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INTRODUCTION TO A MONOGRAPH OF THE NORTH AMERICAN
BATS.*

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The bats constitute the order Cheiroptera. Unlike related groups which are equally extensive, the bats do not vary in sufficient degree to be confounded by any possibility with other creatures. By an untrained observer shrews might be mistaken for mice or voles, some of the smaller marsupials for minks or weasels, conies for marmots. But the popular impression of a bat is accurate, since this creature is the only mammal adapted for true flight, and no other mammal resembles it. If any mammals exist or have existed that are half bats and half moles, half bats and half lemurs, half bats and half marmots, they are quite unknown to the naturalist. Paleontology is silent as to the origin of the bats, though comparison of their bony framework with those of the Insectivora, Lemuroidea, and Rodentia suggest that they may have arisen from the mammalian stem not far from the points at which the differentiation of these branches began.

MEMBRANES.

Let us examine the undissected bat, and endeavor to establish thereby general conceptions of the creature and of some of the signs of the superficies by which its varieties can be named. It is at once seen that the anterior extremities are furnished with greatly elongated fingers, the intervals between which are occupied by two layers of skin. Goldsmith uses a happy phrase when he says "the fingers serve like masts that keep the canvas of a sail spread and regulate its motions."

*The monograph from which this introduction has been extracted will be published as a Bulletin of the National Museum. The printing of the latter having been unavoidably delayed, it has been thought best to publish this introduction in advance.—F W T

Layers of skin thus make up the wing membrane. They are continuous from the last finger and the thumb, or some adjacent surface, to the sides of the body, the neck (both above and below the arm and forearm), and the outer side of the posterior extremity. Each wing membrane reaches below the knee and from this point, in varying degrees, to the ankle and the foot. The space between the posterior extremities is also occupied, as a rule, by two adjoined layers of integument which constitutes the interfemoral membrane. This structure as opposed to the above is less constant in form and dimensions. It may be guided by a long tail quite to its tip, it may allow the tip to project in different degrees beyond its free margin, it may greatly exceed in size that of the stunted tail, it may be defined as a hem along the inner border of the limbs, or it may be entirely absent.

It follows from these statements that all bats are provided with a back and a front skin-expanse from the sides of the body to the extremities in a constant manner, but from the tail to the posterior extremities in an inconstant manner, the last named presenting modifications determined by degrees of outgrowth of the tail itself.

The membranes present many details with respect to the manner of their attachment to the sides of the body and to the various parts of the limbs. Interesting variations of plan are seen where the skin crosses joints. In the elbow joint the skin may be attached entirely to the epicondyle, so that the joint lies quite to the under side of the wing, as in the African fox-bat, *Epomophorus*; or it may be attached midway, namely, to the olecranon, as in many forms, but perhaps best seen in the neotropical American *Saccopteryx*; or it may be attached entirely to the epitrochlea, so that the joint lies quite on the upper surface of the wing, as in *Rhinolophus pearsoni* and *Taphozous*. At the wrist distinctions are seen in the manner in which the tendons of the extensor carpi ulnaris and flexor carpi ulnaris are disposed at the angle which is formed between the radius and the fifth metacarpal bone. When this angle is marked, and skin folds are conspicuous over the tendons named, a radio-metacarpal pouch is defined. The knee always lies on the upper surface of the membrane. It is most free in *Macrotus* and least so in the Molossi.* The membrane attached to the ankle may lie entirely to the pollical side of the joint, but is disposed to cross it by an oblique raised fold and be secured to the minimal, *i. e.*, little toe side.

I have found it convenient to employ a number of names for the subdivisions of the dermal expanse.

The membrane which extends from the sides of the trunk to include the anterior extremity is the wing membrane ("bat wing," patagium).

The membrane between the legs is the interfemoral membrane (uropatagium).

* The group named the Molossi will be held in this essay to be distinct from the group of which *Emballonura* is the central genus. I am of the opinion that these alliances are distinct and co-equal.

The wing membrane above the arm and forearm is the prebrachium (antebrachial membrane, propatagium).

The wing membrane below the arm and forearm would become antithetically the postbrachium. But since the postbrachium could not be separated from the sides of the trunk and the legs, it has been found necessary to discard it.

The part of the wing membrane lying between the body, the humerus, the lower extremity, and a hypothetical line drawn downward from the elbow and intersecting the free margin of the membrane, is the endopatagium.

The boundary at the elbow is often fixed by the vertical terminal branch of the intercosto-humeral line. The subordinate lines (probably platysmal in origin) in the endopatagium incline obliquely either toward the humerus or the trunk.

The part of the wing membrane which is limited by the line at the elbow as above given, by the forearm, and the fifth metacarpal bone and phalanges, is the mesopatagium.* Within the mesopatagium the subordinate lines incline either toward the forearm or the manus.

The part of the wing membrane limited to the manus becomes the ectopatagium (dactylo-patagium). The subdivisions of the ectopatagium are the first, second, third, and fourth interspaces. These are named from the pollex toward the quintus. The series of bones which is embraced in the metacarpal and phalangeal lines being conspicuous in the bat, it is desirable to possess a name in referring to each series taken as a whole. The name digit will be used for the rod of segments embracing the metacarpal element. The nerve which appears at the anterior margin of a digit becomes predigital, and that of the posterior margin, postdigital.

The cartilaginous tip to the terminal bony phalanx, respectively, of the third, fourth, and fifth fingers will receive the name of the third phalanx when three phalanges are present, and of the fourth phalanx when four phalanges are present. The shapes of the terminal phalanges are of interest and some of these will be described.

I have examined a sufficient number of genera to suggest that an account of the markings of the wing membranes and of the shapes of the terminal phalanges enter into all discriminating studies.

The division of the wing membrane into the parts endopatagium, mesopatagium and ectoöpatagium is sustained by what is observed in *Taphozous mauritanus*, since in this species the endopatagium is of a dark color while the rest of the membrane is white, excepting the extreme tip of the end of the third finger. Now when the animal is at rest the surfaces above named are those only which are exposed to the light. In all young bats which cling to the mother, without exposing any other portions of the membrane than those named, it is evident that for a

* The endopatagium and mesopatagium are together the same as plagiopatagium of Kolenati. (Beitr. z. Naturgesch. der Europ. Chir., Dresden, 1857.)

long period the endopatagium has functions which are not exacted of the rest of the wing membrane, and in consequence, in my judgment, it is easy to see how this portion of the wing expanse should be distinguished from those portions which are used only in flight.

The digits on their palmar aspect may be sharply defined as in the Phyllostomidæ and *Corynorhinus*, or they may be obscured by the membrane or the upper part in the forepart of the hand, namely, in the region of the second, third, and fourth digits, as in Molossi, Vespertilionidæ and the genus *Antrozous*. The membrane may lie chiefly on the upper aspect of the digits, as in most bats, or at the lower. That in the second interspace may be attached to the upper border of the second and to the lower border of the third metacarpal bone.

The skin is much more loose about the legs than the arms and on the interfemoral membrane than the wing membrane. The membranes are attached to the lower border of the first two or three caudal vertebræ, thus permitting them to be seen distinctly *above*, and to the upper borders of the remaining vertebræ, thus permitting them to be seen more distinctly *below*.

The skin of the two sides of the body unite in such wise as to permit a very narrow interval to exist between the two layers. The upper layer of the wing membrane is extending directly outward on a level with the back of the chest and of the loin, but the lower layer is variable. It may extend outward as in the upper layer, but a disposition exists for it first to conform to the curve of the side of the trunk and join the upper layer near the union of the side with the upper surface of the trunk. In one remarkable instance, *Chilonycteris davyi*, the under layer extends quite to the middle line of the back, and thence is deflected in an acute angle outward to join the upper layer. The region of the axilla is greatly depressed in bats, owing to the inclination for the under skin layer to extend upward and backward. This space is so large as to suggest the adaptation of the pouch thus formed for the protection of the young. In *Cheiromeles* it must have another significance, since it here constitutes a huge bag-like involution which extends as far as the middle line of the back.

THE WING MEMBRANE AT REST.

