parable to the forked pterygoid of *Apteryx*." In most accipitrids the anterior articulation of the pterygoid, as viewed ventrally, is a straight line; however, notching of one kind or another may occur (fig. 90).

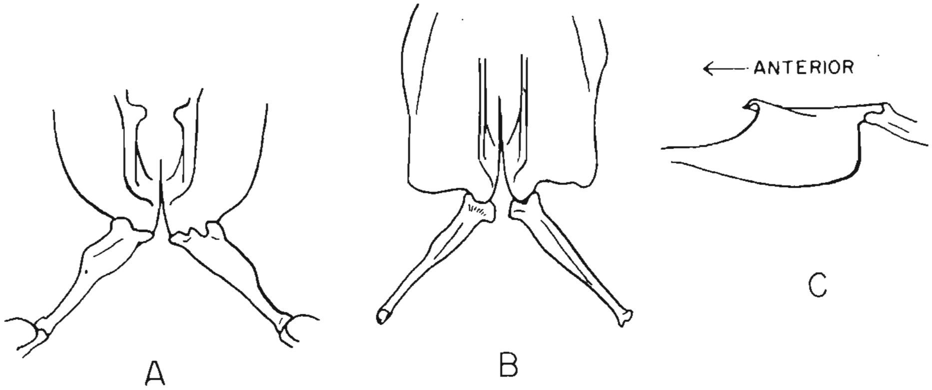


Fig. 90. Posteropterygoid articulation with the palatopterygoid as seen in ventral view in A. *Pandion haliaetus*, B. *Torgos tracheliotus*. C. Lateral view of this articulation in *Aquila chrysaëtos*.

The shape of the upper part of the bill varies; it ranges from the small, sharply ridged form, with elongated narial opening, found in *Machaerhamphus* (fig. 91), to the large inflated one found in *Haliaeetus pelagicus* and *Pithecophaga*. All of the accipitrids show a well-hooked beak, which has been plastic to modification as, for example, the sickle-shaped bill of *Rostrhamus* (fig. 201).

The narial aperture is usually triangular-ovoid (fig. 91). As the form of the bill has varied so has the shape of the narial aperature. The external naris is located in the ventroanterior or anterior portion of the lateral wall of the vestibular chamber (fig. 99). Sushkin (1905:27) stressed that this group, in contrast with the falconid, has the bottom margin of the nostril at the level of the floor of the vestibule (fig. 99).

Among the aegypiins, the external naris has been outlined by ossification in the lateral vestibular wall. Ossifications here are not limited to the aegypiins but are found in *Terathopius*, *Circaëtus*, and some specimens of *Chondrohierax* (fig. 91). Ossification in the lateral vestibular wall may occur in any genus but usually is limited to the posterior margin of the narial opening (*Aquila audax*, *Aquila wahlbergi*, and *Gypohierax angolensis*).

Where the lateral wall is ossified, the vestibular fold is also bony, with the exception of *Chondrohierax*, which lacks the fold. Partial ossification of the posterior portion of this fold may occur in individuals of any species.

The other vestibule walls ossify only slightly in most of this group, forming a part of the median septum, usually perforate, and partial anterior, ventral, and posterior walls (figs. 83, 85, 87). The type of ossification shown in *Aquila* is typical of the group whereas that of *Machaerhamphus*, which has a crack at the angle of the floor and septum, is the most extreme. The

* * *

Evol. Theory 2:209-300 (October, 1977)
Part III received September 9, 1975; May 27, 1977

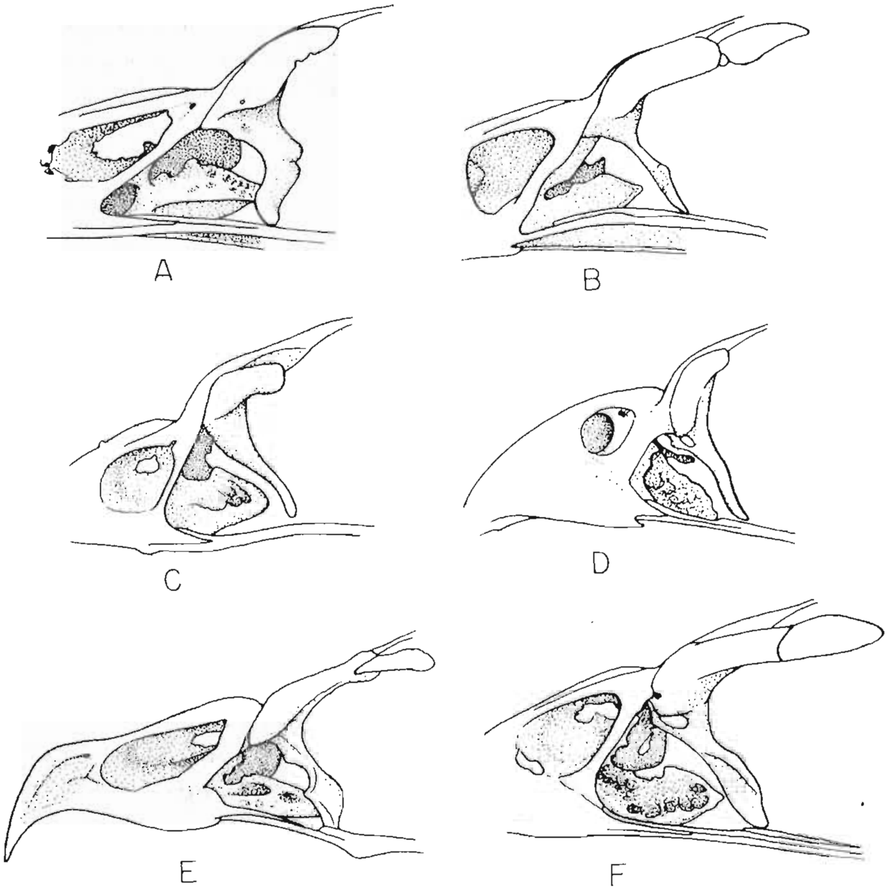


Fig. 91. Lateral view of rostral-cranial articulation in A. *Gypaëtus barbatus*, B. *Gypohierax angolensis*, C. *Gymnogenys typicus*, D. *Chondrohierax uncinatus*, E. *Machaerhamphus alcinus*, F. *Aquila chrysaëtos*.

upper surface of the maxillopalatine usually forms a portion of the entire floor in *Machaerhamphus*. Anteriorly the vestibule is well ossified although a gap or small fissure usually occurs between it and the premaxilla. Posteriorly the wall is incomplete below the median naris. The lateral margin of the median naris is essentially a part of the ventral process of the nasal and the dorsal, nasal process of the maxilla.

The bony nasal septum extends back to the craniofacial gap (figs. 91, 92). It may be imperforate or have an irregular

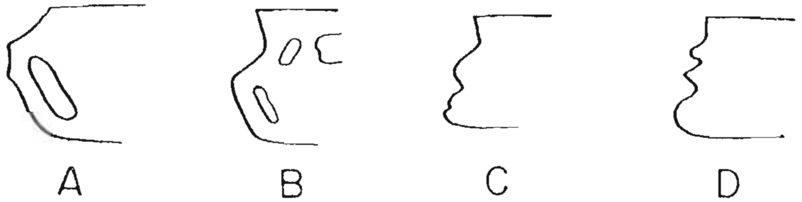


Fig. 92. Posterior outline of the nasal septa of A. *Gyps coprotheres*, B. *Aquila chrysaëtos*, C. *Elanus leucurus*, D. *Pandion haliaetus*.

perforation--the membranous nasal septum is never perforate. the size of the perforation varies with individuals as well as genera and depends apparently upon the general degree of ossification shown throughout. The septum in some genera may be thick and spongy. It appears to be made up of a central ossification over which is added a thin layer of bone from the medial vestibular wall. The posterior margin, at the craniofacial fissure, is irregular.

According to Sushkin (1905:28) "Die Einrichtung der Stirnfortsätze des Nasale ist bei den Accipitres auf zwei Typen zurüchzuführen; entweder sind sie sehr breit und stark nach innen gebogen, wie bei *Tinnunculus*, oder, sie sind schmal und schwach gebogen, wie bei *Astur, Accipiter, Buteo, Pandion, Elanus, Pernis, Gyps, Aquila, Milvus*." (figs. 50A, 111) Not nearly enough of the accipitrids or falconids have been examined to support this contention. As this feature is probably dependent upon the form of the bill, it may be diagnostic of this group and the following one.

The frontonasal hinge is simple (figs. 91, 93). The prefrontal abuts directly, without any overlap, against the side of the frontal and the nasal. This contact (except *Pandion*), when viewed dorsally, is either a straight anteroposterior line or one which curves outward anteriorly. The hinge usually shows a fissure which extends posteromedially along the line of juncture of the outer edge of the nasal where it overlaps the frontal. Movement is possible in this hinge and bending occurs mainly across the nasal at the anterior end of the frontal.

The rostrum-labial bar hinge (fig. 91) might be characterized by the long pointed spine of the premaxilla which projects posteriorly along the labial bar and the slim anterior tip of the jugal.

All accipitrids, except *Pandion*, have a free prefrontal; in the latter it is fused with the frontal and the lateral ethmoid (figs. 93A, 101M). The prefrontal has well-developed , but variable, supraorbital and orbital processes. Generally the supraorbital process is broad with a truncated tip (fig. 93). Every grade of reduction of the supraorbital process occurs from the large broad process of *Aquila* to the short, rounded-tipped one of *Chondrohierax*. The most peculiar supraorbital process is that of *Gymnogenys*; the posterior margin is squared for the reception of the nasal gland, which lies between the prefrontal and the orbit margin. *Machaerhamphus* has an inflated tip at the articulation with the superciliary.

The superciliary is either missing or extremely rudimentary in *Elanoïdes* (Shufeldt, 1909:86, noted none in six specimens), *Rostrhamus, Leptodon, Chondrohierax, Pernis, Aviceda, Pandion, Gymnogenys*, and *Neophron*. In *Gypaëtus* a superciliary is usually not indicated, but in AM 5279 a rudimentary one has been preserved. The question of the occurrency of a superciliary among the aegypiins must await study of nestlings. The presence or absence of the superciliary is relatively unimportant; it is quite evident that it represents a secondary extension of the supraorbital process. Whether it is hinged or not depends upon

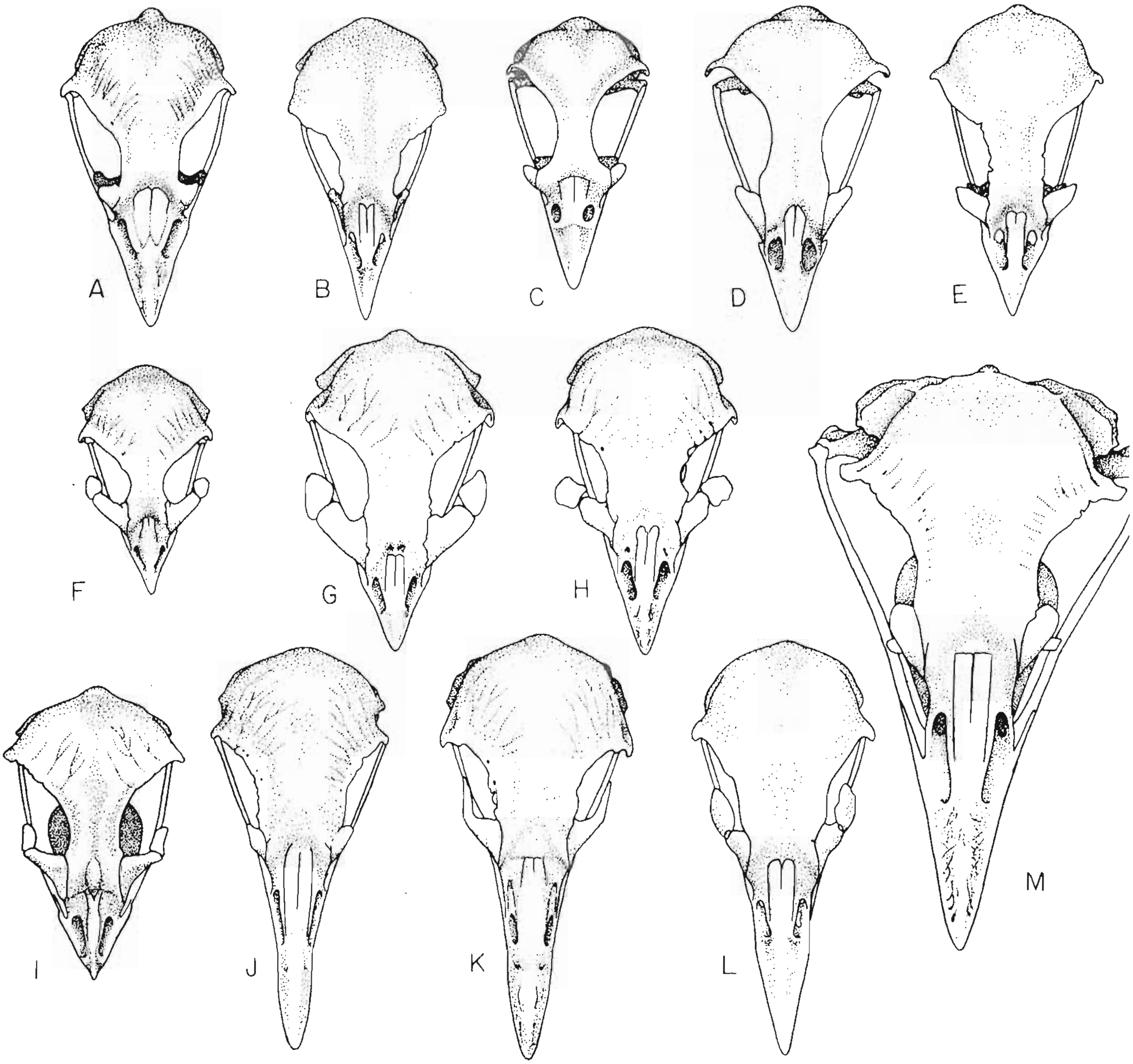


Fig. 93. Dorsal views of skulls of A. *Pandion haliaetus*, B. *Gymnogenys typicus*, C. *Chondrohierax uncinatus*, D. *Leptodon palliatus*, E. *Pernis apivorus*, F. *Accipiter cooperii*, G. *Buteo jamaicensis*, H. *Ichthyophaga ichthyaëtus*, I. *Machaerhamphus alcinus*, J. *Neophron perenopterus*, K. *Necrosyrtes monachus*, L. *Gypohierax angolensis*, M. *Gypaëtus barbatus*.

movement in this area. Its ossification occurs at or after nest leaving in *Buteo*.*

The orbital process of the prefrontal is exceedingly plastic, and, except for *Pandion*, it is free from the lateral ethmoid plate (fig. 101). Most reduced, it is a thin, downward-projecting splint of bone, round in section and fairly straight as in *Chondrohierax*, *Leptodon*, *Elanoïdes*, *Pernis*, *Aviceda* and *Gymnogenys*. More robust processes widen out into a somewhat spatulate ending and appear to represent the primitive form since such an ending is suggested in most species. Somewhat individual processes are found in *Pithecophaga* and *Harpia* in which elongation of the distal portion has taken place (correlated with deepening of the upper mandible). The form of this process in *Gampsonyx* (fig. 101F) is like that of the falconid.

Viewed from above, the skull of the accipitrid is elongate-triangular with a rounded base (fig. 93). The cranium is usually flattened above and rounded behind; it has distinct cerebral bulges and a shallow median gutter. The median depression may extend forward and become accentuated in the brow region.

The supraorbital margins may be extended, but this is never more than enough to contact the very basal portion of the supraorbital process of the prefrontal. These margins are usually less extended in those forms with a reduced prefrontal (*Pandion*, *Pernis*, *Aviceda*, *Chondrohierax*, *Leptodon*, *Elanoïdes*, *Rostrhamus*, and *Gymnogenys*), but such is not the case in *Neophron* and *Gypaëtus*. Reduction of the prefrontal is not necessarily correlated with reduction of the margins, as is seen in some species of *Accipiter*. In these, and in *Gymnogenys*, the margin, for a short distance posterior to the prefrontal, shows a shallowly excavated, squared rim; this is produced by the nasal gland.

The muscle scars in the lateral ear area show considerably more variation than in the other groups. That of the *depressor mandibulae* is of greatest interest (figs. 94, 95). In *Accipiter striatus* the origin of this muscle is restricted to the tympanic rim; *Accipiter cooperii* is intermediate toward the condition of *Accipiter gentilis* in which the origin covers a triangular area posterior to the upper rim as well as the rim more ventrally. The entire area varies somewhat individually. One of the most unique ear regions is that of *Circus* in which the tympanic margin, well back from the head of the quadrate, flares outward as a rectangular plate.

It appears that the tympanic area (fig. 95) has been molded by the temporal and cervical musculature (also by the large ex-

* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *

* Sushkin (1905:28) noted that "bei den grossen Geiern verwächst das Superciliare mit dem Thränenbein, wie das aus einer Vergleichung genannter Vögel mit *Necrosyrtes pileatus* klar zu sehen ist;..." On the same page he stated that "Dagegen fehlt dieses Element bei *Falcones*, *Polybori*, *Microhieraces*, *Micrastur*, *Herpetotheres*, desgleichen bei *Pandion*, *Pernis*, *Baza*, *Pseudogyps*, *Lophogyps*, *Vultur* [*Aegypius*] and *Otogyps*." He also noted that the superciliary is rudimentary and subject to individual variation in *Leptodon*, *Gypohierax*, *Neophron*, *Necrosyrtes*, *Gypaëtus*, and *Gymnogenys*.

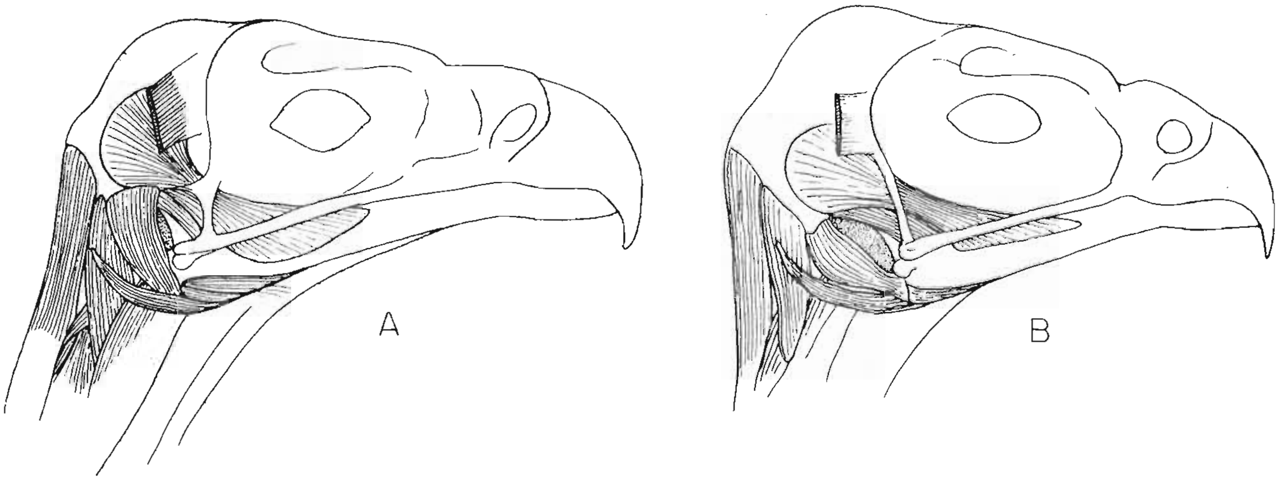


Fig. 94. Muscles of the lateral aspect of the head of A. *Aquila chrysaëtos* and B. *Accipiter cooperii.*

ternal ear opening in *Circus*) and thus reflects directly the variations and development of the muscles of this region. Engels (1940:356, 357, fig. 6) has described the variations of this region in a single genus, *Toxostoma*, and observed that, "The shifting upward of the suprameatic ridge and consequent narrowing of the temporal fossa...is related to changes in the external mandibular adductor muscle..."

Sushkin (1905:22) pointed out, concerning the zygomatic process of the squamosal, that "*Bei allen übrigen Accipitres ist dieser* Fortsatz viel schwacher [than in the Falconidae] entwickelt, und seine Maximallänge übertrifft nicht 1/4 der Langsaxe des Quadratum." The zygomatic process varies from practically lacking in *Elanus* or *Machaerhamphus* to fairly distinct but short and blunt in most accipitrids. Compared with the axillary length of the quadrate, the length of this process ranges from >0 to 25% (16-33% in the falconids, 16-27% in the cathartids).

The articular process of the squamosal is present and ranges in size from the vestige of *Gyps* (fig. 97) or *Pandion* to the well-developed, triangular, bluntly-tipped process of most. The articular process in all accipitrids, vestigial or well developed, is stout and ovoid to triangular in X-section.

The flaring of the dorsal part of the tympanic rim (fig. 96) is somewhat less than in the falconid and the basiparasphenoid plate is somewhat wider. The basitympanic process width, the distance between the lateral points of the basiparasphenoid plate, of the accipitrid skull ranges from 45.2 to 63.5% of the post-temporal width, measured across the skull at the zygomatic process of the squamosal; this compares with 60% in *Sagittarius*, a range of 40.5 to 48% in the falconids and 50 to 54% in the cathartids. Although the ranges for the accipitrids and falconids overlap, most genera of the former exceed 50% while in the latter group

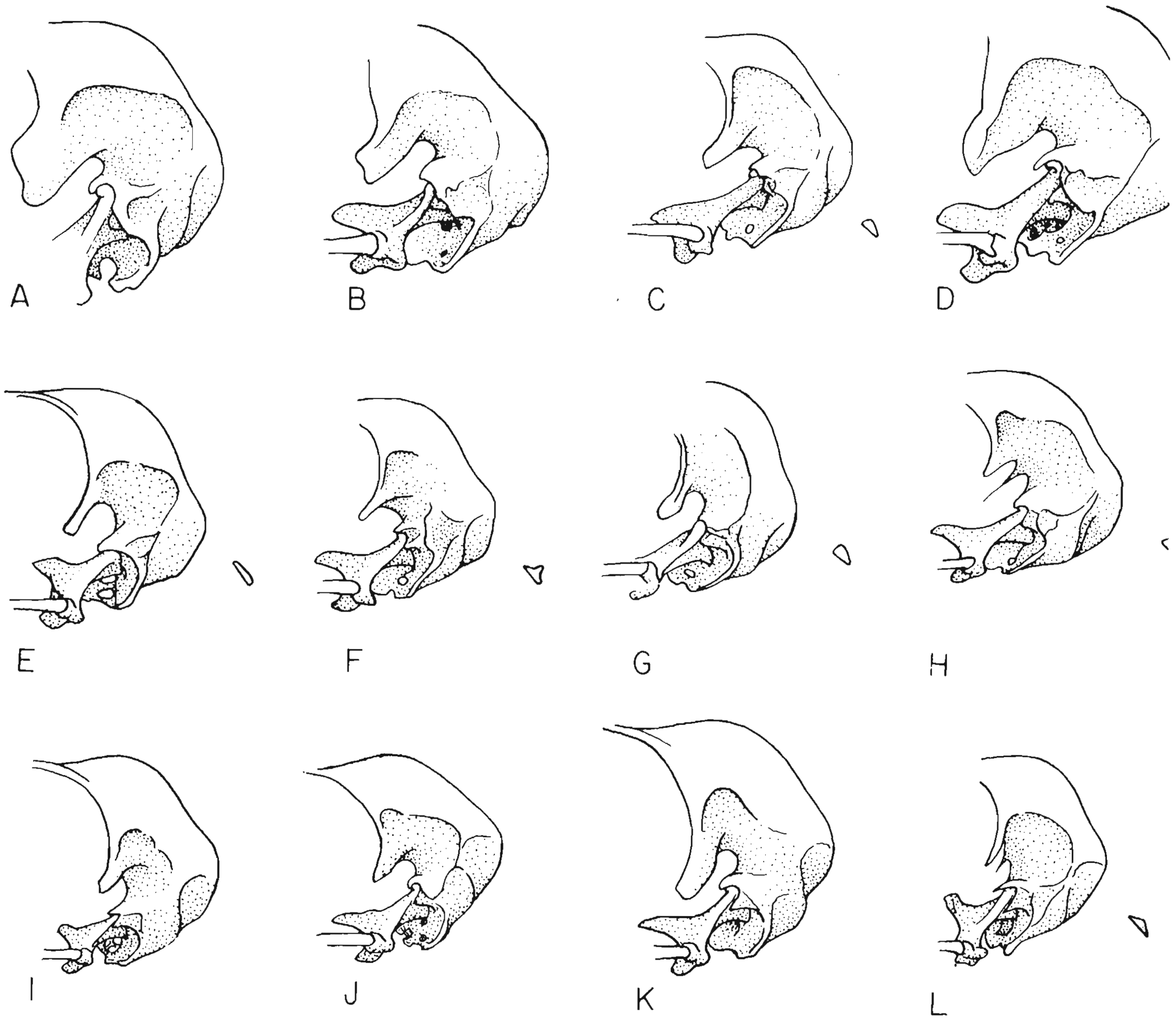


Fig. 95. Lateral views of accipitrid crania, with X-sections of articular process of squamosal of some species to right--*see* Figure 77. A. *Pithecophaga jefferi*, B. *Spizaëtus coronatus*, C. *Buteo jamaicensis*, D. *Aquila chrysaëtos*, E. *Pandion haliaetus*, F. *Circus cyaneus*, G. *Elanus leucurus*, H. *Ictinia misisippiensis*, I. *Pernis apivorus*, J. *Milvus migrans*, K. *Haematornis cheela*, L. *Chondrohierax uncinatus*.

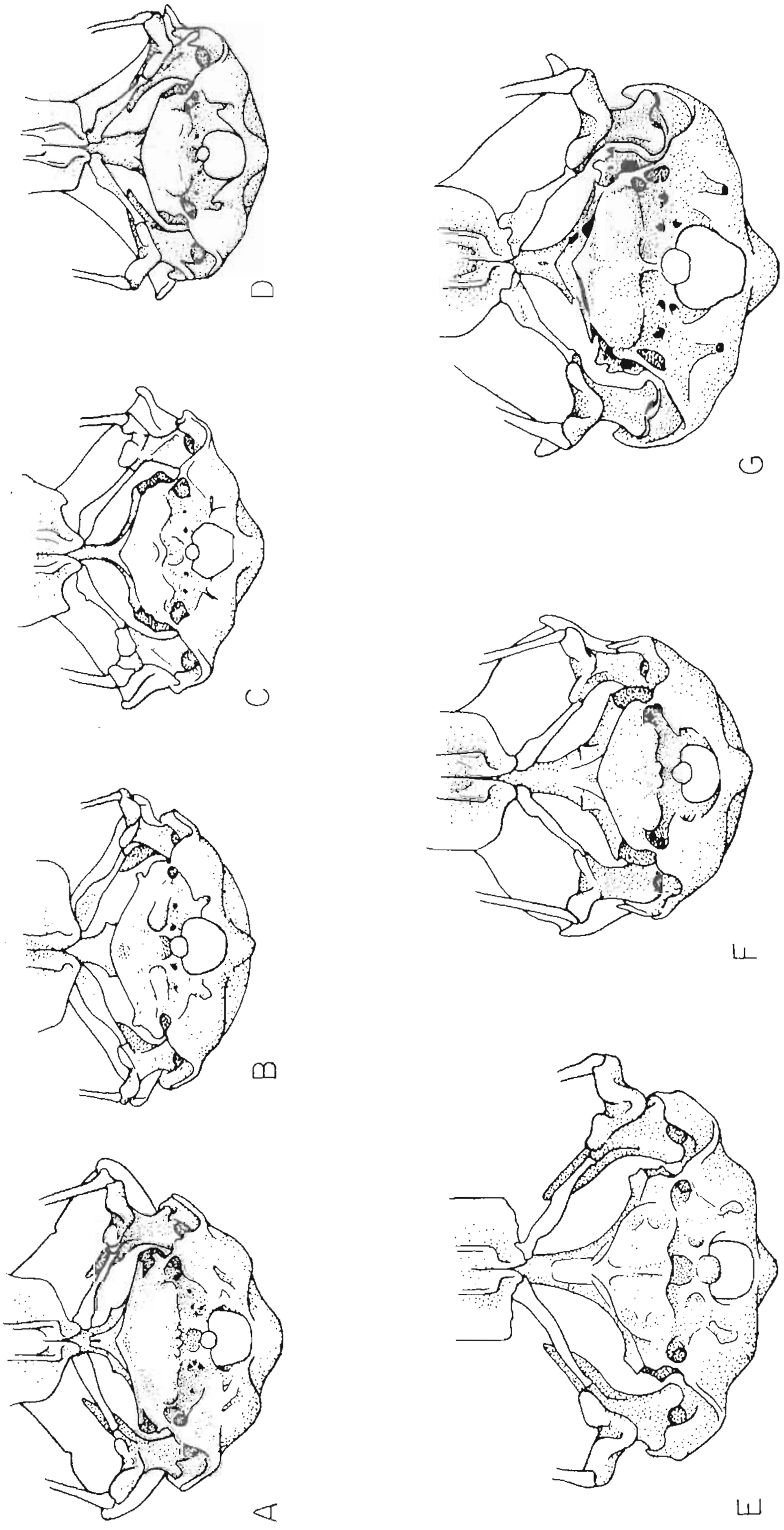


Fig. 96. Base of the cranium in A. *Buteo jamaicensis*, B. *Elanus leucurus*, C. *Machaerhamphus alcinus*, D. *Chondrohierax uncinatus*, E. *Haliaeetus leucocephalus*, F. *Gymnogenys typicus*, G. *Pandion haliaetus*.

the figure is usually below 45%.

Viewed posteriorly, the tympanic margin has a characteristic sigmoid shape. Viewed laterally this margin is more angled at the junction of the squamosal and exoccipital as compared with the more rounded line of the falconid or the even more sharply angled outline of the cathartid. A posterior tympanic process occurs in some accipitrids but involves an outgrowth of the dorsal rim as compared with the posterior margin process of the falconid (fig. 53).

The lateral basiparasphenoidal processes (fig. 96) are usually low rounded lumps showing variously scrawled, minor ridges or tubercles. The exoccipital process is a somewhat triangular, bluntly-tipped, ventroanterior projection at the ventral margin of the tympanic cavity. In *Gyps* and *Pseudogyps* (fig. 97), the development of the exoccipital and lateral basiparasphenoid processes is similar to that found in some cathartids (*Gymnogyps, Vultur,* or *Breagyps*). The cranium of *Gyps* is perhaps the most divergent of the accipitrids due to its elongation and orientation on the neck. In *Pseudogyps* the basal processes are somewhat less prominent, whereas the cranium in general tends more towards the "typical: accipitrid pattern. The plasticity of the base of the cranium, and the cranium in general, is thus indicated in the cathartids by the condors.

The median basiparasphenoid process, when present, is separated by the basioccipital pit from the occipital condyle. The former may be present or absent; when present, it may have the form of a median tubercle, which marks the posterior end of a median ridge, it may be made up of several slightly separated tubercles or be an irregular, tubercled, transverse ridge. The occipital condyle is large and rounded with a median posterior groove.

The jugular fenestra is cut off by a bony tympanic margin; the various foramina are like those of the other groups. The angle of the base of the parasphenoidal rostrum, and the plane of the foramen magnum (fig. 102, basicranial angle) varies among genera (*Gyps* 74° to *Elanus* 30°), within a genus and individually (Golden eagle, 40° to 49°; and 42° to 53° in the fossil La Brea *Aquila*).

The basipterygoids range from pointed structures, which spring from the base of the parasphenoid rostrum, to total absence. These processes are never functional nor do they show an articulatory surface. They are functional from the first stages of bone formation through the first half of nestling life (*Accipiter, Aquila, Buteo*) after which by differential growth the process and posteropterygoid become widely separated (figs. 50B, 51D).*

Remnants of the basipterygoids are usually lacking in adults of the aegypiin genera, and in *Gypohierax, Machaerhamphus, Pandion,*

* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *

* According to Chomjakoff (1901:137, "Bei den Nestjungen von *Pernis apivorus, Astur palumbarius, Accipiter nisus* habe ich auch functionirende Processus basipterygoidei gefunden. In späteren Stadien werden diese Fortsätze hier auch ruckgebildet."

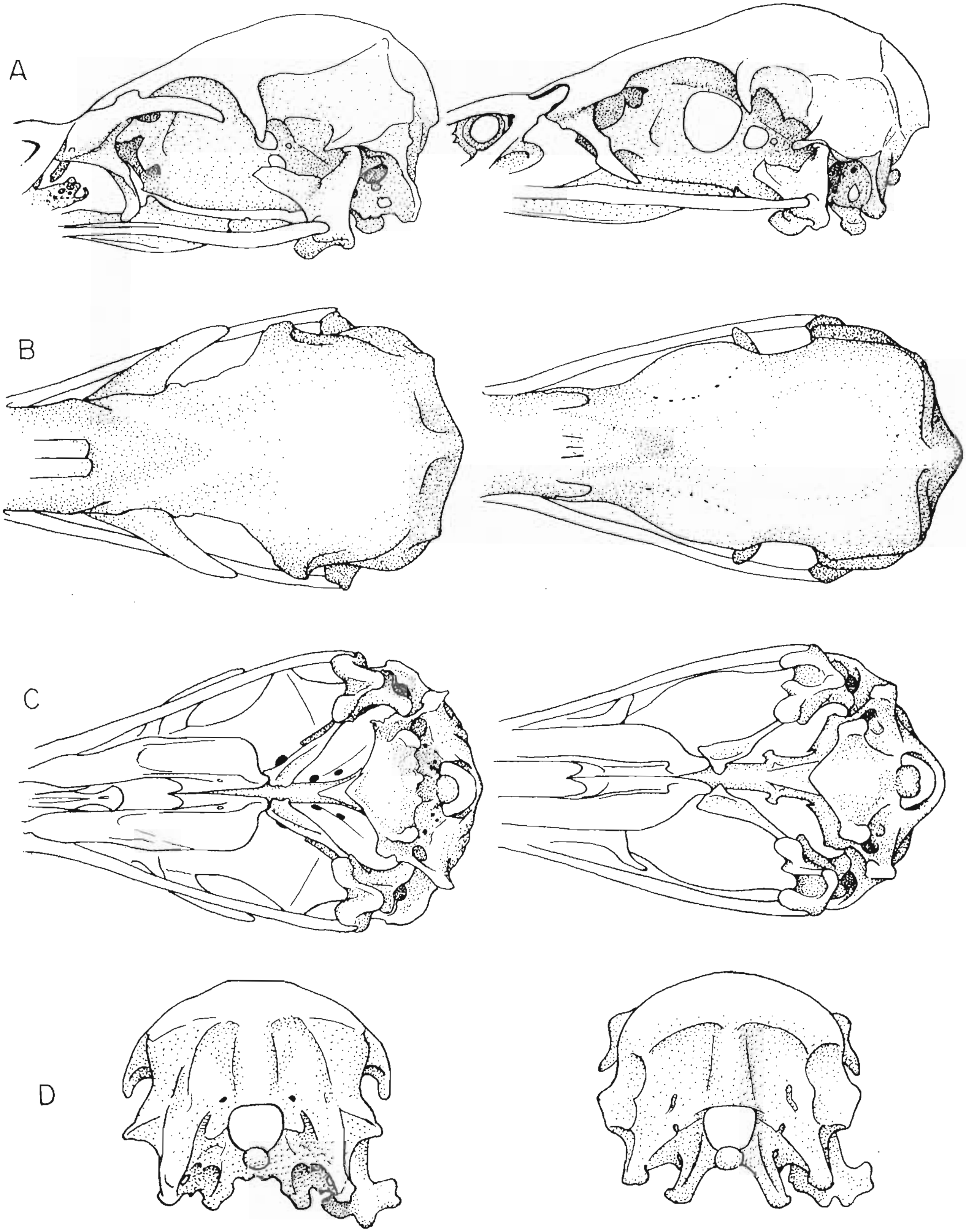


Fig. 97. Comparative figures of the crania of *Gyps coprotheres* left) and *Gymnogyps californianus* (right). A. Lateral, B. dorsal, C. ventral, D. posterior views.

*Uroaëtus*, *Haliaeetus* (excluding the *Concuma* group), and *Ichthyophaga*; they may be absent in some specimens of *Aquila chrysaëtos* (or in specimens of almost any species usually having them).

The eustachian tube may be enclosed within a bony channel or exposed by a narrow crevasse between the alaparasphenoid and basiparasphenoid. Shufeldt (1891a:237) noted that, "*Pandion* is remarkable in having the anterior openings of its eustachian tubes *entirely closed*..." He examined three skulls and one specimen in the flesh. My examination of several skulls, and a specimen in the flesh, failed to substantiate this observation; the tubes open in a normal fashion into the crevasse in the roof of the fleshy palate behind the vomer (fig. 60).

Associated with the lateral opening of the eustachian tube, there is in some accipitrids (fig. 96) a small projection of the aliparasphenoid, here called the tympanic process. This projection is especially well developed in the falconids (fig. 116).

The interorbital septum may be perforate or imperforate. It is imperforate in *Necrosyrtes*, *Gyps*, *Pseudogyps* (a small irregular perforation may occur), *Sarcogyps*, *Trigonoceps*, *Torgos*, *Aegypius*, *Gypaëtus*, *Haliaeetus leucocephalus*, *H. albicilla* (a specimen of *H. albicilla*, USNM 292774, has a minute perforation and a relatively thin septum), and *H. pelagicus*. Among the other accipitrids, the septum has a perforation the size of which varies slightly with species and individual. The interorbital perforation of specimens of the La Brea fossil *Aquila* shows a greater than usual range; in one specimen, UCMPal 28050, the septum is imperforate.

There is no real correlation of perforation size with the size of the bird, although the largest types (also probably the most specialized) tend to show an imperforate septum as suggested by Sushkin (1905:24).*

The nasal passages (fig. 98, 99, 100) differ from those of the falconid, according to Sushkin (1905:26, fig. 2), in that the cartilaginous anlage of the vestibule is incomplete ventrally. Although the nasal passages cannot be characterized beyond this, there is some variation within the group.

The vestibule has a simple fold, the "vestibular concha" of Sushkin (1905), which projects down from the dorsal wall and extends from above the nostril to the posterior wall. The size of the fold varies from a dorsal ridge to a thickened partition which nearly fills the vestibule. This fold could not be seen through the nostrils of many study skins, but it can be assumed to be found in most genera; it is known to be lacking only among the pernins (*Aviceda* and *Chondrohierax*) and in *Necrosyrtes* (and *Neophron*?).

The most peculiar nostril and fold was that of *Pandion*. Here the dorsal and ventral margins of the external naris overlap at the posteroventral corner; this may also occur in *Pernis*. As a

* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *

* Sushkin cited the case of *Haliaeetus* in support of *Fürbringer's* generalization that in larger and more specialized forms the fontanelle is reduced following the pattern of embryological development (misinterpreted by Fisher, 1944:283-284).

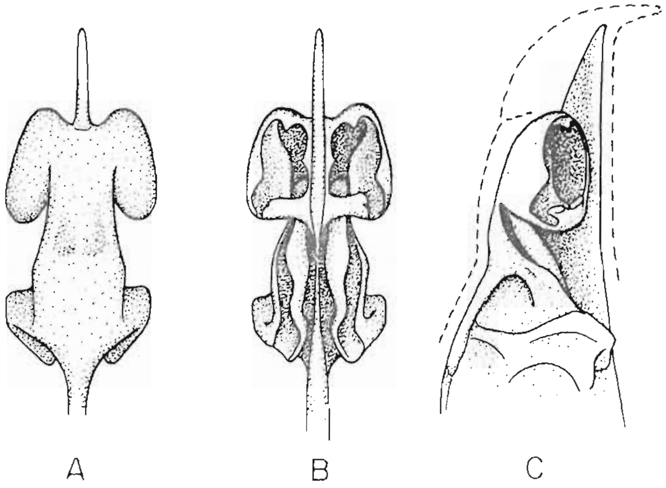


Fig. 98. Cartilaginous nasal structure of nestling *Buteo buteo* (after Sushkin, 1905, figs. 2, 3, 5). A. Dorsal, B. ventral, C. lateral views. Fleshy outline of rostrum shown with dashed line in C.

