorhynchidae, Cracticidae, Artamidae, Grallinidae, Callaeidae, Dicruridae and Oriolidae), but also a few problem genera such as *Pseudopodoces* (discussed under Corvidae), *Prionops* (Laniidae), *Turnagra* (Paradisaeidae, *sensu lato*), *Picathartes* (Muscicapidae), *Pityriasis* (Laniidae), *Platylophus* (Corvidae) and *Ptilostomus* (Corvidae) which have been suggested to be allied to the corvid group (review in Amadon, 1944). I have also included brief remarks on two other groups: 1) the Furnarioidea, in light of the recent suggestion by Feduccia and Olson (1982) of the possible relationship of the Rhinocryptidae to the *Menurae*; and 2) the Vireonidae and a few other oscine groups, in response to Sibley and Ahlquist's findings (1982, in press) that the vireos are closely related to members of the corvid assemblage.

### METHODS AND TERMINOLOGY

In general, I have followed the flat-skin technique described previously (Clench, 1970), but have largely

\*Mailing address: 2239 N.W. 21st Ave, Gainesville, Florida 32605, U.S.A.

omitted the X-ray step from the procedure and studied the undersurface of the skins directly under a binocular dissecting microscope. In a few instances (indicated in the text), I have used already-clipped, alcohol-preserved specimens or the interior of museum study skins when better material was not available. Many of the flat skins used were, of necessity, prepared from specimens in alcohol, and some from specimens that were in very poor condition (e.g., in heavy moult or rotting when preserved, badly shot-damaged, heavily dissected previously). In most instances, however, even the poorest specimens offered at least a general indication of the pterylosis pattern, and the feather rows in some parts of the tracts could be counted. The counting procedure and the discrimination of row patterning are the same as previously described (Clench, 1970). To avoid confusion in this paper, I have adopted the convention of using arabic numerals for the numbers of feathers in a row, and writing out the numbers of rows (e.g., 6 feathers in row six).

The problem of pterylographic terminology remains a knotty one. I follow the concept originated by the founder of pterylography, C. L. Nitzsch (1840, 1867): that a bird's body is feathered by a few large tracts. Each of these major tracts may be further subdivided as the smaller units are discernible and as appropriate for the species under study. Therein lies the most difficult terminology problem: a universally acceptable name for these smaller units. Various pterylographers (those writing in English) have called the subunits 'portions', 'branches', 'regions', 'areas' and 'elements' (Clench, 1970). The other school of thought, most recently expounded in detail by Lucas & Stettenheim (1972), regards each of these discernible units as a 'tract', with no term other than a collective, such as 'capital tracts', for the major divisions. Clearly there is a philosophical difference here that is difficult to resolve.

The International Committee on Avian Anatomical Nomenclature has compiled a comprehensive list of the anatomical structures of birds (Baumel *et al.*, 1979). The pterylosis terms were compiled primarily by A.M. Lucas (Baumel *et al.*, 1979) and follow the concept of many small tracts, although the number is somewhat reduced from that in Lucas & Stettenheim (1972). It is beneficial to standardize nomenclature but, like Homberger (1980), I am unable to accept certain terminology in the *Nomina Anatomica Avium*; my problem is with the basic premise that each small unit of feathers should be called a 'tract.' Accordingly, and in a compromise that should not be confusing, I have revised my terms to conform as far as possible to that of the International Committee (Table 1). My basic departures from the *Nomina* terminology are three: that each major body tract is a single unit, divided into parts (pars); that the 'Ptt. cervicales,' both dorsal and ventral, are properly regarded as parts of the capital tract (Clench, 1970); and that the ventral tract has only two divisions—pectoral and abdominal.

The taxonomy followed here is basically that of

'Peters' (Mayr & Greenway, 1960 and 1962; Traylor, 1979).

## RESULTS

### *Atrichornis clamosus*: Noisy Scrub-bird

The body pterylosis of *Atrichornis* is described here for the first time. It is perfectly passerine and perfectly oscine in its general patterning. Its exceptional aspects are not the tract patterns but the numbers of feathers contained in the tracts; this species is extremely densely feathered.

**Pteryla Spinalis** (Fig. 1). The entire tract, as is usual for a passerine, is composed of chevron-shaped rows, with the central feather of each row lying on the body midline. The anterior portion of the neck skin was not removed from the specimen so as to minimize damage for other studies, thus the length of the pars interscapularis was not determined (nor has this length ever proved to be a taxonomically important aspect of pterylography). Most of the central rows of the pars interscapularis contain 6 feathers on a side (counting the central feather), and the posteriormost three rows have 5 on a side. The pars dorsalis consists of twelve complete rows. They are 'complete' in that they all have a central feather and thus do not form a midline apterium. Two anterior rows, however, have a small gap in their lateral arms, a feature found in many birds and apparently an individual variant of little or no significance (e.g., the extra 'lateral row' in *Passer* and other oscines; Clench, 1970). The first row of the pars dorsalis contains 6 feathers, then a gap of 1 space, followed by 2 more feathers to complete the row, for a count of 9; the second row is entire with 10 feathers on a side; the third is also gapped, with a space of 2 between the 10th and last 2, thus is 14 feathers long; and the remaining rows are all entire, with (one side) counts of 15, 13, 11, 10, 9, 8, 7, 7, 7. The total number of feathers in the pars dorsalis is 228, and the shape is of a rounded rhombus. The pars pelvica consists of eleven rows with the following (one side) counts: 5, 5, 5, 5, 6, 7, 6, 5, 3, 1. It is also very densely feathered for a passerine but otherwise has the normal

Clench (1970)	<i>Nomina Anatomica Avium</i>	This Paper
Dorsal Tract	Pterylae Spinales	Pteryla Spinalis
—	Pt. cervicalis dorsalis	—
anterior element	Pt. interscapularis	pars interscapularis
saddle element	Pt. dorsalis	pars dorsalis
posterior element	Pt. pelvica	pars pelvica
Ventral Tract	Pterylae Ventrales	Pteryla Ventralis
—	Ptt. cervicales ventrales	—
flank element	Pt. pectoralis	pars pectoralis
main element	Pt. sternalis et abdominalis	pars abdominalis

Table 1. Pterylographic terms for the major body tracts.

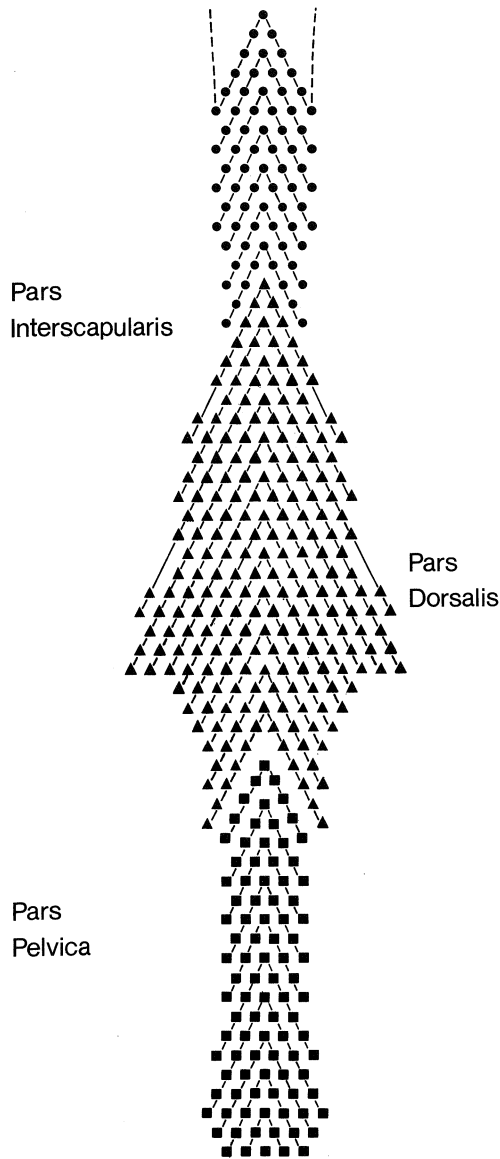


Fig. 1. *Atrichornis clamosus*, Pt. Spinalis.

configuration: straight-sided for the anteriormost half, then expands slightly before ending just anterior to the uropygial gland.

Although all the rows of the Pt. Spinalis are complete, with central feathers, the position of the first row of the pars pelvica relative to the last row of the pars dorsalis forms a small gap or false apterium at the base of the pars dorsalis. This gap is 1 mm wide and 3 mm long (in a formalin-preserved, slightly stretched, dried skin) and is formed by the central feather of the first row of the pars pelvica lying between the 4th feathers of the last row of the pars dorsalis, rather than between the 3rd feathers as it would if the spacing were even (Fig. 1).

**Pteryla Ventralis** (Fig. 2). This tract, like the spinal,

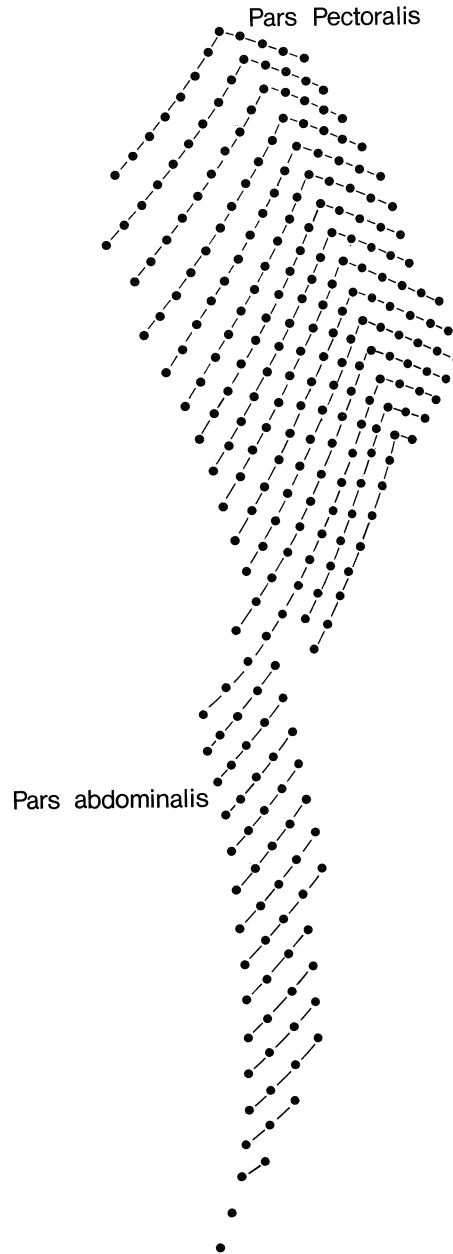


Fig. 2. *Atrichornis clamosus*, Pt. Ventralis.

is typically oscine in pattern but distinguished by exceptionally dense feathering. The lateral arms of the pars pectoralis contain 5 feathers (including the central) for the first eight rows; the next three rows contain 6 feathers per arm, and the pars then ends on the lateral side with counts of 5, 4, 3, 2—a total length of fifteen rows. The medial side of the pars pectoralis contains very long row arms, the first having 8 feathers, the next two having 10, and the next eight having 11. The twelfth medial row arm has 12 feathers, the thirteenth has 14, and the last two have 9. The pars abdominalis begins with seven single-armed rows with 5 feathers, then four rows of 4, one row of 3, one of 2, and two with a single

feather. The complete tract is twenty-eight rows long on each side.

The maximum width of the ventral tract (at row thirteen) is 17 feathers; the majority of the pars pectoralis rows contain 15 or 16. The separation of the pars pectoralis from the pars abdominalis is short, only two rows long.

**Discussion.** As noted in Clench & Smith (1985), I also studied a second specimen of *Atrichornis clamosus*, which was in poor condition. Accurate row counts cannot be made from this old specimen, but in all visible details it is the same as the newly collected one: the feathering is dense throughout; the pars dorsalis of the Pt. Spinalis is twelve rows long and contains well over 200 feathers; a 1 × 3 mm gap at the junction of the pars dorsalis and pars pelvica is clearly visible; the pars pelvica is eleven rows long; the pars pectoralis of the Pt. Ventralis is very wide, and its separation from the pars abdominalis is short—two rows.

#### *Menura novaehollandiae*: Superb Lyrebird

The dorsal body pterylosis of *Menura* is also typically passerine in patterning but is exceptionally densely feathered. Ventrally, however, *Menura* is almost unique within the Passeriformes in the length and type of separation between the pars pectoralis and pars abdominalis.

**Pteryla Spinalis** (Fig. 3). Even taking into consideration the large size of a lyrebird body, the pterylosis of this species can only be described as astonishing in its density of feathering. The pars interscapularis is comparatively weak and sparse anteriorly, but ends in very dense feathering as it joins the pars dorsalis. The pars dorsalis is long and heavy; eighteen rows form a rhombic configuration, with the following counts (one side): 25, 26, 24, 25, 26, 24, 23, 22, 20, 18, 17, 16, 15, 14, 12, 11, 10, 9. The total number of feathers (both sides) is 656. The pars pelvica is similarly heavy and long—approximately seventeen rows and straight-sided for most of its length. Unfortunately, in this specimen (CM Alc. Coll. no. 1834) the fat deposits and connective tissue over the rump feathering make it impossible to count all the feathers in the area.

A small gap at the base of the pars dorsalis is also largely obscured by fat deposits, so the point was verified on two study skins (AMNH 023975 and 554413) which were relaxed and opened. The first of these also seems to have a small gap at the anterior end of the pars pelvica; on the second specimen the gap is clear and is formed in the same manner as that in *Atrichornis*.

**Pteryla Ventralis** (Fig. 4). The lateral arms of the pars pectoralis contain 4 feathers from the first row to the tenth. The eleventh row has 5 feathers; the twelfth and thirteenth, 6; the fourteenth and fifteenth, 5; the sixteenth, 4; and the seventeenth, 2. The medial arm has 4 feathers in the first row, 5 in the second, and 6 in the third through fifth. The sixth through ninth rows have

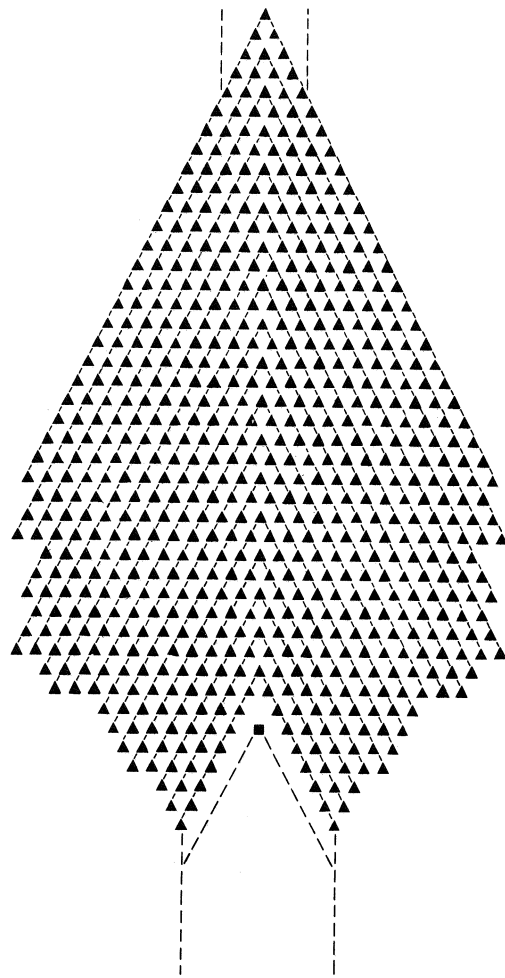


Fig. 3. *Menura novaehollandiae*, Pt. Spinalis, pars dorsalis.

7 feathers, but from the eighth through seventeenth the tract is too obscured by fat and connective tissue to provide accurate counts; the arms all contain either 7, 8 or 9 feathers until the seventeenth, which has 9.

The pars abdominalis does not begin as regularly spaced, additional feathers on the medial ends of the pars pectoralis arms as it does in other passerines (e.g., *Passer*; Clench, 1970). Instead, it first appears as a single, rather small feather opposite the end of row seven, but approximately 7 mm posteromedial to the end of that arm. The next rows (eight through fifteen) contain either 2 or 3 feathers (Fig. 4), and then the pars abdominalis becomes regular rows of 4 feathers (rows sixteen through thirty-four of the tract). The pars tapers and ends with rows of 3, 2, 1, 1, 1, 1 feathers. The total length of the tract is forty rows.

**Discussion.** Nitzsch (1867) figured the pterylosis of *Menura*, showing the very heavy Pt. Spinalis (but without the small gap at the base of the pars dorsalis) and the unusual configuration of the Pt. Ventralis. He commented that *Grallina* was the only other passerine he had examined with what he termed a 'half free' branch of the ventral tract.