The bat when at rest folds the fingers by a movement of the root of the hand (carpus) downward on the wrist end (distal end) of the forearm. This movement is characteristic and when completed brings the fingers in a compact bundle (like the ribs of a closed umbrella) under the forearm and parallel to it. The hand is thus tucked up toward the rest of the anterior extremity, and as the forearm (in the same movement) is sharply flexed on the arm the entire extremity presents the greatest possible contrast to what it exhibited when prepared for flight. The bat now supports the body in one of two ways. It is prone, *i. e.*, with the front of the body downward on the plane of support, or it is pendent, *i. e.*, hung by the claws of the hind feet. If it is prone the base of

the thumb and wrist supports the body and is furnished with a hardened pad of skin (callosity) for the purpose, the thumb being held at the same time well out of the way, and the posterior extremity taking the position nearly the same as that of terrestrial quadrupeds. The best example of those that scurry* when the wings are folded are the Molossi. In this group the phalanges of the third and fourth digits are now no longer held in axial line with the metacarpals as in flight, but are drawn upward and to the side, though well out of the way. The tail in all prone forms remains extended and the tip touches the plane on which the animal rests. If the bat is pendant in rest the base of the thumb and wrist do not support. The thumb is without callosity, is more engaged in the wing membrane, and is drawn more or less in toward the under surface of the wing. In this event the foot is furnished with sharper and more recurved claws, since they are now prehensile. The leg assumes a position quite at variance with the terrestrial position and is different in this regard from all mammals, the sloth alone excepted. The tail in the pendant form, at least in our red bat, is drawn well forward and rests on the lower part of the trunk. It is readily seen that very long digits of the anterior extremity would be more or less in the way in the prone forms, while they might be extended to any degree in the pendant forms, without interference. In fact the first named have smaller digital elements than the last and the wing expanse is correspondingly more restricted.†

THE WING MEMBRANE IN FLIGHT.

While interesting characters are thus observed in the bat when at rest it is in the use of the limbs in flight that the chief peculiarities are noted. The intervals between the digits vary greatly in the different genera. As already remarked the under surfaces of the second and third digits are boldly outlined or are covered with membrane so as to obscure their outlines. In the forms in which this obscuring is noticed the fifth finger is supported by a little rod of cartilage.

The opening of the wing exerts a powerful influence over the posterior extremity. It pulls it outward in the forms in which an interfemoral membrane is present and thus makes tense this membrane. The entire limb is abducted from the terrestrial position and the foot is turned with its plantar surface forward.

*A word was needed to express the terrestrial motion of a bat whose wings are at rest. I venture to use "scurry" in lieu of a better.

†The contrast between prone and pendant positions of bats when at rest is an instructive one. It supposes the existence of a number of adaptive characters, which will be observed in the accounts of members of our fauna. So little is known of the habits of bats that it would be premature to base any generalizations upon these or any other isolated groups of structural peculiarities. I have seen our common brown bat in captivity hang itself up by the claws, but have never seen it other than prone when at rest in its native haunts. I am also aware that *Rhynchonycteris* (which has a flexed thumb and a small potlical callosity) comes to rest like a moth; i. e., with wings expanded yet prone.

The wing membrane may be said to be redundant when the expanse above the arm and forearm extends freely to the carpus and embraces the small thumb to a point beyond the first phalanx of the thumb; when it extends down to the foot beyond an oblique muscle line which extends upward and outward from the lower part of the leg; when the space between the second and third digits is ample, and that between the thumb and second digit is provided with a well-defined hem of membrane.

Skin folds are often disposed along the lines represented by the palmar fascia, at the proximal end of the fifth digit.* The flexor tendons at the radio digital angle are often covered with similar dispositions of the skin.

The membranes are supported not only by the parts of the skeletal frame-work, as these parts are usually defined, but by a number of special adaptations. An accessory cartilage at the somad margin of the terminal fifth digit has been already named (Molossi and Vespertilionidæ, except Plecoti). The interfemoral membrane is supported at the free margin by a special cartilage (calcar) from the tarsus in all bats excepting the Pteropi, Rhinolophidæ, and the Stenodermidæ. The calcar may have a process from its under margin, as in *Noctulinia noctula*. The terminal joint of the tail may be spatulate, as in *Nycteris*. Terminal cartilages of the third and fourth digits are present except in Pteropidæ, Rhinolophidæ, and Emballonuridæ. They are of varying shapes, the whole arrangement having for its object the support of the free margin of the wing membrane. These cartilages, as a rule, are deflected outward, though they may remain axial, as in Phyllostomidæ and Plecoti.

All things remaining the same, the degree of strain may be measured by the extent and variety of these special supports, and may be said to be in the line of specialization for aerial movements. Hence, in forms in which they are absent the membranes are broad and may be said to exhibit more of a parachute arrangement than in other types in which they are present, and the motion of the wings to be like that of a slow fanning rather than a rapid, varied flight.

Strain on the membranes is also shown in the angle form between the portions of the wing farthest away from the body, namely, the region of the second and third digits. These are pulled away from the fourth and fifth digits, which remain nearly passive by the traction of the muscles which extend these bones (extensores carpi radiales longior et brevior), and the whole membrane becomes tense. The contrast between the shapes of the wing in this regard is considerable when such forms as *Artibeus*, *Nyctinomus*, and *Atalapha* are compared.

When the wing of a bat is held up between the eye of the observer and a bright light the membrane is seen to be translucent. The delicate connective tissue lines (trabeculæ) are seen uniting the various

* Vespertilionidæ (excepting Plecoti) and Molossi.

parts of the bony framework, and the positions of the nerves, blood vessels, and muscle-fascicles are displayed. The paths of the nerves and blood vessels constitute one system and may be spoken of together, but the traceulæ and muscles are distinct from these and in some degree from each other. As in the case of the relation which exists between the skin and the bones, so in the arrangement of the parts just named the degrees of strain to which the wing is subjected account in the main for the difference in the various genera. The muscle-fascicles are most numerous in the membrane near the body, and are better developed in the narrow-pointed winged forms, such as *Molossi* and *Atalapha*, than in the broad, parachute-like forms. The muscle element in the wing is especially weak in the *Pteropidæ*, *Rhinolophidæ*, and *Vespertilionidæ*.

The fibrous lines which extend across the membranes are not without system. Many of them are excessively attenuated tendons; such, for example, are the fibres of the palmar fascia, already mentioned. Others are the fibres which connect the joints of digits; more of them yet appear to be parts of a true derm. The nerves and blood vessels pursue the same courses. Since the directions of nerves are of more importance in morphological study than the vessels, the former will be alone named. In each interdigital space a nerve tends to enter at its proximal end and, dividing into two branches, incline along the sides of the opposed metacarpal bones. The departures from this plan are numerous, and are so constant in groups of generic and even specific limitation that they constitute a valuable addition to diagnoses.

The wing membrane, when expanded, exhibits differences in the width of the interdigital spaces. These differences relate in an intimate manner with the behavior of the parts in flight, and consequently with habit. The subjoined table indicates some of these distinctions:

Manal (pteral) formulæ of the widths of second, third, and fourth interspaces.

Species.	II.	III.	IV.	Fore-arm.	Difference between III and IV.
	mm.	mm.	mm.	mm.	mm.
Lophostoma.....	7	17	18	49	1
Schizostoma.....	3	16	21	32	5
Macrotus.....	2	15	22	44	7
Desmodus.....	2	21	37	53	10
Vampyrops.....	3	17	27	36	10
Chilonycteris.....	1½	15	17	40	12
Hemiderma.....	5	20	32	26	9-12
Vampyrus.....	16	41	53	105	12
Lonchoglossa.....	3	19	32	33	12
Monophyllus.....	3	17	34	32	14
Artibeus.....	4	21	39	51	18
Brachyphylla.....	3	25	43	64	18
Mormops.....	3	16	35	50	19
Phyllostoma.....	4	29	62	81	45
Rhynchonycteris.....	5	16	25	40	9
Cynopterus *.....	10	18	27	58	9
Vespertilio †.....	2	11	31	59	10
Epomophorus †.....	13	21	39	83	11
Rhinopoma.....	3	13	30	64	17
Molossus §.....	½	5	35	46	30
Noctilio.....	2	13	58	83	45
Pteropus 	18	17	69	145	52

* *C. marginatus*.
† *V. murinus*.

† *E. franqueti*.
§ *M. rufus*.

|| *P. edwardsii*.

This list is selected in the main for comparison in members of a single family, viz, the Phyllostomidæ. The last eight forms are from families other than the one first named.

It is believed that these distinctions may be conveniently included in the characteristic proportions of bats.

In flight the thumb is extended in Vespertilionidæ, but partially flexed in Phyllostomidæ (excepting *Desmodus* and *Diphylla*) and in *Plecoti*. The degree of inclosure of the thumb in the membrane answers to the amplitude of the membranes generally and when extensive tends to draw the thumb slightly toward the palm, the space between the thumb and index finger being moderately occupied by a skin expansion.

