ANATOMICAL EVIDENCE FOR PHYLOGENETIC RELATIONSHIPS AMONG WOODPECKERS

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ALTHOUGH the functional anatomy of woodpeckers has long been a subject of interest, their internal anatomy has not been used extensively for determining probable phylogenetic relationships within the family. In part this is probably due to the reluctance to use highly adaptive features in phylogenetic studies because of the likelihood of convergent evolution. Bock (1967) and others have pointed out that adaptiveness in itself does not rule out taxonomic usefulness, and that the highly adaptive features will probably be the ones having conspicuous anatomical modifications, and Bock emphasizes the need for detailed studies of function before using features in studies of phylogeny. Although valuable, functional conclusions are often based on inferences not backed up by experimental data. As any similarity between species is possibly due to functional convergence, I believe what is needed most is detailed study of a number of features in order to distinguish between similarities resulting from convergence and those based on phylogentic relationship. Simple structures are not necessarily more primitive and morphological trends are reversible, as Mayr (1955) has pointed out. Individual variation may occur and various investigators may interpret structures differently. Despite these limitations, speculation concerning phylogeny will continue in the future, and I believe that it should be based on more, rather than fewer anatomical studies.

MATERIALS AND METHODS

Alcoholic specimens representing 33 genera and 47 species listed in Table 1 were dissected with the aid of a Zeiss operation microscope. Major items studied include the tongue and hyoid apparatus, salivary glands, certain jaw muscles, and the limb muscles. In order to make direct comparisons between species, an approximate representation of relative size was obtained by the use of a cranial length index, listed for each species in Table 1. This was calculated by dividing the distance from the nasal-frontal hinge to the posterior end of the head by the same measurement in *Dryocopus pileatus*. Relative dimensions were calculated by dividing the actual dimension in each case by the appropriate cranial length index. It is hoped that when more specimens have been studied, the quantitative data can be used in a more sophisticated mathematical treatment, but in this analysis measurements were used only in cases of obvious difference. The criticism that too few individuals of a species were used may be valid, but in order to gain a better perspective in this preliminary study, it was decided to examine a large number of features in a representative series of genera and species. All too often in previous works erroneous conclusions were reached by studying only a few species of a group. Some

TABLE 1
LIST OF SPECIES STUDIED[1] AND SUMMARY OF CERTAIN FEATURES

Species	Cranial index	Iliotib. post w. % biceps	Sartorius origin	
			Thoracic spines	% il. troc. anterior
Jynx torquilla	.59	125	1½	41
Picumnus cirrhatus	.38	52	3	100
Picumnus innominatus	.41	75	3	65
Nesoctites micromegas	.53	120	2½	53
Sasia ochracea	.37	55	3	80
Chrysoptilus melanochloros	.76	91	2½	41
Colaptes auratus (4)	.85	80–97	2–2½	36–83
Piculus flavigula	.63	72	1¾	50
Campethera permista	.58	49	2	100
Celeus flavus	.73	50	1½	0
Celeus sp. (trunk only)	—	58	1½	0
Celeus elegans	.76	54	2	15
Micropternus brachyurus	.70	72	1	0
Picus vittatus	.81	69	2½	56
Dinopium javanense	.76	83	2¼	—
Meiglyptes tristis	.61	—	—	—
Mulleripicus pulverulentus	1.19	36	2¾	0
Dryocopus pileatus (2)	1.00	63–81	2½	51–66
Dryocopus lineatus	.82	66	2¼	39
Asyndesmus lewis	.74	40	2	0
Melanerpes erythrocephalus (2)	.69	38–52	2	100
Melanerpes formicivorus	.68	30	2	100
Centurus striatus	.67	42	2	100
Centurus carolinus (4)	.73	38–47	2–2½	17–67
Centurus pucherani	.66	41	2	100
Sphyrapicus varius	.55	32	2¼	45
Sphyrapicus thyroideus	.54	16	2¼	100
Trichopicus cactorum	.55	52	2	—
Veniliornis passerinus	.54	66	2½	100
Dendropicos fuscesens	.47	49	2¼	100
Dendrocopos villosus	.67	52	2½	100
Dendrocopos pubescens (2)	.50	47	2	100
Dendrocopos scalaris	.53	25	3	89
Dendrocopos nuttallii	.57	67	2	100
Dendrocopos albolarvatus	.62	40	2½	74
Picoides arcticus	.66	68	2¼	100
Sapheopipo noguchii (trunk only)	—	54	2½	100
Xiphidiopicus percussus	.66	39	2	66
Mesopicos goertae	.66	51	1½	84
Thripias namaquus	.70	39	2¼	100
Hemicircus concretus	.55	105	3	47
Blythipicus rubiginosus	.73	74	2½	80
Chrysocolaptes lucidus	.81	61	3	100
Phloeoceastes guatemalensis	.87	43	3	100
Phloeoceastes melanoleucos	.91	44	3	100
Phloeoceastes leucopogon	.83	68	3½	100
Campephilus principalis	1.11	49	3¼	—

[1] Where more than one specimen was examined, the number is shown in parentheses.

indication of individual variation was obtained where several specimens were studied, particularly for *Colaptes* and *Centurus.*

For many of the features to be considered, additional information was available from published works. Descriptions of the salivary glands and hyoid apparatus appear in the works of Leiber (1907), Antony (1920), and Steinbacher (1934, 1957). Information concerning adaptations for climbing and pecking has been obtained from the studies by Burt (1930), Beecher (1953), Bock and Miller (1959), and Spring (1965). For the limb muscles those of Burt, Hudson (1937), Lowe (1946), and Hudson and Lanzillotti (1955) were used. The papers of Lucas (1895) and Scharnke (1931) contain data on the tongue and hyoid horns. For comparison with species outside the family, in addition to use of published information I dissected other specimens, particularly passerines.

The muscle terminology employed by George and Berger (1966) has usually been followed, but for the tracheal and hyoid muscles Leiber's terms have been used in some cases.

As most of the structures studied are uniformly developed throughout the family and some show intraspecific variation, of the hundreds of potentially useful features only a few may be of value as phylogenetic indicators. The first part of the discussion that follows considers about 30 features that may have potential value. An attempt has been made to judge whether a feature is "primitive" or "advanced" depending largely on its occurrence in other birds. Occurrence in *Jynx* or piculets is considered to be supporting evidence of a feature's primitiveness. The next portion of the paper considers groups of individual genera on the basis of anatomical similarity and interrelationships. More descriptions and analyses of function especially of woodpecker limb muscles are needed, but this paper discusses only those structures that may be important for phylogenetic considerations within the family.

Analysis of Individual Features

Latissimus dorsi.—Pars anterior (Figure 1) takes origin in woodpeckers from the last two cervical spinous processes and in most species also from the first thoracic. Pars posterior, not previously reported in woodpeckers, is present in *Jynx*, piculets, *Campephilus,* and *Phloeoceastes* (Figure 1). Origin is by an aponeurosis deep to sartorius. It inserts on the humerus proximal to that of pars anterior. A humeral anchor similar to that described by George and Berger (1966) is present. The presence of pars posterior without doubt represents the retention of a primitive feature.