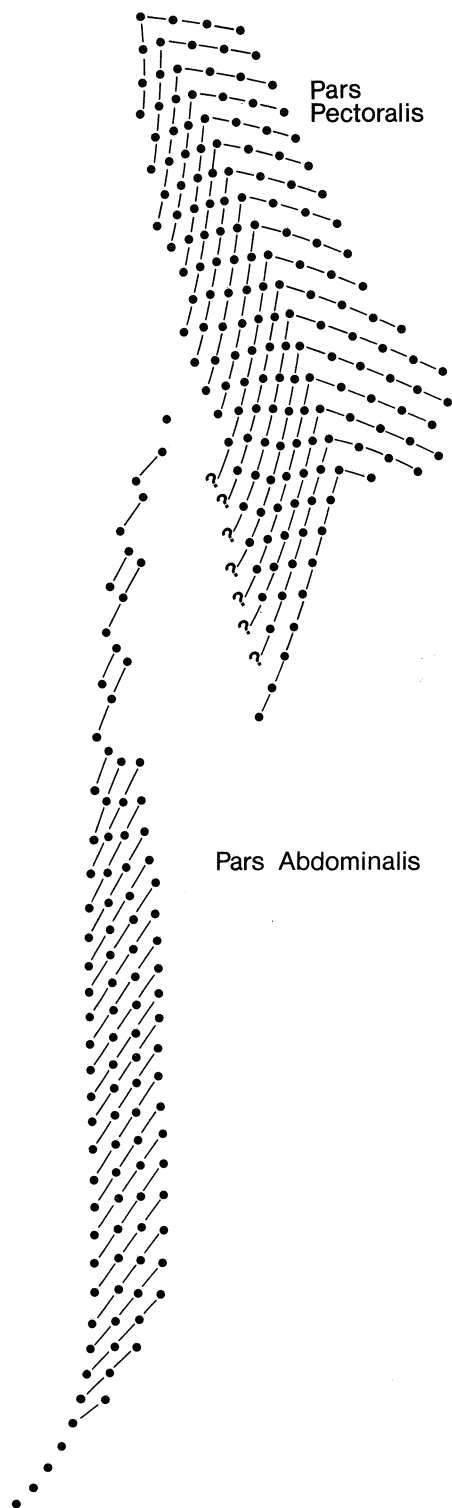


Fig. 4. *Menura novaehollandiae*, Pt. Ventralis.

I also confirmed the pattern and counts of the *Menura* flat skin with the two study skins. Fortunately, lyrebirds are large enough that the pterylosis pattern is relatively apparent in a study skin (in spite of the sawdust or other absorbent from the initial preparation that still adheres to, and may obscure, the calami and muscles of the

tracts). I could see enough details, especially of the Pt. Ventralis, to confirm the counts from the alcohol specimen.

**Paradisaeidae: Birds-of-Paradise**

**Previous studies.** The initial pterylographic study of this family was by Nitzsch (1867), who reported on *Paradisaea apoda* (figured), *Ptiloris paradiseus* ('*Epimachus regius*') and *Epimachus fastuosus* ('*E. superbus*'). Giebel (1877) examined several additional species but used study skins for material; his work was strongly criticized by Pycraft (1905) and Stonor (1938) for its inaccuracy, and I concur. It will not be considered further. Pycraft (1905) studied *Paradisaea minor* (figured) and had *P. apoda*, *Manucodia comrii* and *Ptiloris paradiseus* for comparative material. Stonor (1938) conducted the landmark study of the family, examining 13 of the 20 genera ('Peters' classification) from spirit-preserved material, and 5 from study skins, internally examined. The only genera he was unable to obtain were *Pteridophora* and *Cnemophilus* (the latter then considered to be a bowerbird; Stonor, 1937). Since Stonor's report, there has been only one addition to the pterylographic literature on this family—notes on *Paradisaea rubra* by Berger (1956).

**Material examined.** Cnemophilinae: *Loria loria* (2 specimens), *Loboparadisaea sericea* and *Cnemophilus macgregorii* (2 specimens). Paradisaeinae: *Manucodia chalybatus*, *M. comrii* (2 specimens), *Phonygammus keraudrenii*, *Ptiloris paradiseus*, *Semioptera wallacei*, *Seleucidis melanoleuca*, *Paradigalla (carunculata) brevicauda*, *Epimachus meyeri* (2 specimens), *Astrapia splendidissima*, *A. stephaniae*, *Lophorina superba*, *Parotia lawesii*, *Pteridophora alberti*, *Cicinnurus regius*, *Diphyllodes magnificus* (2 specimens), *Paradisaea apoda*, *P. raggiana* and *P. rubra*. The present series lacks three genera of Paradisaeinae (*Macgregoria*, *Lycocorax* and *Drepanornis*), specimens of which could not be located. The above material came from the AMNH, BM(NH), BPBM, Busch Gardens (through G.E. Woolfenden), the Pittsburgh Conservatory-Aviary (through CM), and the NYZS.

The *Paradisaea rubra* and *Seleucidis melanoleuca* were fresh specimens; all others were in alcohol.

**Cnemophilinae.** Unfortunately, the condition of the specimens ranged from poor to very poor (these are rare taxa in alcohol collections), so it was impossible to count all the feathers and rows in all individual specimens. The following is a conservative appraisal of the pterylosis of this subfamily.

The pterylosis of all three genera is similar. The Pteryla Spinalis is heavily feathered throughout, with a strong and wide pars interscapularis, and a pars dorsalis consisting of thirteen rows in *Loria*, at least eleven rows in *Loboparadisaea*, and approximately thirteen in *Cnemophilus*. I could obtain relatively accurate counts of the pars dorsalis in both *Loria* specimens—254 and 225 feathers, respectively. The

main difference among the specimens is the presence or absence in the outermost row arms of from 1 to 4 feathers in the first and the ninth through thirteenth rows. The pars pelvica is similarly heavily feathered, with little or no expansion posteriorly. Clearly, there is no gap or apterium at the pars dorsalis/pars pectoralis junction. The Pt. Ventralis is unremarkable: there are approximately 9 feathers at the maximum width, the separation between the pars pectoralis and pars abdominalis is three or four rows long, and most of the rows of the pars abdominalis contain 4 feathers. The general configuration of these specimens agrees well with Stonor's figure of *Loria* (1938: 449).

**Paradisaeinae.** More of these specimens were in better condition, hence more specific counts could be made. As noted by Stonor (1938), species with extraordinary development of plumes on certain parts of the body have massive expansion of those portions of the pterylae. Fortunately, in no case do the plumes involve the pars dorsalis/pars pelvica, which is one of the most useful areas of body pterylosis for studying broad familial relationships. Because Stonor described and figured so many of these birds well, I shall simply add details to the material already published.

In strong contrast to the cnemophilines, the pars dorsalis of 'typical' birds-of-paradise is comparatively small and sparsely feathered. The number of rows ranges from seven to eleven. Unlike those of most oscines, the posteriormost rows of the pars dorsalis, and in some instances the feathers within those rows, are more widely spaced, presenting what Stonor termed a 'weakness' at the junction between the pars dorsalis and the pars pelvica. In addition, a small gap often occurs between the two—as in *Menura* and *Atrichornis* (e.g., *Semioptera wallacei*, Fig. 5). To a greater or lesser extent, this weakness and gapping are present in all specimens of paradisaeines examined. The possible exceptions are *Lophorina* and *Parotia* (poor specimens, but they do not seem to have a gap), and *Astrapia splendidissima* in which the central feather of the last row is absent, forming a small apterium (not true of the *A. stephaniae* specimen). The general strength of the pars dorsalis ranges from very sparsely and lightly feathered to moderate. In the specimens examined, the length of the pars dorsalis (number of rows) and its number of feathers are as follows: *Cicinnurus regius* 7/83; *Semioptera wallacei* 7/89; *Seleucidis melanoleuca* 7/97; *Paradigalla brevicauda* 7/?; *Phonygammus keraudrenii* 7/105; *Manucodia chalybatus* 8/92; *M. comrii* 8/116; *Lophorina superba* 8/119; *Diphyllodes magnificus* 8/102 and 8/128?; *Ptiloris paradiseus* 9/147; *Epimachus meyeri* 10/172 and 10/180; *Parotia lawesii* 10/142; *Pteridophora alberti* 10/150; *Paradisaea apoda* 10/144; *P. rubra* 9/155; *Astrapia splendidissima* 11/200; and *A. stephaniae* 11/201. As I have noted before (Clench, 1970), body size *per se* seems to have little to do with the number of feathers in the pars dorsalis; within closely related groups the basic patterns are the same. In paradisaeines, both large species

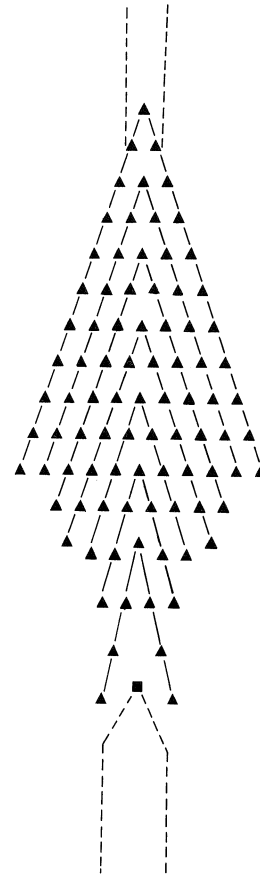


Fig. 5. *Semioptera wallacei*, Pt. Spinalis, pars dorsalis.

(*Seleucidis*) and small (*Cicinnurus*) have similar pterylae, and the most heavily feathered paradisaeines are the medium-sized *Astrapia* spp. *Astrapia* is also the only genus that approaches the cnemophilines in general strength of feathering, but it shows the weakness in the junction of the pars dorsalis/pars pelvica that is typical of paradisaeines.

The Pteryla Ventralis is considerably more variable than is the Pt. Spinalis, largely because of the species that have specialized flank plumes. As Stonor (1938) noted, and I have confirmed, sex apparently has no effect on the basic pterylosis: both males and females have the same pattern and degree of feathering, although the females do not have the long ornamental plumes.

The maximum width of the pars pectoralis ranges from 7 to 10 feathers in the species without specialized plumes (7 in *Phonygammus*, 8 in *Manucodia*, *Lophorina*, *Diphyllodes*, 9 in *Semioptera*, *Paradigalla* [?], *Pteridophora*, *Cicinnurus*, 10 in *Ptiloris*) and from 11 to approximately 28 in the flank-plumed birds (11–12 in *Epimachus*, 13–14 in *Astrapia*, 13 in *Seleucidis*, 18 in *Parotia*, approximately 25–28 in *Paradisaea*.) The separation between the pars pectoralis and the pars abdominalis ranges from three to seven rows long in most species; the longer separations are usually found

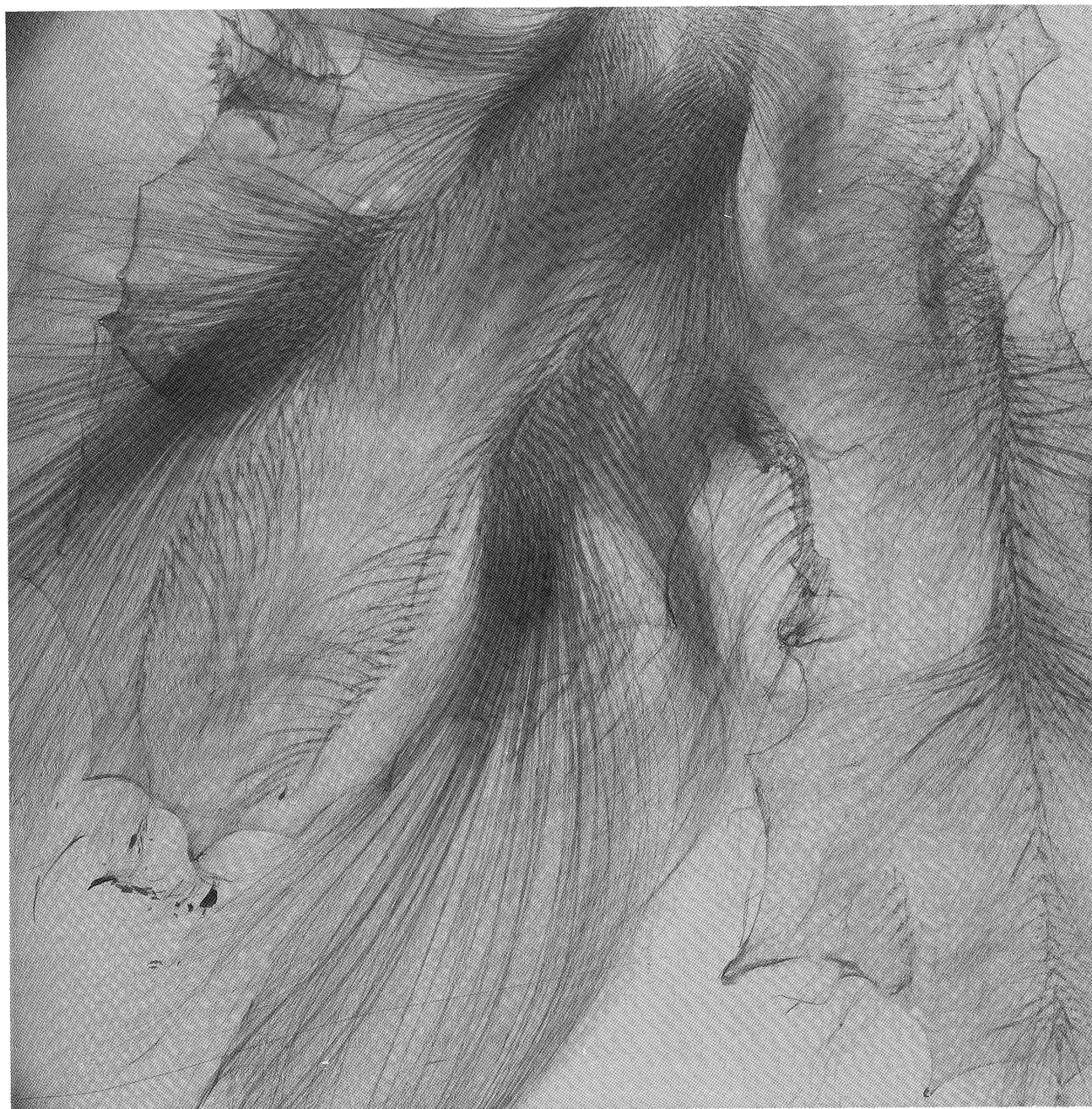


Fig. 6. *Seleucidis melanoleuca*. Radiograph of flat skin. Pt. Ventralis on left, showing extremely heavy feathering of pars pectoralis; paired patches of heavy neck plumes (above) are components of Pt. Capitalis. Lightly feathered Pt. Spinalis on right.

in those forms with flank plumes. The exceptions are *Paradisaea* in which the massive development of the pars pectoralis extends into and partially obscures the separation of the pars abdominalis, and *Seleucidis* and several other genera which have a somewhat separated anterior end of the pars abdominalis, reminiscent of *Menura*.

In *Seleucidis* the first feather of the pars abdominalis is not as widely separated from the pars pectoralis as it is in *Menura*, but the general configuration is similar. The first few rows of the pars abdominalis also consist of 2, then 3, widely spaced feathers; the separated end

of the pars pectoralis is long (approximately eleven rows) and heavily feathered (Fig. 6). The same configuration is apparent but less marked in *Epimachus*, *Cicinnurus* and possibly *Astrapia*.

In all the Paradisaeinae, the pars abdominalis is of normal passerine strength and configuration once it is separated from the pars pectoralis, and it is either 3 or 4 feathers wide through most of its length (5 in *Epimachus* and *Astrapia*).

#### **Ptilonorhynchidae: Bowerbirds**

**Previous studies.** Nitzsch (1867) examined

*Ptilonorhynchus violaceus* (*P. 'holosericeus'*) and *Sericulus chrysocephalus* (*S. 'regens'*) and found the body tracts to be narrow; the pars dorsalis of the Pt. Spinalis was described as rhombic with an elongated interior apterium. Pycraft (1905) studied the same two species, and his brief description agreed with that of Nitzsch. Stonor (1937) described and figured the pterylosis of *Amblyornis* in detail. (Note that the legends of Stonor's figures 6 and 8 were transposed in printing so that the illustration labeled *Semioptera wallacei* is actually *Amblyornis*.) Stonor found the Pt. Spinalis to have a broad rhombic pars dorsalis containing "a long and well-defined ellipsical apterium" (1937: 481). The Pt. Ventralis was typically passerine in configuration. He also described the pteryloses of *Ptilonorhynchus* and *Chlamydera* to be virtually identical to that of *Amblyornis*.

**Material examined.** *Ailuroedus crassirostris*, *Scenopoeetes dentirostris* (from the interior of a study skin only), *Amblyornis macgregoriae*, *Sericulus bakeri*, *S. chrysocephalus*, *Ptilonorhynchus violaceus* and *Chlamydera lauterbachii*. Specimens of *Archboldia* and *Prionodura*, the other genera in the family, could not be located. The specimens of *Ptilonorhynchus* and *Sericulus* were fresh (Pittsburgh Conservatory-Aviary through CM, and NYZS); the others were alcohol-preserved (AMNH).

