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I. ON THE FORM OF THE QUADRATE BONE IN BIRDS.

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I. *On the Form of the Quadrate Bone in Birds.*

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Few descriptions and still fewer figures are extant to show the forms that the quadrate bone assumes in the various groups of Birds. Huxley, in his great paper on the Classification of Birds,* rarely alludes to the quadrate, save in one or two exceptional cases, such as the Ratitæ and the Parrots. Parker, Owen, and Brandt have described the bone carefully in certain particular cases; but no comparative study seems to have been made of it, nor any connected attempt made to use it for purposes of classification. In putting up a set of Birds' skulls for the Museum, and in arranging them to illustrate the Huxleyan classification, I was instructed to prepare also a special set of quadrate bones, and to observe how far an arrangement of these, based on their own special characters, would coincide with the order founded on the general character of the whole palate. It was at once plain that the quadrates differed extremely among themselves, and could all, after a little practice on our part, be easily recognised. We then examined one or two doubtful forms, to see whether the quadrate was likely to help in the matter of classification; and found, for example, that the quadrates of a Goose and a Heron were altogether different, while that of a Flamingo showed the closest possible likeness to the latter. We then proceeded forthwith to a systematic survey.

The following paper is a sketch merely, our Museum not yet containing material enough for a long series, nor possessing more than a very few of the rarer and more interesting forms. I hope to take up some of these in a future paper. Nor does this paper profess to deal with the development or the morphology of the Bird's quadrate, though certain points connected therewith seem to require further study. A short, and indeed preliminary, study of its configuration is all that is attempted here.

In a well-marked quadrate, for example that of a Vulture, we observe the following parts:—The *head*, by which the bone articulates with the temporal region of the skull,

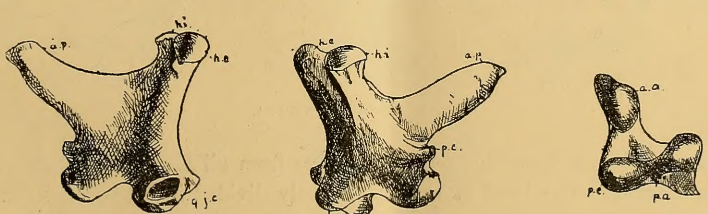

Fig. 1. Neophron percnopterus.

* P.Z.S., 1867.

and which is here (as in most cases) divided by a deep groove [*capitular groove*] into an *internal capitulum* (*h.i.*) for articulation with the prootic, and an *external* (*h.e.*) for articulation with the squamosal; the *shaft* of the bone, leading from the head to the distal extremity, which forms the complicated articular surface for the mandible; an *anterior process,* the *metapterygoid process* of PARKER (*a.p.*), projecting forwards and inwards from the shaft towards the orbit; a smaller process below and to the inner side of this last, which articulates with the pterygoid bone, and which we may call the *pterygoid condyle* (*p.c.*): to it a ridge is directed on the inner surface of the bone, descending from the neighbourhood of the capitular groove; an articular surface at the base of the shaft, on its outer aspect close above the mandibular articulation, for the quadrato-jugal: this articular surface is usually hollowed and cup-like, and may be called the *quadrato-jugal cup* (*q.j.c.*). The articular surface for the mandible is very complicated and variable: in the present case it is divided into two parts, a prominent rounded anterior articular surface or condyle (*a.a.*), and a posterior articular surface transversely elongated, and trochlear in character, presenting an internal (*p.e.*) and external (*p.a.*) condyle, separated by the trochlear groove. The view from below shows also a tract of bone projecting behind the external condyle, which in certain cases becomes more conspicuous.

Of these points those most liable to variation are: the greater or less separation of the two capitula; the form of the anterior process; the presence or absence of the pterygoid condyle; the greater or less completeness of the quadrato-jugal cup; and the whole form and character of the mandibular articulation.

THE RATITÆ.

The quadrate of the Ratitæ has been pretty fully dealt with by PARKER in his memoir on the Skull of the Ostrich. For this reason, and for the better one that we do not yet possess a full series of Ratite skulls, we figure it in one form only, the

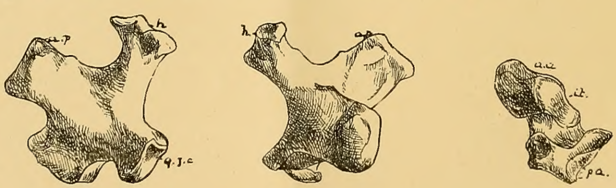

Fig. 2. RHEA AMERICANA.

Rhea. In its clumsy form this quadrate differs from all the others that we shall hereafter describe. The head is very imperfectly divided into two capitula. The anterior process is short, thick, and truncated; the quadrato-jugal cup is imperfect, and is represented merely by an irregular crescentic hollow, the lower part of the cup being absent. The pterygoid condyle is not defined, being merged in a great mass of bone above the inner aspect of the anterior mandibular condyle; the ridge before-mentioned is visible passing down to it from the region of the capitula. The mandibular articulation is peculiar; the posterior portion is disproportionately small, and its inner and outer regions are not clearly separated by a groove; the bulky anterior part (*a.a.*) is bevelled off on its outer side into an accessory trochlear surface (*i.t.*).

No other quadrate that we have studied approaches this in character.

DESMOGNATHÆ: I.—CHENOMORPHÆ.

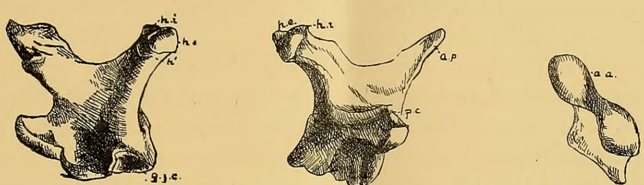

Fig. 3. ANSER DOMESTICUS.

In the Common Goose, the two capitula are only slightly separate; below and to the outer side of the external capitulum is a concave surface, passing below into a small accessory head (h^1). The anterior process is short and pointed, somewhat roughly fashioned on its outer, more concave and delicate on its inner, aspect. The pterygoid condyle and the quadrato-jugal cup are both imperfect—the former, indeed, is quite rudimentary. The mandibular articulation is peculiar; it possesses only the outer moiety of its posterior part, which unites with the (normal) anterior condyle to form an obliquely-placed trochlear articulation. When seen from below, a considerable overhanging stretch of bone is visible posterior to this articular surface. The peculiar form of the joint-surface is connected with the fact that "the angle of the mandible is strongly produced and upcurved," as in the gallinaceous birds. The latter feature and the rudimentary inner lamina of the palatine bone were noted by HUXLEY as features in the skull recalling the Alectoromorphæ. A study of the quadrate emphasises the resemblance. The quadrate of the Goose differs very greatly from that of any other Desmognath that we have examined.