Rhomboideus superficialis.—Origin (Figure 1) is from the last cervical spinous process or first thoracic to mainly the third or sometimes the fourth thoracic spinous process. Probably the area of origin has been reduced in woodpeckers as an origin exists from the last cervical in *Jynx, Nesoctites,* and at least some passerines. In *Jynx, Nesoctites, Campethera, Centurus carolinus, Sphyrapicus varius, Xiphidiopicus, Mesopicos, Blythipicus* (Figure 3), and *Hemicircus* the muscle has a small insertion on the clavicle as well as the scapula.

Rhomboideus profundus.—This muscle is unusual in woodpeckers in that it consists of a small anterior superficial portion and a larger posterior deep portion. Origin of the anterior superficial portion usually is from part or all of the last two cervical spinous processes, and insertion is on the dorsal margin of the scapular blade near the bend (Figure 3). In *Jynx* it has a much broader insertion and is not easily separated from the posterior deep portion. In piculets the origin of the

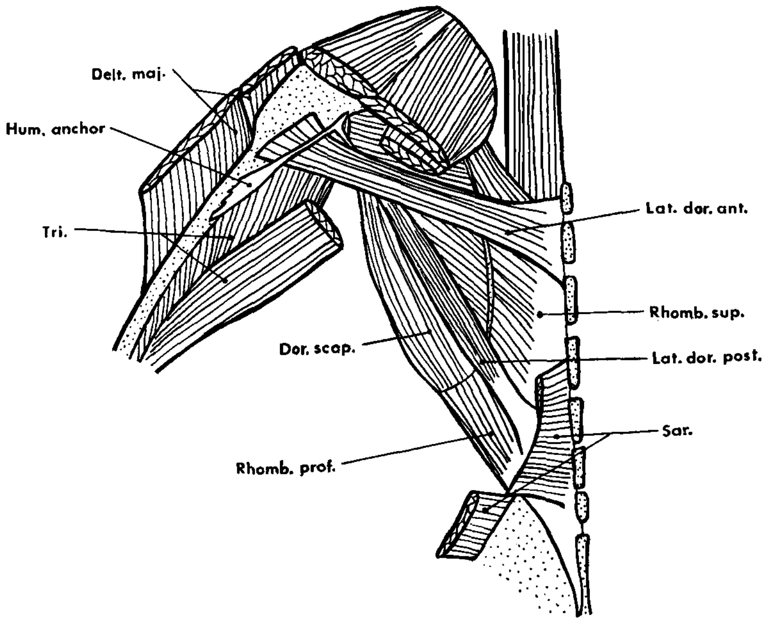

Figure 1. *Phloeoceastes leucopogon*. Dorsal view of left shoulder region. Deltoideus major has been reflected to show insertions of latissimus dorsi.

posterior deep portion is fleshy from the ilium in addition to that from the thoracic spinous processes.

Serratus profundus.—Area of origin of this muscle has been reduced as only *Jynx* has an origin from the last cervical rib; in others it is from two to four cervical transverse processes only. In *Dryocopus*, *Mulleripicus*, melanerpines, *Sphyrapicus*, *Dendrocopos scalaris*, *D. albolarvatus*, *Xiphidiopicus*, *Chrysocolaptes*, and *Phloeoceastes* origin includes the next to the last cervical vertebra. In others it is from two or three more anterior (Figure 2).

Serratus anterior.—Origin in most woodpeckers is from the last cervical rib (Figure 2), but in a few including *Jynx*, *Nesoctites*, *Sasia*, *Campethera*, *Micropternus*, *Dinopium*, *Melanerpes formicivorus*, *Centurus pucherani*, *Xiphidiopicus*, and *Thripias* it is also from the first thoracic rib, and in *Picumnus* and *Mesopicos* from the first thoracic only. Origin from two ribs is usual in passerines and other birds. Origin from only one rib is considered more specialized.

Serratus posterior.—The origin of this muscle is variable. It is most commonly from thoracic ribs 2, 3, and 4 (Figure 2), but in *Jynx*, *Nesoctites*, *Sasia*, and *Picoides* it is from ribs 2, 3, 4, and 5, in *Picumnus cirrhatus*, *Mesopicos* and *Phloeoceastes guatemalensis* from ribs 3, 4, and 5, and in *Campethera*, *Celeus* (one side only in *elegans*), *Mesopicos*, *Blythipicus*, and *Hemicircus* (one side only) from ribs 3 and 4. Although this is a rather plastic feature, origin from a greater number of ribs (as in *Jynx* and others) is considerer primitive.

Serratus metapatagialis.—The most common origin is from thoracic rib 2 ventral to serratus posterior (Figure 2). Origin is from ribs 2 and 3 in *Jynx*, *Micropternus*,

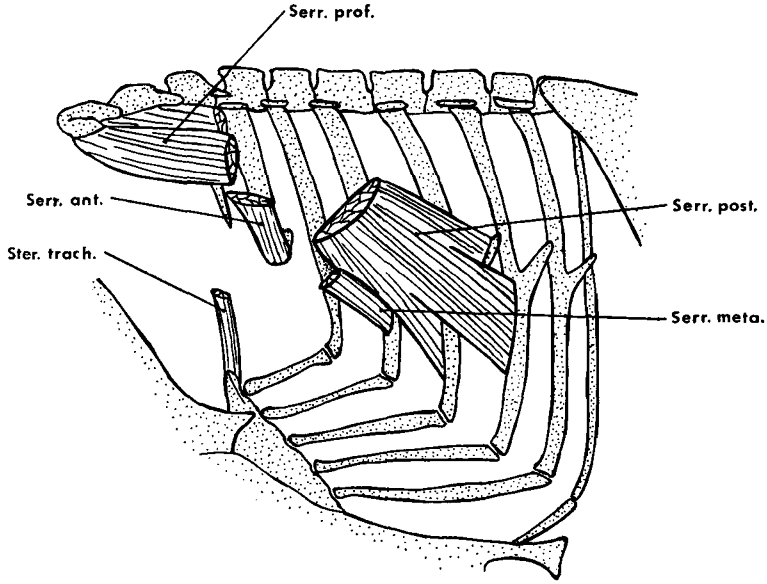

Figure 2. *Centurus carolinus.* Thoracic region, left side, showing origins of serratus muscles and sternotrachealis.

Mesopicos, and *Mulleripicus*. In *Dinopium* the origin is probably from rib 3 only. The origin in *Asyndesmus*, *Melanerpes erythrocephalus*, *Sphyrapicus varius*, and *Trichopicus* is from ribs 1 and 2. Again this may be a highly variable feature, but because of the generally more posterior origin in *Jynx* and other birds, origin from ribs 2 and 3 is considered primitive.

