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**Article I.—ON THE ANATOMY AND CLASSIFICATION OF THE
WEAVER-BIRDS¹**

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My studies of the anatomy of Fringillidæ and allied groups have led me to the conclusion that *Passer* and some other Old World genera are essentially different from the true Fringillidæ and belong, as a matter of fact, to the Ploceidæ. Lafresnaye,² three-quarters of a century ago, was the first to express this idea, on account of the nidification of *Passer*; and the same ornithologist pointed out also that *Plocepasser* may form a connecting link ("le chaînon") between the weaver-birds and sparrows. The prevalent tendency to leave *Passer* with the Fringillidæ remained, however. On examination of the skeletons I have found that the genera *Passer*, *Petronia*, *Chionospina* (= *Montifringilla*³) and *Pyrgilauda* are most intimately related. Besides the skeletal structure, they have in common certain characters of the external anatomy: in the first place, the very characteristic relief of the palatal surface of the horny bill; then too, a total molt (wing-quills and tail-feathers included) of the young bird in the first autumn; the architecture of the nest, which is always domed with a side entrance, if built free, or placed in an enclosed space and thus also covered. The same characters in the external anatomy, post-juvenal molt, and nest-building, are shared by the genera *Gymnoris* and *Onychostruthus*; *Sorella*, according to its external anatomy and the structure of the horny palate, belongs here also.⁴ In this way, these

¹Scientific Results of The American Museum of Natural History Congo Expedition. Ornithology, No. 11.

²1850, *Revue et Magazin de Zoologie pure et appliquée*, (2) II, pp. 315-326.

³In the restricted sense, including only *nivalis* and *alpicola*.

⁴I have been able to examine a good series of *Sorella* in The American Museum of Natural History; unfortunately, it does not contain specimens in the post-juvenal molt. The nest-building seems to be unknown. As for the tenth primary, I found it constantly vestigial, much shorter than the coverts, and displaced to the dorsal side of the ninth primary, as in *Passer* and other members of this group (contrary to the allusion by Prof. E. Lönnberg, 1911, *K. Svenska Vetenskapsakad. Handl.*, XLVII, No. 5, p. 109).

genera form a very close group. By the characters just named, they differ from the true Fringillidæ and agree with the Ploceidæ. I consider them as composing the subfamily Passerinæ of the family Ploceidæ, in addition to the other subfamilies of that group.¹ I have proposed this transfer in the Bulletin of the British Ornithologists' Club for November, 1924, and in the April number of the Auk, 1925; in the first of these papers, I gave also a drawing of the horny palate of *Passer*.²

In 1917, Dr. J. P. Chapin published a very valuable paper on the classification of the Ploceidæ,³ based to a large extent on his field observations and materials collected during his travels in the Congo region. Making use of the presence or absence (as well as the shape) of the gape-markings and appendages observed in the young of some weaver-birds, of the nest-building, and of some characters of external and skeletal anatomy, Dr. Chapin separated *Textor* (now *Bubalornis*) and *Dinemellia* as constituting a family by themselves, the Textoridæ. The rest he divided into the usual subfamilies, which he called Ploceinæ and Estrildinæ (= Viduinæ of authors), but transposed some of the genera from one subfamily to another.

Continuing my studies of the Fringillidæ and their relatives, I took advantage of my visit to New York in 1925 to examine the material collected by Dr. Chapin. I found also some skeletons from other sources in the collection of The American Museum of Natural History in New York, and in the collection of the U. S. National Museum in Washington. It seems opportune to publish some facts and conclusions derived from the study of these materials in hope that they may serve as a starting point for further investigations. I feel deeply indebted to the authorities of the American Museum and the U. S. National Museum for all the facilities which have been placed at my disposal.

Materials Examined

An asterisk indicates a species or genus the skeleton of which has also been examined; an asterisk in parentheses indicates a form of which only part of the skeleton, taken out from the skin, was available, in addition to skins.

¹The genus *Alario* was placed by Sharpe (1909, 'Hand-List of Birds,' V, p. 253) near *Passer*, between that genus and *Auripasser*, which perhaps should not be separated from *Passer*. But *Alario* has little in common with this assemblage. According to its external anatomy, the characteristic relief of the horny palate, and the color-pattern of the young, it is very nearly related to the genus *Serinus* and possibly should even be placed within it, as Shelley (1902, 'Birds of Africa,' III, p. 213) has already done. *Sorella*, on the other hand, belongs to the Passerinæ.

²From personal conversation with Dr. A. Wetmore, in May, 1925, I had the pleasure of learning that he had come to the same conclusions as to the relationship of *Passer*.

³1917, Bull. Amer. Mus. Nat. Hist., XXXVIII, Art. 9, pp. 243-280.

Bubalornis albirostris,^{*1} *Dinemellia*,^{*2} *Plocepasser mahali*,^{*} *Philetairus socius* (*), *Histurgops*, *Pseudonigrita cabanisi* (*), *Sporopipes squamifrons*,^{*} *Sitagra velata*,^{*} *Textor* (*Hyphantornis* auct.) *collaris*,^{*} *Malimbus nitens*,^{*} *Pyromelana franciscana*,^{*} *Coliuspasser*, *Spermospiza ruficapilla*,^{*} *Pyrenestes ostrinus*,^{*} *Uræginthus*,^{*} *Estrilda*, *Lagonosticta*,^{*} *Stizoptera*,^{*} *Staganopleura*,^{*} *Amauresthes*, *Spermestes*,^{*} *Munia*,^{*} *Vidua macroura*,^{*} *Steganura*.^{*}

ANATOMY

STRUCTURE OF THE BILL

I have found that the relief of the horny palate presents features of great value for characterizing large groups. Certainly, it shows also adaptive modifications and adaptive similarities. But the essential plan, so far as I have been able to determine, remains unaffected by these modifications.

In the weaver-birds generally I find the same type of the horny palate which characterizes *Passer* and its nearest allies, as enumerated above. It presents a narrow and sharp ridge, not greatly dilated or split posteriorly, which runs along the middle line of the palate, and a pair of lateral ridges; the latter are low and narrow anteriorly but sharply defined from the tomia; posteriorly they become broader and more elevated, and toward their posterior ends approach the median ridge, being mostly fused together behind it. The furrow which separates the lateral ridges from the tomia gets broader and deeper, but less sharply defined, in the posterior half of the palate. This structure, of course, presents modifications.

In *Dinemellia* (Fig. 1) the median ridge runs back to the posterior limit of the horny palate; the lateral ridges are a little converging but still widely separated behind from the median ridge, and not fused posteriorly. In *Bubalornis* the lateral ridges approach closer to the median one posteriorly, but remain separated therefrom throughout their whole length, and are not fused or connected behind it. The posterior, dilated part of the lateral ridges is coarsely rugose.

In *Plocepasser*, *Histurgops*, and *Philetairus* (Fig. 2) the lateral ridges converge behind towards the median ridge and run for some distance parallel to it, closely embracing its posterior end, which is thickened

^{*1}Besides a mounted skeleton purchased from Verreaux, there were two adult males in non-breeding condition, preserved in alcohol. These two specimens of *Bubalornis albirostris* were obtained by Mr. W. W. Bowen of Gordon College, Khartoum, at the Rahad River, Sudan, in March, 1924, and presented by him to the American Museum.—J. P. Chapin.

^{*2}Including one adult male, preserved in alcohol, of *Dinemellia d. dinemelli*, which died soon after importation to the United States and was generously donated to the American Museum by Mr. L. Ruhe, the well-known New York bird-dealer.—J. P. Chapin.

and elevated, and terminates abruptly. A narrow and deepened bridge, running across between the posterior end of the median ridge and the soft skin surrounding the choanal opening, connects the lateral ridges. In *Plocepasser* and *Histurgops*, the lateral ridges are rugose as in *Bubalornis*, and the median ridge less markedly thickened and elevated behind.

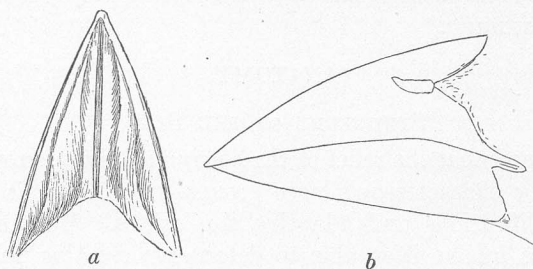


Fig. 1. *Dinemellia*.

a, palatal surface of horny sheath of bill; b, bill from side.

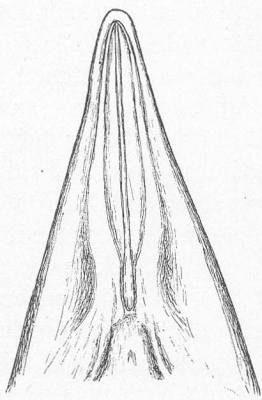


Fig. 2. Horny palate of *Philetairus socius*.

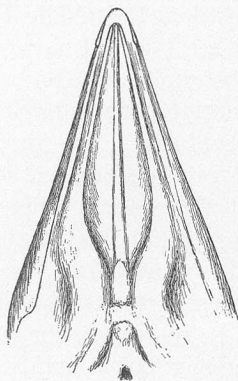


Fig. 3. *Passer domesticus*. Palatal surface of horny sheath of bill.

In *Philetairus*, the lateral ridges are smooth. In *Pseudonigrita* the palate is exactly as in *Philetairus*, only the transverse bridge is wanting.