II.—AMPHIMORPHÆ.

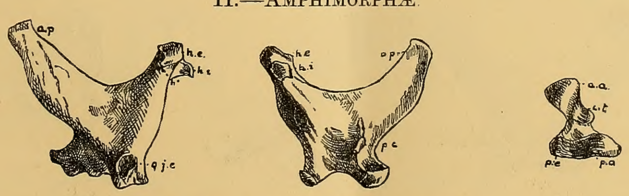

Fig. 4. PHŒNICOPTERUS ANTIQUORUM.

The Flamingo's quadrate is in all important respects totally different from that of the Anserine birds. The two capitula are well apart: the internal one is small, and projects slightly backwards, the external descends on its outer side into an imperfectly developed accessory head (h^1). The anterior process is large, broad, and curved upwards. The pterygoid condyle is well-developed (though not exceptionally so), and is quite separate from the anterior mandibular condyle. It rises somewhat abruptly from the surface of the bone, and does not project forwards, as is more usual with it. The quadrato-jugal cup is deeply sunken, but its margins are not raised above the surface of the bone. The anterior condyle is large, and possesses a well-marked lateral trochlea.

III.—Pelargomorphæ.

We have examined and figured the quadrates of the Heron, Stork, and Ibis, as examples of the three divisions of the Pelargomorphæ—the Herodiæ, Pelargi, and Hemiglottides of Nitzsch.

In all of these, the two capitula are perfectly separate, and there are indications of an accessory head, especially in the Ibis and Heron. In all, the anterior process is large; the quadrato-jugal cup is deep, and its margins raised; the pterygoid condyle is well-marked and large; and the mandibular articulation is very complex.

In the Heron (and Egret) the anterior process is exceptionally large and long,

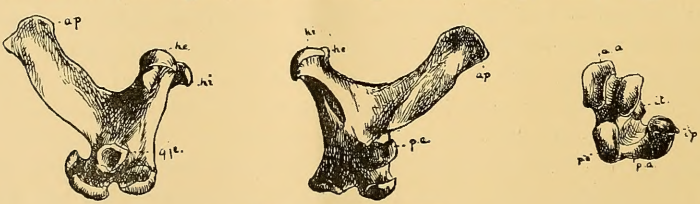

Fig. 5. Ardea cinerea.

with blunt rounded extremity. The pterygoid condyle is also abnormally large. The quadrato-jugal cup is rather far forward, near the base of the anterior process. The posterior portion of the mandibular articulation has its two condyles far apart; the anterior portion is also double, and bears on its side a small accessory trochlea (*i.t.*).

In the Stork the anterior process is very broad, but not so long as in the

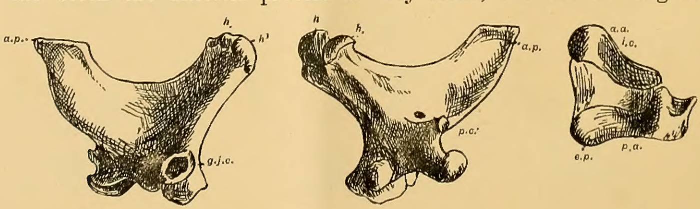

Fig. 6. Ciconia alba.

Heron. The position of the quadrato-jugal cup is more normal. The posterior part of the mandibular articulation is produced on its outer side with a special grooved surface, which in the Heron is very slightly indicated, and in Ibis is absent: the anterior condyle passes gradually into a large accessory trochlear surface.

In Ibis, the capitula are somewhat less separate than in the other two. The angle between the shaft of the bone and its anterior process is very obtuse. The

Fig. 7. Ibis falcinellus.

pterygoid condyle is not so far forward. The posterior portion of the mandibular articulation is normal; the accessory trochlea on the anterior part is very distinct.

It will be observed that these three forms agree closely with one another, and all resemble Phœnicopterus. But Ibis is the most like Phœnicopterus in the characters of its mandibular articulation, its accessory trochlea, the obtuse angle of its anterior process, and the position of its pterygoid condyle. Indeed, the quadrate of the Ibis resembles that of the Flamingo fully more than it does that of either of its Pelargomorph allies.

IV.—Dysporomorphæ.

The three types of Dysporomorphæ that we have examined—the Pelican, Gannet, and Cormorant—show, in several respects, a quite unexpected amount of dissimilarity.

In the Pelican, the two capitula are well defined. The anterior process is

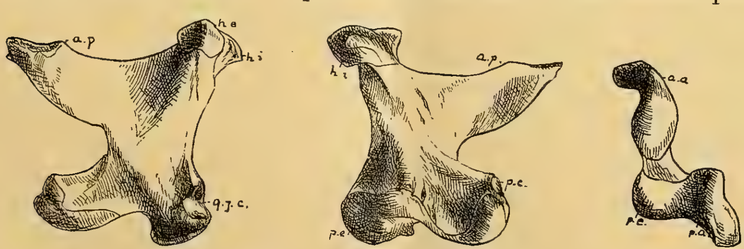

Fig. 8. Pelecanus onocrotalus.

of moderate size, and pointed. The quadrato-jugal cup is imperfect posteriorly, forming merely a crescentic hollow above the posterior portion of the mandibular articulation. The pterygoid condyle is indistinct, and is represented by a slight hollow in the mass of bone above the internal aspect of the anterior mandibular articulation. The mandibular articulation surface is normal in character, and not unlike the Vulture's. The external condyle of the posterior portion is bulky, and the anterior condyle is elongated.

In the Solan Goose, the two capitula are separated by a deep groove, and the

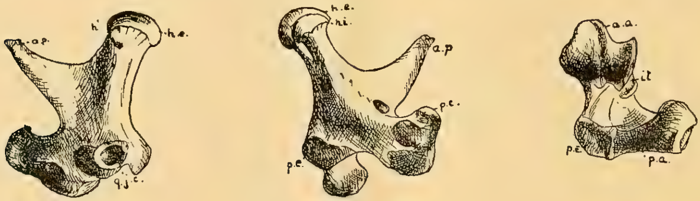

Fig. 9. SULA BASSANA.

accessory head is faintly indicated. The anterior process is small and triangular. The quadrato-jugal cup is deep, with raised margins, and more remote than in the Pelican from the hinder border of the shaft of the bone. The pterygoid condyle is better marked than in the Pelican, but is still not distinctly raised from the surface of the bone. It possesses accessory smooth surfaces on its interior and posterior aspects, which are seen also in the Heron. The mandibular extension possesses on the outer side of its anterior condyle a conspicuous accessory trochlea.