Subcoracoideus.—The coracoid or ventral head of this muscle, which is small in woodpeckers (Figure 3), was not found in *Picumnus* and *Sasia*. A clavicular portion of the dorsal or scapular head is present in *Jynx*, piculets, and many other members of the family (Figure 3). It was not found in *Micropternus*, *Picus*, *Dinopium*, *Chrysocolaptes*, *Phloeoceastes guatemalensis*, *P. leucopogon*, *Celeus elegans*, *Dryocopus pileatus*, *Mulleripicus*, and *Thripias*. Presence of a clavicular portion is considered primitive.

Pectoralis pars abdominalis.—The anterior attachment of this dermal component is variable. It may have a direct attachment to the humerus by fleshy fibers (*Jynx*, *Picumnus*, probably *Sasia*, *Centurus carolinus*, *Dendrocopos albolarvatus*, *Xiphidiopicus*, and *Phloeoceastes guatemalensis*), tendinous and fleshy fibers (*Melanerpes formicivorus*, *Asyndesmus*, *Sphyrapicus*, *and Phloeoceastes melanoleucos*), or by aponeurosis (*Nesoctites*, *Chrysoptilus*, *Colaptes*, *Campethera*, *Micropternus*, *Dinopium*, *Mulleripicus*, *Dryocopus*, *Melanerpes erythrocephalus*, *Centurus striatus*, *Dendrocopos* except *albolarvatus*, *Picoides*, *Sapheopipo*, and *Mesopicos*). It has an attachment to the main portion of pectoralis a few mm from the attachment of the latter to the humerus in *Celeus*, *Piculus*, *Trichopicus*, *Thripias*, *Blythipicus*, and *Chrysocolaptes*. In *Hemicircus* it ends deep to the skin in the axilla. On the basis of its fleshy attachment to the humerus in *Jynx* and piculets, this feature is considered

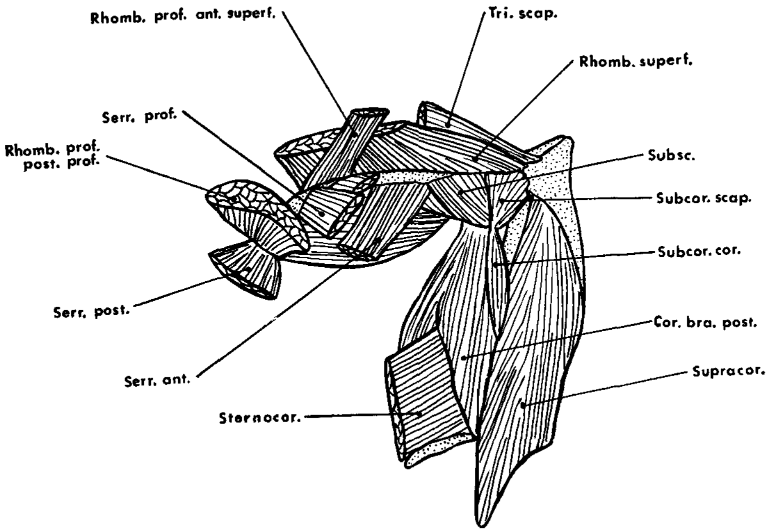

Figure 3. *Blythipicus rubiginosus.* Medial view of muscles having attachments to scapula, coracoid and clavicle. The partial origin of scapulotriceps from the clavicle is unusual in woodpeckers.

primitive, but its considerable variation in other groups of birds makes its significance questionable.

Flexor digitorum superficialis and flexor digitorum profundus.—Melanerpines and sapsuckers have a vinculum between the tendons of these two muscles at the carpometacarpus (Figure 4). Although the tendons may be enclosed by a common sheath in other birds, a vinculum has not been described before and is therefore considered to be a specialized feature.

Flexor carpi ulnaris.—In most woodpeckers (Figure 4) the insertion of this muscle is by two tendons on the os ulnare, but *Phloeoceastes, Campephilus,* and

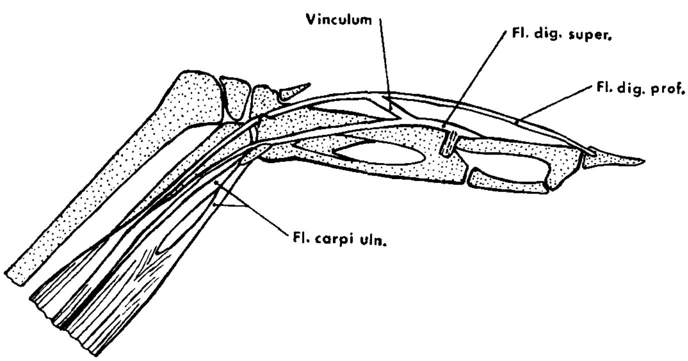

Figure 4. *Centurus carolinus.* Ventral view of distal portion of left wing.

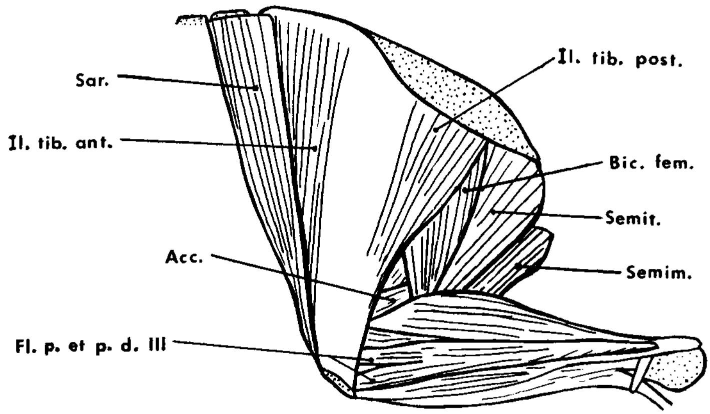

Figure 5. *Micropternus brachyurus.* Superficial muscles of left thigh and leg.

Piculus have only one tendon. The presence of two tendons is considered a primitive feature.

Sartorius.—Origin (Figure 5) is from one to three thoracic spinous processes and from the ilium (see Table 1). A more limited origin from the spinous processes, which is common in other groups and occurs in *Jynx*, is considered primitive. The width of origin from the ilium calculated as a percentage of that of the iliotrochantericus anterior is also given. Because of considerable intraspecific and intrageneric variation this feature may be of limited value.

Iliotibialis.—Table 1 gives width at the origin of the posterior portion relative to that of the biceps. As it is wide in *Jynx* and in passerines, covering the biceps at its origin (as illustrated for *Micropternus* in Figure 5) a relatively wide muscle is considered primitive.

Semitendinosus and semimembranosus.—The accessory semitendinosus is present in most woodpeckers. It is known to be absent only in *Dendrocopos*, *Dendropicos*, *Veniliornis*, *Sapheopipo*, *Picoides*, and *Sphyrapicus*. Its absence is no doubt a specialized condition. The insertions of semitendinosus and semimembranosus are by distinct aponeuroses along the tibial shaft in most woodpeckers (Figure 6B), but in *Jynx*, piculets, *Blythipicus* (Figure 6A), and *Hemicircus* they are united. The latter condition is considered primitive.

