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 I.—On the Systematic Position of Zeledonia coronata, with some Observations on the Position of the Turdidæ. By W. P. PYCRAFT, F.Z.S., A.L.S., &c.

(Plates I. & II.)

I. INTRODUCTORY.

Some time ago Dr. R. Bowdler Sharpe placed in my hands a spirit-specimen of *Zeledonia coronata*, requesting me to endeavour to determine, so far as was possible, the true position of that bird in the system. It was procured for the purpose of this investigation by Dr. F. DuCane Godman, F.R.S., and to him and to Dr. Sharpe I am greatly indebted for many valuable suggestions. Furthermore, I have to record my hearty thanks to Dr. P. L. Sclater, F.R.S., who has throughout taken great interest in the progress of the work and has helped me in many ways.

Zeledonia coronata (Plate I.) is a small bird presenting many very puzzling characteristics. It was first described in 1888 by Prof. Robert Ridgway *, who, however, on account of its

curious appearance, confined himself to a diagnosis of the plumage. Concerning the question of affinity, he remarked: "This remarkable new genus is so peculiar in its characters that I am in much doubt as to which family it belongs. The very short rounded wing with long first primary, full and closely appressed loral feathers, and soft texture of the plumage in general strongly suggest the genus Scytalopus, and I was at first inclined to refer it to the Pteroptochidæ, to which Scytalopus belongs; the coloration of the head strongly suggests that of Basileuterus coronatus, and the loosely webbed rectrices with finely acuminate points, as well as the loosely webbed remiges, slender bill, and long-booted tarsi with sharp posterior edge, remind me of Catharus gracilirostris..... The general resemblance to the genus Xenicus, of New Zealand, is very remarkable, X. longipes being of nearly the same size and proportions..... Xenicus is now referred to the Clamatores; but whether Zeledonia is a related form belonging to the same suborder or an aberrant Oscinine type, cannot, probably, be determined without examination of its anatomy."

Soon after this account was written, skeletons of Zeledonia coronata and Catharus gracilirostris were submitted by Prof. Ridgway to Mr. F. A. Lucas. The result of the investigations of that gentleman * seemed to shew that Zeledonia and Catharus were not related. Further particulars were promised, but Mr. Lucas is a very busy man and doubtless has never had an opportunity of completing his study of this very interesting bird.

A careful comparison of *Zeledonia* with *Basileuterus*, *Xenicus*, and *Scytalopus* made by Messrs. Salvin and Godman⁺ only served to shew that no relationship with any of these forms was probable, and the conclusion was arrived at that " for the present the position of this genus must remain in abeyance pending a full examination of its internal structure."

Here, then, the matter rested until the present writer reopened the question. In a short note, published in the

- * Proc. U.S. Nat. Mus. xi. p. 538 (footnote).
- † Biologia Centr.-Amer., Aves, vol. ii. 1888-97, p. 248.

'Bulletin of the British Ornithologists' Club'*, he was enabled to state definitely that *Zeledonia* could have nothing to do with *Xenicus*, inasmuch as it had a typical Oscinine syrinx. Acting on this, Dr. Sharpe, in vol. iv. (p. 183) of his 'Hand-list,' placed *Zeledonia* in the subfamily Sialiinæ, which contains the genera *Catharus*, *Zeledonia*, *Sialia*, *Grandala*, and *Ridgwayia*.

It was to decide, if possible, whether the position assigned to Zeledonia by Dr. Sharpe, on the evidence of external characters, was at least approximately correct that I was asked to continue the work which I had commenced in 1900. Although, as the sequel will shew, I have been able to confirm Dr. Sharpe's decision in this matter, several points still remain to be settled, while a great number of new questions have arisen. All of these, unfortunately, must for the present remain in abeyance, partly on account of the pressure of other work and partly from lack of material. The latter circumstance has hampered me much during the preparation of the present paper—how much may perhaps be gathered from the fact that I had but a single damaged specimen in spirits and a few skins of Zeledonia, and two skeletons of Sialia. Grandala, Ridgwayia, and Catharus (the remaining genera of the subfamily in which Zeledonia has been placed) I have only been able to study from skins, and these have proved to be of no help whatever in the matter.

II. PTERYLOGRAPHY.

Pteryla capitis (text-fig. 1, pt.cap., p. 4).—This is interrupted only by a small bare space (apt.cap.), arising above the external aperture of the ear, slightly above the level of the posterior canthus of the eye, and passing backwards and downwards and finally forwards to end below this aperture at the base of the mandible. The interramal space is feebly developed.

At the gape are a few short weak rictal bristles.

* Bull. B. O. C. xi. p. 12 (1900).

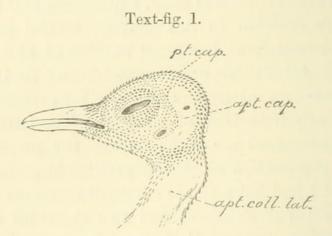
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The nostrils are covered by a membranous operculum having the form of a triangle. So far this operculum appears to be unique.

Pt. colli dorsalis (text-fig. 2, pt.coll.d., p. 5).—This tract is very narrow and passes down into the

Pt. spinalis (text-fig. 2, pt.sp., p. 5).—The only feature of interest about this tract is the broad, more or less shieldshaped expansion which occurs over the pre-iliac (lumbar) region. This contracts again in the space bounded by the antitrochanters of the pelvis, and passes down from this point to the uropygium as a very narrow band.