The quadrate of the Cormorant is very peculiar. The head is undivided, being merely crossed by a faintly indicated capitular groove, as in the Penguin. The

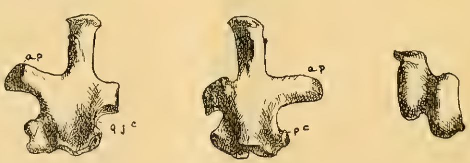

Fig. 10. PHALACROCORAX CARBO.

accessory head is perceptible. The shaft is long, and gives off, at right angles some distance below the head, a short, thick, and blunt anterior process. In place of a quadrato-jugal cup is a crescentic hollow so deeply excavated as to leave projecting above it a process of bone in line with the anterior process on the other side of the shaft. The pterygoid condyle is distinct. The mandibular articulation is exceptional, presenting two lateral surfaces parallel to one another, convex from before backwards, and separated by a deep trochlear groove. Thus the quadrate of the Cormorant, while simple and possibly archaic in character, is not without points of resemblance to the Pelican's, at least in respect of the quadrato-jugal cup; while an inspection of the mandibular articulation in the Pelican may possibly explain the origin of its peculiarity in the Cormorant. The quadrate bone does not help to support the view that the Dysporomorphæ or Steganopodes are a very natural group (BRANDT*), nor that in it the Pelicans form one natural division, the remaining genera another (HUXLEY). For the Pelican differs from the Solan Goose in its imperfect quadrato-jugal cup and its less perfect pterygoid condyle, and in the want of the accessory trochlea on the anterior part of the mandibular articulation; and from both the Solan Goose and the Cormorant in the large size of its anterior process, and in lacking all trace of the accessory capitulum.

The affinity between the Pelargomorph quadrate and that of the Solan Goose and Pelican is more easy to see. The mandibular articular surfaces in the quadrate of the Heron and Gannet are almost identical, the quadrato-jugal cup is similar in both, and indeed they differ in little except the size of the anterior process.

But these quadrates point in other directions besides that of the Pelargomorphæ.

HUXLEY remarks, in dealing with the Cecomorphæ (*loc. cit.*, p. 458), that "the Procellariidæ are aberrant forms tending towards the Cormorants and Pelicans, among the Desmognathæ"; and we find accordingly that the quadrate also shows this affinity between the Cecomorphæ and the Dysporomorphæ. Thus the Gannet resembles the Petrel and Grebe in its accessory trochlea external to the anterior mandibular condyle, and somewhat also in the character of its pterygoid process: its two capitula are more deeply cleft asunder even than those of Larus or Alca; and it resembles the two latter genera in a posterior extension of the posterior mandibular condyles, which is only partially shown in the figures of the side view. But it differs from all Cecomorphæ in its small pointed anterior process. We have already called attention to the resemblance between the head of the bone in the Cormorant and the Penguin.

V.—AËTOMORPHÆ.

We have studied the quadrate in the Vulture (*Neophron*), Owl, and Buzzard. We have not been able to examine Gypogeranus, or the New World Vultures.

The quadrate of the Vulture has already been described. We may recall attention to its widely but not *deeply* separate capitula, its small accessory head, its narrow pointed and rather large anterior process, its distinct pterygoid process, its deep oval quadrato-jugal cup, and its simple and typical mandibular articular surface.

* *Beitr. z. Kennt. d. Naturgesch d. Vögel.* St. Petersburg, 1839.

In the Buzzard the two capitula are still further apart, and the external one is the longer of the two; the pterygoid condyle is more prominent, and the quadrato-

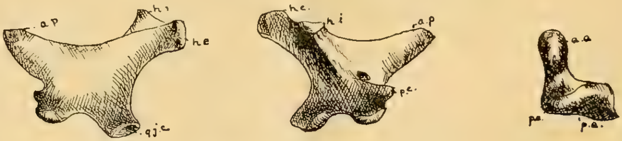

Fig. 11. BUTEO VULGARIS.

jugal cup (oval in form) is placed lower down. The mandibular articulation resembles the Vulture's.

In the Owl, the capitula are yet more widely and more deeply sundered; and the quadrato-jugal cup resembles that of the Buzzard. But the pterygoid condyle

Fig. 12. STRIX ALUCO.

is very faintly marked, and the anterior portion of the mandibular articular surface possesses an external accessory trochlea. We do not propose to discuss on this slender basis the moot point of the relationship of the Owls, beyond merely emphasising the fact that their quadrate differs greatly from that of the true Aëtomorphæ. The Vulture in general outline suggests resemblance to the Geranomorphæ, but the mandibular articulation is very different in the two. On the whole, the likeness to the Gull's quadrate is most striking, and is borne out by the character of the mandibular articulation, and by the situation of the quadrato-jugal cup.

VI.—PSITTACOMORPHÆ.

The very peculiar shape of the Parrot's quadrate is well known. The shaft

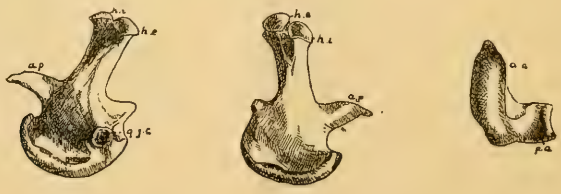

Fig. 13. CACATUA.

long, the capitula are but slightly separate, and the anterior process is very small indeed. The quadrato-jugal cup is small, deep, round, and raised upon an eminence. There is no distinct pterygoid condyle. The mandibular articulation is peculiar, its anterior portion passing uninterruptedly into the posterior by a long, narrow, convex facet.

No resemblance is to be detected between this quadrate and that of the Aëtomorphæ, or any other of the foregoing groups ; but it presents marked affinities with certain Coccygomorphæ.

VII.—Coccygomorphæ.

We have examined the quadrates of the Toucan, Hoopoe, Kingfisher, and *Dacelo;* unfortunately far too small a number of the forms of this polymorphic and most interesting group.

In the Toucan the capitula are widely separate. The anterior process is very

Fig. 14. Rhamphastus tocco.

long and pointed. The quadrato-jugal cup is large but shallow. The pterygoid condyle is indistinct. The mandibular articulation resembles that of the Vulture.

In the Hoopoe the two capitula are distinct. The anterior process is long but

Fig. 15. Upupa epops.

truncated, and makes a very oblique angle (as also in the Toucan) with the shaft of the bone. The pterygoid condyle is not defined. The mandibular articulation is not unlike that of the Toucan, save for a greater transverse elongation of its posterior part.

In the Kingfisher the two capitula are but slightly separate, and the external one is somewhat hollowed out. The shaft is long, and the anterior process rudi-

Fig. 16. Alcedo ispida.

mentary. The pterygoid condyle is very faintly marked. The quadrato-jugal cup is small, deep, and raised. The posterior part of the articular surface is narrow, transversely elongated, and flattened; the anterior is elongated from before backwards, and is bevelled off externally into an accessory trochlea.