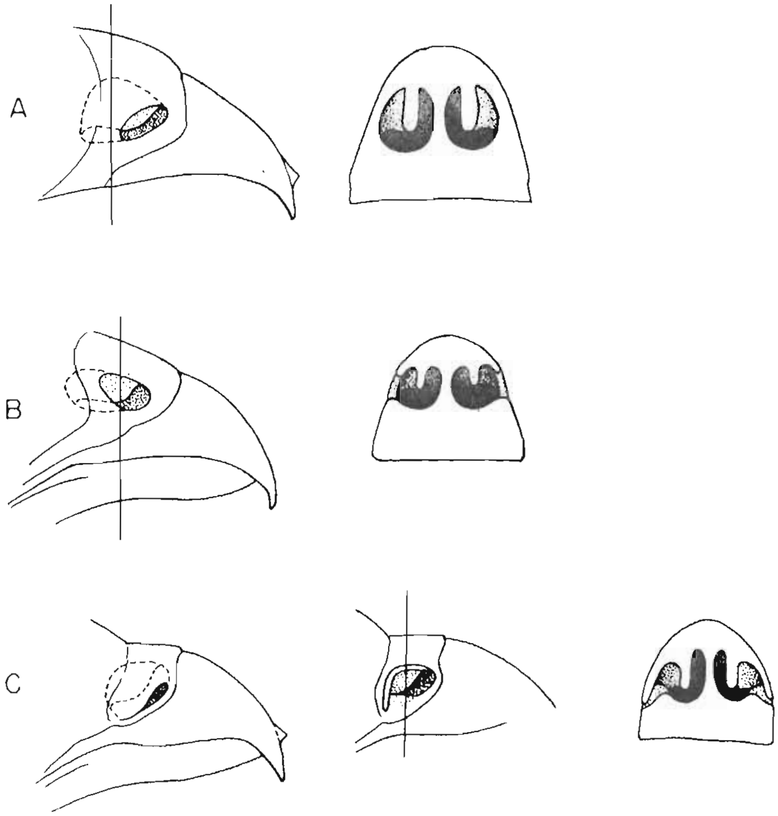


Fig. 99. Lateral view of rostrum to show external naris, vestibule and vestibular fold (dashed lines outline the last two); X-section of vestibule to right. A. Natal chick of *Aquila chrysaëtos*. B. Nestling (1 week) of *Buteo jamaicensis*. C. Natal chick of *Pandion haliaetus*, lateral view of rostrum with side wall of vestibule cut away to show folds (middle).

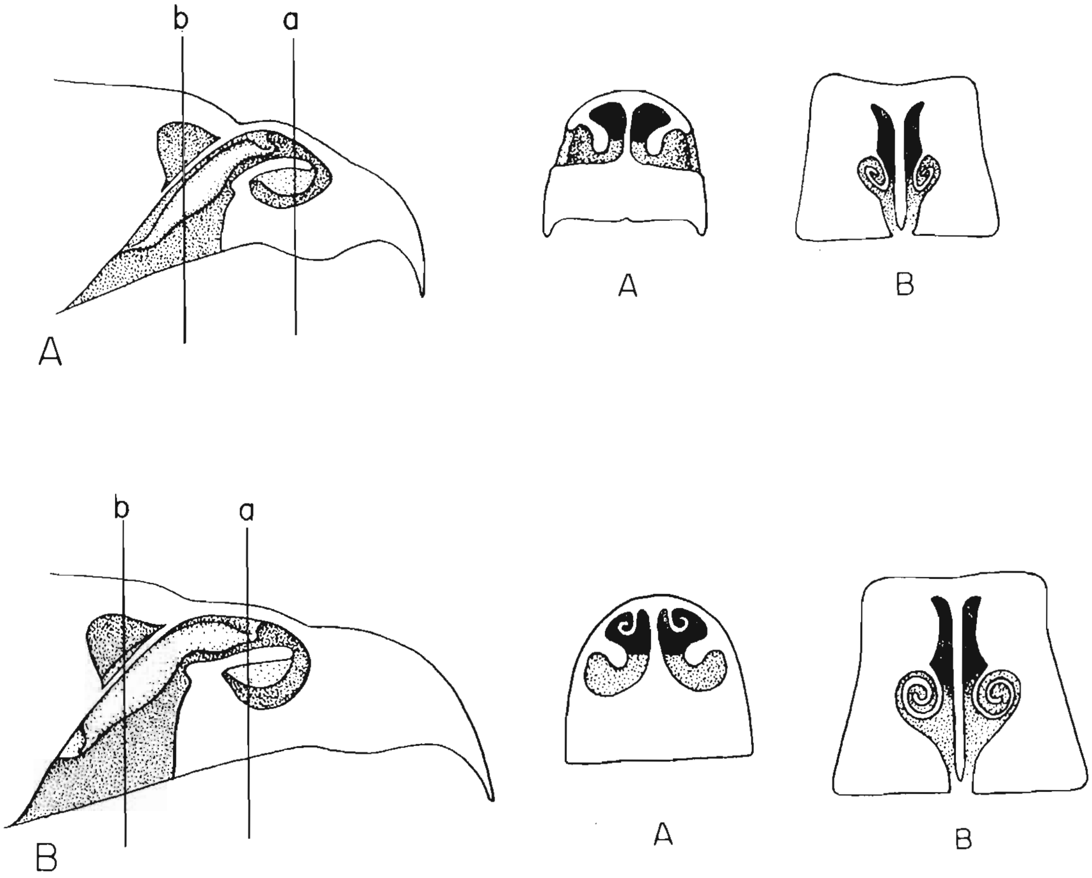


Fig. 100. Nasal passages of A. *Accipiter striatus*, B. *Aquila chrysaëtos*. Lateral outline of rostrum with nasal passage strippled (left), X-section of rostrum as seen with tip of bill cut off along line a (middle) and line b (right).

result of this overlapping, the ventral margin forms a fold jutting into the vestibule (fig. 99C).

The vestibule of *Chondrohierax* is unique in that it consists of little more than tubular extension of the external naris to the median naris. In most of the kites, *Leptodon, Pernis, Aviceda*, and *Gymnogenys* as well as *Pandion, Necrosyrtes, Neophron, Gypaëtus*, and *Gypohierax* the vestibule shows only slight constriction to form the median naris; in most accipitrids it is distinctly constricted here.

Behind the median naris the posterior passage is narrow and slit-like and into this crevasse juts the turbinal with the result that it produces a lateral bulge. The turbinal is a simple roll of highly vascularized tissue showing about two turns. It is attached along a line on the roof of the passage starting just above the median naris and extending down along the dorsolateral wall to just above the posterior end of the internal naris, where it is attached to the ventral margin of the anterior face of the ectethmoid (*see* Sushkin, 1905:25-26).

The olfactory capsule, viewed laterally, is triangular in shape with the apex at the point of entrance of the olfactory nerve. In X-section it is a thin, dorsoventral crevasse which is arched medially. This capsule may be enclosed or only partially outlined by ossification of the lateral ethmoid. *Pandion* agrees with the other accipitrids in the form of its nasal passage and olfactory capsule.

The range of variation in the mesethmoid-ectethmoid structure can be seen by comparing *Haliaeetus* with *Machaerhamphus* (fig. 101). In the former the olfactory capsule is covered by a fenestrated lateral wall whereas in the latter the olfactory bridge (under which the olfactory nerve, the ophthalmic branch of the trigeminal, and blood vessels pass) is extremely narrow and strongly folded. *Pandion* is the only genus in which the lateral ethmoid fuses with the orbital process of the prefrontal. In *Neophron, Necrosyrtes, Sarcogyps*, and *Torgos*, these structures are in contact but do not fuse. In the flesh they are bound together, and to the labial bar by connective tissue. *Gampsonyx* resembles *Falco* in this region.

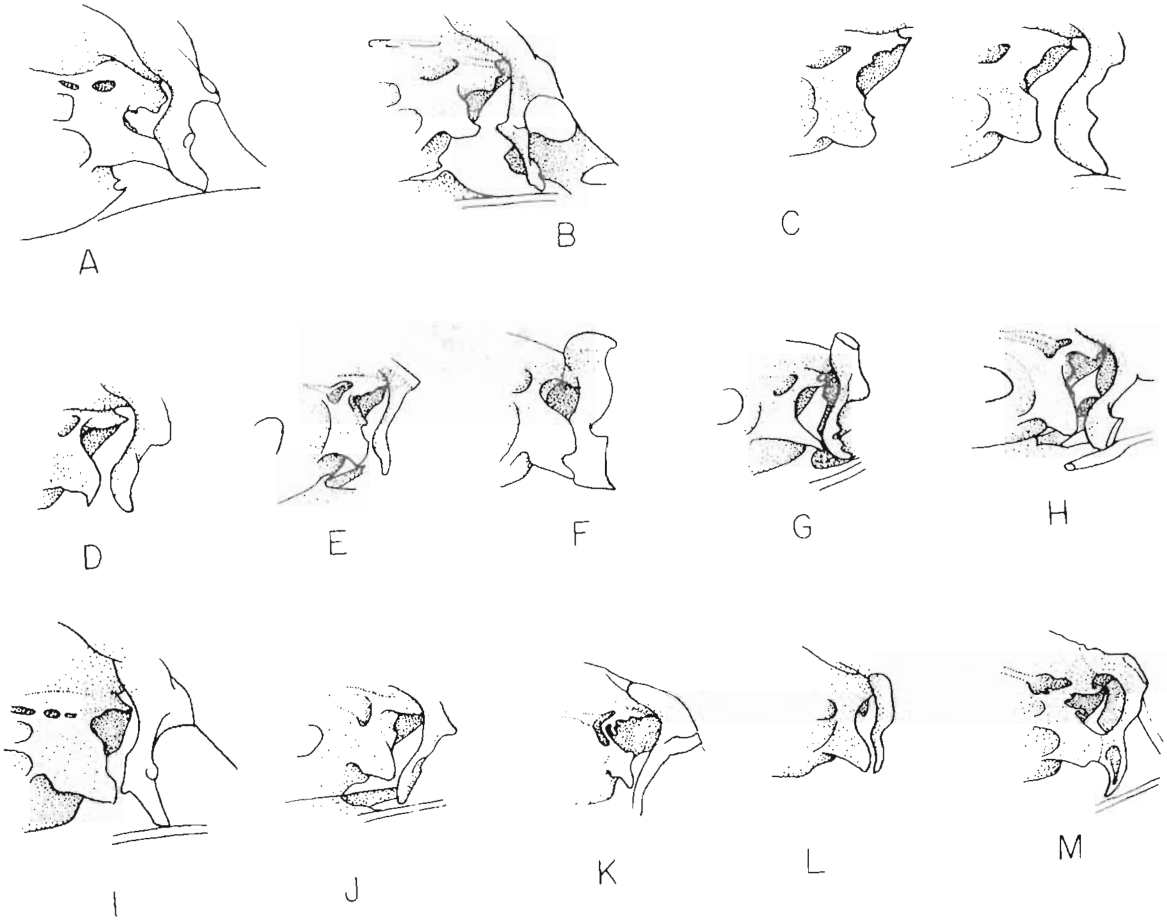


Fig. 101. Orbital views of A. *Sarcogyps calvus*, B. *Gyps coprotheres*, C. Two specimens of *Aquila chrysaëtos*, D. *Buteo jamaicensis*, E. *Milvus migrans*, F. *Gampsonyx swainsonni*, G. *Elanus leucurus*, H. *Machaerhamphus alcinus*, I. *Haliaeetus leucocephalus*, J. *Ichthyophaga ichthyaëtus*, K. *Gymnogenys typicus*, L. *Chondrohierax uncinatus*, M. *Pandion haliaetus*.

The outline of the parasphenoid rostrum and the mesethmoid at the craniofacial fissure is variable and shows nothing characteristic (fig. 102).

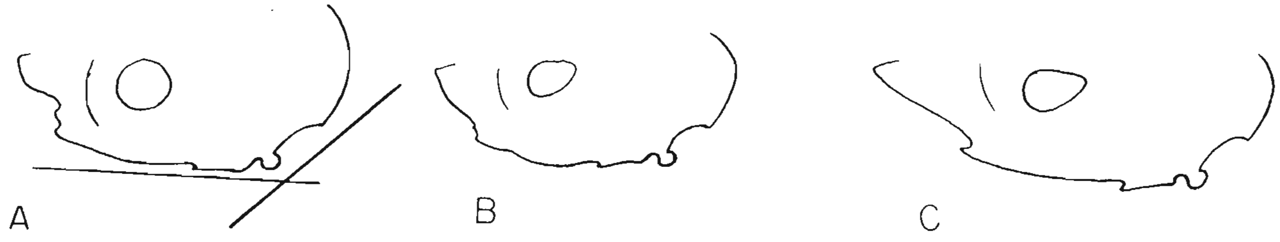


Fig. 102. Median sagittal outline of interorbital septum and back of cranium of A. *Pandion haliaetus*, B. *Chondrohierax uncinatus*, C. *Buteo jamaicensis*. Lines below show angle between base and back of cranium.

The quadrate, when viewed from below, has a distinctly triangular shape, the base forward, the outer side proportionally shortest (fig. 103). *Gyps* resembles *Gymnogyps* in this detail but lacks the cathartid-type articulation. *Rostrhamus* appears to be unique; the outer articular surface is smoothly rounded and blends into the general ventral surface while the medial articular surface is narrow and extends along the posterior margin nearly to the posterior angle. A small notch, suggestive of that in the cathartid, is found in *Necrosyrtes*, *Terathopius*, and *Haliaeetus*. A line can be seen here in other accipitrids.

Sushkin (1905:37) compared the dorsal and posterior aspects of the articular surface of the mandible of the Accipitridae and Falconidae (fig. 104). He noted that as seen from above, the accipitrid has a shallow, rounded notch on its outer posterior margin, and the inner process juts straight medially as part of a relatively straight posterior margin. A pneumatic foramen is found on the dorsal medial surface of this inner process. The cavity of the articular portion is continuous with the tympanic cavity through the foramen.

The details of the bones of the lower mandible differs from those of the cathartid and falconid. The mandible has no indication of a fontanelle (fig. 50F, 50G).

*Pandion* differs from all other falconiforms in that there is a sesamoid ossible in the mandibular ligament. This ossicle is fairly large and corresponds in position to the medial ossicle of a passerine or to the single ossicle of kingfishers, hornbills and gulls.

The hyoid apparatus of the accipitrid is like that of *Sagittarius*. The basihyal is round (or flattened above and rounded below) in section and lacks any indication of the keel of the cathartid (fig. 105). The entoglossal ossifications are elongated rods with articulation areas at their middles, which are more elongated and lateral in this group. Although hyoids were not available for every species, enough were at hand to indicate the constancy of this structure even in the more diverse members of the group.

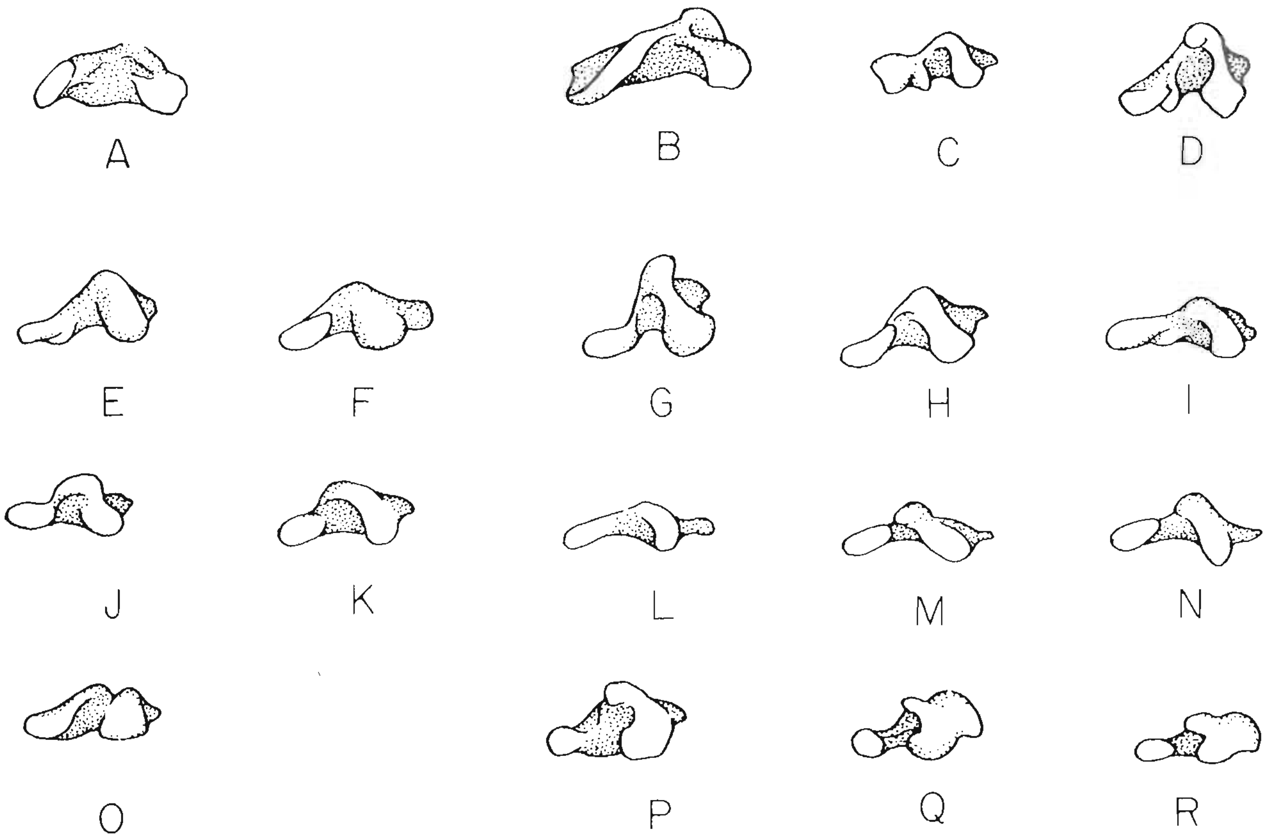


Fig. 103. Distal end of right quadrate of A. *Sagittarius serpentarius*, B. *Teratornis merriami*, C. *Cathartes aura*, D. *Gymnogyps californianus*, E. *Necrosyrtes monachus*, F. *Neophron perenopterus*, G. *Gyps coprotheres*, H. *Trigonoceps occipitalis*, I. *Gypaëtus barbatus*, J. *Gypohierax angolensis*, K. *Aquila chrysaëtos*, L. *Elanus leucurus*, M. *Chondrohierax uncinatus*, N. *Leptodon palliatus*, O. *Rostrhamus sociabilis*, P. *Herpetotheres cachinnans*, Q. *Milvago chimachima*, R. *Falco mexicanus*.

From this survey of features, the accipitrid type can be characterized as follows: the desmognathous palate is formed by the palatal processes of the maxillae meeting at the midline, behind and/or below an ossification of the ventral margin of the nasal septum which extends forward to the tip of the bill; an anterior palatal fossa is lacking; the vomer is a vertical midline plate, which shows evidence of its bilateral nature posteriorly; the nasal vestibule is partly ossified forming a median septum (frequently perforated) and partial walls in front and below; the narial opening, framed by the nasal bone, is roughly triangular in shape and usually not obstructed by ossification in the lateral vestibular wall; the rostrum is relatively small (usually less than 40% of the skull length) and strongly hooked, the premaxillary and narial portions are of about equal length; the frontonasal hinge is simple; the prefrontal is well developed, free, and usually has a superciliary bone associated with its supraorbital process; the cranium is strongly contoured

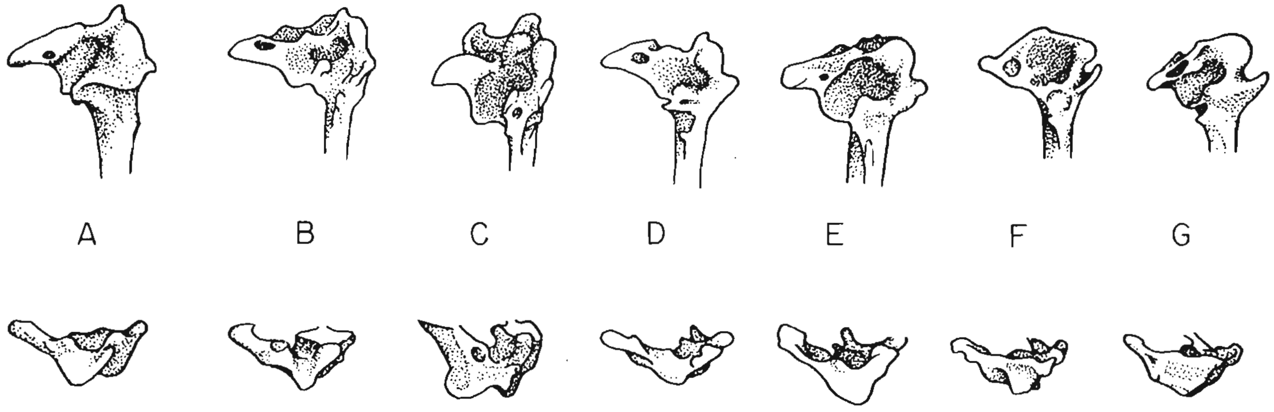


Fig. 104. Proximal end of mandible as seen dorsally (above) and from behind (below) in A. *Sagittarius serpentarius*, B. *Cathartes aura*, C. *Gymnogyps californianus*, D. *Buteo jamaicensis*, E. *Torgos tracheliotus*, F. *Falco mexicanus*, G. *Herpetotheres cachinnans*.

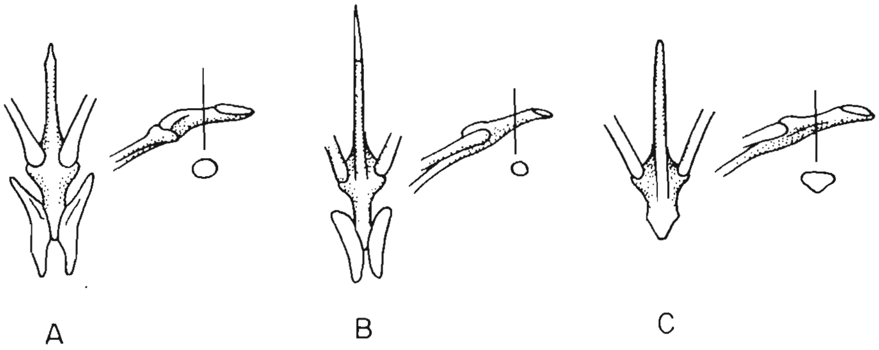


Fig. 105. Hyoid skeletons of A. *Buteo melanoleucus*, (or *Sagittarius serpentarius*); B. *Pandion haliaetus*; C. *Gypohierax angolensis*. Ventral aspect to left (anterior end down); lateral aspect of basihyal, with cross section, to right.

with cerebral bulges, median groove and grooves above the orbital margins; the orbital margins are only slightly extended; the zygomatic and articular processes of the squamosal are usually well developed; the basiptergoid processes are vestigial in the adult but functional in the early stages of the young; the mandible lacks a posterior fenestra; the basihyal is not keeled.

None of the subfamilies can be characterized on the basis of their head skeleton although certain cores of species show some differences. For example, the pernins have reduced supraorbital processes, lack superciliaries, have relatively large orbits--but these features are not limited to the group since there is a positive resemblance to *Pandion*. The aegypiins have ossified lateral walls of the vestibule and lack a separate superciliary, but again this is not always the case. The several groups mentioned--pernins, aegypiins, and accipitrins--grade into other cores of species with the result that identifiable boundaries do not exist.

### The Falconid Type

Sushkin (1899b) studied in detail the development of the head skeleton of *Falco tinnunculus*. A natal specimen of *Falco mexicanus* was cleared and stained to compare with Sushkin's account.

Like the two preceding groups, an ossified nasal septum is continued anteriorly as a bracing bar (fig. 106). In contrast to the accipitrid group, the palatine processes of the premaxilla meet medially below the septal bar. Lateral to the median ridge,

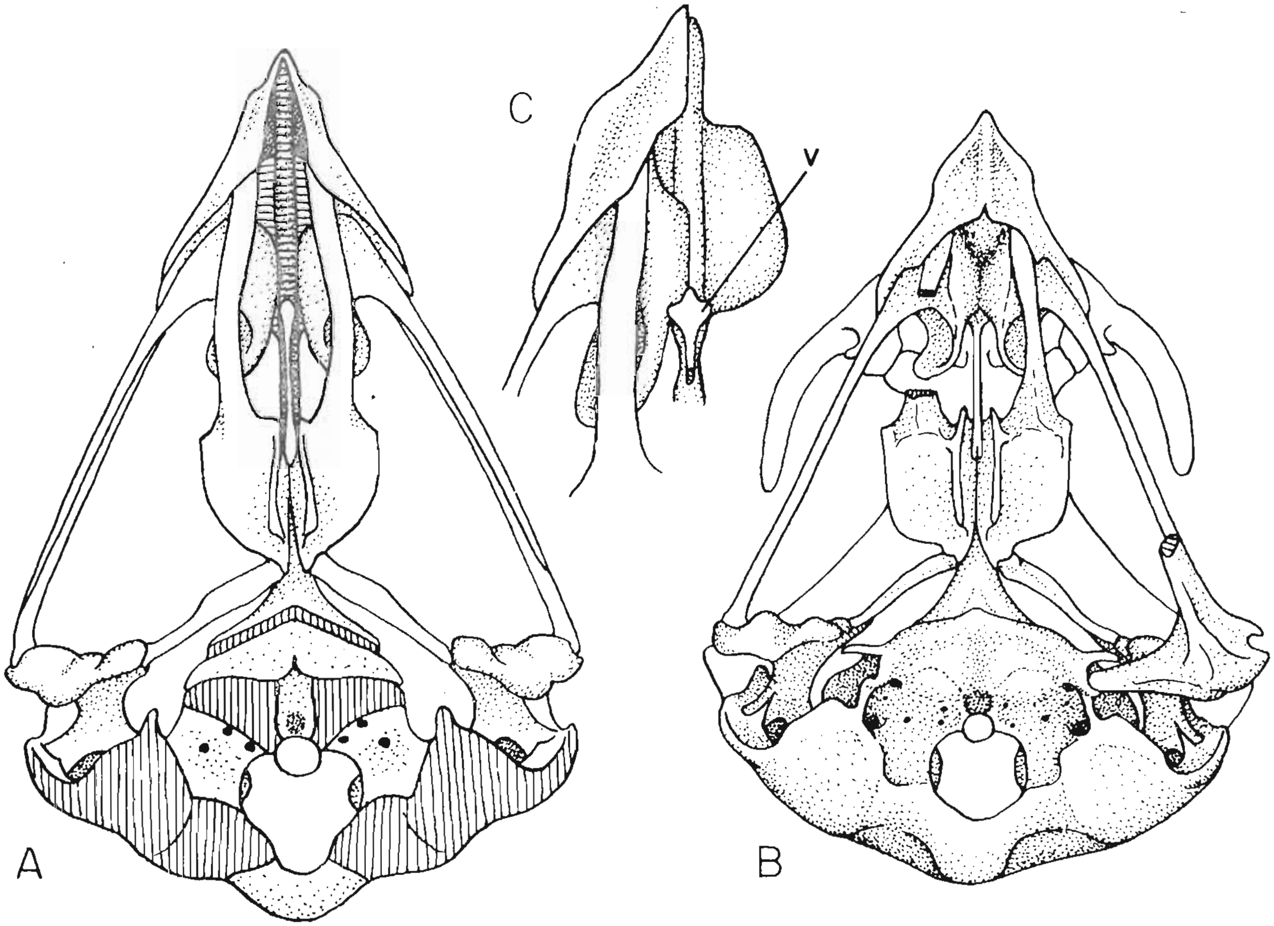


Fig. 106. Palatal views of skull of A. *Falco tinnunculus* nestling (after Sushkin), cartilaginous parts cross-hatched either vertically or transversely; B. *Falco sparverius* adult, part of palatine to left cut away to show palatal process of maxilla, a piece of mandible is shown on right side; C. Diagrammatic structure of rostrum, bones to right removed to show nasal capsule (fig. 117), vomer (V) cut off behind.

formed by the septal bar are excavations, which may be homologous with the lateral grooves of the accipitrid.

Sushkin (1905:63) pointed out that, in the flesh, the horny median palatal ridge near the tip of the upper mandible is characteristic, but such a ridge occurs in all falconiforms (fig. 107). It is not the ridge but rather the lateral depressions, which are more characteristic. In *Falco* the ridge of the prenasal bar disappears posteriorly between the maxillopalatines(fig. 106). The bar is least prominent in *Micrastur* and *Herpetotheres*, where it approaches that of an accipitrid.

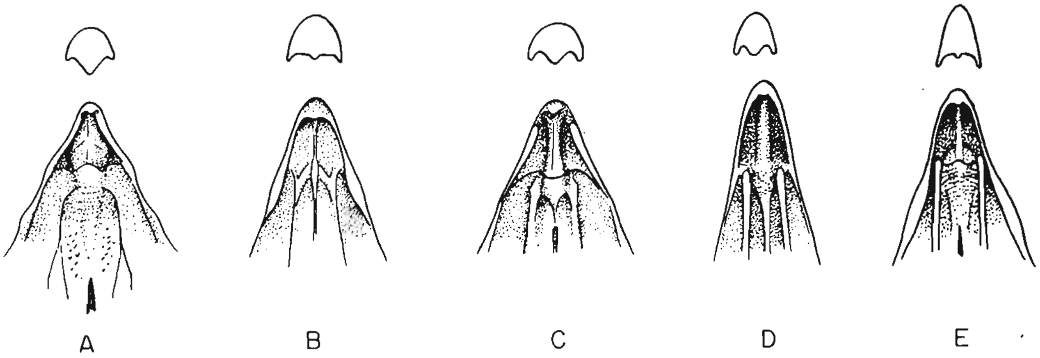


Fig. 107. Palatal aspect of tips of rostra, in the flesh, of A. *Ictinia misisippiensis*, B. *Buteo jamaicensis*, C. *Falco sparverius*, D. *Polyborus cheriway*, E. *Herpetotheres cachinnans*. X-sections through tip of rostrum shown above.

In most falconids, the small posterior palatine process of the premaxilla parallels the lateral edge of the palatine just as in the accipitrid. The relationship of the prenasal cartilage and its associated vestibule are much the same (figs. 106C); comparison indicates differences which seem to be correlated with the shortened rostrum of this group.

The tomium may show a tooth-like projection (lacking in *Polyborinae*, *Herpetotheres*, and *Micrastur*), which in its position is unlike any similar projection in the accipitrid.

The maxillopalatines are fused posteriorly along the midline for a part of their length; they tend to show a median groove at the line of juncture. Among the Polyborinae the maxillopalatines may not come in contact, they fuse with the nasal septum and the septal bar to form a solid palatal surface. The line of contact of the anterior margins of the maxillopalatines and the septal bar is well fused and the suture line is marked by foramina, which may even be observed in some of the stubby-beaked falcons (fig. 108). The posterior parts of the maxillopalatines, lying in the nasal passage wall, are usually laterally compressed and may have closed or perforated dorsolateral walls. They are more-or-less spongy in their interiors. The dorsal walls may contribute to the floor of the vestibule in such forms as *Herpetotheres*, *Micrastur*, or the *Polyborinae*.

There is nothing distinctive in the maxillopalatines, nor are there any significant differences displayed in the development of

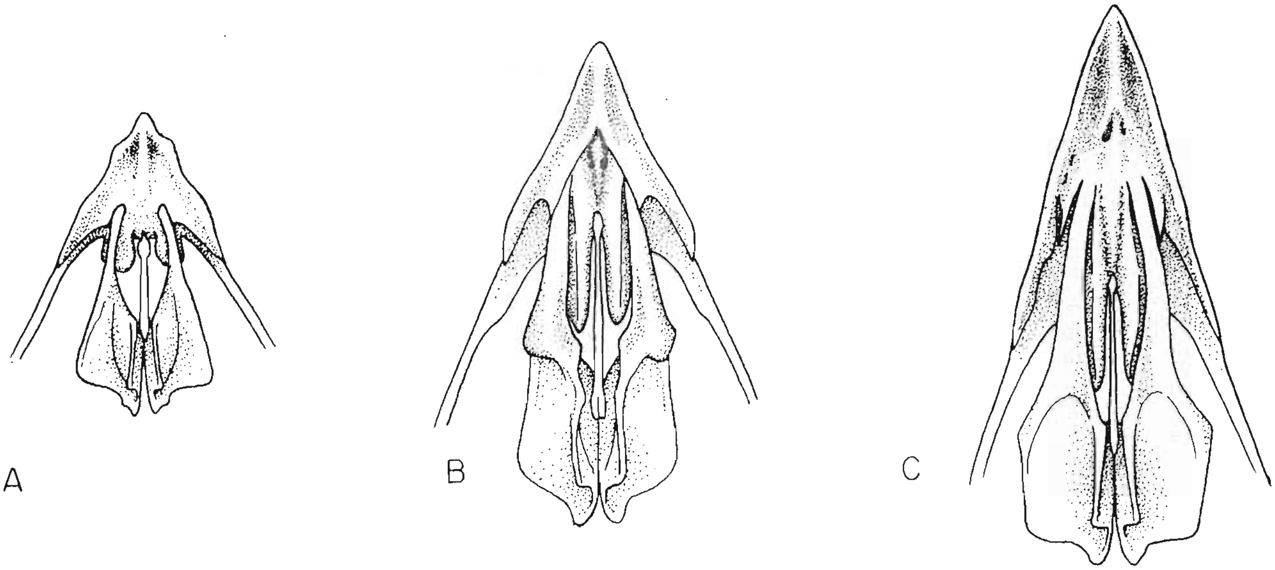


Fig. 108. Palates of A. *Microhierax caerulescens*, B. *Herpetotheres cachinnans*, C. *Polyborus cheriway*.

this palate beyond those involving the shape of the tip. Sushkin's (1905:29-30) remarks on this matter are not clear and certainly do not appear to apply to all of the falconids where the maxillopalatines meet for only a short distance (*Herpetotheres*) or scarcely meet at all (*Polyborus*). The shortened bill of *Falco* is hardly representative of the group, and, until other members have been studied, it is unsafe to generalize.

The anterior end of the palatines lies dorsal to the palatine process of the premaxilla (fig. 106C). The narrow anterior strip expands abruptly, or gradually, beneath the orbit to form the area of attachment of the *pterygoideus* muscle. A well-developed choanal ridge occurs, which is similar to that of the accipitrid (fig. 88). There is a general resemblance of palatines throughout the group, but no absolute feature for their definition.

The vomer is a well-developed splint, separated posteriorly and tipped anteriorly by a small regularly or irregularly shaped expansion, which may fuse to the tissue between the maxillopalatines (figs. 108, 109). Sushkin (1905:35) considered the falconid vomer fairly distinctive, but I cannot agree. Although the anterior knob in *Falco* is much better developed than in any accipitrid, such a knob occurs in certain members of that group (figs. 84I, 89). The knob is much reduced in *Polyborus*, *Milvago*, *Micrastur*, and *Herpetotheres* where it agrees with the accipitrid.

Sushkin (1905:34) considered the anteropterygoids to be missing among the falconid on the grounds of their absence in the nestling of *Falco* (Parker, 1879 , recorded them) and because of the lack of clasping of the parasphenoidal rostrum by the palatines throughout this group. Sushkin's observations were con-

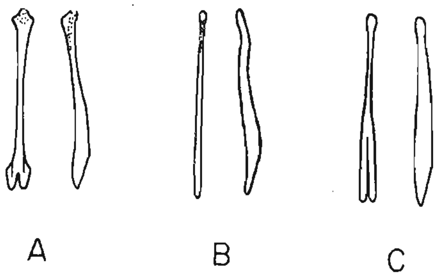


Fig. 109. Ventral (left) and lateral (right) aspects of vomers of A. *Falco peregrinus*, B. *Milvago chimachima*, C. *Micrastur semitorquatus*.

firmed by my natal specimen of *Falco mexicanus*. The situation was not as in *Gallus*, where palatine and anteropterygoid appear fused and separate from the posteropterygoid.

The shape of the upper part of the bill is variable ranging from the somewhat inflated, vaulted rostrum of *Polyborus*, or the accipitrid-like premaxilla of *Herpetotheres*, to the short, stubby premaxillary bill of the genus *Falco* and the Polihieracinae. The bill of *Milvago* is weak and gallinaceous in appearance; it is suggestive of that of *Pernis*.

The lateral walls of the vestibule are usually ossified, thus outlining the nostril. The shape of the narial aperture, as margined by the nasal bone, is triangular-ovoid, with the narrowest angle at the dorsoposterior corner. The margins of this opening are marked by grooves and foramina, especially at the narrowest angle. In *Falco* the narial opening has been reduced in length along with general rostral shortening. In *Polyborus* this opening is situated relatively high on the rostrum.

The nostril in all falconids is located along the anterior margin of the narial aperture and is round in shape. The exception is *Polyborus* in which it is an elongated, vertical opening bent posteriorly in its upper half. The nostril is outlined by the ossified lateral vestibular wall in all except *Micrastur* in which the larger part of the wall remains unossified (Sushkin, 1905, pl. III, fig. 54, shows the margin complete in *M. semitorquatus melanoleucus* and, fig. 76, incomplete in *M. ruficollis*). The vestibular wall flares outward along the posterior margin of the naris in *Herpetotheres* so that the nostril opens somewhat forward. Flaring of the nostril margin is found in *Falco* also. The lower edge of the naris in *Herpetotheres* and *Micrastur* slopes up and inward as the floor of the vestibule; in the Polyborinae the floor of the vestibule is level with the margin while in *Falco* and the Polihieracinae this margin is well above the floor (fig. 118A).

Ossification of the vestibular walls contributes to an imperforate nasal septum. Posteriorly the nasal septum presents a nearly vertical margin at the craniofacial fissure (fig. 110).

Sushkin's comments on the frontal processes of the nasal bone have already been cited (p. 93). Acceptance of this condition in *Falco* (fig. 111) as representative of the group is

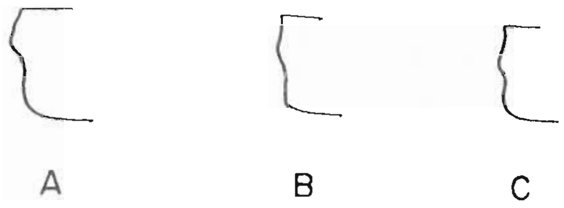
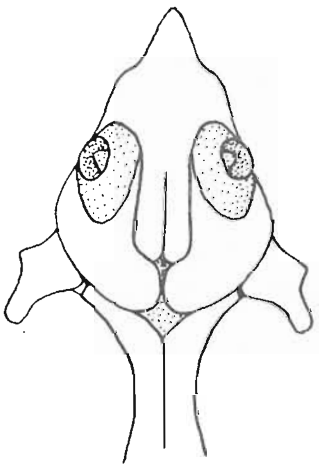
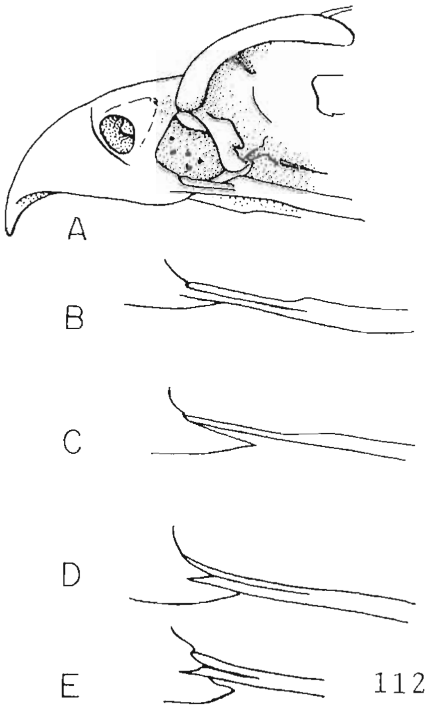


Fig. 110. Posterior outline of nasal septa of A. *Polyborus cheriway*, B. *Milvago chimachima*, C. *Falco mexicanus*.