**Pteryla Spinalis.** The pterylosis of all specimens studied is consistent in pattern: a strong, heavily feathered pars interscapularis, an equally strongly feathered pars dorsalis with a partial apterium, and a moderately strong to strong pars pelvica. The length of the pars dorsalis ranges from eleven rows in *Ailuroedus* and *Amblyornis*, thirteen or fourteen in *Sericulus* and fifteen in *Ptilonorhynchus*. The first rows are complete, with the feathers closely and evenly spaced; the posteriormost rows are incomplete, with the central (and sometimes the next-to-central) feathers absent and forming a midline apterium. In *Ailuroedus* the first six rows are complete and the last five have central feathers absent; the total feather count is 180. For *Scenopoeetes* I was able to examine only the interior of a study skin and could see that the tracts were similar to those of other bowerbirds (heavy pars dorsalis and a long apterium in the Pt. Spinalis), but feather counts were impossible. The *Amblyornis* is in poor condition but the first four rows of the pars dorsalis are clearly complete, the posteriormost seven are incomplete and the total feather count is approximately 228. The specimen of *Sericulus bakeri* is also in poor condition but probably has only four complete pars dorsalis rows and nine or ten incomplete. The *Sericulus chrysocephalus* was prepared from a fresh specimen, X-rayed, and later made into a study skin. It has seven complete rows anteriorly but the central feathers of rows five through seven have gaps to either side (Fig. 7), a not uncommon condition in species with apteria in the pars dorsalis. If these central feathers were not present, the configuration would be identical to that of the *S. bakeri*

specimen. The total number of feathers in the *S. chrysocephalus* pars dorsalis is 235. The *Ptilonorhynchus* is also from a fresh specimen, and its pars dorsalis is shown diagrammatically in Figure 8. Rows one through five are complete, and six through fifteen are incomplete with a feather count of 281. The *Chlamydera* is badly shot-damaged and in moult, and affords little detail other than that the apterium is approximately six rows long in the pars dorsalis.

**Pteryla Ventralis.** This tract is typically oscine in all respects with nothing distinctive in the row patterning. The maximum width is either 10 or 11 feathers wide, the separation between the pars pectoralis and pars abdominalis is short (two to four rows long), and most of the rows in the pars abdominalis have 4 to 6 feathers.

#### *Turnagra capensis*: Piopio (formerly 'New Zealand Thrush')

The only available alcohol material of this enigmatic New Zealand genus consists of two badly shot-damaged specimens in the BM(NH) and the Otago Museum. Nevertheless, the flat skins prepared from them give a general indication of the pterylosis, even if few feather counts are possible.

**Pteryla Spinalis.** Both the pars interscapularis and the pars pelvica are strongly feathered and unremarkable. The pars dorsalis, like that in the cnemophiline birds-of-paradise, scrub-birds and lyrebirds, contains extremely heavy feathering (approximately fifteen rows containing between 300 and 327 feathers in the two specimens). No small basal apterium or gapping is apparent but the condition of the specimens does not preclude the possibility of either.

**Pteryla Ventralis.** This tract is also heavily feathered, with a maximum width of 11 feathers, a separation between the pars pectoralis/pars abdominalis of four rows, and 4 to 5 feathers in most of the rows of the pars abdominalis.

**Discussion.** In a recent study (Olson *et al.*, 1983) I compared the pterylosis of *Turnagra* with that of other members of the 'corvid assemblage' and to various muscicapids with which a relationship has been suggested. *Turnagra* is clearly allied to the Paradisaidae-Ptilonorhynchidae complex and is most similar to the cnemophiline birds-of-paradise.

#### **Grallinidae: Mudnest Builders**

The Australian birds that build mud nests have long been obscure in their relationships, both to one another and to other passerines (McEvey, 1976). They have been variously classified—ranging from separate families for each of the three genera (Mathews, 1930) to being scattered separately through the 'corvid assemblage' in other, larger families (e.g., Sharpe, 1877). In 1950, Amadon tentatively placed all three genera—*Grallina* (including *Pomareopsis*), *Struthidea* and *Corcorax*—





**Fig. 7.** *Sericulus chrysocephalus*. Radiograph of Pt. Spinalis, pars dorsalis. Anteriormost four rows complete; next three complete (with midline feathers) but well gapped; posteriormost six incomplete, forming an apterium.

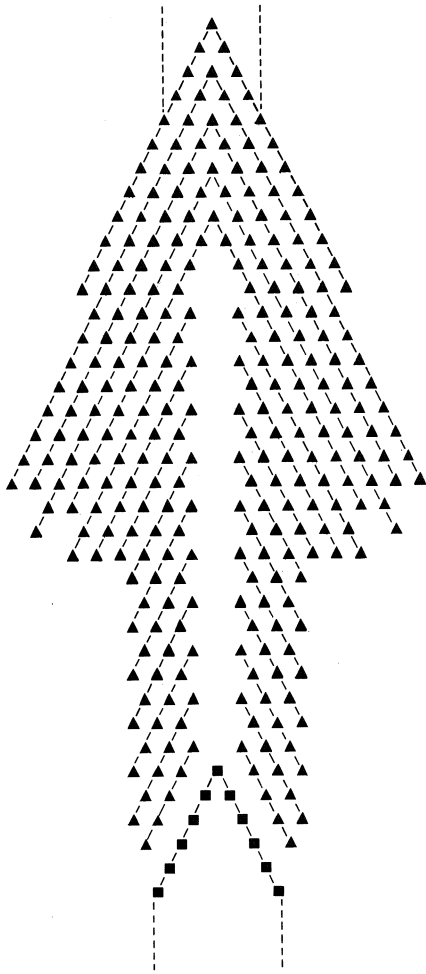


Fig. 8. *Ptilonorhynchus violaceus*, Pt. Spinalis, pars dorsalis. First five rows complete; last ten incomplete, forming an apterium.

together into the family Grallinidae, although he retained *Grallina* in a separate subfamily (Mayr & Amadon, 1951). This arrangement, which was “partly to avoid too many monotypic families” (Mayr & Amadon, 1951: 31), gained general acceptance (e.g., Mayr in Mayr & Greenway, 1962; Keast, 1964; CSIRO, 1969; Macdonald, 1973). It has usually been agreed that *Struthidea* and *Corcorax* are each other’s closest relatives, and the main question has been the relationship of *Grallina* to them and to other passerines. Recently, Schodde (1975) separated them into two families—Grallinidae and Corcoracidae (including *Struthidea*)—but kept them adjacent to each other in his list. Slater (1974) retained *Grallina* in a monotypic family, but placed *Corcorax* and *Struthidea* in the Timaliidae. Chapman (1975) went even further, agreeing that *Corcorax* and *Struthidea* (but merged into a single genus) belonged in the babblers, and placed the Grallinae as a subfamily of the Motacillidae.

As field observations and morphological information accumulate on these birds, their close relationship is becoming more in doubt; their habit of building mud

ests (although of different shapes; Slater, 1974), their geographical distribution (endemic to Australia and New Guinea) and general similarities in skull structure (Amadon, 1950; but see also McEvey, 1976) seem to be about all they have in common. Sibley (1976) reported that egg white proteins of the three were extremely similar to one another but they were also similar to *Corvus* and paradisaeids, as well as generally similar to bowerbirds, *Oriolus*, *Menura*, cracticids, etc.—hardly a discriminating character in the degree of relationship at the family level. Recently, Sibley & Ahlquist (in press), after using a DNA-DNA hybridization technique, have included *Grallina* in the tribe monarchine flycatchers, with the Corcoracinae well separated in another subfamily but both still in a huge superfamily ‘Corvoidea.’ The social structure of *Struthidea* and *Corcorax* is distinctly different from that of *Grallina* (Robinson, 1947; Rowley, 1974; Macdonald, 1973), the skeleton has important differences (Shufeldt, 1923; McEvey, 1976) and the appendicular musculature also shows certain dissimilarities (Borecky, 1977). The pterylosis also supports the conclusion that *Grallina* should be separated from the other mudnest builders.

*Grallina*. The only genus, of the three in question, that previously has been pterylographically studied is *Grallina*. Nitzsch (1867) described the Pt. Spinalis as having an undivided rhombic pars dorsalis and the Pt. Ventralis as sharing with *Menura* the otherwise unique type of separation of the pars abdominalis from the pars pectoralis. Clark (1945) found the same ventral configuration but disagreed on the shape of the Pt. Spinalis, pars dorsalis: “The dorsal tract is thickly feathered and conspicuous. In form it is intermediate between *Motacilla* [rhombic] and *Hirundo* [lobed] as figured by Nitzsch; that is, the outer angles of the anterior half of the tract are thickly feathered while the posterior half is abruptly narrow and the feathers are more widely spaced; indeed, there are but few feathers at the center of the area where widest. Removal of eight to ten feathers there would give a bilobed tract like that in *Hirundo*. These imperfect lobes are densely feathered but not sharply defined.” (1945: 72) His text was accompanied by a sketchy diagram that showed the pars dorsalis as a broad triangle with no suggestion of the features mentioned. A similarly poor figure of *Grallina cyanoleuca* appeared in a report by Parsons (1968): the pars dorsalis was shown as a typically passerine rhombus, the pars pelvica was broadly expanded with an anchor-shaped pattern (heavier feathering?) within the element, and the Pt. Ventralis had an exceptionally broad pars abdominalis that separated from the pars pectoralis approximately halfway down the breast. Parsons stated, however, that the area between the pars dorsalis and the pars pelvica “gets very weak and would be discontinuous but for 5 or 6 small feathers” (1968: 42).

The single specimen of *Grallina cyanoleuca* (YPM alcoholic) available to me was moulting when collected and is in poor condition, which prevents a full count

of the tracts. The posteriormost pars dorsalis of the Pt. Spinalis has a moderately large and striking apterium. The entire element contains nine rows with the feathers of the first four evenly spaced; the fifth and sixth with central feathers slightly separated from the remainder of their rows; and the seventh through ninth clearly lacking a central feather and with a fairly wide space (3mm in a stretched flat skin) between the row arms. The pars pelvica is strong and twelve rows long but the specimen is too heavily in moult to confirm or refute the peculiar internal configuration indicated by Parsons (1968). The Pt. Ventralis is generally heavily feathered. The maximum width is 11 feathers and the pars pectoralis has a long, free segment (eight rows) posterior to its separation from the pars abdominalis. The latter separates from the pars pectoralis in the normal passerine manner—as a regular extension of the medial ends of the rows, not the essentially separate element as seen in *Menura*—but the separation is considerably more anterior than is true of most other passerines. The majority of the pars abdominalis rows have 5 feathers.

**Struthidea.** My single specimen of *Struthidea cinerea* (BM(NH), alcohol-preserved) is also in moult, obscuring some details. The Pt. Spinalis pars dorsalis is nine rows long, with all rows complete (no apterium). The row counts (one side) are: 10, 10, 10, 9, 7, 6, 5, 4, 3, for a total (both sides) of 119 feathers. The midline feathers of the three or four posteriormost rows are slightly set apart but this gapping is so minor that it is visible only under the microscope. The pars pelvica is moderately strong with approximately eleven rows, and is broadly expanded posteriorly. The Pt. Ventralis is typically oscine in general configuration and strength: the maximum width is approximately 9 feathers, the separated pars pectoralis is five rows long and the pars abdominalis rows are 4 to 5 feathers wide.

**Corcorax.** Although I could not obtain a suitable specimen of this genus, I did examine one (BM 1925.11.1.149—specimen in alcohol, not skinned) in heavy molt. It was similar in all visible respects to the *Struthidea*, and clearly did not have a *Grallina*-like apterium in the pars dorsalis.

**Discussion.** *Grallina* differs from *Struthidea* in having an obvious apterium in the base of the pars dorsalis vs. a very slight gapping of the midline feathers in *Struthidea*. The pars pelvica of *Grallina* is also broader and more heavily feathered, especially posteriorly. Ventrally, *Grallina* differs strikingly in the length of the separated pars pectoralis (eight vs. five rows, or 17 mm vs. 9 mm in *Struthidea*).

In regard to the suggested relationship of *Grallina* with the Motacillidae, and *Struthidea/Corcorax* with the Timaliinae (Chapman, 1975), the pterylographic evidence argues strongly against the first and weakly against the second. Nitzsch (1867) and Verheyen (1953) figured *Motacilla*, *Anthus* and *Macronyx*, and I have examined a specimen of *Motacilla alba*: motacillids are typically oscine in all respects and show none of the striking peculiarities of *Grallina*. The babblers are a

large and diverse group and have not yet been studied sufficiently. Those reports that do exist in the literature (Nitzsch, 1867: *Timalia*, *Pomatorhinus*; Shufeldt, 1889: *Chamaea*; Clark, 1914: *Garrulax*; Naik & Andrews, 1966: *Turdoides*) and my own preliminary examination of specimens (*Leiothrix lutea*, *L. argentauris*, *Stachyris pyrrhops*) indicate that the pattern in the pars dorsalis is uninterrupted, unlike the gapping seen in *Struthidea*. Much more material, however, will have to be examined before the relationship can be confirmed or denied by pterylography.

### Artamidae: Wood Swallows

**Previous studies.** Nitzsch (1867: 80) described and figured *Artamus* (*Ocypterus*) *leucorhynchus*. He stated that the pars dorsalis was elongated, rhombic and “narrow, but widened by the two powder-down tracts situated beside it”, and that the pars pelvica was broad. The pars pectoralis was “somewhat separated” at its posterior end and had a band of powderdowns that extended from its posterolateral edge, dorsolaterally into the axillary region. The paired Pt. Femoralis on the base of the thigh similarly had a band of powderdowns on the medial side.

Lowe (1938a: 431) described *Artamus minor* to have “characteristic passerine pterylosis”, with no mention of powderdowns. Parsons (1968) figured *Artamus cyanopterus* (*tenebrosa*) with an elongated, lozenge-shaped pars dorsalis and a broad pars pelvica, without indication of powderdowns. His figure of the Pt. Ventralis, however, showed a lateral extension of the pars pectoralis that almost surely corresponds to the powderdown band illustrated by Nitzsch. Parsons did mention finding feathers with aftershafts in the Pt. Spinalis, mostly on the tract margins; apparently he did not recognize them as powderdowns.

**Material examined.** *Artamus leucorhynchus* and *A. insignis* (one each, CM and AMNH specimens in alcohol).

**Pteryla Spinalis.** The pars dorsalis of a wood swallow is remarkably modified. It is approximately eleven rows long, and a solid rhombus. The first 6 or 7 feathers in each row are normal contour feathers but at feather 7 or 8, to the end of the extended row, they are highly modified powderdown quills in sheath. The pars interscapularis and pars pelvica are generally strong; the latter is nine rows long in the specimen of *A. leucorhynchus* with (one side) counts of 6 feathers in the first six rows, then 4, 3, and 1 feather in the posteriormost.

**Pteryla Ventralis.** The tract is generally heavy, with a maximum width of 10 or 11 feathers in the pars pectoralis and 5 in the pars abdominalis. The separation of the pars abdominalis occurs at row nineteen and the pars pectoralis ends at row twenty-two; the tract as a whole is thirty-nine rows long. A broad band of powderdowns extends dorsolaterally from the posterolateral margin of the pars pectoralis (from near

the ends of rows seventeen to twenty-one) and reaches about halfway to the pars dorsalis on the back. Unlike the situation in the pars dorsalis, however, these powderdown follicles do not seem to be regular extensions of the ventral tract rows, but they are roughly organized and constitute a patch of about six rows of 16 feathers (maximum). There is a sparser and even less organized patch of powderdowns on the medial edge of the Pt. Femoralis and a few scattered powderdown follicles in the Pt. Cruralis.

**Discussion.** When viewed from the underside of the skin, the powderdowns in *Artamus* look like modified contour feathers. The follicles are essentially the same size as a (growing) normal *Artamus* contour feather, and they are either components of the regular body tracts or apparent developments of plumulaceous apterial feathers or ephemeral tracts (e.g., the 'axillary tract'; see comments in Clench, 1970). If one of these artamid powderdowns is plucked and examined, it is a good match to the illustrations of pigeon powder feathers in Lucas & Stettenheim (1972: 337). The same is true of the powderdowns in certain cotingids, although cotinga powderdown follicles tend to be larger than are the adjacent contour feathers (e.g., in *Conioptilon*) and they are very differently arranged on the body (see my comments in Lowery & O'Neill, 1966). In gross morphology, the powderdown patches of herons are even more strikingly different when viewed from the underside of the skin. Heron powderdown follicles are many times smaller than the nearby contour feathers (or than passerine powderdowns); they look like bits of fine thread, and appear to grow randomly in a flat mass of tiny follicles.

#### Callaeidae: New Zealand Wattlebirds

**Previous studies.** Nitzsch (1867) found *Callaeas* ('*Glaucopis*') *cinerea* to have the same pterylosis as that of *Corvus*: a broad, acutely angled, rhombic pars dorsalis with an elongated apterium. Garrod (1872: 644) studied *Heteralocha acutirostris* ('*gouldi*') and stated that "the arrangement of the feathers is completely passerine [the Huia's affinities had been suspected to be with the nonpasserine *Upupa*]. The rhombic saddle of the spinal tract does not enclose any ephippial space, therein differing from the Crow's and resembling the typical Starling's." Stonor (1942) studied all three genera in the family (*Callaeas cinerea*, *Heteralocha acutirostris*, and *Creadion* ('*Philesturnus*') *carunculatus*) and found them to be essentially identical in body pterylosis. His description and figure of *Callaeas* showed the Pt. Spinalis to have a strong pars interscapularis and a broad, rounded, rhombic pars dorsalis without an apterium (contradicting Nitzsch but agreeing with Garrod) and without weakening in its posteriormost rows. The pars pelvica was broad and widened slightly to a triangular base just anterior to the uropygial gland. The Pt. Ventralis was characterized as follows (Stonor, 1942: 4): "The separation of the outer and inner tracts

on the breast, as occurs in all Passerine birds, is but faintly indicated by a narrow 'notch' on the lower breast." He found all three genera to have unremarkably oscine pterylosis, differing among one another only by minor features of the capital tracts.