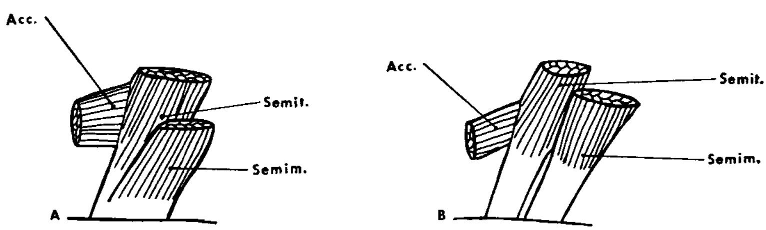

Figure 6. Medial view of insertions of right semitendinosus and semimembranosus on tibial shaft. A, *Blythipicus rubiginosus* with common tendon of insertion; B, *Xiphidiopicus percussus* with separate tendons.

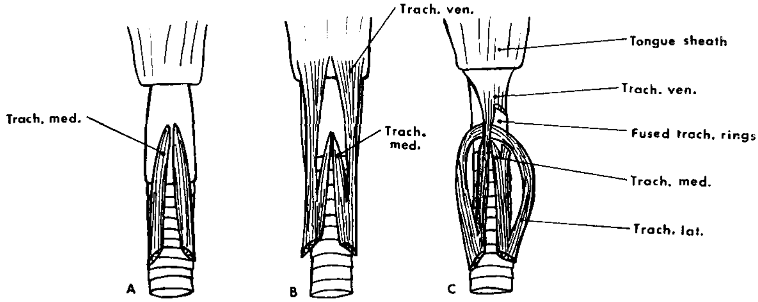

Figure 7. Ventral view of anterior end of trachea to show insertions of trachealis muscle. A, *Asyndesmus lewis*; B, *Picus vittatus*; C, *Dendrocopos villosus*.

Ischiofemoralis.—In woodpeckers the origin is generally more extensive than in other birds, extending ventrally in many to the pubis. Origin in *Jynx* from the ischium only is assumed to be primitive.

Adductor longus et brevis.—Usually anterior and posterior portions were fairly easily separated, but the two portions show some overlap. In a few species the two bellies are better described as deep and superficial. Many species have attachments from this muscle and from the pars media of the gastrocnemius to the meniscus of the knee joint. These were not found in *Jynx, Picmnus, Sasia, Micropternus, Dinopium, Veniliornis, Dendropicos, Dendrocopos, Picoides, Sapheopipo, Mesopicos, Chrysocolaptes, Phloeoceastes guatemalensis*, and *Campephilus*. As these features are quite variable, they are of doubtful phylogenetic significance.

Peroneus longus.—It is absent in *Picumnus* and *Sasia*. The main insertion is on the tibial cartilage and there may be a branch to adjacent fascia, but the latter is difficult to establish with certainty. In some it originates from the fibula. Except that its absence in some piculets is a specialization, the form of the muscle appears to be of little value in determining relationships.

Sternotrachealis.—In most birds the origin is from the sternocoracoidal process of the sternum (Figure 2), but in many woodpeckers it originates from the first thoracic rib. Sternal origin occurs in *Jynx*, piculets, *Micropternus, Hemicircus, Sphyrapicus*, and melanerpines and is assumed to be primitive.

Cucullaris pars dermotemporalis.—Origin of this muscle is variable (Figure 9), but in *Jynx*, piculets (Figure 9A), *Sphyrapicus*, and most melanerpines (Figure 9B) it is from the posterior orbital rim. This feature, which is also found in some passerines, is considered primitive.

Trachealis.—This muscle, also termed tracheolateralis, is attached posteriorly to the first bronchial ring. Anteriorly (Figure 7) it may consist of one to three parts. A medial part (Figure 7A, 7B, 7C), which is present in all the woodpeckers studied, inserts ventrally near the midline on the fused portion of the trachea posterior to the larynx. A thin ventral part may extend anteriorly to the base of the tongue sheath (Figures 7B, 7C). It is present in *Jynx*, piculets, and several other species. A lateral part when present (Figure 7C) passes lateral to the tracheohyoid muscle and inserts on the trachea close to the insertion of the medial part. It occurs in *Jynx, Dendrocopos, Picoides, Mesopicos, Veniliornis, Sapheopipo*, and probably *Dendropicos*. It is also found in some passerines and Leiber (1907) considered it a primitive feature.

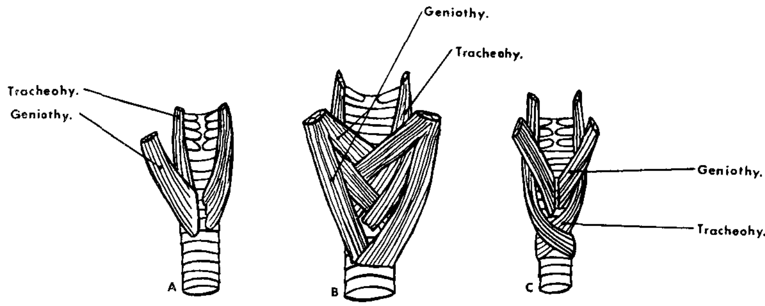

Figure 8. Dorsal view of anterior end of trachea to show attachments of geniothyroid and tracheohyoid muscles. A, *Celeus flavus* (right geniothyroid has been removed to show origin of tracheohyoid); B, *Dryocopus pileatus*; C, *Campethera permista.*

Geniothyroid.—This muscle, first noted by Huber (1821) and discussed and well-illustrated by Leiber (1907), is known only in woodpeckers and is perhaps homologous to the genioglossus of other birds. Origin is from the medial surface of the mandible posterior to that of geniohyoid. In those woodpeckers where it is well-developed a broad band of muscle fibers has one or two points of attachment to the trachea in the vicinity of the tracheohyoid (Figures 8A, 8B, 8C). In other species it is represented only by a few fibers to the floor of the mouth. Without knowing its history outside of the Picidae it is difficult to decide whether a well-developed muscle represents an advanced state or whether it became large early in the evolution of woodpeckers and later regressed. As it is well-developed in *Jynx,* the latter alternative seems more likely.

Tracheohyoid.—The winding of this muscle (which may not be homologous to the tracheohyoid of other birds) around the trachea (Figure 8C) is frequently illustrated, but for the family as a whole it is an uncommon specialization. In other species the muscles of each side meet in the midline (Figure 8A) or interdigitate (Figure 8B). The coiled condition, which apparently has occurred independently more than once, is considered an advanced feature.

Geniohyoid and hyoid horns.—The long horns and associated geniohyoid muscles that encircle the head and enter the upper bill in *Picus*, *Dinopium*, and *Colaptes* (Figure 9C) are also unusual in the Picidae. Most commonly they extend to or near the base of the bill (Figure 9D). In some individuals they deviate to the left rather than to the right. In *Dendrocopos villosus, Hemicircus,* and *Picumnus innominatus* (Figure 9A) the horns are wound around the right orbit, an obvious case of convergent evolution. Short hyoid horns are considered primitive, but a secondary reduction in length particularly in sapsuckers must be considered.