111



112

Fig. 111. Dorsal view of rostrum of nestling *Falco tinnunculus* (after Sushkin, 1899b, Pl. V, fig. 86); compare with figures 50, 51.

Fig. 112. Lateral views of rostrum-labial bar articulation of A. *Herpetotheres cachinnans*, B. *Micrastur semitorquatus*, C. *Polyborus cheriway*, D. *Falco mexicanus*, E. *Falco albigularis*.

dangerous since it is probable a correlary of the short stubby beak of this genus. However, it can be noted that among passerines the long bill of the magpie or crow and the short bill of the junco share this type.

The frontonasal hinge may be simple, as in the accipitrid, or, in the Falconinae and Polihieracinae, the hinge may appear as a transverse straight line similar to that found among parrots (fig. 113). Usually *Microhierax* is cited in this regard (*see* Pycraft, 1902:287); a similar hinge occurs in *Falco cuvierii* (USNM 18963, 18964). Such a hinge is a result of an arched brow with an abrupt angle between the brow and the rostrum proper. The hinge is capable of easy movement. Anteriorly the nasal and prefrontal are not fused and in *Polyborus* and *Milvago* a crack appears between the nasal and frontal process of the premaxilla as in the accipitrid.

The rostrum-labial bar hinge (fig. 112) is variable but not distinctive. Sushkin (1905:36) pointed out that "eine Jugale bei *Tinnunculus* immer fehlt, dagegen bei jungen *Astur, Accipiter* und *Buteo* vorhanden ist. Vielleicht ist dieses Merkmal von noch grösserer bedeutung, daruber ist jedoch ohne eingehender Kenntniss der Jungen einer grösseren Zahl von Vertretern der *Accipitres* schwer zu urteilen, da ein Vorhandensein oder Fehlen des Jugale am Schädel eines erwachsenen Vogel nicht zu konstatiren ist." A hinge similar to that of the Accipitrid is found in *Falco peregrinus* and a jugal may be present in the adult labial bar of most genera.

The supraorbital process of the prefrontal may be reduced or well developed but never has a free superciliary bone or even an indication of such (fig. 113).* There is a positive resemblance between the condition of the supraorbital processes of aegypiins and falconids; it can be assumed that they are convergent developments.

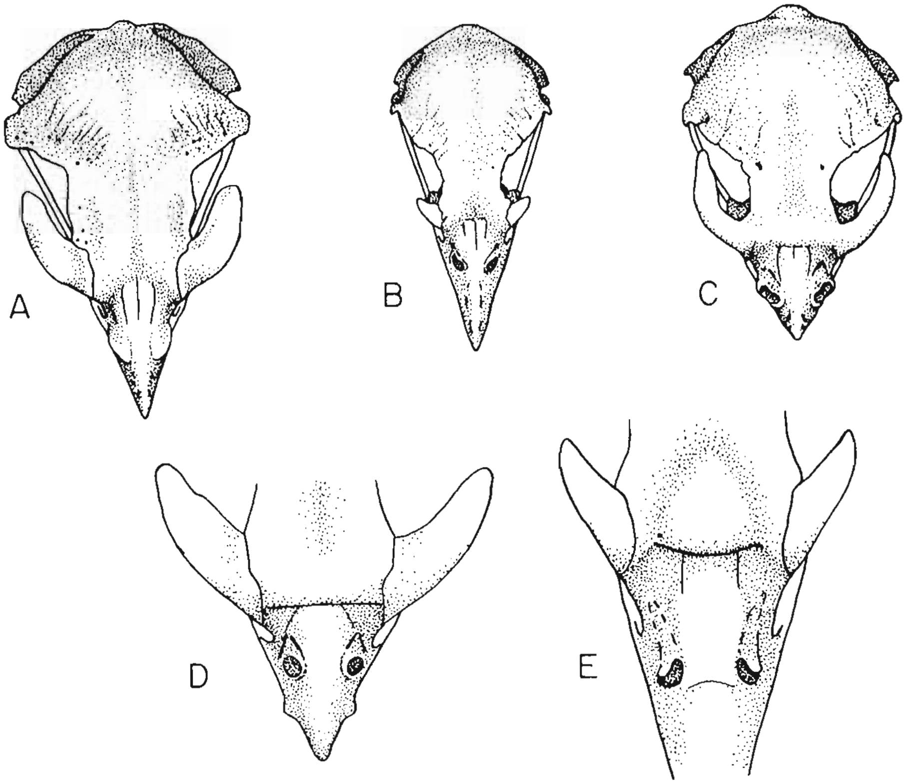


Fig. 113. Dorsal views of skull and frontonasal hinge of A. *Herpetotheres cachinnans*, B. *Milvago chimachima*, C. *Falco mexicanus*, D. *Microhierax caerulescens*, E. *Polyborus cheriway*.

* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *

* Sushkin (1905:28) in a footnote commented that "Pykraft wiederholt die irrthümliche Meinung der älteren Autoren, es sei bei den Falken das Lacrymale [should read Superciliare] am oberen Aste des Thränenbeins angewachsen."

The antorbital process of the prefrontal is characterized by a narrow, dorsolateral tear-duct notch (fig. 119). This process may be in contact, or fused over a large part of its length, with the lateral ethmoid; this condition varies within both subfamilies and genera.

The skull of the falconid may be similar in outline, as viewed dorsally, to that of the typical accipitrid; it is more rounded in *Falco*. The cranium shows the cerebral swellings and the median depression from brow to occiput, which is so characteristic of the falconiform skulls (excluding the cathartids).

The orbital margins show a certain amount of extension, and in *Herpetotheres* (and others as well) they come in contact for a short distance with the inner margin of the supraorbital process of the prefrontal. Reduction in width or length of the supraorbital process is paralleled by reduction in extension of the supraorbital margins (c.f., *Herpetotheres* to *Falco* to *Milvago*).

The tympanic region of the cranium is molded by the jaw musculature (fig. 114). This area in the falconid is especially variable in the appearance of a posterior tympanic process (fig. 115), which gives additional area for origin of the *depressor mandibulae*. In *Milvago*, *Microhierax*, or *Falco*, this process is only indicated, whereas in *Polyborus* if reaches its maximum development. In contrast to the accipitrid, the process tends to extend more from the posterior than the dorsal margin of the tympanic cavity. As a result of the presence of this process, the tympanic margin has an angle at the level of the head of the quadrate and also at the point of junction of the squamosal and exoccipital.

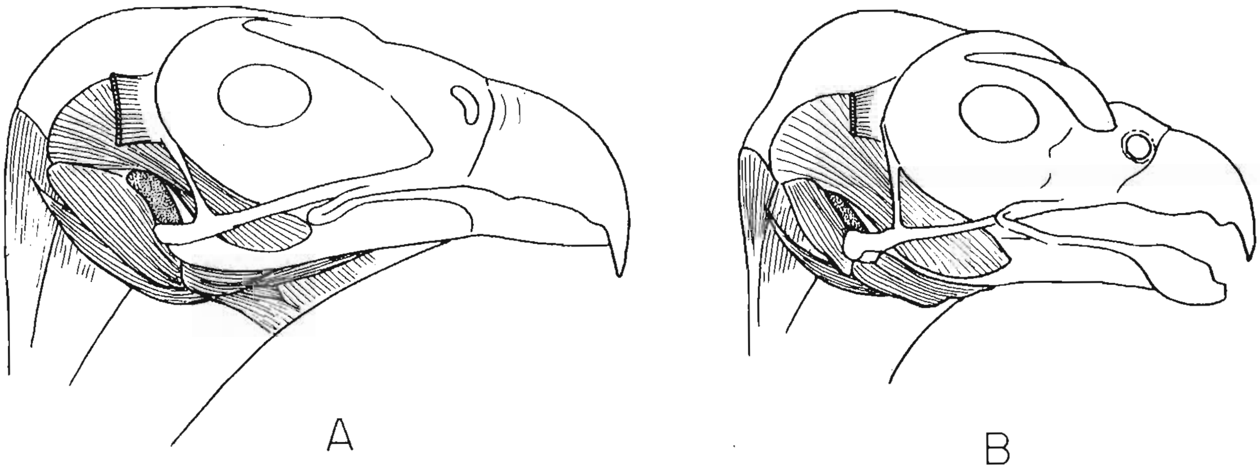


Fig. 114. Lateral view of head musculature of A. *Polyborus cheriway*, B. *Falco sparverius*.

Sushkin (1905:22) characterized the Falconidae as having a zygomatic process of the squamosal of a length equal to 2/5 or more of the quadrate length. The significance of this character is questionable and measurements are difficult to make because

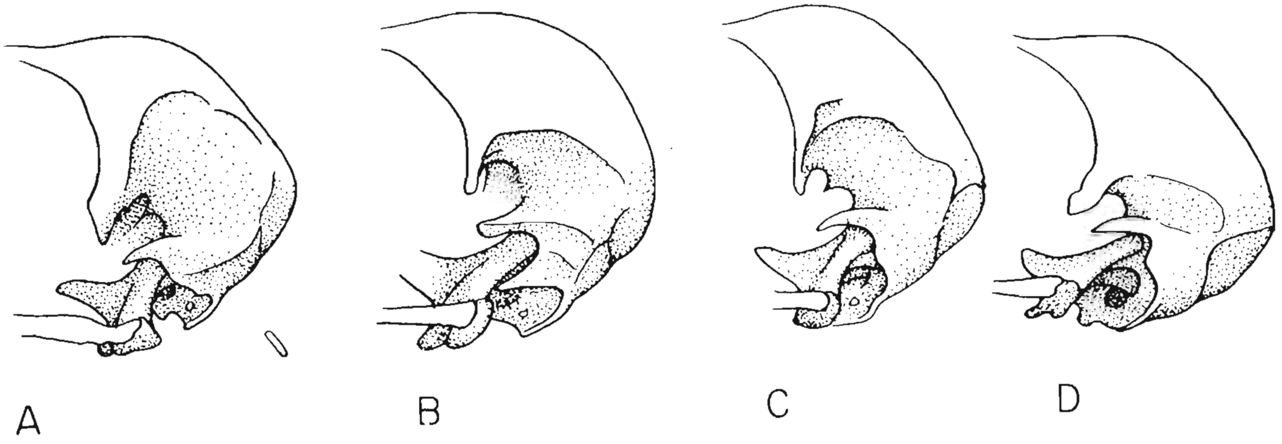


Fig. 115. Lateral aspect of the posterior part of the cranium of A. *Herpetotheres cachinnans*, B. *Polyborus cheriway*, C. *Milvago chimachima*, D. *Falco mexicanus*.

of lack of consistent reference points (*see* p. 114).

The articular process of the squamosal is a sharp-pointed structure with a thin X-section (fig. 115A). In the flesh this process is connected with the alaparasphenoid process by a ligamentous band (*see below*). Among the falconids, ossification nearly encircles the tympanic membrane.

As indicated (p. 114), in the discussion of the previous group, the proportion of the width of the basitympanic processes to the greatest posttemporal width is fairly characteristic of the group. The basitympanic porcesses of the falconid may act also as a point of articulation for the medial process of the mandible (fig. 106B). This feature appears to be unique to the group. The somewhat characteristic form of the tympanic margin and the exoccipital process width is indicated by the more rounded outline as viewed posteriorly.

Viewed ventrally, the outline of the basal depression is more rounded in the falconid than in the accipitrid (fig. 116), a subtle difference which may be more apparent than real. Otherwise the bases of the crania in these two groups are much alike in showing only slight development of the basal processes. Lateral basiparasphenoid processes are at best indistinct. As in the accipitrid the fallopian fenestra is closed, but it is usually much reduced in size. The eustachian tubes are enclosed in all.

The pointed, spine-like alaparasphenoid process on the anteroventral margin of the rostral air sac cavity, the anterior auditory recess, is characteristic, although a blunt process may occur here in some accipitrids (fig. 96). This process reaches its maximal proportions in *Milvago* in which its tip almost contacts that of the articular process of the squamosal.

Basipterygoid processes may be present or absent. They are distinct spines in *Herpetotheres* and *Micrastur*, whereas in *Polyborus* they are extremely rudimentary. Their rare occurrence

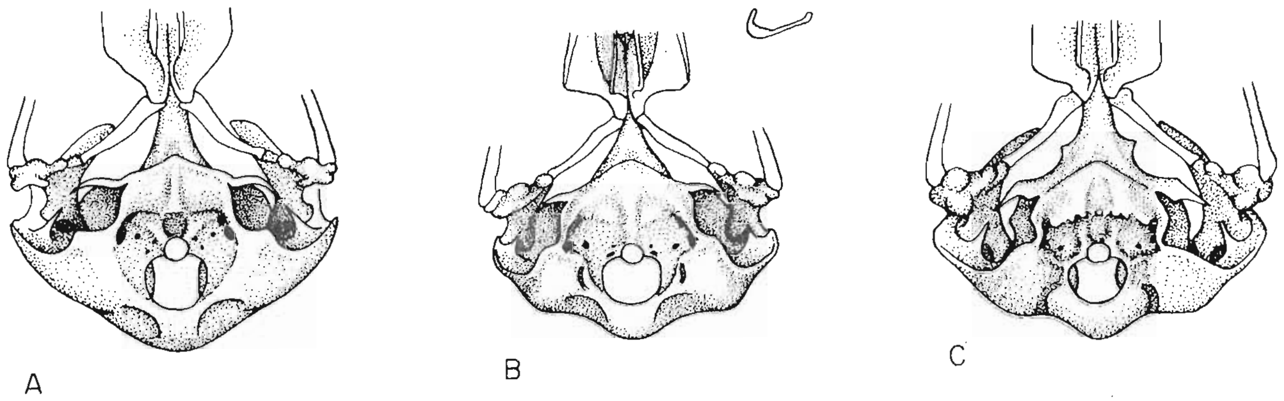


Fig. 116. Base of cranium of A. *Milvago chimachima*, B. *Microhierax caerulescens*, X-section of palatine to right, C. *Herpetotheres cachinnans*.

in adults of *Falco mexicanus* represents an atavism, since they are lacking in most species of *Falco* and in the natal specimen examined (fig. 106). Sushkin (1905:24) noted that these processes appear in the development of the skull of *Falco* but are never functional.

The interorbital septum usually has a large fenestra. The fenestra may have irregular margins (*Daptrius*), or there may be several openings (*Micrastur*). This is the only situation in which ossification is reduced as compared with the accipitrid.

The cartilaginous capsule of *Falco* differs from that of *Buteo* in that the vestibule is completely enclosed (fig. 117). The form of the vestibule is somewhat variable, it is expanded and globular in *Falco* or laterally compressed in *Polyborus*; in all it constricts posteriorly and dorsally to the median naris (fig. 118). The vestibular fold of *Falco*, *Ieracidea*, *Polihierax*, and *Spiziapteryx* is cupshaped and well ossified; it is associated with a second, anteromedially directed fold from the lateral wall. The remainder of the falconids (including *Microhierax*) have a simple vestibular fold like that of the accipitrid.

The median naris is high and somewhat restricted with the result that the nasal turbinal does not appear to project into the vestibule. This turbinal of *Falco* has a T-shaped X-section, especially midway along its length (fig. 118). Its length is not proportional to that of the previous group due probably to shortening of the rostrum. Sushkin (1905:25) stressed the point that posteriorly it is not fused to the lateral ethmoid as in the accipitrid. The form of the turbinal of *Polyborus* and its relationships to the lateral ethmoid is just as in *Buteo*. *Polihierax* is peculiar in that the turbinal has only an indication of the roll observed in *Buteo* or *Polyborus*, being little more than a plate extending down into the nasal passage.

The olfactory capsule is similar to that of the accipitrid.

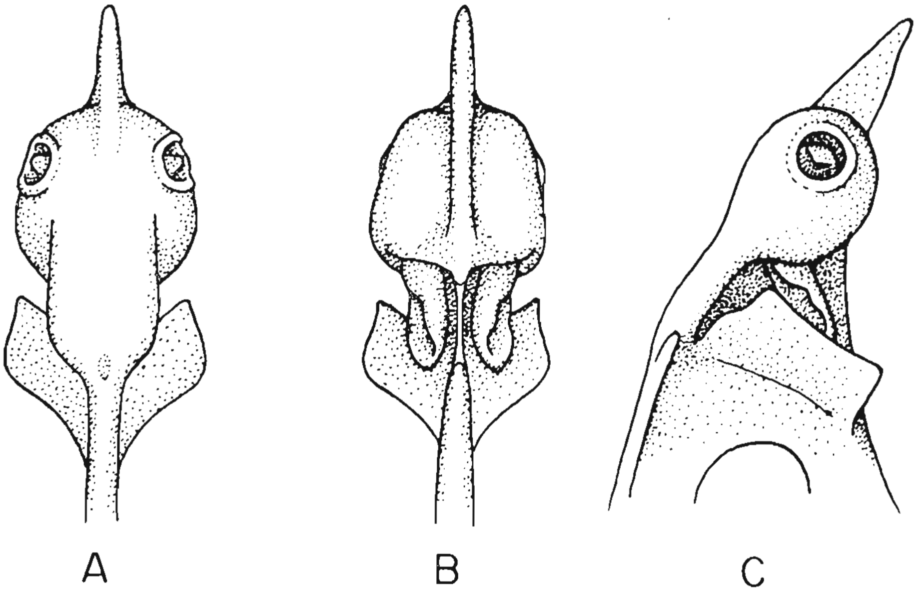


Fig. 117. The cartilaginous nasal capsule of an embryo of *Falco tinnunculus* (after Sushkin 1899b and 1900). A. Dorsal, B. ventral, C. lateral views.

In X-section it is a narrow, vertical fissure which arches medially; viewed laterally it is triangular, the apex at the point of entrance of the olfactory nerve. It lies just posterior to the craniofacial fissure. The opening of this capsule lies medial to, and is partially obstructed by, the nasal turbinal.

The lateral ethmoid (fig. 119) is well developed throughout the group and laterally contacts or fuses with the orbital process of the prefrontal for a significant part of the length of that process. The olfactory loop of the lateral ethmoid may be wide, as in *Herpetotheres*, or reduced, as in *Falco*. In *Polyborus* and *Milvago* (also one specimen of *Falco albigularis*) it is missing entirely. Sushkin (1905:27) mentioned that the passageway between the orbital and rostral cavities, between the ectethmoid and the orbital process of the prefrontal, is much reduced as compared with the accipitrids. The condition of the falconid is approached by *Gampsonyx* (fig. 101).

The outline of the parasphenoidal rostrum and the craniofacial fissure may be significantly different (fig. 120). Sushkin (1905:24-25) stated that, "Im allgemeinen, ist der Unterrand des Septums gerade, oder er ist gekrümmt in Form eines liegenden S bei Falken, Karakaren, Microhieraces..., *Micrastur*, *Herpetotheres*;..." The latter form seems to be more applicable.

The outer articular surface of the quadrate has its axis running posteriorly and shows only a partial median curve in *Herpetotheres* (fig. 103). In *Falco* this surface is constricted anteroposteriorly. The over-all configuration and outline is not matched in other falconiforms.

The articular surface of the mandible has a deep lateral notch with the anterior process elongated and hooked posteriorly

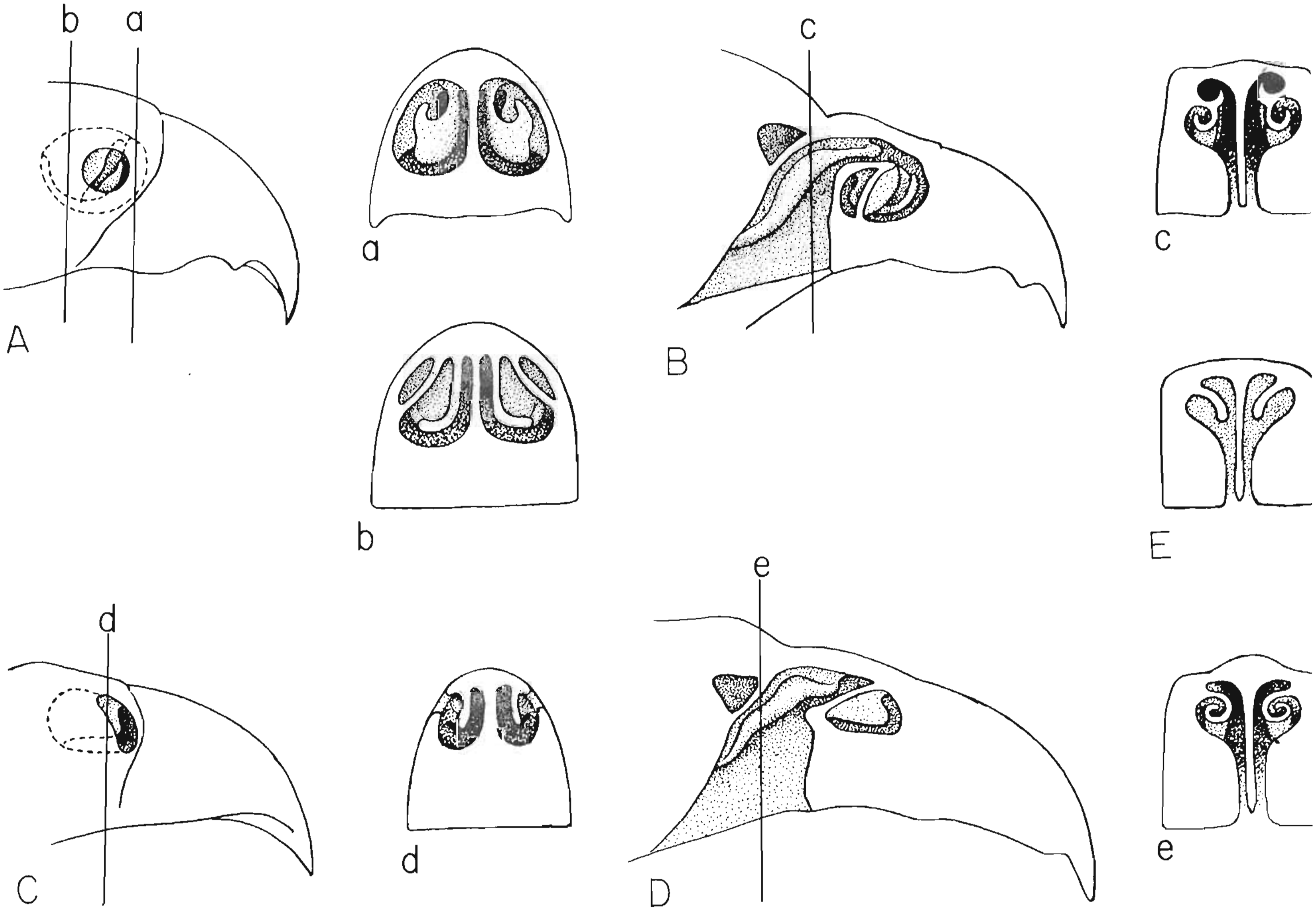


Fig. 118. Nasal passages of A-B. *Falco sparverius*, C-D. *Polyborus cheriway*; lateral view of rostrum with outline of vestibule and folds in dashed line (left), X-sections of rostrum as seen with tip cut off along lines a, b and d (left of middle), B-D. sagittal sections of rostrum showing vestibular and nasal turbinals, X-section of rostrum as seen with tip cut off along lines c (above) and e (below). E. Section similar to c or e but for *Polihierax*.

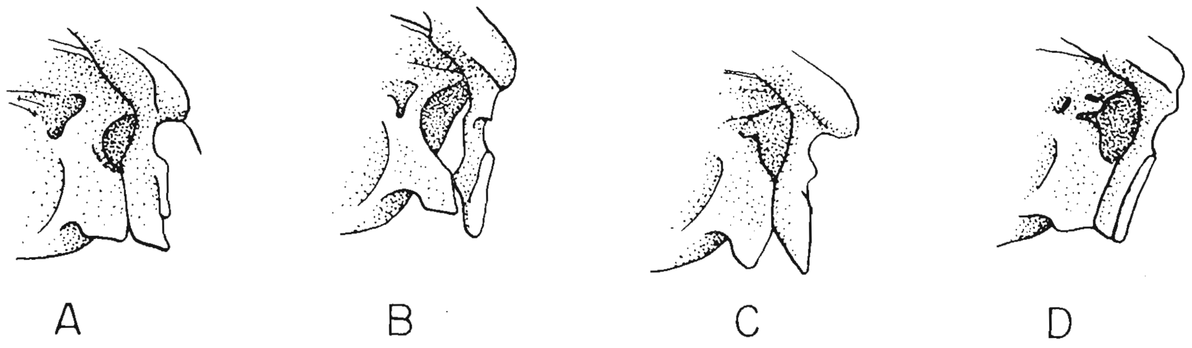
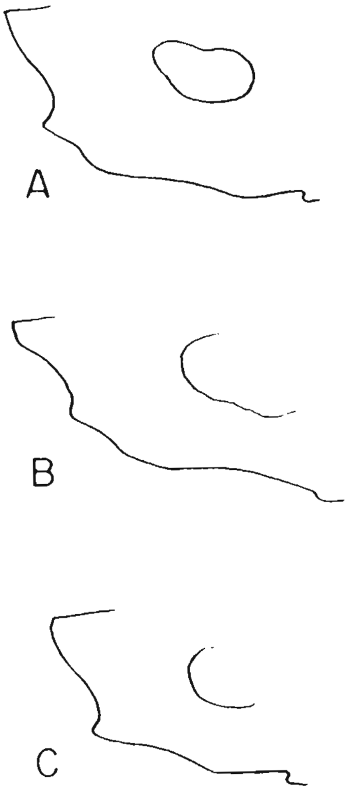
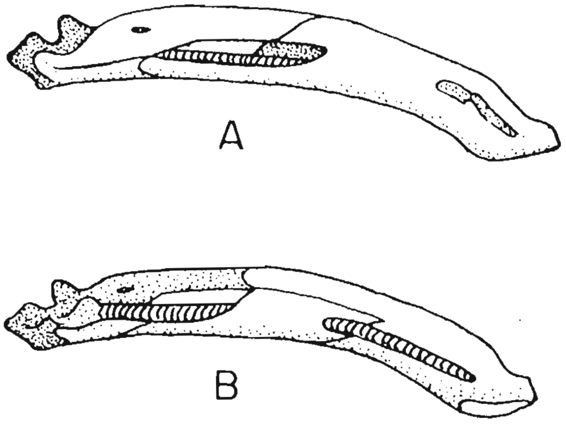


Fig. 119. Orbital views of ethmoid area of A. *Herpetotheres cachinnans*, B. *Micrastur semitorquatus*, C. *Polyborus cheriway*, D. *Falco mexicanus*.





121

Fig. 120. Median sagittal outline of interorbital septum and back of cranium of A. *Herpetotheres cachinnans*, B. *Polyborus cheriway*, C. *Falco mexicanus*.

Fig. 121. Lateral (A) and medial (B) views of the mandible of a natal *Falco tinnunculus* (after Sushkin, 1905, fig. 9). See fig. 50 for labels.

(fig. 104). In its structure (fig. 121) the mandible differs from the accipitrid or cathartid in that the prearticular is small. There is usually a large posterior fontanelle. In *Microhierax* and some specimens of *Falco* (*Falco albigularis*, USNM 289804, and *Falco peregrinus*, USNM 291184) the inner and outer plates (splenial and supraangular) lap to close the fontanelle. In agreement with Sushkin's (1905:36-37) conclusions, the presence of a fenestra in most species is a useful feature.

The basihyal (fig. 122) of the falconid has a distinctive surface for the entoglossal articulation. In *Falco* and *Polyborus* this element is laterally compressed and is not matched by that of any of the accipitrids. *Microhierax* differs in having a slight keel on the basihyal. The entoglossal ossifications are much like those of the accipitrid or sagittariid, although usually more squared and meeting (or fusing) anteriorly.

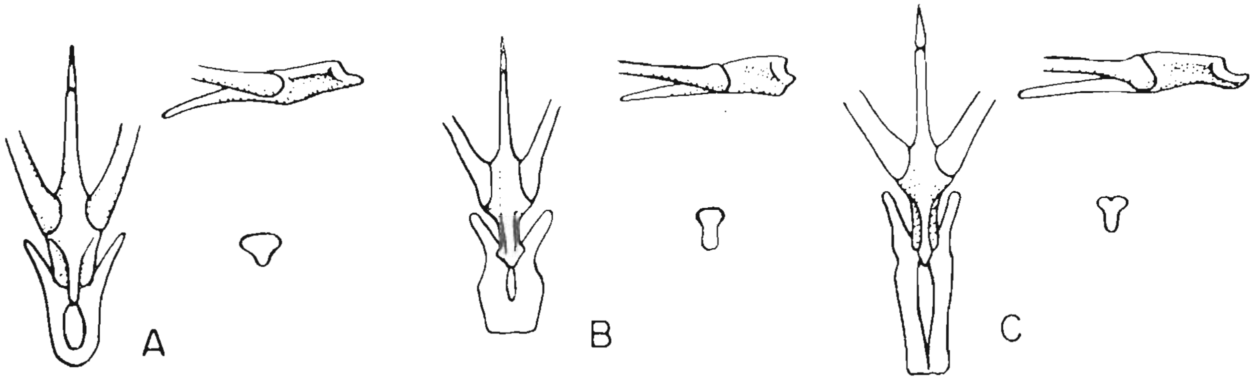


Fig. 122. Hyoid bones of A. *Microhierax caerulescens*, B. *Falco sparverius*, C. *Polyborus cheriway*.

In summary, the falconid skull can be characterized as resembling the accipitrid in most features and differing only in having the palatine processes of the premaxillae fused anteriorly below the septal bar; in more complete ossification of the nasal capsule, including its lateral wall; in lacking a superciliary; in the better development of the articular process of the squamosal, the tip of which is associated with a distinct alaparasphenoid spine; in greater reduction of the basipterygoid processes, perhaps never functional; in lacking identifiable anteropterygoids; in having a posterior fenestra in the mandible and a reduced prearticular.

Most of these are quantitative differences, but there are apparent gaps between the "averages" of the two groups. In other features that might be cited, such "gaps" are not as convincing. Of the above, only the lack of the superciliary is striking, although the fusion of the premaxilla below the septal bar and the condition of the mandible may in the final analysis be more important. In this first detail the falconid agrees with *Sagittarius*; it differs from *Sagittarius* in the premaxillary feature, lacking functional basipterygoids, and in having a posterior fontanelle in the mandible.

The falconid type shows a restricted range of variation without any sharp subdivision. Minor details could be cited to support some of the existing subfamilies; for example, the Polyborinae have a distinct posterior palatal process of the premaxilla and a reduced supraorbital process of the prefrontal. In terms of the head skeleton the Falconinae blend with the Polihieracinae.

## Summary and Conclusions

The structure of the palate has been much utilized in comparing different kinds of birds; a part of this comparison has been the use of the terms "schizognathous" and "desmognathous." These terms have been variously defined and subtypes of the latter identified. Pycraft (1902:289) described the palate of the cathartid as, "Of the indirect desmognathous type on account of the fact that the nasal septum expands ventrally into a horizontal plate, fusing on either side with a pair of strap-shaped laminae arising from the inner dorsal border of the maxillopalatine processes." The use of "indirectly desmognathous" in reference to the cathartids obscures the basic similarity of this palate to that of other "schizognathous" forms and assumes a similarity to the "desmognathous" plates of the other falconiforms.

The facts presented by the falconiforms, in terms of adult anatomy and development combined with similar information from other birds, suggest that the dromaeognathous type of palate, as expressed in part by the embryo of *Struthio* (Hofer, 1949, fig. 15A; Lang, 1956, fig. 14), is the more primitive type from which various types have evolved. Thus, the primitive palate had a complete pterygoid in contact with the vomer. For many of the Neognathae (including certainly the cathartid) a schizognathous type, suggestive of the charadriiform or bustard, appears to have been the point of origin. It is possible that all of the falconiforms started from this last ancestral type. Ossification of the nasal capsule as well as medial extension of the palatine processes of the premaxillae and maxillae have produced various types of "desmognathous" palates. Those of three of the falconiform groups (sagittariid, accipitrid, and falconid) are directly comparable and have been the main support for the continued union of these in a common order. It is unlikely that this trio shared an immediate common ancestor with the schizognathous cathartid, but surely, along with other orders, they share a distant ancestor which was "schizognathous".

None of the other features of the skull or mandible appears to be as useful as the palate. There can be little doubt that functional basipterygoid processes are primitive, but these processes range from functional to lacking in the procellariiforms, the charadriiforms, and the falconiforms. A complete pterygoid (as in the palaeognath or in foetal accipitrids) is primitive but among the neognaths there is some, apparently erratic, variation in the adult form. The form and relationships of the individual bones in the cranium--i.e., the frontal processes of the nasal--may supply useful features, but this area of knowledge has not yet been explored. The narial aperture is relatively constant in the falconiform array. The prefrontal is sometimes useful. It separates the accipitrids and the cathartids from the others and from each other. Among the accipitrids the trend appears to have been from a small prefrontal, without a superciliary--i.e., like most birds, to one with a large supraorbital process and a superciliary. In the aegypiins extension into the supraorbital membrane occurred, as in the falconid, without development of the superciliary. The superciliary is probably a functional modification related to rotation of eyes forward for binocular vision in the "keener-eyed" predators.

As a functional modification, Wetmore (1944:60) assumed that the venation of the cranium of the cathartid is the result of increased blood supply to a thickened naked skin covering the head. Such a view may be correct, but it must remain purely speculative as the available facts do not support it. The heads of cathartids are no more "naked" than those of aegypiin vultures, which show no more venation than types with feathered heads. Pelicans are not bare-headed, but the tops of their crania resemble those of the cathartids.

The general form of the cranium, its basal processes and tampanic rim are certainly plastic as is indicated in the convergence of the condor and the gryphon vulture. The drastic tympanic margin alteration of *Circus* or *Polyborus* dissuades one from placing much trust in its configuration. The interorbital septum and the ethmoid structure vary widely. The form of the mandible identifies at least some falconids.

What similarity the skulls of the sagittariid, accipitrid, and falconid show needs further consideration. There is little question that these types find only a poor match elsewhere in the Class Aves. Yet on inspection what are their common attributes? The cranium is not unlike that of the owl or *Cariama*; the prefrontals are matched fairly well by those of *Cariama*, the Alcedinidae, and others. This leads one to the thought that perhaps the critical difference lies in the rostrum. The shape of the upper part of the bill is the classic feature, but this is shared with the owls in remarkable detail. The desmognathous palate is not critical since many other types (pelecaniforms, ciconiids, etc.) share this style. The really significant points are the lack of an anterior palatine fossa and the ossification of the septal bar and vestibule, however, these features are shared with some of the desmognathous types and even with some of the passerines. Resort to a combination of features reduces the similarity to the shape and structure of the rostrum. Certainly this could be the result of convergence!

A case for convergence is supplied by a comparison of the falconid and accipitrid. Assuming common ancestry, some overlap in physical features should occur in view of the wide range of size, shape and adaptive variation within the latter group; such overlap is not evident. Surely one of the several kinds of falconids would have a free superciliary, or lack ossification of the lateral wall of the vestibule; or perhaps some of the accipitrids could have a large posterior mandibular fontanelle or a tomial "tooth" like that of the falconid. Some might accept the resemblance of the falconid prefrontal to that of some kites, *Pandion*, and the aegypiins as an instance of overlap and evidence that the former group separated very early from the line that continued on to the accipitrids (or vice versus). The details of form of the prefrontal argue against such a conclusion, and thus the head skeleton presents no evidence of interrelationship.

As one seeks proofs of lack of relationship so also can evidence of relationship be sought. The variations of these styles of falconiform head skeletons have convinced previous investigators of interrelationship, but the features used to indicate relationship are those that have been either rejected here or used to support independent origin. The above discussion can only be interpreted as suggestive; we must, therefore, turn to other areas for additional evidence.

## OSTEOLOGY--THE TARSOMETATARSUS

### Definition and Orientation

The avian tarsometatarsus has become increasingly important in systematics as it is frequently fossilized. Many species are known only from it. Milne-Edwards (1867-1871:19) described this element and compared its taxonomic value to that of mammalian teeth. Pycraft (1902) in his osteological study scarcely mentions it and Sushkin (1905) gives only a superficial account, basing most of his discussion on its musculature. Recent authors of fossil species have confined their comparisons to small numbers of living species; but fairly detailed comparisons have been made by Howard, especially in her description of *Spizaëtus willetti* 1935). More recent authors have placed great faith in the diagnostic value of the tarsometatarsus (for example, Cracraft and Rich, 1972). In view of the literature, the value of this bone should be determined for such a group as the falconiforms.

The development of the tarsometatarsus is assumed to be much the same in all birds (fig. 123), but it has never been fully described (*see* Holmgren, 1933, 1955). It is compounded from three metatarsals (II, III, IV) and a proximal tarsal component. The metatarsals of the red-tailed hawk are partly fused when ossification begins--well before hatching. In the chick the tarsal unit ossifies, soon after hatching, from bilateral centers; it lies above the end of the third metatarsal. Late in the nestling period the three metatarsals fuse and the suture lines are obliterated. The ossified tarsal mass covers the proximal end and acts as an epiphysis. Fusion of the tarsal mass to the metatarsals occurs with the completion of growth, at or shortly after nest leaving.

The tarsometatarsus is molded by the musculature and tendons passing along it (Table 6). The tarsal component is particularly plastic and gives rise to a variety of hypotarsal processes. The plasticity of this unit is related to the fact that ossification takes place from the center of the mass outward and is not completed until full growth is achieved.