**Material examined.** Through the courtesy of J.D. Macdonald, I was given permission to remove the body skin from two BM(NH) spirit specimens: the long-extinct *Heteralocha acutirostris* (BM Reg. no. 1940.12.8.107) and the rare *Callaeas cinerea* (1940.12.8.109). The former had been collected in 1894, may have been originally preserved in rum (judging from its pungent odour), and was in heavy moult; it was in remarkably good condition for its museum age and stage of moult when collected. The *Callaeas* was collected at about the same time (data illegible — 1896?) and in excellent condition.

**Pteryla Spinalis.** In *Heteralocha* and *Callaeas* the pars interscapularis is broad and strong; its posteriormost row has 6 feathers per arm. The pars dorsalis in both genera is fourteen rows long and contains 298 feathers. The rhombic shape of the pars dorsalis in *Heteralocha* is slightly wider and more flared posteriorly than in *Callaeas*, which is a result of minor differences in the row arm lengths (11, 18, 18, 18, 17, 15, 12, 11, 9, 8, 7, 5, 4, 3 in *Heteralocha* vs. 18, 18, 17, 16, 14, 13, 11, 10, 9, 8, 6, 6, 5, 5 in *Callaeas*). The occurrence of an apterium or gap will be discussed. The pars pelvica is strong and slightly expanded at its posteriormost end as illustrated by Stonor (1942).

**Pteryla Ventralis.** Both *Heteralocha* and *Callaeas* have the same highly unusual configuration of this tract. Throughout, the feathering is extremely heavy and there is no separation of the pars pectoralis from the pars abdominalis in the flank area. The maximum width above the flank is 10 feathers per row, and the lateral row arms contain 4 feathers. The flank ends by a gradual shortening of the lateral arms but, aside from a few slight irregularities in feather placement where the separation normally occurs in passerines, no true break occurs between the two pars. The pars abdominalis below the flank is wide, 7 feathers in *Callaeas*, 6 (perhaps 7? — obscured by moult) in *Heteralocha*.

**Discussion.** The major difference between the two specimens lies in an apparent apterium in the posterior pars dorsalis of *Callaeas*. In that specimen the first six rows are normal with the feathers evenly spaced. At row seven there is a small gap between the midline and first arm feathers; at rows eight and nine the gap is slightly wider and the apparent apterium (visible macroscopically) begins. The midline feathers from row eight through fourteen become progressively smaller. At the last (fourteenth) row the feather is so small as to be almost invisible under a microscope, and the gap of the 'apterium' is 4 to 5 mm wide across the centre of the pars. At row eleven the central feather is 3 mm from its nearest lateral neighbor (feather number 3 of row ten), compared with an average distance of 1 mm between the rest of the saddle feathers. In the



*Heteralocha* specimen no apterium is apparent, except for a suggestion of a gap on either side of the midline in the posteriormost rows. Unfortunately, the heavy stage of moult in this bird precludes detailed analysis.

This variation, an apparent apterium formed by gaps in the spacing between (progressively smaller) midline feathers and their corresponding row arms, is also found in other passerines such as corvids (q.v.). I suspect this phenomenon explains the discrepancies reported by Nitzsch vs. Garrod and Stonor. All three were careful workers, and I have seldom found cause to doubt their results. In answer to my query whether Stonor's specimen of *Callaeas* (registration number unknown) still existed in the BM(NH) spirit collection and was thus available for re-examination, P.J.K. Burton reported (in litt.) that the collection now contains no clipped specimens of *Callaeas* (Stonor normally clipped the feathers from birds he studied pterylographically). Stonor also carried out other dissections for his study, so I can only conclude that he did not return what was left of the specimen to the collection (although he often did return clipped specimens of other species). Dr Burton also examined several other spirit specimens of *Callaeas* for me, and he reports (in litt.) that they seem to have small apparent apteria in the posterior pars dorsalis, but without clipping or skinning the specimens, he cannot be sure. I suggest, therefore, that members of this family may have a weakening in the posterior midline of the pars dorsalis, which may not be apparent in preserved specimens unless skins can be stretched out slightly to improve visibility.

Stonor (1942: 4) also described a condition in the Pt. Ventralis of *Callaeas* that is different from my findings: "The separation of the outer and inner tracts on the breast, as occurs in all Passerine birds, is but faintly indicated by a narrow 'notch' on the lower breast." Without Stonor's specimen to re-examine, I can only guess that it showed even more pattern interruption at the usual flank separation area than does mine, but more material would have to be examined to prove the point. Because my specimen of *Heteralocha*, and another of *H. acutirostris*, BM(NH) Reg. no. 1940.12.8.158, which I was able to examine superficially while it was on loan to R.J. Raikow, both lacked a true separation of the two pars of the Pt. Ventralis, I believe this feature is characteristic of the family.

### Cracticidae: Australian Magpies

**Previous studies.** Nitzsch (1867: 80) described *Strepera graculina* (? = *Barita strepera*), *Cracticus torquatus* (? = *Barita destructor*) and *C. cassicus* (? = *Barita varia*) as "saddle short, broadly rhombic, acutely angled." Degen (1903) noted *Gymnorhina tibicen* as having a typical passerine configuration and agreeing well with the cracticid species described by Nitzsch. Leach (1914) described the pterylosis of *Strepera graculina* and, although his illustration showed peculiar differences from the standard passerine pattern

(e.g., the Pt. Femoralis merging with the pars pelvica of the Pt. Spinalis, and the Pt. Ventralis continuous with the Pt. Cruralis and the wing feathering), he did not comment on these anomalies, stating just (p. 34) that "*Strepera, Gymnorhina* and *Cracticus* agree closely in the feather tracts." Clark (1945) re-examined and figured *Strepera graculina* and also described *Cracticus nigrogularis*. He criticized Leach's figure and stated that the Pt. Spinalis was heavy but of standard passerine configuration, that the connection between the pars pelvica and the Pt. Femoralis was "very incomplete", and that the Pt. Ventralis, especially the expansion of the pars pectoralis, was strong and similar to the pattern of *Paradisaea* in Nitzsch's illustration. Clark described *Cracticus nigrogularis* as being like *Strepera* but with a narrower, less densely feathered Pt. Ventralis. Parsons (1968) figured the dorsal pteryloses of *Gymnorhina tibicen leuconota* and *Strepera versicolor (intermedia)*, and both dorsal and ventral tracts of *Cracticus torquatus* ('*destructor*'). All three were shown with essentially similar pteryloses, the pars dorsalis being slightly narrower in *Cracticus*, broader and more rounded in *Gymnorhina*, and more angled in *Strepera*. *Cracticus* was figured with heavy ventral feathering in the pars pectoralis (except on its medial margin) and light feathering in the pars abdominalis.

**Material examined.** *Strepera graculina, Cracticus nigrogularis* (1 each, BM(NH) alcohol-preserved) and *C. torquatus* (YPM alcohol-preserved).

**Pterylya Spinalis.** The pterylosis of the three specimens is generally similar with relatively heavy feathering throughout, and the pars dorsalis in a rounded rhombic configuration. The pars dorsalis of *Cracticus nigrogularis* has 201 feathers in ten rows, with counts of 15, 16, 14, 12, 11, 10, 8, 7, 6, and (-)6. The posteriormost two rows show some gapping at the midline and the last row lacks a central feather, thus forming a small apterium. The specimen of *C. torquatus* is in poor condition (heavy moult) and cannot be fully counted, but the posterior end of the pars dorsalis (ten rows) shows similar gapping, with the last row clearly complete, although the midline feather is small.

*Strepera graculina* has a pars dorsalis of 198 feathers in eleven complete rows, with less posterior gapping but with the 1st midline feather of the pars pelvica lying between the 4th feathers (rather than the usual 3rd) of the last pars dorsalis row and hence forming a small space.

The pars pelvica is strongly feathered (84 feathers in ten rows in *C. nigrogularis*) and of the usual passerine configuration. In the *Strepera graculina* specimen, however, a few weak feathers lead off from the posteriormost rows and suggest the 'very incomplete' connection between the pars pelvica and the Pt. Femoralis reported for this species by Clark (1945) and Leach (1914) but not by Nitzsch (1867) or Parsons (1968). I consider that these small feathers are individual anomalies and have seen similar situations in a number of unrelated birds (e.g., *Pycnonotus leucogenys*;

Heimerdinger, 1964).

**Pteryla Ventralis.** This tract is similarly strong and of typical oscine configuration. The flank separation is clear and relatively long (five rows in all three specimens) but not as extreme as that in *Paradisaea* (*contra* Clark 1945). The maximum width of the pars pectoralis is 10 or 11 feathers and the pars abdominalis is predominantly 5 feathers wide.

**Discussion.** The pterylosis of this family seems to be relatively uniform with strong feathering throughout the body tracts. The only noteworthy variation lies in the extent of the midline gapping and presence or absence of a small apterium in the posteriormost rows of the pars dorsalis.

#### Oriolidae: Old World Orioles

**Previous studies.** Nitzsch (1867) figured *Oriolus oriolus* ('*galbula*' [sic]) with a typical passerine pterylosis except that the pars dorsalis was lanceolate rather than rhombic in configuration, and the pars pectoralis was not separated from the pars abdominalis. Verheyen (1953) figured *Oriolus auratus* (*notatus*) with a similar shape dorsally and a complete lack of differentiation ventrally. Urik (1983) studied *Oriolus chinensis*, *O. auratus*, *O. oriolus* and *Sphecotheres flaviventris*; his findings of a lanceolate pars dorsalis with ten (*Sphecotheres*) to twelve (*Oriolus*) rows and the details of the Pt. Ventralis are essentially similar to mine (this study).

**Material examined.** Two fresh specimens of *Oriolus trailli* (♀ and ♂ from the NYZS).

**Pteryla Spinalis.** The tract is heavily feathered throughout with the pars dorsalis long and lanceolate in shape. The pars dorsalis is composed of 234 feathers in twelve rows (16, 16, 15, 14, 13, 11, 9, 7, 7, 6, 5, 4) in the female specimen; the male (in moult) seems to be identical. The pars pelvica is eight rows long and of the usual oscine configuration.

**Pteryla Ventralis.** The total length is forty-one rows. The first row is a chevron of 6 feathers and the maximum width of 9 is reached at row ten. The pars pectoralis separates at row twenty-two and ends at twenty-six. The pars abdominalis posterior to the separation has 6 feathers per row for most of its length. Both specimens are identical.

**Discussion.** The heavy feathering of the Pt. Ventralis may have caused Nitzsch to miss the separation of the pars pectoralis from the pars abdominalis—as apparently has been the case with many pterylographers in many instances. Verheyen's figure of the Pt. Ventralis is so generalized as to be completely misleading.

#### Dicruridae: Drongos

**Previous studies.** Nitzsch (1867) described *Dicrurus macrocercus* ('*Edolius bilobus*') as having a very small

apterium at the base of the rhombic pars dorsalis and a broad Pt. Ventralis with a slight separation of the pars pectoralis and pars abdominalis. McDowell (1947: 303) published a short description of *Dicrurus adsimilis* ('*modestus*') based on the examination of an unclipped specimen in alcohol (AMNH). Accuracy is impossible using his method, so until the same species (perhaps the same specimen) can be re-examined, I put little reliance on McDowell's description of a pars dorsalis without an apterium, one side of the posterior Pt. Ventralis "uniting with its fellow to surround the cloaca", and other anomalies. Urik (1983) examined *Dicrurus macrocercus*, *D. hottentottus* and *Chaetorhynchus papuensis*. Both *Dicrurus* specimens had wide gapping or a true apterium in the posterior pars dorsalis, and a pars dorsalis that was nine rows long; both tracts were similar to my findings. *Chaetorhynchus* differed dorsally by lacking an apterium and by having a posteriorly expanded pars pelvica.

**Material examined.** A fresh specimen of *Dicrurus paradiseus* (NYZS) but in heavy moult.

**Pteryla Spinalis.** The pars interscapularis is moderately broad, with most of its rows having 5 feathers per arm. The pars dorsalis is long, narrow and lanceolate; an apterium is formed by the last two rows being incomplete on the midline. The pars dorsalis is approximately nine rows long (too many feathers lost to be certain). The pars pelvica is narrow and expanded at the base in the usual passerine configuration.

**Pteryla Ventralis.** The maximum width above the flank area is 8 feathers, the pars pectoralis separates approximately three rows before it ends at row twenty-one, and the entire length is about thirty-five rows (uncertainty the result of missing and growing feathers). The two horns of the pars abdominalis clearly do not meet or enclose the cloaca.

#### Laniidae: Shrikes

The shrikes are considered here because several genera that were long thought to be allied to starlings have been removed to the Laniidae and their allies (Amadon in Mayr & Greenway, 1962). Rand (in Mayr & Greenway, 1960) listed *Pityriasis* and *Prionops* within the Laniidae, and the vanga shrikes as a separate family; but Morony, Bock & Farrand (1975) consider *Vanga* and its relatives as a subfamily within shrikes, and thus they shall be treated here.

**Previous studies.** Nitzsch (1867) described several species of this family (both unspecified and specified, and including European *Lanius* spp. and *Prionops plumata*) as having a broad, uninterrupted, rhombic pars dorsalis that was "posteriorly abbreviated". Miller (1931) made a thorough study of *Lanius ludovicianus*. The Pt. Spinalis was described and figured with a heavy pars interscapularis; a broad, rhombic, almost fan-shaped pars dorsalis; and a pars pelvica ending in a triangular base. The Pt. Ventralis was shown to have a wide pars pectoralis with a single line of feathers

leading dorsally from its posterolateral margin almost to join the pars dorsalis. The pars abdominalis contained approximately 3 feathers per row and narrowed to a single line, meeting "its counterpart of the opposite side at a point just anterior to the anal circlet" (p. 129). Verheyen (1953) figured the Pt. Spinalis of four species: *Tchagra senegala*, *T. minuta*, *Laniarius ferrugineus* and *Telophorus nigrifrons*. All showed the same rhombic shape in the pars dorsalis and slightly triangular base in the pars pelvica, although the pars dorsalis of *Telophorus* was more oval than that of the others. Berger (1957: 237) studied the pterylosis of *Leptopterus* ('*Artamella*') *viridis*. He described the pars dorsalis as being diamond-shaped and similar to Nitzsch's figure of *Motacilla*. The pars pelvica was generally similar to Miller's figure of *Lanius*. Berger found the Pt. Ventralis to be wide anteriorly (the pars pectoralis) and two or three rows wide in the pars abdominalis. He also described "a discrete lateral thoracic tract (two to three rows wide), which extends dorsocephalad from the posterodorsal margin of the sternal tract [pars pectoralis] to the axilla". Dorst (1960) studied several species (unspecified) of vanga shrikes and wood shrikes, and described the former as having an uninterrupted, lozenge-shaped pars dorsalis and a narrow pars pelvica, and the latter as having a wider Pt. Spinalis. De Vree (1969) made a detailed study of *Tchagra minuta*. His figures are excellent and allow feather counts: the Pt. Spinalis is of typical passerine configuration, the pars dorsalis contains nine rows (7, 12, 11, 10, 9, 7, 6, 4, 3) with a total of 129 feathers, and the pars pelvica has seven rows with 27 feathers. The Pt. Ventralis is also of normal passerine shape, the maximum width of the pars pectoralis is 10 feathers, its length is about sixteen rows long and it separates from the pars abdominalis at row eleven. Most of the rows of the pars abdominalis are 4 or 5 feathers wide, and the entire tract is thirty-one rows long. De Vree used eleven specimens of *Tchagra minuta* for his study and found in only one a weak axillary tract of four or five small downy feathers.

**Material examined.** One fresh specimen of *Lanius schach* (YPM), single alcoholic specimens of *Pityriasis gymnocephala* (FMNH), *Prionops retzii* (YPM) and *Leptopterus chaberti* (YPM).

**Pteryla Spinalis.** These specimens have very similar pteryloses, both dorsally and ventrally, and are of the type common to most oscines. The pars interscapularis is moderately strong, the pars dorsalis is expanded into a solid rhombic configuration, and the pars pelvica is relatively narrow and weak. The specimen of *Lanius schach* is somewhat different in that it has 126 feathers in only eight rows in the pars dorsalis (vs. 129 feathers in nine rows in *Tchagra*, approximately nine rows in *Leptopterus*, and ten in *Prionops* and *Pityriasis*); the first six *Lanius* rows are closely arranged and the last two are more spaced out with a very small gap before the beginning of the pars pelvica.

**Pteryla Ventralis.** The maximum width is nine or

ten rows, the separated portion of the pars pectoralis is three to five rows long, and the pars abdominalis is 4 or 5 feathers wide through most of its length.

**Discussion.** Whether *Pityriasis* and *Prionops* are appropriately included within the shrikes cannot be answered with pterylography, but certainly the two genera show no pterylographic relationship with the Corvidae and allies (see below) and agree well with the Laniidae (albeit also agreeing with the patterns in many other passerine families).

