

“Acrobatic” display. It has been witnessed on different days to his “Juggling” display. While giving his Acrobatic performance he sings the whole time, but never shews his side-plumes; and when he is in the pendulous position his body sways gently as if it were influenced by a fitful breeze. The whole of this performance takes but a very few seconds.

The drawings by Mr. G. E. Lodge (Plate V. and text-figures 8 & 9) were sketched from life, the bird having given him a continuous exhibition of his display of nearly an hour’s duration.

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X.—*On the Anatomy and Systematic Position of the Colies.*

By W. P. PYCRAFT, F.Z.S., A L.S., M.B.O.U., &c.

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I. INTRODUCTION.

WHEN, some months since, Dr. Sclater asked me to contribute a paper to ‘The Ibis’ on the anatomy of the Colies, with especial regard to the systematic position of these aberrant birds, it seemed to me that little that was new remained to be said. For, in addition to Dr. Murie’s monograph on the skeleton (II) which appeared in ‘The Ibis’ so far back as 1872, a number of contributions have been made by other writers dealing with the pterylosis, myology, and intestinal convolutions.

Nevertheless, I have been enabled to add some new facts, as well as to correct, here and there, mis-statements or errors of interpretation, such as will creep in, even when the greatest care is taken to ensure accuracy.

In the course of my work I have received very material assistance from Dr. Sclater, and also from my friend Mr. D. Seth-Smith; both these gentlemen having furnished



me with spirit-specimens of species hitherto undescribed except from the skins. But for their help this paper would never have been written. I therefore take this opportunity of thanking them. Further, and finally, I am also indebted to Mr. F. E. Beddard for the loan of spirit-specimens from the prosectorium at the Zoological Gardens.

## II. PTERYLOGRAPHY.

Since, in some respects, pterylosis can most easily be studied in nestling birds, wherein the contour-feathers are just making their appearance, I have selected the nestling of *Colius affinis* for the following description. For the unexpected opportunity of so doing I have to thank Mr. D. Seth-Smith, who kindly presented two nestlings of that species to the Museum some little time since. These are here figured for the first time.

For the sake of clearness the pterylosis of *C. affinis* will be first described in detail without reference to other species: after which the points wherein these differ one from another will be stated.

*Pteryla capitis* (text-fig. 10, p. 231, *pt.cap.*).—The only adult examples of *C. affinis* which I have been able to examine I owe to the kindness of Mr. D. Seth-Smith, but unfortunately the pterylosis of the head-region was too much damaged for me to make out. From the examination of the nestlings, however, it would seem that the parietal apterion in this species is crescentic in shape, has the limbs of the crescent continued outwards into the ocular area, and is small in size.

The upper jaw in the nestlings, I may remark, is of a lemon-yellow colour, while the under jaw is black; the inside of the mouth is also black, but the tongue is of a bright orange colour.

The anterior nares are small oval apertures, piercing the membranous outer wall of the nasal chamber.

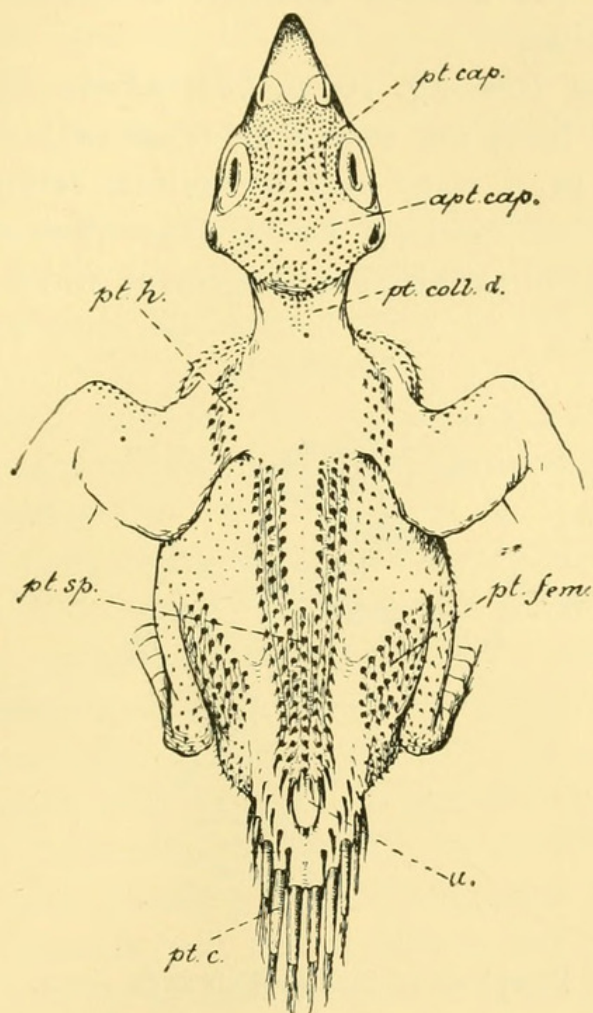
*Pt. colli dorsalis* (text-fig. 10, *pt.coll.d.*).—This tract is of moderate width and just behind the head ceases to closely



invest the neck, becoming supported by a median vertical fold of skin continued caudad into the

*Pt. spinalis* (text-fig. 10, *pt.sp.*).—This tract must be regarded as commencing at a point about level with a line

Text-fig. 10.



Dorsal aspect of *Colius affinis*, shewing the pterylae. The neck is deeply flexed so that the *pteryla colli* is almost entirely concealed. The anterior portion of the *pt. spinalis* is wanting. There are 10 rectrices. The tail, as distinct from the rectrices, is of abnormal length.

*pt. cap.* = pteryla capitis.

*pt. coll. d.* = pteryla colli dorsalis.

*pt. fem.* = pteryla femoralis.

*pt. h.* = pteryla humeralis.

*pt. sp.* = pteryla spinalis.

*pt. c.* = pteryla caudalis.

*apt. cap.* = apterion capitis.

*u.* = uropygium.