Nasal gland.—The nasal gland is a compact structure lying adjacent to the nasal cavity in most woodpeckers, but it enters the orbit in *Jynx*, *Picumnus* (Figure 9A), and *Sasia*. This form is similar to that of passerines, and its failure to enter the orbit in other woodpeckers (Figure 9B, 9C, 9D) is assumed a more advanced feature.

Maxillary gland.—An unusual and specialized feature in woodpeckers is the large expanded posterior portion that lies in the floor of the orbit (Figure 9), and which some authors have confused with the nasal gland. In *Jynx* the posterior portion

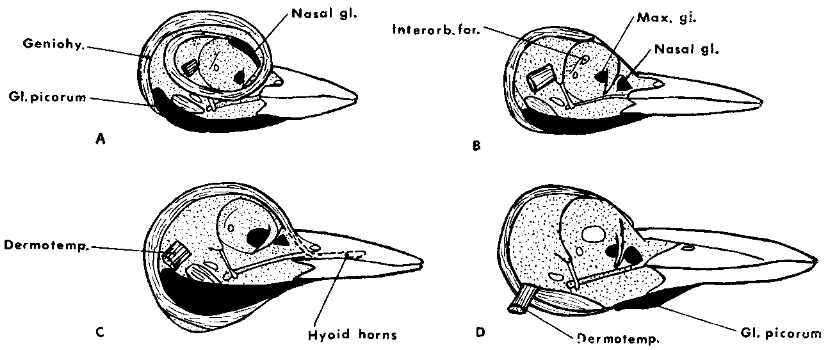

Figure 9. Dissection of right side of head and orbit. A, *Picumnus innominatus*; B, *Asyndesmus lewis*; C, *Chrysoptilus melanochloros*; D, *Phloeoceastes guatemalensis*.

enters the orbit but is not expanded and in *Nesoctites* it just reaches the pars plana.

Mandibular gland.—The large portion of this gland, which may be termed glandula picorum, is a specialized feature of woodpeckers (Figure 9). It is large in *Jynx*, piculets, and many other species. Reduction in size is believed a secondary specialization.

Interorbital foramen.—This foramen (Figures 9B, 9D), present in some woodpeckers, possibly is of phylogenetic significance, but defining an evolutionary trend for it within the family is difficult. It is absent in *Jynx*, *Nesoctites*, *Colaptes*, *Campethera*, *Dinopium*, *Centurus carolinus*, *Sphyrapicus*, *Celeus elegans*, *Piculus*, and *Hemicircus*.

Other features.—The great development of the protractor pterygoideus discussed by Spring (1965) was not studied in detail, but it is much smaller in *Jynx*. Well-developed in piculets, it probably indicates an early specialization for pecking in that group. The assumption that specialization for climbing has developed more than once within the family is considered with the other evidence.

WRYNECKS (JYNGINAE)

Several features distinguish *Jynx* from all other Picidae. These include the form of rhomboideus profundus, origin of serratus profundus from the last cervical rib, the limited origin of ischiofemoralis, origin of adductor longus et brevis from ischium and the smaller protractor pterygoideus. In addition, deltoideus minor has a clavicular origin, caudofemoralis has a fleshy as well as tendinous attachment to the pygostyle, and iliacus inserts on the anterior rather than the medial surface of the femur. Three features found only in *Jynx* and some or all piculets are the soft rectrices, nasal gland in the orbit, and smaller maxillary gland. Most of these features I consider primitive on the basis of their widespread occurrence in other birds, suggesting that *Jynx* resembles most closely the ancestral members of the family. The barbless tongue is probably primitive as Leiber (1907) suggested, but possibly a secondary reduction of spines has occurred. The geniothyroid and tracheohyoid are attached to fused tracheal rings (according to Leiber 5-18) some distance posterior to the larynx. The posterior attachment of tracheohyoid (like its coiling around the trachea in other species) provides a mechanism for greater protrusion of the tongue. Possibly the geniothyroid became well-developed independently and its enlargement in other woodpeckers is not truly a primitive feature. The large glandula picorum, the specialized hyoid apparatus, and lack of modification of the feet, tail, and jaw muscles for climbing and pecking give evidence that ground feeding preceded the development of other specializations typical of woodpeckers. The morphological evidence clearly justifies recognition of the subfamily Jynginae.

Piculets (Picumninae)

The considerable morphological variation among the piculets is not surprising in view of their discontinuous distribution. In general they are more primitive than other members of the family, but show some specializations. Primitive features found in all of the piculets studied include the presence of an accessory semitendinosus, the common tendon for semitendinosus and semimembranosus, origin of ischiofemoralis and adductor longus et brevis dorsal to the pubis, the anterior origin of dermotemporalis (Figure 9A), sternal origin of sternotrachealis, large glandula picorum (Figure 9A), and the presence of the ventral part of trachealis. Other primitive features include a clavicular origin for rhomboideus superficialis, the shorter maxillary gland, and the broad iliotibialis in *Nesoctites*. The nasal gland enters the orbit in *Picumnus* (Figure 9A) and *Sasia*. Specialized features in piculets include origin of serratus metapatagialis from second thoracic rib only, origin of sartorius from two or three spinous processes, absence of a lateral part of trachealis, and a poorly developed geniothyroid. Possibly the latter two muscles have developed independently in *Jynx* and true woodpeckers and their absence in piculets represents the primitive condition. The loss of the coracoid head of subcoracoideus in *Picumnus* and *Sasia* and the fleshy insertion of rhomboideus profundus on the ilium do not occur in other members of the family. Origin of serratus anterior from the last cervical and first thoracic rib in *Nesoctites* and *Sasia* is primitive, and origin from the first thoracic only in *Picumnus* is unusual. The origin of serratus posterior shows considerable variation, but the generally more extensive origin probably is primitive. *Sasia*, which lacks a hind toe, has lost extensor hallucis longus and flexor hallucis brevis. The hyoid horns are relatively short in *Picumnus cirrhatus*, *Sasia*, and *Nesoctites*, but in *Picumnus innominatus* (Figure 9A) they coil around the right orbital rim and the tracheohyoid makes two turns around the trachea. In *cirrhatus* the muscles meet in the midline without crossing, in *Sasia* they cross slightly, and in *Nesoctites* they interdigitate.

The piculets are more like true woodpeckers than *Jynx*, but they show enough differences from both other groups to justify recognizing the subfamily Picumninae. The fact that the Asian *Picumnus innominatus* differs somewhat from the South American *P. cirrhatus* suggests a possible generic separation, but more species should be studied.

Nesoctites is perhaps closer to the ancestral members of the Picinae. The strongest evidence for this is the failure of the nasal gland to enter the orbit. On the other hand the maxillary gland is expanded in the orbit in *Picumnus*, but not in *Nesoctites*.