The several reports of 'axillary tracts' and of the two horns of the pars abdominalis meeting above the cloaca are almost surely due to individual variation (and freshness of the specimens examined) rather than to any important variation.

### Sturnidae: Starlings

**Previous studies.** Nitzsch (1867) found the Pt. Spinalis of starlings to be variable. *Gracula religiosa*, *Lamprotornis* and perhaps *Sturnus* ('*Pastor*') *roseus* (his wording is unclear) had a solidly feathered, rhombic pars dorsalis, whereas that element contained a very small apterium in *Sturnus contra* ('*capensis*'), *Acridotheres* ('*Pastor*') *tristis* and *Buphagus africanus*. Lowe (1938b) described the pars dorsalis of *Sturnus vulgaris* as broad and rounded, lacking an apterium. Berger (1957) made a careful study of the pterylosis of *Fregilupus varius*. His descriptions and figures showed the expanded portion of the pars pectoralis to be unseparated from the pars abdominalis. The Pt. Spinalis also presented an unusual configuration: the pars dorsalis was narrow and lobed but continuous with the pars pelvica which, in turn, ended in a barely expanded and pointed shape. *Sturnus vulgaris* and *Aplonis tabuensis*, in contrast, had a rhombic pars dorsalis. Berger also described *Sturnus* to have an expanded pars pelvica posteriorly and a wide, separated pars pectoralis in the Pt. Ventralis.

**Material examined.** Alcohol-preserved specimens of *Aplonis opaca*, *Poeoptera lugubris* (nestling, not skinned), *Onychognathus morio*, *Lamprotornis chalybaeus*, *Neocichla gutturalis*, *Cosmopsarus unicolor* (2 specimens), *Saroglossa aurata*, *Acridotheres cristatellus*, *Mino dumontii*, *Scissirostrum dubium* and *Buphagus erythrorhynchus* (YPM, BM(NH), USNM, AMNH), and fresh specimens of *Lamprotornis purpureus*, *Cinnyricinclus sharpii*, *C. leucogaster*, *Spreo superbus*, *Creatophora cinerea* (2), *Sturnus malabaricus*, *S. vulgaris* (3), *S. contra*, *Leucopsar rothschildi* (2), *Ampeliceps coronatus*, *Sarcops calvus* and *Gracula religiosa* (2) (CM, NYZS). This sample of 29 specimens represents 23 species of 19 genera in the family; 7 genera were not located.

**Pteryla Spinalis.** Within this sample of starlings, several distinct patterns are apparent in the pars dorsalis. In *Mino*, *Ampeliceps*, *Sarcops* and *Gracula* the element is relatively short, narrow and sparsely feathered, ranging from 47 feathers in five rows in *Gracula* to 79

feathers in seven rows in *Sarcops*. The feathers of the anteriormost two or three rows are slightly more closely arranged than are those of the posterior rows, and the spacing between the posteriormost midline feathers and the first feathers of their respective row arms is wider. In *Ampeliceps* the central feathers of the last three rows (four through six) are absent, as is the central feather of the last (fifth) row in one specimen of *Gracula*; neither *Mino*, *Sarcops* nor the other specimen of *Gracula* has an apterium.

In the other genera studied, the pars dorsalis is longer, wider and more abundantly feathered, with seven (*Sturnus* only) to nine rows containing from 100 to 136 feathers. The anteriormost rows are closely and evenly spaced, and the posteriormost show a gap of variable width between the midline feathers and the remainder of their rows; the posterior rows are also fairly closely and evenly spaced relative to each other.

The midline gap is very slight (visible only under microscopic examination) and otherwise the element appears to be a solidly and evenly feathered rhombus in *Aplonis*, *Saroglossa*, *Scissirostrum* and *Buphagus*. The gap is somewhat wider in *Lamprotornis*, *Neocichla*, *Cosmopsarus* and *Acridotheres*. In *Cinnyricinclus*, *Spreo*, *Creatophora*, *Sturnus*, *Leucopsar* and probably *Poeoptera*, the gap is moderately wide and clearly visible macroscopically. (The uncertainty about *Poeoptera* results from my being able to examine only an unskinned nestling; it has either a moderately wide gap or an apterium.) In addition to the midline gapping, these last genera tend to have the posteriormost rows more widely spaced from each other; the general appearance suggests a lobed pars dorsalis (formed by the more densely arranged anteriormost rows), with sparser feathering connecting the 'lobes' to the pars pelvica. Figure 9 is a radiograph of an adult *Sturnus vulgaris* showing the midline gapping (not extreme in this individual) and row spacing. In other preparations, such as direct examination of the underside of the skin or the study of a clipped alcoholic specimen, this 'lobed' effect is more apparent.

The pars dorsalis of *Onychognathus*, with 99 feathers in eight rows, has a long apterium; only the first three rows are complete, the apterium is wide, and the anteriormost rows are only slightly more closely feathered than are the posteriormost. The general appearance, however, is not like that of the *Mino* group because of the denser feathering.

Within the entire sample of starlings, the pars pelvica is strong (heaviest in *Sturnus vulgaris*) and variable in the width of its posterior expansion, but generally unremarkable.

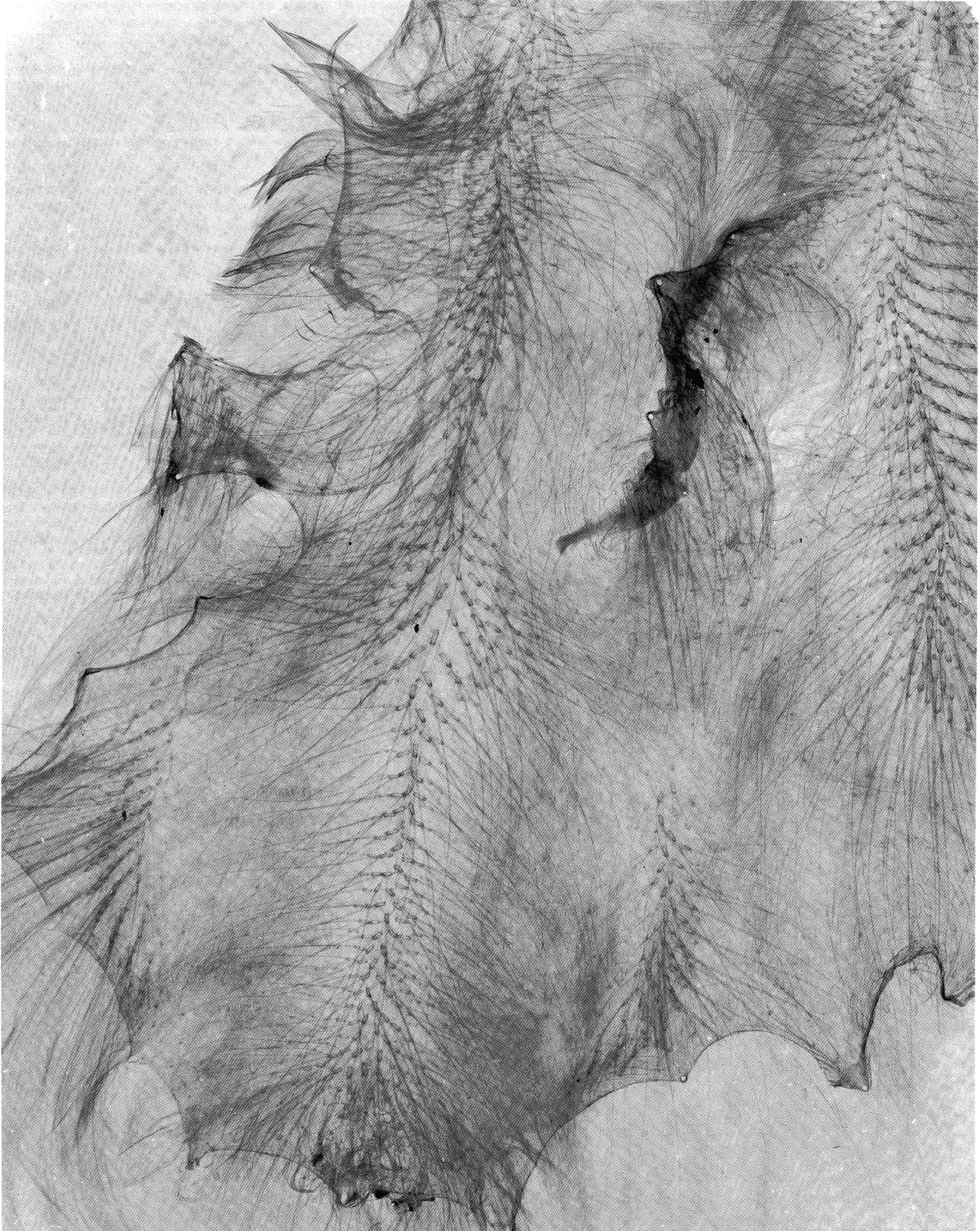
**Pteryla Ventralis.** The maximum width of the pars pectoralis ranges from 8 to 11 feathers, the separated portion is three to five rows long, and most of the pars abdominalis rows are 4 to 6 feathers long. There is comparatively good retention of the group of small feathers that extends laterally from the posterolateral margin of the pars pectoralis ('axillary tract') as well

as the minute feathers that extend across the abdomen from the posteriormost row of the pars abdominalis (see remarks on both these features in Clench, 1970). I believe these feathers tend to be retained in starlings because of the generally tough nature of sturnid skin. In most birds these small feathers tend to 'slip' easily and are often lost in preparation.

**Discussion.** The Sturnidae show more variation in the Pt. Spinalis than does almost any other passerine family (Heimerdinger, 1964; Clench, ms.). Yet, in spite of the several variants seen, a common pattern emerges: the feathers in the anteriormost rows tend to be more closely arranged than those of the posteriormost. The degree of spacing can lead to different appearances, from an almost solidly feathered rhombus to a seemingly lobed element with only a few feathers connecting it to the pars pelvica. There is also a tendency for midline weakness, ranging from slight gapping between the central posterior midline feathers and their row arms, through a wide gapping, to an actual apterium in a few forms. Morphologically speaking, the patterns in the Sturnidae can be arranged into a continuum, illustrating the stages that might be expected when a group was losing (or acquiring) an apterium. Therefore, despite the gradations in this family, the common, though variable, features of closely arranged vs. more loosely arranged rows, anterior to posterior, and the posterior midline weakness, seem to argue that the starlings are a natural group.

The explanations for the contradictory reports in the literature lie, I believe, in both the variability in the family, and in the condition of study material and the method of examination. It has long been customary to clip the feathers of an alcoholic specimen and study the pterylosis from the stubs of the calami remaining in the follicles. Depending on how strongly the feather musculature contracted when the specimen was fixed, small spaces between or within tracts could either be obscured or be plainly visible. Nitzsch (1867) reported a very small apterium in the pars dorsalis of *Sturnus contra* but probably not in *S. roseus*. I studied three species of *Sturnus*, including *S. contra*, and found all essentially similar; none had apteria but all had enough row-spreading and midline gapping in the posterior pars dorsalis that the spacing might be mistaken for an apterium in one specimen and covered by bunched follicles in the next. Similarly, Nitzsch's report of small apteria in *Acridotheres tris* and *Buphagus africanus* may have resulted from the condition of the specimen; my specimens of *A. cristatellus* and *B. erythrorhynchus* had no apteria. Berger's report (1957) of *Fregilupus* contained two strong anomalies—the lack of a separated pars pectoralis and a lobed pars dorsalis. The former may reflect strongly contracted muscles in that region, for I have found numerous such reports in passerines to be in error; the separation is almost always there if one stretches the skin slightly and looks for the characteristic row patterning in the flank. The lobed pars dorsalis may be an extreme development of the





**Fig. 9.** *Sturnus vulgaris*, Pt. Spinalis. Pars dorsalis shows starlings' characteristic wider spacing between posteriormost rows.

condition I described for the *Sturnus* group, or it may be the result of poor external condition of the sole available specimen. Berger stated: "Though the plumage was badly discolored and most of the remiges and rectrices were broken, the muscles were, surprisingly, in excellent condition" (1957: 231). Yet, because Berger described *Sturnus vulgaris* as essentially the same as I found it, the lobed pars dorsalis of *Fregilupus* may well be a further extreme of the 'lobing' tendency and not an artifact.

### Corvidae: Crows, Jays and Allies

**Previous studies.** The pterylosis of the crows and jays and their allies probably has been studied more than that of any other single passerine family. All authors found the ventral pattern to be relatively constant (e.g., Morlion & Vanparijs, 1979), but the Pt. Spinalis, pars dorsalis, showed variation. In most species this element contained a large, posterior midline apterium, but in a few others the pars dorsalis was a solidly feathered rhombus. Three species, *Pica pica* (Lowe, 1938b; Bock, 1962), *Corvus albus* (Dekeyser & Derivot, 1958) and perhaps *Nucifraga columbiana* (Bock, 1962) were described as having a 'forked' pars dorsalis, but this was almost certainly the result of a large apterium merging into a weak anterior end of the pars pelvica. Tables 2 and 3 summarize earlier findings and the results of the present study.

**Material examined.** Alcoholic specimens of *Calocitta formosa*, *Cissa chinensis*, *Cissilopha beecheii*, *Cissilopha sanblasiana*, *Crypsirina temia*, *Cyanocorax yncas*, *Cyanolyca mirabilis*, *Cyanolyca nana*, *Cyanolyca pumilo*, *Cyanopica cyana*, *Dendrocitta vagabunda*, *Gymnorhinus cyanocephala*, *Nucifraga columbiana*, *Perisoreus canadensis*, *Platylophus galericulatus*, *Psilorhinus morio*, *Ptilostomus afer*, *Temnurus temnurus* and *Zavattariornis stresemanni* (AMNH, BM(NH), CM, MLZ, SDMNH, USNM, YPM), and fresh specimens of *Aphelocoma coerulescens* (5 specimens), *A. ultramarina*, *Cissa chinensis*, *Corvus brachyrhynchos* (2), *Corvus corax*, *Corvus ossifragus*, *Cyanocitta cristata* (3), *Cyanocorax affinis*, *Cyanocorax caeruleus*, *Pica nuttalli* (2) and *Urocissa erythrorhyncha* (CM, FSM, NYZS, YPM, K.C. Parkes). I also examined alcohol-preserved specimens, but could not prepare flat skins from *Platysmurus leucopterus*, *Podoces hendersoni*, *Pseudopodoces humilis* and *Pyrrhocorax pyrrhocorax* (BM (NH)). This sample of 42 specimens represents 34 species of 25 genera in the family; the remaining genus, *Garrulus*, was well described by Morlion & Vanparijs (1979).