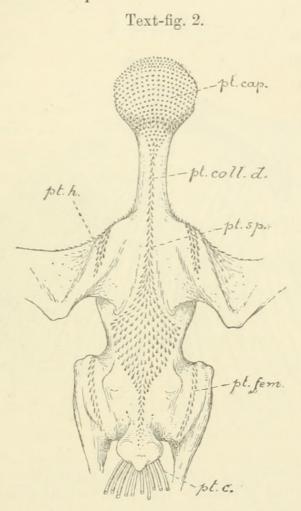
Head of Zeledonia coronata, shewing the form of the pteryla capitis and the apterion extending from the base of the lower jaw upwards. *apt.cap.*=apterion capitis; *apt.coll.lat.*=apterion colli laterale; *pt.cap.*=pteryla capitis.

Pt. caudalis (text-fig. 2, pt.c., p. 5). — There are 10 rectrices. The shafts of these feathers are continued beyond the vanes to form minute filiform processes. The length of the whole tail is about equal to the combined length of the tarso-metatarsus and outer toe—minus its claw. The filiform extensions of the shafts of the tail-feathers are also distinctly traceable in Grandala cœlicolor.

Pt. colli ventralis.—Contracting at the throat to run down the middle line of the neck, this tract divides high up, sending backwards two relatively broad bands to pass at the base of the neck into the

Pt. ventralis.-This, at its origin, and for some way down,

is of considerable breadth, but near the lower third of the breast the outer border of the tract becomes suddenly emarginate, and is continued forwards from this point as a narrow band to terminate in the region of the cloaca. Whether the right and left portions of this tract join in the middle line in front of the cloaca I am unable to say, the specimen from which the description was taken having been too much damaged to settle this point.



Dorsal aspect of Zeledonia coronata, prepared to shew the form of the pterylæ. *pt.cap.*=pteryla capitis; *pt.c.*=pteryla caudalis; *pt.coll.d.* =pteryla colli dorsalis; *pt.fem.*=pteryla femoralis; *pt.h*=pteryla humeralis; *pt.sp.*=pteryla spinalis.

Pt. femoralis (text-fig. 2, *pt.fem.*).—This tract is well defined, crossing the femur near its upper third and running backwards to the base of the oil-gland.

Pt. cruralis.-Sparsely feathered and not well defined.

Pt. humeralis (text-fig. 2, pt.h., p. 5).—This tract, perhaps rather narrower than usual, calls for no special remark.

Pt. alaris (text-fig. 3).

Metacarpo-digital remiges or primaries.—These are actually 10 in number, but the 10th remex is reduced to the merest vestige and is even smaller than its covert. According to the usual ornithological custom, this wing would be considered to have but 9 primaries.



Right wing of Zeledonia coronata, dorsal surface, shewing the relative lengths of the primaries. 1, 2, 3-9, 10=primaries 1-10; 1, 2, 3= secondaries; c.c.=carpal covert; t.m.=tectrices majores.

Reckoning from the wrist outwards, the first 6 remiges may be regarded as subequal in length, the remaining 3 being remarkably shorter, the 9th especially so. The 10th remex, as I have just remarked, is practically non-existent. There is no diastema between the primary and secondary remiges.

The great reduction which has taken place in the length of the outermost primaries is to be attributed to the comparative disuse of the wings. Furthermore, this reduction has given to the wing a peculiarly rounded form, the primaries passing insensibly into the secondaries.

Cubital remiges or secondaries.—These are 9 in number, the 9th being but little longer than its covert. The wing, of course, is eutaxic. These remiges decrease in length rapidly from without inwards.

A peculiar feature about the remiges of the wing is their extreme breadth, which would be just as noticeable even had no reduction in the length taken place, as in the case of the outer primaries. This feature also appears to be correlated with the disuse of the wings.

Tectrices : upper surface :---

T. majores.—Those of the primaries are small and rapidly decrease in size from within outwards (text-fig. 3, t.m., p. 6). The secondary series is normally developed. The transition to shorter coverts is somewhat abrupt, commencing with the covert of the 7th remex. The 9th remex and its covert are barely distinguishable from one another.

The remaining coverts of the upper surface present the usual Passerine arrangement and call for no comment.

The coverts of the under surface are also of the normal type and therefore need no description here.

Plumulæ or down-feathers occur very sparingly on the trunk.

Rhamphotheca (Pl. II. fig. 11).—The only feature that requires special notice here is the form of the external nostril. This appears, so far, to be unique, inasmuch as it is protected by a membranous fold or operculum, the free edge of which may be described as triangular; the apex of the angle overhangs the mouth of the narial aperture, which is still further increased by the extension backwards of the inner angle of the base of the triangle.

Podotheca (text-fig. 4, p. 8).—This is a complex formed by the fusion of several distinct elements. The acrotarsium is covered by a single shield extending from the proximal end of the tarso-metatarsus to within a short distance of its extreme distal end, which is protected by three small scales, the last overlapping the toes. The inner edge of the large scute runs along near the middle line of the inner side of the shaft, while the outer edge extends as far as the middle line of the planta; the space between the two edges is filled up by a long plate extending the whole length of the planta and inner side of the tarso-metatarsal shaft. The large sheath covering the acrotarsium, when carefully examined, is found to be formed by a fusion of four separate scutes, traces of which can be distinctly seen.