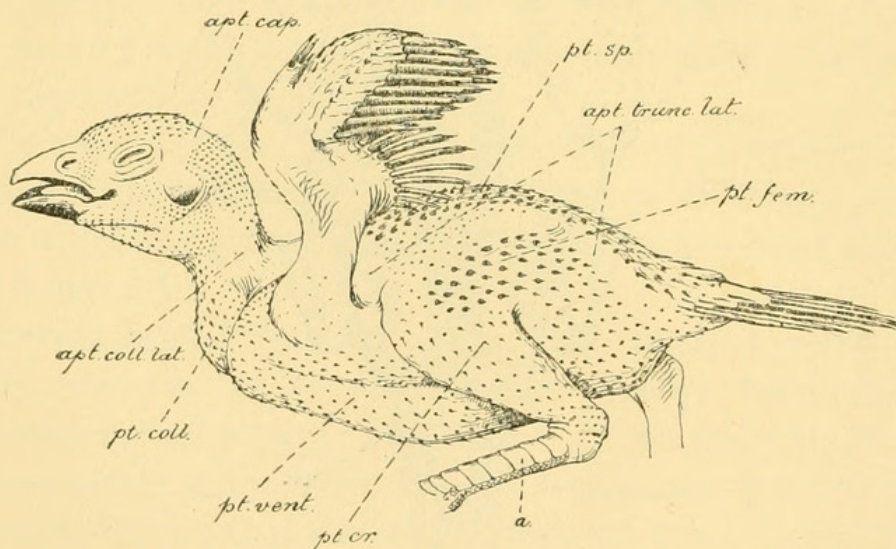
drawn across the body from the free ends of the humeral tract, and is thus separated from the *pt. colli dorsalis* by a wide apterion. From its commencement it forms a



tract of unusual width, and passing downwards on either side merges insensibly into the femoral tract, while further backwards, over the acetabular region, it suddenly tapers to be continued caudad in the form of a narrow band to the uropygium. In the mid-dorsal line the tract is marked by a narrow but distinct apterion terminating over the acetabular region.

*Pt. caudalis* (text-fig. 10, p. 231, *pt.c.*).—There are 10 rectrices, and these are somewhat remarkable in that they are inserted as it were into a conical, rather than into the normal semicircular base; thus they approximate towards the more primitive arrangement which obtained in *Archæopteryx*.

Text-fig. 11.

Pterylosis of *Colius affinis* (side view).

Side view of the same specimen as in fig. 10. Note the great width of *pt. ventralis*, which posteriorly joins the *pt. femoralis*.

*pt.coll.* = pteryla colli.

*pt.cr.* = pteryla cruralis.

*pt.sp.* = pteryla spinalis.

*pt.fem.* = pteryla femoralis.

*pt.vent.* = pteryla ventralis.

*apt.cap.* = apterion capitis.

*a.* = acrotarsium.

*apt.coll.lat.* = apterion colli lateralis.

*apt.trunc.lat.* = apterion trunci lateralis.

*Pt. colli ventralis* (text-fig. 11, *pt.coll.*).—This tract is ill-defined and sparsely feathered; at about the middle of the neck it divides, to pass, in the form of a broad band on either side, into the



*Pt. ventralis* (text-fig. 11, p. 232, *pt.vent.*).—This tract is not divisible into the usual short outer and long inner branches, but forms a band of great width, extending from the shoulder backwards to the cloaca, and meeting its fellow of the opposite side, so as very nearly to obliterate the *apt. mesogastrei*; indeed this is only traceable with difficulty.

*Pt. femoralis* (text-fig. 11, p. 232, *pt.fem.*).—This tract is of great width, confluent above with the *pt. spinalis*, and below with the *pt. ventralis* caudad of the thigh. Antero-ventrally it passes into the

*Pt. cruralis*.—This tract is unusually well developed, the tibial region of the leg being completely covered externally with weak feathers: the inner surface of the leg, however, is bare.

*Pt. humeralis* (text-fig. 10, p. 231, *pt.h.*).—Short and narrow, this tract presents no special characters of note.

*Pteryla alaris*:—

*Metacarpo-digital remiges or primaries*.—These are ten in number, the 10th being comparatively long. The outer primaries are particularly short, giving the expanded wing the much rounded appearance characteristic of birds which live among undergrowth and fly little.

*Cubital remiges or secondaries*.—These are eight in number, but the two innermost are greatly reduced in length, so much so as to be hardly distinguishable from their coverts. The wing is eutaxic, and this condition has probably been reached through the earlier diastataxic. Many of the Swifts have similarly become eutaxic.

*Tectrices*: upper surface:—

*T. majores*.—Those of the primaries are rather below the normal relative size. The carpal remex is long and downy, while its covert, of equal length, is pennaceous.

*T. mediæ*.—These present no characters demanding comment. The specimen having been in spirit I found it impossible to determine the overlap of this row and the remaining coverts.

*T. minores*.—There are three cubital rows of these coverts, but neither this series nor the preceding occur on the manus.



*T. marginales*.—These afford no facts of interest, except that they are throughout relatively long feathers, not forming a series of small, closely overlapping feathers, as in so many birds.

*Tectrices*: under surface :—

The *T. majores* appear to be wanting, but the *T. mediæ* are represented by small weak feathers. In addition to this row the under surface of the wing is very sparsely covered by a few straggling feathers representing the minor and marginal coverts. The latter in their shortness contrast with the same feathers in the Passeres, where the most preaxial rows are drawn out into long plumes masking the whole of the fleshy portion of the forearm.

*Plumulæ* or *down-feathers* are wanting.

The *Uropygium* is tufted.

The *Rhamphotheca* is Finch-like in shape and has the tomium entire. The nostrils are circular, have a slightly swollen rim, and are placed close to the feathers of the lores.

The *Podotheca*.—The acrotarsium (text-fig. 11, p. 232) is covered by five large scutes, which fail to meet in the middle line behind. The gap—along the planta—is filled in by soft skin covered with small granulations. The acropodium is peculiar, the back of each toe being covered with a number of small scutes, all of equal size.

In all the spirit-specimens examined, the hallux occupies the normal position, its under surface being apposed to that of D. II.: without difficulty, however, it can be brought round to the pamprodactylous position.

*Claws*.—On the toes these are moderately long, laterally compressed and hook-shaped; they are of equal size on D. II.–IV., but that of the hallux is slightly smaller than the rest. The pollex of the nestling bears the vestige of a claw, but this is entirely lost in the adult.

*Neossoptiles*.—The nestling-down plumage is vestigial, being represented only by a few minute rami borne on the tips of the contour-feathers.