The quadrate of Dacelo is surprisingly different from that of Alcedo, in respect of its large anterior process, otherwise the two are not so different as owing to this

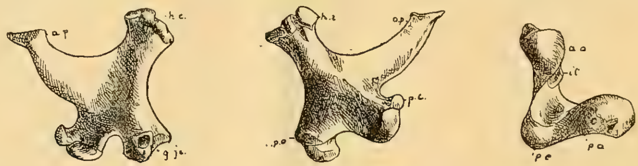

Fig. 17. Dacelo gigas.

fact they at first sight appear. The two capitula in Dacelo are slightly separate, and the external one is hollowed out. The quadrato-jugal cup is small and deep. The pterygoid condyle is more distinct than in Alcedo, but yet is imperfectly severed from the mass of bone below. The anterior portion of the mandibular articular surface possesses an accessory trochlea.

Our four Coccygomorph quadrates, differing greatly among themselves, unmistakeably suggest divergent resemblances with other Desmognathous groups. That of the Toucan recalls the Vulture and Buzzard among the Aëtomorphæ, save that the condition of the pterygoid condyle and the lateral outline of the lower part of the bone perhaps suggest a closer likeness to the Pelican and Gannet.

The quadrate of Alcedo is eminently suggestive of affinity with the Parrot, in respect of its long shaft, its indistinct capitula, its aborted anterior process, its imperfect pterygoid condyle, and the antero-posterior extension of its anterior mandibular condyle.

With regard to that of Dacelo, the resemblance to an Owl's would be extremely close, were it not for the widely-separate capitula of the latter; but the affinity with the Pelargomorphæ (hinted at by Huxley) is but hazy, the accessory trochlea being almost the only point to support it.

The quadrate of Upupa has points of resemblance with Rhamphastus or Alcedo within its own group, and we may perhaps hazard also a suggestion of likeness to the Woodpecker.

Celeomorphæ.

In this group we have been confined to a single species, the green Woodpecker.

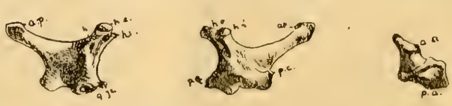

Fig. 18. Picus viridis.

In the Woodpecker's quadrate the capitula are small, but distinctly separate. The shaft of the bone is short and very broad, especially in its lower part. The anterior process is long, swollen at the extremity, and set on to the shaft at an obtuse angle. The quadrato-jugal cup is small, and low down. The pterygoid condyle is perceptible, but not well defined. The posterior portion of the mandibular articular surface is bulky, especially on its outer side; the anterior is also large. These points indicate a certain resemblance to the Hoopoe, and an inspection of the figures will show that the quadrate bone well bears out the suggestion that the Celeomorphæ are intermediate between the Coracomorphæ and the Coccygomorphæ (HUXLEY, *loc. cit.*, p. 468).

We have not yet any examples of the Swifts, Humming-birds, or Goatsuckers.

CORACOMORPHÆ.

In the Rook the capitula are distinct and separate. The shaft of the bone is

Fig. 19. CORVUS FRUGILEGUS.

very stout and broad, the anterior process long and thick. The quadrato-jugal cup is small, deep, and round, and is placed quite at the postero-inferior angle of the bone. The pterygoid condyle is distinct, but is not so neatly defined as in most of the Desmognathæ. The mandibular articulation is of the simple type that we have spoken of as "normal;" its anterior condyle is rather large.

The Lyre-bird furnishes us with an example of the lower Coracomorphæ

Fig. 20. MENURA SUPERBA.

extremely remote from the Corvidæ; but the quadrate bones of the two are very similar indeed. The two capitula, however, are not so distinctly separate, or rather, perhaps, the external one is in part degenerate.

In both of these forms the quadrate strikes us as somewhat thick and clumsy, and less specialized or more primitive than that of the majority of the Desmognathæ.

Schizognathæ: I.—Cecomorphæ.

This is one of the more polymorphic groups, and we have studied the quadrate in four members of its principal types, the Petrel (and Albatross), the Grebe, the Razorbill, and the Gull.

In the Fulmar Petrel (*Procellaria glacialis*) the quadrate is short and broad. The capitula are small, rounded, and distinctly separate. The anterior process is of

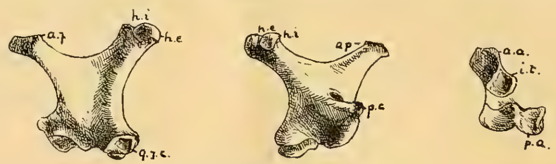

Fig. 21. Procellaria glacialis.

moderate size. The quadrato-jugal cup is well marked, and placed low down at the postero-inferior angle. The pterygoid condyle is imperfectly severed from the mass of bone below. The mandibular articular surface has a large accessory trochlea on the outer sides of its anterior condyle, and the posterior portion is transversely elongated, and its external half is somewhat hollowed out.

The Albatross is quite similar to the above.

In the Grebe the quadrate is more delicately formed. The capitula are small, the anterior process very long, and the pterygoid condyle distinct. The quadrato-

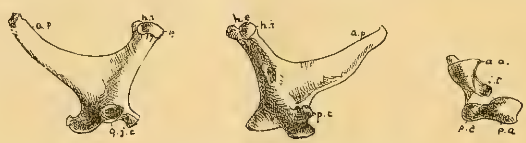

Fig. 22. Podiceps cristatus.

jugal cup is more nearly in the middle of the inferior border of the bone. The anterior mandibular condyle has a very perfect external accessory trochlea.

In the Gull the bone is broad, but with a slender neck. The capitula are rather more deeply cleft than in the former species. The anterior process is short,

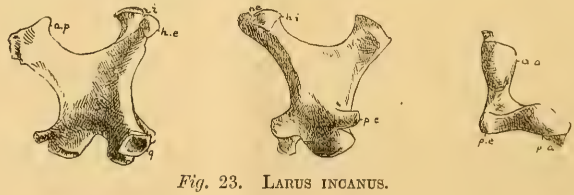

Fig. 23. Larus incanus.

broad, and truncated. The pterygoid condyle is elevated in an exceptional degree. The deep ovoid quadrato-jugal cup is placed at the postero-inferior angle. The mandibular articular surface is normal, lacking the accessory trochlea.

The quadrate of the Tern very closely resembles that of the Gull in all essential

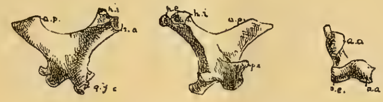

Fig. 24. Sterna hirundo.

features. The quadrato-jugal cup is singularly small.