Text-fig. 4.



Left foot of Zeledonia coronata, shewing the podotheca. Only the faintest traces remain of the originally separate scales which compose the main sheath of the acrotarsium.

Discretion must be used in employing the fusion or nonfusion of the scales of the acrotarsium as a character of systematic value. Even in different species of the same genus I find that great variation obtains. Age doubtless has much to do with the matter, the traces of scutes, where fusion of an originally separate series has taken place, being often visible only in young birds and absent in adults. But let it be distinctly understood that I do not mean to decry the value of the squamation of the leg as an aid in distinguishing members of different "Families" of Passeres. There it is often very useful. Thus, to take a case at random : the squamation of the acrotarsium of the Sturnidæ differs

distinctly from that in the Turdidæ, and can be distinguished even in the embryo. Even where fusion is taking place it would always be possible to distinguish the acrotarsium of the one group from that of the other by counting the number of disappearing elements.

Planta.—By the backward extension of the outer border of the acrotarsial shield this forms a knife-like edge. The inner side of this is clothed by a long narrow plate.

Claws.—These are not conspicuously large, that on the hallux being the largest.

General Remarks on the Pterylosis of Zeledonia and of the Turdidæ in general.

In its pterylological characters Zeledonia, so far as I have been able to discover, agrees more nearly with the Turdidæ than with any other group.

But what are, precisely, the pterylological characters of the Turdidæ? Unfortunately, owing to lack of material, I cannot at present say, nor can I find any scientific contribution to this subject. So much, however, seems apparent, that the Turdidæ, as a group, present certain common characters, which may be regarded as distinctly Turdine. It is possible, however, that these distinctions, which are of a somewhat subtle description, will break down when the pterylosis of the Timeliidæ (revised), Pycnonotidæ, Alaudidæ, Motacillidæ, Mniotiltidæ, and Sylviidæ—of Dr. Sharpe's 'Hand-list'—come to be studied. These several "families" will, I believe, prove to be more closely related than has been supposed.

Among the Turdidæ the spinal tract is found to assume two distinct forms— (α) in which *pteryla spinalis* runs down the back as a broad band, and (β) where it expands in the lumbar region into a diamond-shaped patch.

Since, however, the same features obtain in other families of Passeres, the form of this tract can have but a limited value for the systematist. But it promises to be of some use in determining the generic distinctness or otherwise of allied species. To take a case in point, *Merula merula* differs from our native species of Turdus in that in the former the tract has the saddle-shaped expansion, while in the latter it is straight. The Ruticillinæ, Saxicolinæ, and Sialiinæ of Dr. Sharpe's 'Hand-list' appear to possess the saddleshaped type. I have, however, examined very few of the genera of these subfamilies, though among these I have discovered certain small differences which, at the present time, appear to be of uncertain value. Thus Zeledonia and Cossypha-genera which belong apparently to two distinct subfamilies-agree in that the broad dorsal saddle contracts over the pre-ilia to form a narrow band running evenly to the oil-gland. Saxicola appears to be peculiar in that the band immediately behind the saddle is much broader than in Zeledonia, and behind the level of a line passing through the antitrochanters suddenly expands to form a roughly quadrangular patch extending backwards to the oil-gland. But as no less than forty-seven species of Saxicola are recognised by Dr. Sharpe, it seems doubtful whether a detail like this will persist throughout the whole of themsupposing them to be really members of the genus. I have only examined eight.

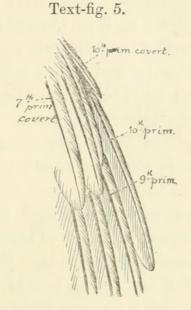
Daulias luscinia appears to be intermediate in the matter of this lumbar saddle between Saxicola and Zeledonia, the region bounded by the antitrochanters being very broad and expanding into a still broader caudal patch, which, however, is narrower than in Saxicola.

In the possession of the semilunar apterion capitis, Zeledonia appears to be peculiar among the Turdidæ.

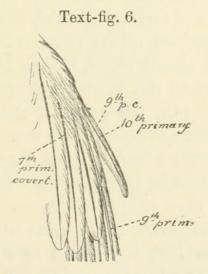
If any proof were needed as to the inutility, for the purposes of classification, of the number of the primaries, it could be abundantly furnished by the Turdidæ. This character, it will be remembered, has been used by several workers in systematic ornithology; and especially by Wallace*, who, indeed, made it the basis of a scheme for the classification of the Passeres.

^{*} Wallace, A. R., "On the Arrangement of the Families constituting the Order Passeres," Ibis, 1874, p. 406.

Zeledonia would be reckoned, by those who follow this system, as one of the 9-primaried Passeres, since only the merest vestige of the 10th remex remains (text-fig. 3, p. 6). On the other hand, in Cossypha (text-fig. 5) and Saxicola



Portion of the primary region of the wing of Cossypha, to shew the great length of the 10th primary.



Portion of the wing of *Saxicola*, to shew the relatively large 10th primary.

(text-fig. 6), and in *Cisticola*, one of the Sylviidæ—which group, I hope to be able to shew, is also to be reckoned among the allies of the Thrushes,—the 10th remex is a relatively long feather.