**Pteryla Spinalis.** The Corvidae may be divided pterylographically into three groups:

1. THE CROWS, OLD WORLD JAYS AND ALLIES — *Platysmurus*, *Garrulus* (data from Morlion & Vanparijs, 1979), *Urocissa*, *Cissa*, *Cyanopica*, *Dendrocitta*, *Crypsirina*, *Temnurus*, *Pica*, *Zavattariornis*, *Nucifraga*, *Pyrrhocorax* and *Corvus* (Fig. 10) — are characterized

Species	Apterium Present	Apterium Absent	Reference <sup>1</sup>
<i>Platylophus galericulatus</i> <sup>2</sup>		×	1, 13
<i>Platysmurus leucopterus</i>	×		1, 13
<i>Gymnorhinus cyanocephala</i>	×		7, 13
<i>Cyanocitta cristata</i>	×	×	2, 9, 13 (see text)
<i>Cyanocitta stelleri</i>		×	4 (sp.?), 7
<i>Aphelocoma coerulescens</i>	×	×	4, 7, 9, 13 (see text)
<i>Aphelocoma ultramarina</i>		×	4, 13
<i>Aphelocoma unicolor</i>		×	4
<i>Cyanolyca pumilo</i>	×		13
<i>Cyanolyca nana</i>	×		13
<i>Cyanolyca mirabilis</i>	×		13
<i>Cissilopha sanblasiana</i>	×		13
<i>Cissilopha beecheii</i>	×	×	7, 13 (see text)
<i>Cyanocorax caeruleus</i> <sup>3</sup>	×		1, 13
<i>Cyanocorax affinis</i>	×		13
<i>Cyanocorax chrysops</i>	×		7
<i>Cyanocorax yncas</i>	×	×	7, 13 (see text)
<i>Psilorhinus morio</i> <sup>4</sup>	×		1, 7, 13
<i>Calocitta formosa</i>	×		7, 13
<i>Garrulus glandarius</i>	×		3, 7 (sp.?), 9, 12
<i>Perisoreus canadensis</i>		×	7, 9 (sp.?), 11, 13
<i>Urocissa erythrorhyncha</i>	×		13
<i>Cissa chinensis</i>	×		7, 13
<i>Cissa thalassina</i>		×?	1 (see text)
<i>Cyanopica cyana</i>	×		13
<i>Dendrocitta vagabunda</i>	×		1, 13
<i>Crypsirina temia</i> <sup>5</sup>	×		1, 13
<i>Temnurus temnurus</i>	×		13
<i>Pica pica</i>	×		1, 3, 7, 9, 12
<i>Pica nuttalli</i>	×		13
<i>Zavattariornis stresemanni</i>	×		13
<i>Podoces hendersoni</i>		×	13
<i>Pseudopodoces humilis</i>		×	13
<i>Nucifraga columbiana</i>	×		7, 9, 13
<i>Nucifraga caryocatactes</i>	×		9
<i>Pyrrhocorax pyrrhocorax</i>	×		13
<i>Ptilostomus afer</i>		×	13
<i>Corvus monedula</i>	×		12
<i>Corvus frugilegus</i>	×		3, 9, 12
<i>Corvus brachyrhynchos</i>	×		7, 13
<i>Corvus ossifragus</i>	×		13
<i>Corvus corone</i>	×		3, 9, 12
<i>Corvus orru</i>	×		10
<i>Corvus coronoides</i>	×		5
<i>Corvus albus</i>	×		8
<i>Corvus corax</i>	×		6, 7, 9, 13

**Table 2.** Pteryla Spinalis, pars dorsalis, of the Corvidae.

<sup>1</sup>References: 1. Nitzsch, 1867; 2. Peck, 1900; 3. Lowe, 1938b; 4. Pitelka, 1945; 5. Boehm, 1945; 6. Friant, 1948; 7. Mewaldt, 1958; 8. Dekeyser & Derivot, 1958; 9. Bock, 1962; 10. Parsons, 1968; 11. Ouellet, 1971; 12. Morlion & Vanparijs, 1979; 13. present study. <sup>2-5</sup>*Lanius scapularis* Licht., '*Corvus azureus*', '*Corvus fuliginosus*' and '*Glaucopsis varians*,' respectively, of Nitzsch, 1867.

by having a strong pars interscapularis, a pars dorsalis with a long and wide apterium, and a moderately well

Genus	No. Rows	% True Apt.	% Apparent Apt.	No. Feathers	n <sup>1</sup>
<i>Platylophus</i>	6	0	0	50	1
<i>Platysmurus</i>	—	'long'	'long'	—	(1)
<i>Gymnorhinus</i>	10	50	50	c.139	1
<i>Cyanocitta</i>	10	0-30	20-30	157 [1] <sup>2</sup>	3
<i>Aphelocoma</i>	10-11	0-30	27-40	157-178	6
<i>Cyanolyca</i>	10	20	20	c.162 [1]	3
<i>Cissilopha</i>	11	18-27	18-27	170-177	2
<i>Cyanocorax</i>	9-11	27-36	44-45	149 [1]	3
<i>Psilorhinus</i>	10	30	50	159	1
<i>Calocitta</i>	10	20	40	152	1
<i>Perisoreus</i>	13 (+?)	0	23	—	1
<i>Urocissa</i>	11	36	36	163	1
<i>Cissa</i>	10	30	50	163 [1]	2
<i>Cyanopica</i>	9	33	33	—	1
<i>Dendrocitta</i>	9	22	44	143	1
<i>Crypsirina</i>	10	40	40	c.130	1
<i>Temnurus</i>	9	33	33	122	1
<i>Pica</i>	9	33	44	147-156	2
<i>Zavattariornis</i>	9	33	33	114	1
<i>Podoces</i>	c.10	0	0	—	(1)
<i>Pseudopodoces</i>	c.9-10	0	0	—	(1)
<i>Nucifraga</i>	12	33	42	162	1
<i>Pyrrhocorax</i>	—	'long'	'long'	—	(1)
<i>Ptilostomus</i>	8	0	0	90	1
<i>Corvus</i>	11-12	55-67	55-67	110-198	4

**Table 3.** Pterylosis of the Corvidae: Pt. Spinalis, pars dorsalis.

<sup>1</sup>The specimens noted with parentheses were examined from unskinned alcoholic specimens and could not be counted completely.

<sup>2</sup>The numbers in square brackets denote the number in the sample that could be counted completely.

developed pars pelvica that ends in a triangularly expanded base. The length of the pars dorsalis ranges from nine to twelve rows (Table 3), and the apterium involves from two to eight (22% to 67%) of the posteriormost rows. The apterium is longest in *Corvus* and best developed in the species with the largest body size, *C. corax*: eight of the twelve rows (67%) lack central feathers in an otherwise strong element of 198 feathers. *Corvus ossifragus*, with a much smaller body size, has seven of eleven rows (64%) incomplete, with 110 feathers in the element; and the intermediate-sized *C. brachyrhynchus* (2 specimens) has six of eleven rows (55%) incomplete, with total feather counts of 155 and 165. In addition to the extent of the true apterium (midline feathers lacking), several of the genera have longer apparent apteria, caused by the posteriormost midline feathers being smaller than those more anterior, and by having wider spaces between them and the first feathers of the row arms — a 'gapping' mentioned previously. Thus, of this group, although *Dendrocitta* has the smallest apterium by percentage (two of nine rows, 22%), the midline feathers of rows six and seven are well gapped and the apterium appears longer than it actually is.

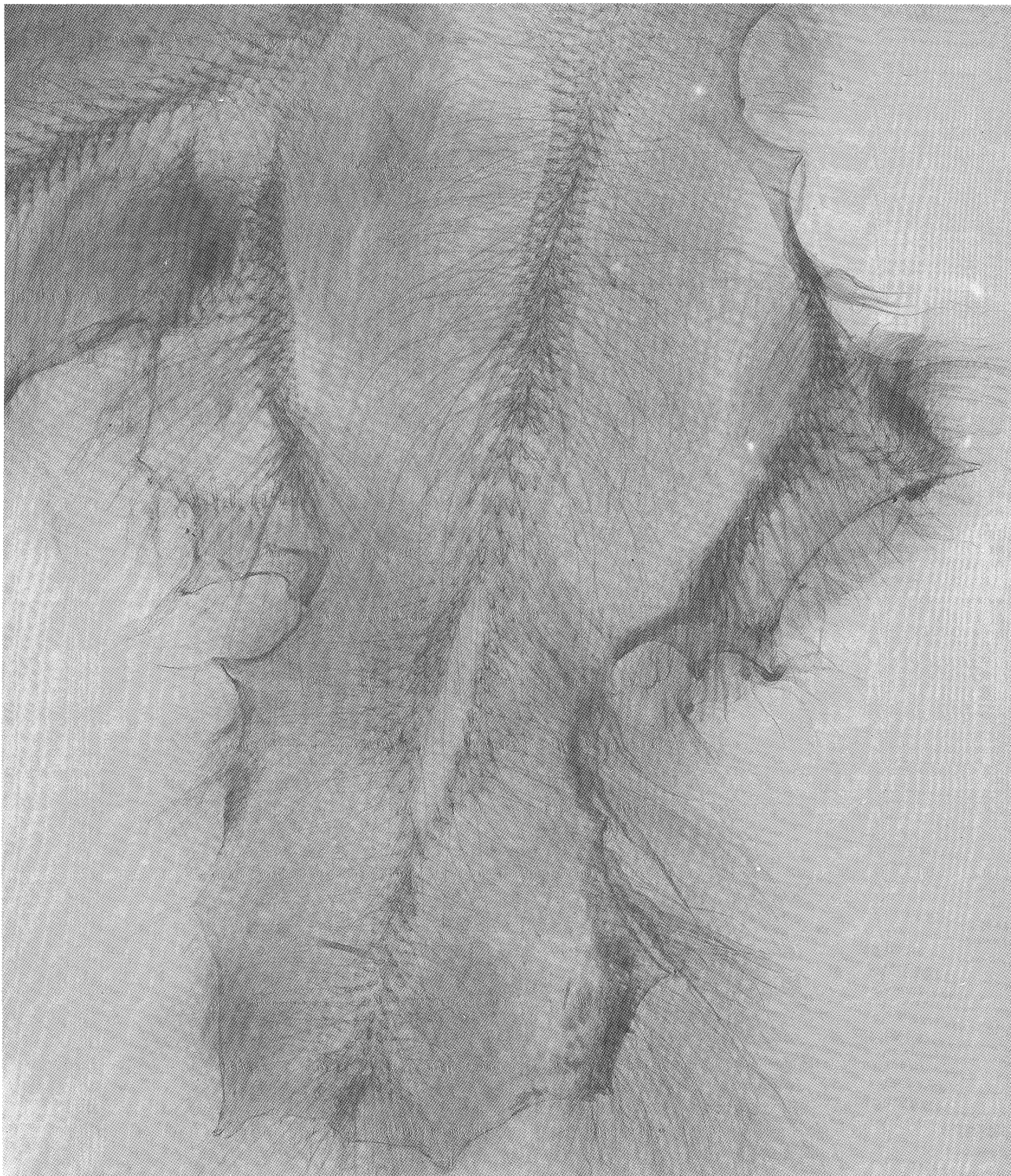
Nitzsch (1867) figured '*Kitta thalassina*' with a solidly rhombic pars dorsalis and with a line of feathers extending posteriad from either side of the pars. I have never seen a passerine with such a configuration and am sure that whatever Nitzsch's '*Kitta thalassina*' was, it was not *Cissa thalassina*. Both Mewaldt's (1958) and

my specimens (3) of *Cissa (chinensis)* had large and obvious apteria. '*Kitta*' Temminck has erroneously been used in the past for *Cissa* (Blake & Vaurie in Mayr & Greenway, 1962). Nitzsch did not include '*Kitta thalassina*' in his group of 'Corvinae', but instead placed it in his 'Paradisidae' [sic], a grouping of birds-of-paradise and starlings. '*Kitta*' is also a synonym for *Ptilonorhynchus*, but that bowerbird has a large apterium in the pars dorsalis—as Nitzsch correctly reported. It is unfortunate that the system of terminology common in Germany during Nitzsch's period of activity (the first third of the Nineteenth Century) has largely fallen into disuse; it is now difficult or impossible to trace to modern taxa all the names he used.

2. THE NEW WORLD JAYS — *Gymnorhinus*, *Cyanocitta*, *Aphelocoma*, *Cyanolyca*, *Cissilopha*, *Cyanocorax*, *Psilorhinus* and *Calocitta*—have a strong pars interscapularis, a pars dorsalis of nine to eleven rows with a variably long-to-absent apterium, and a weakly to moderately developed pars pelvica that ends in a triangular base. *Gymnorhinus* has the best developed apterium (50% of its ten rows) and, along with *Psilorhinus* and *Calocitta*, has never been found to lack an apterium. The other genera of New World jays (with the possible exception of *Cyanolyca*) seem to be variable in this regard. Of my series of five *Aphelocoma coerulescens* (four from California, one a cage bird of unknown origin), one of the California birds lacks an apterium. My single *A. ultramarina* also lacks an apterium, as does one of three *Cyanocitta cristata*. Judging from the current results and from those of earlier studies (see Table 2), I believe that these New World jays may be in the process of losing (or gaining) the midline apterium. However, in all my specimens that have all the midline feathers present, and thus lack a true apterium, the birds show a semblance of an apterium by having the last rows gapped away from the midline feathers. In addition, the specimens with true apteria often have a longer apparent apterium by similar gapping (see Fig. 11 and Table 3).

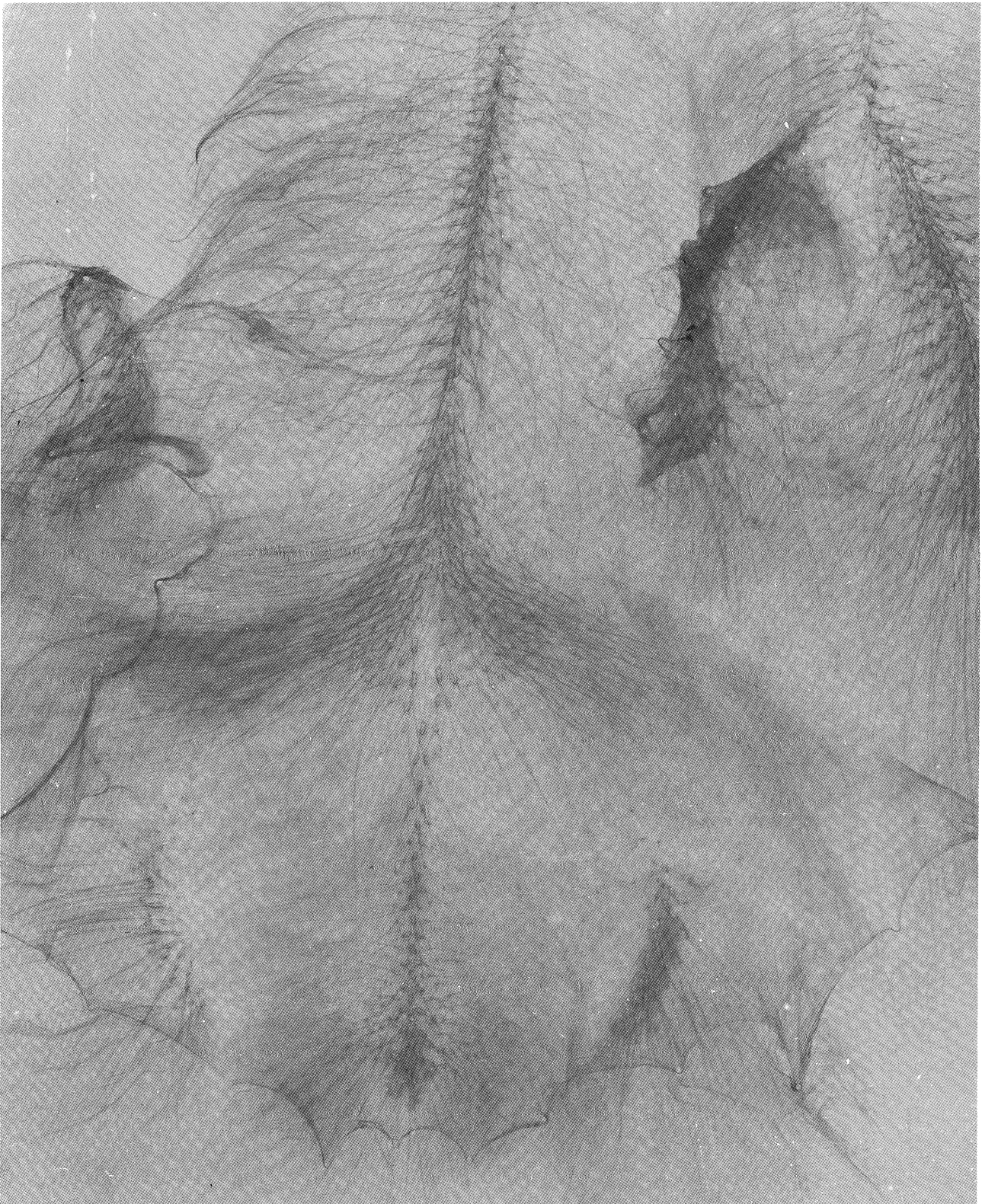
3. ATYPICAL JAYS — *Platylophus*, *Perisoreus*, *Podoces*, *Pseudopodoces* and *Ptilostomus*. This assemblage of Old World or Holarctic jays falls together here only because, like most oscines, these genera have no apterium in the pars dorsalis; no particular relationship is implied. *Platylophus* strongly differs from any other corvid by its very short (six rows) and sparsely feathered (50) pars dorsalis. *Ptilostomus* has a relatively short (eight rows), lightly feathered (90) pars dorsalis, whereas *Perisoreus* lies at the other end of the scale with the longest (thirteen or fourteen rows) pars dorsalis, and one that is very densely feathered (not countable in my specimen). The base of the element in *Perisoreus* clearly has all the midline feathers present, but the posteriormost two to four rows are gapped, which gives the appearance of an apterium. The specimens of *Podoces* and *Pseudopodoces* were very unsatisfactory material (whole, alcohol-preserved





**Fig. 10.** *Corvus brachyrhynchos*, Pt. Spinalis.





**Fig. 11.** *Cyanocitta cristata*, Pt. Spinalis. Specimen has lost some feathers from lower right area of pars dorsalis but empty follicles are visible.

specimens, not flat skins), and I can state only that neither has an apterium in the pars dorsalis which is about nine or ten rows long.

**Pteryla Ventralis.** With exception of *Platylophus*, the ventral tract in this sample is unremarkable (Fig. 12). The maximum width of the pars pectoralis ranges from 8 to 11 feathers (12 in *Pica*), the separated portion is from three to five or six rows long (eight in *Pica*), and the pars abdominalis rows are primarily 3 to 5 feathers long. *Platylophus* is more lightly feathered, with a maximum width of the pars pectoralis of 7 feathers, the separated portion four rows long, and most of the abdominal rows having 3 feathers.

**Discussion.** In general, the Corvidae are characterized by having a relatively well developed apterium in the pars dorsalis. The New World jays differ somewhat by having a less developed apterium and sometimes none at all, although gapping in the posteriormost part of the element suggests a tendency toward an apterium. *Perisoreus* probably fits perfectly well into the New World jay group because it has the gapping, although it is generally more heavily feathered. However, birds that live in colder climates often have more feathers than do their tropical relatives (Clench, 1970); that tendency could be acting in the gray jays.