In the Razorbill the capitula are small and deeply separate. The shaft of the bone is slender, and the anterior process of moderate size. The quadrato-jugal cup

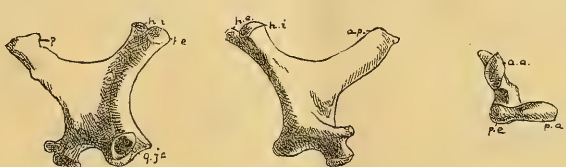

Fig. 25. Alca torda.

is deep, and situated postero-inferiorly. The pterygoid condyle is much raised. The mandibular articulation is of the normal pattern.

We have examined, by Dr Traquair's permission, the quadrate of a Great Auk's skeleton, recently acquired for the Museum of Science and Art, Edinburgh. It corresponds with the Razorbill's very exactly, the only difference perceptible being that the mandibular condyles are rather more massive.

From the foregoing description and figures, it is plain that the quadrates of the Gull and the Razorbill are, comparatively speaking, alike, and that in a less degree the Petrel and the Grebe resemble one another.

The Gull and the Razorbill agree in the deeply-cleft capitula, the blunt square anterior process, the high pterygoid condyle, and the absence of the accessory trochlea.

The Petrel and the Grebe differ indeed in general form, but possess in the accessory trochlea a common feature.

There are not wanting other characters, as, for instance, Nitzsch's pterylographic figures will show, to corroborate this alliance of the Procellariidæ and Colymbidæ on the one hand, and of the Laridæ and Alcidæ on the other. A close alliance between the Gulls and the Grebes, as suggested by Huxley (*la. cit.*, p. 458), is not borne out at any rate by the quadrate bone.

As regards affinity with other groups beyond the limits of the Cecomorphæ, it will be seen that the quadrate of Larus is exceedingly like that of the Godwit, our one example of the Charadriomorphæ, a fact in support of a long-suspected relationship maintained by NITZSCH, L'HERMINIER, GARROD, PARKER, NEWTON, FÜRBRINGER, and others. But if any resemblance is to be found with the Spheniscomorphæ, it appears not in Alca, as we might be led to expect, but in Procellaria.*

II.—SPHENISCOMORPHÆ.

In the Penguin, the body of the quadrate bone is broad and stout, but the

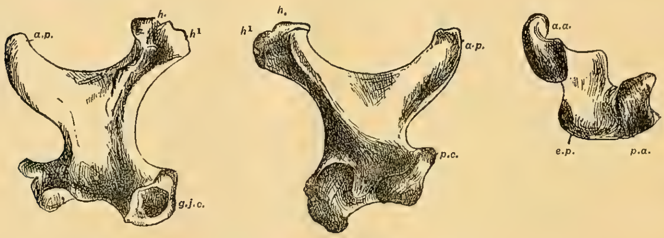

Fig. 26. SPHENISCUS DEMERSUS.

neck is slender and rather long. The head is crossed by a faint groove, which imperfectly divides it into two rudimentary capitula. The accessory process is of moderate size, and curved upwards. The quadrato-jugal cup is very deep, and situated at the postero-inferior angle. The pterygoid condyle is not separated off from the mass of bone beneath it. The posterior portion of the mandibular articular surface seems to be deficient on its inner side, or rather, perhaps, its internal condyle is diminished by the breadth of the trochlear groove; the anterior condyle passes into a broad trochlear surface on its outer side. A low grade of specialisation is indicated by the undivided head and the undifferentiated pterygoid condyle, which, however, are not sufficient to give the Penguin's quadrate the least resemblance to that of a Ratite. It is hard, indeed, to compare the Penguin's quadrate with any other.†

* FORBES *(Report on Challenger Petrels*, p. 62) denies the existence of any close connection between the Gulls and Petrels, and approximates the latter to the Ciconiidæ and to the Steganopodes. "I cannot understand," he says, "Professor HUXLEY's remark (P.Z.S., 1867, p. 455) that the Gulls grade insensibly into the Procellariidæ." It will be seen that the quadrate bones help to support this conclusion.

† FÜRBRINGER (*Morphologie d. Vögel*, 1888, Vol. II., p. 1147) finds it likewise hard to connect the Penguins with any other order. He denies their close affinity with Alcidæ, and finds a more probable direct relationship with the Colymbo-Podicipidæ.

III.—Charadriomorphæ.

We have only examined a single Charadriomorph quadrate, that of the Bar-tailed Godwit. The two capitula are not deeply cleft asunder; there is an indication

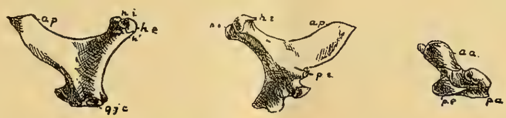

Fig. 27. Limosa rufa.

of an accessory head. The anterior process is long, broad, compressed, and set on at a very obtuse angle to the shaft. The quadrato-jugal cup is distinct but small. The pterygoid process is very well marked. In the mandibular articular surface the anterior condyle is bevelled off on its external aspect, without exactly forming an accessory trochlea.

The quadrate bears out the received affinity of the Charadriomorphæ to the Cecomorphæ and the Geranomorphæ. Its resemblance to the Gull's has been already noted, and is shown particularly in the imperfect separation of the capitula, and in the great size of the pterygoid process. It is more like the Crane's than either of our other types of Geranomorphæ.

IV.—Geranomorphæ.

Of the members of this Huxleyan group, we have studied the Crane, the Bustard, and the Water Rail.

The quadrates of all these forms are comparatively alike, and on the whole support the naturalness of the group.

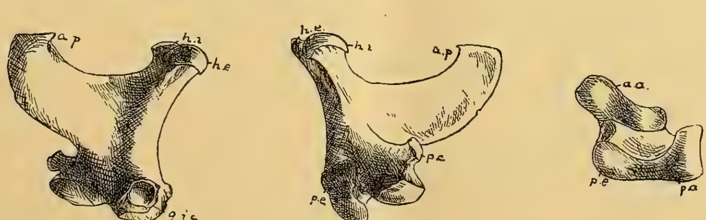

Fig. 28. Grus cinerea.

In all the capitula are distinctly separate: the anterior process is large, broad, and upcurved: the pterygoid condyle is on a prominent eminence: the quadrato-jugal cup is deep, with raised margins, and is placed close to the postero-inferior angle of the bone.

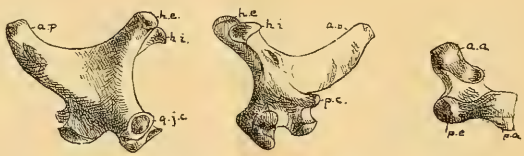

Fig. 29. RALLUS AQUATICUS.