It is a tendency under certain conditions for all growth processes to dominate functions other than those which are essential to their own activities. The best general conception of the manner of extending a fold of skin between the limbs is seen in the Batrachia. In the water newts a longitudinal ridge is often seen extending along the sides of the trunk. This is continuous along the hinder border of the anterior extremity (well developed in *Menopoma*) and reaches as far as the tip of the fifth digit. This fold is supplied by the ulnar nerve, which appears to be in its earliest expression a nerve for the skin of the posterior border of the forearm, of the fifth digit, and the muscles found in these regions. The phenomena of a fold of skin extending between the toes is one already familiar, so that the general plan of the skin expanse in a creature so low as the *Menopoma* prefigures that of so highly specialized a form as the bat without violence and without leaving a single line obscured. Difference of degree and not of kind separates them.

The very exceptional disposition in the bat for the skin from the trunk to extend the entire lengths of the limb, and in the case of the anterior extremity to form enormous webs between the produced digits, is associated with an inclination for the ears to become greatly expanded and for cutaneous offshoots to appear at the muzzle, chin, and the sides of the face. Even the prepuce is disposed to be redundant. Together with this inclination, dermal structures are highly specialized, so that the sebaceous glands, hair follicles, and tactile bodies are well developed. It can be readily surmised that special adaptations for a variety of purposes occur in this group of structures, so that secondary sexual characters are found in the gland masses of the skin of the neck, and of the skin folds, the details in the ears, the pouches of skin, etc., are available for purposes of classification.

THE EXTERNAL EAR.

In this connection let us glance at the peculiarities of the external ear. The external ear is markedly modified from the type usual in quadrupeds. Its simplest expression is seen in the Pteropidæ and the Rhinolophidæ. In these families the widely separated auricular carti-

lages are closely enwrapped by integument and the tragus is absent. In such an ear the terms *inner* and *outer borders* and *tip*, exhaust the list which are demanded in their description. In the ears of the remaining families it is far different. The auricle here is expanded to degrees which bring the outer parts to a greater or less degree downward and forward on the upper parts of the neck and reach the region of the mouth, or even the chin, while the inner border, being guarded by a skin fold which connects the ear to the crown, is disposed to be united with the corresponding part of the ear of the opposite side and extend in varying degrees toward the snout. Skin lappets arise from both inner and outer borders. Those from the inner border form a long appendage which lies in advance as defined in the simple ear and becomes the *internal hem*. As a rule it ends as a free lobe inferiorly, which thus becomes the *internal basal lobe*. The line of the true internal border being always discernible becomes the *internal ridge*. The external border, which is distinguished from the true external border which now becomes the external ridge is also disposed to form a hem (*external hem*), which, however, in contrast to the inner is apt to be divided into an upper and a lower part; the upper part forms the *first scallop*, and the lower the *second scallop*. The free lower end of the outer border becomes the *external basal lobe*, which may be separated from the lower scallop by a deep *basal notch*, or the second scallop may extend across this notch and the external basal lobe and becomes continuous at various distances with the face or that over the lower jaw. These parts will not receive distinctive names. In most examples the auricle is also conveniently divided into an anterior and a posterior part, the anterior part is marked, if marked at all, by lines repeating that of the internal border, while the posterior part is marked, if marked at all, by conspicuous transverse lines or striæ. The hair when it extends upward on the ear from the crown is usually of the color and character of that of the crown, while that of the posterior is of the color and character of that of the neck.

The *tragus* varies exceedingly in form. The following terms are employed in its description, viz, the *inner* and *outer border*, the *tip*, the *notch*, which is near the base of the outer border, and the *basal lobe*, which lies below the notch. The tragus is said to be absent in Pteropidæ and Rhinolophidæ, but in some examples of the family last named a rudimental tragus can be discerned. The tragus always arises from the ridge which lies in front of the auditory meatus and connects the inner and outer auricular borders. It is of interest to observe that while this connection with the borders is imperfectly defined in most bats that in the recently discovered *Euderma* it is markedly so united and tends to constrict the basal parts of the enormous auricle.

Not only is this the case, but the ears are often united by a band (*inter auricular membrane*) which extends obliquely forward. In *Corynorhinus* and *Macrotus* it is on the face, and in *Promops perotis* reaches quite to the snout.

In illustration of the value of the ear in classification the following table is drawn up from the members of the bats described in this memoir.

Phyllostomidæ.—External ear without internal basal lobe. External ridge rudimental or absent. External basal lobe not marginal, but lies well within the large second scallop, which is continued well in front; tragus prorect, coarsely crenulate or spinose on outer border.

Molossi.—Ears without internal basal lobe. Internal ridge produced forming a "keel." External ridge marginal, produced, bounding external basal lobe. External basal notch open, *i. e.*, not covered by lower scallop; tragus rudimental.

Vespertilionidæ.—Ears with internal basal lobe. Internal and external ridges rudimental, not produced. External basal lobe marginal (except *Plecoti*), not touching external basal ridge. External basal notch occupied by produced lower scallop. Tragus obscurely crenulate on outer border, or smooth.

SECONDARY SKIN DEVELOPMENTS.

At the muzzle the skin folds are median and lateral. The margins of the nostrils expand above and at the outer side while they are separated by a groove or a ridge in the middle line, as is seen in *Brachyphylla* and *Nyctinomus*. Or the two lines of perinarial expansion may meet below in the space between the nostrils and the lip to form a swollen ridge as in *Glossophaga* or a lappet as in most *Vampyri*, while the internarial ridge is continuous with a vertical leaflet. This is the type seen in most of the *Phyllostomidæ* as exemplified in this memoir in *Artibeus* and *Macrotus*. The nostrils may remain simple with upper border advanced upon lumen of the opening so as to divide it into two cornua as in most *Vespertilionidæ* or the lumen may be oval as in *Euderma*.

The lower lip is firmly held to the gum of the lower incisor teeth, as in *Vespertilio*, or it is free and forms a protrusile, membranous fold as in *Atalapha*. It may be entire or divided in the center so as to form two chin plates as in *Macrotus* and as a variation in *Nycticejus*. In *Atalapha* a distinct lappet extends entirely across the chin and in degrees of development distinguishes the sexes. The chin itself and the space directly back of it is adorned with scattered warts in all forms, but in *Phyllostomidæ*, as shown in *Artibeus*, the entire chin is conspicuously adorned with verrucæ arranged in median and lateral groups. In *Chilonycteris* and *Mormops* these are the sites of curiously complex leaflets.

The sides of the face are furnished with skin-folds of various lengths, which are continuous with the external border of the auricle, or a large wart lies directly back of or below the angle of the mouth, while the sides of the muzzle are apt to be more or less thickened by swollen gland-masses, which tend to embrace the side of the nose-leaf as in

Artibeus and *Macrotus*, or ascend toward the vertex of the face, where they either approach each other on the top of the muzzle as in *Antrozous*, or end free as in *Corynorhinus*.

HAIR.

The hair of the body is arranged in regions having well-defined boundaries. The crown of the head, the region directly in front of the ear, the neck, especially the side and back, inclusive of a line across the top of the chest, the shoulder itself, the sides of the under surface of the body, the rump, and pubis are all regions which are often separately colored, or clothed with hair of distinct texture, or rate of development than that of the other portions of the body. The sides of the neck are always furnished with longer hair than is the front and ordinarily than is the back. The hair of the pubis is more woolly than that seen elsewhere. The hair extends farther on the dorsum of the face in *Vespertilio* than in most genera. The same region is naked in *Adelonycteris*. The shoulders are occasionally furnished with shades of color contrasting with that of the rest of the body.

The membranes are clothed with hair in varying degrees. The greater area is naked. The interfemoral membrane is more thickly clothed on the upper than the lower surface, a tendency reaching its maximum in *Atalapha*, while the lower surface of the wing membrane between the body and the border of the manus—a tendency also marked in *Atalapha*, but most marked in the Asiatic form of the noctule bat (*Noctulina noctula lasiopterus*). As a rule the fur from the under surface of the body extends from the upper third or half of the arm to the knee. The presence of a clump of hair on the dorsum of the forearm is a good peripheral character for *Atalapha cinerea*. The interfemoral membrane as a rule is covered with an extension of hair from the rump to the basal third in most Vespertilionidæ. In *Vespertilio* an interesting character is noted in this clump, not being well defined, but straggles downward in an irregular manner and is lost near the ankle. This disposition is especially developed in *Vespertilio capaccini* and in the Nevadan variety of *Vespertilio nitidus ciliolabrum*. The lower border of the membrane is constantly fringed in some forms of *Vespertilio*, but as an individual variation in the North American species. It is rare to have the lower border of the wing membrane from the foot to the manus fringed as in *Pteropus*, but *Vespertilio*, as seen in North America exhibits a singularly constant, minute bristle which overlies the membrane at the tip of the fifth finger. The ears are apt to be sparsely haired on the inner surface near the anterior border, on the outer surface at the basal third or half, and on the external basal lobe. On the whole the bats which take the prone position in rest are less heavily furred than those which are pendent. In one of the most marked forms of the former group (*Cheiromeles*) the skin is nearly naked. Interesting contrasts can be made in this way between the hunters of

caves, attics, and old tree trunks and those which are caught hanging from the smaller branches and twigs of trees and bushes.