Goodwin (1976), Amadon (pers. comm.) and others have suggested that *Platylophus* may not be appropriately placed in the Corvidae. The pterylographic evidence indicates that the Crested Jay is not a corvid, although its generalized oscine pattern (a solidly feathered, rhombic pars dorsalis) is of little help in the search for its true affinities. Borecky (1977) found *Platylophus* to be perfectly corvid in its limb musculature. In contrast, Borecky (1978) reported that the musculature and other traits of *Pseudopodoces* were very uncorvid and suggested that *Pseudopodoces*, but not *Podoces*, be removed from the family. Borecky and I used the same specimens of both genera. Again, the pterylosis patterns of *Pseudopodoces* and *Podoces* are of little assistance in answering the question because they are of the generalized oscine type. *Zavattariornis*, on the other hand, fits well pterylographically into the Corvidae, although its position in that family has been questioned by Goodwin (1976) and others.

*Ptilostomus* does not seem to be a corvid. I have not seen any recent suggestions to the contrary, aside from Goodwin's (1976) uncertain placement of the genus at the base of the corvid family tree, with *Zavattariornis* possibly branching off from *Ptilostomus* (the latter suggestion not borne out by the pterylosis). Unfortunately, the pars dorsalis of *Ptilostomus* is of the generalized passerine type, so it is of little assistance other than to support the argument against a relationship with the crows and jays. Judging from the behavior, zoogeography and other published information on the Piapiac, I would be inclined to consider the Sturnidae (near *Buphagus*?) as the most fruitful area to look for relationships, but *Ptilostomus* would also be a fairly aberrant starling; the general

strength of the pterylosis fits that of starlings, but the single specimen I was able to locate had no suggestion of the pars dorsalis basal gapping so characteristic of (but not universal in) the Sturnidae. The specimen was very old, alcohol-preserved and in moult at the base of the pars dorsalis, so the pattern was not clear. Better material might answer the question.

#### Furnarioidea: Woodhewers, Ovenbirds, Antbirds and Tapaculos

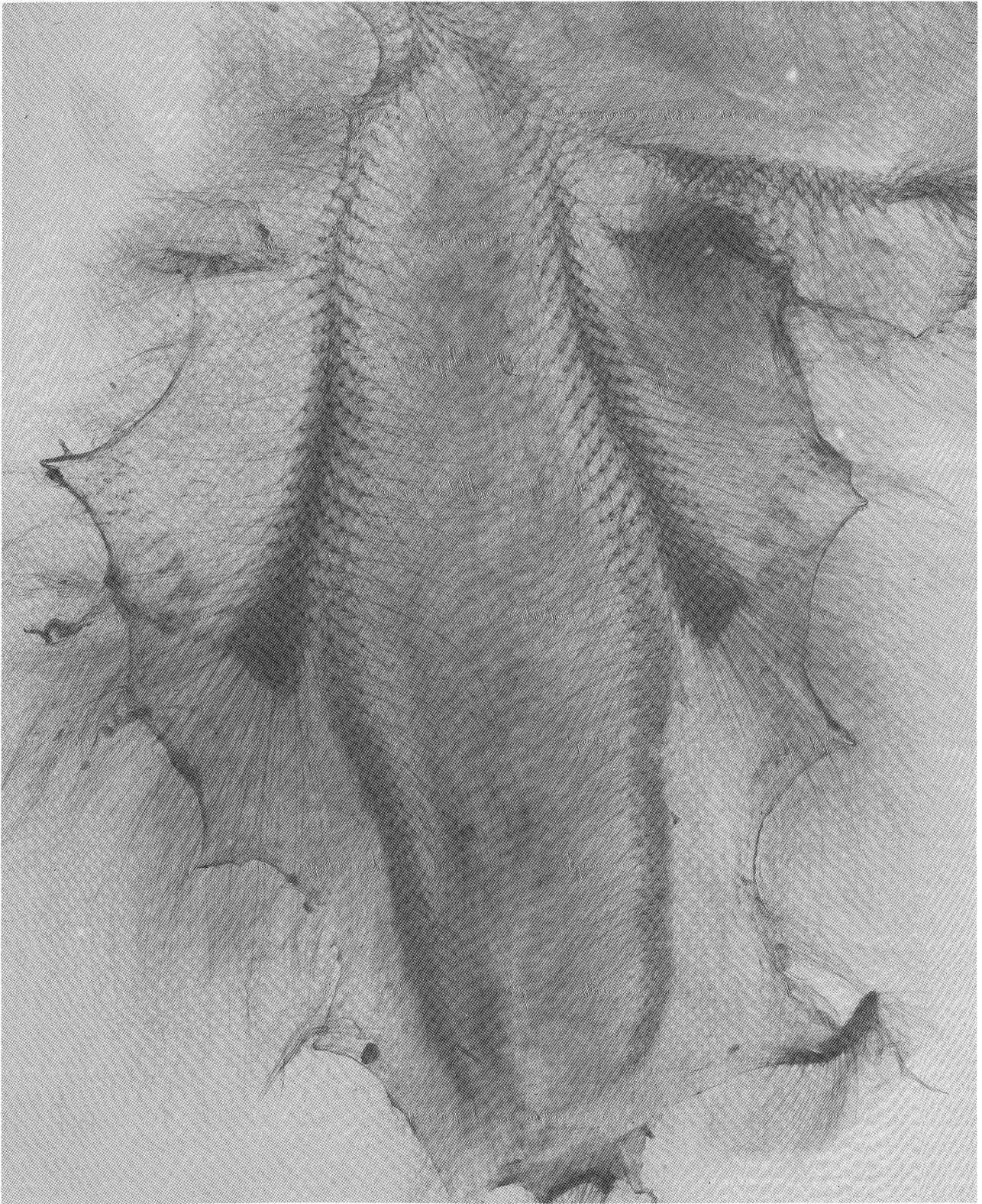
Feduccia & Olson (1982) have found a strong similarity between the Menurae and the Rhinocryptidae. The Rhinocryptidae, as well as other families in the Furnarioidea, have a complex array of pterylosis patterns (Clench, ms.), and a discussion of them is beyond the scope of this paper. However, in my current series of 133 flat skins representing 92 species of 73 genera in this superfamily (including 8 of 11 genera of Rhinocryptidae and 37 of 53 Formicariidae), no specimen shows the unusual configuration of the Pt. Ventralis seen in *Menura* and some Paradisaeidae. I have not counted the feathers in the entire series, but preliminary study also indicates that no furnarioidean has the density of ventral feathering as that in *Atrichornis* and *Menura*. A few have superficially similar Ptt. Spinales, notably *Chamaeza* (but not other formicariids) and some, but not all, rhinocryptids. Until I have the opportunity to report on my series of New World subspecies in detail, I can only state that pterylography only mildly suggests a relationship between the Menurae and the Furnarioidea.

#### Muscicapidae, Vireonidae and other Oscines

The problematical African genus *Picathartes* has been known pterylographically for many years (Lowe, 1938b) but, unfortunately, that information has been of little help in taxonomically placing the 'bald crow'. I have confirmed Lowe's description of *Picathartes oreas* with a fresh, but moulting, specimen of *P. gymnocephalus* (NYZS). It is of the typical oscine type, although with an exceptionally wide pars interscapularis; a broad, rounded and solidly feathered pars dorsalis; and a narrow pars pelvica. Ventrally, it has a wide pars pectoralis, well separated posteriorly from the pars abdominalis. In general strength, *Picathartes* surpasses the pterylosis of the few Timaliinae that have been studied (see above under Grallinidae) or of the small sample of Muscicapinae I have examined (briefly noted in Olson *et al.*, 1983). This is another instance of a bird, with the generalized oscine pattern, that cannot be placed by pterylosis except for being excluded from certain families (e.g., Corvidae, Sturnidae) that do have distinctive pterylosis patterns.

Sibley & Ahlquist, using a DNA-DNA hybridization technique, have begun to publish a series of papers that include many surprising suggestions on relationships within the Passeriformes (Sibley & Ahlquist, 1982; in





**Fig. 12.** *Corvus brachyrhynchos*, Pt. Ventralis. Typical passerine pattern of this tract, especially in type of separation between pars pectoralis and pars abdominalis.

press). It would be both premature and outside the scope of this paper to comment on many of their suggestions as to the relationships involving the Menuridae and what has been called the corvid assemblage. Because I have seen only the bare classification, without the text, of the paper in press, I shall note only a few points.

Their Superfamily Menuroidea is made up of the Family Menuridae (*Menura*, *Atrichornis*), the Family Ptilonorhynchidae, and perhaps the Family Climacteridae. *Climacteris affinis* has a pars dorsalis that is long, lanceolate and heavily feathered (172 in ten rows in my single specimen, from a BM(NH) alcoholic). This is unlike *Certhia familiaris* which has a more lightly feathered, and shorter and rounder pars dorsalis (105 feathers in nine rows in one fresh specimen from Connecticut), and is very unlike *Rhabdornis inornatus* and *R. mysticallis* (three specimens of the genus, one from CM, two from USNM) which have a large apterium in the pars dorsalis. Sibley & Ahlquist may be correct in their suggestion about *Climacteris*, for the general type and shape of the pars dorsalis is not unlike that of *Menura*, considering the great difference in body size between them, but the Pt. Ventralis shows almost nothing distinctive (maximum width of 8 feathers, a rather long, separated pars pectoralis of seven rows, and abdominal rows with 5 feathers). The general pterylographic similarity of *Climacteris* to other oscines such as *Sitta* is at least as reasonable.

Sibley & Ahlquist (in press) erect a large Superfamily Corvoidea which is separated from the Menuroidea by the Superfamily Meliphagoidea; their Corvoidea includes a wide array of crows and their traditional allies, most of which have been discussed here. The birds-of-paradise are listed as a tribe immediately after the tribe of crows and jays, and immediately before the 'Cracticini, *Artamus*, *Strepera*, etc.', and then the orioles and cuckoo-shrikes. Sibley & Ahlquist also include in their Corvoidea a group of Old World, especially Australasian, groups that have hitherto been included in other (often 'wastebasket') families such as the Muscicapidae (s.l.) and Timaliidae. The few specimens I have representing these groups (e.g., *Pachycephala flavifrons*) have the common oscine pterylosis pattern that is no help in elucidating relationships.

Sibley & Ahlquist (in press) also include several groups as *incertae sedis* within their Corvoidea — the shrikes, the vireos and allies, and *Irena*, *Aegithina* and *Melanocharis*. The shrikes have already been discussed here. *Vireo* pterylosis is not unlike that of some of the traditional corvid allies and very unlike that of the New World, nine-primaried oscines. The latter have the typical and undistinguished oscine pattern, with minor exceptions. The vireos, in contrast, have a pars dorsalis that is nine or ten rows long, with the posteriormost three rows gapped away from the midline feathers which tend to be small or sometimes absent, forming a basal apterium. Whether or not a true apterium exists, the general vireo configuration is that of a lobed pars

dorsalis, barely connected to an anteriorly weak pars pelvica. I have examined 10 specimens of *Vireo* (seven species, and including both subgenera *Vireo* and *Vireosylva*), and one specimen each of *Hylophilus flavipes*, *Vireolanius pulchellus* and *Cyclarhis gujanensis*.

Urik (1983) has studied *Irena* and *Aegithina*, as have I, and the pterylosis is not distinctive enough (a solidly feathered, lanceolate-to-rhombic pars dorsalis) to show relationships. I have also examined one specimen of *Melanocharis nigra* which has a pars dorsalis that is small (nine rows, 129 feathers), rounded and slightly lobed, without an apterium. The pars pelvica is weak anteriorly, producing the superficial appearance of a discontinuity between the pars dorsalis and pars pelvica.

Two final comments about the Sibley & Ahlquist classification: the starlings are far removed from the corvid groups — indeed, are included in the Parvorder Muscicapae — whereas all the others already noted (including the Menuridae) are in the Parvorder Corvi; and Sibley recants somewhat from his previous opinion, based on egg-white protein and other evidence, that *Menura* (and he presumed *Atrichornis*, for which he then had no material) is most closely related to the 'bowerbird/bird-of-paradise assemblage' (Sibley, 1974). He stated in the earlier paper (1974: 78) that "*Menura* is more closely related to the bowerbirds than to the birds-of-paradise, although all three groups are members of a single natural cluster". In the new DNA study, the bowerbirds (with the Menuridae) are far removed from the birds-of-paradise.

## DISCUSSION AND CONCLUSIONS

In this study of 154 specimens representing 126 species of 98 genera, I have attempted to compare the body pterylosis of *Atrichornis* and *Menura* with that of all the passerine groups to which they might conceivably be related. The availability and quality of specimens put some constraints on these comparisons because I could not locate satisfactory (or any) material of some of the genera I would like to have looked at, but I believe there are no serious lacunae in the present series. The most important pterylographic findings are summarized in Table 4.

Within this series, *Atrichornis* and *Menura* are singular in many respects. They have extremely dense feathering, both dorsally and ventrally. Their pars dorsales of 228 feathers in *Atrichornis* and 656 in *Menura* are comparable in view of the great disparity in their body sizes — the *Atrichornis* weighed 34 g and the *Menura* 921 g (both were females). They show the same basic passerine patterning in the Pt. Spinalis, similarly modified to accommodate their extraordinary number of feathers. The small gap they both have between the pars dorsalis and pars pelvica seems to be of some systematic importance. *Atrichornis* and *Menura* are less similar ventrally, with the scrub-bird having a very wide pars pectoralis (17 feathers at the maximum)

Taxon (with No. Genera Studied)	Pt. Spinalis, Pars Dorsalis			Pt. Ventralis		
	Length (rows)	Tot. No. Feathers	Aptorium	Max. Width	Free Pect. Rows	Width Abdom. Rows
<i>Atrichornis</i>	12	228	D/P gap <sup>1</sup>	17	2	5
<i>Menura</i>	18	656	D/P gap	c.13	10	4
Paradisaeidae						
Cnemophilinae (3/3)	c.13	225-254	no	9	3-4	4
Paradisaeinae (14/17)	7-10	83-180	gap, D/P gap, or weakness	7-28 <sup>2</sup>	3-7	3-5
<i>Astrapia</i>	11	200-201	gap or 1-row apt.	13-14	5-6	5
Ptilonorhynchidae (6/8)	11-15	180-281	5-10 rows	10-11	2-4	4-6
<i>Turnagra</i>	c.15	300-327	none apparent	11	4	4-5
Grallinidae (3/3)						
<i>Grallina</i>	9	-	3 rows	11	8	5
<i>Struthidea, Corcorax</i>	9	119	slight gap	9	5	4-5
Artamidae (1/1)	c.11	-	no	10-11	4	5
Callaeidae (2/3)	14	298	gap	10	0	4
Cracticidae (2/3)	10-11	198-201	gap, 1-row apt., or D/P gap	10-11	5	5
Oriolidae (1/2)	12	234	no	9	5	6
Dicuridae (1/2)	c.9	-	2 rows	8	3	-
Laniidae (4/21)	8-10	126-129	slight gap	9-10	3-6	4-5
Sturnidae (19/26)	5-9	47-136	gap or 1-3 rows; characteristic pattern	8-11	3-5	4-6
Corvidae (26/26)	9-13	110-198	2-8 rows, a few with gaps, or no apt.	8-21	3-8	3-5
<i>Ptilostomus</i>	8	90	no	9	4	4
<i>Platylophus</i>	6	50	no	7	4	3

Table 4. Summary of pterylographic differences.

<sup>1</sup>D/P gap = gap between pars dorsalis and pars pelvica; other gap notations refer to the posterior rows and midline area of the pars dorsalis.

<sup>2</sup>7-10 rows in spp. without ventral plumes, 11-28 in spp. with ventral plumes.

and a short (two-rowed) separation of the pars abdominalis from the pars pectoralis; the separation is otherwise typically passerine. *Menura* differs strikingly in this separation, having a pattern that is unique within the Passeriformes, insofar as is known. The lyrebird is also generally heavily feathered below, with a maximum width of the pars pectoralis of approximately thirteen rows.

As I have stated earlier (Clench, 1970), the taxonomic significance of the number of feathers on a bird's body (but not the pattern of feather insertion) must be assessed in light of the overall body size. This is easy to do in a subjective manner but difficult to accomplish with precision because of the problems involved in measuring body size accurately. The three customary body size measurements (overall length, wing length, or weight) all present problems when considering a group of birds with the wide diversity present here. Weight is probably the most accurate measure, even given its natural variation — the differences in a single individual's weight throughout a day, week, season or year (Clench, unpublished data). The fact remains,

however, that not until recent years has a specimen's weight become a standard label datum, and even single weight records do not exist in the published literature for the majority of the species treated here. Wing length is a more available datum, but it would be highly misleading to compare the wing length/pterylographic counts of such birds as *Atrichornis* and *Menura*, which are notoriously weak fliers and short-winged, with most of the birds in the 'corvid assemblage', which have normal powers of flight and proportionately longer wings. One is left, then, with overall body measurement to try to compare with pterylosis density. Again, difficulties arise because *Menura* and some of the birds-of-paradise have extraordinarily long plumes or tails. I have tried, however, to use conservative measurements to achieve a rough numerical index of feather density (the number of feathers in the pars dorsalis/overall body length in mm).