In describing this bone the following orientation terms have been utilized: proximal, for the end attached to the tibiotarsus; distal, for the opposite end; medial or inner, for the side facing toward the midline plane in opposition to lateral or outer; anterior and posterior, for the front and back aspects respective-

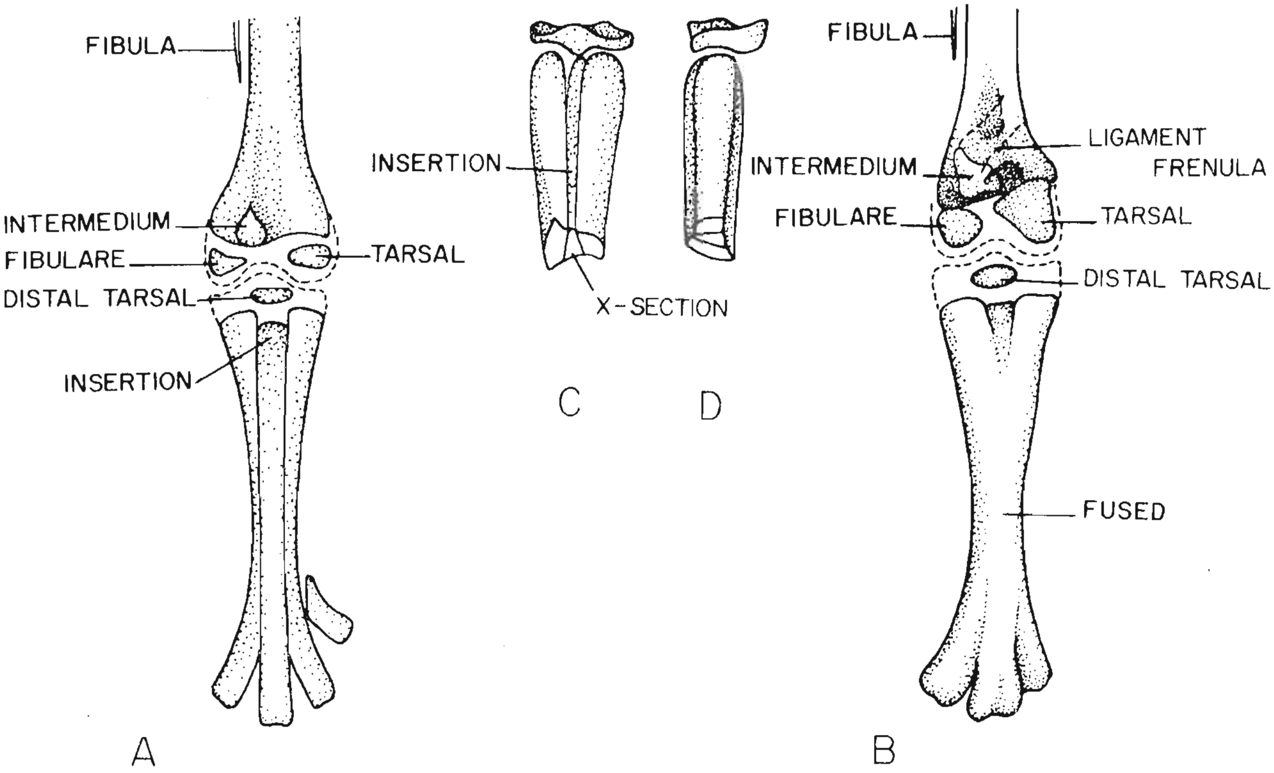


Fig. 123. The developing tarsometatarsus. A. Anterior view of right leg of *Gallus domesticus* 2 days old. B. 1½ weeks old. C. Anterior and D. medial view of proximal end of this bone in a 2½-week-old *Buteo jamaicensis*.

* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *

Table 6. Synonymy of Tarsometatarsal Muscles.

| Bird (Fisher, 1945; Hudson, 1937, etc.) | Mammal (Man) |
|---|---|
| 1. extensor hallucis | extensor hallucis brevis (pt. of the extensor digitorum brevis) |
| 2. abductor digiti II | pt. of extensor digitorum brevis |
| 3. extensor digiti III | pt. of extensor digitorum brevis |
| 4. adductor digiti IV (=extensor brevis digiti IV) | pt. of extensor digitorum brevis |
| 5. abductor digiti IV | pt. of interossei plantaris |
| 6. adductor digiti II | pt. of interossei plantaris |
| 7. flexor hallucis brevis (2 parts) | flexor hallucis brevis (2 parts) |
| 8. lumbricales | pt. of lumbricales |

Names used in this account, short form underlined.

1. extensor digitorum brevis pars hallucis.

2. extensor digitorum brevis pars abductor digiti II.
3. extensor digitorum brevis pars extensor digiti III.
4. extensor digitorum brevis pars adductor-extensor digiti IV.
5. interossei plantaris pars abductor digiti IV.
6. interossei plantaris pars adductor digiti II.
7. flexor hallucis brevis.
8. lumbricales.

* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *

1y. The processes are identified in Figure 124 and in the text (*see* Howard, 1929).

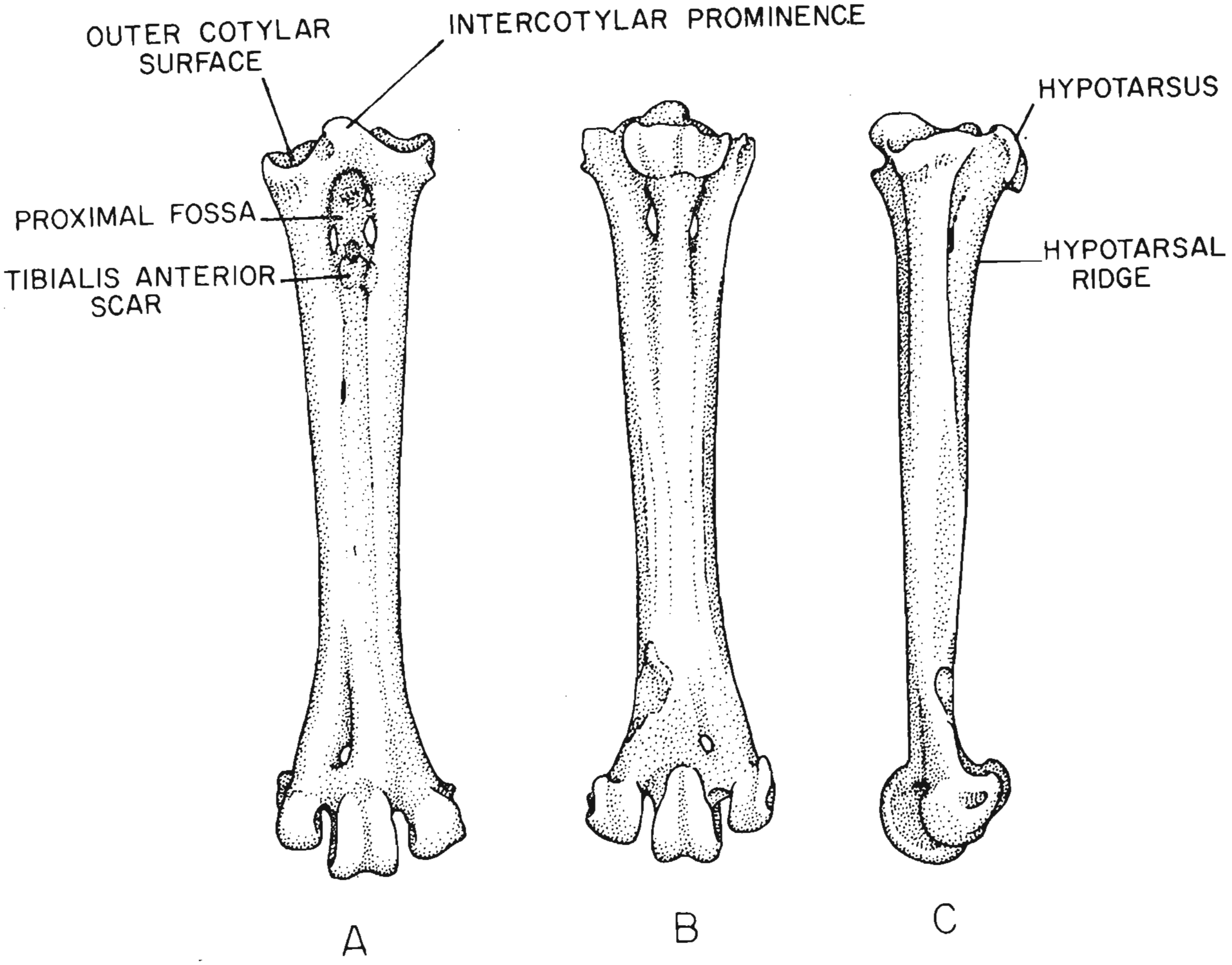


Fig. 124. Right tarsometatarsus of fully grown nestling of *Gymnogyps californianus*. A. Anterior, B. posterior, C. medial views.

## Comparative Anatomy

### The Cathartid (Cathartoid) Type

The inner cotylar surface is more deeply hollowed than the outer and the intercotylar prominence rises well above either of these surfaces. The hypotarsus is a low transverse block with two, broad, shallow grooves on its posterior surface, a groove down either side and across the proximal aspect, and a thick, rounded hypotarsal ridge extending a short distance down the shaft from about its middle.

The shaft of the tarsometatarsus is somewhat ovoid in section (fig. 125); it is deeply grooved anteriorly, and flattened posteriorly. *Teratornis* has relatively the thickest shaft, whereas that of *Cathartes* or *Coragyps* is thinnest. The anterior aspect has a deep proximal fossa (posterior displacement of the proximal part of the third metatarsal) in which are two or more pairs of foramina, symmetrically placed and marking the suture lines between the metatarsals. The largest, distal pair of foramina pierce the shaft of the tarsometatarsus for the passage of blood vessels.

The *tibialis anterior* scar (fig. 125, row b) lies distal to these foramina and is made up of two tubercles; the larger rising from the middle metatarsal and the smaller from the lateral margin of the second metatarsal (scar described as single by Fisher, 1946:675).

The anterior surface of the second metatarsal may be marked by one or two slight, irregular parallel ridges (frenula scars--fig. 125 C b,D b). These scars, in the modern species, are at about the level of that of the *tibialis anterior*. The frenula is relatively wide (up and down) but short (across the tarsometatarsus); it holds the extensor *digitorum longus* tendon (fig. 126) close to the lateroanterior angle of the second metatarsal. The anterior, proximal rim of *Teratornis* is peculiar in having a prominent lateral tubercle, which arises from the lower edge of the proximal rim and hooks medially (fig. 125 D a).

Distally, the anterior aspect of the tarsus shows a short tendinal groove for the *adductor-extensor digiti* IV, which passes through a canal between metatarsals III and IV. Coincident with the proximal end of this canal is the distal foramen--passage for a small, round impression marking the origin of the *extensor digiti* III.

The canal of the *adductor-extensor digiti* IV emerges in the intertrochlear notch next to the posterior surface. In most cathartids a small pit marks the notch anterior to the opening of this canal. *Teratornis* differs in that this canal usually is exposed posteriorly, a small bridge occurs in some specimens. In *Cathartes*, the posterior wall of this canal may be slightly cut back at its distal margin. Also peculiar to *Teratornis* is the fact that a small pit or foramen occurs, at the level of the distal foramen, on the posterior surface between metatarsals II and III.

The posterior surface of the tarsus is flattened and has a series of longitudinal grooves, impressions of the three muscles which cover this area: the *flexor hallucis brevis, adductor digiti* II and *abductor digiti* IV. The *abductor digiti* IV tendon makes an impression just above the fourth trochlea, which extends down and out onto the lateral aspect of that trochlea.

The distal outline of the trochleae, as viewed anteriorly (fig. 125, rows e,g), has the middle trochlea extending beyond the second and fourth which terminate at slightly different levels, the inner one nearly equalling the third while the fourth is smallest and shortest. The trochleae are rounded and have only slight

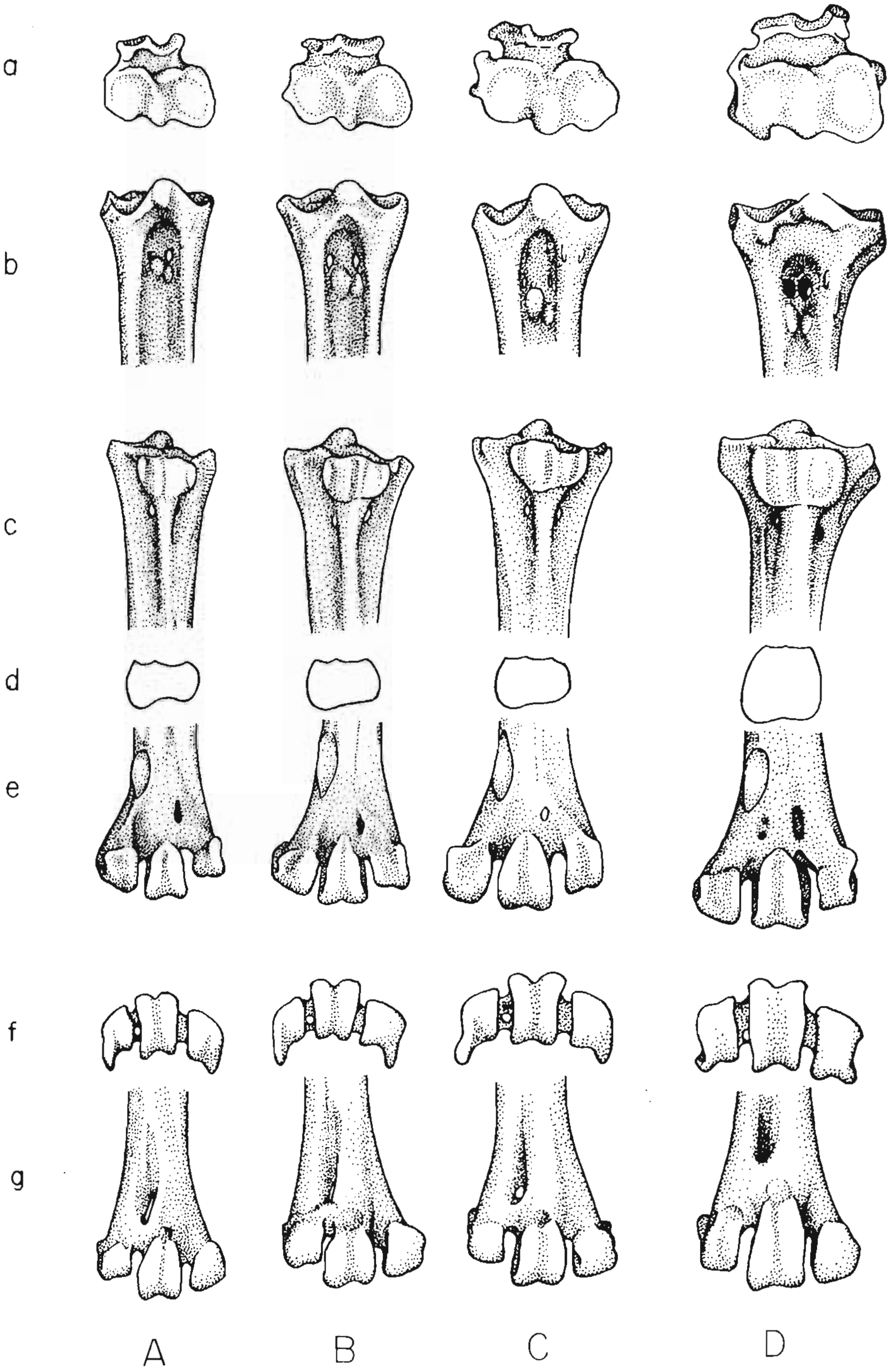


Fig. 125. Comparative sketches of right tarsometatarsi of A. *Cathartes aura*, B. *Sarcoramphus papa*, C. *Gymnogyps californianus*, D. *Teratornis merriami*. From top to bottom; row a, proximal end, anterior aspect down; row b, anterior view of proximal end; row c, posterior view of proximal end; row d, X-section through shaft, anterior aspect down; row e, posterior view of distal end; row f, distal end, anterior aspect up; row g, anterior view of distal end.

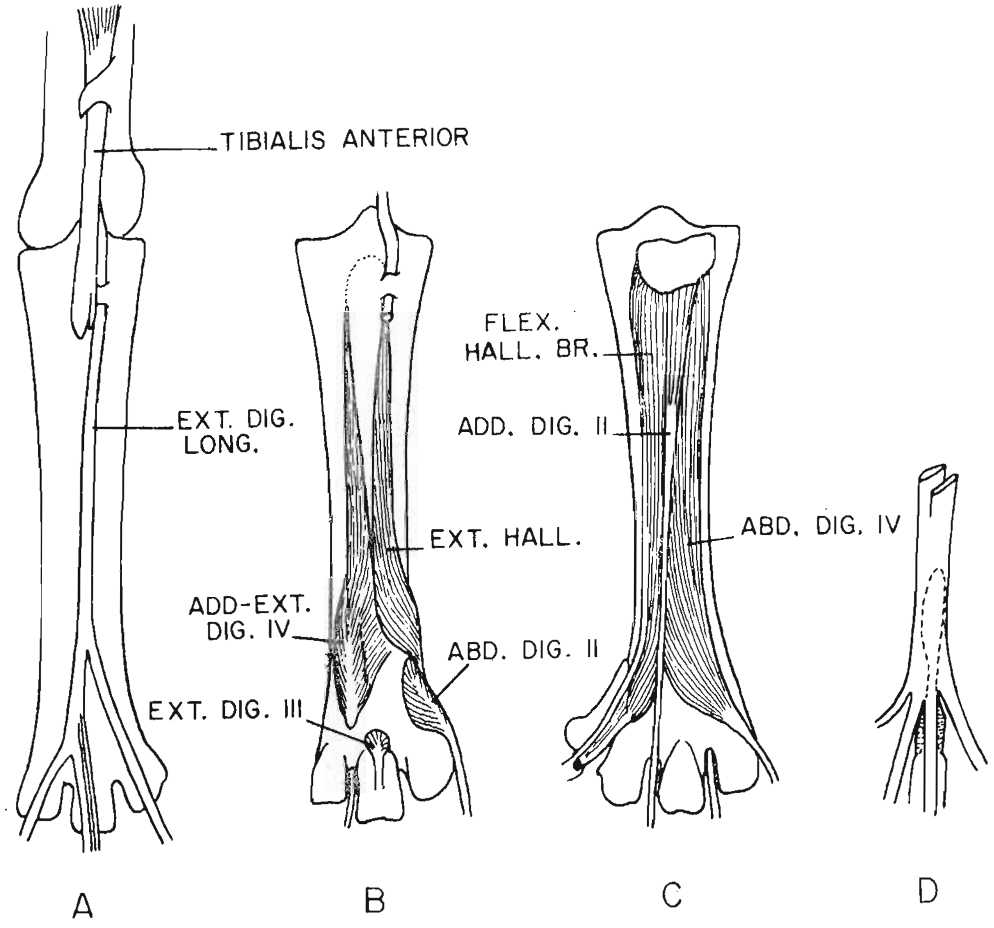


Fig. 126. Right tarsometatarsal muscles of *Cathartes aura*. A. Superficial tendons of anterior aspect, B. muscles of anterior aspect, C. muscles of posterior aspect, D. deep flexor tendons of posterior aspect, lumbricales outline dashed.

projecting articular ridges; these are best developed on the inner edge or trochlea II and the outer edge of IV.

The trochleae show certain peculiarities in that the medial articular ridge of the second trochlea is drawn slightly medially and up. The articular facet of the middle trochlea ends sharply above, both in front and behind, as a highly arched line extending well above the intertrochlear notches. The outer trochlea shows nothing of significance. Other aspects of the trochleae are noted under the accipitrid type.

The cathartid tarsometatarsus shows remarkable constancy throughout the group so that subgroups cannot be defined. It can be characterized as follows: cotylar surfaces of approximately equal size separated by a well-elevated intercotylar prominence; hypotarsus simple with low rounded hypotarsal ridge running distally; proximal anterior fossa deep and symmetrical; *tibialis anterior* scars distinctly proximal and paired; lateral and median aspects of shaft convex (as seen in X-section), anterior and posterior surfaces slightly grooved; metatarsal scar regular without strong ligamentous attachment scars; distal trochleae fairly symmetrical, with rounded articulations, round scar on anterior aspect above middle trochlea.

## The Sagittariid Type

The tarsometatarsus of this type is long and slim. The outline of the proximal end, as viewed anteriorly, is similar to the cathartid; the lateral cotylar surface is lower and more deeply hollowed than the medial one (fig. 127). The intercotylar prominence is well elevated, rounded, and almost median in position.

Anteriorly the tarsus is grooved for most of its length; the groove increases in depth and width proximally and terminates in a well-hollowed fossa. Close to the proximal end, in the fossa, the shaft is pierced by foramina on either side of the middle metatarsal. Just distal to, and in touch with, the foramina are the scars of the *tibialis anterior* muscle insertion. In contrast to the cathartid, the medial tubercle of this insertion is larger than the lateral one. Only the lateral frenula scar is present on metatarsal II (fig. 128).

The hypotarsus shows some resemblance to that of the cathartid but it is less massive; its narrowly rounded ridge extends down the middle of the shaft (metatarsal III) for one sixth of the length of this bone, where it gives way to the posterior flexor surface. To either side of the hypotarsal ridge are the posterior proximal fossae the outer margins of which are marked by ridges.

The lateral aspect of the shaft is wide (widest in its middle half); the posterolateral angle is sharp. The medial aspect is narrower and almost flat, becoming rounded distally. The "flexor surface" begins in the second sixth of the length of the shaft and extends distally to the region of the metatarsal I scar where it fades out.

Viewed anteriorly the distal foramen pierces the shaft somewhat above the entrance of the *adductor-extensor digiti* IV canal. The latter passes between the third and fourth metatarsals and opens midway in the intercondylar notch rather than posteriorly as in the cathartids. The medial trochlea (II) lies in the same or at a slightly higher plane than the outer; the former is distinctive in its shape, its distal outline curves up slightly from the lateral to the medial margin. The middle trochlea (III) is disproportionately large. Anteriorly it arises sharply from the shaft along an arched line, whereas posteriorly its articular surface terminates at the level of the tops of the intertrochlear notches. The outer (IV) trochlea is not distinctive. Additional features of the trochleae are mentioned under the accipitrid type.

The long, crane-like tarsometatarsus of the secretary bird resembles in many ways that of *Mycteria* or *Cariama*, to select only two non-related genera (fig. 127). There are similarities to other falconiforms, particularly the cathartids, and few unique features. This type can be characterized as: much like the cathartid but hypotarsus less symmetrical as seen from behind, hypotarsal ridge continuous with posterior surface of shaft which has strong posterolateral angle; lateral and medial aspects of shaft grooved; medial trochlea longer than lateral one but smaller, when viewed anteriorly.

## The Accipitrid Type

The tarsometatarsus of this group shows a wide range of

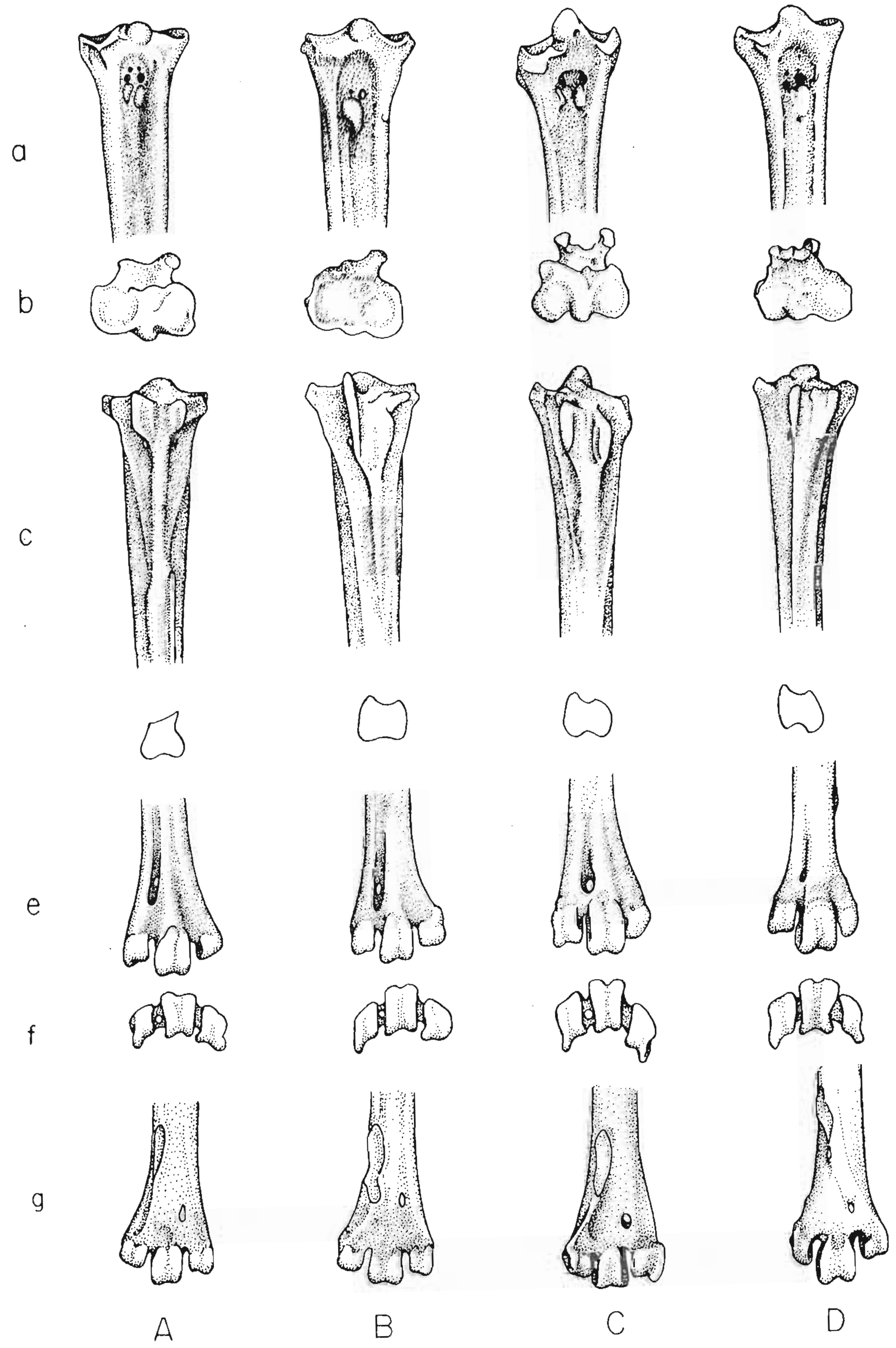


Fig. 127. Right tarsometatarsi of A. *Sagittarius serpentarius*, B. *Amynoptilon robustum*, C. *Mycteria americana*, D. *Cariama cristata*.

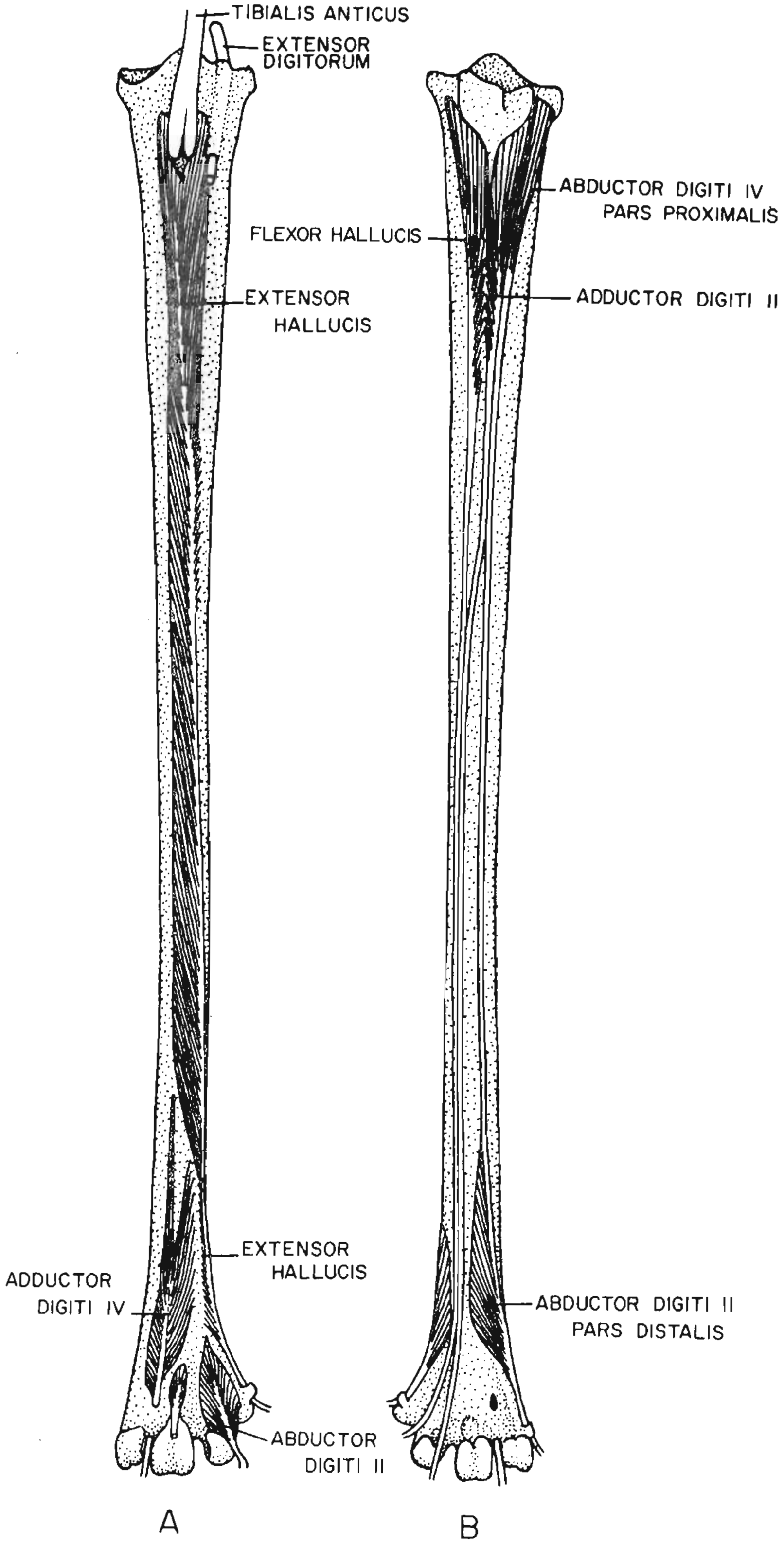


Fig. 128. Muscles of right tarsometatarsus of *Sagittarius serpentarius*. A. Anterior, B. posterior aspects.

variation. The most distinctive feature is the style of hypotarsus and its attendant ridges (figs. 129, 131). In most there is an inner and outer calcaneal process between which the flexor tendons pass. The degree of separation of these processes varies. They are widely set in *Elanus*, *Stephanoaëtus*, *Harpia*, and *Pithecophaga*, and close together in *Rostrhamus*. In *Pandion*, *Pernis*, and *Elanoïdes* (fig. 137) this tendinal groove is roofed over forming a calcaneal canal. *Aviceda* represents a transitional stage from the open to the closed canal.

The outer calcaneal process is usually lower and broader than the inner. In *Torgos* it is nearly equal in size to the medial process whereas in *Haliaeetus* and *Ichthyophaga* it has been displaced laterally and flattened so as not to be visible from above. From above, the outer process usually is separated from the head of the tarsometatarus by the notch of the peronaeus nerve. This notch is well developed in *Buteo* and *Leptodon*, wide but recognizable in *Torgos* and *Elanus*, indistinct in *Neophron* and *Circaëtus*, and absent in *Haliaeetus* and *Ichthyophaga* (figs. 129, 137).

The lateral (outer) calcaneal process gives rise to a rounded ridge, which extends down the shaft and fades into the outer posterior margin. This ridge, distally, is notched by the accessory tendon of the *peronaeus longus*. This tendinal scar begins on the lateral face of the tarsus, passes down and backward across the posterior angle to the flexor surface for about one third of the tarsal length, where the tendon fuses with the *pars perforatus digiti* III tendon. The length of the outer calcaneal ridge varies; it is short in the small forms, longer in the larger ones. It is clearly delimited medially by the fossa of the *abductor digiti* IV muscle and the lateral vascular foramen (fig. 130).

In the vulturine species, the lateral ridge has been shifted medially and fused with that of the medial process (the present subfamily Aegypiinae plus *Terathopius*). Transitional from this type is a series of genera starting with *Circaëtus* and passing through *Haematornis* and *Gypohierax* to certain fossils such as *Buteo ales* and finally to the typical accipitrid type represented by the living species of *Buteo* or *Accipiter*.

A typical lateral calcaneal ridge is also wanting in the pernin kites and *Pandion*. In this group the posterior aspect of the tarsus is fairly flat and the lateral ridge is little more than a line marking the margins of the *abductor digiti* IV and the *adductor digiti* II impressions (figs. 132 D, 137).

The medial calcaneal process varies from pillar-like in *Elanus* or *Gampsonyx* to an elongated plate in *Leptodon*, *Chondrohierax*, *Gypohierax*, *Spilornis*, *Gymnogenys*, or *Pandion* (figs. 136, 137). Proximally the margin of this process usually is bent medially at a right angle. The posterior margin is thickened and expanded where it contacts the fascia enclosing the flexor tendons and anchoring the gastrocnemius sheet. Distally its margin curves toward the shaft and fades out as a low rounded ridge of short length.

Among the vulturines this terminal ridge and that of the lateral process are fused (formed by the posterior displacement of metatarsal III (fig. 129 B,C,D). The product of this fusion

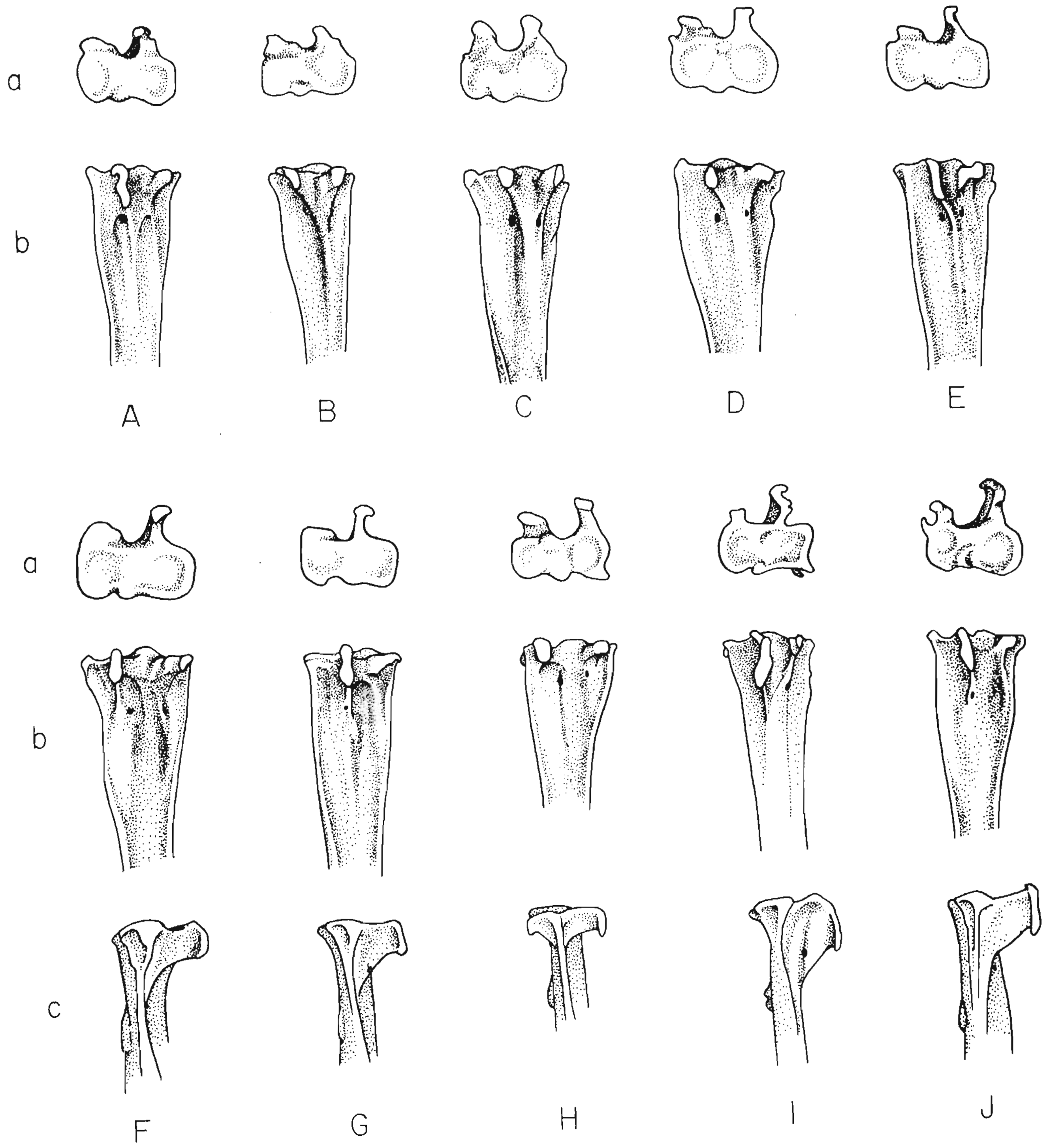


Fig. 129. Proximal ends of right tarsometatarsi of A. *Circaëtus gallicus*, B. *Neophron perenopterus*, C. *Torgos tracheliotus*, D. *Gypaëtus barbatus*, E. *Gypohierax angolensis*, F. *Haliaeetus leucocephalus*, G. *Ichthyophaga ichthyaëtus*, H. *Elanus leucurus*, I. *Chondrohierax uncinatus*, J. *Buteo jamaicensis*. Row a, end view, anterior aspect down; row b, posterior aspect; row c, medial aspect.

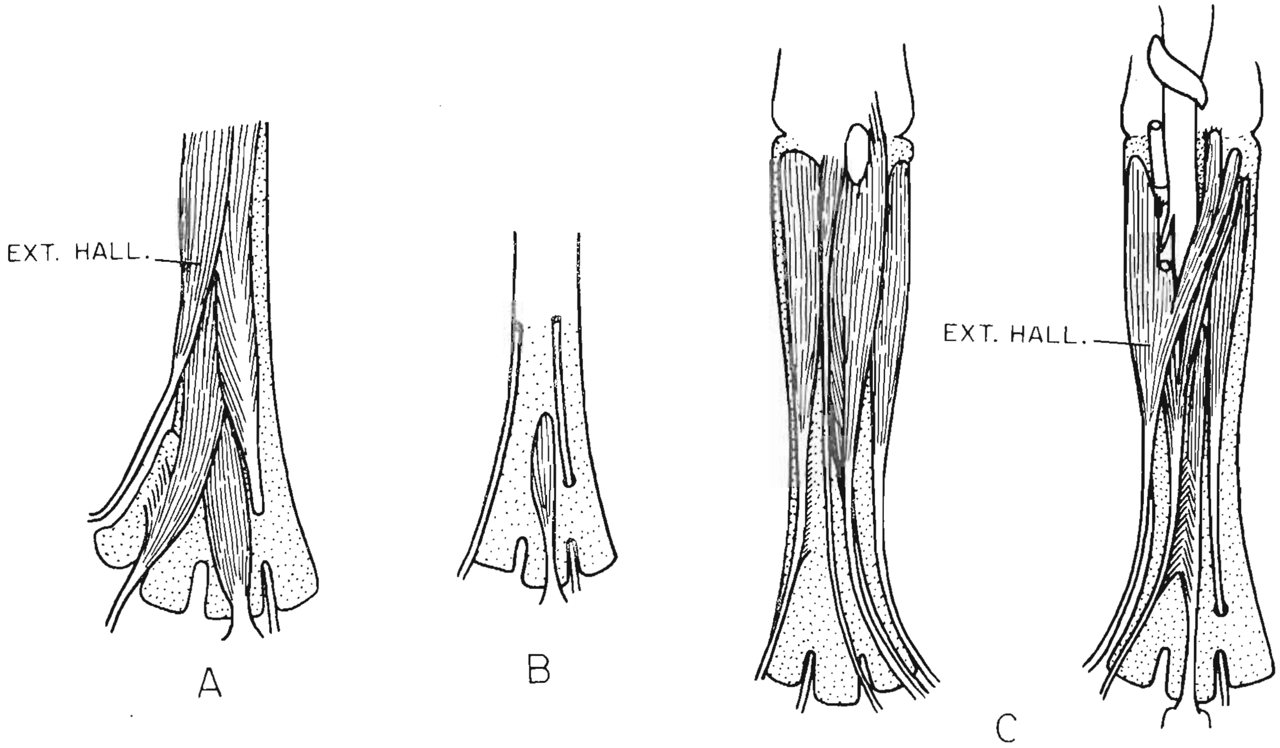


Fig. 130. Muscles of the right tarsometatarsi of A. *Torgos tracheliotus*, anterior aspect of distal half; B. *Accipiter striatus*, anterior aspect of distal end; C. *Aquila chrysaëtos*, anterior aspect right, posterior aspect left.

extends proportionally further down the shaft and lies more laterally (as indicated by the position of the lateral vascular foramen) than does the medial ridge of most accipitrids. In transitional forms, the increase in bulk of the flexor tendons (correlated with strength of grasping) is responsible for the separation of these ridges.