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In Saxicola the 10th remex is longer than the covert of the 9th, but shorter than the remainder of the primary-coverts. In Cossypha this remex is nearly as long as the 4th primary reckoning from the wrist—and markedly longer than the remaining primary-coverts. The covert of the 10th remex, by the way, is vestigial both in Cossypha and Saxicola. In Cisticola the coverts of both the 9th and 10th remiges are vestigial. In Turdus the 10th remex is longer than the series of primary-coverts; its covert is wanting, whilst the covert of the 9th remex is extremely reduced.

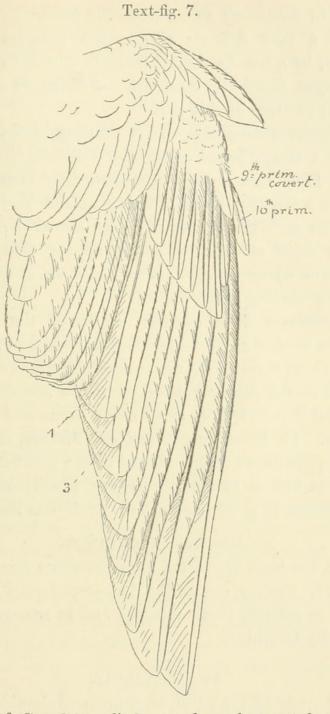
The carpal covert in Zeledonia, Cossypha, Saxicola, and Erithacus is large, in Cisticola small. There is no carpal remex in Zeledonia.

The general form of the extended wing is rounded in *Zeledonia*; and therein it contrasts strongly with the wings of *Saxicola* or *Cossypha*, for example. But this is a character utterly valueless for systematic purposes. The shortening and rounding of the wing apparently follows upon a lessened use of this member or is brought about by adaptation to flight in thick woods or undergrowth.

The great range of variability which is to be met with even among those members of the group which are admittedly and undoubtedly closely allied, should be regarded as good evidence in favour of this contention—that the form of the wing is correlated with the habits of the bird, and is therefore of no value for systematic purposes.

Grandala cælicolor affords a good illustration of this. A close ally of Zeledonia, an indubitable Thrush, yet its wing recalls strongly that of the Swallows—or of Artamus, for example. The primaries are of great length, and the 9th is the longest. The 10th is reduced to a vestigial condition, and although, even when thus reduced, it is longer than the covert of the 9th remex, it is several times shorter than others of the primary-coverts. The covert of the 10th remex has disappeared entirely.

The peculiar shape of this wing suggests a habit of flight resembling that of the forms with which it is compared.



Right wing of *Grandala cælicolor*, to shew the great length of the 9th primary and the vestige of the 10th primary and of the 9th primary-covert.

III. MYOLOGY.

Nothing of importance appears to be derivable from the study of the myology of *Zeledonia*. Typically Passerine, the only features that call for comment are those which concern the wing- and thigh-muscles. Whilst in *Erithacus* and *Turdus* the *tensor patagii brevis* sends off a very delicate slip to the patagial fold, and ultimately, by a few extremely delicate fibres, to the *tensor patagii longus*, *Zeledonia*, *Saxicola*, and *Cossypha* only present the merest vestiges of this slip.

The latissimus dorsi posterior is wanting in Zeledonia, but occurs as a strap-shaped muscle in Saxicola, Cossypha, and Turdus. Since this muscle in undoubtedly Timeliine forms appears as a triangular sheet, filling up the V-shaped space between its anterior border and the hinder border of the latissimus dorsi anterior, it would appear that the strapshaped form which it presents in Saxicola is a degenerate condition preceding extinction.

The *latissimus dorsi anterior* is in all the forms just described a narrow strap-shaped muscle, broadest in *Saxicola*.

Of the thigh-muscles the only one which offers any features of interest is the *femoro-caudal*, which, in *Zeledonia*, is very slender and is inserted by a relatively broad and long sheet of tendon. In *Erithacus*, *Cossypha*, *Merula*, and *Cisticola* the muscle continues fleshy almost to the point of insertion. *Saxicola*, as well as *Crateropus* among the Timeliidæ, agree with *Zeledonia* in presenting a long tendinous insertion.

Muscles of the Syrinx.

Since it has been suggested that Zeledonia might prove to be an ally of Xenicus, one of the Anisomyodean Passeres, it is necessary to refer to these muscles and to remark that they are typically Oscinine.

IV. OSTEOLOGY.

Careful study of the skull, sternum, and shoulder-girdle of *Zeledonia* leaves little doubt but that this bird must be regarded as one of the Turdidæ. The skull, however, presents one or two relatively important features, which may, perhaps, be regarded as primitive characters.

The Skull (Pl. II. figs. 7, 9).—The Thrush-like characters of the skull are to be found in the form of the tympanic cavity and of the palate. These points of common resemblance, it must be remarked, by no means leap to the

eyes on a first examination, nevertheless they are real. They seem to indicate that *Zeledonia* should be regarded as a primitive Thrush, in the wide sense of the word; but to this point we shall return later.