MICROPTERNUS, *MEIGLYPTES*, AND *CELEUS*

In these genera the glandula picorum is large, the geniothyroid is well-developed, hyoid horns are short, and the tracheohyoids are simple. *Micropternus* has several primitive features. The posterior portion of the iliotibialis is broad (Figure 5), sartorius takes origin from the last thoracic spinous process only (Figure 5), sternotrachealis comes from the sternum, and serratus anterior from the first thoracic as well as the last cervical rib. Origin of dermotemporalis was not determined. Geniothyroid inserts anterior and posterior to the origin of tracheohyoid. Trachealis has ventral and medial parts, but no lateral. *Meiglyptes* is apparently similar, but the specimen was not dissected completely. Sternotrachealis takes origin from the sternum. Origin of the dermotemporalis is 4 mm posterior to the orbital rim. Only the medial part of trachealis was found. On the basis of the available evidence *Meiglyptes* is related to *Micropternus*.

Celeus is in many ways similar to *Micropternus*, but has fewer primitive features. Geniothyroid has only one attachment to the trachea (Figure 8A). Only the medial part of trachealis is present, origin of sternotrachealis is from the first rib, and dermotemporalis originates 5 to 7 mm posterior to the orbital rim. Serratus anterior originates from the last cervical rib only. In the *Celeus elegans* specimen examined serratus posterior originated from ribs 2, 3, and 4 on one side and from ribs 3 and 4 on the other. In the other two species studied origin was ribs 3 and 4 only. In woodpeckers flexor perforans et perforatus digiti III usually has two heads (Figure 5), but it has only one head in *elegans*. Insertion of pectoralis abdominalis is to pars thoracicus 3 to 5 mm from the humerus. Origin of sartorius is only slightly more extensive than for *Micropternus*, and the posterior portion of iliotibialis is narrower. Despite these differences *Celeus* appears to belong to the same evolutionary line as *Micropternus*.

Piculus and *Campethera*

Both *Piculus* and *Campethera* have a large glandula picorum and a well-developed geniothyroid. In *Piculus* the origin of sternotrachealis is from the first rib. The origin of dermotemporalis is posterior to the ear opening. Tracheohyoid reaches the base of the right nostril and the tracheohyoids cross and make a three-fourths turn around the trachea. Origin of pectoralis abdominalis is similar to that of *Celeus*, but that of serratus posterior is thoracic ribs 2, 3, and 4. Origin of sartorius is limited to 1¾ thoracic spines, and the posterior portion of iliotibialis is of moderate width. Both medial and ventral parts of trachealis are present.

The hyoid horns of *Campethera* are shorter, but the tracheohyoids (Figure 8C) make a three-fourths turn around the trachea as in *Piculus*. The geniothyroid has only one attachment anterior to the tracheohyoid (Figure 8C), whereas in *Piculus* it also has a small posterior attachment. Previous dissection prevented determining the origin of sternotrachealis. Origin of dermotemporalis is dorsal to the ear opening. A primitive feature is the origin of serratus anterior from the last cervical and first thoracic ribs. As in *Celeus* the origin of serratus posterior is from thoracic ribs 3 and 4, but pectoralis abdominalis has a humeral origin. On the basis of their anatomy *Piculus* and *Campethera* appear to be related and both show similarities to *Celeus*, but the similar winding of the tracheohyoid around the trachea in *Piculus* and *Campethera* may represent convergence in New and Old World lines even though both may have evolved from the same general group.

Colaptes, *Picus*, and *Dinopium*

These are similar to the genera discussed under the previous heading in having a large glandula picorum and well-developed geniothyroid, but they show greater coiling of the tracheohyoid and extension of the hyoid horns into the upper bill (Figure 9C).

Chrysoptilus and *Colaptes* are similar, and this discussion makes no distinction between the two genera. In *Colaptes* the posterior portion of iliotibialis is broad and the origin of sartorius is from 2 to 2½ spinous processes. Pectoralis abdominalis is attached to the humerus by aponeurosis. Dermotemporalis is attached to the skull posterior to the ear opening (Figure 9C). In *Colaptes*, as in *Piculus*, *Campethera*, and *Celeus elegans*, no interorbital foramen is present, but one was noted in *Celeus* *flavus*. The origins of the serratus muscles are all of the more advanced type. Trachealis has a ventral as well as a medial part (Figure 7B).

Few differences were noted between *Picus* and *Colaptes*. In *Picus* the posterior portion of iliotibialis is somewhat narrower, subcoracoideus has no clavicular head, and the geniothyroid has an additional attachment to the larynx. *Dinopium* has a similar morphology; the posterior portion of iliotibialis is broad as in *Colaptes*, but as in *Picus* the geniothyroid has an attachment to the larynx and the subcoracoideus has no clavicular head. *Dinopium* lacks the interorbital foramen as does *Colaptes*; specimen damage prevented determining its presence or absence in *Picus*. Origin of serratus anterior from the first thoracic and last cervical ribs, serratus posterior from ribs 1, 2, 3, and 4 and the origin of serratus metapatagialis from rib 3 are considered primitive features in *Dinopium*. It has lost the hind toe, but the extensor hallucis longus is well-developed and flexor hallucis brevis is present although very small. Flexor perforans et perforatus digiti III has only one head instead of the usual two. Their similar anatomy suggest that *Colaptes*, *Picus*, and *Dinopium* derive from the same general ancestral group, but such similarities as the coiling of the tracheohyoid and the entrance of the hyoid horns into the bill may be due to convergent evolution. Further study is needed, but I favor the view that the three genera are related and that the hyoid horns have grown into the bill only once.

DRYOCOPUS AND *MULLERIPICUS*

Dryocopus and *Mulleripicus* are similar to the three preceding groups in having well-developed geniothyroids (Figure 8B). Glandula picorum is somewhat smaller in *Dryocopus*, but is well-developed. Dermotemporalis inserts on the skull posterior to the ear opening. Trachealis has medial and ventral parts, the hyoid horns reach the base of the bill and the tracheohyoids interdigitate (Figure 8B). Iliotibialis is of moderate width and sartorius originates from 2¼ to 2½ spinous processes. Only one head of flexor perforans et perforatus digiti III is present in *D. lineatus*. An interorbital foramen is present. The feet have become more specialized for climbing. *Mulleripicus* differs little from *Dryocopus*, but a primitive feature is the origin of serratus metapatagialis from thoracic ribs 2 and 3. Glandula picorum is larger and the posterior portion of iliotibialis is narrower. They resemble *Micropternus* in having an attachment of geniothyroid anterior and posterior to tracheohyoid and a short hind toe, and in *Mulleripicus* the origin of serratus metapatagialis from thoracic ribs 2 and 3. Unlike *Micropternus* origin of sternotrachealis is from the first rib and serratus anterior has an origin from the last cervical rib only.