In the Passerinae as defined above the median ridge ends posteriorly in a small but sharply defined knob; the lateral ridges closely embrace the posterior end of the median ridge and are connected by a transverse bridge behind it (Fig. 3). It is evident that the condition of the horny

palate in the *Plocepasser* group presents a very near approach to that in the Passerinae. Among the latter the palate of *Gymnoris* is especially similar to that of *Philetairus*. In the Ploceinae (Fig. 4, *h*, *i*), at least in the genera examined by me, the lateral ridges are fused only well to the rear, without embracing the median ridge, and the last runs along nearly the whole length of the horny palate. In the Estrildinae the lateral ridges are fused posteriorly to a large extent, and the median ridge is exposed only in the anterior two-thirds or half of the palate; mostly, but not constantly, the furrow which bounds the lateral ridges forms a deep pit-like depression behind, and the posterior half of each lateral ridge is emarginate externally. *Sporopipes* (Fig. 5) has the structure of the palate as in the Ploceinae.

Some of the modifications are worthy of mention here. In *Pyrenestes*, extremely heavy-billed, the bill is strongly deflected; the tomia are irregularly shaped by wear. The lateral pits of the palatal surface are very deep; they seem to sustain the maximum pressure, as the maximum thickening of the horny sheath of the lower mandible is working against them, and the horny tissue of the palate is particularly thick here, causing deep excavations of the underlying palatal surface of the pre-maxillae. In *Spermospiza*, which is nearly as thick-billed, the horny palatal surface has a different structure; there are no pits; the lateral ridges are strongly thickened behind, and their surface is rough from wear. In spite of a certain similarity with the hawfinches in the shape of the bill, the palatal surface and the lower mandible are formed quite differently, just in the functional details, and do not show anything of the special crushing pads characteristic of that group (cf. my paper in the Auk, April, 1925). In *Malimbus* the horny palate extends posteriorly much farther than in other genera examined. The base of the bill in *Bubalornis* and *Dinemellia* (Fig. 1*b*) is well marked off from the soft integuments of the head by a sharp fold of the skin which runs all around it. In *Plocepasser* and *Pseudonigrita* such a fold is well marked on the dorsal side of the maxilla and on the sides of the mandible, and less so on the sides of the maxilla below the nostril; in *Philetairus* it is quite indistinct on the sides of the upper bill. Vestiges of the fold at the base of the culmen seem to be common to the whole family and occur sporadically in the Fringillidae.

THE FEATHERING AT THE BASE OF THE BILL is variable.—In *Bubalornis* and *Dinemellia* the feathers of the forehead and lores become shorter anteriorly but are not otherwise modified. There are some strong bristles above the angle of the mouth; the nostrils are completely exposed (in

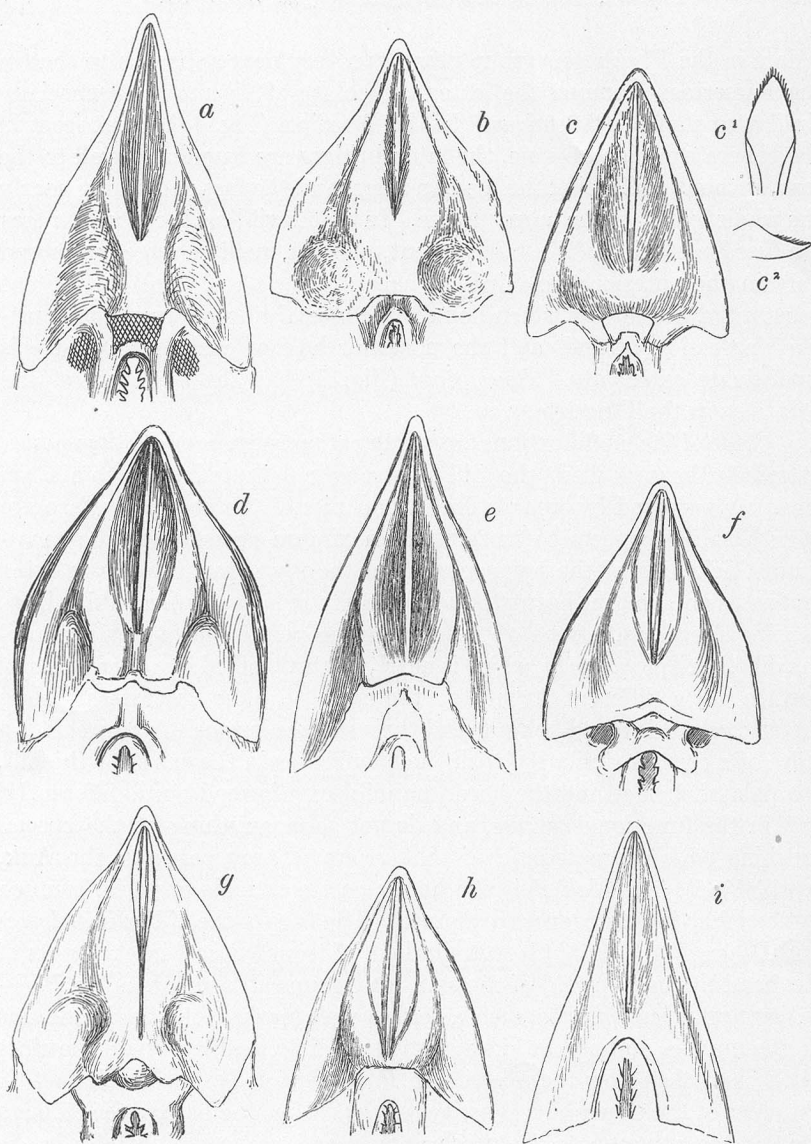


Fig. 4. Palatal surface of rhamphotheca in various genera.

a, *Uraginthus bengalus* (black palatal markings in the adult indicated by cross-hatching); b, *Pyrenestes ostrinus rothschildi*; c, *Spermospiza ruficapilla* (tongue; c¹, dorsal view; c², side view); d, *Spermestes cucullatus*; e, *Amauresthes fringilloides*; f, *Estrilda paludicola*; g, *Vidua macroura*; h, *Coliuspasser* sp.; i, *Malimbus nitens*.

Dinemellia there is in addition a bare loreal stripe). In *Plocepasser*, *Philetairus*, *Pseudonigrita*, and *Histurgops* the foremost feathers of the sides of the forehead stand upright or are inclined forward, partly overhanging the posterior margin of the nostril, the loreal feathers are also partly inclined forwards and their shafts are produced in bristles; there are also some rictal bristles. In *Sporopipes* we find the same condition, but rictal bristles are absent. The rest of the Ploceinae and Estrildinae present no constant characters in this regard; generally, the feathers at the base of the bill are more or less directed forwards, and are stiffer; in the Ploceinae the shafts of the loreal feathers are mostly prolonged into bristles; in the Estrildinae, these bristly tips are often weak or absent. Among the Passerinae, the feathers of the sides of the forehead are stiff, bristly, and directed forward, more or less covering the nostrils—least so in *Gymnoris*.

TONGUE

It is remarkable that in several forms the tongue is fringed. In *Bubalornis* it is rather long, narrow, and pointed, with subcylindrical ventral surface. The horny plate which covers its ventral surface projects beyond the fleshy part of the tongue for about $1\frac{1}{2}$ mm. anteriorly, and is provided with a well-developed fringe of flat horny filaments. In *Dinemellia*, the structure seems to be the same.¹ Unfortunately, I had no alcoholic specimens of *Plocepasser*, *Philetairus*, or *Pseudonigrita*. In *Spermospiza* the tongue, although short and fleshy, shows a clearly developed fringe of short horny filaments (Fig. 4c¹, c²); a vestigial fringe is present in *Malimbus*.

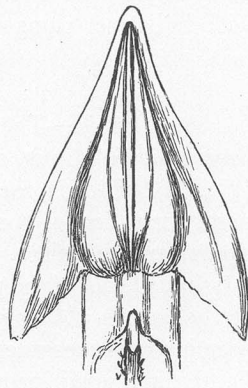


Fig. 5. *Sporopipes squamifrons*. Palatal surface of rhamphotheca.

INTEGUMENTS OF THE TARSUS

In most cases, the tarsus is typical for the Oscines, laminiplantar and acutiplantar, that is, the back of the tarsus is covered, internally and externally, by a pair of horny plates which by their meeting form the posterior ridge. In *Bubalornis*, however, the plantar laminae are partly broken, the external plate showing two distinct scutes proximally, and the internal plate two scutes distally; between both laminae there runs,

¹In the only alcoholic specimen available most of the horny filaments are lost.

from the ankle-joint to the base of the hind toe, a narrow strip of distinctly granulated skin—true integument of the plantar surface, which in other genera is squeezed out, as it were, by meeting of the posterior lateral laminae. In *Dinemellia*, both plantar laminae are continuous; the posterior granulated strip is interrupted in the middle third of the tarsus, but is well developed at its basal and distal ends. *Plocepasser* and *Histurgops* are normally acutiplantar and laminiplantar. *Philetairus* is similar but a strip of granulated skin descends from the ankle-joint farther down than usual, for about one-third of the length of tarso-metatarsus. In *Sporopipes* again the plantar laminae are partly divided, and between them runs a very narrow continuous plantar strip of skin with indistinct elongated granules.¹

SKELETON

Bubalornis.—The most prominent feature is the condition of the processus palatinus maxillæ, commonly called the maxillo-palatine (Fig. 6a), which is, for an oscinine bird, extraordinarily developed. The base, consisting of spongy bone, is thick and excavated anteriorly, the tip flat and spatulate. Into the excavation of the base fits the posterior sac-shaped wall of the nasal vestibulum; and below it, horn-like processes of the vomer abut against the base of the maxillo-palatine. Another peculiarity is presented by the olfactory fontanel of the brain-case (Fig. 7). It is divided incompletely² into the fontanel proper and the orifice which transmits the olfactory nerve. The incomplete bony bridge is formed in its dorsal part by a process of the lower surface of the frontal bone, and in its ventral part by a process of the interorbital septum which represents a vestige of the side wall of the primordial skull.³ There is a large fontanel of the interorbital septum and the foramen opticum is not closed anteriorly.

Of other characters, the most noteworthy are the following.

Upper border of the occipital muscular area nearly straight, notched at the mid-line, and its lateral outline close to the border of the exoccipital wing.