The tympanic cavity in Zeledonia is extremely shallow. Bounded posteriorly by the conch-like tympanic wing of the exoccipital (Pl. II. fig. 9, l.o.w.), it passes upwards into the squamosal prominence to terminate some distance above the squamosal head of the quadrate in the form of a low hook-shaped ridge. The termination of this hook, which, it must be remembered, is the termination of the free edge of the tympanic cavity, lies behind and beneath the base of a conical process of the alisphenoid. The articular surface for the squamosal head of the quadrate, it should be observed, lies, relatively, remote both from this alisphenoid process and the termination of the free edge of the tympanic wing. Another point of some importance to be noted here is the fact that. after the removal of the tympanic membrane, the aperture of the recessus tympanicus posterior will be found only after a careful examination in the form of a minute foramen which leads into a small chamber formed by the absorption of the cancellated tissue around the semicircular canals, and is strictly confined to this region. The aperture of the recessus tympanicus anterior, though small, is guite normal in position.

Turning now to the palate, the chief point of interest will be found in the maxillo-palatine processes, here reduced to slender stylets of bone, the free ends of which are bent at a sharp angle so as to lie parallel with the vomer and on either side thereof (Pl. II. fig. 7, mx.p.).

In the lateral view of the skull it will be noted that the postorbital process is barely visible (Pl. II. fig. 9, p.o.p.), whilst the interorbital septum is much fenestrated, only a very slender bar of bone remaining, which runs forwards from the membranous orbito-sphenoids to join a small pillarlike remnant of the septum that remains at the anterior wall of the orbit.

The anteorbital plates are large and have entirely replaced

the lachrymal, of which no trace remains (Pl. II. fig. 9, *a.p.*). In a much-damaged skull of *Grandala* cælicolor I find the lachrymal represented by a minute scale.

The palato-pterygoid articulation is formed, as in the typical Passeres, by the extension of the distal end of the ptervgoid into a slipper-shaped plate embracing the parasphenoidal rostrum. The anterior edge of the plate is opposed to one side of the triangular plate of bone which rises up from the dorsal surface of the palatine so as to be closely applied to the rostrum (Pl. II. fig. 9, h.pt.). This triangular plate, though now forming part of the palatine, is evidently the remnant of the hemipterygoid. Sialia, Grandala, and Erithacus resemble Zeledonia in the presence of this triangular vestige of the hemipterygoid, but in the genera Turdus and Merula, for example, no such vestige remains, and the ptervgoid articulates with the palatine by the approximation of two oblique and almost linear glenoid surfaces, that afforded by the palatine being developed upon the hinder end of its distal border (Pl. II. fig. 12).

The Sternum and Shoulder-girdle (text-fig. 8, p. 17).— The sternum of Zeledonia affords indubitable evidence that this bird possesses but limited powers of flight, inasmuch as the keel, relatively to the size of the corpus sterni, is extremely small. Compared with the keel of Sialia, Erithacus, Pratincola, Phylloscopus, for example, the extent of the reduction which has taken place is very striking. While in Zeledonia its free edge is slightly concave, in the several forms just referred to it is markedly convex. Again, in Zeledonia the keel decreases in depth rapidly from before backwards, so that for about one-third of its length it is little more than a median ridge of bone. In any of the forms compared above it will be noticed that the keel is continued backwards to the extreme end of the sternal plate, there to fan out into a V-shaped plate.

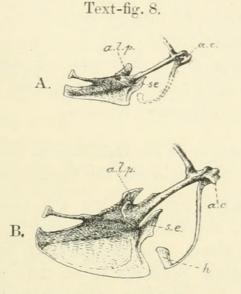
The peculiar shape of the wing further strongly supports the view that this bird has gone far on the road to flightlessness. In this connexion it is interesting to note that the reduction of the wing-area correlated with this lack

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of use has not taken place by the shortening of all the remiges, but only of the outer primaries. This method of wing-reduction appears to be the invariable rule in the early stages of flightlessness.

Five ribs articulate with the sternum, and all are attached to the anterior lateral process—as appears to be the rule among the Passeres. These processes in Zeledonia are relatively short, as also is the bifurcate spina externa.

The relative length of the anterior lateral processes and the spina externa will possibly prove of some use in defining



- A .- Sternum and shoulder-girdle of Zeledonia coronata, shewing the degenerate condition of the keel and the long and slender coracoids. a.l.p.=anterior lateral process; a.c.=acrocoracoid; s.e.=spina externa.
- B.-Sternum and shoulder-girdle of Sialia wilsoni. Note the deep keel, the large hypocleideum, and strong coracoid. Additional letter: h = hypocleideum.

the smaller groups of Passeres, though these proportions must always be rigorously scrutinized, since they may vary individually with the power of flight. But Turdus, Pratincola, and Phylloscopus, for example, present so many distinct generic types, though the differences are small.

The coracoid in Zeledonia shews, like the keel of the sternum, evidence of degeneration. Relatively to the corpus sterni it is longer than in Sialia; this is due to the reduction of the sternum. Further, it has lost the strong SER. VIII.-VOL. V.

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external lateral ridge which runs forward from the base to the middle of the shaft in such genera as *Turdus*, *Pratincola*, and *Erithacus*, for example. It differs, too, from the coracoid of *Sialia*, firstly, in that the width at the base is greatly increased in *Sialia* by the development of a large lateral plate formed by the expansion of the external angle of the base of the shaft; and, secondly, in that, while in *Sialia* the acrocoracoid (fig. 8 B, *a.c.*, p. 17) is well marked, and at its free end turns inwards and downwards to form a hammershaped process grooved on its inner surface for the furcula, in *Zeledonia* this region of the coracoid is much reduced, and has the hammer-shaped process reduced to a hook-shaped, which is not grooved for the furcula on its inner side.