Melanerpine Woodpeckers and *Sphyrapicus*

In this group and the ones to follow, in contrast to those previously discussed the geniothyroids are poorly developed with only a few fibers to the floor of the mouth, and glandula picorum in general is less well-developed (Figure 9B). The distal horny part of the tongue is usually longer and the foot is more adapted for climbing. *Centurus, Melanerpes, Asyndesmus,* and *Tripsurus* are morphologically similar and in this analysis they are usually considered together.

The melanerpine woodpeckers have several primitive features including origin of sternotrachealis from the sternum (Figure 2), origin of a dermotemporalis from near the orbital rim (Figure 9B), and the lack of specialization of the tracheohyoids and hyoid horns. Glandula picorum is moderately long and slender. Origin of serratus metapatagialis from the first and second thoracic ribs in some species and the presence of a vinculum (Figure 4) between the tendons of flexor digitorum superficialis and flexor digitorum profundus (except in *Centurus striatus*) are distinctive features. Subcoracoideus has a clavicular head. Serratus anterior originates from the last cervical rib (Figure 2) except in *Melanerpes formicivorus* and *Centurus pucherani* in which the origin is the last cervical and first thoracic. Posterior portion of iliotibialis is narrow to moderate in width and the origin of sartorius is from 2 to 2½ spinous processes. Origin of dermotemporalis is more posterior in *Centurus striatus.* The interorbital foramen is small in most species (Figure 9B) and absent in the specimens of *Centurus carolinus* studied. A small ventral part of trachealis was found on one side in *Centurus pucherani,* but it was absent in the other species (Figure 7A). Tracheohyoids interdigitate markedly in *striatus* and *carolinus,* less so in *pucherani* and *Melanerpes formicivorus,* and not at all in *Asyndesmus* and *Melanerpes erythrocephalus.* The length of the hyoid horns is also variable with the longest reaching the base of the bill.

In *Trichopicus* serratus posterior originates from thoracic ribs 1, 2, and 3 and glandula picorum is larger, but it is otherwise similar. The posterior portion of iliotibialis is relatively wide and the glandula picorum not reduced in size, but the vinculum between the flexor tendons and the origins of serratus posterior and metapatagialis are specialized features.

Sphyrapicus resembles *Dendrocopos* by the absence of accessory semitendinosus and, according to Burt (1930), by the greater folding of the frontal region of the skull, but in other ways it resembles the melanerpines. Unlike *Dendrocopos,* it has a vinculum between the tendons of flexor digitorum superficialis and flexor digitorum profundus, origin of sternotrachealis is from the sternum, dermotemporalis originates from the orbital margin, glandula picorum is long and slender, and trachealis has no lateral part. As in most melanerpines the interorbital foramen is absent, and in *Sphyrapicus varius* serratus metapatagialis takes origin from thoracic ribs 1 and 2. The very short hyoid horns and the origin of the tracheohyoids from the lateral surface of the trachea may represent a secondary reduction.

DENDROCOPOS WOODPECKERS

In *Mesopicos, Dendrocopos, Picoides, Sapheopipo, Dendropicos, Veniliornis,* and *Thripias* the glandula picorum is short, trachealis has a lateral part (Figure 7C), sternotrachealis is from the first thoracic rib, dermotemporalis originates dorsal to the ear opening, geniothyroid is poorly developed, and an interorbital foramen is present. The foot has become specialized for climbing.

In *Dendrocopos* accessory semitendinosus is absent. Posterior portion of iliotibialis is narrow to moderately broad, and sartorius originates from 2 to 3 spinous processes. The tracheohyoids extensively interdigitate. Hyoid horns are of moderate length, except in *villosus* in which they coil around the right orbital margin.

I examined only a trunk specimen of *Sapheopipo,* but found no differences to support its separation from *Dendrocopos. Picoides* is similar to *Dendrocopos,* but the origin of serratus posterior from thoracic ribs 2, 3, 4, and 5 may be evidence for a more basal position. Flexor hallucis brevis is of moderate size, but extensor hallucis longus is weakly developed. Although the loss of the hind toe is not fundamental, this along with the different origin for serratus anterior (if the latter is a consistent difference) favors the separation of the two genera. No distinctive features were noted for *Veniliornis.* It may represent a relatively recent offshoot from North American *Dendrocopos,* or possibly it is more primitive.

Mesopicos is clearly related to *Dendrocopos,* but it has several features thought to be primitive. These include the presence of accessory semitendinosus, origin of serratus anterior from the first thoracic rib, serratus posterior from ribs 3, 4, and 5, serratus metapatagialis from ribs 2 and 3, and the more limited origin of sartorius from 1½ spinous processes. The tracheohyoid muscles interdigitate. *Dendropicos* closely resembles *Dendrocopos,* but serratus posterior originates from thoracic ribs 2 and 3 only. No ventral part of trachealis was found and the presence of a lateral part was somewhat doubtful. This point needs further study, but apparently *Dendrocopos* and *Dendropicos* are related. The specimen of *Thripias* studied was so poorly preserved in some parts it is discussed with some reservation. No determinations were made for trachealis or tracheohyoids, but for other features such as the loss of the accessory semitendinosus, *Thripias* is similar to *Dendropicos*. A primitive feature is the origin of serratus anterior from the first thoracic and last cervical ribs. Origin of pectoralis abdominalis is from pars thoracicus.

Xiphidiopicus

The Cuban Green Woodpecker is similar to *Dendrocopos* woodpeckers in having a short glandula picorum, a posterior origin for the dermotemporalis, poorly developed geniothyroid, interdigitation of the tracheohyoids, origin of sternotrachealis from the first rib, and the presence of an interorbital foramen. Like *Mesopicos*, an accessory semitendinosus is present (Figure 6B). As in melanerpine woodpeckers ventral and lateral parts of trachealis are absent. A primitive feature is the origin of serratus anterior from the last cervical and first thoracic ribs. Perhaps *Xiphidiopicus* is an isolated remnant of the ancestral stock that gave rise to *Dendrocopos* and its relatives. No morphological evidence indicates that *Xiphidiopicus* is a recent offshoot from *Dendrocopos* or the melanerpines.

Ivory-billed Woodpeckers

Latissimus dorsi posterior is present in *Campephilus* and *Phloeoceastes leucopogon* and was found on one side in *melanoleucos*. Glandula picorum is short and the distal portion is narrow (Figure 9D). Only the medial part of trachealis is present and the tracheohyoids meet in the midline or interdigitate slightly. Geniothyroids are poorly developed although, *P. leucopogon* and *Chrysocolaptes* have a few fibers to the trachea or larynx. The hyoid horns are of moderate length. An interorbital foramen is present (Figure 9D), except that this feature was not examined in *Campephilus*. Origin of sternotrachealis is peculiar in *Campephilus* and *Phloeoceastes* in that in addition to the attachment to the first rib there is a small slip to the wall of the interclavicular air sac. *Campephilus*, *Phloeoceastes*, and *Chrysocolaptes* are similar in that dermotemporalis inserts posteriorly and is far ventral in position, being immediately dorsal to depressor mandibulae (Figure 9D). Sartorius takes origin from 3 to 3½ spinous processes, posterior portion of iliotibialis is of moderate width, peroneus longus arises in part directly from the fibula, extensor hallucis longus has an additional attachment to the first phalanx, and flexor perforans et perforatus digiti III has only one head. In *Campephilus* and *Phloeoceastes* the tendon of flexor carpi ulnaris to the os ulnare is not divided.