The zygomatic process of the squamosal presents a narrow external border and smooth, concave ventral outline (Fig. 7). The impression

¹This strip is very distinct in the alcoholic specimens; in the skins sometimes partly concealed by desiccation, as it may also be in *Bubalornis*.

²Chapin's allusion to a complete bridge (1917, Bull. Amer. Nat. Hist., XXXVII Art. 9, p. 250, Fig. 3C) is inexact, and due to incomplete cleaning of the skull.

³Well developed in some birds in their early ontogeny. Cf. Sushkin, 'Zur Morphologie des Vogel-skelets, 1. Schädel von *Tinnunculus*'; Nouveaux Mémoires de la Société Impériale des Naturalistes de Moscou, XVI, Livr. 2, 1899.

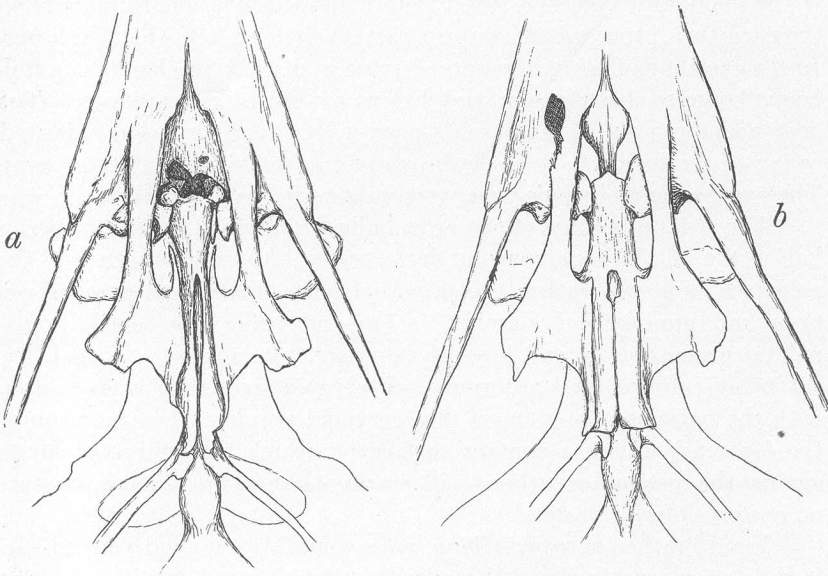


Fig. 6. Bony palate.

a, *Bubalornis albirostris*; *b*, *Plocepasser mahali*, end of the right anterior palatal process partly broken, to expose the base of the maxillo-palatine process.

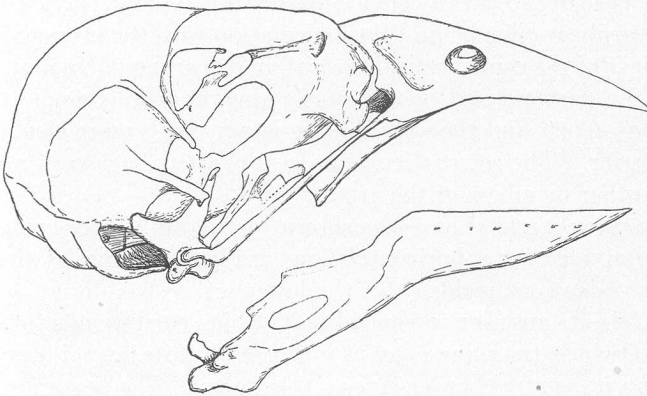


Fig. 7. *Bubalornis albirostris*. Skull and mandible, side view.

of the temporalis muscle is incompletely divided by a line running from the zygomatic process, and its upper part is a little broader than the lower. In the ectethmoid plate, the outer border is sharply notched, the notch being bounded both above and below by hook-like processes. The descendent process of the nasal is narrow, but its lower part is dilated owing to the fusion to it of the broad base of maxillo-palatine process. The nasal wing and whole nasal vestibulum are ossified.

The palatal laminæ of the premaxillæ are divided, in the posterior half of the bill, by a narrow and deep furrow. Anterior processes of the palatines (Fig. 6a) rather broad, without any dilatations or constrictions, and running nearly parallel, the fore-ends being wide apart. Transpalatal process short and broadly laminate. Palatines not fused, the slit being rather broad anteriorly. Pterygoid free, that is, not fused with the palatine; the stem of the pterygoid slender; the expansion of the fore end, giving a contact surface by which the pterygoid abuts against the rostrum, is rather small, smaller than in *Passer*, and presents no postero-inferior process.

Vomer rather narrow or long, with smoothly rounded ventral surface; its fore end is rounded medially and presents laterally a pair of knob-like processes connected with the fore edge of the dilated tip of the maxillo-palatine, dorsally to them, a pair of thick horn-like processes arise which abut against the base of the palatine process, between it and the vestibulum nasi.

The base of the parasphenoid rostrum is comparatively narrow, and rather sharply swollen behind the articulation with the pterygoids. The mandible is of the same vertical breadth in its coronoidal region as at the base of the part covered by the horny sheath; the coronoid tubercles are set far apart, and the anterior one is not much more elevated than the posterior. The retroarticular process projects backward more than in most other members of the group.

The spina sterni (Fig. 8), as shown by Chapin,¹ is perforated. The orifice is divided by a horizontal bony bridge; the mesial tips of the articular ends of coracoids enter the lower orifice but do not touch one another. In its anterior or ventral part, which corresponds to the spina of other Oscines, the spina is set as in *Passer*, but its lateral branches are short, and its ventral border gives a third apex. The posterior or post-coracoid part of the spina is as broad as the anterior or ventral one. The middle part of the corpus sterni is narrower than in *Passer*, the posterior lateral processes are broader and more dilated distally.

¹1917, Bull. Amer. Mus. Nat. Hist., XXXVII, Art. 9, p. 250, Fig. 4B.

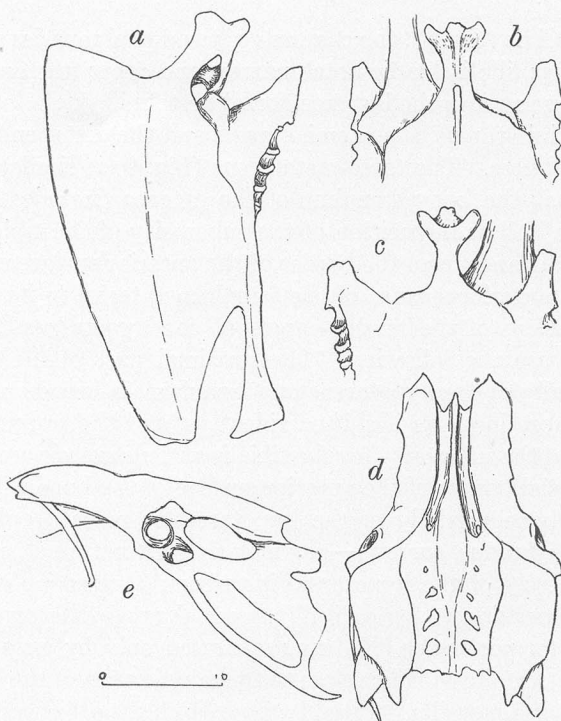


Fig. 8. *Bubalornis albirostris*.

Sternum: *a*, side view; *b*, anterior end, front view; *c*, back view of same. Pelvis: *d*, dorsal view; *e*, side view.

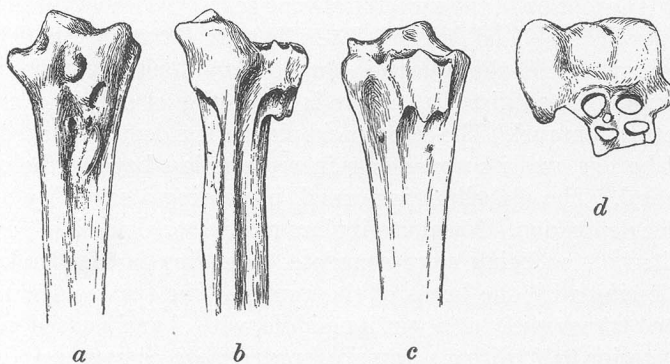


Fig. 9. *Bubalornis albirostris*.

Right tarso-metatarsus: *a*, front; *b*, inner side; *c*, back; *d*, top view.

In the pelvis (Fig. 8), the channels of the dorsal muscles are broadly open all along; ilio-ischiadic notch narrow and deep; the anterior ends of the ilia overlap also the last free dorsal vertebra.

In the tibio-tarsus, the cnemial crests and the distal end are essentially as in *Passer*. The tarso-metatarsus (Fig. 9) is similar to that of *Passer* in that the bony frenulum of the extensor muscles is set very obliquely, as well as in position of the tuberosity of the tibialis anticus muscle at a distance from the border of the anterior surface of the bone, the rounded anterior surface of the fourth metatarsal in its basal part, and the relations of the tendon-canals of the hypotarsus. Important peculiarities are the following. The proximal part of the tarso-metatarsus, mesially of the hypotarsus and frenulum, is broader; the hypotarsus therefore looks as if shifted sideways, and the frenulum for the extensors and the tuberosity for the tibialis anticus muscle are set farther from the mesial border of the anterior surface of the bone. The plantar side of the bone mesially of the hypotarsus is more deeply furrowed (peroneus profundus furrow)—particularly distinct in the top view. The mesial crest of the hypotarsus is narrow; the tendon of the flexor perforans-et-perforatus for digit II passes through the external angle of the canal for perforatus III, being separated only by an aponeurosis; the canal for perforatus II lies close to the middle crest of the hypotarsus, as in *Passer*, and is well separated by bone from the other canals.