Bristles (setæ) usually surmount warts (verrucae). They are best developed on the face of *Molossi*, though they may be found in the group last named on the upper surface of the interfemoral membrane. The very long hairs of the sides of the muzzle, which are so conspicuous in many of the small mammals of other orders, notably the Rodentia and Carnivora are absent. The best examples are met with in *Vespertilio* and *Choeronycteris*. Fringes of bristles adorn the margins of the toes in *Molossi*.

In describing bats in this manner the attention which has been given to the details of the coloring and the markings on membranes require an exact use of terms.

When hair arises from the membrane it will be seen that the clumps follow the directions of the trabeculae and are detected in the translucent wing as minute black dots arranged in rows. These must not be confounded with pigment spots which dot the naked spaces of the wing in some species.

GLANDS.

The skin glands are best developed on the sides of the face directly back of the muzzle. In *Molossi* a large, median, coarse sebaceous gland lies on the under surface of the neck. It is best developed in the male. The mammae are large during the lactating period when the nipples are projecting and the areolar space naked. At other times the nipple disappears and the gland is reduced to the smallest possible proportions. In *Saccopteryx* and its allies the wing membrane above the anterior extremity is furnished with a sack which is lined with folds which yield a fetid secretion. The position and size of this sack furnish excellent characters to distinguish genera as well as sexes of individuals.

COLORATION.

It is necessary to state that the colors for the most part are described from alcoholic specimens which have been removed from the spirit and permitted to dry. Mr. F. W. True writes in the Smithsonian Report for 1888 that alcohol disturbs the color scheme of a mammal. The character of alcohol is not especially here named and the remark is undoubtedly correct for specimens which have been preserved in wood spirit. However, none of the specimens used for study have been preserved in other than commercial alcohol which has been variously diluted with water. I have observed no differences of the kind named between the few living individuals I have seen, the fur of the dried skin prepared in the usual way with arsenic and in skins dried after prolonged immersion in commercial spirit. It must also be remembered that since all the material available for my study has been preserved

in the same medium the comparisons are sufficiently exact for purposes of identification of museum alcoholics. It is barely possible that the color description may require some modification as contrasted with these drawn up from living specimens.

SKELETON.

Skull.—In describing the skull in bats, I have borne in mind that the form of the brain gives expression to the shape of the brain-case to a far greater degree than is the case in other mammals. The divisions of the brain are readily outlined externally, and yield convenient boundaries, since the shapes of associated parts harmonize in some degree to them. Thus the region of the proëncephalon, of the mesencephalon, and of the metencephalon are defined. In like manner the impressions made by the lines of attachment of the temporal and masseter muscles, the former on the cranium, the latter on the lower jaw, are valuable. For the temporal muscles I have named the median line between the two the sagittal crest or line, and the anterior and posterior temporal impressions the anterior and posterior temporal ridges or lines.

On the under surface of the skull the size and direction of the process (sphenoidal tongue) which extends backward and outward from the basisphenoid is worthy of notice. As compared to other mammals, the cochlea is unusually large at the base of the skull, and is, as a rule, but partially concealed by the tympanic bone.

The otic capsule varies in the degree in which bony laminae occupy the spaces created by the semicircular canals. On the side of the skull the surface (opisthotic) which adjoins the squama in mammals generally is in bats crossed by a process of the squama uniting with one from the exoccipital, as in *Atalapha*, or the surface is free as in *Nyctinomus*. The old-world genus *Hipposideros* resembles *Nyctinomus* in this particular. When the otic capsule falls out, as it is apt to do in the over-macerated skull, a foramen or a notch is always defined between the squama and the occipital bone. Sometimes a foramen of the same significance, viz, one occupied by the opisthotic during life, is seen on the occiput.

The otic capsule in Pteropidæ alone is inclosed in bone, to form a triangular wedge comparable to the *os petrosa* of other mammals. As a rule, the form of the cochlea and semicircular canals are outlined as though in the human skull the encapsuling petrosal bone had been chiseled away, the degrees in which thin plates of bone fill in the semicircular canals being alone subject to change. The horizontal loop in all forms examined is filled with bone.

The following scheme of the otic element will be found useful:
External loop entirely occupied with bone:

Superior loop angulated, open.....	<i>Artibeus</i> .
Superior loop nearly filled.....	<i>Nyctinomus</i> (<i>N. brasiliensis</i>).
Superior loop about half filled.....	<i>Atalapha</i> .

External loop almost entirely occupied with bone:

Antrozous.

Vespertilio.

Adelonycteris (*A. fuscus*).

External loop and superior loops not occupied with bone:

Noctilio.

Macrotus (occasionally excepted).

Hemiderma.

Chilonycteris.

The tympanic bone is sometimes incomplete, as in *Vespertilio*, at its upper arc, where it limits the zona tympanica superiorly. The bone constitutes the bulla, which presents various degrees of extension over the cochlea or forward along the side of the glenoid fossa. The width of the origin of the sterno-mastoid muscle is much greater than in mammalia generally. This interval in *Artibeus* equals one-seventh of the greatest length of the skull, which in *Canis* it equals one-nineteenth.

Seen from above, the face is described as forming a vertex. This extends from the region of the proencephalon to the upper border of the anterior nasal aperture. On the side the region of the face is equal to the length of the dental series. The orbit is, strictly speaking, that portion of the skull which accommodates the eyeball; but this is much smaller than the space as defined by the bony limits, as seen in many other mammals. Since custom has sanctioned an acceptance of an orbital region which would be limited posteriorly if a process were present extending from the anterior temporal ridge toward the zygoma, a similar region so restricted is held to be a valid one in all bats. In some genera, indeed, as those of the Emballonuridæ, the post-orbital process is constantly present, and in the Pteropidæ varying degrees of posterior limitations of the orbital region are seen. The face, including a part of the frontal bone, is inflated at the side in bats. I have called this the fronto-maxillary inflation. It forms a ridge or swelling at the upper border of the orbit. The inflation of the skull at the anterior part of the frontal bone to form the frontal sinus is much less conspicuous in the Cheiroptera than in some other orders, but the maxillary inflation is greater. This peculiarity gives the face a broad effect at its junction with the brain-case and modifies the shape of the orbit. The ethmoidal plates variously change the shape of the inner wall. As a rule, the frontal bone here permits the ectoturbinal parts to be in part defined. The region of the lachrymal bone appears to resist the disposition to inflation; hence the peculiarities of the inflation give character to this portion of the cranium. On the vertex the inflation causes the face to widen from the proencephalon to near the anterior nasal aperture, where it is abruptly narrowed, and to create depressions of inconstant kinds in the line of the conjoined nasal bones. The extent to which the recession of the nasal bone from the anterior nasal aperture occurs, as well as of the palatal notch, due to the rudimentary state of

the premaxillæ, afford bases for some characters of minor value. The length of the infra-orbital canal and the peculiarities of the outer wall of the canal are of interest. In *Artibeus* the canal is long and for the most part smooth externally, as in *Canis*, while in the fauna generally it is short, as in *Felis*, and is often elevated.

The hard palate may be either in the main axis of the skull, as in most forms, or deflected upward and forward. The characters furnished by the pterygoid processes, the palatal plates, are here as useful as in other mammalian groups. The premaxillæ are rarely firmly united to one another. When they are so united, as in Phyllostomidæ and Molossi, the median incisors are disposed to be contiguous. When they are not united, a large median interspace separates them and is continuous with the vacuity which in other mammals represent the incisorial foramen. The presence or absence of the spheno-palatine foramen is used in some groups, as Molossi and in Plecoti, in separating genera. The disposition of the turbinals is also of interest, the peculiarities of the arrangement being definitive of the families as established on other structural characters. If in mammals generally an outer and an inner turbinal group is recognized, then in the bats we have a median lamina which bears upon its inner surface one or more scrolls (endoturbinals), and an outer lamina with much simpler accessories (ectoturbinals). The simplest arrangement of the turbinals is seen in the Nycteridæ and Rhinolophidæ, the most complex in Pteropidæ. In *Natalus* alone is the ectoturbinal rudimental or absent. (Bull. Mus. Comp. Zool., Feb., 1880.)

In addition to the peculiarities of the masseteric impression on the lower jaw, already noticed, characters are furnished in the height of the coronoid process and the degree of deflection as well as the size and shape of the angle. The post-symphysal spine which is conspicuous in some extinct forms has not been seen by me in any of the extant forms, and I have examined most of the genera of the order.