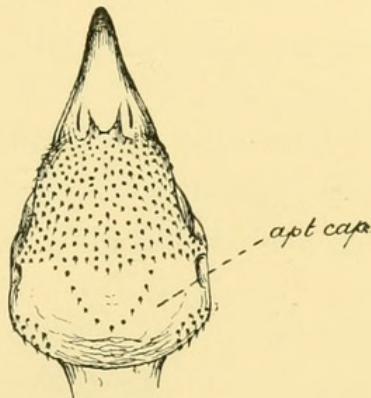


*The Pterylosis of some other Species of Colius compared with that of C. affinis.*

The differences in the matter of pterylosis between *C. affinis* and *C. striatus*, *C. capensis*, *C. castanotus*, and *C. erythromelon* appear to be very small, and are confined almost entirely to the *pt. capitis*.

*C. striatus* (text-fig. 12).—The parietal apterion of this species differs from that of the other species herein described in that it is larger and has assumed an oval shape, laterally passing, as before, into the ocular area; while from the anterior margin of this area there runs backwards a horse-shoe-shaped loop.

Text-fig. 12.



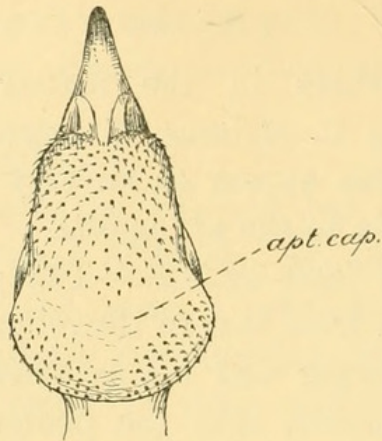
Dorsal aspect of the head of *Colius striatus*, shewing the parietal apterion.

*apt.cap.* = apterion capitis.

*C. erythromelon* (text-fig. 13, p. 236).—The *pt. capitis* differs conspicuously from that of *P. affinis* (text-fig. 10, p. 231) in the great size of the parietal apterion and the larger size of the ocular area, which runs into the parietal area on either side. The parietal apterion takes the form of a broad T-shaped space, the limbs thereof narrowing immediately above the auricular aperture and passing insensibly into the ocular area. The anterior boundary of the space does not extend beyond the level of the posterior border of the orbit; while the median stem of the "T" runs downwards to the occiput, tapering slightly to its base.



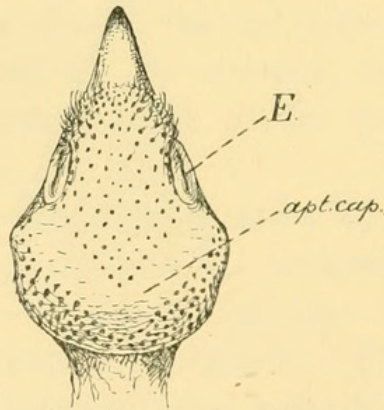
Text-fig. 13.



Dorsal aspect of the head of *Colius erythromelon*, shewing the parietal apterion.

*apt. cap.* = apterion capitis.

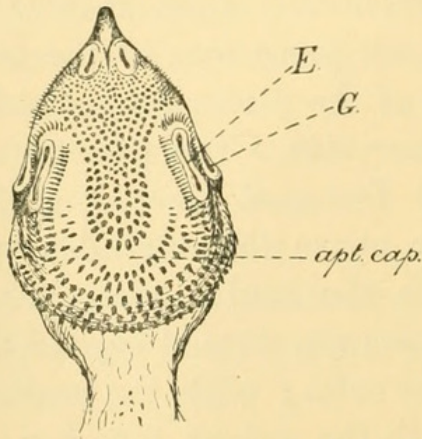
Text-fig. 14.



Dorsal aspect of the head of *Colius capensis*, shewing the parietal apterion.

*apt. cap.* = apterion capitis. *E.* = Eye.

Text-fig. 15.



Dorsal aspect of the head of *Cypselus apus*, shewing the parietal apterion (see p. 249).

*apt. cap.* = apterion capitis. *E.* = Eye. *G.* = Gape.



*C. capensis* (text-fig. 14, p. 236). The parietal apterion is V-shaped, and extends backwards, on either side, from the eye to terminate in a pointed apex above the occipital region. A small apterion surrounding the eyelids may be traced backwards into the limbs of the V-shaped parietal apterion. The malar and ramal areas and the region round the aperture of the ear are densely feathered. The inter-ramal area is bounded, on either side, by a narrow apterion.

### III. MYOLOGY, SYRINX, AND INTESTINAL CONVOLUTIONS.

I have but little that is new to add on the subject of the Myology of the Colies, in so far as systematic work is concerned.

Garrod (6), it may be remembered, shewed that the ambiens was wanting, that the femoro-caudal was well developed, but had no accessory head, and that the semitendinosus and its accessory head were both fairly developed. Thus the muscle-formula, as laid down by Garrod, is A . XY. The *tensor fasciæ* of the thigh does not in any way overlap the biceps.

In the plantar tendons *Colius*, according to Garrod, "exactly resembles the feeble-footed Alcedinidæ, and hardly differs from the Coraciidæ, Meropidæ, and Caprimulgidæ," while, according to Dr. Gadow, these tendons agree with his type V. *a*—where the tendon of the *flexor longus hallucis* fuses with the *flexor perforans digitorum* along its fibular side, the united tendons split up, successively, into four, running first to the hallux, and lastly to D. IV. Therefore, according to this, *Colius* agrees with *Buceros* and *Cypselus*.

My own dissections of these tendons seem, however, to shew that neither of the interpretations just given can be correct, inasmuch as a careful examination of the fused tendons shews that the *flexor longus hallucis* never completely fuses with the deeper tendon: the line of junction is always visible. Further, this tendon, the *fl. long. hall.*, splits up into two, one branch going to the hallux and one to D. II. (text-fig. 22, p. 251), while the *flex. perf. digit.* splits



up to serve D. III. IV. This arrangement so far appears to be unique ; yet it has probably been derived from an earlier and more primitive condition, shared in common with the Swifts and Humming-birds, a possibility which is discussed on p. 250. I would remark here, however, that, in the Swifts, as in the Colies, though the two tendons appear to fuse after the ankle-joint is passed, they, in reality, still shew traces of their originally separate condition. And from this it is clear that in the Swifts the *flexor longus hallucis* serves digits I. and IV., while II. and III. are served by the *fl. perf. digitorum*. This point is of no small interest and importance, as will be shown later (p. 252).