Dinemellia.—Very near to *Bubalornis*. The skull is in most respects the same as in *Bubalornis*, but with the following differences. The outline of the area of attachment of the occipital muscles runs laterally as near to the margin of the exoccipital wing as in *Bubalornis*, but dorsally it is convex medially and descends laterally as in *Plocepasser* and *Passer*. Zygomatic process of the squamosal broader and longer, with its lateral margin more dilated distally. There is no vestige of a bridge crossing the olfactory fontanel. The ectethmoid plate is less deeply notched on its external border, and its upper margin projects less beyond the margin of the nasal. The glabellum is normal, presenting a smoothly arched, transverse depression. Nasal vestibulum more strongly ossified, ossification of its bottom being more complete, extending farther backwards, and coalescing with the horns of the vomer. The vomer is somewhat contracted transversely at about its middle, with sharply edged margins in its posterior half, with its anterior border more convex, and ventral side more concave. Lateral knob-like prominences of the anterior border, into which abut the anterior edges of the maxillo-palatines (cf. *Bubalornis*), are less developed than in *Bubalornis*, but are present.

As mentioned before, the horns of the vomer are fused with the ossified floor of the vestibulum. The maxillo-palatines are as strongly developed as in *Bubalornis*, but their base is strongly concave ventrally. Anterior processes of the palatine are accompanied by a narrow supplementary plate, very closely adjoining the lateral border of each process. It is of a regular occurrence in the cardinals, also in many buntings, but does not seem to be found in the forms related to the typical weaver-birds. Pterygo-palatal suture is distinct only in its lower half; its upper half—which, as a matter of fact, separates the hemipterygoid from the rest of pterygoid—is not developed here. Pterygoids are broader than in *Bubalornis*; their anterior end, which establishes the contact with the parasphenoid, is dilated but in a different way than in *Passer*, the supplementary part lying more dorsally. The mandible is a little more massive, with the coronoid region broader dorsoventrally; coronoid tubercles set far apart as in *Bubalornis*, but the anterior tubercle being more elevated, as in *Passer* and *Plocepasser*; retroarticular process a trifle shorter than in *Bubalornis*. The sternum, as I was shown first by Dr. Chapin, presents the same remarkable peculiarities of the spina. The only difference I was able to find is that the lateral and middle processes of its tip are less developed, and the upper perforation nearly filled up. The antero-ventral angle of the keel projects less strongly than in *Bubalornis*.

The peculiarities of the tarso-metatarsus are generally less prominent than in *Bubalornis*. The part of the bone lying mesially of the extensor frenulum, tibialis tubercle, and hypotarsus is less broadened and less deeply furrowed on its plantar side; the frenulum, tibialis tubercle, and hypotarsus are consequently set nearer to the median line of the bone. The furrow of the lateral surface of the proximal end, serving for the tendon of the superficial peroneus, is less sharply bounded anteriorly. Hypotarsus somewhat different: the canal for flexor perforatus III and perforans-perforatus III is flattened antero-posteriorly and extended transversely; the canal for perforatus II is closed behind only by connective tissue; the canal for perforatus IV not quite closed up.

Plocepasser.—Intermediate in many respects between *Bubalornis* and *Dinemellia* on the one hand, and the average *Ploceinæ* and *Passer* on the other. *Dinemellia* presents, in several respects, an approach to *Plocepasser*. With *Bubalornis* and *Dinemellia*, this bird shares strongly developed maxillo-palatines (Fig. 6b), and the same relations thereof to the horns of the vomer.

The bill is relatively smaller. The outlines of the occipital muscle areas are much as in *Passer*, the dorsal outline being convex, but with a median notch, and the lateral outlines lying farther from the margin of the exoccipital wing, which forms the posterior wall of the tympanic cavity and external ear. The exoccipital wing itself is little broader or deeper and its upper end lies somewhat higher up than in *Bubalornis*. Lower outline of the zygomatic process of the squamosal slightly dentate, recalling that of *Passer*; its external border angulate and feebly thickened; lower portion of the impression of the temporalis muscle decidedly broader than the upper, approaching again the condition in *Passer*. The olfactory fontanel shaped as usual, presenting no trace of a bridge. Small interorbital fontanel persistent and optic foramen not closed anteriorly. Ectethmoid plate less deeply notched externally than in *Bubalornis* and *Dinemellia*, and sharply limited only above. The glabella as in *Dinemellia* and *Passer*, forming a smooth arched depression. Of the nasal labyrinth, the septum, most of the bottom of the vestibulum, and the root of the vestibular concha are ossified. Palatal processes of the premaxilla divided by a furrow in the hind part of the bill, as in *Bubalornis* and *Dinemellia*. Maxillo-palatines as in *Bubalornis*. Vomer comparatively shorter and broader, with sharply edged lateral borders as in *Passer*, and rounded anterior end, which bears no knobs connected with the maxillo-palatine, such as have been described for *Bubalornis* and *Dinemellia*. Palatines and pterygoids essentially as in *Bubalornis*, but the anterior processes of palatines converging anteriorly, ventral palatal crests truncated and showing no spur-like anterior process, and the contact surface of the pterygoid for the parasphenoid rostrum intermediate between *Bubalornis* and *Passer*. Base of the parasphenoid rostrum a little narrower and distinctly keeled behind the swelling as in many Ploceidæ but not in *Passer*.

The lower mandible presents an approach to *Passer*. The region of the horny sheath is more feeble than in *Bubalornis* and *Dinemellia*, and the coronoid region is comparatively broader. The coronoid tubercles are set as in *Passer*, more closely than in *Bubalornis* and *Dinemellia*, the anterior tubercle being more elevated and shifted back. The retroarticular process is as in *Dinemellia*, longer than in *Passer*.

Spina sterni as in *Passer*, the post-coracoid part of the spina of *Bubalornis* and *Dinemellia* being represented by a narrow ligament. Middle part of the corpus sterni as in *Bubalornis*, posterior lateral processes but little broader than in *Passer*. Pelvis as in *Bubalornis*. In the tarso-metatarsus, only the very base, proximal to the tibialis

tubercle, is broadened in the mesial direction, as compared with *Passer*; the tibialis tubercle is shorter than in *Bubalornis* and *Dinemellia* and is, like the extensor frenulum and hypotarsus, set more closely to the inner margin of the bone; the last-mentioned surface is more rounded, showing no sharp ridge at the head of the bone. Canals of hypotarsus for flexor perforatus IV and III are closed late and in one specimen not closed at all; canal of perforatus III is extended transversely; canal of perforatus II lies more closely to that of flexor perforans and is divided by a thicker septum from the canal of perforatus III, the relations being also different from those of *Dinemellia*. Median crest of the hypotarsus narrow, as in *Bubalornis* and *Dinemellia*.

Of *Philetairus* and *Pseudonigrita* only the hind limbs and parts of the skull were available by sacrificing one skin of each genus. Both birds are especially near to *Plocepasser*, presenting at the same time some features of further approach to the Passerinae.

In *Philetairus*, the maxillo-palatines are almost exactly as in *Plocepasser*, but with somewhat narrower base, and presenting the same relations to the nasal labyrinth. Ossification of the nasal labyrinth as in *Plocepasser*. Vomer approaches that of *Passer* by being relatively shorter, and by showing the beginning of a median notch of the fore-end, but its lateral borders are parallel, and the horns of the fore-end are shaped as in *Plocepasser* and *Bubalornis*. Form of the bill, descendent process of the nasal, and antorbital fontanel as in *Passer*. Palatines recall especially those of *Plocepasser*, with truncated fore-end of the palatal crest; the posterior, dilated part is shorter antero-posteriorly; the anterior processes run more parallel, as in *Bubalornis*, and grow anteriorly somewhat broader. Notch of the lateral margin of the ectethmoid shallow and rather broad, as in *Passer*. Olfactory fontanel as usual. There is certainly an interorbital fontanel; but, unfortunately, nothing can be said as to the condition of the optic foramen, the zygomatic process of the squamosal, impression of the temporal and occipital muscles, transpalatine process, and base of the skull. The lower mandible as in *Plocepasser*. Tarso-metatarsus nearer to *Passer*, but the external border of the proximal part formed as in *Plocepasser*, and posterior hypotarsal canals not closed.

Pseudonigrita is very similar to *Philetairus*, but the vomer is shaped as in *Plocepasser*, with its fore-end rounded and not notched; interorbital fontanel seems to be closed; lateral border of the zygomatic process of the squamosal straight, not angular as in *Plocepasser*, and forming a laminar dilatation; transpalatine process nearly as in *Passer*.

Lower mandible somewhat broader dorsoventrally in the coronoid region, as in *Passer*. Tarso-metatarsus as in *Philetairus*, with the canals of the perforatus III and IV still less closed.

In the Ploceinæ and Estrildinæ—with the exception of *Sporopipes*—as well as in the Passerinæ the basal part of the maxillo-palatine (see Figs. 10 and 14) is reduced to a narrow stalk; the sac-like posterior part of the nasal vestibulum—ossified in most of the Ploceinæ—encroaches

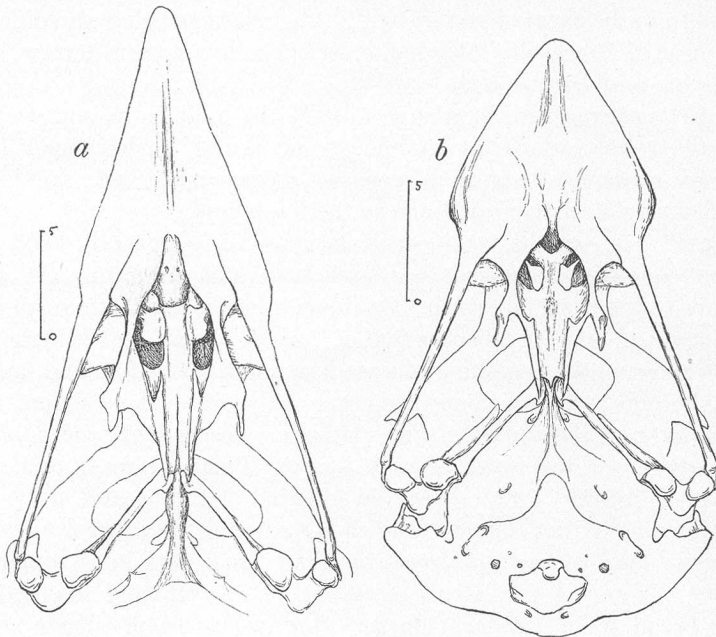


Fig. 10. Palatal surface of the skull.

a, *Textor collaris*; b, *Munia maja*.

upon the base of the maxillo-palatine, which lies now NOT BEHIND the posterior end of vestibulum as in *Bubalornis* and *Plocepasser*, but BELOW it.