The medial process is separated in most members of this group from the margin of the tarsometatarsus by the deep rounded fossa of the *flexor hallucis brevis*. *Elanus* and *Gampsonyx* are singular in lacking a distinct proximal fossa medial to this process. In these genera the medial process arises as a pillar almost from the margin of the bone (only a small part of the muscle arises medially, most of it arising from the distal aspect of the process and lateral to this area).

Associated with these calcaneal processes are vascular foramina piercing the shaft from the anterior proximal fossa. The position of these foramina is quite inconsistent especially that of the inner (as viewed posteriorly). The medial foramen may open on the inner face of the medial calcaneal process (*Aquila chrysaëtos*), well above the ventral margin, or at any position from this to one well lateral to the distal end of the process (*Haliaeetus*--fig. 129). Slight variation occurs within a species and more within a genus (Table 7).

The lateral vascular foramen may be of value as a position marker. In the bulk of the accipitrids, it appears on the medial side of the lateral ridge, while in the vulturine species it lies laterally or on the lateral slope of the hypotarsal ridge. Among the pernin kites and *Pandion*, this foramen marks the proximal lateral head of the *adductor digiti* II (fig. 130).

This outline of the cotylar surfaces, as viewed from in front, is fairly distinctive of most accipitrids (fig. 131). The outer cotylar surface is higher than the medial one and less deeply hollowed. The anterior margin presents only a slight, somewhat laterally displaced intercotylar prominence, in contrast to the cathartid or *Sagittarius*. Among the vulturines, the pernin kites and *Pandion*, the level of the outer and inner cotylar surfaces may be equal or that of the medial one higher, but in every case the intercotylar prominence is somewhat laterally displaced.

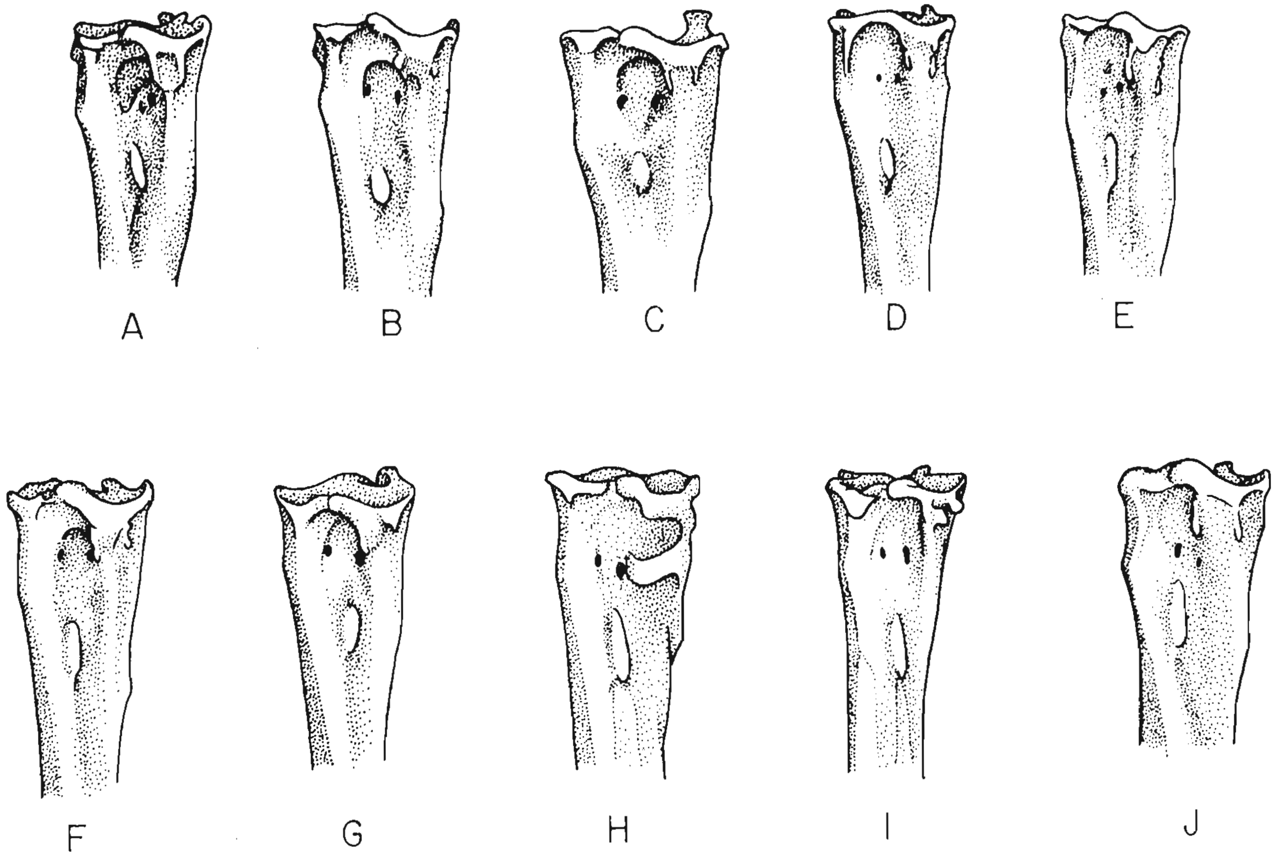


Fig. 131. Anterior views of proximal end of right tarsometatarsi of A. *Neogyps errans*, B. *Aquila verreauxi*, C. *Spizaëtus coronatus*, D. *Spizaëtus ornatus*, E. *Spizaëtus grinnelli*, F. *Aquila chrysaëtos*, G. *Elanus leucurus*, H. *Pandion haliaetus*, I. *Chondrohierax uncinatus*, J. *Haliaeetus leucocephalus*.

Table 7. Position of the medial foramen in reference to the medial calcaneal process and its distal ridge (*see* fig. 129). The width of the name indicates approximately the range of variation in position.

<table>
<tr><th>medial to and well above the distal margin of the process</th><th>medial and above the distal margin</th><th>medial to the distal margin</th><th>on ridge below distal margin</th><th>just lateral to ridge</th><th>well lateral to ridge</th></tr>
<tr><td>Pandion</td><td>Pernis</td><td colspan="2">Elanoïdes</td><td>Elanus</td><td></td></tr>
<tr><td>Leptodon</td><td>Ictinia</td><td></td><td></td><td></td><td></td></tr>
<tr><td>Chondrohierax</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>Gypohierax</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td colspan="2">aegypiins</td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td>Aquila chrysaëtos</td><td colspan="2">Aquila rapax</td><td></td><td>Haliaeetus</td></tr>
<tr><td></td><td>Hieraaëtus</td><td></td><td></td><td></td><td></td></tr>
<tr><td>Haematornis</td><td>Polemaëtus</td><td>Buteo plagiata</td><td></td><td>Buteo lagopus</td><td></td></tr>
<tr><td>Harpia</td><td></td><td colspan="2">most species of Accipiter</td><td></td><td></td></tr>
<tr><td colspan="2">Pithecophaga</td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td></td><td>Hypomorphus</td><td colspan="2">Geranospiza</td><td></td></tr>
<tr><td></td><td></td><td colspan="2">Heterospizias</td><td></td><td></td></tr>
</table>

The anterior aspect (fig. 131) has a well-developed, but shallow, proximal fossa in which are found two vascular foramina, lying at about the same level, one on either side of the middle metatarsal component. Proximal to these are lesser foramina entering the bone itself.

The distance between the main vascular foramina varies and does not seem to show any constant relationship. The *tibialis anterior* tubercle is well down from the proximal end of the tarsometatarsus and usually lies just lateral to the midline. It is just medial to the midline in *Gypaëtus, Sarcogyps, Elanus, Gampsonyx*, the pernin kites, *Pandion*, and *Geranospiza.* It varies in shape from circular in *Gyps* to an elongated, distally elevated ridge in *Necrosyrtes.* Most accipitrids have an elongated tubercle; the extreme is *Pandion.* Among the vulturines, the *tibialis anterior* tubercle is close to the proximal foramina, thus approaching the style of the cathartid or *Sagittarius* (fig. 138). This relationship varies from close together in *Gyps* or *Necrosyrtes* through *Terathopius* (which equals *Circaëtus*) to the bulk of the group. *Circus* also shows a close approximation of tubercle and proximal foramina as do the pernin kites, *Pandion, Icthyophaga, Haliaeetus, Milvus, Haematornis, Hypomorphnus*, and *Heterospizias.*

The length of the power arm of the tarsus was the subject of some speculation by Loye Miller (1911:313; 1912:93), who noted that long tarsi have a short power arm whereas short, broad tarsi have a relatively longer one. Table 8 summarizes measurements on this matter and shows the percentage of the total length of the tarsus represented by the distance from the proximal end to the center of the tibialis anterior scar. It is notable that *Pandion* stands apart in the length of the "power arm."

Medially the anterior proximal fossa is bounded by the lateral metatarsal, which varies in prominence from scarcely discernable among the pernins, *Pandion*, most vulturines and some species of *Aquila*, through *Torgos*, and other species of *Aquila*, to well defined in the buteonin species.

On the lateral metatarsal, just below the proximal rim, are located the frenula scars (figs. 131, 136, 137, 138, 139). These scars represent ossifications of the points of attachment of the ligamentous loop for the tendon of the *extensor digitorum longus.* In *Chondrohierax* these scars are drawn out into distinct processes. The inner one projects from the posteromedial angle of the proximal margin of the tarsometatarsus and is shorter than the lateral one which lies somewhat below its level. The frenula in this genus lies more toward the medial margin than in any other genus and the scar processes are relatively closer together. Among the other pernins, these scars lie somewhat more toward the midline of the tarsometatarsus near the proximal rim and on about the same level.

In *Elanus* the medial scar appears as a projection from the medial rim of the tarsometatarsus. The more lateral one lies at the level of the top of the proximal fossa; it marks the lateral edge of a broad distal extension of the tarsal rim which, below the level of the proximal foramina, fades into the medial meta-

Table 8. The length of the lever arm X 100 / length of the tarsometatarsus for selected species of each of the four basic types. An * denotes a fossil species.

| | |
|---|---|
| Cathartid | |
| Coragyps atratus | 14.6 |
| Gymnogyps californianus | 19.1 |
| Sagittariid | |
| Sagittarius serpentarius | 5.2 - 6.2 |
| Accipitrid | |
| Pandion haliaetus | 32.2 |
| Leptodon palliatus | 29.2 |
| Gymnogenys typicus | 16.1 |
| Haliaeetus leucocephalus | 26. |
| Gypohierax angolensis | 18.4 |
| Gypaëtus barbatus | 23.3 |
| Neophron perenopterus | 17.3 |
| *Neophrontops americanus | 12.5 - 13. |
| Haematornis cheela | 15.2 |
| Terathopius ecaudatus | 22. |
| Necrosyrtes monachus | 15.7 |
| Aegypius monachus | 19.8 |
| *Neogyps errans | 21.1 - 23.3 |
| Aquila chrysaëtos (30 measured) | 25.3 - 29.1 |
| *La Brea Aquila (50 measured) | 23.8 - 28.1 |
| Aquila rapax | 20.3 |
| Aquila audax | 25.9 |
| *Buteo ales (my measurements) | 17.9 |
| (Wetmore's measurements) | 16.5 |
| Accipiter striatus | 13.2 |
| Circus cyaneus | 13.3 |
| Falconid | |
| Polyborus cheriway | 11.2 |
| Herpetotheres cachinnans | 20.2 |

* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *

tarsal. The frenula in this genus is broad; it extends from its medial attachment outward and down to the lateral one. *Elanus* is peculiar in the distance of separation of the scars (approaching *Pandion* in this detail) and also in the extreme midline position of the more lateral scar.

In *Pandion* the frenula is completely ossified and extends from the lateral margin almost directly across the tarsometatarsus to its midline. The lateral attachment lies just below the level of the medial one and is at the level of the proximal foramina. This loop is well down from the proximal end.

In general the frenula scars tend to lie at different levels, the medial higher than the lateral; however, this varies within a genus (*Buteo*). An opposite extreme is reached in *Haliaeetus*. *Neogyps errans* (a LaBrea fossil form) has the surface of the metatarsal raised between these scars, a peculiarity which is just suggested in *Aquila chrysaëtos*. The scars themselves are equally developed, with an average separation, and at the same level as in the golden eagle.

Frenula scars are absent in the vulturine species and *Circaëtus*. In *Torgos* there is a fascial sheath which encloses the extensor tendon from the joint region for a distance of about one-half inch (like *Sagittarius*). In *Necrosyrtes* there is a narrow but very weakly developed frenula.

The shaft of the tarsus is typically triangular in cross section (fig. 132): flat on the outer (somewhat anterior) aspect, hollowed posteriorly, with the anterior medial surface sloping posteriorly. Among the vulturines the variation ranges from strongly triangular in *Neophrontops*, *Neophron*, *Necrosyrtes*, and *Terathopius* to the round tarsi of the larger members. In *Geranospiza* and *Gymnogenys* (fig. 138) the triangular tarsus is altered as it is among the pernin kites and in *Pandion* (fig. 137).

Fig. 132. X-sections of the right tarsometatarsal shafts of A. *Buteo jamaicensis*, B. *Geranospiza nigra*, C. *Leptodon palliatus*, D. *Pandion haliaetus*, E. *Necrosyrtes monachus*, F. *Gyps coprotheres*, G. *Torgos tracheliotus*.

The posterior flexor groove is well hollowed and usually unmarked (may show the impression of the adductor digiti II).* The flexor surface in *Pandion*, *Aviceda*, *Pernis*, *Chondrohierax*, *Leptodon*, and *Elanoides* is relatively flat and has a series of shallow impressions for the three posterior muscles.

Distally (fig. 133) the first metatarsal scar may be directed almost medially (*Elanus*) or posteriorly (*Neophrontops* fig. 138). In most accipitrids the strong binding of the first metatarsal is indicated by a line of irregular bumps extending to the level of the distal foramen. Proximally the scar is rounded; it becomes elongate and acute distally. The proximal edge of the articular surface is raised and separated by a notch from the projecting line of the medial edge of the tarsus, except in such genera as *Chondrohierax* and *Leptodon* where the margin of the tarsus is not distinctly raised.

On the distal half of the anterior aspect of the tarsometatarsus the tendon of the *adductor-extensor digiti* IV produces a groove, which leads into the distal foramen and canal. The proximal margin of the canal may not correspond exactly with the edge of the foramen so that there are two openings at the distal

* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *

* Sushkin (1905:54) assumed that the *adductor digiti* II was well developed and produced a distinct impression in the bone only in the Falconidae.

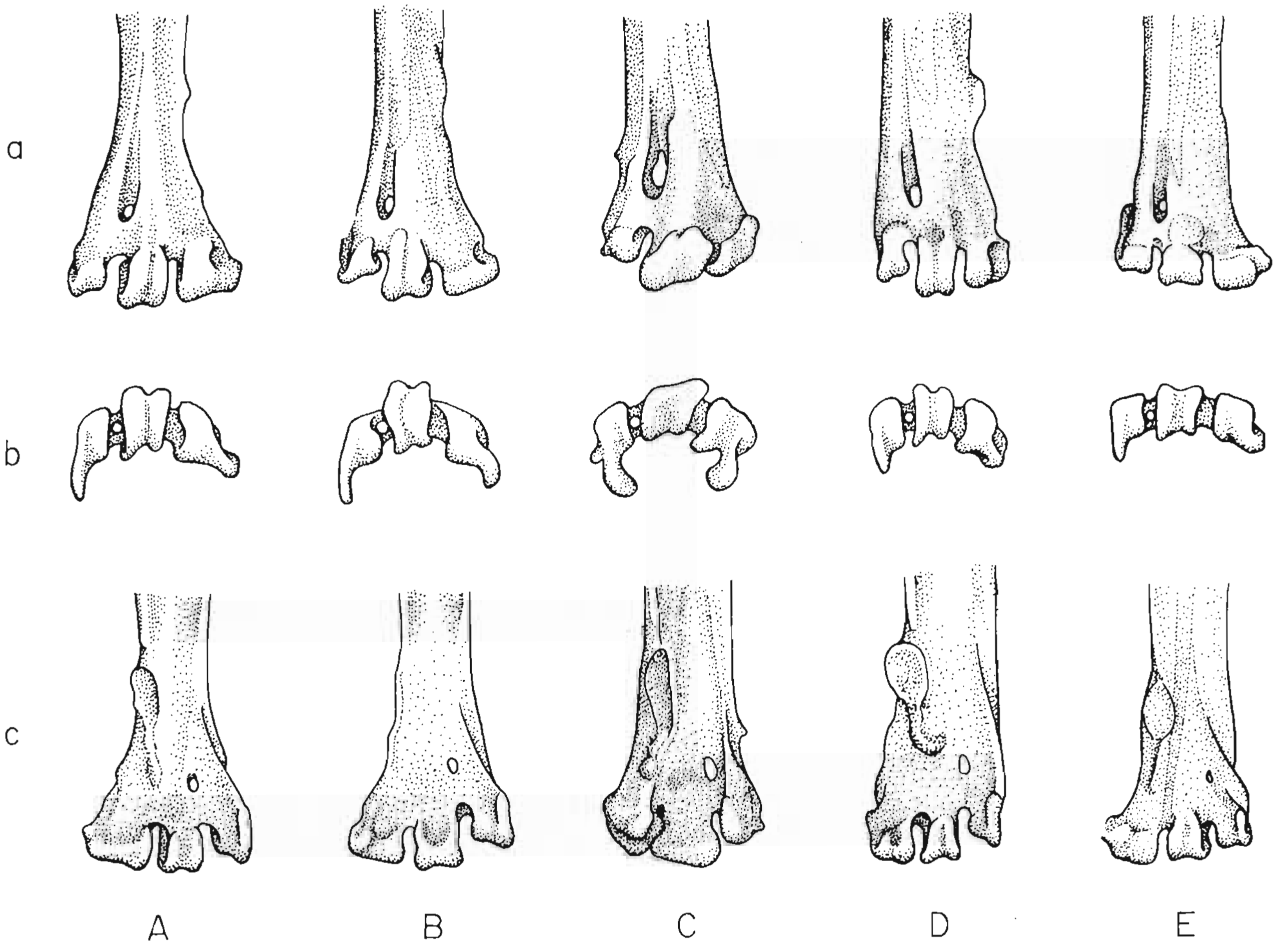
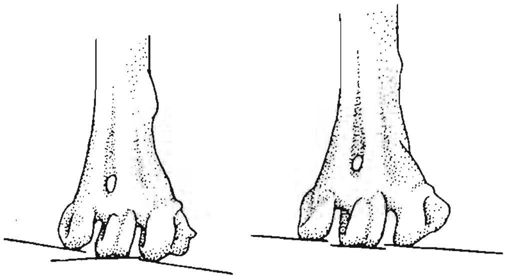


Fig. 133. Distal ends of tarsometatarsi of A. *Aquila chrysaëtos*, B. *Elanus leucurus*, C. *Pandion haliaetus*, D. *Geranospiza nigra*, E. *Chondrohierax uncinatus*. Row a, anterior aspect; row b, end view; row c, posterior aspect.

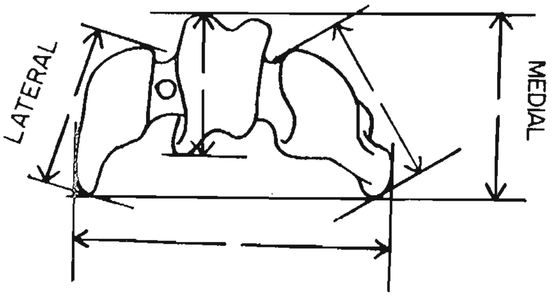
end of the tendinal groove in *Necrosyrtes*, *Chondrohierax* and occasional specimens of other genera. In one specimen of *Leptodon* the right tarsus has no distal foramen (an anomaly). Among the accipitrids the adductor-extensor canal opens into the intertrochlear notch equidistant from either margin.

The *extensor digiti* III may have the upper and medial margins of its origin indicated by a scar. *Leptodon* and *Chondrohierax* have a pit above the middle trochlea like that seen in the cathartid. The *abductor digiti* II may have a fairly distinct, roughened area of origin which extends from the *tibialis anterior* tubercle to the upper and lateral margin of the first metatarsal articulation.

Viewed anteriorly the outline of the trochleae is fairly characteristic. The inner trochlea usually extends furthest, but the middle one may exceed it (*Necrosyrtes* and *Neophron*); in *Gypaëtus*, *Sarcogyps*, *Trigonoceps*, *Torgos*, and *Aegypius* the inner and middle are equal in length, if the former does not actually exceed the latter. The outer trochlea is the smallest and shortest in all. There is much individual variation in the relative lengths of the trochleae (fig. 134) but little significance is attached to it. However, birds having feet adapted for walking or running show a much extended medial one (like those of the cathartids and *Sagittarius* among the falconiforms).



134



135

Fig. 134. Anterior view of distal ends of tarsometatarsi of two specimens of *Aquila chrysaëtos* to show variations in the trochleae. Lines below emphasize these variations.

Fig. 135. Distal end of tarsometatarsus to show refrence points of measurements referred to in tables 9, 10.

The inner (medial) and outer trochleae usually have well-developed wings. The outer wing extends posteriorly while the inner one projects posteromedially. These wings seem to be correlated with grasping and are best developed in those forms having the most robust feet.

The inner trochlea is characteristic in that the anterior articular surface shows no distal grooving; it extends outward and backward to the tip of the posterolateral process with only a simple dip. Howard (1932:72) has assumed that the length of this inner wing is of use in identifying members of the "*Aegypiinae*." The only satisfactory (and admittedly incomplete) test of a character lies in an examination of all the known members of the group; such an examination shows that this feature does not identify any subfamily. Table 9 presents the percentage

* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *

Table 9. The greatest depth of the trochlea II X 100 / the distal width of the tarsometatarsus for selected species of each of the four basic types. An * denotes a fossil species.

| | |
|---|---|
| Cathartid | |
| Cathartes aura | 54.8 |
| Gymnogyps californianus | 47.7 |
| Sagittariid | |
| Sagittarius serpentarius | 49. - 50.5 |

| | |
|---|---|
| Accipitrid | |
| Pandion haliaetus | 55.8 |
| Elanus leucurus | 51. |
| Pernis apivorus | 47.8 |
| Rostrhamus sociabilis | 56.1 |
| Haliaeetus leucocephalus | 58. |
| Gypohierax angolensis | 52.4 |
| Gypaëtus barbatus | 53.5 |
| Neophron perenopterus | 51.2 |
| *Neophrontops americanus | 48.2 - 50.7 |
| Haematornis cheela | 53.3 |
| Terathopius ecaudatus | 60. |
| Necrosyrtes monachus | 57.3 |
| Trigonoceps occipitalis | 50.4 |
| *Neogyps errans | 54. - 57. |
| Aquila (range of five species) | 54. - 60. |
| Aquila chrysaëtos (30 measured) | 54. - 60. |
| Spizaëtus ornatus | 62.7 |
| Geranospiza nigra | 51.5 |
| *Buteo ales | 52.4 |
| *Palaeastur atavus | 50. |
| *Palaeoborus howardae | 53.3 |
| Falconid | |
| Polyborus cheriway | 58.6 - 63.8 |
| Falco Peregrinus | 50. |

* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *

of the total distal width represented by the deepest measurement of the second trochlea (measured as indicated in fig. 135). The actual measurements are not listed since any reevaluation should be based upon independent measurements. The percentages indicated are those for the right tarsus of specimens listed in Table 4. Only in the case of *Aquila chrysaëtos* was a sufficient number measured to give an accurate representation of the range of variation within a single species; the range within this species equaled that of the genus.

The posterolateral length of the second trochlea varies from 47.8% to 62.7% of the total width of the distal end of the tarsus, being least among the pernins and greatest among some of the large powerful species (*Spizaëtus ornatus*). The length of this process appears to be a crude measure of the predatory capacity in the species or at least the clenching strength of the foot. It is relatively short in fossil species as compared with more modern types.

Among the vulturines there is a tendency for shallow trochleae, but there is every gradation to that of *Aquila* or *Buteo*. Among the members of the Aegypiinae the inner wing is least developed in *Neophrontops* and increases through the group in the following order (on the basis of general appearance): *Aegypius* to *Necrosyrtes*, which equals *Torgos*, *Trigonoceps* and *Gyps*; to *Sarcogyps*, which equals *Gypaëtus*. From here the series extends to *Terathopius*, which equals *Aquila wahlbergi* or *Circaëtus*. On the basis of measurements the series is somewhat different since such measurements do not capture the three dimensionality of the "whole" process. Among the vulturines there is a tendency for this projection to be more posteriorly directed, but here again the range of variation overlaps that of the core genera of the Accipitridae (*Buteo, Accipiter*).

The inner trochlea of *Pandion* is the most distinctive in the group; it has the posteromedial process bent toward the midline of the tarsus. Its form is probably related to the wide angle of medial movement of which the digit is capable; superficially it resembles that of the owl. Another peculiar inner trochlea is that of *Gymnogenys* (fig. 139); here the posterolateral process is short and thick and distinctly separated from the articular surface by a groove. This groove extends up onto the anterior medial face where it ends as a distinct pocket. The trochlea of *Gymnogenys* appears to an adaptation for its peculiar climbing habits (*see* Swann, 1924-1945; 98-99, quoting Shortridge; or Chapin, 1932:596).

The middle trochlea is usually clearly delineated from the anterior face of the shaft. The outline of its upper margin is gently rounded. In some genera, *Neophrontops, Sarcogyps, Aegypius, Torgos, Aquila* (*verreauxi*), *Geranospiza, Heterospiza, Hypomorphnus*, there may be an indistinct pit at the apex of its upper margin just as in the cathartids. *Leptodon* and *Chondrohierax* show larger impressions above the middle trochlea. The middle trochlea is grooved around its entire arc, the groove being least evident behind. This groove in *Pandion* is exceptionally wide. *Elanus* and *Gampsonyx* are distinctive (fig. 133B) in having the posterior dorsal margin either indistinct, the articular surface of the trochlea fading into the shaft, or truncated, and not extending much above the tops of the intertrochlear notches.

Howard (1932:72) used the depth of the third trochlea as a distinguishing character of the Aegypiinae. The depth of this trochlea was measured for species which appear to show extremes (Table 10). Among the accipitrids it ranges from 33.9% to 53.6%; the range in the Aegypiinae is from 40.8% to 53.6%. On the basis of proportions, *Haliaeetus* or *Aquila* could be called vulturine. The lapping of percentages from one group to another indicates the unreliability of this character for the identification of fossil subfamilies.

The outer trochlea shows little significant variation. It has a posterior lateral projection, which varies in length with that of the medial trochlea. This process is rounded posteriorly, in contrast to the dorsally pointed process of the cathartid, and usually it ends bluntly. *Pandion* is peculiar in that his process has a truncated margin, pointed at its ventroposterior angle; its form reflects the wide lateral movement of which the digit is capable.

The posterolateral margin of the shaft just above the outer trochlea shows a shallow groove for the *abductor digiti* IV tendon. The form of this groove varies within the group; it is most apparent and widest amongst the pernins.

Viewed end on, the trochlea may lie nearly in one plane, as in *Leptodon*, or may be strongly arched around the flexor tendons as in *Pandion*. In most accipitrids the trochleae are well arched (figs. 133, 136, 137, 138, 139).

From the description of the tarsus of this group, five subtypes are largely or partly definable: elanin, pernin, pandionin, vulturine and the remainder of the Accipitridae.

The elanin tarsometatarsus (*Elanus* and *Gampsonyx*) is unique in many features (fig. 136A). The calcaneal processes are reduced to flat-topped pillars, widely separated and lacking distinct hypotarsal ridges. The inner process is located located nearly on the margin so that there is only a small medial origin for the *flexor hallucis brevis*. The outer process has a well-defined notch at its base for the passage of the peronaeus nerve. Anteriorly the *tibialis anterior* scar is on the medial side of the midline (as in many other kites). The shaft is strongly triangular in section; the posterior flexor groove is deeply hollowed. The trochleae do not resemble those of any other genus in the family. This style of tarsus seems to be distinctly specialized for easy flexion of the toes; the foot itself is proportionally small and not particularly powerful.

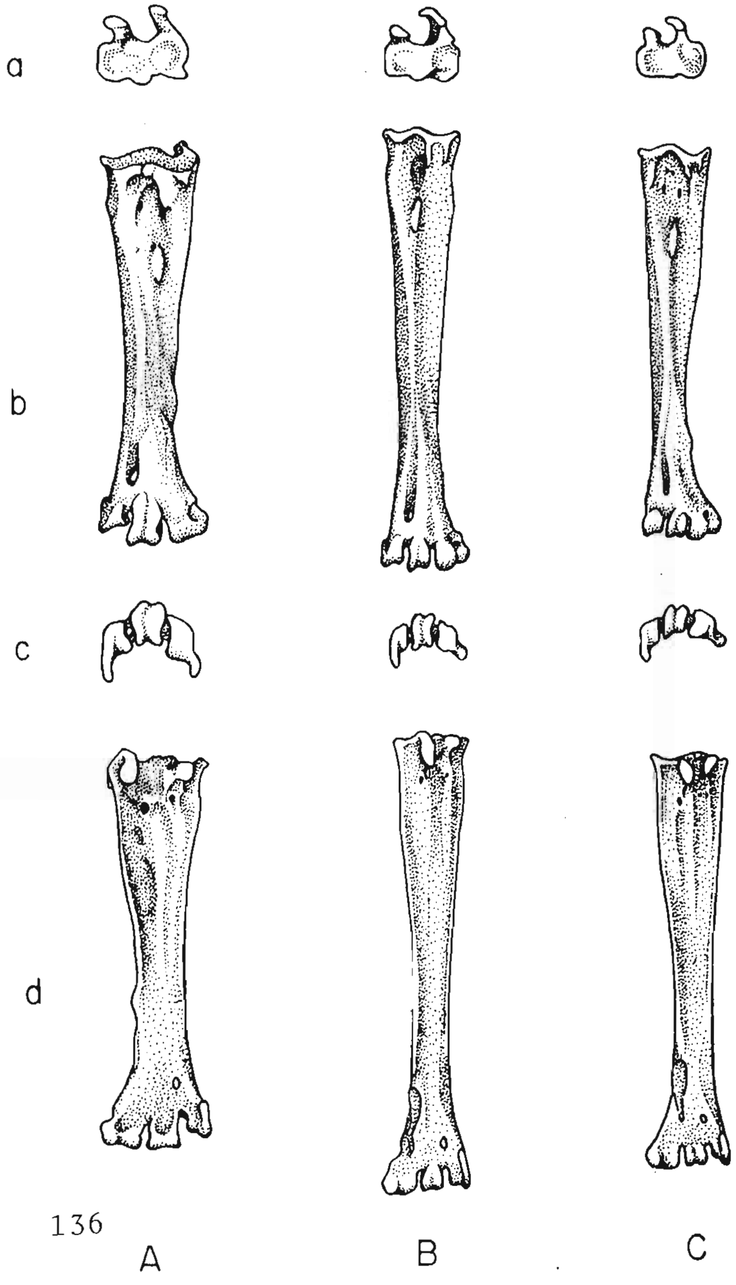
The hypotarsus of the pernin varies from the perforated type of *Pernis* or *Elanoïdes* (resembling *Pandion*) through *Aviceda* to the open type found in *Chondrohierax* and *Leptodon* (fig. 137). The proximal frenula is very weak in *Aviceda*; strongly ossified in *Chondrohierax*. This type is not strongly triangular in section; it has a flattened, grooved anterior surface and posteriorly the flat flexor surface has distinct impressions of the *flexor hallucis brevis*, *adductor digiti* II, and *abductor digiti* IV muscles. Viewed end on, the trochleae lie nearly in one plane.

In *Pandion* the hypotarsus is relatively enormous, extending well down the tarsus and enclosing a canal for the *flexor digitorum* and *flexor hallucis longus* tendons. The ossified frenula is peculiar. Distally the trochleae are distinct in form and strongly arched around the flexor tendons, resembling more closely the owl than any of the hawks. The tarsus (and foot) is extremely powerful and does not resemble in detail that of any of the other falconiforms.

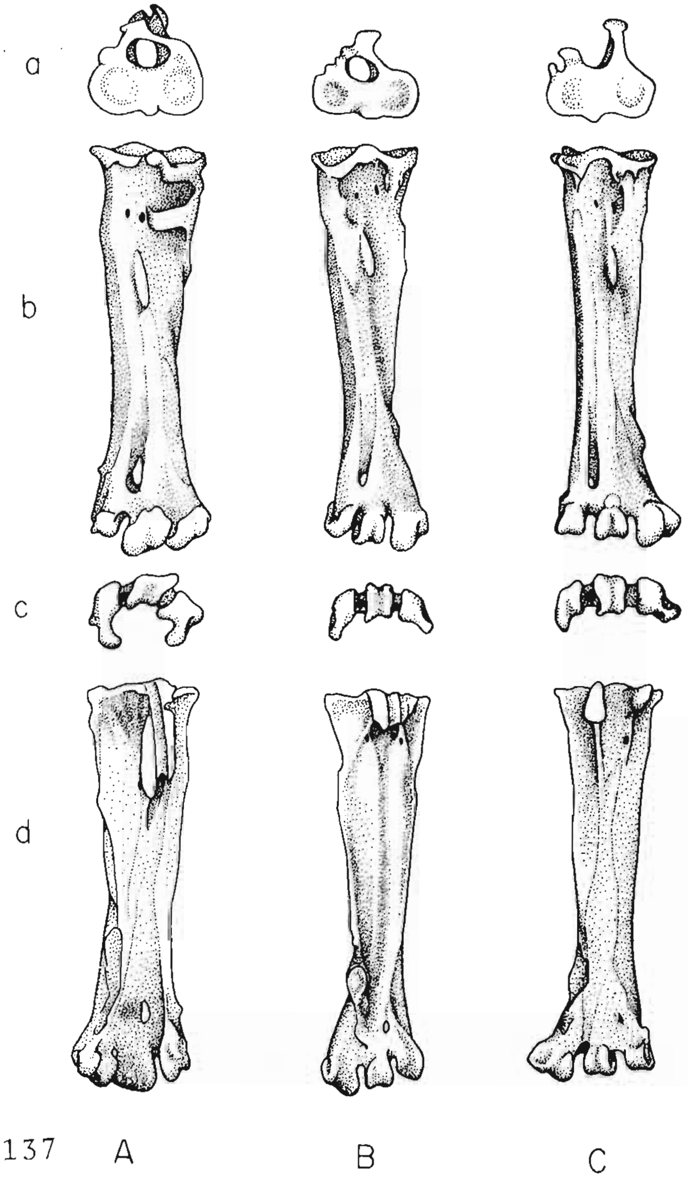
The relationship between the bulk of the accipitrids and the other kite genera (*Machaerhamphus*--fig. 136B, *Rostrhamus*--fig. 136C, *Milvus*, *Ictinia*, and *Harpagus*) cannot be ascertained from the tarsus as every stage of transition seems to be present. The tarsus of *Ictinia*, for example, agrees in detail with that of *Accipiter* or *Circus* (*see* L. Miller, 1937, on *Harpagus*).

The vulturine type (fig. 138) has a weak foot, which is not used for clutching prey in the fashion of the more active hawks, as a result the tarsometatarsus is less modeled, the flexor groove less developed so that the calcaneal processes share a rounded distal ridge. This style of hypotarsus is connected with the typical accipitrid through such transitional genera as *Circaëtus*, *Haematornis* and *Terathopius*.

Miller and Howard (various publications) have attempted to define a type of tarsometatarsus for the Aegypiinae by the use of proportions based on the depth of the second and third trochleae Tables 9 and 10). If the vulturine style were confined to the Aegypiinae, a combination of hypotarsus, lack of frenula scars,



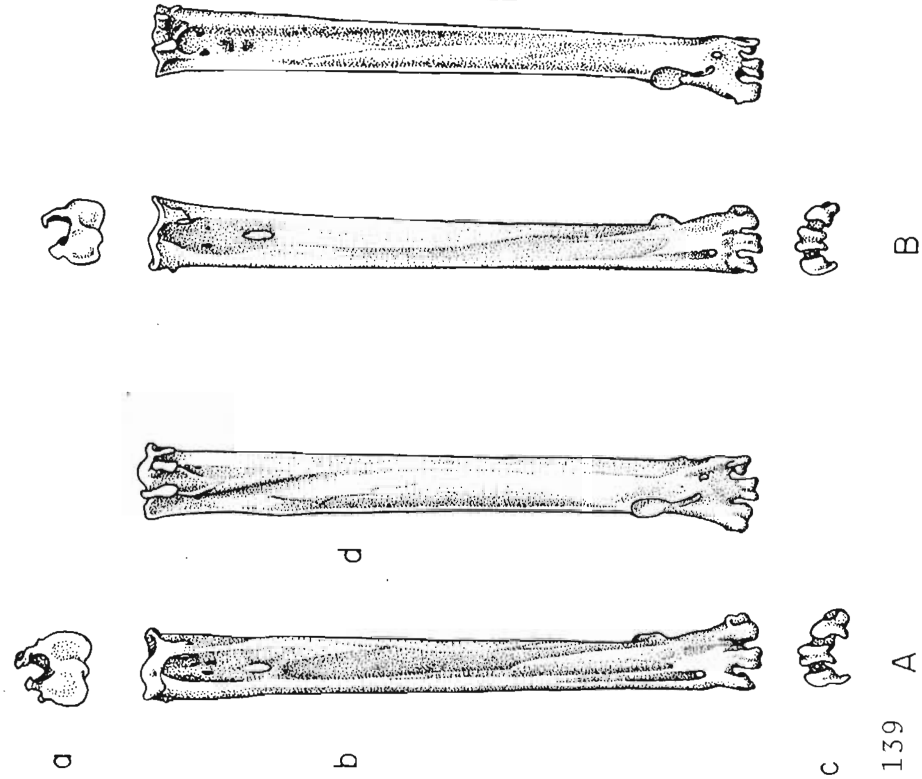
136



137

Fig. 136. Right tarsometatarsi of A. *Elanus leucurus*, B. *Machaerhamphus alcinus*, C. *Rostrhamus sociabilis*. Row a, proximal end; row b, anterior aspect; row c, distal end; row d, posterior aspect.

Fig. 137. Right tarsometatarsi of A. *Pandion haliaetus*, B. *Elanoïdes forficatus*, C. *Leptodon palliatus* (rows a,b,c,d, as in Fig. 136).