In the Crane and the Rail the anterior mandibular condyle is produced on its external side into a broad flat accessory trochlea, precisely like that of the Stork. The Bustard differs from the other two in the absence of this trochlear surface, as

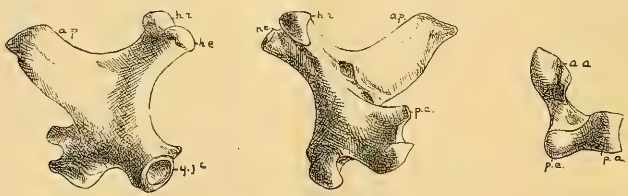

Fig. 30. OTIS TARDA.

well as in the somewhat wider separation of the capitula. These characters scarcely indicate an affinity on the part of Otis to the Charadriomorphæ rather than to the Gruidæ, as FÜRBRINGER suggests; but, on the other hand, the unmistakable likeness of the Crane's quadrate to that of the Stork adds another to the long list of characters summed up by FÜRBRINGER, in which Grus resembles the Pelargo-Herodii (*loc. cit.*, II. 1205).

V.—ALECTOROMORPHÆ *(excluding Pterocles).*

The quadrates of the Fowl and the Turkey are very similar. We have chosen the larger species for representation.

Fig. 31. MELEAGRIS GALLOPAVO.

The quadrate is exceedingly peculiar. The neck of the bone is unusually long and slender, and is terminated by a round capitulum, representing apparently* not the undivided head of the Ratitæ, but the outer or squamosal capitulum of other birds. The inner or prootic capitulum is almost aborted, and is represented only by a roughened facet some way down the neck of the bone. The anterior process is long and narrow. The quadrato-jugal cup is quite imperfect, and is represented by an irregular notch cut out of the postero-inferior angle of the bone. The pterygoid condyle is not separate from the mass of bone below. The articular surface is peculiar, and consists of a single oblique trochlear surface.

In the condition of the quadrato-jugal cup and the pterygoid process we have features which we have regarded as distinctly archaic; but the degenerate inner capitula and the peculiar mandibular articulation seem to be acquired features. This quadrate gives us no help in deducing the relationship of the Fowls to any of the foregoing groups.

VI.—Peristeromorphæ.

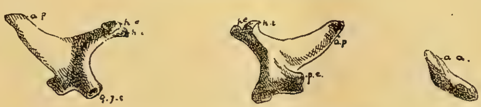

Fig. 32. Columba palumbus.

In the Common Pigeon the neck of the quadrate is moderately long, and directed somewhat backwards. The capitula are distinct and separate. The anterior process is rather long, broad, and pointed. The quadrato-jugal cup is very small but neatly formed, and placed quite at the postero-inferior angle. The pterygoid process is confluent with the mass of bone below. The mandibular articulation is similar to, but even less perfect than that of the Fowl. The two last characters are manifestly points of affinity with the Alectoromorphæ.

Fig. 33. Pterocles arenarius.

In the Sandgrouse the capitula are distinct and widely separate, and the neck has a backward inclination even more marked than in the Pigeon. The anterior process is moderately large, and the body of the bone below is curiously narrow. The quadrato-jugal cup is small, well-formed, and low down. The pterygoid process is more distinct than in Columba. The mandibular articulation is almost normal, with a slightly unusual antero-posterior extension of its anterior part. In

* See Parker, *Skull of Fowl*, Phil. Trans., Vol. 159, p. 793, 1870.

spite of this well-formed mandibular articulation, the quadrate of Pterocles is not very dissimilar to the Pigeon's. It is much more divergent from the Fowl's, however, instead of being intermediate between the two.

ODONTORNITHES.

In commencing this study, we had from the first the hope of finding some evidence as to the relationship of the Odontornithes in the quadrate bone, which Professor MARSH figures* for the two genera *Hesperornis* and *Ichthyornis*, without drawing any conclusions from its characters.

Professor PARKER, commenting on OWEN'S account of the skull of *Notornis*,† says, "this knob-like [pterygoid] process on the os quadratum of the great Notornis is to the morphologist 'a nail fastened in a sure place;' and on it, supposing a mere fragment of this os quadratum had been all we possessed of this bird, might have been hung the whole weight of my assertion, viz., that the bird in question is not a congener of the *Dinornis*." We should be inclined to make precisely the same observation regarding the quadrate of the *Hesperornis* and *Ichthyornis*.

The positions in which Professor MARSH has figured his quadrates are somewhat different from those that we have adopted; and it is far from easy to understand from his figures the exact shape of the bones. But we see from his figures of the quadrate of *Hesperornis* that this quadrate is a bone with a long, slender, well-formed shaft, a head whose two capitula are defined though not deeply cleft, a slender pointed (?) anterior process springing from the shaft at some distance from the head, a distinctly prominent pterygoid process, and a deep quadrato-jugal cup. By everyone of these characters the bone is far removed from the Ratite type. It seems to resemble the Grebe's more than any other quadrate that we have figured, and if we rightly understand MARSH'S view of the inferior surface (*loc. cit.*, Pl. ii. fig. 6*c*), which appears to show chiefly what we have called the anterior condyle, with its external trochlear surface, that region of the bone does not discredit the affinity that its other characters suggest.

The quadrate of Ichthyornis appears to be less perfectly preserved. In MARSH'S figures (*loc cit.* p. 121, woodcuts) we are struck by the bulkiness of its lower extremity, by its exceedingly prominent pterygoid condyle, and by its minute quadrato-jugal cup. The anterior process is lost, but from the appearance of its broken base it seems to have been stout and broad. In all these characters, the quadrate of Ichthyornis very strikingly resembles that of the Tern.

* *Odontornithes*, 4to. Washington, 1880.

† *On the Skull of the Ostrich*. Phil. Trans., Vol. 156, p. 166. 1866.

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Studies from the Museum of Zoology

IN UNIVERSITY COLLEGE, DUNDEE.

EDITED BY

D'ARCY W. THOMPSON,

Professor.

II. RECHERCHES SUR LA MORPHOLOGIE DE LA MAIN

CHEZ LES PINNIPÈDES.

PAR

HENRI LEBOUCQ,

Professeur à l'Université de Gand.

DUNDEE:

Printed for the Museum.

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Recherches sur la morphologie de la main chez les Pinnipèdes.

Par H. LEBOUCQ, *Professeur à l' Université de Gand.*

Après les remarquables monographies de MURIE [1] il semble qu'il doive rester peu de chose encore à signaler sur la morphologie des extrémités des Pinnipèdes. Aussi me suis-je proposé d'examiner seulement quelques points sur lesquels l'attention a été appelée d'une façon moins spéciale, ou qui ont été inexactement interprétés par les auteurs.

Pour faire suite aux recherches que j'ai publiées antérieurement,[2] j'ai examiné d'une manière spéciale la structure du carpe.; j'ai étudié ensuite le mode de développement des extrémités des doigts qui, chez les carnassiers amphibies ont évolué dans une direction totalement différente de celle de leurs congénères terrestres.