In most features *Chrysocolaptes* resembles the American ivory-bills. It resembles *Blythipicus* in the origin of sternotrachealis from the first rib only, the attachment of pectoralis abdominalis to pars thoracicus instead of the humerus, and the insertion of flexor carpi ulnaris. *Blythipicus* (Figure 6A) and *Hemicircus* have a common tendon of insertion for semitendinosus and semimembranosus, a feature found also in *Jynx* and piculets, but not in other woodpeckers.

Hemicircus has more features in common with *Blythipicus* than the other ivory-bills, but resembles them in the posterior ventral origin of dermotemporalis, and the origin of sartorius from 3 spinous processes. It differs from the others by the attachment pectoralis abdominalis to skin only, origin of sternotrachealis from sternum, lack of an interorbital foramen, the very broad posterior part of iliotibialis, the coiling of the hyoid horns around the orbit, and the winding of the tracheohyoid around the trachea.

Campephilus and *Phloeoceastes* are clearly related and do not show a close relationship to *Dryocopus*. The resemblance of *Chrysocolaptes* to the American ivory-bills is difficult to explain on the basis of convergence. *Blythipicus* and *Hemicircus* are less like the American species, but they do have features in common with *Chrysocolaptes*. Primitive features present in some ivory-bills are the presence of latissimus dorsi posterior, common tendon for semimembranosus and semitendinosus, sternal origin of sternotrachealis, and broad posterior portion of iliotibialis. Superficial resemblances exist between *Chrysocolaptes* and *Dinopium*, *Hemicircus* and *Meiglyptes*, and *Blythipicus* and *Micropternus*, but most of the anatomical evidence does not support these relationships. Flexor perforans et perforatus digiti III has only one head in *Dinopium* as in *Chrysocolaptes*, but this was true also for *Dryocopus lineatus* and *Celeus elegans*. In such other features as the origin of the serratus muscles, the size of the glandula picorum, the relative development of geniothyroids, tracheohyoids, and the hyoid horns, *Dinopium* and *Chrysocolaptes* are dissimilar. *Hemicircus*, *Meiglyptes*, and *Micropternus* are alike in having a sternal origin for sternotrachealis, but the two ivory-billed genera *Hemicircus* and *Blythipicus* resemble closely neither *Meiglyptes* nor *Micropternus*.

General Discussion

In his consideration of convergence in sympatric species Cody (1969) compares the genera of ivory-billed woodpeckers *Hemicircus*, *Blythipicus*, *Campephilus* and *Phloeoceastes* with the "logcock" genera *Meiglyptes*, *Micropternus*, *Dinopium* and *Dryocopus* which, in spite of striking similarities in plumage among species pairs from the two groups, can be distinguished by differences in morphology, behavior, and ecology. Bock (1963) doubts that these similarities of complex plumage patterns can be explained on the basis of convergence, but the evidence obtained in the present study tends to support Cody's view. One argument against the independent origin for the different ivory-bill genera from less specialized ground woodpeckers is that in general the ivory-bills have other primitive features not found in their supposed ancestral groups. *Phloeoceastes* and *Campephilus* have a latissimus dorsi posterior and a different origin for sternotrachealis, which seems to rule out an origin from *Dryocopus*. *Chrysocolaptes* lacks the specialization of the tracheohyoid and hyoid horns of *Picus* and *Dinopium*. *Blythipicus* and *Hemicircus* have retained the common tendon for semitendinosus and semimembranosus, unlike their possible relatives *Micropternus* and *Meiglyptes*. If features such as the presence of a latissimus dorsi posterior were present throughout the ivory-bill group their close relationship would be on much firmer ground, but they no doubt represent an earlier radiation from the ground woodpeckers and their anatomical diversity is therefore to be expected. In summary convergence in plumage patterns, although remarkable, is probably more easily accepted than the opposite view, which demands a great deal of structural convergence.

General morphological similarity is evident in *Micropternus*, *Meiglyptes*, *Dryocopus*, *Mulleripicus*, *Celeus*, *Piculus*, *Campethera*, *Picus*, *Colaptes*, and *Dinopium*, and despite certain specializations of the hyoid apparatus, all appear to be related at least distantly. In forms specialized for a more arboreal habitat, the hind toe is small or absent. A major question is whether the great resemblance of *Picus* to *Colaptes* indicates close relationship or is the result of convergent evolution in the Old and New Worlds. Certainly more species, particularly of *Picus*, need to be studied.

Burt (1930) and Howell (1952) concluded that *Sphyrapicus* is a derivative of *Dendrocopos*, but I agree with Short and Morony (1970) that sapsuckers are more closely allied to the melanerpine woodpeckers. Possibly the melanerpines and pied woodpeckers had a common origin, but in any case the evidence strongly favors a closer relationship of *Sphyrapicus* to the melanerpines than to *Dendrocopos*.

Goodwin (1968) favors the position that all the sub-Saharan African woodpeckers are more closely related to one another than to non-African forms. His alternative that they are polyphyletic is supported by the anatomical evidence, but I suggest that *Mesopicos*, *Thripias*, and *Dendropicos* are related to *Dendrocopos*, whereas *Campethera* is closer to *Picus*. Goodwin concludes that similarities in plumage of certain *Dendropicos* and *Veniliornis* species are due to convergence, but the anatomical evidence supports a relationship of the latter to *Dendrocopos* also. *Geocolaptes* was not studied, but its relationship to other African forms or to *Picus* or *Colaptes* could probably be determined by its internal morphology.

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SUMMARY

An anatomical study of 33 genera and 47 species of woodpeckers was carried out to learn more about interrelationships and the evolutionary history of the Picidae. About 30 features of possible phylogenic significance are described. The wrynecks and piculets possess many primitive features and on the basis of their anatomy can be distinguished from the Picinae. Some primitive members of the latter subfamily have retained adaptations for ground feeding, with well-developed salivary glands and probing tongues with little specialization for pecking in more solid wood. An early radiation of the ivory-billed woodpecker group apparently occurred with the development of specializations for climbing and pecking. *Dryocopus* and *Mulleripicus* are not directly related to the ivory-bills, but probably evolved more recently from the "ground woodpeckers." *Picus* and *Colaptes* with their highly specialized tongue and hyoid apparatus are probably closely related and represent terminal branches in the radiation of the "ground woodpeckers." The melanerpine woodpeckers and sapsuckers are related and comprise another group that has evolved a climbing foot and specialized feeding apparatus, although retaining many primitive features. The pied woodpeckers comprise another group whose members also have more arboreal habits and a bill more highly developed for pecking.

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