The shortening of the face, *pari passu*, with reduction of teeth, is seen in Carnivora. The tendency is seen in *Vesperugo*, and in bats generally. In *Vespertilio* the shortening of face is accompanied by displacement inward of the premolars. In a mechanical sense it amounts to the same as reduction in number. In pteropine bats a remarkable persistence of facial length remains, while the disposition to reduction is evident. One may conclude from the instance last named that the shortening of face and reduction of teeth are independent. The same is true of the Ungulata.

In *Atalapha* the lower jaw closes in front of the upper. The lower canines articulate with the anterior surfaces of the upper laterals their entire length. The upper canines are free, *i. e.*, do not articulate with anything.

Vertebral column.—The vertebral column is without large processes other than the hæmopophyses which are well developed in the cervical region.

The atlas is broadest in Pteropidæ. In both *Pteropus* and *Epomophorus* the bone extends downward posteriorly and at the sides so as to conceal the lower opening of the canal for the vertebral canal. The upper border of the conjoined laminae is boldly rugose. In *Artibeus*, a member of a group in the New World analogous to the foregoing, the atlas is greatly reduced in the proportions of the laminae and the transverse process, the lower opening of the canal for the vertebral canal is exposed on the posterior aspect of the bone, while the upper border of the conjoined laminae is scarcely rugose. In the vespertilionines, molossines, and phyllostomines minor peculiarities distinguish the atlas. These are given in the diagnosis of genera and species. In a general way it may be said that the pteropines are broadly separated from all the other bats by the characters presented by this bone. In *Pteropus* and *Epomophorus* the axis possesses a large neural spine which almost equals the length of the body inclusive of the cylindroid odontoid process. In *Artibeus* the spine is but one-half the length of the body inclusive of the tubercle-like odontoid process. The remaining portion of the cervical is curved more or less antero-posteriorly. This is less marked in the pteropine and phyllostomine genera than in the vespertilionine where the curve is so great as to bring the occiput almost to the first dorsal vertebra. The sacrum, at its upper portion, exhibits a compressed projecting ventral surface. The spinous processes are flat, distinct, and increase in size from above downward in molossines and *Atalapha*, but they are low and confluent in many forms as in the pteropines. The first coccygeal vertebra in tailed forms is large and resembles those of the sacrum. The caudal vertebrae below this are cylindroid. They vary greatly in length, especially at the beginning of the series.

Ribs.—The ribs are flat, broad, with wide intercostal spaces (coalescent in *Natalus* and *Hipposideros* for the region of the first and second ribs). The other interspaces are also well defined in Pteropidæ, but as a rule they are narrow, and in *Natalus* and *Hipposideros* are practically obliterated. The costal cartilages are relatively inelastic and are disposed to become early calcified. Indeed, the entire chest is rigid, and the ribs often become ankylosed to the spine, and in some forms, as in old individuals of *Vespertilio murinus*, the contiguous ribs to each other. Hence the respiratory movements are for the most part performed by the diaphragm and the flank muscles.

Sternum.—The sternum possesses a massive, broad prosternum and a narrowed mesosternum and metasternum. The prosternum sends a conspicuous process forward into the neck (as in many terrestrial mammals) in molossines; all the others are without this process. The first joint is usually conspicuously keeled, and in Pteropidæ this keel is divided by a deep notch. The mesosternum in the same family is also keeled its entire length, but in the other groups it is barely ridged or smooth.

Anterior limbs.—The *clavicle* is present in all bats. It is firmly attached at both the acromial and the sternal end. The last named

effects an important articulation with the cartilage of the first rib and in the sterno-claviculo-costal joint; in Molossi, at least, it is of enormous strength. The *scapula*, as in other clavicate forms, with few exceptions, in which the large anterior extremity is not supported on the ground, possesses an infraspinus fossa very much larger than the supraspinatus. The bone lies well up on the side of the neck in the forms in which the cervical series of vertebræ is bent forward. Excellent characters are yielded by the coracoid process. It is always long and slender, simple, and gently curved in various arcs in Pteropidæ, Rhinolophidæ, Emballonuridæ, and Phyllostomidæ, but bifid in most Vespertilionidæ. It is interesting to find the genus *Vespertilio* aberrant in this respect, the process being simple and curved quite as in the larger groups first named. The posterior tubercle is prolonged to form an oblique posteriorly-directed process in the molossines and in *Chalinolobus*.

With the exception of the tuberosities of the *humerus* no check processes exist anywhere in the bones of the limbs, thus presenting marked contrasts with the limbs of birds. The trochlear end of the humerus yields in the shape and direction of the epitrochlea valuable characters. This process conforms to the terrestrial type, *i. e.*, it is transversely inclined in pteropines and the genus *Saccopteryx*; is deflected downward parallel or nearly so to the shaft in phyllostomines, but is absent in vespertilionines. In vespertilionines again the articular surface is axial, *i. e.*, is in the middle line of the humerus, but in phyllostomines it is thrown well off to the outer side. Narrow-winged forms, as the molossines and the genus *Atalapha*, exhibit large tubercles on the humerus and wide trochlear surfaces. Thus these characters harmonize with rapid flight. On the other hand, the forms with smaller tubercles and narrow poorly defined trochlear surfaces have broad wings and presumably slow flight.

The *radius* constitutes the main support of the forearm and presents few variations from a single type. As a rule it is nearly straight, but is much bent in *Hipposideros*. It is always obliquely grooved by the tendon of the extensor ossi metacarpi pollicis. The size of the large deep fossa for the insertion of the biceps flexor is variable. Since the ulna does not enter into the composition of the anterior arc of the trochlea, and its place is here taken by the radius in addition to the work this bone does in articulating with the humerus at its outer half, it is easily seen that the radius is provided with two facets at its proximal end, and that the main ridge on the distal articular surface of the humerus fits in between these two radial facets. So far as the degree of invasion of the radius into the trochlea has been noted it appears to correlate with the degree of activity of the prone form in scurrying. It is thus marked in *Cheiromeles* and *Molossus*, and is small in *Kerivoula*.

The *ulna* is more inconstant in form than the radius; in all it is incomplete and is composed of a proximal and a distal rudiment. The proximal rudiment is free at the weak olecranon, which resembles the parts in the sloth, and is continuous in most genera with an arched rod-like shaft of uniform width, which is ossified, as a rule, with the radius at about its proximal third. Exceptions are noted to this arrangement in some of the vespertilionine genera, *e. g.*, *Scotophilus* and *Miniopterus*, as well as in the molossine *Promops*, in which a small ankylosed olecranon unites by a filiform shaft to the proximal third of the ulna. But the vespertilionine forms as a rule (*Harpiocephalus* not examined) retain a free olecranon which is continuous with a filiform tapering shaft, which ends free in the muscles of the forearm. *Corynorhinus*, *Nyctophilus*, *Chalinolobus* are exceptions even to this arrangement, for here the shaft is entirely absent, the rudimental fixed olecranon constituting the entire proximal end. The tendon of the triceps muscle as it is inserted into the ulna is occupied by a sesamoid bone. No other animals possess a bone in this situation. It is either a separate ossicle developed in the tendon, or the disjuncted epiphysis of the ulna. This relatively unimportant bone receives the muscle which alone extends the powerful forearm. The extensor carpi ulnar is—a muscle as constant in this group as in others—arises from it. All the relations of the ulna, therefore, are with the extensors. The distal end is ankylosed to the radius at the wrist. The form may be that of a quadrate plate which is usually entire, though it may retain a minute foramen of insufficiency, as a rule, in the vespertilionines. The plate may be absent when a hook-like process directed proximally, as in molossines and *Atalapha*; it may project nearly at right angles to shaft and be conoidal, as in phyllostomines, rhinolophines, and the genera *Saccopteryx* and *Natalus*; or it may be absent, as in the pteropines.

The carpus of bats exhibits some valuable characters. In all forms the first row of bones is composed of two bones only—viz, a large bone which constitutes the greater part of the row and will here receive the name of the scapho-lunar, and a small separate bone at the ulna border of the scapho-lunar which appears to be the cuneiform.

The second row is composed of the trapezium, trapezoid, os magnum, unciform, and pisiform. The os magnum and unciform always unite to form a convex surface for articulation with the second row. With the exception of the pisiform all these integers are easily recognized. The carpus on the whole is simple, since the first, second, and third metacarpal bones are in axial articulation with trapezium, trapezoid, and os magnum, respectively, while the fourth and fifth metacarpal bones articulate with the unciform.