The olfactory fontanel is formed as usual. Optic foramen closed; interorbital fontanel absent, or—in some Estrildinæ—vestiges of it are present.

In the Ploceinæ (Fig. 10a) the distal end of the maxillo-palatine is broadly spatulate as in *Passer*; and in some is connected with the vomer in the way described above for *Bubalornis*. The interpalatal

space represents the same shape, size, and relations as in *Passer*. Anterior processes of the palatines converging anteriorly, constricted at the basal half and rather suddenly dilated in their anterior half, this dilatation being of equal breadth all along, and differing thus from the spur-like dilatation characteristic of the *Carduelinæ*.¹ The slit between the posterior leaves of the palatines variable: complete in *Pyromelana*; hind half persistent in *Malimbus*; the same, or completely closed, in *Textor* (= *Hyphantornis* of authors). Transpalatal process tapering; palatal crests much shorter than in *Bubalornis* and *Plocepasser*. The pterygoid may be free, or fused with the palatine; its anterior end, abutting against the parasphenoid rostrum, is shaped as in *Bubalornis*. Vomer broad and flat, its borders forming sharp edges pointing ventrally; anterior tip formed either as in *Plocepasser* (e. g. in *Malimbus*), or emarginated and provided with lateral knobs connected with the dilated tips of the maxillo-palatine in the same way as in *Bubalornis* (e. g. in *Textor*). The base of the parasphenoid rostrum, behind its contact with the pterygoids, is generally narrow, swollen anteriorly and compressed posteriorly (in *Malimbus* very narrow and nearly blade-like). Ala nasi ossified in the majority at least.

In the Estrildinæ (Fig. 10b) the interpalatal space is greatly shortened anteriorly, the vomer being sometimes completely hidden. The anterior processes of the palatines converge anteriorly, their basal half being more strongly constricted, and distal half more strongly dilated than in the Ploceinæ, though the distal half keeps an equal breadth throughout. The palatal crests are set more widely apart; in *Munia* (*sensu lato*) and *Spermestes* they are conspicuously shortened, with abbreviated anterior spur. Slit between the bases of the palatines mostly closed. Pterygoid fused to the palatine; its anterior head, articulating with the parasphenoid rostrum, gives off posteriorly a conspicuous spur which does not, however, touch the rostrum. Ala nasi never ossified.

Vomer variable; in *Lagonosticta* and *Spermospiza* narrower than in others and conspicuously furrowed ventrally, its anterior horns directed nearly transversally in *Munia oryzivora*. In other species of *Munia* (e. g. *maja*, *brunneiceps*) and in other genera examined, the horns are directed obliquely antero-laterally. Vestiges of the interorbital fontanel persist in *Stictopleura* and *Lagonosticta*. Base of the parasphenoid rostrum very variable: very broad and flat in *Pyrenestes*; more narrow generally in others; in *Lagonosticta* and *Spermospiza* feebly swollen

¹Sushkin, 1925, *Auk*, pp. 257, 258, Fig. 2.

anteriorly, and furrowed behind; in *Uræginthus*, *Stictospiza* and *Stagano-pleura* feebly keeled; in *Spermestes*, and especially in *Munia*, sharply keeled.

The base of the brain-case in *Munia* and *Spermestes* exhibits a very peculiar relief of the basitemporal plate: its lateral parts strongly shifted backwards, and the middle part, which retains its normal position, projecting much forward. In other genera the basitemporal plate is normal.

Some aberrant genera are worthy of mention. *Pyrenestes* (Fig. 11) is strikingly modified. Its bill, very massive, is extraordinarily strongly

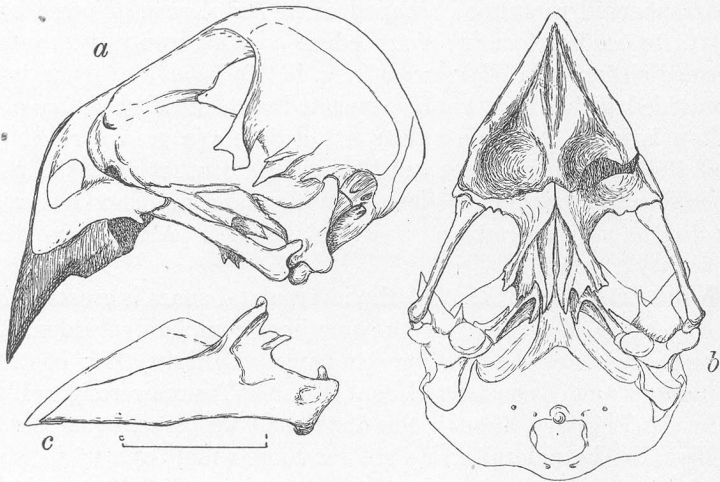


Fig. 11. *Pyrenestes ostrinus rothschildi*.

Skull: a, side view (horny sheath of bill is partly removed); b, palatal view (on the left side part of the horny sheath is cut off); c, mandible, bone exposed but outline of horny sheath preserved.

bent and deflected. Interpalatal space much shortened, the vomer and the ends of palatal crests being concealed. The palatal surface of the upper jaw is strongly excavated laterally for the reception of the very thick horny lining of the lateral pits of the horny palate. The slit dividing the palatines is preserved. The tip of the postorbital process, the zygomatic process, transpalatal processes, posterior face of the pterygoid, dorsal surface of the palatine, and coronoid region of the mandible all present exaggerated muscular asperities. The lower mandible (Figs. 11 and 12) is peculiar for its strongly developed and uplifted coronoid asperities, and the limit of the horny part shifted far backwards; the mandibular fontanel, constant in others, is closed.

Vidua and *Steganura* are peculiar in other respects. The shape of the skull is of an average type for the Estrildinæ. A vestigial interorbital fontanel present. Palatal crests set widely apart, typical for the Estrildinæ. But the interpalatal suture persistent, although narrow; anterior palatal processes much less strongly dilated, their shape and the shape and size of the interpalatal space being rather of a type usual among the Ploceinæ. Pterygoid fused with the palatal bones. Vomer broad, its lower surface bordered with sharp edges pointing ventrally. Base of the parasphenoid rostrum rather broad, feebly swollen anteriorly and very feebly keeled posteriorly. Inner head of the quadrate in *Steganura* spongy, this being exceptional for the group; in *Vidua* it is pierced only by 2-3 small pneumatic orifices. Descending process of the nasal narrow. Most of the distinctive characters enumerated seem to be primitive.

Sporopipes (Fig. 13) is in many respects intermediate between the typical weavers and *Bubalornis* and *Plocepasser*. General shape of the skull and of the bill rather estrildine. Maxillo-palatine reduced, with stalked base and scarcely dilated apical part, the relation of the base of the maxillo-palatine being as in the typical Ploceidæ. Olfactory fontanel formed as usual. Interorbital fontanel present, and optic foramen not closed anteriorly. The surface occupied by the occipital muscles is shaped as in *Bubalornis*. Zygomatic process of the squamosal with sharp external border. Impression of the temporalis muscle small, upper portion reduced and narrower than the lower. Exoccipital wing extends farther up than in other genera. Ectethmoid as in *Plocepasser*. Descending process of the nasal narrow. Ossification of the nasal labyrinth nearly as in *Plocepasser*. Vomer the same, but its horns vestigial and not extending to the base of the maxillo-palatine. Palatine laminae of both premaxillæ divided by a long furrow. Anterior processes of the palatines converging anteriorly, much constricted at the base and then dilated strongly but gradually. Transpalatine processes as in *Plocepasser*. Palatal crests as in *Plocepasser*, differing from other Ploceidæ by the absence of a projecting anterior spur. Slit between the palatines persistent, though narrow. Pterygoid not fused with the palatine. Support of the articular surface for the inner head of the quadrate, and whole

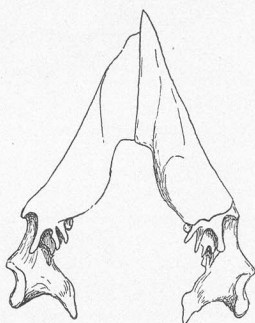


Fig. 12. *Pyrenestes ostrinus rothschildi*. Mandible, dorsal view. Horny sheath preserved on the right half.

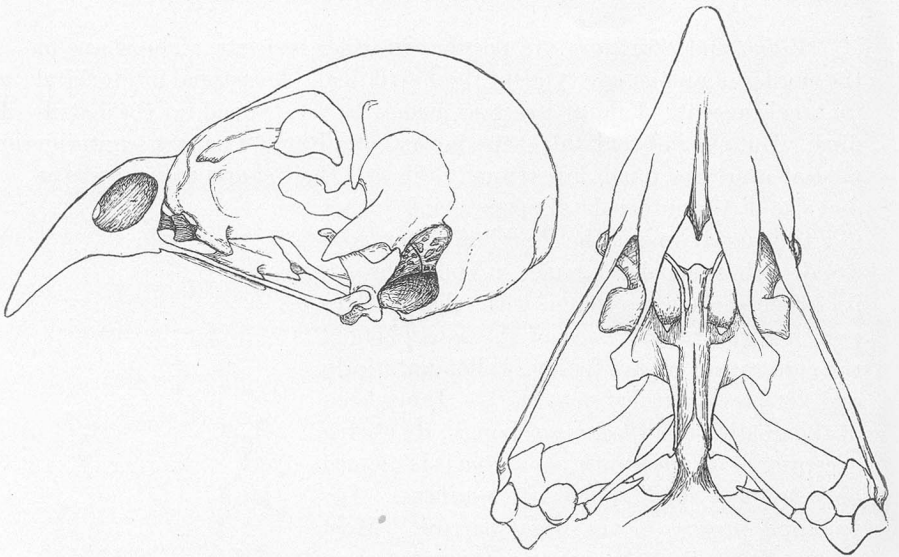


Fig. 13. *Sporopipes squamifrons*. Skull, side view and palatal surface.