The furcula was much damaged. From the fragments that I have been able to dissect out it can be seen that the hypocleideum was extremely reduced.

General Remarks on the Osteological Characters of Zeledonia and the Turdidæ.

That in general conformation the skull of Zeledonia resembles that of the Turdidæ more closely than that of any other family is clear. Furthermore, it would seem that among the Turdidæ Zeledonia must take its place with or near the Sialiinæ: the likeness which the skull presents to those of Sialia and Grandala, at least, seems to support this view. Unfortunately I have but a damaged skull of Grandala cælicolor, and this is too much broken to admit of a comparison of the tympanic region.

Probably these small forms, and with them the equally diminutive members of the Ruticillinæ and Saxicolinæ, should be regarded as more primitive than the typical Thrushes, such as *Geocichla*, *Turdus*, *Merula*, &c. 'The forms of the external auditory meatus (tympanic cavity) and of the palato-pterygoid articulation both point in this direction. In *Zeledonia* the tympanic cavity seems to be of a very simple type, and this, coupled with the large size of the hemipterygoid element of the palatine and the nonpneumaticity of the skull, would seem to indicate that *Zeledonia* is one of the lowest members of the Turdiformes.

Of the larger Thrushes, *Geocichla* seems undoubtedly one to take a very low position. This is borne out partly by the form of the tympanic cavity (Pl. II. fig. 2), which is intermediate in character between that of *Sialia* and *Turdus*, and partly by the presence of vestigial basipterygoid processes. The presence of the latter is somewhat remarkable (Pl. II. fig. 6). Unfortunately I have but one skull of the genus *Geocichla* — *G. monticola*. But traces of these processes probably occur in other species of this genus. Few other Passerines retain any vestige of these buttresses.

The Tympanic Cavity.—The study of the free edge of the tympanic cavity reveals some curiously interesting facts. The simplest condition, perhaps, which this region presents among the Passeriformes is to be met with in Menura (Pl. II. fig. 5). Here the free edge of the lateral occipital wing meets, at a sharp angle, a sinuous ridge running from the squamosal head of the quadrate. To the inner edge of the lip of this ridge the tympanic membrane is attached, and stretching across becomes attached to the lateral occipital wing very near its free edge, so that the tympanum lies very close to the surface.

This type appears in a large number of widely different groups, and the fact may be regarded as an additional indication of its primitive character.

The Turdiformes appear to have departed from this type along two different lines.

The ground-type of both forms appears to be represented in *Sialia* (Pl. II. fig. 3). In this genus the line formed by the lateral occipital wing, after meeting the ridge described in *Menura*, which runs from the squamosal head of the quadrate, is continued upwards and forwards, then sharply downwards on to the squamosal process in the form of a low and barely perceptible ridge.

In the Ruticillinæ the free edge of the lateral occipital wing is continued upwards and forwards in the form of a strong ridge to the postorbital process, so that the ridge forming the anterior border of the meatus in *Menura* now becomes overhung by a sort of cave. This feature is still

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more marked in *Daulias luscinia* (Pl. II. fig. 4) and *Erithacus rubecula*.

Pratincola and *Saxicola* also belong to this type. So also, it is significant to note, do *Phylloscopus* and *Cisticola*, and probably the Warblers generally.

The tympanic region of the skull in Zeledonia (Pl. II. fig. 9) is undoubtedly specialized in one respect, since the processus zygomaticus squamosi has apparently been replaced by a process of similar size furnished by the alisphenoid. Pneumatic tissue is practically wanting. Indeed the peculiar features of this region of the skull appear to have resulted from a modification of the type of tympanic region in Sialia, not as it is in adult life, but as it appears during its earlier stages of development.

As I have already remarked, the free edge of the lateral occipital wing, which is relatively longer than in *Menura*, terminates in a low ridge above the squamosal head of the quadrate, leaving a notch between itself and what appears to correspond to the zygomatic process, which, it is to be especially noticed, is some distance from the squamosal articulation of the quadrate. In this respect *Zeledonia* is quite remarkable. In *Cossypha* and *Geocichla* the free edge of the lateral occipital is continued upwards and forwards on to the zygomatic process (Pl. II. fig. 2, *l.o.w.*) in the form of a strong sharp ridge overhanging the bony ridge which formed the external boundary of the meatus in *Menura*. From this the passage to the more specialized form is easy.

In Merula (Pl. II. fig. 1, *l.o.w.*) the lateral occipital wing passes upwards into what corresponds to the overhanging ridge in *Geocichla*. But both the occipital wing and the ridge continued therefrom are immensely developed, so as to form a spacious chamber around the tympanic membrane. Externally this chamber has the form of a bulla. The incipient stages in the formation of this bulla are easily traceable in *Zeledonia*.

The skulls of *Anthus* and *Motacilla*, it should be remembered, resemble *Sialia* in the form of the tympanic cavity.

The three great air-sinuses of the cranium are not very largely developed in any of the Passeres.