With regard to the wing-muscles. The *deltoides propatagialis* has the *brevis* portion large, fleshy, and continued downwards to the level of the *extensor carpi radialis* before becoming tendinous, the tendon running obliquely backwards after the fashion seen in the Passerine wing, but quickly becoming lost in the fascia of the forearm. The *longus* portion is given off unusually low down—from the middle of the belly of the *brevis* portion—and in the form of a slender muscular slip, which quickly gives place to tendon. The origin of this muscle is from the far end of the clavicle.

*Biceps brachialis*.—This is thick and fleshy, arising from the acrocoracoid laterad of the articulation for the furcula, and joins the humerus by one broad sheet of tendon running obliquely from acrocoracoid to humerus.

*Biceps propatagialis*.—Is represented by a short, thick, fleshy band or slip, a fact which is to be reckoned among the many peculiarities of the Colies.

*Deltoides major* (text-fig. 16, p. 239).—These muscles seem to present a very unspecialized condition, the *longus* and *brevis* portions being confluent and extending the whole way down the humeral shaft. *Pars longa* arises in the form of a broad fleshy band from the clavicle, extending nearly half-way down the limb, and from the scapula immediately caudad of the glenoid cavity for the humerus. The *brevis* portion arises from the *os humeri scapulare* and from the rim of humeral cotylus of the coracoid and scapula, and is attached along the whole preaxial border of the humeral shaft.

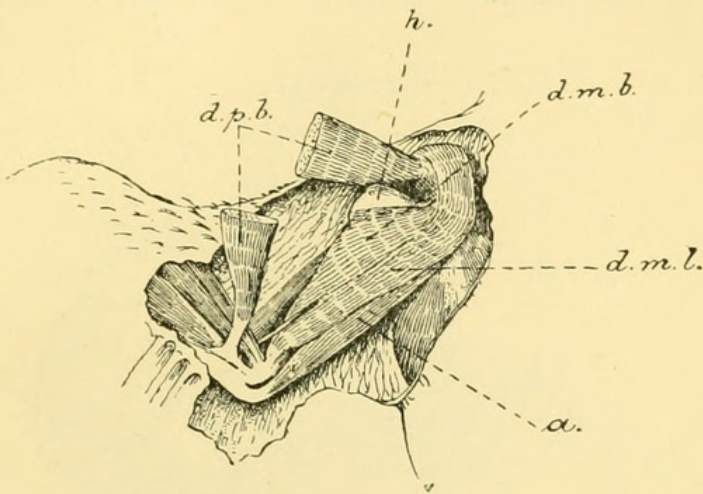


In *Acanthidositta*—one of the “Tracheophone” Passeres—the *pars longa* has separate furcular and scapular heads as I have recently shown elsewhere (13), and it is evident that the heads have been derived by the splitting-up of an origin, such as that seen in *Colius*.

Besides the Hornbills and the Macrochires, the Colies are, as Mr. Beddard has remarked, the only flying-birds in which the *latissimus dorsi metapatagialis* is absent.

The *syrinx* is of the typical tracheo-bronchial type.

Text-fig. 16.



Wing-muscles of *Colius*, to shew the confluent condition of the *pars longa* and *brevis* of the deltoideus major.

*d.m.b.* = deltoideus major pars brevis.

*d.m.l.* = deltoideus major pars longus.

*d.p.b.* = deltoideus propatagialis brevis.

*a.* = anconeus.

*h.* = humerus.

In the matter of the intestinal tract, Dr. Chalmers Mitchell (10) has shown that the Colies stand alone in the extreme shortness of the gut and the great width of its lumen—a modification which he attributes to the frugivorous habits of these birds. The duodenum is of great width. Meckel's tract similarly forms but a simple loop, bearing a small diverticulum; while the rectum is short and wide. The cæca are altogether wanting.

In the general conformation of the tract, *Colius*, as Dr. Mitchell shews, closely agrees with the *Cypseli*, both being apocentricities of the archicentric Caprimulgine type.



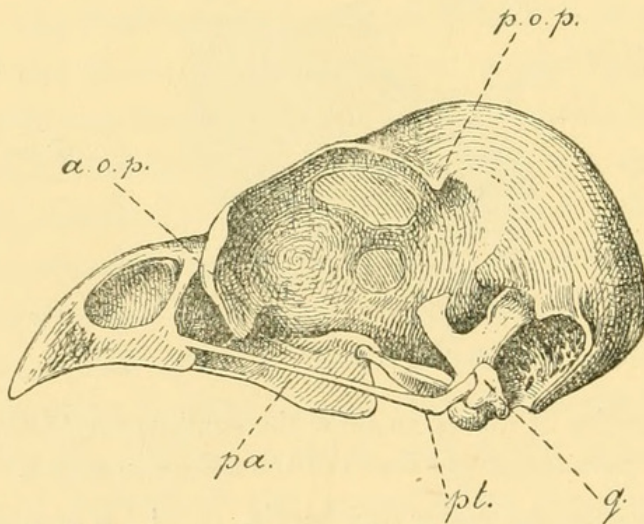
## IV. OSTEOLOGY.

Osteologically, the Colies present many peculiarities which, so far as the adult skeleton is concerned, make this group appear more isolated than is really the case; and this is especially true of the skull.

*The Skull of the Adult.*

*The Skull* (text-fig. 17).—The most conspicuous feature of the skull, in the adult, is the spherical shape of the cranium, the feeble development of the postorbital process (which may be described as obsolete), the vestigial lachrymal, and the

Text-fig. 17.

Lateral aspect of the skull of *Colius capensis*.  $\times 2$ .

*a.o.p.* = antorbital plate.

*p.o.p.* = postorbital process.

*pa.* = palatine.

*pt.* = pterygoid.

*q.* = quadrate.

palate (which is indirectly desmognathous); while the inter-orbital septum is complete and the nares are divided by a bony septum.