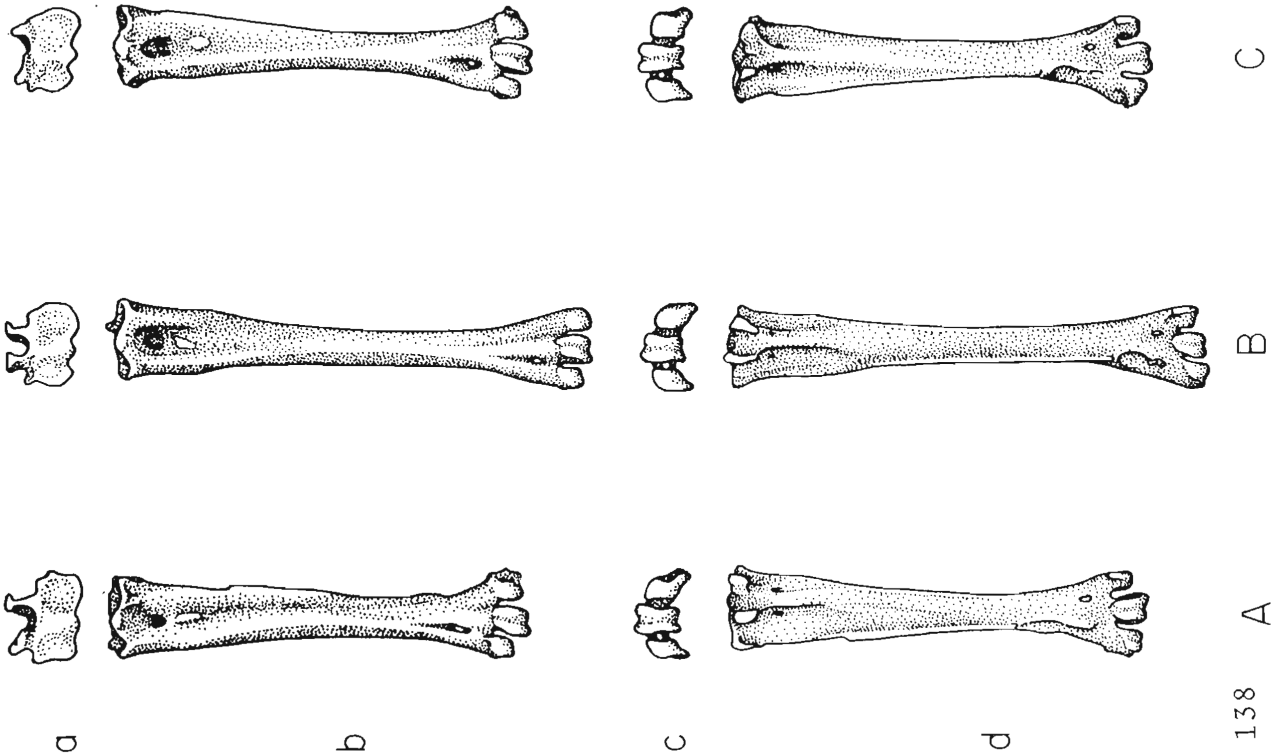


Fig. 138. Right tarsometatarsi of A. *Necrosyrtes monachus*, B. *Neophrontops americanus*, C. *Neophron perenopterus* (rows a, b, c, d, as in fig. 136).

Fig. 139. Right tarsometatarsi of A. *Gymnogenys typicus*, B. *Geranospiza nigra* (rows a, b, c, d, as in fig. 136).

Table 10. The depth of the trochlea III X 100 / the distal width of the tarsometatarsus for selected species of each of the four basic types. An * denotes a fossil species.

| | |
|---|---|
| Cathartid | |
| Sarcoramphus papa | 50. |
| Coragyps atratus | 58.8 |
| *Teratornis merriami | 56.4 - 62. |
| Sagittariid | |
| Sagittarius serpentarius | 44. - 45.7 |
| Accipitrid | |
| Pandion haliaetus | 39.6 |
| Leptodon palliatus | 33.9 |
| Pernis apivorus | 41.7 |
| Elanus leucurus | 37. |
| Rostrhamus sociabilis | 35.3 |
| Haliaeetus leucocephalus | 46.1 |
| Gypohierax angolensis | 40.8 |
| Gypaëtus barbatus | 50.7 |
| Neophron perenopterus | 44. |
| *Neophrontops americanus | 46.2 - 47.3 |
| Sarcogyps calvus | 49.4 |
| Necrosyrtes monachus | 53.6 |
| Aquila chrysaëtos | 43.7 - 46.5 |
| *La Brea aquila | 40.7 - 47. |
| Aquila audax | 41.9 |
| Aquila rapax | 47.2 |
| *Spizaëtus grinnelli | 48.7 |
| *Neogyps errans | 41.5 - 44.1 |
| Buteo lagopus | 37.3 |
| Buteogallus anthracinus | 36.8 |
| *Buteo ales | 41.5 |
| *Palaeaster atavus | 48.1 |
| *Palaeoborus howardae | 47.7 |
| Accipiter cooperii | 47.2 |
| Falconid | |
| Falco peregrinus | 41.3 |
| Polyborus cheriway | 51.8 |

* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *

and lack of well-developed processes on the second and fourth trochleae might be used to define it. However, *Necrosyrtes*, *Terathopius*, *Gypaëtus*, and *Circaëtus* show a combination of well-developed processes and aegypiin hypotarsus, thus bridging any gap that might exist. The tarsometatarsus of *Gypaëtus*, although agreeing in matters of the hypotarsus, is not vulturine distally. *Gypohierax* lacks the aegypiin hypotarsus, has well-developed frenula scars and, in general, approximates the pernin type. The result is that *Terathopius*, if not *Circaëtus*, must be included in the aegypiin group while *Gypaëtus* and *Gypohierax* should be excluded.

The bulk of the accipitrids show some agreement but much variation. Certain features indicate that the same specialization has occurred several times within the group; examples include the details of the hypotarsus and its attendant ridges and the form of the trochleae. Independent variation in detail has left nothing by which one can separate the different subfamilies. The tarsometatarsus in some cases is even a poor indicator of generic affinity *(depending on how one defines a genus). Such genera as *Polemaëtus*, *Spizaëtus*, and *Hieraaëtus* cannot be distinguished from *Aquila* whereas *Harpia*, *Pithecophaga* and *Stephanoaëtus* show a remarkable parallelism. (Some might feel that relationship is indicated.)

General resemblance of tarsometatarsi would tend to link *Accipiter*, *Circus*, and *Ictinia*, while transitional forms of *Buteo* link these to *Aquila*. The length of the outer hypotarsal ridge suggests that *Accipiter*, *Circus*, and *Ictinia* represent "advanced" types; in an opposite view these are the most primitive, or least modified. *Busarellus* has a distinctive tarsometatarsus at the end of a series extending from *Buteo* through *Buteogallus*, *Hypomorphnus*, *Heterospizias*, and *Leucopternis*. *Haliaeetus* and *Icthyophaga* are also distinct from the central type, but paralleled in some features by *Busarellus*. This kind of tarsometatarsus has an extremely flattened outer calcaneal process, no peronaeus notch, and a deeply hollowed fossa for the median part of the *abductor digiti* II. *Gymnogenys* and *Geranospiza* show some agreement in their highly modified tarsi (fig. 139). This similarity leaves one confused as to whether relationship or convergence is indicated.

A characterization of the accipitrid type necessarily is a description of an "average" form since wide variation is observable in every detail. Thus, the hypotarsus usually is divided by the flexor tendons into two calcaneal processes, which extend distally only a short distance, the medial one is sheetlike and extends further than the lateral one; the intercotylar prominence is low; proximally the lateral margin is notched by the peronaeus nerve; the anterior proximal fossa is shallow and indistinct; the proximal foramina lie midway between the laterally displaced *tibialis anterior* tubercle and the proximal end; the shaft tends to be triangular in cross-section (strongly concave posteriorly, slightly convex anteromedially, and flat lateroanteriorly); the distal trochleae are asymmetric, the medial one appearing to be the largest (seen anteriorly) and the inner tapers out as a long, blunt-tipped posteromedial wing.

### The Falconid Type

The outer calcaneal process of the hypotarsus is always reduced in size (fig. 140); it represents a posterior and somewhat lateral projection of the proximal rim separated by a well-defined flexor groove from the large inner calcaneal process. There is no notch for the peronaeus nerve on the lateral aspect. The lateral hypotarsal ridge is short, extending medially and forming the proximal margin of the lateral fossa. Distally this fossa is continuous with the flexor groove; it has distinct muscle impressions in *Herpetotheres*, but these do not change its

---

* A paper by Martin (1975, Wilson Bull., 87:413-416) is an example of ill founded speculation.

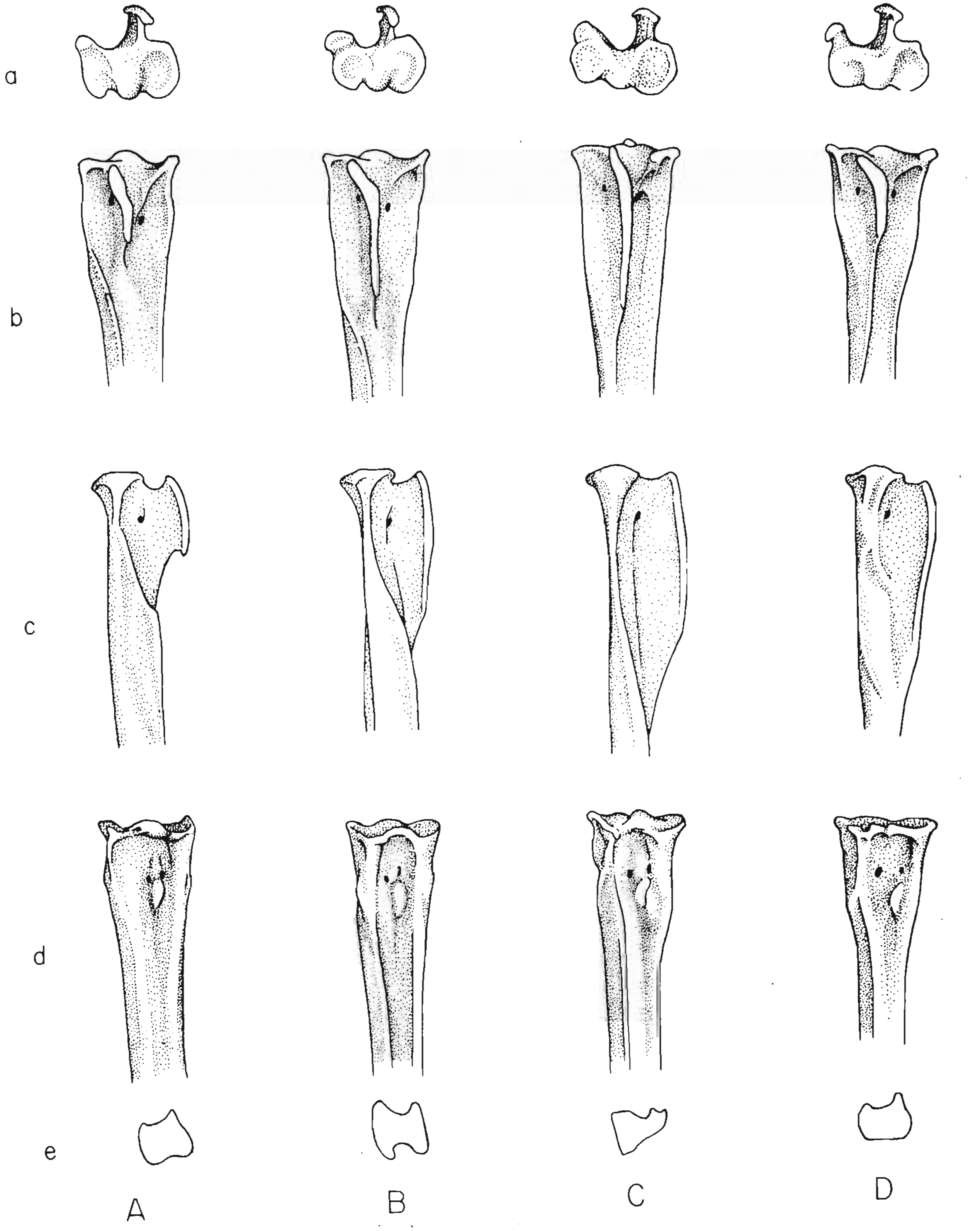


Fig. 140. Proximal ends of right tarsometatarsi of A. *Polyborus cheriway*, B. *Micrastur semitorquatus*, C. *Herpetotheres cachinnans*, D. *Falco mexicanus*. Row a, proximal end; row b, posterior aspect; row c, medial aspect; row d, anterior aspect; row e, X-section of shaft.

general appearance.

The medial calcaneal process is large (as in some gallinaceous birds). It extends well down the tarsus as a sheet of bone, the hypotarsal ridge, which is continuous with the inner margin, either directly as in *Falco* or indirectly by a rounded ridge in the Polyborinae. *Herpetotheres* is singular in that this process continues distally, as a slight ridge lateral to the medial margin, as far as the upper margin of the metatarsal scar. The medial calcaneal ridge is shortest (reduced) in *Polyborus* or *Milvago* and longest in *Falco* and *Herpetotheres*. The fossa of the *flexor hallucis brevis* is confined by the medial calcaneal process, and its distal ridge, to the medial aspect of this bone in contrast to the condition of the accipitrid.

The relationship of the medial proximal foramen to the calcaneal process is constant; it lies at the base of the process on the medial side.

The outline of the top of the tarsus, as viewed from in front, is similar to that in the accipitrid. The outer cotylar surface is just slightly higher than the inner. The intercotylar prominence is generally reduced; it is best developed in the more terrestrial Polyborinae.

Anteriorly the proximal foramina are closely associated with the *tibialis anterior* tubercle which lies well to the medial side and, in all genera, seems to be a part of the medial metatarsal.

The medial metatarsal lacks the frenula scars on its proximal surface, this ligamentous loop is shifted up onto the connective tissue of the joint (fig. 141). The position of the frenula appears to be involved in the clutching power of the foot.

The X-section of the tarsometatarsus has a wide variety of forms. *Herpetotheres* approaches the accipitrid in triangularity, while *Micrastur* shows the extreme of the tetragonal form. In general there is a medial flat surface as well as a small lateral one. Anteriorly the tarsometatarsus tends to be grooved for a greater part of its length; grooving is least in *Falco*, which resembles the accipitrid, and most in *Micrastur*. *Micrastur* is unique in its deeply grooved anterior and posterior surfaces; it probably has the strongest clutching foot of the group.

Distally the tendon of the *adductor-extensor digiti* IV passes into its tendinal canal either above, or at the level of the distal foramen (fig. 141. *Herpetotheres* resembles the accipitrid in this detail. In other falconids, various levels of separation exist between the foramen and the point where the tendon passes into the canal. Separation is widest and also least within the genus *Falco*.

Posteriorly the *adductor digiti* II impression is best developed in *Herpetotheres*; in addition, there is a good impression of the tendon of that muscle (figs. 140C, 142C). In most falconids the tendon can be traced as far as the upper end of the metatarsal scar (also in *Chondrohierax* and *Elanoïdes*).

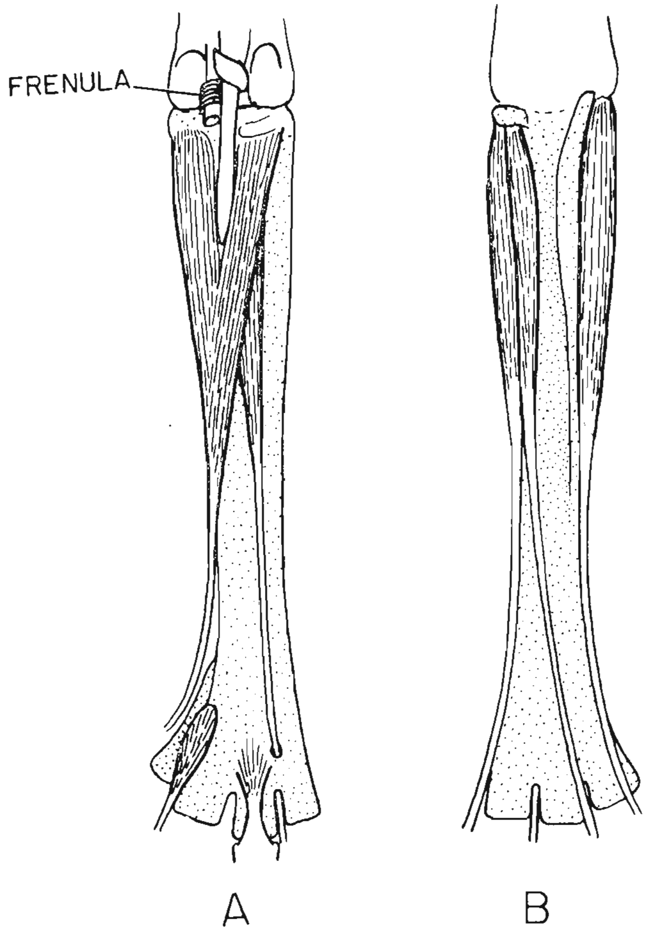


Fig. 141. Muscles of the left tarsometatarsus of *Falco sparverius*, A. Anterior, B. posterior aspects (*see* fig. 130 for labels).

The lateral margin of the metatarsal scar lacks the irregular ridge which extends distally in the accipitrid (fig. 142). The posterior surface has a small pit above the medial intertrochlear notch. This pit is absent in *Herpetotheres* as it is in the accipitrid.

Distally the canal of the *adductor-extensor digiti* IV opens on the posterior margin of the intertrochlear notch. The posterior cover of this canal may be entirely lacking from the level of the distal foramen to the intertrochlear exit in some specimens of *Herpetotheres* or *Falco*, or it may show various stages of incompleteness distally. The intertrochlear notch of *Herpetotheres*, as viewed distally, has a pit above the opening of the extensor canal just as do some cathartids.

The falconid trochleae are fairly distinctive (tables 9, 10). The medial process of the second trochlea is thinner (less tapered), has a more truncated tip, and is more pointed ventrally; it is more sharply differentiated from the body of the trochlea. The articular surface of this trochlea may show

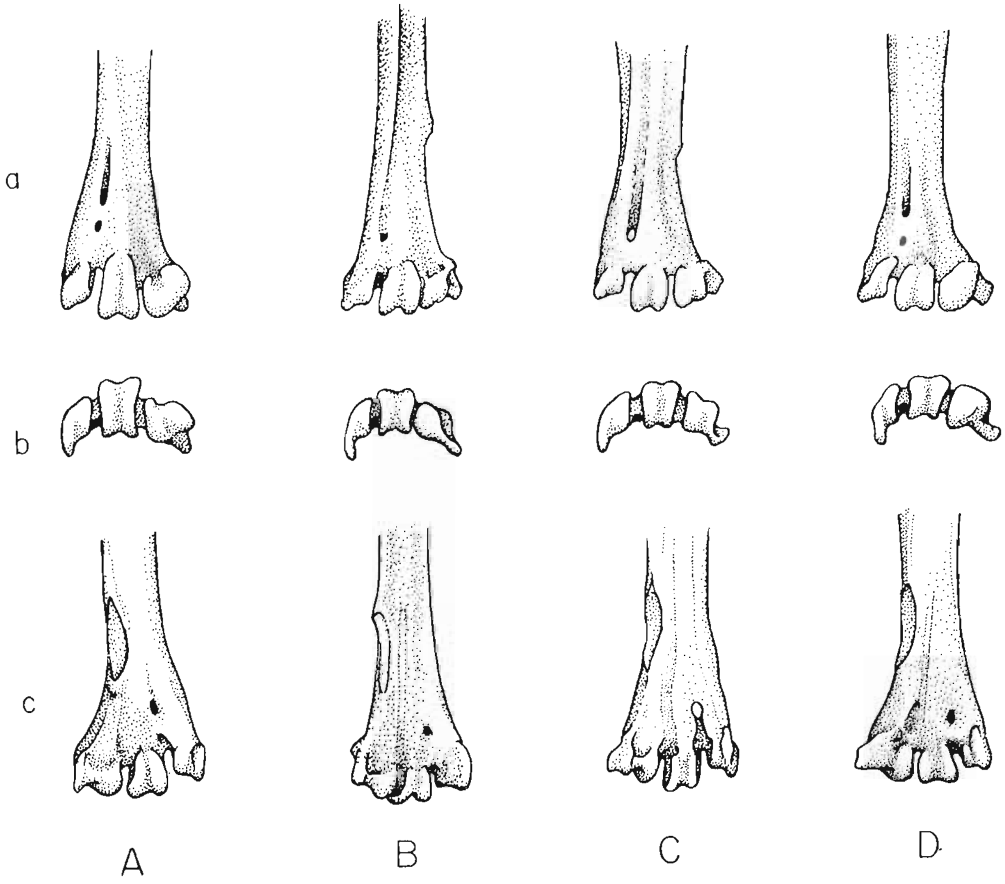


Fig. 142. Distal ends of right tarsometatarsi of A. *Polyborus cheriway*, B. *Micrastur semitorquatus*, C. *Herpetotheres cachinnans*, D. *Falco mexicanus*. Row a, anterior view; row b, distal view; row c, posterior view.

a slight, middle groove. The medioanterior aspect lacks the deep pit of the accipitrid. As viewed posteriorly the upper and lower margins of the articular surface form an hourglass.

The falconid type shows extreme variations, but it can be characterized as having: a short, thick, lateral calcaneal process, and a sheet-like medial one, which projects well out from the shaft and separates the fossa of the *flexor hallucis* from that of the other posterior muscles; a shallow anterior proximal fossa in which the proximal foramina are just above the medially displaced *tibialis anterior* tubercle; usually a square cross-section to the shaft; asymmetric distal trochleae, the inner one of which has a less tapered, more sharply differentiated posteromedial process and a distinctively formed articulatory body.

Within this array, four subtypes appear: micrasturin, herpetotherin, polyborin and falconin. Three of Sushkin's (1905) subfamilies are thus separable on the basis of this bone.

The micrasturin subtype is most unique and shows little similarity to that of *Herpetotheres* with which it is usually allied. The hypotarsal ridge is shortened and resembles that of the polyborin. The *tibialis anterior* scar is separated from the medial ridge whereas the proximal anterior fossa is deep and continuous with an anterior extensor groove. The shaft has an H-shaped cross section. In *Micrastur ruficollis* the anterior aspect is less grooved than in *M. semitorquatus*. The distal scar of the *adductor digiti* II tendon is weak.

*Herpetotheres* resembles *Falco* on the one hand and the accipitrid on the other. The hypotarsal ridge is like that of *Falco* but the impression of the *adductor digiti* II is distinct both proximally and distally. The proximal anterior fossa is shallow and not continuous with an extensor groove; the shaft is nearly triangular in section. Posteriorly, the small pit above the medial intertrochlear notch found in the other styles, is lacking. The distal trochleae show an independent style of modeling.

The polyborin has a shortened hypotarsal ridge, which extends less than one quarter of the length of the tarsometatarsus. This appears to be a parallelism to the vulturine species of the accipitrid group, perhaps an adaptation for walking. The shaft is square in section as in *Falco*. This style of tarsus is also found in *Spiziapteryx*.

The falconin style is found in *Falco, Ieracidea, Polihierax,* and *Michrohierax* (*see* Sushkin, 1905: 165, 170). It has a long hypotarsal ridge, weak proximal impression of the *adductor digiti* II, and a square cross-section to the shaft. *Falco* is peculiar in that the tibial or gastrocnemius mass, associated with the hypotarsus. is ossified as a sesamoid (fig. 143).

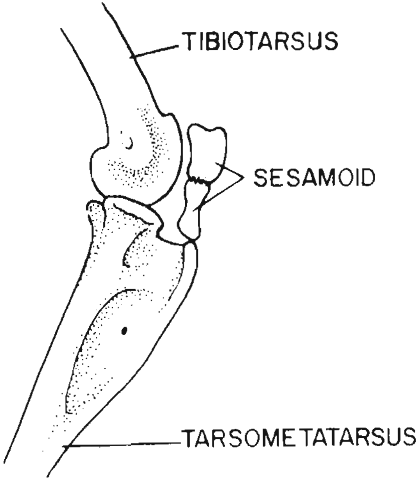


Fig. 143. Medial view of heel joint of a specimen of *Falco rusticolus* (USNM 345380) to show sesamoids.

## Summary and Conclusions

The taxonomic value of the tarsometatarsus has never been thoroughly investigated. From this study it is evident that this bone has the same limitations as the pterylosis or the head skeleton. Some orders cannot be characterized by this element (i.e., gruiforms, ralliforms, charadriiforms) while others, such as the parrots, are easily distinguished. The form of the tarsometatarsus is dependent in part upon muscular development, which in turn reflects the adaptations of the leg. The molding effects of the musculature are not always parallel, as for example the differences in the equally powerful bones of hawks, falcons, owls, and parrots.

The tarsometatarsi of each of the several types of falconiforms are distinctive and are not easily compared with each other or with those of other orders. The cathartid can be superficially compared with *Sagittarius* or the procellariiform, pelecaniform, ciconiiform, ralliform, gruiform, or charadriiform. An interrelationship between the cathartid and sagittariid is neither substantiated nor refuted by this element. *Sagittarius* shows some similarity to *Cariama* (ralliform-gruiform) or the storks, a similarity which is not revealing as to relationship. The accipitrid and falconid types share modifications imposed by a thick bundle of flexor tendons and can be considered as superficially similar although no real overlap is evident.

In terms of evolution, the cathartid-sagittariid hypotarsus and trochleae are probably least modified from that of the ancestral bird in which the tarsometatarsus was already strongly modified from the reptile (*Archaeopteryx*). The cathartid type is possibly very close to that of the theoretical ancestor, more so than *Sagittarius* in which elongation has occurred. That a less modified type than the cathartid exists among living birds is possible but cannot as yet be identified.

The falconid type appears to be somewhat less specialized (less grasping power) than the accipitrid, although the micrasturin or herpetotherin style may represent an equal degree of modification. Of the falconids, the polyborin style (best typified by *Milvago*) can be considered the most primitive. That of *Polyborus* is modified (lengthened) for walking, while the other styles might be correlated with variations in use of the legs. The lengthened medial calcaneal process of the herpetotherin and falconin is unique among birds.

The accipitrid type is a product of an even stronger clutching musculature than the falconid. If the tarsi of early Tertiary hawks give some indication of the evolution of this bone, the primitive form was similar to that of *Leptodon* or *Gypohierax*, among the living species, but larger.

In terms of size and the form of the tarsometatarsus the ancestral accipitrid was already distinctively specialized in the Eocene. From this ancestral form a series of vulturine types appeared as well as large powerful predators--many of these lines have become extinct. The range of adaptive variation within this group, following its initial radiation, has probably always been large.

## OSTEOLOGY--THE PECTORAL GIRDLE

### Definition and Orientation

Three bones, the coracoid, scapula, and clavicle, are involved in the pectoral girdle and form the area of articulation of the humerus. The first two are cartilaginous in origin and the latter membranous. There is nothing of significance in the development of this trio of bones (each ossifies from a single center); nor is the anatomy of this region complex.

The first effective use of the anatomy of the pectoral girdle was made by Ridgway (1875) to separate the Falconidae from the Accipitridae. Fürbringer (1888) made an extensive study of this region in birds. It is suggested that some details of the coracoid and clavicle can be used in determining the phylogeny of the falconiforms. This is true even though this region shows restricted variation and often the individual elements cannot be distinguished from those of other orders. For lack of recognizable features, the scapula will not be discussed.

## Comparative Anatomy

### The Cathartid (Cathartoid) Type

The brachial tuberosity of the coracoid (fig. 144) is an irregular rounded knob. The clavicular facet on its medial aspect is more or less triangular in outline and is peculiar in that it is only slightly raised from the shaft and is without sheet-like projections. Just below the anterior margin of the facet there is a small fossa with pneumatic openings into the shaft (fig. 144) except in *Cathartes* where this fossa is indistinct.

Below the head, posterolaterally, are the articulations of the humerus and scapula. The coracoidal portion of the glenoid fossa is a shallowly hollowed area with rounded margins (especially dorsolaterally). The scapular articulation is a transverse area extending from the ventromedial margin of the glenoid fossa to the tip of the procoracoid. The glenoid fossa tends to be more linear-ovoid in shape, rather than elliptical, and it is not as deeply hollowed as in the accipitrid group.

The elongate, triangular procoracoid projects inward below the glenoid fossa. Its upper margin forms a part of the scapular articulation. The free margin is thick and rounded as compared with the other groups where it is thin edged. The coracoidal canal pierces the shaft near the distal end of the procoracoid process. Through this canal passes the nerve of the *supracoracoideus* muscle. The position of the canal varies; it approaches the margin of the bone in some specimens of *Coragyps* but is usually set well back.

The shaft of the coracoid is relatively short; it constricts gradually to the level of the distal end of the procoracoid then expands to form the flattened sternal portion. The anterior intermuscular line (between the medial lying *supracoracoideus* and the more lateral *coracobrachialis longus* muscle) lies well to the lateral side.

The lateral outline of the sternal end (sternocoracoid process) is characteristic. The margin of the shaft sweeps down and out to a truncated tip (insertion of *sternocoracoideus pars costalis*) and then down and inward to a point distal to the end of the intermuscular line. The ventral margin, from the end of the intermuscular line to the medial angle, articulates with the sternum. The medial tip of the articular surface is rotated outward so that it is exposed to view from an anterolateral angle.

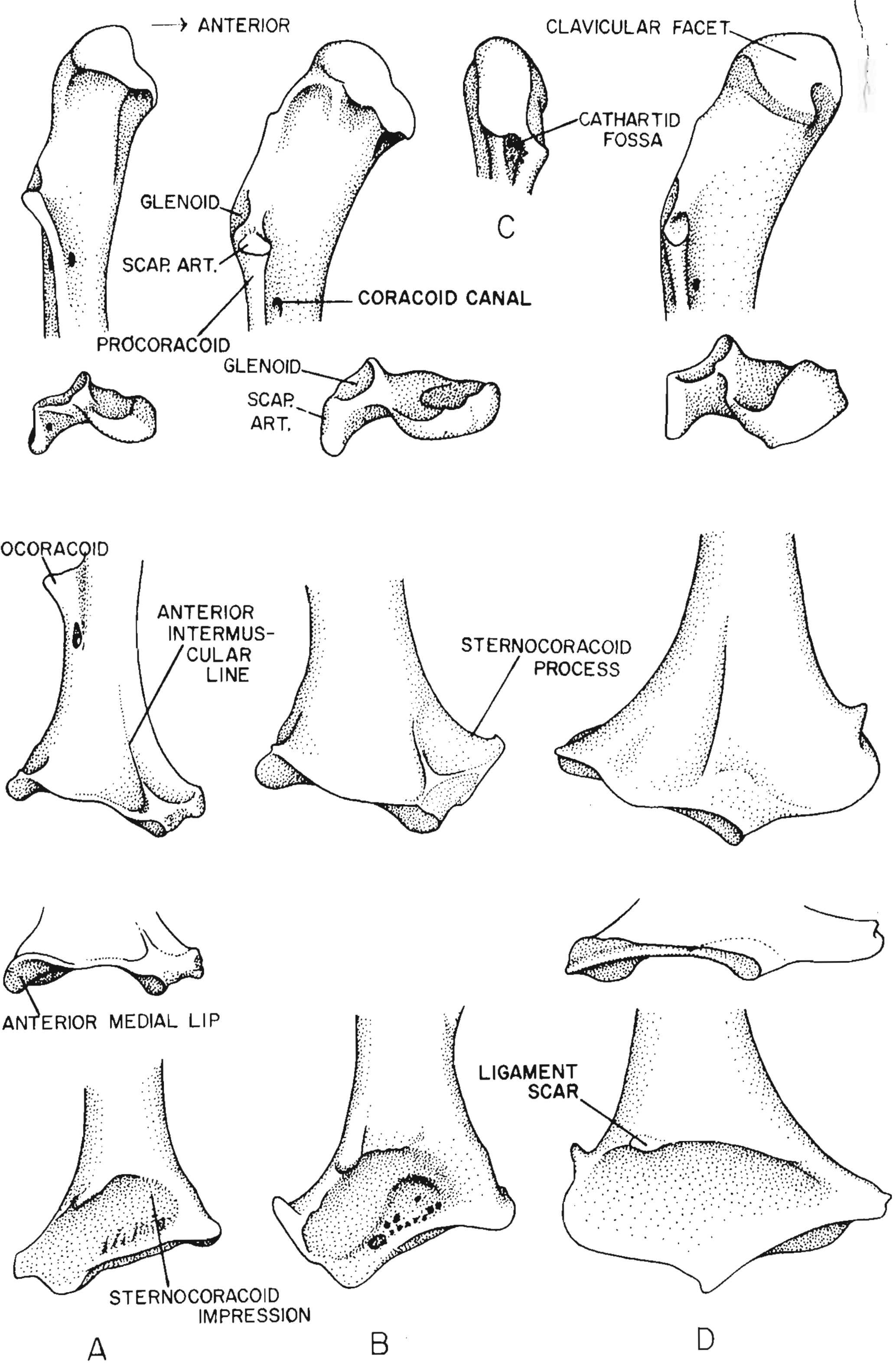


Fig. 144. Left coracoids of A. *Cathartes aura*, B. *Gymnogyps californianus*, C, *Gymnogyps californianus* (anterior aspect of coracoid head) D. *Teratornis merriami*. Row a, medial view of head; row b, end view of head; row c, anterolateral view of shaft and sternal end; row d, ventroanterolateral view of sternal end; row e, posteromedial view of sternal end.

The sternocoracoid impression of the posterior aspect (which is largely unoccupied in the flesh) has irregular pneumatic openings, especially along its ventral margin. There is a ligamental scar near the lateral margin but, in the flesh, the entire dorsal margin of the sternocoracoidal fossa serves for attachment of a ligamentous sheet which covers the fossa. This sheet is somewhat heavier laterally, where it overlies the area of insertion of the sternocoracoid muscle.

Among the modern genera the above description holds, but *Teratornis* does not agree in detail (fig. 144C).* The outline of the head is distinctive both as viewed medially and from above. There is a general resemblance to the living cathartids in the lack of a well-hollowed fossa below the clavicular facet and in the questionable presence of a fossa on the anterior margin. The shaft is more elongated and fans out more extensively distally. The intermuscular line is on the medial side of the shaft. The sternocoracoidal process is much expanded and has a rounded margin, which arches down from the lateral dorsal point to the lateral end of the distal articular surface. The articular surface is exposed medially but is distinctly ridged as the result of an anteriorly projecting margin. Posteriorly the fossa is shallow and non-pneumatic in contrast to the other members of this group.

The clavicle of the cathartid has a large broad head and a relatively short, straight shaft set at a right angle to its axis (fig. 145). The head, viewed from the side, has the outline of a bird's head (duck), the beak pointed posteriorly. The lateral face of the head is largely occupied by a fossa, which begins abruptly along a line almost parallel with the anterior margin and extends posteriorly almost to the rounded tip. The high rounded anterior margin of this fossa lacks a distinct

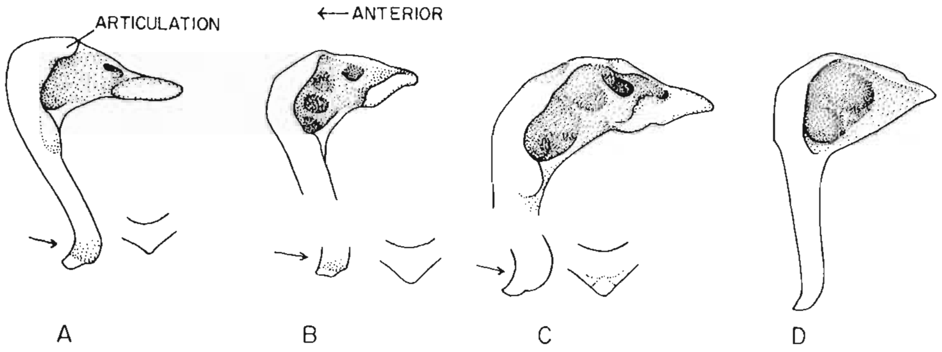


Fig. 145. Lateral views of the furcula of A. *Cathartes aura*, B. *Coragyps atratus*, C. *Gymnogyps californianus*, D. *Teratornis merriami*. At bottom, lateral (anterior aspect to left) and anterior (right) views of the clavicular symphysis.

---

* Fisher (1945:729) remarked that the coracoid of *Teratornis* is "essentially cathartid in pattern."

articular area for the coracoid, although there is a small area of contact here in *Cathartes* and *Coragyps* when examined in the flesh (not a distinct facet as suggested by Fisher, 1946:567). The posterior tip is swollen laterally in the modern genera but not in *Teratornis*. In *Cathartes* and *Coragyps*, the dorsal margin of this swelling supplies a large part of the area of origin of the *teres minor* (the *deltoideus minor* of Fisher, 1946).

The configuration of the bones at the region of their shoulder articulation is distinctive in the lack of a broad contact between an articular pad on the clavicle and the head of the coracoid (fig. 146B).

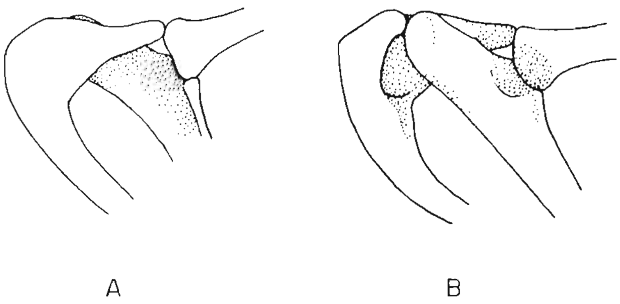


Fig. 146. Region of glenoid fossa of *Cathartes aura*. A. Medial, B. lateral views.

The cathartid type can be characterized as follows: clavicular facet with a distinct but not projecting ventral margin, the anteroventral angle projecting only slightly or not at all; presence of a small fossa under the anterior margin of the clavicular facet; sternal end variable, but medial angle blunt and with part of the articular surface exposed as viewed from in

* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *

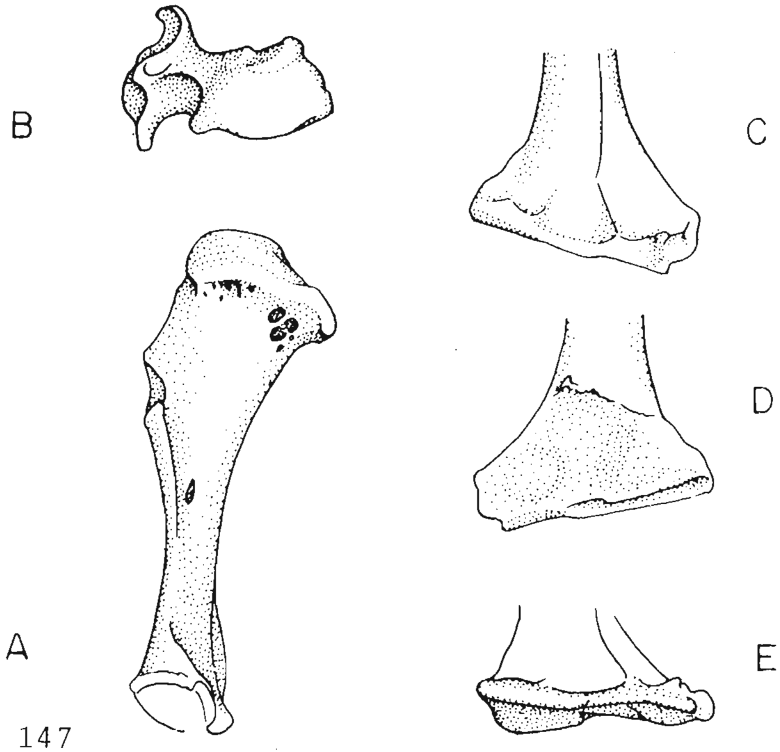
* Fisher (1946:567 said about the furcular shafts: "Another interesting variation is in the direction assumed by the furcular process at the symphysis; it points posteriorly in the Accipitridae and anteriorly in the Cathartidae....In the vultures the anterior and internal surfaces are very smooth in contrast to the sharp edges and the prominent symphysial ridge in the...[accipitrid]. Perhaps...The smooth surface of the furcula in vultures is adapted to support the relatively thin [food-gorged] crop that might be injured by sharp ridges; the furcular process extends forward beneath this weight to give added support and protection." Fisher's directional implications concerning the furcular process (fig. 145) are not accurate, nor is his assumption concerning rough or sharp edges on which to injure a "thin crop". The form of the furculum, as a membrane element, conforms strictly to that of the pectoral musculature and could not be adapted for supporting an inflated crop without these muscles also showing a modification in their form for such a function (*see* Böker, 1929). These comments lead to the conclusion that the pectoral muscle mass of the cathartid will show a difference in form when contrasted to that of the accipitrid.

front (has upturned lip), posterior articular flange at about same level as articular margin; head of clavicle of bird-head shape, lacking distinct articular pad for coracoid; hypocleidium a small tapered anteroventrally directed point.