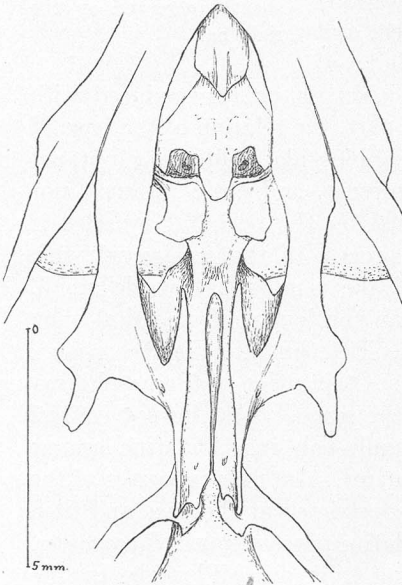


Fig. 14. *Passer domesticus*. Bony palate.

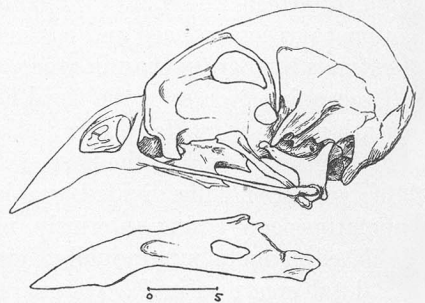


Fig. 15. *Passer domesticus*. Side view of skull and mandible.

inner head of the quadrate strongly spongy; in other genera, with the exception of *Steganura*, only the support of the inner articular surface is spongy. Base of the parasphenoid rostrum swollen anteriorly.

Sternum as in *Plocepasser*. Pelvis with deep ilio-ischiadic incisure as in *Plocepasser* and *Bubalornis*, but the canals of the dorsal muscles closed behind as in the typical Ploceidæ. Hypotarsus without any definite distinction from *Plocepasser*.

For the Passerinæ (Figs. 14 and 15) may be given as typical the following combination of characters. Maxillo-palatine with stalked base and dilated, spatulate tip. Olfactory fontanel formed as usual, inter-orbital fontanel absent, optic foramen closed anteriorly. External border of the zygomatic process of the squamosal extremely dilated, laminate, lower border dentate. Descending process of the nasal rather broad. In the nasal labyrinth, the septum and part of the bottom of the vestibulum are ossified. Furrow between the palatal processes of the premaxillæ closed up. Interpalatal space large, as in the Ploceinæ, and the vomer exposed. Anterior processes of the palatines converging, rather broad, not definitely constricted at the base and feebly dilated in the middle. Palatal crests with a strong anterior spur. Slit between posterior portions of the palatines complete. Vomer broad, notched anteriorly, with strongly developed horns. Pterygoids not fused with the palatines, their stem rather thick; the head articulating with the parasphenoid rostrum gives a rather strong postero-inferior spur articulating with the rostrum posterior to the articulation with the palatine. Base of the parasphenoid rostrum broad, rounded, with no swelling or keel.

PHYLOGENETIC RELATIONS

Bubalornis, as has been shown, is characterized by a number of features of which some are certainly primitive. As such I consider:

(a) The fold of skin encircling the base of the bill. In others it is reduced or disappears, its vestiges occurring sporadically in Fringillidæ also.

(b) Non-modified feathers of the forehead.

(c) Lateral ridges of the horny palate not fused behind. A majority of the members of the group show progressive fusion of the lateral ridges.

(d) Persistent plantar strip of granulated skin, and postero-lateral plates partly broken up into separate scutes.

(e) Very long tenth primary. Reduction is progressive within the group.

(f) Narrow exoccipital wing. Primitive, judging by its ontogeny in *Cerchneis* (= *Tinnunculus*).

(g) Narrow lateral border of the zygomatic process of the squamosal.

(h) Presence of an interorbital fontanel, and optic foramen not closed. It is shown, by ontogeny, that primarily—in the cartilaginous skull—the interorbital septum is continuous, and the optic foramen is not closed ABOVE. The next stage is the forming of a fontanel, which later may disappear by ossification of the membrane which closes the fontanel.

(i) Presence of a vestigial bar bordering posteriorly the olfactory foramen. In ontogeny of birds, the olfactory nerve enters into the orbit through an orifice in the cartilaginous wall of the brain-case; later on, this part of the primary wall of the brain-case disappears in most birds altogether.

(j) State of the maxillo-palatine. In nearly all Oscines it is strongly reduced. The maxillo-palatines are found in the condition described here among many of the non-oscine Passeres.

(k) *Spina sterni*, probably primitive. In Passeres it is typically single, non-perforated; the post-coracoid part of the spina of *Bubalornis* being replaced by a ligament. But as an abnormality, a perforated spina, built much as in *Bubalornis*, has been found in Fringillidæ and Tanagridæ. I have found it in three specimens of *Fringilla cælebs*—one in the British Museum, and two in the U. S. National Museum. Of the last two specimens, one has the post-coracoid part of the spine narrow, whereas in the other it is as broad as the precoracoidal part; the foramen is single but divided into a basal and an apical part by a ligament which corresponds to the bony bridge present in *Bubalornis*. In *Fringilla montifringilla* I have never found the postcoracoidal spina; it is replaced by a ligament, but the base of it is sometimes ossified. Once I found a perforated spina in *Sicalis* (among five specimens examined). Clark has discovered a perforated spina in *Rhodinocichla* and some other tanagers¹ but has erroneously described this character as constant for tanagers. It seems thus that this feature disappeared in the phylogeny of Oscines, being preserved sporadically as an anomaly.

(l) A part of the characters of the tarso-metatarsus—position of hypotarsus, and its narrow median crest. These characters change gradually within the series of Ploceidæ.

The problematic penis-like organ of *Bubalornis*, of which some details are given below (see Supplement to this paper), cannot be classed here

¹1913, Auk, p. 14.

as it is not homologous with the penis found in some less advanced groups of birds.

In *Dinemellia*, which is generally very near to *Bubalornis*, many of the characters enumerated, supposedly primitive, are present, namely those marked *a, b, c, e, f, g, h, j*, and *k*. In the state of the horny palate, and perhaps in the incomplete closure of some canals of the hypotarsus, *Dinemellia* is even more primitive than *Bubalornis*. But in most of the features distinguishing it from *Bubalornis*, *Dinemellia* is advanced or else stands nearer to the bulk of the Ploceidæ. Such are: (*a*) condition of the tarsal integument, halfway between that of *Bubalornis* and the usual oscinine; (*b*) outline of the occipital muscular area; (*c*) dilated lateral border of the zygomatic process of the squamosal; (*d*) disappearance of the olfactory bridge; (*e*) some features of the mandible; and (*f*) of the tarso-metatarsus. I was unable to appreciate the significance of the additional ossification accompanying the anterior process of the palatines, and of the state of the pterygo-palatine suture as observed in *Dinemellia*. Though strongly characterized in this way, *Bubalornis* and *Dinemellia* are, nevertheless, intimately connected with the more advanced Ploceidæ through *Plocepasser*, *Philetairus*, and *Pseudonigrita*. For this reason, the whole assemblage, which is rather advanced in its typical forms, is to be considered as a branch separated off from the common stem at a comparatively low morphological level.

Some characters of the Phytotomidæ may seem to entitle that small family to an ancestral relation to *Bubalornis*: the very similar shape of vomer and maxillo-palatines; tarso-metatarsus covered posteriorly by three rows of large scales, of which the outer consists of larger elements, although, individually, the internal row may also consist of large scales, leaving out the middle or medio-plantar row consisting of smaller scales; tenth primary large; bill conirostral. But the ends of the maxillo-palatines ARTICULATE with the ventral side of the antero-lateral angle of the vomer; the zygomatic process of the squamosal is of a different shape, pointing to a different structure of the temporalis muscle; spina sterni simple; hypotarsus with five canals too, but of the canal for the tendon of *M. flexor perforans* much smaller than the canal for *M. flexor hallucis*.

Plocepasser, *Philetairus* and *Pseudonigrita* form another small group of nearly related genera, which presents a decided advance leading to the Passerinæ and Ploceinæ + Estrildinæ, and may be considered as perhaps ancestral to both. Only one character found in *Plocepasser*—namely the structure of the base of the parasphenoid rostrum—seems to

be incompatible with a direct relationship to the Passerinæ. Unfortunately, *Philetairus* and *Pseudonigrita*, more advanced generally and more decidedly sparrow-like in several characters, are insufficiently known generally, and just this feature is unknown. The structure of the vomer seems to indicate that *Philetairus* is nearest to the sparrows. The structure of its horny palate recalls very closely that of the Passerinæ, the condition of the tenth primary likewise is the same as in sparrows, although this character cannot be relied upon. But, at the same time, *Philetairus* shows peculiar stiff feathers on the interscapulum and flanks which recall the ornamental feathers of some Ploceinæ and are quite unusual for Passerinæ. The condition of the tenth primary is very variable in this group. It is rather well developed in *Plocepasser*—certainly one of the less advanced forms; in the more advanced genera it is much reduced, being shorter than the primary coverts in *Pseudonigrita*, though keeping still its position on the under side of the ninth primary; and in *Philetairus* being even displaced to the dorsal side of the ninth primary as in the Passerinæ.