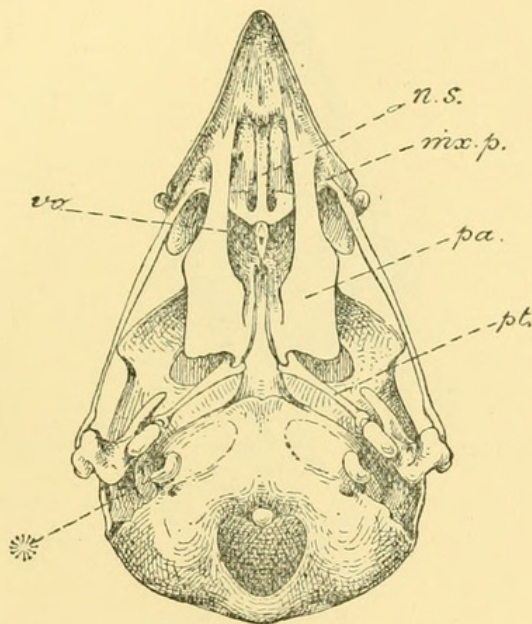
The tympanic cavity is relatively small, oval, and rather shallow. The lateral wing of the exoccipital, which forms the posterior boundary of this cavity, rises upwards to pass insensibly into the *processus articularis squamosi*, but there is no squamosal prominence. The *recessus tympanicus anterior*, which opens into this cavity, is small; while the



*recessus tympanicus posterior* and *superior* are only feebly developed. In this region of the skull *Colius* resembles *Cypselus*.

The palate (text-fig. 18) has never been properly interpreted. Generally it is described as directly desmognathous; but this is not the case. As a matter of fact, the maxillo-palatines are extremely reduced—so much so, that they cannot be exposed without first carefully removing the underlying palatines. This done, it becomes manifest that

Text-fig. 18.



Ventral aspect of the same skull, to shew the arrangement of the palatine bones.  $\times 2$ . The asterisk marks the articular surface for the lower jaw (p. 243).

*mx.p.* = maxillo palatine process.

*n.s.* = nasal septum.

*pa.* = palatine.

*vo.* = vomer.

*pt.* = pterygoid.

the desmognathism is due to the inflation of the inferior border of the nasal septum and the ossification of the cartilage of the floor of the vestibulum, which forms two descending wings expanding, laterally, to fuse with the vestigial maxillo-palatine plate (text-fig. 19, p. 242).

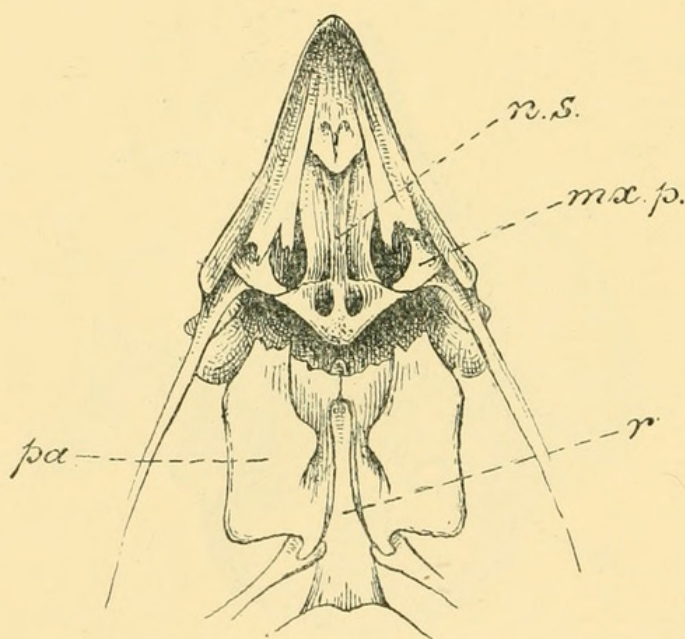
Murie (11), in describing the palate of *Colius leucotis*, wrote: "As respects the presence of a vomer, there is



apparently a short one, tapering rather than abruptly truncate anteriorly, and not visibly deeply cleft behind." But Garrod (6), in describing the skull of *C. castanotus*, stated that, after careful maceration, he was unable to find a vomer. I have carefully dissected the skulls of *C. capensis* and *C. affinis* (three of the former), and find that the vomer is present, but only in the form of a very small nodule of bone (text-fig. 18, p. 241).

The *palatines* posteriorly expand into broad, oblong plates,

Text-fig. 19.



Anterior portion of the ventral aspect of the same skull, further enlarged and dissected to display clearly the relation of the maxillo-palatines to the nasal septum.

*mx.p.* = maxillo-palatine process.

*n.s.* = nasal septum.

*pa.* = palatine.

*r.* = rostrum.

and do not meet in the middle line beneath the parasphenoidal rostrum, in this particular recalling the skull of the Touracos.

The *pterygoids* are moderately long, round, and slender rods articulating with the palatines by means of a well-developed joint.

The *quadrate* has the orbital and squamosal limbs subequal; while the articular surface for the quadrato-jugal bar



is hollowed out of a laterally projecting spur. The external mandibular condyle is elongate and directed obliquely outwards; while the internal condyle is also elongate and runs parallel with the long axis of the pterygoid.

Basipterygoid processes are wanting.

With regard to the articulation of the lower jaw, a curious feature is noticeable in the skull of *Colius* that I do not remember to have seen elsewhere. This is the development of a distinct elliptical glenoid surface, for the articulation of the internal angular process of the lower jaw. It is borne on the antero-inferior angle of the lateral occipital wing, mesiad, and slightly caudad, of the internal mandibular condyle of the quadrate (text-fig. 18, \*, p. 241).

The *lachrymal* is reduced to a short tear-shaped rod, fused with the superior angle of the antorbital plate; yet Murie described a lachrymal in *C. leucotis*, which was "nearly perpendicular, its inferior limb spongy . . .," but there was no "backward upper orbital process" nor any *os crochu*. Some mistake has probably been made here, as also in the statement that the beak joined the skull by a nasal hinge.

The antorbital plate is large and quadrangular. The superior external angle of this plate projects laterad of the nasals, and represents the lachrymal, which has fused with the plate.

The mandible has a moderately long symphysis, a large lateral vacuity, and a short internal angular process, but is abruptly truncated posteriorly.

*The hyoid*.—The *basihyal* is completely ossified and arrow-headed in shape, being pointed in front and having the posterior angles produced backwards into a pair of spurs answering to the ceratohyals; further, the centre of the basihyal is perforated by a fan-shaped fenestra.

The *basibranchial* is elongated, laterally compressed, keeled, and produced backwards into a cartilaginous style—the 2nd basibranchial (urohyal). The *ceratobranchials* are relatively short, and so also are the epibranchials. These two rods—the cerato- and epibranchials—are subequal in length.



*The Skull of the Nestling* (text-fig. 20).