Les principaux matériaux pour ces recherches m'ont été fournis par mon collègue et ami M. D'ARCY THOMPSON, de Dundee, qui a généreusement mis à ma disposition des pièces précieuses de son laboratoire. Je suis heureux de saisir cette occasion pour lui témoigner toute ma gratitude. Je dois également remercier bien vivement M. L. CAMERANO, de Turin, qui m'a envoyé des doigts d'un fœtus d'otarie. Il ne m'a pas été possible d'examiner des extrémités d'adultes à l'état frais ou conservées en chair dans l'alcool. C'est une lacune regrettable que l'étude de squelettes de collections n'a pu que très imparfaitement combler. Sur ceux-ci en effet, toutes les parties non osseuses sont racornies par la dessiccation ou ont même été enlevées. C'est donc surtout sur des pièces fœtales qu'ont été faites les recherches dont l'exposé va suivre.

I.

Carpe.—Au point de vue du nombre des éléments, le carpe des pinnipèdes ressemble à celui des autres carnassiers. Il y a dans la première rangée un grand os correspondant au radius, un plus petit sous le cubitus et un pisiforme intercalé entre le précédent et le cubitus.

Le grand os de la première rangeé, le *radio-intermedium* des auteurs est un *radio-intermedio-centrale.* Telle est aussi la signification de ce premier os chez les

(1) *J. Murie.*—Researches upon the Anatomy of the Pinnipedia.—Transact. Zool. Soc. London. Vol. vii. et viii., 1872-74.

(2) *H. Leboucq.*—Recherches sur la morphologie du carpe chez les mammifères.—Archives de Biologie, v., 1884.

carnassiers terrestres comme Flower l'a déjà demontré en 1871[1] sur un squelette de jeune chien, et comme je l'ai trouvé d'une manière constante chez le chien et le chat à l'état fœtal.[2] Chez un fœtus de *Phoca grönlandica* long de 5 centimètres, on voit le cartilage subdivisé en trois parties dont les deux supérieures sont le radial et l'intermédiaire, et l'inférieure allongée est un central. De même que chez le plus grand nombre des mammifères la soudure des trois éléments a déjà commencé du côté palmaire, alors que du côté dorsal ils sont encore parfaitement libres. C'est donc sur les coupes les plus rapprochées de la face dorsale que la division se voit le mieux (Fig. 1). La soudure des trois éléments paraît marcher assez rapidement. Chez un fœtus de phoque de la même espèce que le précédent mais de grandeur double, le *radio-intermedio-centrale* n'est plus formé que d'un cartilage unique et la trace de la séparation primitive n'est plus que vaguement indiquée. Chez un fœtus de morse long de quinze centimètres les trois cartilages sont soudés, mais la disposition des capsules cartilagineuses et de la substance fondamentale indiquent encore manifestement la division primitive (Fig. 2).

Je n'ai pas examiné le carpe fœtal de l'otarie, mais je ne doute pas que le même fait s'y présente.

Le central soudé au radio-intermédiaire se retrouve chez l'adulte sous forme d'une apophyse portée par le premier os de la première rangée du côté distal de sa face dorsale, et s'enfonçant entre les os de la seconde rangée (Fig. 5). Cette apophyse est partout très évidente, voir par exemple le squelette fœtal d'otarie qui a servi à la monographie de Camerano,[3] et le *scapho-lunatum* d'otarie adulte représenté par Murie.[4]

Le cubital du carpe, second élément de la première rangée, est petit, cuboïde, et n'est pas toujours articulé directement avec le précédent. Sur un squelette de *Leptonyx monachus* de la collection de l' Université de Gand, les deux os du premier rang sont unis par un ligament de manière que le quatrième os du second rang s'intercale entre les deux du premier.[5] Chez les fœtus de phoque que j'ai examinés il y a aussi entre les cartilages du premier rang un écartement plus considérable qu' entre les autres.

Le pisiforme est petit chez le phoque et engagé entre le cubitus et l'os cubital du côté palmaire. Il est plus considérable chez le morse, surtout à l'état fœtal. La seconde rangée renferme quatre os ; les *carpalia* 1, 2, 3 et 4+5. Sur un squelette

[1] *W. H. Flower.*—On the composition of the carpus of the dog.—Journ. of Anat. and Phys., VI., 1871, p. 62.

[2] *H. Leboucq.*—Recherches, &c., pg. 72. Fig. 45—48.

[3] *L. Camerano.*—Ricerche intorno all' anatomia di un feto di otaria jubata.—Mem. dell' Accad. delle Scienza, Torino, 1882. Tav. II., fig. 25.

[4] *J. Murie.*—Descriptive Anatomy of the Sea-lion.—Trans. Zool. Soc. London. Vol. VIII., pl. 77, fig. 24.

[5] V. aussi : *Cuvier.*—Ossements fossiles. Paris, 1823. Tom. V. 1er p. Pl. 17, fig. 12.

de jeune phoque (fig. 5) le premier, le trapèze semble divisé en deux par un sillon vertical sur la face dorsale. Chez le fœtus j'ai trouvé un étranglement sur le premier cartilage carpien (fig. 1) mais pas de division proprement dite. Il est possible qu'à un stade plus jeune la moitié radiale du trapèze forme un nodule cartilagineux distinct se soudant rapidement avec le reste de cet élément du carpe. Cette partie serait ce que l'on appelle généralement un sésamoïde radial, et que l'on doit interpréter probablement comme la base d'un rayon précédant le pouce. (1) Ce rudiment de praepollex est très répandu chez les mammifères (Bardeleben).

Le trapézoïde, articulé avec le deuxième métacarpien, se dirige obliquement du côté radial de manière que chez le fœtus de phoque et de morse il atteint le bord et sépare complètement le trapèze du premier os de la première rangée. A première vue, ce trapézoïde engagé entre les deux rangées du carpe ressemble à un central. Giebel (2) dit d'une façon formelle que le central existe chez le phoque et il reproduit la figure de Cuvier (Ossem. Foss.) sur laquelle il désigne le trapézoïde comme central et le carpien comme l'extrémité proximale du deuxième métacarpien. L'interprétation de Cuvier est exacte. Le central existe en effet, nous avons vu plus haut où on doit le chercher.

Il n'y a rien de particulier à ajouter à propos des deux derniers éléments de la rangée distale du carpe.

II.