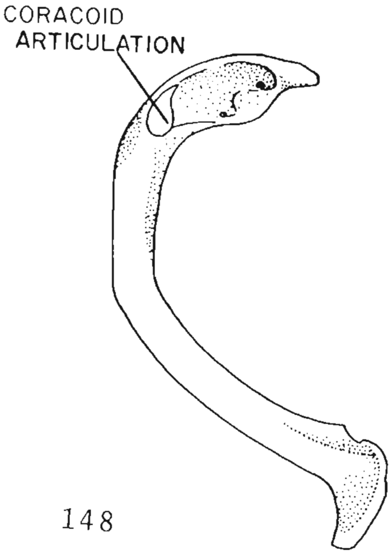
The cathartids differ from all other birds in the details of their pectoral girdle. The form of the coracoid is not exactly matched elsewhere although the sternal end, as it occurs in the highly modified *Teratornis*, is approached by that of *Fregata* or *Diomedia*. Similarly the head of the clavicle finds its closest match in the accipitrids but differs significantly from that type in the lack of a distinct coracoid articulatory pad. Some objection might be raised to the inclusion of *Teratornis* in this type, but it appears to represent only a specialized extreme.

### The Sagittariid Type

The head of the coracoid is slightly arched, viewed anterolaterally, and transversely flattened; viewed from above it is somewhat rectangular in outline (fig. 147). The clavicular facet is reduced to a belt along the medial margin of the head. Below the clavicular facet rim, the head has a series of irregular pneumatic foramina.



147



148

Fig. 147. Left coracoid of *Sagittarius serpentarius*. A. Medial view of entire bone, B. top view, C. anterolateral view of sternal end, D. posteromedial view of sternal end, E. ventroanterolateral view of sternal end.

Fig. 148. Lateral view of the furculum of *Sagittarius serpentarius*.

The glenoid fossa is rounded and deeply hollowed, the scapular articulation is a line extending out from that fossa along the upper edge of the procoracoid. The shaft is not distinctive as compared with that of some vulturines (accipitrids), although the margin of the procoracoid is thinner.

Ventrally the outline differs little from the accipitrid type. The articulatory surface is similar, but as viewed anterolaterally it forms nearly a straight line or is even somewhat convex. Posteriorly the sternocoracoid impression is shallow and non-pneumatic (sternocoracoid muscle inserts over much of its surface). The posterior ligament scar is on the lateral margin, associated with the dorsal margin of the sternocoracoid impression.

The head of the clavicle (fig. 148) is scarcely expanded as compared with the thin, blade-like shaft. Because of the thinness of the head, the lateral fossa is shallow and indistinct. The posterior point of the head is slightly bulbous for the scapular attachment. The coracoid articulation is lightly raised; in shape it is rounded below and pointed above.

The shaft curves down and then back in a continuous arc from the head. At the line of fusion of the clavicles, there is a massive posteriorly and ventrally directed hypocleidium. This process fans out, especially ventrally, fitting into the curve of the keel of the sternum to which it is partially or completely fused.

The shoulder articulation of the clavicle, coracoid, and scapula agrees with that of the accipitrid (fig. 149).

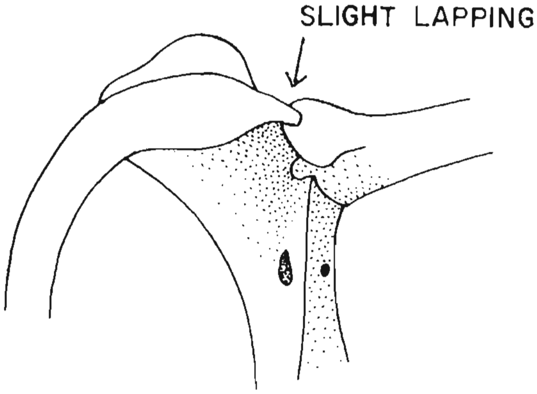


Fig. 149. Medial view of shoulder articulation of *Sagittarius serpentarius*.

The sagittariid type is best characterized by the flattened top of the head of the coracoid, rounded margins of the clavicular facet (lack of extension as a sheet at the anteroventral angle), sternal articular margin straight or convex, medial angle blunt; sternocoracoid process short and blunt; a clavicle which has a relatively small head, with a distinct coracoid articular pad, a long and evenly curved shaft, and a plate-like hypocleidium, which fits into the curve of, or fuses to, the anterior margin of the keel of the sternum.

This type is best matched by that of the storks in which the tip of the sternocoracoid process of the coracoid is drawn out vertically, the procoracoid process is larger, and the hypocleidium contacts the ventroanterior point of the sternal keel. The sagittariid type can be compared only superficially with the accipitrid or cathartid; it agrees even less with the other falconiform types.

### The Accipitrid Type

Viewed medially the head has a well-defined clavicular facet, (fig. 150) which may be separated into anterior and posterior parts by a shallow depression, as in most buteonins (*Buteo*, *Buteogallus*, etc.) and miscellaneous accipitrids (*Elanus*, *Accipiter*, *Ictinia*, *Rostrhamus*, *Pernis*, *Gymnogenys*, *Gypohierax*, *Milvus*, *Icthyophaga*, and *Haliaeetus*). It may be a single, well-defined facet the anterior part of which ends ventrally along a sharp projecting line, as in some kites (*Machaerhamphus*, *Chondrohierax*, *Leptodon*) or some eagles (*Aquila*, *Spizaëtus*, and *Stephanoaëtus*). Intermediate types are found among the vulturine species and in *Elanoïdes*. There is no sharp line of distinction between these purely arbitrary groups. The anteroventral angle of the clavicular facet projects out from the shaft in all. Viewed from above (fig. 151), the head has a more triangular outline (apex anterior). This triangularity is lost in some of the smaller species.

Below the clavicular facet there is a fossa which may or may not have pneumatic openings in it. This fossa may be a small pit or an extensive one covering most of the medial surface. This pit may be subdivided by ridges. Variation in the clavicular facet, and the fossa below it, is marked even within a species.

The procoracoid process is a sheet-like projection from the shaft, pierced by the coracoid foramen (canal). In *Elanus* the foramen is high up, nearly at the top, whereas in the remainder of the group it is lower. In *Accipiter* and *Circus* this process is reduced in size; the foramen is either absent or indicated by a notch in the margin. *Ictinia* has a well-developed process and an oblong foramen in about the same position as the notch of *Accipiter*.

The position of the coracoid foramen varies within a species. In *Aquila chrysaëtos* it ranges from an opening well back from the margin of the procoracoid to a mere notch in the margin. In spite of individual variation, there is some agreement within genera as to the position of this opening. The fenestra is characteristically large and ovoid in the accipitrid.

The coracoid is a short stout bone, which is ventrally widened and flattened (fig. 152). The anterior intermuscular line extends down along the lateral margin of the bone to its ventral rim where it ends in a slight projection.

The sternocoracoid process of *Elanus* is short; it is much elongated in *Leptodon*, *Ictinia*, *Accipiter* (gentilis), and *Milvus*. Usually this process has a truncated tip (insertion of the *sternocoracoideus pars costalis*), which is pointed at its dorsolateral angle. The medial line of the shaft swings out and ends as a point, the internal angle. This point is most attenuated in *Elanus*.

Viewed end on (fig. 152, row b), the articular surface is an upward arched line; viewed anterolaterally it is the same. The

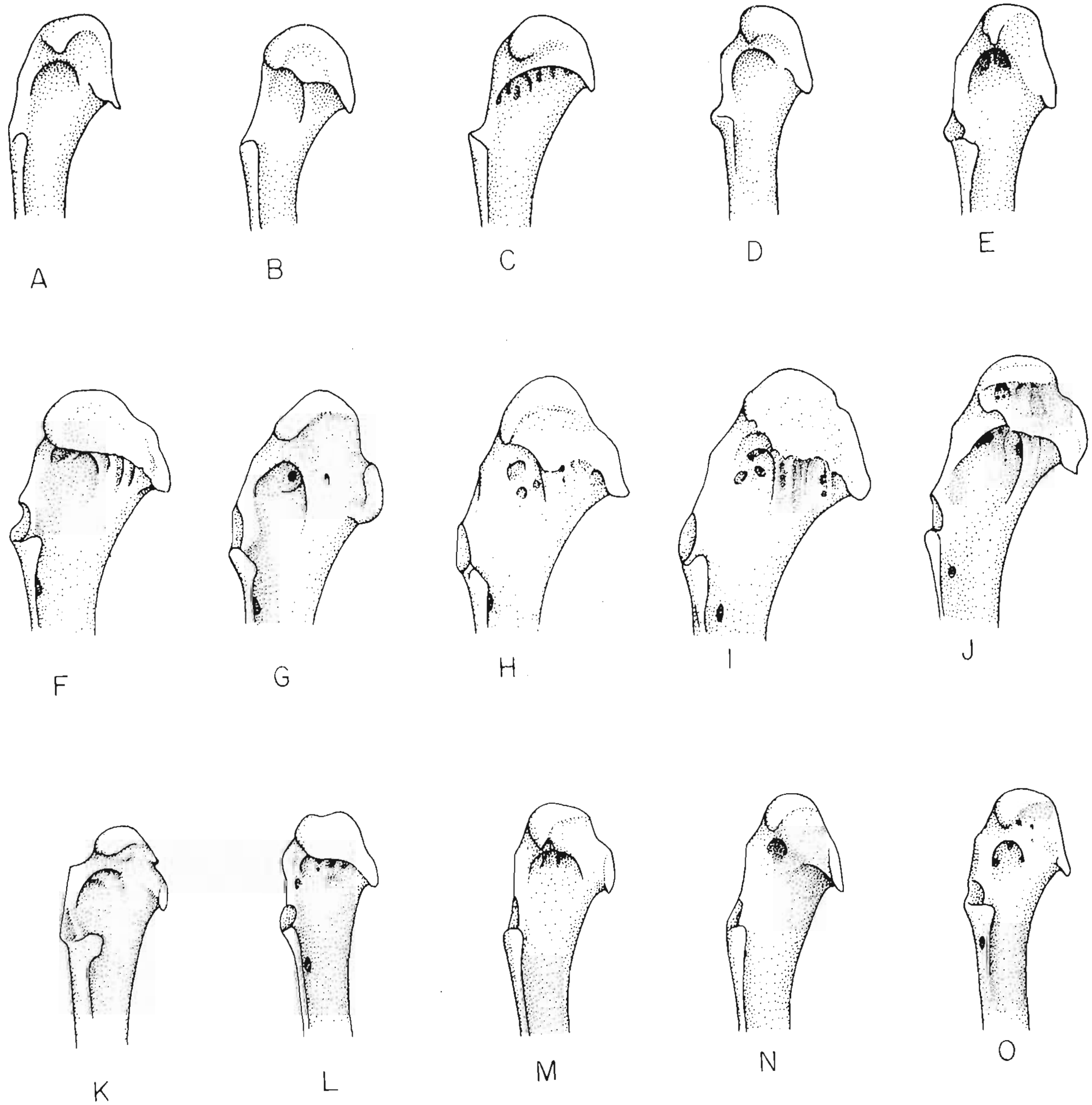


Fig. 150. Medial view of heads of left coracoids of A. *Elanus leucurus*, B. *Machaerhamphus alcinus*, C. *Elanoïdes forficatus*, D. *Rostrhamus sociabilis*, E. *Gymnogenys typicus*, F. *Aquila chrysaëtos*, G. *Haliaeetus leucocephalus*, H. *Trigonoceps occipitalis*, I. *Torgos tracheliotus*, J. *Terathopius ecaudatus*, K. *Accipiter gentilis*, L. *Chondrohierax uncinatus*, M. *Haematornis cheela*, N. *Icthyopaga ichthyaëtus*, O. *Buteo jamaicensis*.

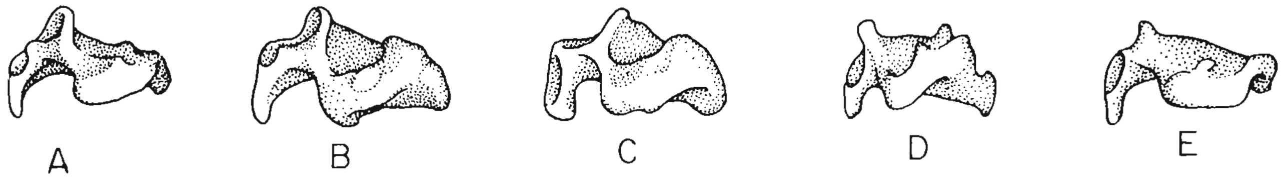


Fig. 151. Dorsal end of left coracoids of A. *Buteo jamaicensis*, B. *Aquila chrysaëtos*, C. *Necrosyrtes monachus*, D. *Chondrohierax uncinatus*, E. *Elanus leucurus*.

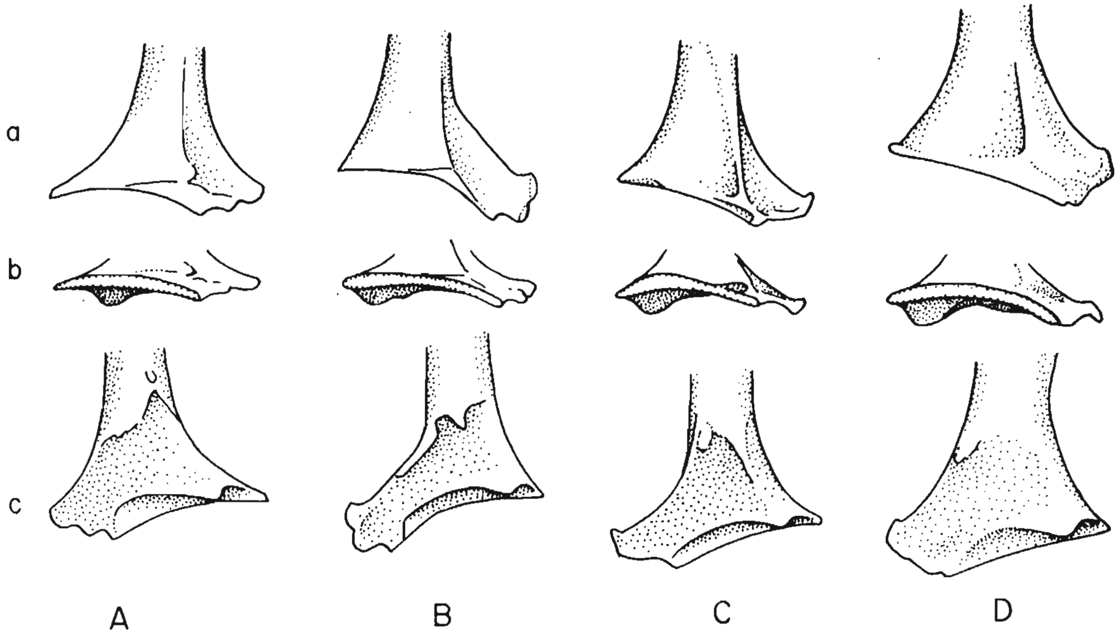


Fig. 152. Sternal end of left coracoids of A. *Elanus leucurus*, B. *Leptodon palliatus*, C. *Buteo jamaicensis*, D. *Torgos tracheliotus*. Row a, anterolateral view; row b, ventroanterolateral view; row c, posteromedial view.

rounded articular margin (in X-section) extends across the greater width of the coracoid, from the medial angle to a point just lateral to the end of the intermuscular line (it fits into the articular groove of the sternum). Behind this margin is a groove formed by a posterior flange, which completes the articular surface. This flange is largest medially and it has a distinct posterior projection (fig. 152, row b).

The sternocoracoid impression is shallow and covers most of the posterior aspect. The impression is most distinct medially, the area of muscle insertion. This impression generally lacks pneumatic openings although *Gypaëtus* has a pneumatic area laterally.

The posterior ligament scar (formed by the ligament anchoring the corcoid to the sternum) usually lies laterally above the sternocoracoid impression; it occurs in various positions ranging to well up on the shaft and toward the medial margin. In some genera such as *Elanus, Ictinia,* and *Pandion*, this scar could not be located, while in others there was a well-developed irregular tubercle.

The head of the clavicle (fig. 153) has a shallow, often pneumatic lateral fossa with a raised posterior margin. This margin forms a distinct articular area for the coracoid which is least developed, but still evident, in *Gypaëtus*. The outline of the head cannot be catagorized, although it terminates more or less acutely posteriorly. Among the kites there seems to be a tendency for short, ovoid, irregular heads. *Pandion* is unique in the form of the head (and in the degree of variation shown by this entire structure--fig. 153D). The head is much like that found among geese; it is attenuated and pointed posteriorly. The fossa appears to be eliminated, although a pneumatic foramen

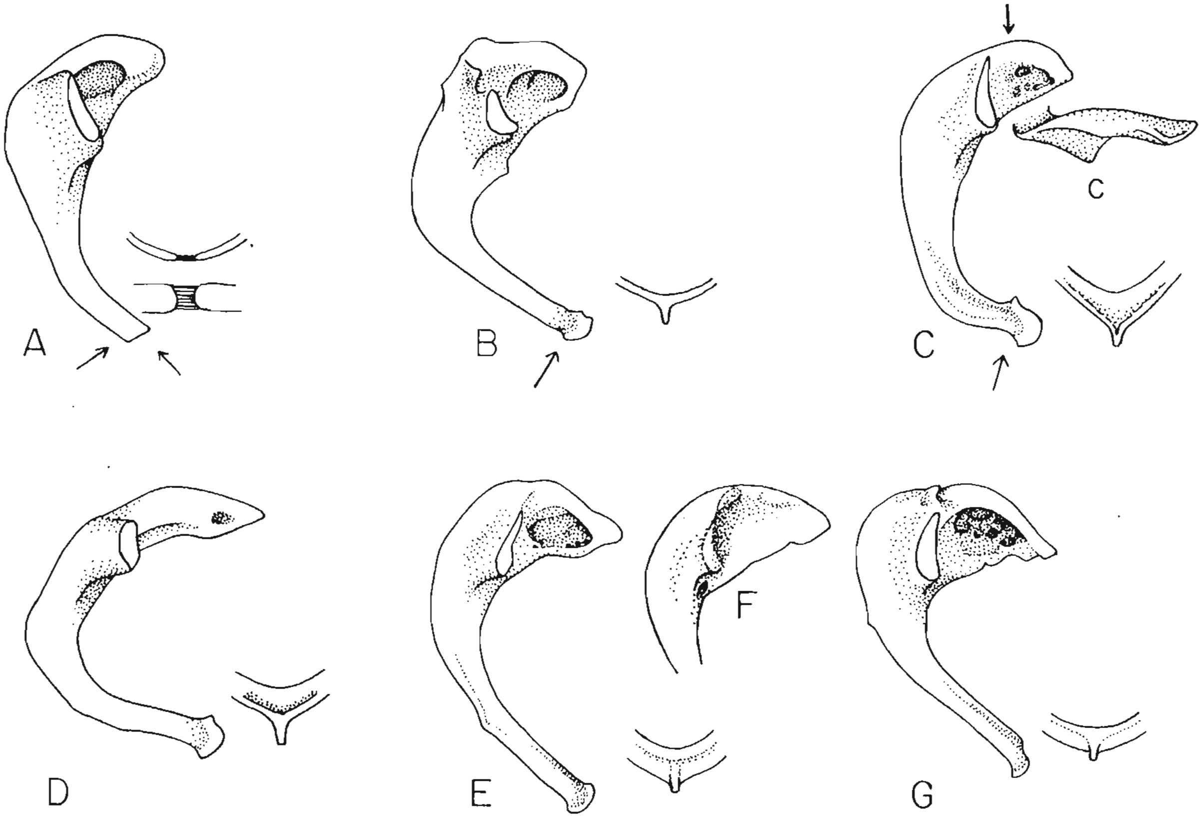


Fig. 153. Lateral views of furcula of A. *Elanus leucurus*, B. *Leptodon palliatus*, C. *Buteo jamaicensis*, D. *Pandion haliaetus*, E. *Sarcogyps calvus*, F. *Gypaëtus barbatus*, G. *Terathopius ecaudatus*. Insets show anteroventral views (along line of arrow) of symphysis, inset c shows a dorsal view of the head along the line of the arrow.

occurs on this surface. The coracoid articulation is sharply raised from the shaft both above and below and is nearly ovoid in outline.

The shaft extends in a continuous arc with the head. The width of the shaft varies, especially in the symphyseal region. At the symphysis a posteriorly and ventrally projecting hypocleidium is formed in all genera with the exception of *Elanus* where the tips of the shafts are somewhat separated and joined by a band of osseus tissue. The form of the hypocleidium appears to correlate with the proximity of the ends of the shafts to the anterior margin of the sternal keel or to the sternal spine; it cannot be employed in the recognition of subgroups.

The articulation of the clavicle, coracoid and scapula (fig. 154), is similar to that found in either the cathartid or *Sagittarius*. The tip of the clavicle usually lies in contact with, or slightly overlaps, the acromial process of the scapula. In *Terathopius*, *Gyps*, *Pseudogyps*, *Aegypius*, *Torgos*, *Sarcogyps*, *Trigonoceps*, *Gypaëtus*, and *Elanus*, there is a distinct gap between these points, bridged only by connective tissue. Some of the kites show quite different and in some cases transitional forms.

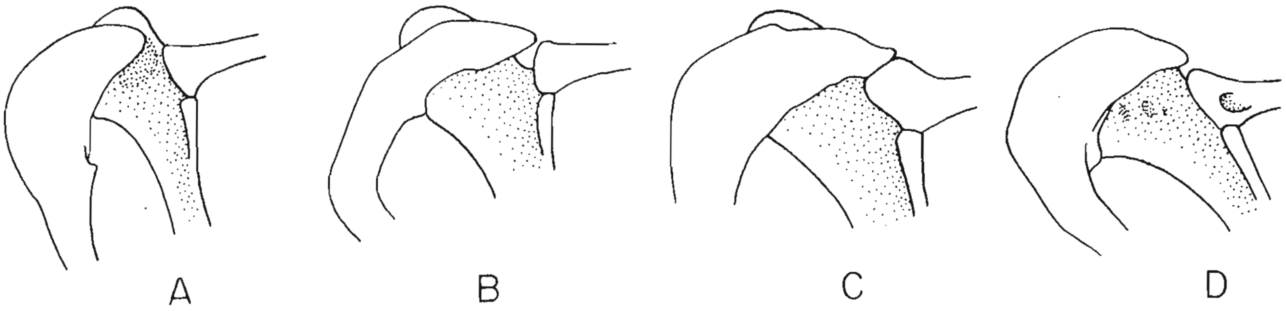


Fig. 154. Medial view of shoulder articulation of A. *Elanus leucurus*, B. *Pandion haliaetus*, C. *Aquila chrysaëtos*, D. *Terathopius ecaudatus*.

Despite the variation, the pectoral girdles of the accipitrids belong to a single type. Subtypes can be defined only poorly. *Elanus* is singular in having an attenuated ventral medial angle on the coracoid; a strongly triangular procoracoid with a highly-placed, small, round foramen; a nearly vertical clavicular facet which projects as a thin sheet ventrally; and in lacking a posterior ligament scar. The furculum lacks a hypocleidium.

The pernins certainly do not have a characteristic coracoid and, similarly none of the other kites can be associated with any group, pernin or otherwise. The kites, considered together, show certain tendencies such as a distinct ventral projection of the margin of the clavicular facet; wide, evenly rounded, proximal outline as viewed medially; and strongly projecting sternocoracoid processes (weak in *Pernis* and *Gymnogenys*). The kites might be characterized by their variability and general disagreement with the bulk of the accipitrids. This may be because of the wide variation in their sluggish flight and in their soaring ability. The aegypiin genera (not the subfamily Aegypiinae) have a fairly distinct style, grading, however, into the bulk of the accipitrids, and from this other individual styles can be said to stick out from the central mass of species.

*Pandion* is separable from the general plan on the basis of the clavicle; its differences are scarcely radical enough to remove it from the accipitrid type. (The head of the clavicle of the fossil, *Palaeoplancus sternbergi*, suggests that found in *Pandion* usually resembles the pernin genera, but here it marks the opposite extreme.

The accipitrid type can be characterized as follows: the head of the coracoid is bent noticeably forward (in contrast to the falconid), the clavicular facet is variable but projects noticeably from the head at its anteroventral angle, below the clavicular facet is a wide fossa which usually is pneumatic, the sternal end has an acute medial angle, the sternocoracoid process ends in a dorsolateral blunt-tipped angle, the articular margin lacks an anterior medial lip, the posterior flange is about on the level as the margin; the clavicle has a relatively large head with a well-developed coracoid articular pad, a slightly curved to sharply bent shaft, and a small plate-like hypocleidium.

This type finds no meaningful comparison with other birds. It has a resemblance to the cathartid or sagittariid--but certainly not to the falconid--and to other birds such as the storks and herons. However, agreement is not close enough with any of these to indicate relationship.

### The Falconid Type

The ventral margin of the clavicular facet lies at a steeper angle than in the previous types (fig. 155). It has a thin, downward-entending marginal plate. The procoracoid is attenuated its tip extending forward to a point below the anterior margin of the clavicular facet. The coracoidal canal is generally small and round, but in *Falco* it is larger and ovoid. Individual variations include having the canal set well back from the margin, as in the Polyborinae, *Micrastur*, *Herpetotheres*, and some species of *Falco* to a marginal notch in other species (specimens) of *Falco*. Even a notch is lacking in the specimen of *Microhierax* examined.

Ventrally the lateral outline arches out and down to a point on the articular margin; the latter arches up and medially. The tendon of the *sternocoracoideus pars costalis* muscle inserts along the whole lateral margin of this process. In *Polyborus* (and some specimens of other genera) this margin bulges somewhat in its middle course marking, perhaps, the initial step in the establishment of the truncated process found in other groups.

The articular margin is thin and rounded in X-section, the posterior articular groove is formed by a posteriorly projecting flange lying well above this margin; the latter is higher and smaller than that of the accipitrid.

There is no, or only a weak, posterior ligament present in the flesh and, therefore, no ligament scar. There is a high point

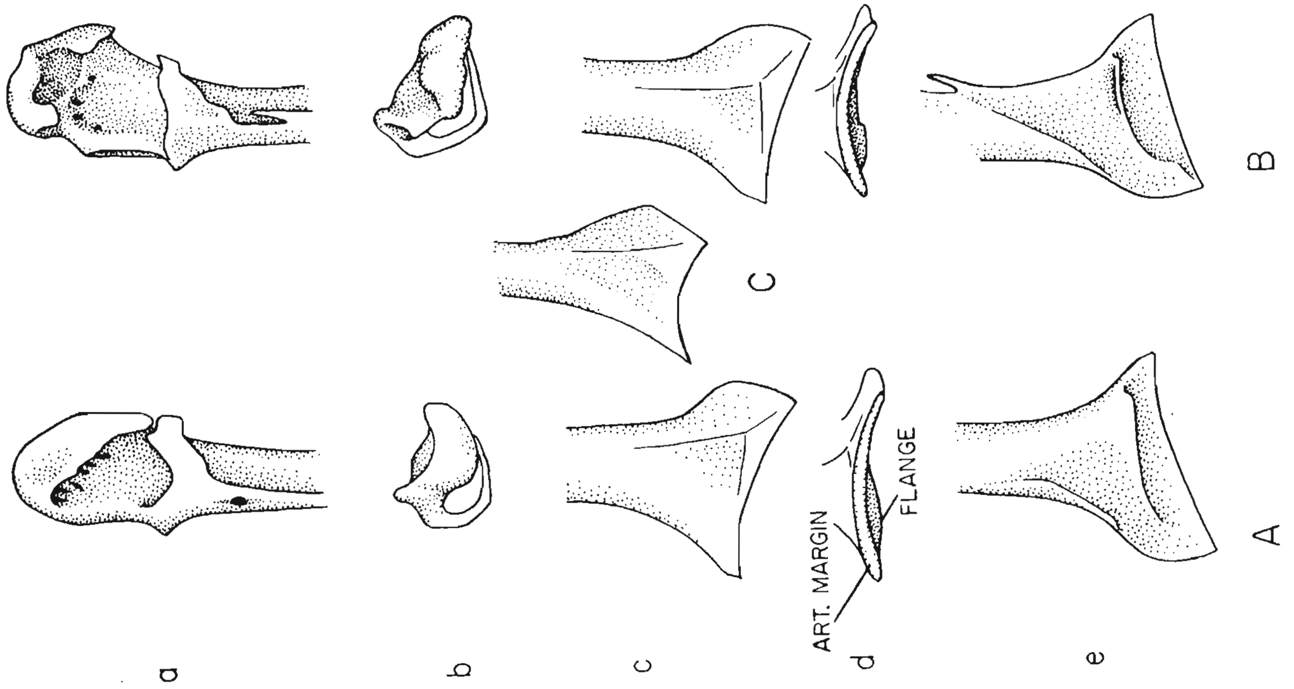


Fig. 155. Left coracoids of A. *Herpetotheres cachinnans*, B. *Falco mexicanus*, C. *Microhierax caerulescens*. Row a, medial view of head and upper part of shaft; row b, top view of head; row c, anterolateral view of sternal end; row d, ventroanterolateral view of sternal end; row e, posteromedial view of sternal end.

at the dorsal angle of the sternocoracoid impression in *Falco*, which is the ventral culmination of the medial, procoracoid ridge. The sternocoracoid fossa (insertion impression of the sternocoracoid muscle) lacks rugosities and pneumatic openings; it extends further up the shaft medially than in the accipitrid.

In outline, the head of the clavicle does not taper to a posterior point but ends in a single rounded knob, which is directed slightly upward, rather than backward as in the accipitrid (fig. 156). The lateral fossa is obscure and, in *Falco* only irregularly marked with pneumatic openings. There is a well-developed coracoid articulatory pad. In *Herpetotheres* or *Micrastur* there is a procoracoid process and notch directly below the coracoid articulation; the process is indicated in *Falco* but lacking in *Polyborus*.

The shafts curve only slightly, and there is usually a marked angle between the head and the shaft. As viewed anteriorly the furculum is narrowly U-shaped. At the point of symphysis, there is an indistinct hypocleidium, except in *Falco*.

The shoulder region of the falconid is very distinctive and was used by Ridgway (1875) to separate this group from the Accipitridae (fig. 157). The short blunt furculum abuts against the scapula; the procoracoid process projects anteriorly to

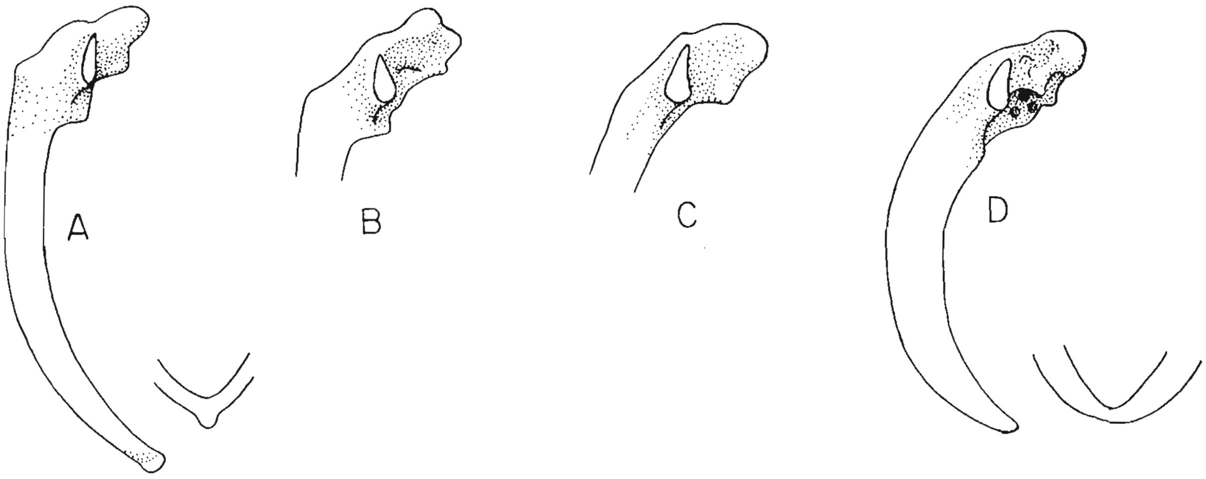


Fig. 156. Lateral views of furcula of A. *Herpetotheres cachinnans*, B. *Micrastur semitorquatus*, C. *Polyborus cheriway*, D. *Falco mexicanus*. Inserts are anteroventral views of symphysis.

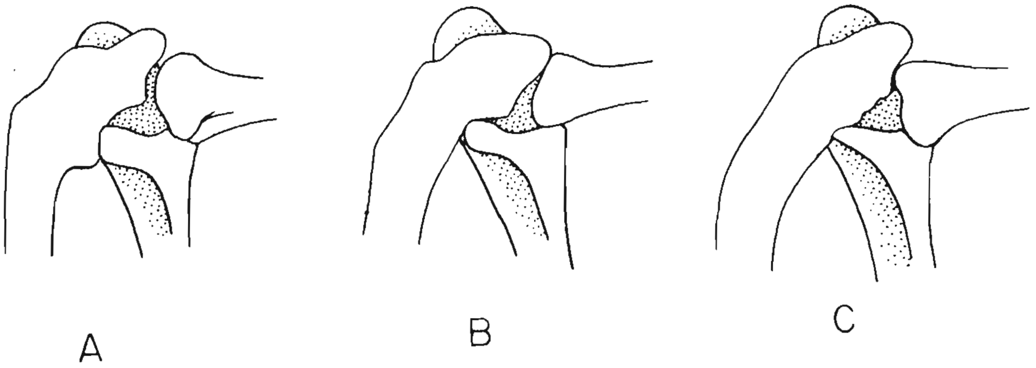


Fig. 157. Shoulder articulations of A. *Herpetotheres cachinnans*, B. *Polyborus cheriway*, C. *Falco mexicanus*.

contact the head of the furculum at the slight procoracoid notch and process (it attaches mainly through connective tissue with the anteroventral margin of the clavicular facet). No subtypes can be defined.

The falconid type can be characterized as follows: the head of the coracoid is not bent forward; the clavicular facet is steeply inclined; the procoracoid almost encloses the triosseal canal, its anterior end lying below the anterior tip of the clavicular facet; the sternal end does not flare out as strongly as in the other groups; the medial angle is acute or blunt; the lateral margin is rounded rather than forming a distinct sternocoracoid process; the articular margin is thin, lacking an anterior lip; the posterior flange is high above this margin; the head of the clavicle is nobby and directed slightly upward rather than posteriorly; the shaft is slightly curved; the hypocleidium is small or absent; viewed anteriorly, the furculum is U-shaped rather than V-shaped (as in the other three types).

Summary and Conclusions

On the basis of the shoulder region, the same four groups of the falconiforms can be defined. Of these the falconid is the best marked, being a radical departure in almost every way from the others.

The cathartid has a fairly distinctive coracoid and furculum. The shoulder articulation might be considered unique on the basis of the lack of a broad contact between the coracoid and clavicle. The lack of a defined articular pad on the latter can be considered a specialization.

Separation of *Sagittarius* from the accipitrid assumes the significance of various features of the head and sternal ends of the coracoid as well as such points as the slight development of the head of the clavicle and the greatly developed hypocleidium, which may fuse to the sternum. The girdle of the secretary is best matched by that of *Cariama* or a stork (*Jabiru*), particularly the latter. The match may not be exact enough to support relationship; it could be explained as convergence.

The variations of the accipitrid girdle appear to range around a central type. The arbitrary selection of the buteonin or accipitrin style as representative is based on the assumption that these genera are least specialized. The "archetype" must remain somewhat anonymous since as yet we do not know what is specialized and what is advanced.

The accipitrid type, in terms of individual details, can be matched in other "primitive" birds. As a whole it comes closest to the sagittariid. It is not strongly differentiated from the cathartid, but there is no overlap in terms of the clavicular and coracoid heads so that one can conclude that there is a "real" difference. Within this type there are no distinctive subgroups, although certainly there are some aberrant genera.

Howard (1932:62) assumed that the coracoid of the Aegypiinae can be characterized (exceptions perhaps of *Neophron* and *Neophrontops*,) by the ventral projection of the anterior part of the clavicular facet, as well as the forward projection of this surface. This feature is best presented by *Gypaëtus* but *Necrosyrtes* hardly differs from *Aquila* whereas *Neophron* is like *Buteo* (figs. 150H, I; 158). *Neophronotops* distally is also buteonin while *Neophron* resembles *Necrosyrtes*. These three genera which otherwise seem to be so alike show remarkable disagreement as to detail.

Howard also used the broad symphyseal region of the furculum and its sharp posterodorsal angle as distinctive of the Aegypiinae. These criteria, used to indicate the relationship to *Neogyps* to this subfamily, are fairly constant among the vulturine species but are not confined to this group. Comparison of the furculum of *Neogyps* with that of the aegypiin finds no more agreement than with *Aquila* or with such a wide, straight furculum as that of *Morphnus woodwardi*. *Terathopius* follows the general pattern of the aegypiin (although it is not included in the Aegypiinae) even to the straight shaft. These shafts are narrow in the symphyseal

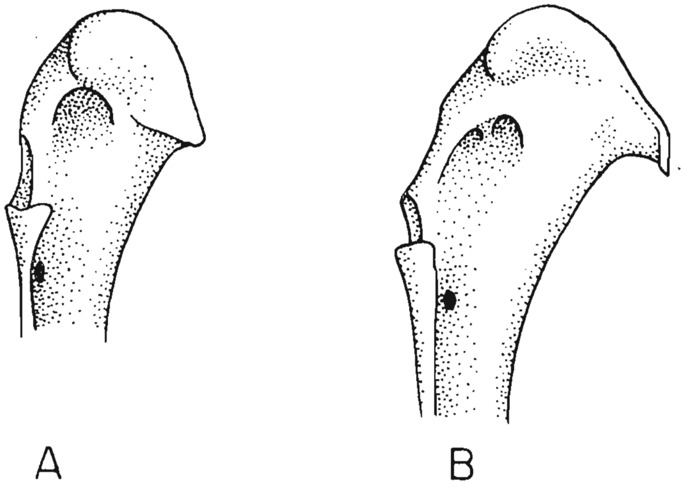


Fig. 158. Medial views of heads of left coracoids of A. *Neophrontops americanus*, B. *Gypaëtus barbatus*.

region as in *Aquila*. There is doubt that any significance can be placed on straight opposed to strongly curved or angled shafts, or wide contrasted to narrow symphyseal regions; these crop up quite at random throughout the Accipitridae.

The type of pectoral girdle Howard (1932) described applies best to the aegypiin genera. It does not apply to all of the members of the present subfamily and particularly to some of the fossil genera which have been placed in this subfamily.

The falconid type is not too dissimilar to that of the cuckoo, parrot, or owl. It is of interest to note the remarkable likeness between the coracoids of *Strix stygius*, a South American owl, and *Herpetotheres*, especially in details of the sternal end. The falconid coracoid shows interesting similarities to that of *Plegadis*, *Larus*, or *Bubo* (to select genera from various orders); it finds only poor comparisons with any of the other falconiforms.