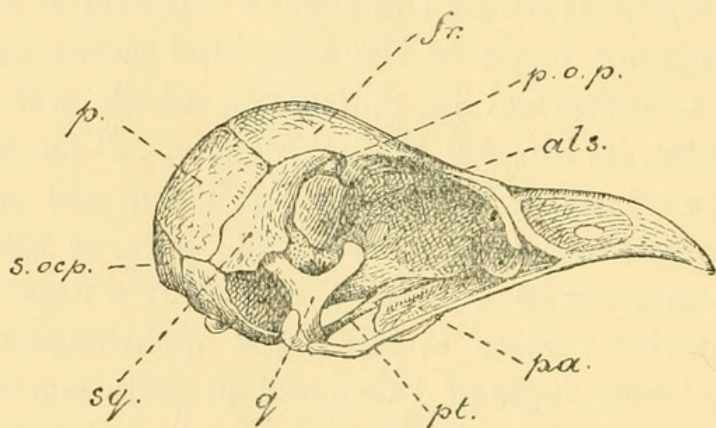
For an opportunity of studying the skull of the nestling Coly, I am indebted to the kindness of Mr. D. Seth-Smith, who furnished me with three nestlings of *C. affinis*.

*The Cartilage-bones.*

The *basioccipital* is short, rather narrow, and sharply cut off in front from the basitemporal plate.

The *exoccipital*, or lateral occipital, in these skulls is not yet completely ossified, the tympanic ring being cartilaginous.

Text-fig. 20.



Lateral aspect of the skull of nestling *Colius affinis*, to shew the form and relations of the squamosal.

*als.* = alisphenoid.

*fr.* = frontal.

*p.* = parietal.

*p.o.p.* = postorbital process.

*pt.* = pterygoid.

*pa.* = palatine.

*q.* = quadrate.

*s.ocp.* = supraoccipital.

*sq.* = squamosal.

Only by means of its extreme supero-internal angle does it come into contact with the parietal; and in this it differs from that of the Cypselidæ, wherein almost the whole dorsal border is apposed to the parietal.

The *supraoccipital* is paired, and extends upwards for a considerable distance to form, with its fellow, a full rounded contour.

The *pro-*, *epi-*, and *opisthotic* bones are now completely



concealed from the outside ; and so also is the *basisphenoid*, which is underfloored by the basitemporal plate.

The *alisphenoid* is at present unossified, and forms a large cartilaginous plate extending outwardly to join the squamosal, terminating immediately above and in front of the free end of this element to form the postorbital process, which appears to be represented by the *alisphenoid* alone.

The *orbito-sphenoid* and *mesethmoid* are still cartilaginous, while the quadrate differs in no way from that of the adult.

#### *The Membrane-bones.*

The *parietal* is roughly quadrangular in form, but has the inferior border slightly hollowed to receive the supra-occipital.

The *frontal* has a straight posterior border, and immediately in front of the squamosal sends down a narrow tongue to the orbito-sphenoid. In the supraorbital region it is reduced to a very narrow band, and finally terminates as usual under the nasals.

The *squamosal* takes the form of a cone, having its apex slightly bent forwards ; the inner half of its base rests upon the tympanic ring of the lateral occipital, while its outer half forms the margin of the tympanic cavity. Superiorly it extends far beyond the parietal, forming the outer boundary of the frontal and terminating at the base of the postorbital process.

The *lachrymal* is represented here by a slender rod of bone running parallel to the descending process of the nasal, and sending backwards a long delicate supraorbital rod of cartilage along the frontal. In later life the lachrymal fuses completely with the antorbital plate and frontal.

The *premaxilla* has moderately long palatine processes.

The *maxilla* is small, while its palatine processes are greatly reduced, forming an "oat"-shaped plate of bone concealed from below by the palatine rod. These processes are, however, relatively larger and more distinct than in the adult.

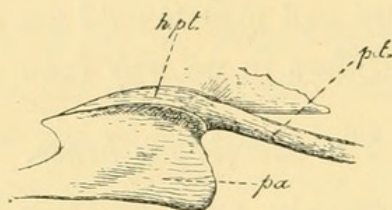
The *palatine* differs from that of the adult in that its mesial



border has not yet received the addition of the hemipterygoid which is made to it later.

The *pterygoid* is rod-shaped and is continued forward along the whole length of the mesial rostral border of the palatine, terminating in a point (text-fig. 21). Thus at present there

Text-fig. 21.



Hemipterygoid region of the pterygoid of the same skull (text-fig. 18).

*pa.* = palatine.      *pt.* = pterygoid.      *h.pt.* = hemipterygoid.

is no trace of the segmentation resulting in the formation of the temporary hemipterygoid, the ultimate fusion of which takes place with the palatine; while this element and the pterygoid come to articulate by a joint (figs. 17, 18, 19).

### *The Vertebral Column and Ribs.*

All the presynsacral vertebræ are free and heterocœlous. The lower cervicals bear very small hypapophyses; while 1–4 of the dorsals are similarly protected, though these are relatively larger than in the cervicals. The last rib-bearing dorsal is included in the synsacrum, which is made up of 12 vertebræ. The dorsi-lateral processes of the sacra are wanting. There are 7 free caudals, including the pygostyle, which is peculiar. Superiorly it is expanded to form a large pentagonal plate, which sends forward a long blunt spine, apparently representing an hypertrophied hypapophysis.

There are 7 pairs of free ribs, of which all but the last two bear uncinæ processes. Of these ribs, however, only four pairs articulate with the sternum, though the sternal segments of the last three pairs are of great length.

### *The Sternum and Shoulder-girdle.*

The sternum of the Colies resembles that of the Capitonidæ in that the posterior border of the sternal plate is deeply



notched by two pairs of notches. It differs, however, in that the keel is hollowed along its anterior border, leaving a long *spina externa*; while in the Capitonidæ, as in so many Coraciiformes, the keel is continued forwards to a point corresponding with the level of the free end of the *spina sterni*. In the Colies, as among the majority of the Coraciiform types, the ribs articulate with the outer border of the anterior lateral process. There is no *spina interna*. The coracoids do not cross one another, have long shafts broad at the base, and lack the procoracoid.

In the great depth of the carina *C. macrurus* is remarkable among the Colies; while in this species also the *posterior lateral* and *intermediate processes* terminate in unusually large hastate expansions.