The recessus tympanicus anterior appears to be invariably present and well defined; but in the small Turdiform skulls e. g. Sialia, Pratincola—the superior and posterior recesses are ill-defined, passing insensibly into the general diploid tissue of the skull.

In Zeledonia this diploid tissue is extremely reduced and the superior tympanic recess is wanting. The posterior is present, however, but is very small; it opens externally by a small foramen above the fenestral recess. Only among Laniine skulls have I noticed a similar lack of diploid tissue. But even there some vestiges of the superior recess are to be found. These are present in the form of a number of small foramina arranged in a semicircle, leading from the articular surface for the squamosal head of the quadrate backwards and downwards to the top of the fenestral recess.

In the larger Thrushes, e. g. *Merula*, the superior and posterior recesses are moderately large. The aperture of the former lies between the squamosal and the articular surfaces of the quadrate, while the entrance to the latter is through a cribriform plate above the fenestral recess.

The Palate.—That the form of the pterygo-palatine articulation in Zeledonia is more primitive than that which obtains in Sialia or Erithacus for example, there can be little doubt. In support of this view I would cite the conditions which obtain in Menura. In this bird the hemiptery-goid element does not fuse with the palatine till late in life (Pl. II. fig. 10, h.pt.), but when this has taken place the appearance of the palatine is precisely the same as that of Zeledonia.

The nature of the palato-pterygoid articulation in Menura, and the transformation in the details of this articulation which can be traced in Zeledonia, Erithacus, Sialia, and Turdus for example, on the one hand, and the peculiar modifications which obtain in forms like Bucco and Megalama for example, on the other, seem to shew conclusively that the fusion between the pterygoid and the palatine, which takes place in the latter and in some Passeres, has resulted from fusion between a sometime free pterygoid and palatine, which articulated by a flexible joint formed between the pterygoid shaft and the segmented extremity of that bone and the palatine. This anchylosis took place when the movement between pterygoid and palatine became too restricted to allow of free movement between the two bones. In other words, the unsegmented pterygoid of the forms in question is not a primitive condition, but has been derived from the fusion of a segmented pterygoid such as obtains in the majority of the Neognathæ *.

The style-shaped maxillo-palatines of Zeledonia represent an undoubtedly specialized condition. In the typical Turdiform palate—e. g. Merula, Cossypha—these structures are larger, spoon-shaped, and inflated at the free end to form a kind of pocket. The spoon-shaped plate underlies the body of the vomer. The linear form seen in Zeledonia is obviously a degenerate condition of a maxillo-palatine of the type found in Erithacus or Sialia, for example. Here these elements are rod-shaped, and much inflated to form delicate shells of bone open along the outer side. Phylloscopus and Anthus shew the Turdiform type.

V. SUMMARY.

As to the precise position of *Zeledonia* I regret that I can say nothing definite until I have had an opportunity of examining much more material than is procurable at present. Before any sound deduction can be framed on this particular question it will be necessary to obtain examples in immature plumage and a series of birds for dissection. The specimen submitted to me for the purpose of this paper was not wellpreserved, and, furthermore, was so much damaged that reliable data on many questions concerning the soft parts were impossible. Quite as necessary are examples of other species allied to *Zeledonia*.

* Pycraft, "On the Morphology of the Palate in the Neognathæ," Journ. Linn. Soc., Zool. xxviii. p. 333.

Nevertheless, it seems to me that there can be no doubt about the Turdine affinities of *Zeledonia*. Whether further research would justify the formation of a separate subfamily for this bird, as has been proposed, remains to be seen. Its nearest allies seem to be among the Sialiinæ.

That it is an isolated form, primitive in some respects, highly specialized in others, seems beyond dispute. Its powers of flight must be of a very limited description; the small size of the keel of the breast-bone and the peculiar form of the wing bear out this contention. In this matter of the reduction of the wing it is significant to remark that it takes place, not by a decrease in the length of *all* the remiges, but by the shortening of the outer primaries only, leaving the inner primaries and secondaries still unreduced. This is exactly what takes place during the early stages of the degeneration of the wing throughout the class Aves.

To keep this paper within the smallest possible limits I have been obliged to omit the results of comparisons with the more distant allies of the Turdidæ and of those reputed to hold such a position; but I would say here that there seems good ground for believing that further research will demand the formation of one large group of Turdiform birds.

This would include the Timeliidæ of Dr. Sharpe's 'Handlist' (in part.), the Pycnonotidæ, Mimidæ, Turdidæ, Sylviidæ, Mniotiltidæ, Regulidæ, Cinclidæ, Troglodytidæ, Alaudidæ, and Motacillidæ. The relationship of these groups one to another is a matter upon which I am now engaged, and is one of extreme difficulty.

I am equally unable, at the present juncture, to say anything definite as to the probable nearest allies of this great Turdiform group. Suffice it to say, I do not think that this group stands so low in the scale as some have imagined, if we may give any weight to the form of the maxillo-palatine processes and the relations of the squamosal in the nestling; and to my mind these are characters of some importance. Neither do I believe that they stand so high as others have contended; but, as I have just remarked, this is a matter which I am now trying to sift.

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EXPLANATION OF THE PLATES.

PLATE I.

Zeledonia coronata, p. 1.

PLATE II.