The PASSERINÆ present a compact group which is nearer to the Ploceinæ than to the Estrildinæ, and in some respects (e. g., state of the anterior process of the palatine) more primitive than either, in others (for instance, specialized feathers at the base of the bill) more advanced. The connection downward is pretty well established through *Philetairus*, *Pseudonigrita*, and *Plocepasser*. It should be noted, however, that *Bubalornis*, *Dinemellia* and *Plocepasser* (*Philetairus* and *Pseudonigrita* unknown in this regard) present a feature—swelling of the base of the parasphenoid rostrum—which is absent in the Passerinæ. We have no reason as yet to consider this a primitive character and its absence in the Passerinæ as due to subsequent reduction. By the incipient condition of the feathery covering of the nostrils, as also by special similarity of the palatal surface of the bill to that of *Philetairus*, *Gymnoris* may prove the most primitive member of the sparrow group; unfortunately, I have had as yet no opportunity of examining its skeleton.

PLOCEINÆ AND ESTRILDINÆ.—For the understanding of the broad and diversified groups of Ploceinæ and Estrildinæ much more work is needed than I have been able to do with the material at my disposal. Nevertheless, some points of interest may be indicated. *Pyromelana* and (from the structure of the horny palate) *Coliuspasser* prove to belong to the Ploceinæ, where these genera have been placed by Chapin,¹

¹1917, Bull. Amer. Mus. Nat. Hist., XXXVII, pp. 252, 256, 261.

contrary to the opinion of other classifiers of the group. As a rule, the Estrildinæ are more advanced than Ploceinæ (maxillo-palatines more reduced; anterior processes of the palatines more specialized, and inter-palatine space more closed), but in the persistently cartilaginous ala nasi they seem to be more primitive. *Vidua* and *Steganura*, while showing unmistakable features of the Estrildinæ, differ less strongly than usual from the Ploceinæ. I think that both groups should be considered as having started from a common ancestor and converging in their respective lower forms. As to the group bearing the name Estrildinæ, it certainly consists of several branches or secondary groups. *Munia* and *Spermestes* form one of them, as has been already been indicated by Chapin,¹ after the palatal markings of the nestling. It is to be noted that "*Munia*" *oryzivora* differs anatomically from other species included in that genus, and so the generic name *Padda* is to be retained for it. *Spermospiza* is decidedly related to *Lagonosticta*. *Pyrenestes* is extremely modified; there is no reason, in its anatomy, for considering it as a descendant of *Spermospiza* or in any close degree related to it. *Vidua* and *Steganura*, which show some unmistakable features of the Estrildinæ, and none of the characters common to the Ploceinæ that could not be interpreted as primitive, are in their skeletons the most primitive of all Estrildinæ. I see no reason for placing them at the top of the phylogenetic tree as Dr. Chapin does; certainly they are strongly modified in their nuptial plumage, but on a very low base. Perhaps the munias, the whydahs, possibly *Pyrenestes*, and the remainder (including *Lagonosticta* and allies) should form separate subfamilies. The difficulty of discriminating between Ploceinæ and Estrildinæ by external characters may result from the very fact that in the last group certainly, and in both perhaps, forms are included which should be kept separate.

As to the characters used, I agree with Dr. Chapin who rejects totally as a criterion the state of the tenth primary. Besides many instances where the development of the tenth primary affords indications contradictory to those given by other characters, the review by Dr. Chapin contains several cases where the state of the tenth primary is quite ambiguous, or variable even within one genus. Very limited material at my disposal has enabled me nevertheless to confirm the opinion of Dr. Chapin in two critical cases, namely as to the position of *Pyromelana* and *Coliuspasser*, which belong in the Ploceinæ notwithstanding their short tenth primary. It is to be taken into account that

¹1917, Bull. Amer. Mus. Nat. Hist., XXXVII, pp. 247, 252, 261.

the state of a declining organ cannot serve as a taxonomic criterion. Such organs are notoriously variable because, being useless, they elude the sifting out of variations by natural selection. I have alluded to the variability of the tenth primary in the group consisting of *Plocepasser*, *Philetairus*, and *Pseudonigrita*, which certainly belong close together by their structure of the skeleton and horny palate. Other instances of the variability of the tenth primary in groups where it is declining are:

Vireo, in which, after careful study of their anatomy by Dr. Alexander Wetmore (*in litt.*) the tenth primary may be present or absent in birds belonging surely to the same genus; and

Urocynchramus, a typical bunting in all characters of external anatomy, structure of the horny palate included, but with long tenth primary.

Sporopipes is another genus of intermediate position. While having lost some of the morphologically primitive characters of the *Bubalornis* and *Plocepasser* groups, it is very little specialized; in one character—integuments of the tarso-metatarsus—it is even as primitive as *Bubalornis*. Concerning its relations to the more advanced groups, it presents no characters pointing to the Passerinae but certainly shows some characters of both Ploceinae and Estrildinae. It is more difficult to fix its relation to either one of these subfamilies owing to some uncertainty as to the groups themselves, and to the fact that most of the features of the Estrildinae are of advanced character and are undeveloped in *Vidua* and *Steganura*, which are surely primitive Estrildine birds. Judging by the shape of the skull and bill, by the rather pronounced abortion of the maxillo-palatines and by certain characters of the palate (strongly constricted base of the anterior process of the palatine, and long posterior part, behind the root of transpalatine process), I consider *Sporopipes* as leading towards primitive Estrildinae but certainly not incorporable into that group. The state of the internal head of the quadrate, very spongy and pierced by numerous openings both in *Steganura* and in *Sporopipes*, is very suggestive. The whole structure of the skeleton of *Sporopipes* forbids considering it as ancestral to *Plocepasser*¹ and its nearest relatives.

OUTLINES OF CLASSIFICATION

The inadequacy of material at my disposal, which has been just sufficient to show the extent of morphological differences and the intricate relations, as well as the character of the relations themselves, makes a satisfactory classification of the group a very difficult task. It may be set forth now only in its general features.

¹Cf. Chapin, 1917, Bull. Amer. Mus. Nat. Hist., XXXVII, Art. 9, p. 264.

Bubalornis and *Dinemellia* are very closely allied, and are so strongly characterized as to seem to justify their separation as a family proposed by Chapin. But already *Dinemellia* lacks some of the exclusive and primitive features proper to *Bubalornis*, and points, as I hope to have shown, in the direction of the more advanced Ploceidæ. And *Plocepasser* with *Philetairus* and *Pseudonigrita* fill the gap to a large extent, making the isolation of *Bubalornis* less striking. As a matter of fact, the whole sum of the characters of *Plocepasser*, *Philetairus* and *Pseudonigrita* is such as to make nearly arbitrary the decision whether they should be placed in the same group with *Bubalornis* or with more advanced forms, or separated as constituting a group (family?) by themselves. I consider that in principle there should be no objection to an augmenting of families when it is required by increasing knowledge of morphology, taking it for granted that the classification should mirror the phylogenetic relations. But, for the same considerations, an increase of minor groups if not held together is an evil. And in the same way I consider that the establishing of higher systematic groups consisting of but one genus or perhaps one species should be admitted only with greatest care. In practice, I admit, subfamilies may be small and numerous, giving thus expression of detailed relations of genera, but they should be united in comprehensive families. The sentence *omnis divisio est magis artis quam naturæ* is the more justified, the more complete the material we are dealing with, and this "art of dividing" consists in expressing genetic relations by distributing the material into co-ordinate and subordinate groups to which an exact definition may be given. Forms which break down the definition of a group are to be removed therefrom. I consider that *Bubalornis* and *Dinemellia* constitute a close group separated from the rest of the assemblage and certainly more primitive. Another small group of closely related genera form *Plocepasser*, *Philetairus*, and *Pseudonigrita*. For the last group, the presence of such a character as the condition of the maxillo-palatine process alone forbids their union with *Passerina*, or with *Ploceina* and *Estrildina*. When acquainted with the inner organization of *Bubalornis* and *Plocepasser* only, I was inclined to put the last-named together with *Bubalornis* and *Dinemellia* as a more advanced member of the same group, but now I consider the separation of *Plocepasser* and its allies more justified, as all three genera are closely related and differ in the same advanced features from *Bubalornis* and *Dinemellia*. I make of *Plocepasser*, *Philetairus*, and *Pseudonigrita* a subfamily, **Plocepasserina**, to which *Histurgops* seems also to belong. And, as the *Plocepasserina* break down the apparently isolated position

of *Bubalornis* and *Dinemellia*, I prefer to treat these also as a subfamily, Bubalornithinæ.

The Ploceinæ and Estrildinæ form subfamilies by themselves; I have said already that the Estrildinæ almost surely are to be split up after further investigation; of the genera known anatomically in the latter subfamily, *Steganura* and *Vidua* are the least advanced in many respects, and least different from the Ploceinæ.

Less related to them is another group of advanced Ploceidæ which contains the true sparrows and their kindred as enumerated already in this paper. They have been placed hitherto in the family Fringillidæ. I make of them a separate subfamily, Passerinæ, of the Ploceidæ. It cannot be considered as standing in direct ascendent or descendent relation with the other two, but presents a separate branch of evolution. Thus the Passerinæ on the one side and Ploceinæ and Estrildinæ on the other, present advanced branches of Ploceidæ, flourishing now as evidenced by the large number of species and extensive geographical distribution, whereas the Bubalornithinæ present a remnant of the ancestral stock reduced numerically. The Plocepasserinæ form an intermediate group which leads from the more archaic Bubalornithinæ upwards. Most of its advanced features point in the direction of the Passerinæ, and the relation seems to be especially near between *Gymnoris* on the one side and *Philetairus* on the other. But even *Philetairus* shows at least one feature, seemingly of advanced character—namely, modified feathers of the back and flanks,—which may point in the direction of Ploceinæ and does not reappear among the Passerinæ. Another feature of this kind is, at least in *Plocepasser*, the structure of the base of the parasphenoid rostrum.