The *furcula* is U-shaped and has a small *hypocleideum*. So far as I can make out, except in *C. macrurus*, it is slender; but in the last-named species its rami are broad and twisted upon themselves. The free end of the furcula is expanded, and, being applied to the acromion of the scapula and the acrocoracoid, shuts in the *foramen triosseum*.

The *scapula* is long, slender, and scimitar-shaped.

#### *The Pelvic Girdle.*

The pelvic girdle is of moderate length, and has the preacetabular region of the ilium very narrow, pointed, and applied, low down, to the base of the neural plate of the synsacrum: the postacetabular region is wide, the dorsal plane inflated, curiously transparent, and extremely broad, the transverse processes of the synsacrum having become suppressed.

The ischium is narrow and produced backwards into a long downwardly directed pointed plate, which affords attachment to, but does not fuse with, the pubis.

The pubis is long, slender, and rod-like, and produced backwards beyond the level of the ischium.

The *fovea lumbalis* is small; while the *fovea ischiadica* and *pudendalis* are confluent.



*The Pectoral Limb.*

The pectoral limb of the Colies presents no very marked peculiarities. It is non-pneumatic, and has the humerus and manus subequal and longer than the forearm. The humerus has the *crista superior* triangular in shape, an unusually small *fossa subtrochanterica*, a feebly marked *sulcus transversus*, and a moderately deep *incisura capitis*. There are no ectepicondylar or entepicondylar tubercles, nor is there any tubercle on the palmar surface for the attachment of the *extensor metacarpi ulnaris*.

The ulna has but a feebly developed olecranon process, and the radius is straight.

The manus is moderately long, has the Mc. III. strongly bowed, while the Mc. II. develops a small intermetacarpal plate. The pollex shews a vestige of an ungual phalanx.

*The Pelvic Limb.*

The femur, which is moderately long and slender, presents no characters of importance in the present connexion.

The tibio-tarsus is long and slender, and has the entonemial crest well developed and produced upwards to a rather considerable extent. The fibula is short. The condyles at the lower end of the shaft are laterally compressed; the inner condyle is conspicuously the larger of the two, and separated from its fellow by a deep intercondylar gorge, which is crossed above by an ossified extensor bridge.

The tarso-metatarsus has the trochleæ placed all in the same horizontal plane, the mesotrochlea being the largest and projecting slightly beyond the level of its neighbour on either side. Trochlea II. is much reduced, forming a small rounded knob with a faint median groove. In this arrangement of the condyles the tarso-metatarsus of *Colius* differs conspicuously from that which obtains in *Cypselus*, a fact which is all the more peculiar since both are pamprodactylous.

The hypotarsus is compound, taking the form of a flat



plate perforated by a single foramen. The shaft is flattened antero-posteriorly, and has the outer border produced into a sharp edge, which, as it approaches the hypotarsus, widens out into a thin flange pierced by a small fenestra.

#### V. SUMMARY.

It must be evident, to those who have read the earlier sections of this paper, that the question of the systematic position of the Colies is not one that can be easily or over-confidently answered. But all the available evidence tends to shew that the nearest allies of this group are the *Cypseli*; though, as will be seen, in many points the two groups do not agree very closely, and this more especially with regard to the skeleton.

In the matter of their pterylosis the *Colii* and *Cypseli* shew a remarkable and significant likeness, and this is most apparent, perhaps, when nestlings are compared. In the present paper these comparisons have been made between *Colius affinis* and *Cypselus apus*.

In both groups the *pteryla capitis* is interrupted by an apterion; but while this apterion in *Colius* is of considerable size, and extends outwards to join the ocular area *behind* the eye, in *Cypselus apus* (for example) it is very narrow and joins the ocular area in *front* of the eye. Moreover, the feathers are arranged differently in the two types. In *Cypselus apus* there is a sharply defined, tongue-shaped, frontal area, wherein the feathers are closely set, contrasting with the more sparsely feathered parietal area.

In both the *Colii* and *Cypseli* the spinal tract is interrupted by a long narrow apterion, while the pterylæ are of unusual width throughout the body, thus reducing the apteria to a minimum. The difference in the form of the wing is entirely due to the difference in habit between the two groups, the one being of a sedentary habit and flying little, the other extremely active and depending for sustenance on insects caught in mid-air.

The myology of the two groups, when compared in this connexion, is less convincing. A comparison of the wing-



muscles, for example, reveals nothing, so far as the question of relationship between the two groups is concerned; inasmuch as the *Cypseli* have undergone very profound modifications with regard to the wing—a degree of extreme specialization which has obliterated all the more normal, more primitive characters.

In the muscles of the thigh the *Cypseli* shew no less extreme modifications, or, as Dr. Chalmers Mitchell has it, apocentricity.

The plantar tendons of these two groups appear, at first sight, to be no more helpful in this connexion, inasmuch as, so far as the matter has been investigated, three very distinct combinations of these tendons have been brought to light, combinations represented respectively by the Colies, Swifts, and Humming-birds. If correctly interpreted they shew, however, that they must be regarded as so many modifications of a common and primitive plan, wherein the *flexor longus hallucis* split up to serve each of the four toes, while the *flexor perforans digitorum* was restricted in its ramifications to digits II., III., IV., the two tendons being unconnected by a vinculum. Such an arrangement, among living birds, has been found, so far, only in *Heliornis*, an aberrant Gruine bird. It would be beside the purpose of the present paper to enter into a discussion of the evolution of all the known types of plantar tendons, but we may gain a most instructive insight into the matter by the tendons in the Colies and the forms therewith associated—the Swifts and Humming-birds.