In pteropines the trapezium and os magnum are greatly larger than are the other bones of the second row, and give a peculiarly massive appearance to the carpus when the wing is folded. The bone first named is without nodosity on the palmar aspect. Wedged between

the two bones last named is the insignificant trapezoid. Owing to the abruptly curved line formed by the heads of the metacarpals the second and fifth bones lie at the level of the plane, which would unite the ends of the curve, while the third and fourth form the bottom. The cavity defined by the curve as indicated is almost entirely occupied by a large hatchet-shape prolongation of the os magnum. Thus the os magnum, beside its axial attachments, is held on the one side to the second and on the other to the fifth metacarpal bone. The heads of these bones are so disposed as not to approach each other. The pisiform is absent unless it is represented in the palmar prolongation of the os magnum.

In rhinolophines the plan is that of pteropines. Though the bones are less massive than in that group, the methods of articulation are the same, and the pisiform is also apparently absent.

In *Artibeus* the palmar part of the os magnum articulates with a separate but much smaller element, which occupies the place of the hatchet-shape plate in *Pteropus*. The heads of the metacarpals are scarcely curved, and those of the second and fifth are disposed not to approach each other.

Among the vespertilionines we notice the following: *Corynorhinus* closely resembles *Artibeus*. In *Adelonycteris* the trapezium possesses a tubercle on the palmar aspect; the os magnum is without palmar plate either united or separate. The heads of the second and fifth metacarpals approach each other and almost touch. In *Atalapha* the tubercle to the trapezium is retained, while the palmar extension of the os magnum is absent. Articulating on the pollical side of the fifth metacarpal bone is a separate ossicle, which appears to take the place of the part last named. It is elongated and much larger than any of the carpal elements. I have named it the pisiform. *Antrozous* is much the same as *Atalapha*; the ossicle by the side of the fifth metacarpal bone is triangular in shape. The plate of bone which is continuous with the os magnum on its palmar aspect in pteropines appears to be the same as the separate ossicle in the same situation in *Artibeus*.

The bone which articulates by its base with the fifth metacarpal bone in *Atalapha* and *Antrozous* would appear to be identical with the above plate, since when it is present the os magnum ends in a simple manner toward the palm. It would appear to be the pisiform, since in *Atalapha* it was observed to receive the tendon of the extensor carpi ulnaris.

Sesamoid bones.—The sesamoid bones are found in locations where great motion is permitted on the side opposite to which the bones are lodged—the purpose being apparently to prevent stretching of the muscles which carry the sesamoids. At the point at which stretching would begin the bones lock with the joint surface and takes the strain. They are best developed on the dorsum of the carpus in phyllostomines.

The tendency above noted for the second and fifth metacarpal bones to incline toward one another on the palmar aspect of the carpus, and

as a result for the second bone to lie in front of the third and for the fifth to lie in front of the fourth, is a notable feature in the manus of the bat. Minor differences are seen in the relative lengths of the bones. They are shortest in pteropines and rhinolophines. The second metacarpal is usually slightly shorter than the others, but in *Hipposideros* it is much shorter. The fifth metacarpal bone is apt to be the largest, as in *Pteropus*, but in *Hipposideros* and in the molossines it is the shortest. In the group last named and the related genus *Atalapha* the bones are marked by grooves for the powerful metacarpo-phalangeal flexors. The third metacarpal bone is commonly the largest, the fifth the shortest, the fourth being intermediate, yet in North American species of *Vespertilio* the fourth bone, being slightly shorter than the fifth, is sometimes an individual variation. *Megaderma* is remarkable for having the above order reversed—the fifth metacarpal is the largest and the third is the shortest. Viewed as a whole the manus, notwithstanding its enormous longitudinal development in the third, fourth, and fifth elements, is singularly unimportant in the first and second. The second, however, while unsupported by elongated phalanges, has strong architectural functions at the line of its union with the carpus.

The phalanges present few points of contrast. They are uniformly elongated rods. As a rule the second digit possesses a single rudimentary phalanx which may be free or semianchylised to the metacarpus. The highest degree of development is attained in the pteropines and in the genus *Rhinopoma*, the former having three and the latter two phalanges. In the pteropines the third is ordinarily furnished with a claw. They vary greatly in the range of motion, those of the second and fifth digits being the least mobile; in their relative lengths in the pteropines and the genera *Noctilio* and *Miniopterus*, these forms being remarkable for the degrees present of lateral and dorsal flexion. It has been noted on p. — that the disposition and relative sizes of the phalanges vary in the scurrying and pendant forms. In the position of flight the row of first phalanges is flexed downward, but the row of second phalanges is at the same time deflected laterally; *i. e.* toward the body. In the position of rest the parts either remain axially disposed or the row of the first phalanges is laterally or dorsally flexed, as in the molossines and emballanourines. The terminal cartilages are apparently absent in pteropines and rhinolophines. When present they remain in axial line with the phalanges, as in phyllostomines (excepting *Vampyrus*), or they are deflected from that line, as in vespertilionines and molossines. These little rods appear to be indices of the amount and direction of strain to which the membranes are subjected, and point, therefore, to distinctions in methods of flight. It may be said that they are absent, or, if present, axially disposed in the broad-winged forms, but are deflected in the narrow winged. In vespertilionines and molossines (excepting *Kerivoula* (?) and *Antrozous*) the fifth digit is provided with an accessory cartilage, which lies to the outer side of the

terminal cartilage. It slightly projects from the margin of the wing membrane.

The much greater length of the third digit, as compared with that of other digits, is a noteworthy feature of the bat wing. Its relative length in different forms serves as a guide to generic and sometimes to specific distinctions.

The peculiarities of the thumb are so marked that they can be best considered apart from the other manal parts. The thumb, as a rule, is free from membrane beyond the basal third of the first phalanx, but may be almost entirely inclosed, as in *Thyroptera*. The extent of the enwrapping membrane determines the size of the little fold of skin which lies between the thumb and the second metacarpal bone. The thumb is relatively large in pendent forms, since it is here of value in prehension; *per contra*, in *Thyroptera*, in which genus a suction disk takes the place of a prehensile thumb, this digit is also small, though the animal is unadapted to activity in the prone attitude. It has been already noted (p. 5) that the thumb is bent downward and the under surface of the first metacarpal bone fairly well outlined in the pendent forms. It is not known how *Desmodus* and *Diphylla*, which process with large projecting thumbs, support the body when at rest. The claws on the feet are weak, and the animals are probably not pendent at rest. With these exceptions, the phyllostomines possess the semi-flexed thumb, as do all the other families excepting the molossines and vespertiliones.

Posterior limbs.—The innominate bone always exhibits a narrow rod-like ilium which occasionally projects slightly above the line of the ilio-sacral articulation, but as a rule is level therewith. The dorsum of the ilium is flat, in most forms, but it may be concave and broad, as in molossines, *Atalapha* and *Chilonycteris*. The pubis is, as a rule, defined in the males, but is absent and has a wide interval defined between the innominate bones anteriorly in the females. The shape of the ischium and of the thyroid foramen is subject to slight variation in genera and even in species. The innominate bone is in most forms distinct from the vertebral column. In molossines, *Chilonycteris*, and in rhinolophines, it is ankylosed, both at the sacro-iliac junction and the ischio-sacral or ischio-coccygeal junctions. *Chilonycteris* is an instance of the union last named. In all bats a disposition exists for the tuberosity of the ischium to approach the vertebral column, thus presenting a marked contrast to that seen in terrestrial quadrupeds. *Antrozous* exhibits a facet between the tuberosity and the first joint of the coccyx. The sloth is the only animal I can recall which exhibits a fixation of the ischium similar to that found in the bats. The ilio-pectineal spine is marked; often a large tubercle, it may be a needle-like spine. In *Hipposideros* it is of enormous length and is ankylosed to the ilium near its upper border.

The interest which attaches to the osteology of the hind extremity has led me to give in more detail the following:

In pteropines the ilium is curved outward to a slight degree at the crest. The ridge from the upper border of the acetabulum is inconspicuous and does not extend entire length of ilium; thus the ventral and dorsal surfaces are not separated and there is no special external border near the crest. The tuberosity of the ischium is deflected markedly from the line of the ilium and lies against the coccyx. The pubis is thickened inferiorly; the pectineal spine is absent or scarcely discernible.

In *Hipposideros* among the rhinolophines the ilium is expanded and is concave on both dorsal and ventral surfaces. The broad crest extends outward and unites by a broad thin flange to the tip of the long pectineal spine. Tuberosity of the ischium not projected backward; nearly the entire pubis and ischium converted into a broad plate of bone at the expense of the thyroid foramen. Symphysis pubis long, entire. The trochanters of the femur are drawn backward and approximated; the inner trochanter is the longer; the outer side of the shaft below the head furnished with a flange. The condyles small and separated by a wide notch. In the tibia the spine for hamstrings compressed. Internal tuberosity prolonged; no malleolus.