- Figs. 1-5 shew the various forms of the tympanic cavity from the right side for comparison with that of *Zeledonia*, seen in the side view of the skull of fig. 9.
- Fig. 1. The tympanic cavity of *Merula*. $\times 2$. Here the lateral occipital wing (*l.o.w.*) is much inflated to form a large chamber in front of the tympanic membrane. This wing, it will be noticed, curves upwards and forwards to terminate on the zygomatic process. This is an extremely specialized type.
- Fig. 2. The simpler form of the tympanic cavity in *Geocichla*, intermediate in type between that of *Turdus* and *Sialia*. $\times 2$.
- Fig. 3. The tympanic cavity of *Sialia*, representing probably the simplest type among the Turdidæ. $\times 2$. Letters as before.
- Fig. 4. The tympanic cavity of *Daulias luscinia*. $\times 2$. A specialized type, inasmuch as the lateral occipital wing (*l.o.w.*) is continued upwards to the base of the postorbital process (*p.o.p.*).
- Fig. 5. The tympanic cavity of *Menura superba*. Nat. size. The tympanic cavity as seen here is possibly of a more primitive character than in any of the Turdidæ.
- Fig. 6. Palate view of the skull of *Geocichla*, shewing vestigial basipterygoid processes (bp.p.). $\times \frac{1}{3}$.
- Fig. 7. Palate view of skull of Zeledonia coronata. $\times 2$.
- Fig. 8. Palate view of skull of *Sialia wilsoni*, to compare with that of *Zeledonia*. $\times 2$. Note the larger and inflated maxillo-palatine processes (mx.p.).
- Fig. 9. Lateral view of skull of Zeledonia coronata. \times 2. Note the position of the zygomatic process (z.ps.).
- Fig. 10. Hemipterygoid of *Menura superba*. This does not appear to fuse with the palatine till comparatively late in life. $\times 2$.
- Fig. 11. Rhamphotheca of Zeledonia coronata, to shew the remarkable operculum (op.). $\times 2$.
- Fig. 12. Hemipterygoid region of skull of *Turdus*, to compare with that of *Menura* and *Zeledonia*. $\times 2$.

Explanation of the Lettering.	
a.p. = antorbital process.	pa. = palatine.
a.tb. = alinasal turbinal.	pt. = pterygoid.
bp.p. = basipterygoid process.	p.o.p. = postorbital process.
h.pt.=hemipterygoid.	q.=quadrate.
<i>l.o.w.</i> =lateral occipital wing.	vo. = vomer.
mx.p. = maxillo-palatine process.	z.p.s.=processus zygomaticus
op. = operculum.	squamosi.
o.s.=otic articular surface for	z.s. = squamosal articular surface
quadrate.	for quadrate.

Explanation of the Lettering.



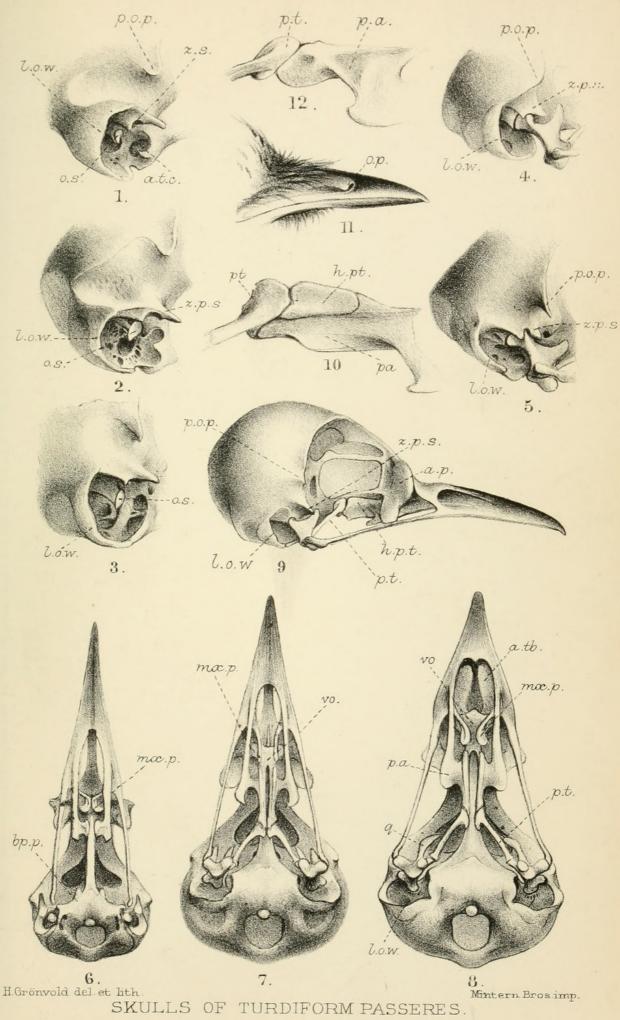
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ZELEDONIA CORONATA.

Mintern Bros.imp.

Ibis.1905, Pl.II.



SKULLS OF TURDIFORM PASSERES.



Pycraft, W. P. 1905. "I.On the Systematic Position of Zeledonia coronata, with By some Observations on the Position of the Turdida?" *Ibis* 5(1), 1–24. <u>https://doi.org/10.1111/j.1474-919x.1905.tb05581.x</u>.

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