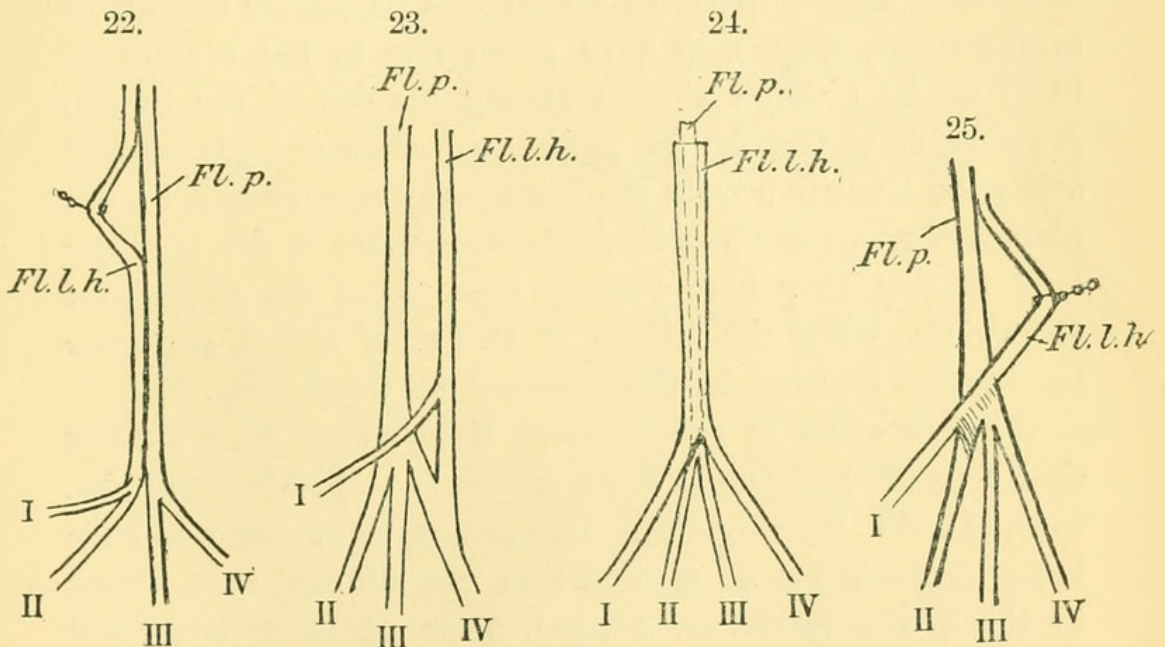
Curiously enough, the Humming-birds approach nearest to this primitive type, though even there a considerable degree of specialization has continued to mask the evidence of the earlier condition of things \*.

\* Before proceeding further it would be well to remark that the description and figure of the plantar tendons of the Humming-birds given in Prof. Newton's 'Dictionary of Birds' by Dr. Gadow are incorrect. This fact was pointed out by Mr. F. A. Lucas in 'The Ibis,' 1895 (8), and appended to this correction will be found an acknowledgment by Dr. Gadow (5) of the accuracy of Mr. Lucas's remarks and the figure accompanying them. I have now, by dissection, been able to further confirm Mr. Lucas.



In the Humming-birds, then, the *flexor longus hallucis*, by means of a broad sheet of delicate tendinous strands, joins the anterior, *flexor perforans*, tendon at the level where it branches (text-fig. 25). This sheet undoubtedly represents all that remains of four separate and independent branches. The fibres of this sheet, which are attached to the tendon to D. II., are furthermore, it is to be noted, rather more strongly developed than those running to the other branches. Now in *Macropteryx* (one of the Swifts) the plantar tendons appear to differ markedly from those of all other Cypselidæ in that

Text-figs. 22-25.



Diagrammatic figures of the plantar tendons of *Colius* (22), *Macropteryx* (23), *Cypselus* (24), and a Humming-bird (25).

I., II., III., IV.=Tendons to digits I.-IV.

*Fl.p.* =Flexor perforans.

*Fl.l.h.*=Flexor longus hallucis.

the *flexor longus hallucis* runs, as a separate tendon, directly into that branch of the *flexor perforans* which runs to D. IV.; it sends off, however, above the point where the three tendons of the *f. perforans* diverge, a branch to the hallux. A reference to the accompanying diagrams (text-figs. 22-25) will shew that if this branch to the hallux were connected by



strands of tendons to D. II. & III. we should have the same arrangement as that which obtains in the Humming-birds, except that the strongest strand would be that to D. IV.

The peculiar arrangement of these tendons in the remainder of the Swifts appears to have been derived by a further modification of the plan seen in *Macropteryx* (text-fig. 23, p. 251). Thus, from the tarsal region downwards the two tendons have fused, while at the base of the toes a further change has taken place. The *flexor perforans* branch to D. IV. as seen in *Macropteryx* has disappeared, so that this tendon now supplies only D. II.-III., while D. I. & IV. are supplied by the *fl. longus hallucis*. Thus it is clear that the plantar tendons of *Macropteryx*, or rather this particular method of arrangement, may well have given rise to the system of fused tendons which obtains among the rest of the Swifts. A reference to text-fig. 24, p. 251, will shew at a glance how easily the transition from the one to the other is made, for the plantar tendons of *Cypselus* differ from those of *Macropteryx* only in that they have become fused from the ankle-joint downwards, while the tendon of D. IV. of the *fl. perforans* has become replaced by the tendon from the *fl. long. hall.*

We now come to the Colies. Here, as we have already shown (p. 237), *fl. longus hallucis* runs to D. I.-II., *fl. perf. dig.* to D. III.-IV. (text-fig. 22). This arrangement may well have been derived by a modification resembling that found in the Swifts (text-figs. 23, 24), a strong connecting-band from the tendon to the hallux—the relic of branch II. of the originally complete *fl. long. hallucis*—grafting itself on to the tendon of the *fl. perforans* to D. II., and ultimately causing the severance of this branch with its original stem, and its incorporation with the *fl. long. hallucis*, this connecting band answering to that shown in text-fig. 23 running to D. IV. In other words, as *Cypselus* has preserved tendons I. & IV. of the original complete set, so *Colius* has kept I. & II.

Thus, then, the apparent differences in the plan of the plantar tendons of the Colies, Swifts, and Humming-birds are all, in reality, but modifications of a common type. This type is sufficiently distinct from all other known types



to render it tolerably certain that the birds in which it is found must be more or less closely related.

In the convolutions of the intestines the Colies, as Dr. Chalmers Mitchell has shown, undoubtedly agree very nearly with the *Cypseli*, and this in spite of very extensive specialization in adaptation to a frugivorous diet.

So far as the known facts go, there is really little in the skeleton of the Colies to connect them with the *Cypseli*; and a study of nestling skeletons of both groups will undoubtedly add to the scanty evidence so far to hand. But the Colies are *indirectly* desmognathous, not *directly* so as is commonly stated; nor is the vomer absent, though reduced to the merest vestige.

Inasmuch as the Colies are undoubtedly related to the *Cypseli*, they are also related, though more remotely, to the *Caprimulgi*, since this last group represents the stock from which the two former have descended.

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