In phyllostomines the ilium is not deflected at crest. As seen in *Artibeus* the ridge above the acetabulum rudimental as in pteropines—the ventral and dorsal surfaces therefore scarcely distinguished. The external border below the crest is rugose and enormously thickened. The ischium is turned but slightly toward the coccyx. The inferior border of the pubis produced inward as a long blunt process and the upper border forms a long acicular process (pectineal eminence) which extends one-half the length of the ilium. The trochanters of the femur not carried back, the outer not separated from the head by a notch. The inner is much longer than the outer. The shaft at its inner side at the proximal fifths exhibits a conspicuous crest. The condyles are of equal size. Above them posteriorly is a depression (best marked over inner condyle) to receive in forced flexion the posterior border of the articular surface of the tibia. Intercondylar notch, pit-like. Proximal end of the tibia with scarcely any inward projecting process; malleolus none; tubercle for insertion of hamstrings markedly developed; surface for articulation with the fibula rugose.

In *Hemiderma* the innominate is much as in *Artibeus*, but the pubis not projecting or thickened; the pectineal spine but one-third the length of the ilium. The femur quite as in this genus, but the outer trochanter separated by a notch from the head. In *Macrotus* the innominate bone much the same as above, but the pectineal spine over one-half the length of the ilium. The trochanters of the femur approximated and carried well to the back of the shaft. The fibula only half the length of the tibia.

In *Mormops* the ilium is greatly compressed between the ventral and dorsal surfaces; first joint of the tail very long. The femur and tibia as in *Macrotus*. *Chilonycteris* in like manner exhibits a compressed ilium ossified to sacrum with broad rugose external border adjoining crest. Dorsal surface slightly concave and expanded. In both *Mormops* and *Chilonycteris* the tuberosity of the ischium is anchylosed to the sacrum. The pubis in the male of *Mormops* is bony and entire; in *Chilonycteris* it is less firmly defined. The pectineal spine in *Mormops* is two-thirds the length of the ilium. In *Chilonycteris davyi* it is remarkable for being nearly as long as this bone and bound by fibrous tissue to the vertebræ. In both of the genera of Lobostomidæ the trochanters of the femur are approximate, confluent, and carried well back of the head. Tibia and fibula much as in *Macrotus*.

In *Molossus* the innominate bone is compressed, expanded. It is concave dorsally with narrow iliac upper border slightly projecting. Pectineal spine one-third the height of the ilium. Pubic symphysis entire, bony. Tuberosity of the ischium projects well backward, but is free from the sacrum. The inner trochanter much larger than the outer; truncate with a downward projecting spine, not carried backward. The outer trochanter separated from the head by a slight notch. Condyles equal in size; notch wide, shallow. Tibia straight with large malleolus.

In *Promops* the pelvis entire as in *Molossus*; characters much the same as in this genus, but the upper border of the ilium without spine and the tuberosity articulating with the sacrum, but not anchylosed thereto. Femur and tibia of the same character—the distal epiphysis of the femur narrower than the expanded shaft. In *Nyctinomus* the ilium as in *Molossus*, but the pubic bones free; femur and tibia the same.

In *Atalapha* the ilium is quite as in *Molossus*, but is not anchylosed to the sacrum. The pectineal spine blunt, rudimental; tuberosity of the ischium lies in the same line with ilium approaches sacrum, but is not articulated therewith. Both trochanters of the femur are carried backward as in *Vampyri*, but are not approximate; *i. e.*, they are visible from in front; the inner is the narrower, though they are of the same length. Condyles high and narrow, the inner scarcely the wider; notch narrow, deep. Tibia curved with medianly projecting inner tuberosity, malleolus scarcely discernible. Fibula entire; upper portion membranous. In *Antrozous* the ilium is anchylosed to the sacrum and in the male at least the symphysis pubis is well defined; the tuberosity of the ischium extends back of the line of the ilium and almost touches the sacrum. The pubic bone without a thickened inferior border. The femur and tibia much as in *Vespertilio*.

In *Vespertilio* the ilium is narrow, not expanded above and not concave posteriorly; the outer border scarcely thickened near the crest. The pectineal spine low, compressed, directed slightly forward, blunt,

scarcely higher than the acetabulum. The inferior border of the pubic bone greatly thickened near the symphysic line in the male. The innominate bone is lightly held to the sacrum and at the symphysis pubis. The inner trochanter of the femur equals the external. Both are small and the gluteal crest is scarcely larger than a flange which unites the inner trochanter to the shaft, thus making the femur unique. The inner condyle is slightly the larger and the notch narrow. The tibia with large projecting median spine at the proximal end; malleous distinct.

In *Adelonycteris* and *Lasionycteris* the parts quite as in *Vespertilio*, the pectineal spine slightly longer; the shaft of the femur just below the head less expanded.

Corynorhinus much as in *Vespertilio*, but the upper part of the femur much less expanded, the shaft near the trochanter scarcely at all.

The femur is without neck. The outer and inner trochanters are subequal, and of large size, the outer tending to become the larger as in the molossines. The outer side of the shaft below the trochanter is often marked by a flange in position of the third trochanter. *Hipposideros* and all phyllostomines show an inclination to the development of a conspicuous flange on the inner side of the shaft near the inner trochanter. This is most marked in *Chilonycteris*, *Mormops*, and *Natalus*. In the genera last named the trochanters are drawn backward, lie on the posterior surface of the bone, and are in close relation (resembling, with the head, the anterior end of a geometric larva), while as a rule they are on lines which answer to the lateral ligaments of the knee joint. The condyles are approximate markedly unequal with a narrow intercondylar notch, the inner condyle being the larger, as is the rule, or wide apart with small condyles, as in molossines and rhinolophines. The tibia may be shorter than the femur, as in *Artibeus* and *Molossus*, but it is, as a rule, longer than that bone. The inner tuberosity is furnished with a horizontally-projecting process in vespertilionines; this is an excellent character defining the family. The tubercle for insertion of the hamstrings is most marked in strictly arboreal forms, as the pteropines. The malleolus is often rudimentary or absent, as in phyllostomines and rhinolophines. The fibula is uniformly imperfect above save in the molossines, where it is complete, or in *Antrozous*, where a membranous fillet continues the form of the bone to the inner tuberosity of the tibia.

The toes retain two phalanges to the first toe; all the others have three, but differ in their relative lengths. The first phalanx of the first toe is, so far as examined, longer than that of the other toes. In *Pteropus* the lengths of the toes from the second to the fifth gradually diminish. In *Chilonycteris* they abruptly increase, that of the second toe being one-third shorter than the fifth. In all bats the tarsus and calcaneum are elongate and exhibit the general character of these bones in mammals, in which little or no weight is borne upon the posterior extremities. Both bones are so disposed that the larger end of each is

directed proximally. In *Rhinolophus* the calcaneum enters into the ankle joint. In other forms the calcaneum is independent of the joint. In *Phyllostomidae*, including *Natalus*, as well as in the genus *Rhyconycteris*, the calcar* is placed in axial line with the calcaneum. In other families it joins the calcaneum to its outer side at a well-defined angle. As a rule the astragalus and calcaneum are nearly of one size, but in the genus last named the calcaneum is notably the smaller (Am. Naturalist, Feb., 1886, 176).

GENERAL PLAN OF ANTERIOR EXTREMITIES IN FLYING VERTEBRATED ANIMALS.

From the above consideration it will be seen that the wing membranes possess various features which can be used in distinguishing the members of the order. But after what manner are the flying mammals distinguished from other flying vertebrates?

There are two distinct types of modification which the vertebrate skeleton has undergone in adapting the animal for flight, both of which depend upon some peculiarity in the structure of the anterior extremities; and in order to obtain a correct opinion of them we propose to cast a glance at each in turn.

Plan of bony structure of the wings of flying vertebrate animals.