The species or generic groups that have the heaviest feathering are *Climacteris* (1.23), *Turnagra* (1.18), the Cnemophilinae (1.12), *Atrichornis* (0.99), *Oriolus* (0.88), *Certhia* (0.81), *Menura* and the

Ptilonorhynchidae (both 0.77), and the Callaeidae (0.70). The index figure for *Menura* is probably artificially low, weighted by the extremely long tail, even of females. Those with an intermediate degree of feathering are *Lanius* (0.53), the Cracticidae (0.51) and *Astrapia* (0.48). Birds with light feathering are *Struthidea* (0.36), the Corvidae (0.35), the Sturnidae (0.30) and the Paradisaeinae (0.20). I urge that not too much importance be placed on these figures, based as they are on broad averages of body length and limited numbers of feather counts, but I believe they offer at least a rough index to the degree of body feathering.

To further assess the general accuracy of this method, I computed the indices for several New World corvids for which data were readily available. Members of the first group (crows, Old World jays and allies, that were grouped on the basis of pterylographic pattern) gave similar index numbers: *Pica* (0.34), *Corvus ossifragus* (0.28), *Corvus brachyrhynchos* (0.36) and *Corvus corax* (0.32). The three species of *Corvus* were originally selected for the series because they represented the wide range of variation in body size seen in this genus, yet their index values were within 0.08 of each other. A similar calculation of the *Corvus* series, based on body weight, also resulted in close values — within 0.10. The single exception in the series of New World members of the first group was *Nucifraga*; nutcrackers had heavier feathering (0.52). All of the genera of the second group tested (New World jays) gave similar values: *Cyanocitta* (0.56), *Aphelocoma* (0.58), *Gymnorhinus* (0.51) and *Cyanocorax* (0.55).

Many genera in the full comparative series showed dense feathering like that of *Atrichornis* and *Menura* — the cnemophiline birds-of-paradise, the bowerbirds, *Turnagra*, *Climacteris* and the Callaeidae (Table 4). These groups, and the related Paradisaeinae, also show pattern similarities in aspects of their pterylosis that may suggest a relationship, although not a very close one. The Cnemophilinae are generally similar in dorsal feathering, both in density and pattern. Certain of the Paradisaeinae have a pars pectoralis/pars abdominalis separation that is suggestive of, but not precisely the same as, that in *Menura*, and the entire subfamily has a weakness in the base of the pars dorsalis, including a small gap in some genera. The Callaeidae also have a heavily feathered pars dorsalis with a basal gap, but they lack any separation at all between the pars pectoralis and pars abdominalis (unique within oscines, in my experience, but found in a few suboscines, notably in all the Rhinocryptidae I have studied except *Melanopareia*). *Turnagra* most closely resembles the cnemophiline birds-of-paradise, as I have stated earlier (Olson *et al.*, 1983).

The primary conclusion from this study is that *Menura* and *Atrichornis* are each other's closest relatives, but the degree of similarity is such that they should remain separated taxonomically, at least in different families. In turn, their closest relationships lie with the Paradisaeidae-Ptilonorhynchidae-Callaeidae

complex. Again, the degree of similarity is not close, but is closer than it is to any other group of passerines.

Other pterylographic findings of this study are: 1) if the 'corvid assemblage' is a strong natural entity, it is not apparent from pterylography. The true Corvidae generally have a well developed basal apterium in the pars dorsalis that I have not found elsewhere in oscines except in the Ptilonorhynchidae and *Grallina*, although a less well developed apterium, gapping, or basal weakness occurs in the Paradisaeinae, *Struthidea* and *Corcorax*, the Cracticidae, Sturnidae, Vireonidae, Laniidae and Dicruridae. A small apterium or gapping is also found in a few other, clearly unrelated oscines (e.g., Dicaeidae, *Arachnothera* but not *Nectarinia*, *Ploceus* but not other weavers, and some Sylviinae) as well as in certain suboscines. Other types of apteria characterize the Alaudidae, Hirundinidae and many New World suboscines (Heimerdinger, 1964). 2) *Astrapia* has a somewhat unusual pterylosis; it lies between the normal pattern for paradisaeines and cnemophiline birds-of-paradise, but also may show a small apterium, possibly reminiscent of bowerbirds. In his diagram of paradisaeine relationships, Schodde (1976) shows this genus (along with *Lophorina*) as one of two core genera for the subfamily. Pterylography suggests that *Astrapia* may be a bit deeper into the core of the entire bird-of-paradise/bowerbird complex. 3) *Platylophus* is not a corvid and *Ptilostomus* is probably not, either. *Ptilostomus* may be an aberrant starling. 4) *Grallina* shows no pterylographic relationship to *Struthidea* and *Corcorax*; the old family 'Grallinidae', constituting these three genera, should be abolished. Although the pterylosis does not strongly suggest affinities that would assist in new placements, *Grallina* shows no similarities to motacillids, but *Struthidea* and *Corcorax* may be babblers.

ACKNOWLEDGEMENTS. This long-term study reflects the help of many people over many years of accumulating series of specimens. I am indebted to the curators of the following institutions for lending me material, often of rare and difficult, or impossible-to-replace genera; the American Museum of Natural History (AMNH), the British Museum (Natural History) (BM(NH)), the Bernice P. Bishop Museum (BPBM), Carnegie Museum of Natural History (CM), the Field Museum of Natural History (FMNH), the Florida State Museum (FSM), the Moore Laboratory of Zoology at Occidental College (MLZ), the National Museum of Natural History (USNM), San Diego Natural History Museum (SDMNH) and Yale Peabody Museum of Natural History (YPM). I also thank the officials of the Pittsburgh Conservatory-Aviary, the Highland Park Zoo in Pittsburgh, and the Bronx Zoological Park (New York Zoological Society, NYZS) for permission to skin freshly dead specimens from their collections. The key specimens for this study were acquired through the kind efforts of G. T. Smith and H. J. deS. Disney and their respective institutions, the C.S.I.R.O. and the Australian Museum. Additional important assistance of various kinds was received from curators at the Otago Museum, the Museum of Victoria and the Western Australian Museum, and from D. Amadon, J. J. Baumel, P. J. K. Burton, J. E. duPont, J. D.



MacDonald, A. R. McEvey, K. C. Parkes, A. M. Rea, R. W. Schreiber, G. E. Woolfenden, and R. J. Raikow and his former students S. R. Borecky and J. A. Urik. Nancy Perkins prepared the drawings, Alice Cullu gave advice on the manuscript and Anne Crawford typed the final draft. I thank them all.

### References

- Amadon, D., 1944. The genera of Corvidae and their relationships. *American Museum Novitates* 1251: 1-21.
- 1950. Australian mud nest builders. *The Emu* 50: 123-127.
- Baumel, J. J., A. S. King, A. M. Lucas, Y. E. Breazile & H. E. Evans, eds, 1979. *Nomina anatomica avium*. London, Academic Press, pp. xxv + 637.
- Berger, A. J., 1956. On the anatomy of the Red Bird of Paradise, with comparative remarks on the Corvidae. *The Auk* 73: 427-446.
- 1957. On the anatomy and relationships of *Fregilupus varius*, an extinct starling from the Mascarene Islands. *Bulletin of the American Museum of Natural History* 113: 225-272.
- Bock, W. J., 1962. Feather tracts in the Corvidae — a correction. *The Ibis* 104: 257-259.
- Boehm, E. F., 1945. Notes on the pterylography of the Australian Raven. *The Emu* 44: 230-231.
- Borecky, S. R., 1977. The appendicular myology and phylogenetic relationships of the avian 'corvid assemblage'. Unpublished Ph.D. thesis, University of Pittsburgh, Pittsburgh, Pennsylvania.
- 1978. Evidence for the removal of *Pseudopodoces humilis* from the Corvidae. *Bulletin of the British Ornithologists' Club* 98: 36-37.
- Chapman, G., 1975. Recent observations on the family Grallinidae and comments on its taxonomy. *The Emu* 74: 307.
- Clark, H. L., 1914. Anatomical notes on *Trochalopteron* and *Sicalis*. *The Auk* 31: 461-463.
- 1945. The pteryloses of some Australian birds. *The Auk* 62: 70-74.
- Clench, M. H., 1970. Variability in body pterylosis, with special reference to the genus *Passer*. *The Auk* 87: 650-691.
- 1975. Pterylography of the Menurae: taxonomic considerations (an abstract). *The Emu* 74: 278.
- Clench, M. H. & G. T. Smith, 1985. Morphology of the Noisy Scrub-bird, *Atrichornis clamosus* (Passeriformes: Atrichornithidae): introduction, with remarks on plumage and systematic position. *Records of the Australian Museum* 37(3): 111-114.
- Commonwealth Scientific and Industrial Research Organization, 1969. An index of Australian bird names. CSIRO Division of Wildlife Research Technical Paper 20: 1-93.
- Degen, E., 1903. Ecdysis, as morphological evidence of the original tetradactyle feathering of the bird's forelimb, based especially on the perennial moult in *Gymnorhina tibicen*. *Transactions of the Zoological Society of London* 16: 347-418.
- Dekeyser, P.L. & J. Derivot, 1958. Etude d'un type d'oiseau Ouest-Africain: *Corvus albus*. *Institut Francais D'Afrique Noire, Initiations Africains* 16: 1-58.
- De Vree, F., 1969. The pterylosis of the African Bush Shrike *Tchagra m. minuta* (Hartlaub). *Le Gerfaut* 59: 157-191.
- Dorst, J., 1960. A propos des affinites systematiques de deux oiseaux Malgaches: *Tylas eduardi* et *Hypositta corallirostris*. *L'Oiseau et Revue Francaise d'Ornithologie* 30: 259-269.
- Feduccia, A. & S. L. Olson, 1982. Morphological similarities between the Menurae and the Rhinocryptidae, relict passerine birds of the Southern Hemisphere. *Smithsonian Contributions to Zoology* 366, pp iv + 22.
- Friant, M., 1948. Le développement de la ptérylose au cours de l'ontogénie, chez les Passeriformes. *Bulletin de la Societe Zoologique de France* 72: 114-117.
- Garrod, A. H., 1872. Notes on the anatomy of the Huia bird (*Heteralocha gouldi*). *Proceedings of the Zoological Society of London* 1872: 643-647.
- Giebel, C. G. A., 1877. Pterylose der paradiesvögel. *Zeitschrift fuer die Gesamte Naturwissenschaft* 49: 143-144.
- Goodwin, D., 1976. *Crows of the world*. British Museum (Natural History), London, pp. vi + 354.
- Heimerdinger, M. A., 1964. A study of morphological variation in the dorsal and ventral pterylae of Passeriformes. Unpublished Ph.D. thesis, Yale University, New Haven, Connecticut.
- Homberger, D. G., 1980. [Review of] J.J. Baumel *et al.*, *Nomina anatomica avium*. *The Auk* 97: 912-914.
- Keast, A., 1964. Magpie-lark. In 'A new dictionary of birds' (ed. A. Landsborough-Thomson): 442-443. McGraw-Hill, New York.
- Leach, J. A., 1914. The myology of the bell-magpie (*Strepera*) and its position in classification. *The Emu* 14: 2-38.
- Lowe, P. R., 1938a. Some anatomical notes on the genus *Pseudochelidon* Hartlaub with reference to its taxonomic position. *The Ibis* 80: 429-437.
- 1938b. Some anatomical and other notes on the systematic position of the genus *Picathartes*, together with some remarks on the families Sturnidae and Eulibatidae. *The Ibis* 80: 254-269.
- Lowery, G. H., Jr. & J. P. O'Neill, 1966. A new genus and species of cotinga from eastern Peru. *The Auk* 83: 1-9.
- Lucas, A. M. & P. R. Stettenheim, 1972. *Avian anatomy. Integument*. U.S. Department of Agriculture, *Agricultural Handbook* 362, pp. xii + 750.
- Macdonald, J. D., 1973. *Birds of Australia*. Witherby, London, pp. 552.
- Mathews, G. M., 1930. *Systema avium Australasianarum*. Part II. London, British Ornithologists' Union, pp. iv + 427-1048.
- Mayr, E. & D. Amadon, 1951. A classification of recent birds. *American Museum Novitates* 1496: 1-42.
- Mayr, E. & J. C. Greenway, Jr., 1960. Check-list of birds of the world, a continuation of the work of James L. Peters, vol. 9. *Museum of Comparative Zoology, Cambridge*, pp. viii + 506.
- 1962. Check-list of birds of the world . . . , vol. 15. *Museum of Comparative Zoology, Cambridge*, pp. x + 315.
- McDowell, S., 1947. Pterylography of the drongo (*Dicrurus modestus coracinus*). *The Auk* 64: 303.
- McEvey, A., 1976. Osteological notes on Grallinidae, Cracticidae and Artamidae. *Proceedings of the 16th International Ornithological Congress: 150-160*. Australian Academy of Sciences, Canberra.
- Mewaldt, L. R., 1958. Pterylography and natural and experimentally induced molt in Clark's Nutcracker. *The Condor* 60: 165-187.
- Miller, A. H., 1931. Systematic revision and natural history

- of the American shrikes (*Lanius*). University of California Publications in Zoology 38: 11-242.
- Morlion, M. L. & P. Vanparijs, 1979. The pterylosis of five European corvids. *Le Gerfaut* 69: 357-378.
- Morony, J. J., Jr., W. J. Bock & J. Farrand, Jr., 1975. Reference list of the birds of the world. American Museum of Natural History, New York, pp. x + 207.
- Naik, R. M. & M. I. Andrews, 1966. Pterylosis, age determination and moult in the Jungle Babbler. *Pavo* 4: 22-47.
- Nitzsch, C. L., 1840. *System der pterylographie*. (ed. E. Burmeister). Halle, Germany, pp. xii + 228.
- 1867. *Pterylography*. (English transl. by W. S. Dallas; ed. P. L. Sclater). Ray Society, London, pp. xii + 181.
- Olson, S. L., K. C. Parkes, M. H. Clench & S. R. Borecky, 1983. The affinities of the New Zealand passerine genus *Turnagra*. *Notornis* 30: 319-336.
- Ouellet, H., 1971. Contribution à l'étude de la pterylose chez *Perisoreus canadensis* (Linnaeus), (Aves: Corvidae). *Canadian Journal of Zoology* 49: 147-158.
- Parsons, F. E., 1968. *Pterylography*. Libraries Board of South Australia, Adelaide. *Occasional Papers in Zoology* 1:1-60.
- Peck, M. E., 1900. The plumage of the Blue Jay (*Cyanocitta cristata*). *Western Ornithologist* 5: 1-6, 23-33, 48-52.
- Pitelka, F. A., 1945. *Pterylography, molt, and age determination of American jays of the genus Aphelocoma*. *The Condor* 47: 229-260.
- Pycraft, W. P., 1905. On the pterylography and dermal myology of the Lesser Bird-of-Paradise, with especial reference to the 'display.' *The Ibis* 47: 440-453.
- Robinson, A., 1947. Magpie-larks — A study in behaviour. *The Emu* 46: 256-281 *et seq.*
- Rowley, I., 1974. *Bird life*. Taplinger, New York, pp. 284.
- Schodde, R., 1975. Interim list of Australian songbirds. Royal Australasian Ornithologists' Union, pp. vi + 46.
- 1976. Evolution in the birds-of-paradise and bowerbirds, a resynthesis. *Proceedings of the 16th International Ornithological Congress*: 137-149. Australian Academy of Sciences, Canberra.
- Sharpe, R. B., 1877. *Catalogue of the birds in the British Museum*, vol 3: xiii + 343. British Museum, London.
- Shufeldt, R. W., 1889. On the position of *Chamaea* in the system. *Journal of Morphology* 3: 475-502.
- 1923. Comparative osteology of the Australian mud-builders. *The Emu* 23: 4-19.
- Sibley, C. G., 1974. The relationships of the lyrebirds. *The Emu* 74: 65-79.
- 1976. Protein evidence of the relationships of some Australian passerine birds. *Proceedings of the 16th International Ornithological Congress*: 557-570. Australian Academy of Sciences, Canberra.
- Sibley, C. G. & J. E. Ahlquist, 1982. The relationships of the vireos (Vireonidae) as indicated by DNA-DNA hybridization. *The Wilson Bulletin* 94: 114-128.
- in press*. The phylogeny and classification of the passerine birds, based on comparisons of the genetic material, DNA. *Proceedings of the 18th International Ornithological Congress*, Moscow.
- Slater, P., 1974. *A field guide to Australian birds. Passerines*. Livingston, Wynnewood, Pa., pp. xv + 309.
- Stonor, C. R., 1937. On the systematic position of the Ptilonorhynchidae. *Proceedings of the Zoological Society of London* 107: 475-490.
- 1938. Some features of the variation of the birds of paradise. *Proceedings of the Zoological Society of London* 108: 417-481.
- 1942. Anatomical notes on the New Zealand Wattled Crow (*Callaeas*), with especial reference to its powers of flight. *The Ibis* 84:1-18.
- Traylor, M. A., Jr., 1979. Check-list of birds of the world, a continuation of the work of James L. Peters, vol. 8. Museum of Comparative Zoology, Cambridge, pp. xv + 365.
- Urik, J. A., 1983. *Anatomy and evolutionary relationships of the avian family Irenidae*. Unpublished Ph. D. thesis, University of Pittsburgh, Pittsburgh, Pennsylvania.
- Verheyen, R., 1953. Oiseaux. In 'Exploration du Parc National de l'Upemba', fasc. 19: 135-156. Institut des Parcs Nationaux de Congo.