The features of this girdle do not appear important at first glance but might assume significance with further analysis of this region (Fürbringer, 1888, must have started with just such an hypothesis). Within each of the groups of the falconiforms there is a basic agreement in the pectoral girdle structure in spite of the wide range of specialization in body size and styles of flight, this is true particularly of the Accipitridae. In a survey of all kinds of birds it can be said that the pectoral girdle is relatively constant within an order and in some cases several orders can be united on the basis of it. If anything this girdle is conservative. Even in such a highly specialized form as *Stringops* (*see* Böker, 1929) this region retains its phylogenetic identity.

The fact that the various elements of the girdle can be matched in different orders (*Teratornis* with *Fregata* or *Diomedea*, *Herpetotheres* with *Strix*), suggests that both specialization and conservatism are involved. In the first instance, convergence seems like the only logical explanation, but one can also assume a comparable common starting point and parallel development with specialization of flight and feeding. The comparison of the falconid and owl could easily be explained as retention of a primitive style; the degree of relationship thus indicated could be close or quite distant.

These views refute certain conclusions of Fürbringer (1888) or Fisher (1946). The later assumed that soaring was a specialized style of flight involving marked structural changes. This is a common style among the falconiforms and occurs in probably every group of birds, birds having very different styles of shoulder apparatus. There is no necessity for two species which fly "exactly alike" to have comparable shoulder bones (or musculature, viz. *Torgos* and *Cathartes*). The raven and the crow are structurally almost identical and yet one is given to soaring whereas the other indulges in soaring only on special occasions.

If locomotor specialization does account for variations in this girdle, the explanation does not involve such things as flapping or soaring but rather particular movements for landing or taking off; for control and stability in flight; or for the plane at which the wings are held while soaring and the arc through which the wings are moved when flapping.

The different types of pectoral girdles in birds represent a very early radiation of styles of flight upon which have been superimposed refinements accompanying radiation within the present families or orders. The fact that significant differences in styles of locomotion do not exist between the several types of falconiforms strongly suggests that we are, in fact, dealing with different heritages. It is inconceivable that two groups such as the accipitrid and falconid, which are presumed to be so much alike, should differ so markedly in this region (which should be relatively conservative).

## OSTEOLOGY--THE STERNUM

### Definition and Orientation

The sternum functions in anchoring the pectoral muscles employed in flight. Modeling of this bone and the development of its keel seem to be responses to the requirement of sufficient area for the origins of these large muscles. A sternum somewhat similar to that of the bird was developed by the Pterosauria.

This element develops from a cartilaginous precursor, which seems to arise by the fusion of bilateral contributions from the tips of the thoracic rib anlagen. It ossifies from two, three, or five centers in different kinds of birds (seven centers are reported for *Turnix*). In the red-tailed hawk there is a pair of lateral centers, equivalent to fused pleurosteon and metosteon centers of the chicken, which appear when the nestling is nearly full grown (half feathered), and a diffuse center (the lophosteon), which appears shortly afterward. The secondary nature of this bone is indicated by the late appearance of its centers of ossification.

The sternum was seized upon early as a structure which might be useful for the classification of birds. As pointed out by

Fürbringer (1888:1027), it was viewed as of primary or of no importance; the latter view appears to prevail at the present time although some still use the designations, ratite and carinate. As regards the falconiforms, Shufeldt (1878:728) said "It seems to me that this...bone would be particularly unreliable to adopt for any such purpose (taxonomy), for we will soon see in the Cathartidae that its shape appears to vary with the age of the individual, and a description of the bone in one bird, apparently an adult, would not answer for another of the same species, and perhaps of the same, or nearly the same, age."

The utility of the sternum cannot be based on the failures of the past; we should assume some value, perhaps as yet undiscovered. Examination of the sterni of the falconiforms supports this view.

## Comparative Anatomy

### The Carthartid (Cathartoid) Type

The manubrial spine of this family is blunt and heavy; it projects forward for a short distance and has a rounded lateral outline (fig. 159). No dorsal spine (*see* figs. 166, 167) is present although in some there are questionable lateral-dorsal processes formed by the ligaments anchoring the coracoids. The coracoid is braced, on its visceral aspect, to the dorsal margin

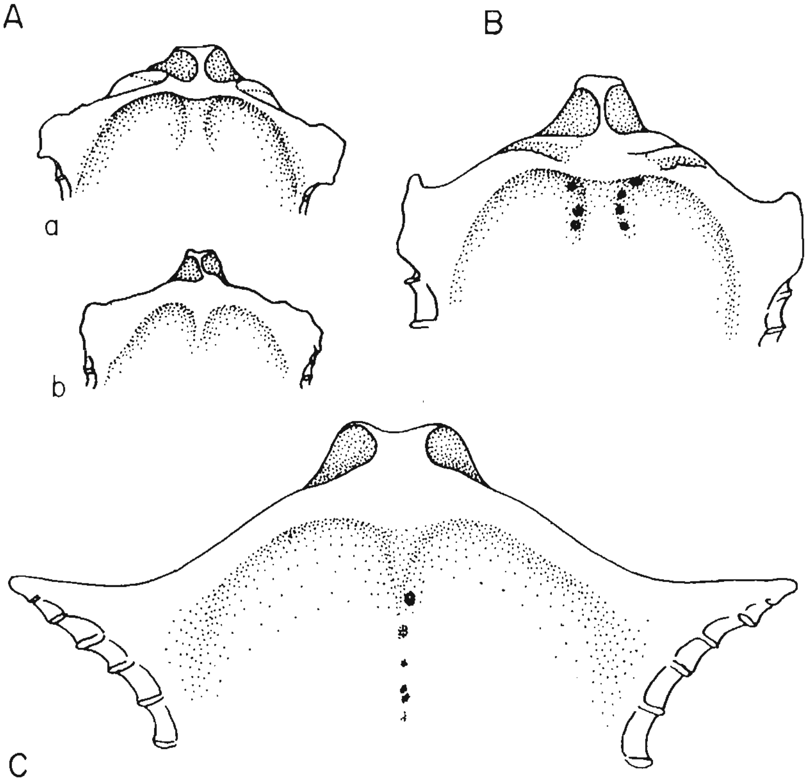


Fig. 159. Dorsal views of the anterior part of the sterna of A. *Cathartes aura*, two extremes shown (a and b); B. *Gymnogyps californianus*, C. *Teratornis merriami*.

of the sternum by a broad ligamentous sheet; this is continuous with that overlying the empty sternocoracoid impression of the coracoid which in turn is continuous with the aponeurosis covering the sternocoracoid muscle. The line of sternal attachment of this sheet may be drawn up as a thin lip, which terminates medially in a prominence. This prominence, in *Cathartes*, is the area of origin of the *sternotrachealis* muscle.

The coracoid sulcus is shallow and divided into a well-defined medial and a smaller, lateral articular impression. The sulci of either side do not lap on the dorsal surface of the manubrial spine, although they approach this condition in some specimens of *Cathartes* (fig. 159b). The medial margins of the sulci serve in anchoring the tendinous origin of the *supracoracoideus* muscles. There is no, or only an indistinct, articular pad behind the sulcus (*Cathartes, Coragyps,* and *Teratornis*). Midway above the sulcus there is a hollowed pit, overhung by a dorsal lip (fig. 160).

Except in *Teratornis* the sternocoracoid impression extends back to the first or second rib articulation and is largely occupied by deep pneumatic openings. In *Teratornis* it is similar in form, but alteration of the costal margin has changed relationships with the ribs. In this type the posteromedial angle bears a diffuse scar formed by the ligament, which anchors the coracoid laterally.

The lateral and dorsal margins of the sternocoracoid process are distinctive, except in *Teratornis*, in that they are broadly parallel to the axis of the sternum. In *Gymnogyps* the anterior angle of this process is drawn out suggesting a narrow-bellied *sternocoracoideus* muscle or attachment of a powerful ligament.

The costal margin of the sternum has five or six rib articulations separated by fairly deep, pneumatic cavities. The lateral plates of the sternum are only slightly arched (cupped) around the visceral cavity.*

The keel is well developed and peculiar in that it is of nearly uniform depth for at least one half the length of the sternum, except in *Teratornis* (fig. 160). It terminates at the extreme posterior margin of the sternum. The edge of the keel is thickened and irregular with the exception of *Cathartes* and *Teratornis*. According to Fisher (1946:562), "the ventral border is especially wide...correlated with the habit of placing the carina on the perch when resting, there are great extensions in width in the second and third quarters of the ventral border of the carina in all cathartids except *Cathartes*..."

* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *

* Fisher (1946:561) measured the relative depth of the visceral cup of the sternum and remarked that, "These ratios show the depth to be greatest in the accipitrines and least in *Cathartes* and *Coragyps*; the other genera form an intermediate froup. However, the depth in *Aquila* and *Buteo* is slightly more than in the vultures. From these facts it appears that greater depth of the trough is correlated with greater use of the flapping mode of flight." He concluded this subject by observing, "I am unable to discover any reason for the lesser depth in *Cathartes* and *Coragyps* which flap more than the other vultures."

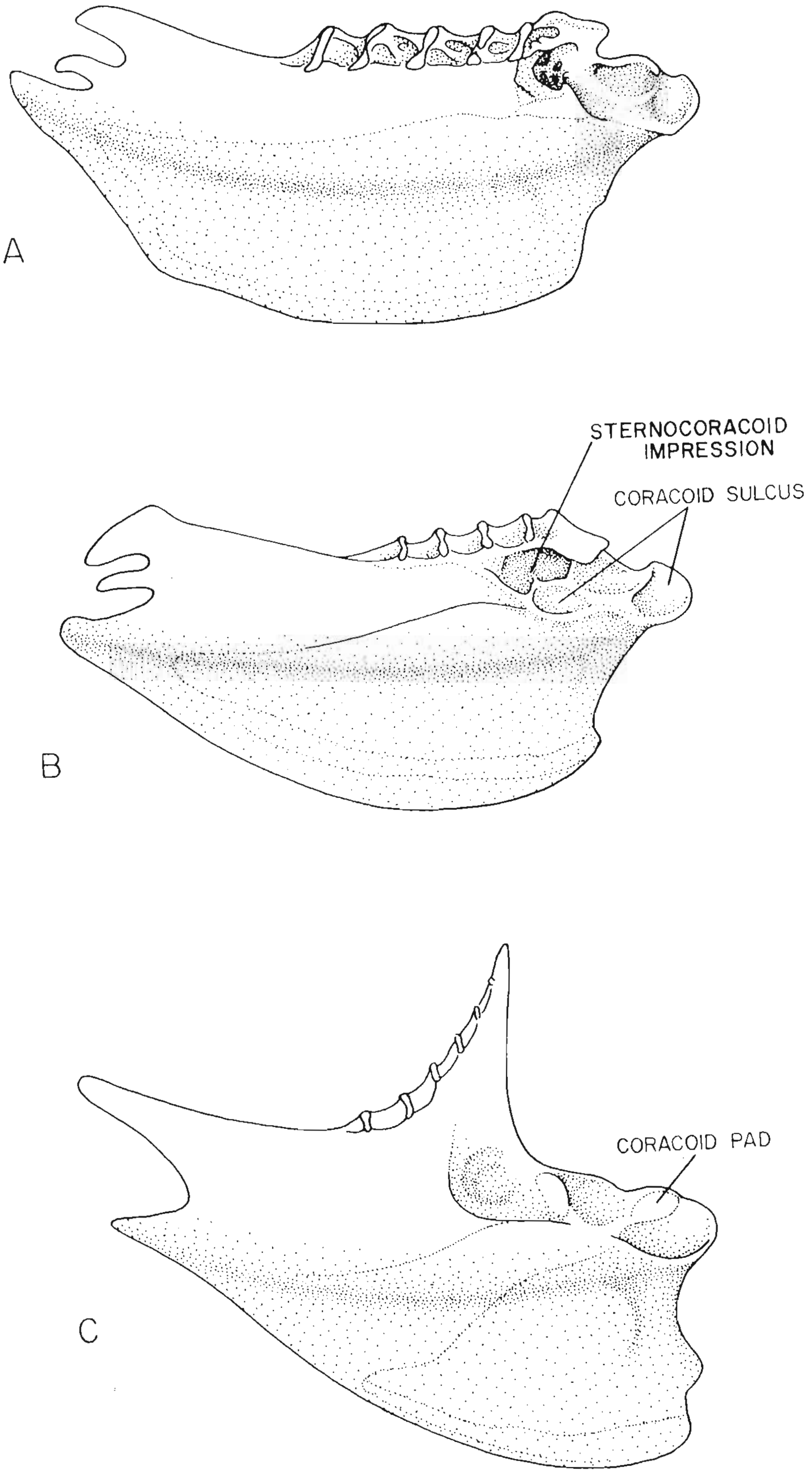


Fig. 160. Lateral views of the sterna of A. *Gymnogyps californianus*, B. *Cathartes aura*, C. *Teratornis merriami*.

Posteriorly the margin of the sternal plates has a deep, single (*Teratornis*) or double incision (fig. 161). The outer surface of the plates and keel show plainly the outline of the *supracoracoideus* muscle. In this group the muscle is well developed and extends nearly to the posterior margin of the sternum and to the ventral margin of the keel, except in *Teratornis* where it is limited to the anterior half. In no other group of the falconiforms is the area of origin of this muscle on the sternum proportionally so large as in the living members of this group.

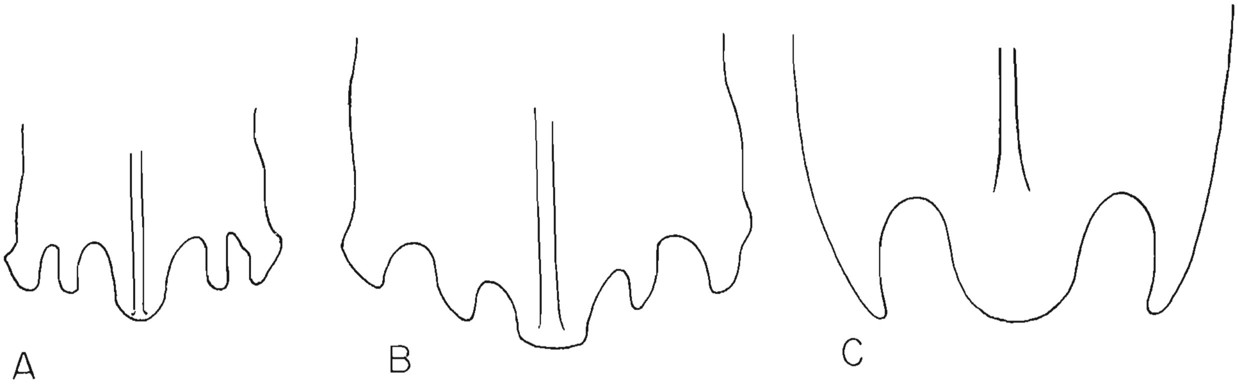


Fig. 161. Ventral view of posterior part of sterna of A. *Cathartes aura*, B. *Gymnogyps californianus*, C. *Teratornis merriami*.

The fossil genus *Teratornis* disagrees in many ways with the living species. It does not show a distinct pneumatic pit in the sternocoracoid impression, and the sternocoracoid process is drawn out dorsally and laterally into a point. The structure of this area (and the coracoid) indicates that the sternocoracoid muscle is either vestigial or lacking (as in *Fregata*). There are good articular pads for the coracoid above the sulcus. The keel is deepest anteriorly and tapers rapidly posteriorly. The posterior transverse margin has a single embayment on either side rather than two. Fisher (1945:727) pointed out that, "The anterior and lateral margins of this bone are decidedly concave in *Teratornis*; in the California Condor the lateral edges are straight, and the anterior margin is sharply convex." It could be added that the rib articulations are along a nearly vertical line rather than the horizontal characteristic of the living genera.

The features of the sternum of this group, based only on the living genera, can be summarized as follows: *simple manubrial spine with unlapped coracoid sulci*, poorly developed coracoid pads, *no dorsal process along the anterior margin* (may have a thin elevated line terminating medially at the scar for the *sternotrachialis* muscle), *coracoid sulci well impressed only medially and laterally, shallow fossa between the middle of the sulcus and the dorsal margin*, pneumatic pit in the relatively small sternocoracoid impression, *scar for anchoring ligament of outer point of coracoid weak or lacking,* shallow keel extending length of bone, large supracoracoideus scar (with thin *pectoralis* muscle), and two pairs of incisions in the posterior margin.

If *Teratornis* is included in the group, only the italicized portions of the above characterization apply. Although Fisher (1945:727) concluded that the sternum of this fossil is not of a "cathartid type," I cannot agree and suggest use of the italicized version.

The cathartid type has a strong resemblance to the sternum of *Sagittarius*; it can only superficially be compared with such divergent groups as the cranes and procellariiforms. It is not matched well enough with the latter to indicate relationship.

### The Sagittariid Type

The manubrial spine of *Sagittarius* is blunt; it has a slight medial groove and a triangular cross section, with the apex down (fig. 162). The coracoid sulcus is deepest medially and laterally; laterally there is a distinct ventral lip. Dorsomedially there are relatively flattened coracoid pads. The two sulci are well

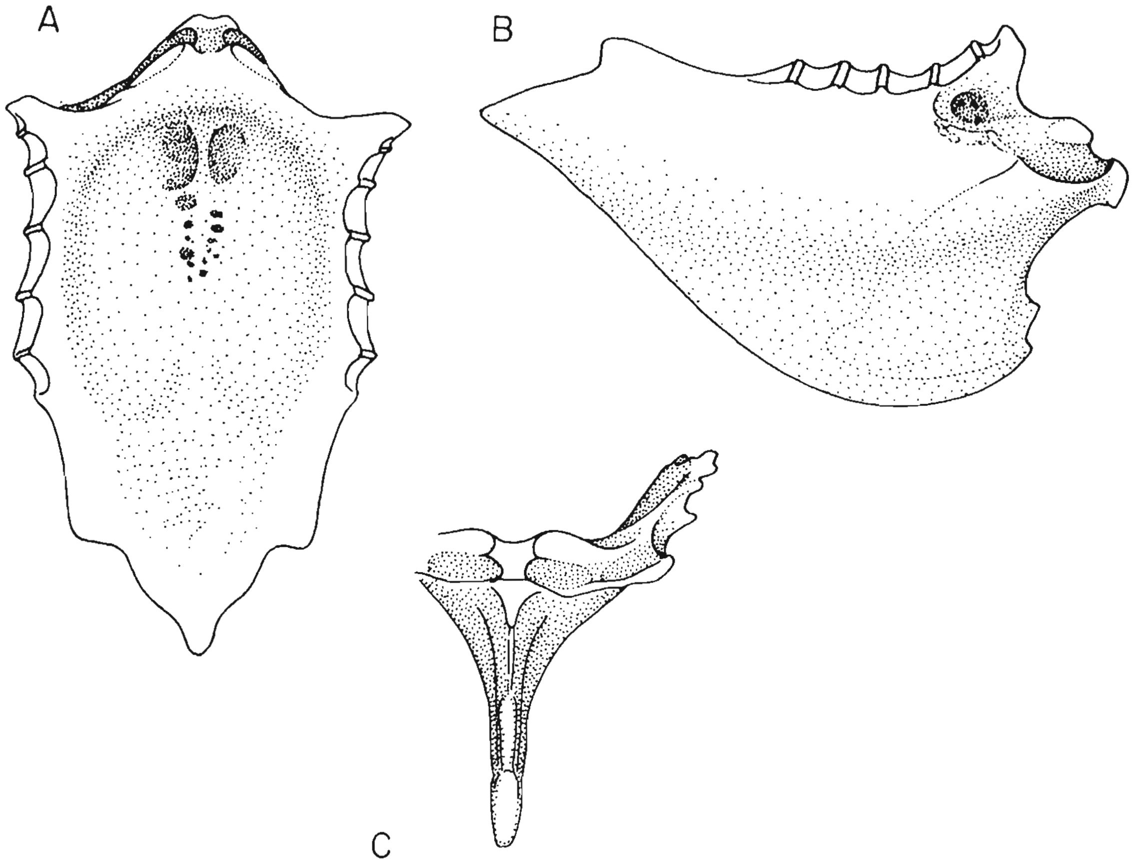


Fig. 162. The sternum of *Sagittarius serpentarius*. A. Dorsal, B. lateral, C. anterior views.

separated on the manubrial spine. The dorsal anterior margin curves out smoothly and lacks processes. Laterally, the margin ends at the tip of the sternocoracoid process.

The costal margins have five rib articulations separated by pneumatic cavities. The sternal plates are well hollowed for the viscera. The keel does not join the sternal plates at a sharp angle but gradually tapers into them in a smooth arc. The keel is relatively deep; its ventral margin arches upward posteriorly and ends on the apex of the posterior margin. The anterior line of the keel is deeply incurved, paralleling the margin of the hypocleidial process of the clavicles to which it is closely bound (or fused). The transverse posterior margin is peculiar in its thickened, triangular form; laterally slight projections occur.

Muscle and ligament scars are weak; that of the *supracoracoideus* is restricted to the anterior half and has an indented posterolateral margin. The ventral (medial) margin of this muscle lies close to the edge of the keel.

The sternocoracoid impression has a pneumatic fossa resembling that found in the cathartid. The ventral margin has a weak, diffuse scar formed by the attachment of the ligament from the lateral angle of the coracoid; in this it resembles the cathartid.

The sagittariid type can be summarized as follows: manubrial spine short and blunt, coracoid sulci well separated, distinct coracoid pads present, tips of sternocoracoid processes pointed, sternocoracoid impression has cathartid pneumatic fossa, lack of a distinct marginal tubercle for ligament bracing coracoid, keel deep anteriorly and extending to the posterior thickened and triangular margin.

### The Accipitrid Type

The manubrial spine of the accipitrids ranges from broad and blunt in *Gypaëtus* to thin and projecting in *Accipiter* (fig. 163). The tip of this spine is triangular in section, with the apex down, and there is a slight median groove dorsally. Correlating in general with the type of spine is the overlapping of the medial ends of the coracoid sulci. In *Gypaëtus* the medial edges of the sulci are widely separated, and the spine is short and broad; in most accipitrids the sulci overlap, the medial process of the right coracoid extends across in front of the left and the manubrial spine is proportionally narrower.* The narrowest spine, found in *Accipiter*, appears to be a result of need for a point of attachment of the furculum in addition to the lapping of the coracoids. The degree of lapping corresponds nicely with the length of the medial process of the coracoid. Lapping reaches its extreme in Elanus, where approximately one sixth of the coracoid widths are involved. The tendinous origin of the supracoracoideus muscle arises from the sulcal margins on the manubrial spine as in the cathartids.

The coracoid sulci of this group are deep and show only a

* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *

* The lapping of the coracoids of *Pandion* has been noted to be unique, but I find no disagreement with the typical accipitrid; occasionally there may be a reversal of the lapping.

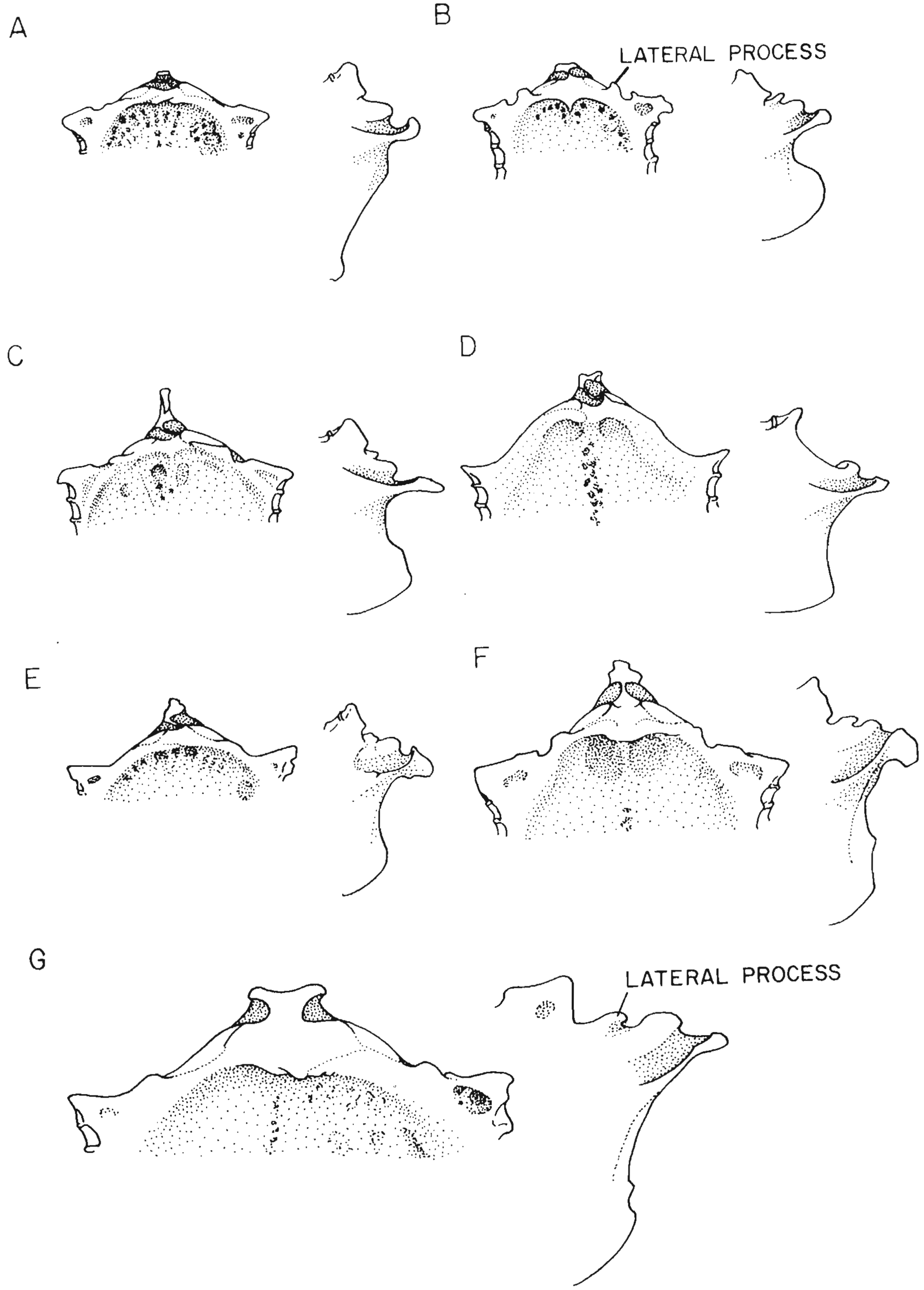


Fig. 163. Dorsal (left) and lateral views (right) of the anterior part of the sterna of A. *Elanus leucurus*, B. *Leptodon palliatus*, C. *Accipiter gentilis*, D. *Pandion haliaetus*, E. *Buteo jamaicensis*, F. *Terathopius ecaudatus*, G. *Gypaëtus barbatus*.

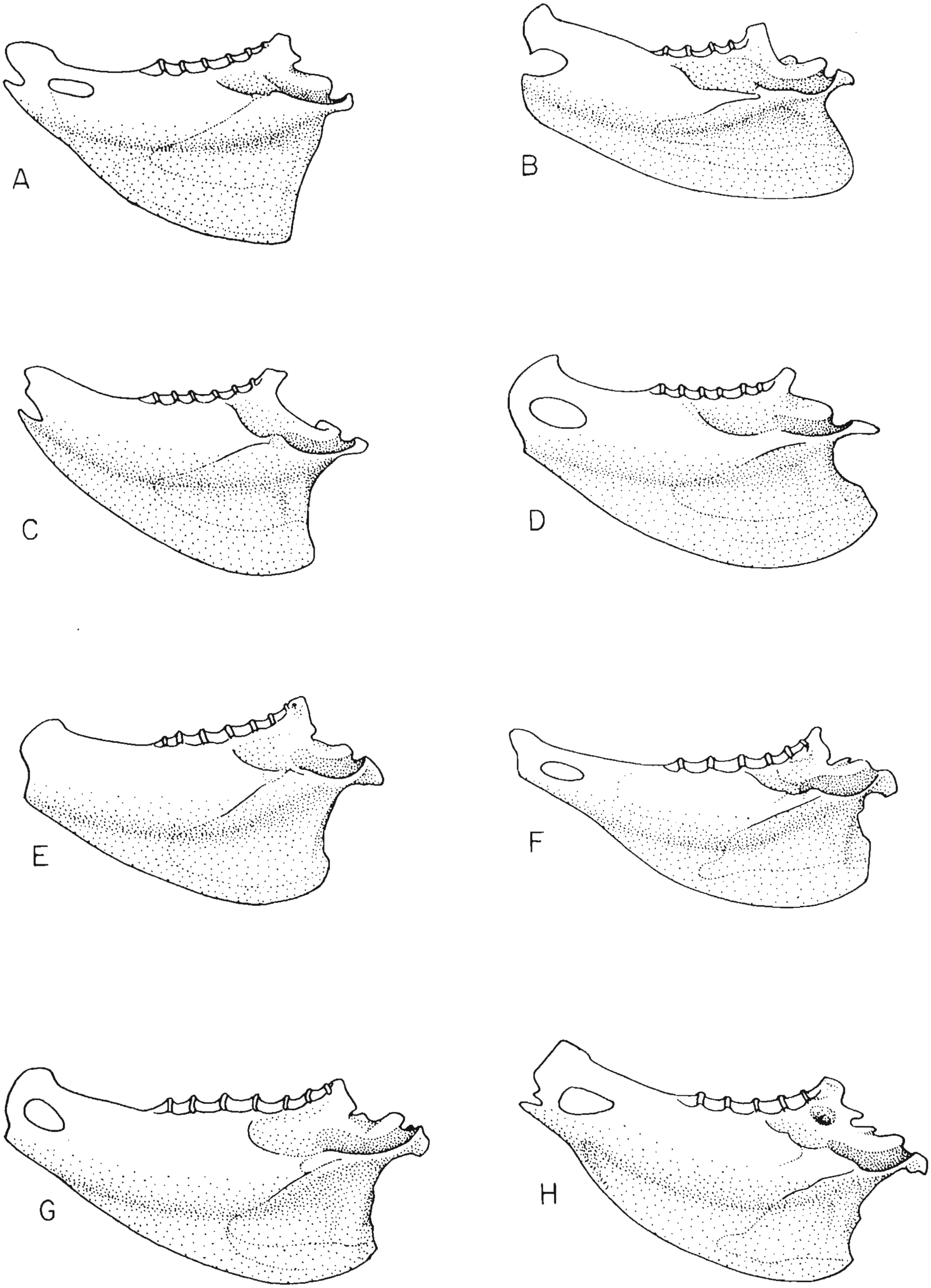


Fig. 164. Lateral views of sterna of A. *Elanus leucurus*, B. *Chondrohierax uncinatus*, C. *Pandion haliaetus*, D. *Accipiter cooperii*, E. *Buteo jamaicensis*, F. *Terathopius ecaudatus*, G. *Aquila chrysaëtos*, H. *Necrosyrtes monachus*.

slight midway shallowing due to the forward-curving nature of the articular margin of the coracoid (fig. 164). Dorsally there are well-developed, rounded coracoid pads. The anterior dorsal margin of the sternum may have well-developed lateral processes (attachment of ligament bracing coracoid) or these may be lacking (Table 11).

* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *

Table 11. The relative development of the lateral dorsal process on the anterior transverse margin of the sternum.

| well developed | distinct | vestigial | absent |
|---|---|---|---|
| | | | Pandion |
| Pernis | | | Elanus |
| Chondrohierax | | | Machae-rhamphus |
| Leptodon | | | |
| Elanoīdes | | | |
| Rostrhamus | | Ictinia | |
| | Gymnogenys | | |
| Haliaeetus leucocephalus | | Haliaeetus leucogaster | |
| | | Haliaeetus vociferoides | |
| | Gypohierax | | |
| | Gypaëtus | | |
| | Neophron | | |
| Terathopius | Haematornis | | |
| Necrosyrtes | | Aegypius | |
| | Gyps | Trigonoceps | |
| | Pseudogyps | | |
| | Aquila | Spizaëtus | |
| | Harpia | Pithecophaga | |
| | Buteo magnirostris | | Buteo jamaicensis |
| | Busarellus | Asturina | |
| | Accipiter striatus | Circus | |
| | Accipiter cooperii | | |
| | | Accipiter gentilis | |

* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *

The sternocoracoid fossa is usually well developed; generally it extends posteriorly to the third rib articulation. The fossa is smallest in *Pandion* where the costal margin parallels the medial margin of this fossa. A pneumatic pit occurs in the impression of *Necrosyrtes*, *Pseudogyps*, and *Gypaëtus*.

The ventral margin of the sternocoracoid fossa appears as a posterior continuation of the ventral margin of the coracoid sulcus. The position of this margin relative to that of the *supracoracoideus* muscle scar varies from well separated to lying in contact. The margin of the sternocoracoid fossa has at its anterior medial angle a strong point of attachment for the ligament from the outer tip of the coracoid.

The sternocoracoid process may have a small, anteromedial projection (fig. 163B, *Leptodon*), formed by a part of the sternocoracoid muscle arising here. In the aegypiins (fig. 169) this process is largest, whereas in most genera it is weak to indistinguishable. The costal margin of the sternum has four to seven, usually seven, rib articulations separated by pneumatic fossae.

The sternal plates are usually well hollowed for the viscera, and the keel descends as a thin plate at their point of junction. The shape of the keel differs widely among the various genera; it projects forward in *Accipiter* (*cooperii*), *Machaerhamphus*, or in *Chondrohierax* or sweeps strongly backward as in *Gyps* or *Pseudogyps* (fig. 164). Usually the deepest portion of the keel is forward, just behind the anterior pillar, but *Elanus* and *Chondrohierax* are deepest at the anterior margin. The keel tapers to the sternal plates before or at the posterior margin of the sternum. The depth of the keel is proportionally least in some of the large aegypiins (*Gyps*, *Pseudogyps*) and greatest in *Pandion* or *Elanus*.

The posterior margin of the sternum is usually square, it may have a pair of incisions or fenestrae. (These are laid down in the cartilaginous anlage of the sternum.) *Pandion* shows evidence of two pairs of incisions (fig. 165). The fenestrae are largest in the aegypiin genera and in some of the kites; they are lacking in some kites and in adults of some other genera. The nestling of *Buteo* has two large sternal fenestrae, which are closed by ossification in fully grown individuals.

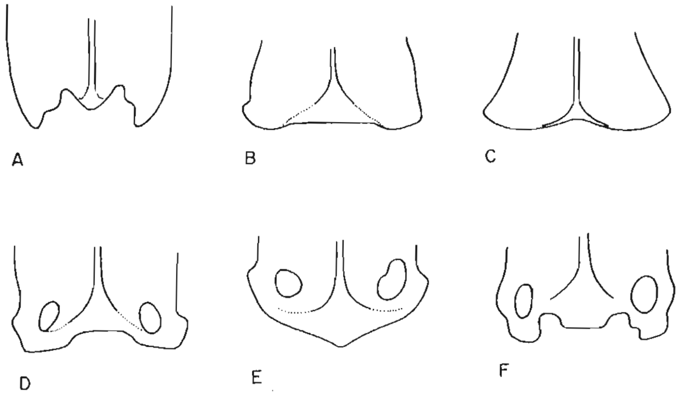


Fig. 165. Ventral views of posterior part of sterna of A. *Pandion haliaetus*, B. *Buteo jamaicensis*, C. *Leptodon palliatus*, D. *Terathopius ecaudatus*, E. *Gyps coprotheres*, F. *Gypaëtus barbatus*.

There has been some speculation on whether the size of a fenestra varies with age. After full growth is achieved variation is slight. In a series of skeletons of the golden eagle of known ages it was found that juveniles had the same range of variation (from no fenestrae to large ones on either side) as did the adults.

The sternal plates and keel, viewed from the side and below, show a fairly distinct *supracoracoideus* scar. Usually this scar is simple and more or less restricted to the anterior three fifths of the sternum. Certain of the Aegypiinae (excluding *Neophron*, *Gypohierax*, and *Terathopius*) show a lobed scar. This scar is misleading in that the muscle itself is not lobed (as it is in Sagittarius); the line is a composite. The area of this muscle scar is proportionally least in the larger aegypiins and greatest in the kites, in *Pandion*, and *Accipiter*.

The sternum of *Pandion* marks the extreme in several features: the form of the keel in terms of depth and shape, the style of sternocoracoid fossa, the incisions of the posterior margin, and the lack of dorsal processes on the anterior margin, which are usually developed in the kites. All these extremes suggest convergence toward the accipitrid rather than relation with that group. The sternum of *Elanus* is also quite distinctive. Except for these aberrant genera, however, subtypes cannot be defined.

The special features of the accipitrid type can be summarized as follows: simple to modified manubrial spine; coracoid sulci separate to lapped; sulci fairly deep and rounded at the bottom; coracoid pads well developed; distinct tubercled scar at angle of sternocoracoid impression for ligament anchoring tip of coracoid; sternocoracoid process rectangular in form, its tip a rounded point; usually only a single pair of incisions or fenestrae in posterior margin.

### The Falconid Type

The falconid manubrial spine is thin and elongated except in *Herpetotheres* where it is blunt and triangular (accipitrid-like, fig. 166). The coracoid sulci are usually well lapped, more so than in the accipitrid. In *Spiziapteryx* and *Polihierax* the sulci may touch, whereas in *Micohierax* they are slightly separated on the manubrium; *Herpetotheres* has approximately one sixth of the width of the coracoid involved, while one fourth is typical of other falconids.

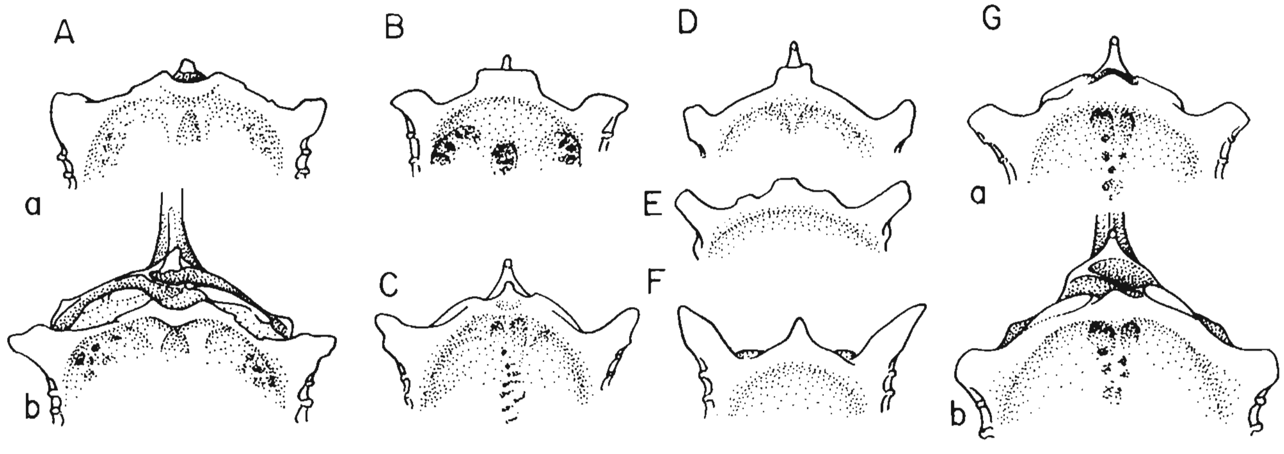


Fig. 166. Dorsal views of anterior part of sterna of A. *Herpetotheres cachinnans*, B. *Micrastur semitorquatus*, C. *Falco mexicanus*, D. *Milvago chimachima*, E. *Spiziapteryx circumcinctus*, F. *Microhierax caerulescens*, G. *Polyborus cheriway*. Anteroventral views are shown in b.