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|----|-------------------------------------------------------------------------|---|---------------------------------------------------------------------------------------------------------------------------------------------------------------|
| a. | Bones of carpus ununited distinct; flight maintained by dermal expanse. | { | I. Wing membrane supported by all fingers.
<i>Bats</i> (<i>Vespertilio</i>), order of MAMMALIA. |
| | | { | II. Wing membrane supported by the fourth finger only (which is immensely developed), the others remaining free.
<i>Pterodactyles</i> , order of REPTILIA. |
| b. | Bones of carpus united; flight maintained by dermal appendages. | { | III. Bones of metacarpus, two to three in number; feathers not radiating.
<i>Living birds</i> (AVES)—class. |
| | | { | IV. Bones of metacarpus, four in number; feathers radiating.
<i>Archæopteryx</i> (AVES)—subclass. |
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- | | | |
|----|---|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| a. | { | I. The Bat, in which the humerus is long and slender, with a small pectoral ridge. Ulna rudimentary. The radius constitutes the bulk of the forearm; carpus composed of six bones; the metacarpal bones, five in number, separate and distinct; the phalanges generally, two in number; thumb, and in some genera the index finger, surmounted by a claw. |
| | { | II. The Pterodactyle, in which the humerus is short and straight, very broad at head, with angular and prominent pectoral ridge; ulna and radius distinct, of nearly equal size; carpus composed of five bones; metacarpus of four bones, separate and distinct; first finger with three joints, second with four, third with five, fourth with four joints, all provided with claws, with the exception of the fourth, which is remarkable for the extraordinary development of its several joints. It is from this last-mentioned finger to the base of the foot that the skin was stretched by which the animal was enabled to fly. |

*The calcar is an element of doubtful homology. It supports the free border of the interfemoral membrane, and is of the same significance as the accessory cartilage of the fifth manal digit.

- III. The Bird, in which the humerus is curved, more or less slender; pectoral ridge prominent, not angular; ulna large, curved, not united with the slender and more diminutive radius; carpus or two bones; metacarpus of two, sometimes of three bones—the first being small and cylindrical, the other two of larger dimensions and united so as to form a bone resembling those of the forearm; ulnar phalanx of one joint, united to the radial, which is composed of two.
- b. The power of sustaining flight not dependent upon the expansion of skin, but upon the excessive development of dermal appendages (feathers).
- IV. The Archaeopteryx agrees with the typical bird in general particulars, but differs in the number of metacarpal bones, which are here four in number: the first and second are slender, free and separate from one another; the third and fourth bear considerable resemblance to those of extant birds, in being large, stout, and closely approximated; but are not, however, united.
- Flight is supposed to have been maintained in the same manner as in living birds.

In addition to the instances already given, certain fishes, as the *Exocoetus* and *Dactylopterus*, possess the power of sustaining true flight. The mechanism that lifts the body of the fish from the water, and upholds it for a short time in the air, is obtained in the pectoral fins, which, in these animals, are enormously developed. The structure of these fins is homologous to that of the anterior extremities of other vertebrates—their form alone being modified to adapt the animal to the medium in which it is placed. Thus we have, in each great subdivision of vertebrate animals, a representative capable of sustaining flight.

Another somewhat similar modification of the animal economy is met with in a few animals of arboreal habits. Here a peculiar arrangement of the skin is observed, which enables the possessor to break the force of downward leaps. In the Flying Lemur (*Galeopithecus*), in the Flying Squirrel (*Pteromys*), and in the Flying Opossum (*Petaurista*), the furred skin extends laterally from the sides of the body, and is attached to anterior and posterior extremities at the metacarpal and metatarsal regions respectively. The only instance of osteological development is obtained in the Dragon (*Draco volans*), a small lizard from Sumatra, in which long, transverse processes from either side of the lumbar vertebræ support a thin membranous growth which is capable of being opened and shut by means of muscles attached to the bony frame-work.

TEETH.

In describing the teeth the nomenclature of Prof. H. F. Osborn will be followed. The diagram herewith presented is copied from this writer's paper in the *American Naturalist*, December, 1888, p. 1072.

UPPER MOLARS.

Antero-internal cusp	Protocone.	pr.
Postero-internal cusp or sixth cusp	Hypocone.	hy.
Antero-external cusp	Paracone.	pa.
Postero-external cusp	Metacone.	me.
Anterior intermediate cusp	Protoconule.	pl.
Posterior intermediate cusp	Metaconule.	ml.

LOWER MOLARS.

Antero-external cusp.....	Protoconid. pr ^d
Postero-external cusp.....	Hypoconid. hy ^d
Antero-internal cusp or fifth cusp.....	Paraconid. pa ^d
Intermediate or antero-internal cusp (in quadritubercular molars).....	Metaconid. me ^d
Postero-internal cusp.....	Entoconid. en ^d

The upper molar in most bats presents to an extraordinary degree depressions on the outer or buccal surface of the crown. Such depressions receive the name of "flutings" and are seen in the teeth of many mammals other than the bats, as for example in the moles and shrews among the Insectivora, in the Ungulata, and in a marked degree in an extinct genus described by Prof. Cope, *Lambdotherium*. "Flutings," while of no homological significance, furnish systematic characters, and will therefore be noted in the descriptions. Disposed so as to define two V-shaped figures the "flutings" extend as a sinuate commissure between the paracone and the metacone. Of the two Vs an anterior and a posterior will be distinguished. Each V has two limbs, a first and a second. In the third molar various degrees of loss of the system of flutings occur. Commonly the anterior V is retained while the second is lost, excepting the buccal half of the first limb, as in *V. fuscus*, or the "fluting" is reduced to the anterior V, the palatal half of the second limb being lost, as in *Macrotus* and *Atalapha*. In the Bats of North America the least reduced last molars are seen in *Nyctinomus* and *V. hesperus*.

The tri-tubercular tooth which results from the presence of the three cusps, the protocone, the paracone, and the metacone, may be connected with a triangular figure by bands which unite the cusp-points. These bands will be named in this monograph the commissures. In the molars of the bat such a triangle is seen whose apex is palatal and constituted of the protocone and whose commissure extends from this cusp to the paracone and metacone. Its base is the extraordinarily sinuate ("fluted") buccal surface of the crown. A careful search must be made for the true positions of the sides of this triangular figure for they lie on the opposed sides of the teeth and are inconspicuous. The crown at the "flutings" is of great vertical extent and dwarfs even the proportions of the protocone. When seen in profile the proportions between the size of the "columns" of the two V's and the "cusp" of the protocone afford materials for interesting comparisons in the different genera. The hypocone presents excellent subordinate characters. It is a development of the cingulum. Usually flat, as in *Macrotus*, it may be a sharply defined as in *Promops perotis*, or provided with a sharp cusp as in the exotic genus *Noctilio*. The cingulum can be traced as a delicate ridge which lies basal to the sides of the tritubercular triangle. It varies greatly in extent, being best developed in *Nyctinomus*.

In the lower molar scarcely any fluting is present and the plan of the tooth is simple. The protoconid, paraconid, and metaconid are united

by commissures. The apex of the triangular figure is buccal. The heel or hypoconid is large. It is united to the triangle by a commissure at the lingual side. Such a commissure is provided with a sharp cusp in *P. perotis*, but as a rule it is smooth.

KEY TO GENERA.

- I. Bats with median appendage to nose, four incisors in lower jaw... PHYLLOSTOMIDÆ.
- a.* Body massive, auricle shorter than head, not united with its fellow... *Artibeus*.
- a*¹. Body slender, auricle as large or longer than head, united with its fellow
 *Macrotus*.
- II. Bats without median appendages to nose.
- b.* Nostrils circular, wings narrow and pointed; tail long, produced far beyond
 interfemoral membrane; marginal toes fringed with coarse hair. MOLOSSI.
- Lips grooved..... *Nyctinomus*.
- Lips not grooved..... *Promops*.
- b*¹. Nostrils elliptical, wings broad, ample; tail as long or only slightly longer
 than the broad interfemoral membrane; marginal toes naked
 VESPERTILIONIDÆ.
- c.* Two incisors in upper jaw.
- † Six incisors in lower jaw.
- * Interfemoral membrane more or less hairy.
- Premolars $\frac{1}{2}$ *Dasypterus*.
- Premolars $\frac{2}{2}$ *Atalapha*.
- ** Interfemoral membrane not hairy *Nycticejus*.
- †† Four incisors in lower jaw *Antrozous*.
- c*¹. Four incisors in upper jaw.
- † Premolars $\frac{1}{2}$; greatest width of tragus at base equals one-half of inner
 border..... *Adelonycteris*.
- †† Premolars $\frac{2}{2}$.
- * Greatest width of tragus equals much less than one-half inner border;
 nose simple, ears separate..... *Vesperugo*.
- ** Greatest width of tragus equals one-third height of inner border;
 auricles united.
- ♂ Nose with lateral club-shaped gland-masses..... *Corynorhinus*.
- ♂♂ Nose without lateral club-shaped gland-masses..... *Euderma*.
- ††† Premolars $\frac{2}{3}$; greatest width of tragus at middle and equals two-thirds
 height of inner border *Lasionycteris*.
- †††† Premolars $\frac{3}{3}$. Lips whiskered, dorsum of face furred..... *Vespertilio*



Allen, Harrison. 1893. "Introduction to a monograph of the North American bats." *Proceedings of the United States National Museum* 16(919), 1-28.

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