Sporopipes stands in pretty much the same relation to both the Ploceinæ and the Estrildinæ, connecting them downward. Standing halfway between the primitive Estrildinæ and *Plocepasser*, or even *Bubalornis*, it cannot be grouped with either without damage to the definitions of the characters, and there remains nothing but to separate it as a subfamily **Sporopipinæ**.

Thus, I propose the following divisions:

Family Ploceidæ

Subfamily Bubalornithinæ

“ Plocepasserinæ

“ Passerinæ

“ Sporopipinæ

“ Ploceinæ

“ Estrildinæ

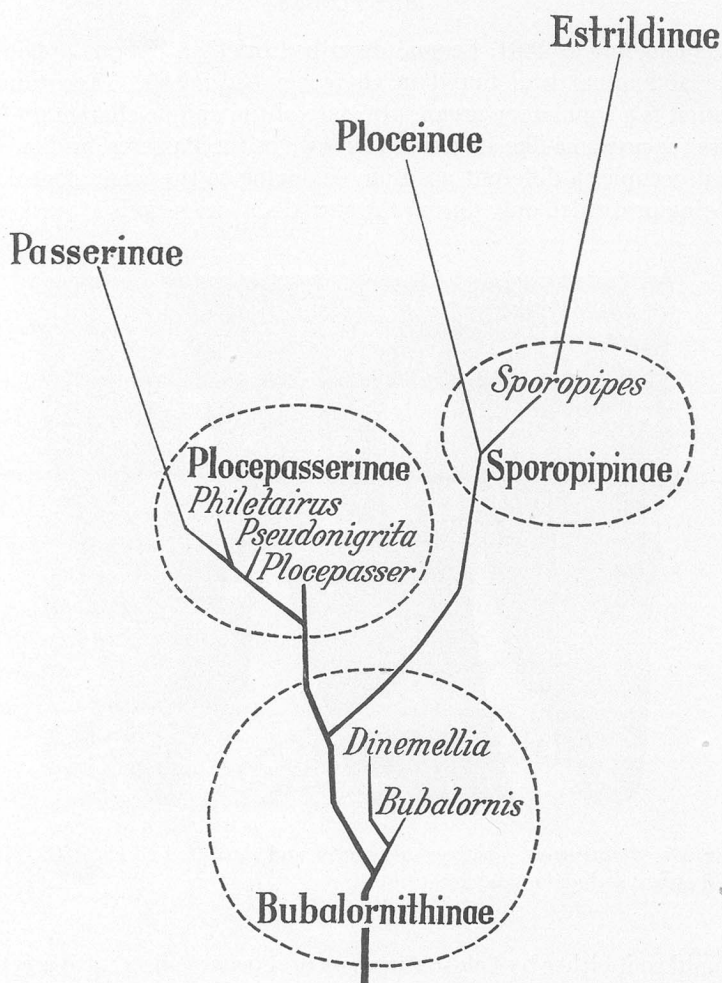


Fig. 16. Diagram illustrating relations of the main groups of Ploceidæ.

The diagram (Fig. 16) represents my understanding of the relations, which cannot be displayed by a linear arrangement.

SUPPLEMENT.—ON THE SUPPOSED COPULATORY ORGAN IN
BUBALORNIS

As long ago as 1831, Lesson¹ described briefly a curious appendage of the abdominal wall found in the male *Bubalornis*. According to Lesson, it is a copulatory organ. In spite of the unique character of this feature (as no penis-like structure is known in the Passeres, and in other birds it occupies a different position, belonging to the inner cloacal wall and being protruded only during the sexual act) no serious attention has

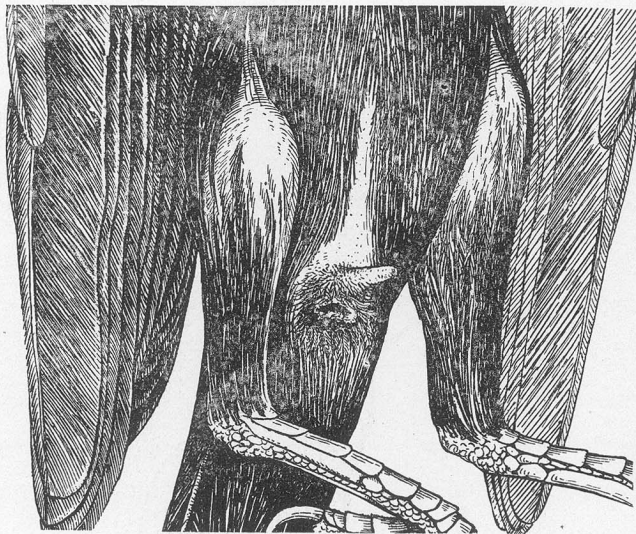


Fig. 17. *Bubalornis*. Feathers moistened and separated to show the cloaca, phalloid organ, and abdominal apertures.

been paid to it either by field-naturalists or morphologists until recently. In 1902, Dr. E. Hartert, at the meeting of the British Ornithologists' Club, mentioned this curious organ and called the attention of his colleagues to the subject.² In 1917, Dr. Hartert returned to this theme again, giving some details and alluding to the field-notes made on the labels of the skins by W. J. Ansorge. Hartert came to a definite conclu-

¹'*Traité de d'Ornithologie*,' p. 433.

²*Bull. Brit. Orn. Club*, XII, pp. 77, 78.

sion that this organ cannot be considered as a penis and so its physiological meaning remains enigmatic, the only allusion as to its copulatory functions by Lesson being mere surmise. No description has been given except that the organ lies in front of the cloaca, is not perforated, is stiff during life, and vestiges of it are present in females.

When I was working at the American Museum in 1925 on the anatomy of the weaver-birds, Dr. J. P. Chapin proposed that I make use of his material (several skins and two alcoholic specimens) in order to elucidate the question. I am also indebted to Dr. Chapin for the figure (17) prepared under his direction.

The "phalloid" organ, as it may be named (Fig. 17), presents a conical prominence of the abdominal wall arising quite close to the ventral side of the swollen border of the cloacal opening. The form is simply conical, bluntly pointed and perhaps somewhat bent, with the convexity behind. In the early-spring birds—both the alcoholic specimens—the dimensions of the phalloid organ are 8 mm. in length and 6 mm. across at the base; in the skin of birds taken in the breeding season it is more developed, and according to Ansorge its length may be about 25 mm. In the alcoholic specimens, the cloacal opening is directed more backward than ventrally, and the phalloid structure is directed nearly at a right angle to the abdominal wall or somewhat forward. The organ is not perforated, and bears no furrows or special rugosities.

As has been said already, the phalloid arises close to the swollen rim of the cloaca; the rim is provided, as usual, with a row of stiff feathers, and is not interrupted or marked in any way at the base of the phalloid. The skin which covers the organ is just a continuation of the abdominal skin. The base of the organ is covered by small downy feathers which are more dense and ascend farther up on the caudal side.

The dissection (Fig. 18) shows that the skin is attached firmly, especially near the tip, being here lined with a thin layer of fat-tissue. The axis of the organ consists of a stiff fibrous core which is closely attached to the outer wall of the cloaca, but is not contiguous with it, being separated by a thin layer of loose connective tissue. The core pushes out, as it were, the muscular sheet formed by *M. transversus cloacæ* and is completely enwrapped by muscular tissue, excepting perhaps at the tip. As is shown in Fig. 18, the *musculus transversus cloacæ* is subdivided into two portions, the anterior starting from the end of the pubis, and the posterior arising partly from the aponeurosis which covers the caudal muscles and partly contiguous with the sphincter ani and encircling the cloaca. Both portions of the muscle take a share

in forming the phalloid; the pubic portions of either side meet just at the root of the anterior surface of the phalloid, forming here a rather distinct raphe; no raphe is formed on the posterior side of the organ.

Without making microscopical sections of the phalloid it is difficult to tell whether its core consists of erectile tissue. At any rate, the phalloid, as seen in the alcoholic specimens, is stiff and resistant; and so it is

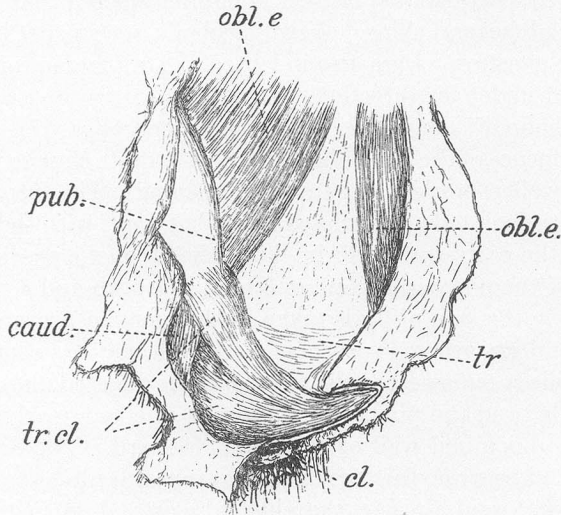


Fig. 18. *Bubalornis*. Abdominal wall and phalloid organ, in same position as in Fig. 17 but with skin split open.

cl., cloaca; *caud.*, caudal muscles; *obl. e.*, obliquus externus muscle; *pub.*, pubis; *tr.*, transversus muscle; *tr. cl.*, musc. transversus cloacæ.

described in freshly killed birds. According to Ansorge (field notes quoted by Hartert), there is a vestigial phalloid in the females, too.

As is evident from this description, the phalloid is very different from the cloacal penis present in *Struthionidæ*, *Rheidæ*, and *Anatidæ*. Nothing like it is known in other birds, and even in *Dinemellia*, the nearest relative of *Bubalornis*, no trace of the phalloid has been found. As to the possible function of the phalloid, the following features of its structure are to be considered. It is a stiff organ, firmly attached to the outer cloacal wall near its orifice and dominated by the same muscles which govern the movements of the cloaca; the subdivision of its muscular sheet in separate portions may show that the organ can be moved and inclined in different ways. Hence, I think it quite possible that the phalloid, even if its core is not erectile, may serve as an auxiliary organ in the act of copulation.