Les extrémités des pinnipèdes sont profondément modifiées dans leur forme extérieure ; elles sont élargies et aplaties de manière à être transformées en nageoires. Cette adaptation à la vie aquatique est phylogéniquement de date récente. En effet l'adaptation s'accentue davantage pendant le développement ontogénique. Chez le fœtus, la forme des extrémités se rapproche plus de celle des autres carnassiers que chez l'adulte. En comparant, par exemple, l'extrémité antérieure de fœtus de morse (Fig. 3) avec celle d'adulte (Fig 4) on y constate une différence assez sensible. La main du fœtus rappelle encore assez bien celle du phoque (qui s'écarte le moins de la main des carnassiers terrestres). La palmure des doigts n'est pas très développée, le bout des doigts est libre, et des ongles crochus font saillie à la face dorsale. La main du morse adulte est devenue une véritable nageoire large et plate, rappelant déjà la nageoire des cétacés. Les ongles sont devenus rudimentaires et au lieu de terminer le bout des doigts ils semblent avoir opéré une migration dans le sens proximal. Je ne sais comment se présente l'extrémité antérieure de l'otarie dans les premiers stades de son développement. Le fœtus de Camerano déjà très avancé dans son évolution, a une nageoire assez semblable à celle de l'adulte ; sur

(1) Le correspondant de ce nodule existe au pied à l'état libre. Chez les fœtus de phoque et de morse la base d'un *praehallux* se présente comme un cartilage bien développé du côté tibial du 1er tarsien.

(2) *Bronn's* Thierreich.—Mammalien, p. 520. Pl. 88, fig. 1.

cette dernière toutefois on remarquera en la comparant à celle du fœtus, l'atrophie des ongles et leur migration proximale beaucoup plus prononcées encore que chez le morse. Examinons les changements de structure qui correspondent à ces transformations extérieures.

La section dorso-palmaire du premier doigt de fœtus de morse (Fig. 6) nous montre la phalange unguéale à l'extrémité de laquelle commence à apparaître la coiffe d'ossification périchondrale. L'ongle est bien formé et dépasse le bout de la phalange. Du côté palmaire se voit une saillie beaucoup plus considérable que l'extrémité terminale du doigt dans laquelle s'engage la phalange. Dans l'axe de cette saillie se trouve du tissu conjonctif fibrillaire, très peu vasculaire, partant de la face palmaire de la base de la phalange distale et recevant une expansion du tendon fléchisseur qui se termine en cet endroit. Différemment de cet axe, le tissu sous-dermique est très riche en vaisseaux. Si nous comparons cette coupe de doigt de morse à celle d'un autre mammifère, il ne sera pas difficile de voir que cette saillie répond à la pulpe du doigt. L'encoche profonde entre celle-ci et le lit unguéal, remplie de grandes cellules épidermiques, est une formation constante chez tous les mammifères d'après les recherches de Boas ; [1] cet auteur l'a désignée sous le nom de *Sohlenhorn* (corne plantaire) par extension d'une appellation surtout applicable aux ongulés.

Il nous sera facile d'interpréter maintenant la coupe de doigt fœtal d'otarie [2] (Fig. 7). L'ossification assez avancée de la phalange distale nous montre que le développement est plus avancé que chez le morse. L'ongle forme une lamelle cornée mince dépassant le sommet de la phalange. La pulpe du doigt a acquis un volume énorme, elle a le double de la longueur de la phalange. Pour le reste la structure est la même que celle du morse. La partie axiale est formée de tissu conjonctif condensé et la fig. 8 montre à un grossissement plus fort, l'épanouissement du tendon fléchisseur dans cet axe. Remarquons aussi que la partie cornée intermédiaire entre l'ongle et la pulpe du doigt s'est considérablement réduite de manière à ne plus former qu' une simple encoche épidermique. Il résulte de là, que le prolongement pulpaire s'est redressé dans la direction dorsale et tend à se mettre dans l'axe du squelette osseux du doigt.

En fail de pièces provenant d'animaux adultes je n'ai pu examiner qu' une phalange terminale de la main de l'otarie. Le squelette conservé à sec fait partie de la collection de l'Université de Liége ; mon collègue M. Ed. Van Beneden a bien voulu mettre la pièce à ma disposition. Le prolongement axial de la pulpe du doigt est conservé en rapport avec le bout de la phalange et se présente comme une lamelle d'aspect fibreux ou de cartilage desséché se plaçant directement dans l'axe

(1) *J. E. V. Boas.*—Ein Beitrag zur Morphologie der Nägel, Krallen, Hufe und Klauen der Säugethiere.—Morphol. Jahrb. IX., 1884.

(2) Fœtus décrit par Camerano ; long de 43 ctm. de l'extrémité du museau au bout de la queue.

de la phalange osseuse. A première vue on dirait que toute l'extrémité distale de la phalange est restée cartilagineuse, mais il suffit de faire une coupe à travers cette lamelle pour pouvoir s'assurer, après l'avoir fait gonfler dans l'eau, qu'elle est formée surtout par du tissu conjonctif condensé de même que le prolongement de la pulpe du doigt chez le fœtus (Fig. 9).

La position de la lamelle fibreuse est-elle aussi directement axiale à l'état frais, ou dépend-elle de la dessiccation ? Je ne saurais me prononcer sur ce point d'une manière positive. Je crois, cependant, que la direction axiale est plutôt la position naturelle puisque nous avons déjà vu par une transition progressive la pulpe du doigt se redresser vers la face dorsale chez le fœtus. En outre, cette position est la même sur toutes les phalanges des mains et des pieds du squelette que j'ai observé. Enfin ces appendices sont décrits par les auteurs comme cartilages *terminaux* des phalanges.[1]

Ces modifications dans le domaine de la pulpe des doigts sont directement en rapport avec celles dont les ongles sont le siége. Nous avons déjà constaté en examinant les caractères extérieurs des extrémités chez le morse et l'otarie à l'état fœtal et adulte, que dans le premier état les ongles sont plus rapprochés de l'extrémité terminale du doigt que dans le second. Cette différence de position est surtout remarquable chez l'otarie ; d'après la figure de Murie, le rudiment d'ongle du pouce se trouve à près de 20 centimètres du bord libre de la nageoire. Il est évident qu' il n'est pas question ici de migration proprement dite de l'ongle dans le sens proximal. Nous voyons seulement se présenter d'une manière exagérée ce qui d'après les recherches de Zander[2] se rencontre même chez l'homme : la prédominance d'accroissement des parties situées du côté palmaire ou plantaire des doigts sur les parties dorsales. La migration de l'ongle n'est donc qu' apparente. Il continue à occuper le véritable bout du doigt correspondant à l'extrémité distale de la dernière phalange. Il en résulte que toute la partie de la face dorsale de la nageoire comprise entre le bord libre et l'ongle rudimentaire est en réalité une partie palmaire.

A cette pseudo-migration de l'ongle sont intimement liées la réduction de la bordure cornée entre l'ongle et la pulpe du doigt (*Sohlenhorn*), et la rudimentation de l'ongle lui-même. Déjà chez le fœtus d'otarie que j'ai examiné, cette bordure n'est plus représentée que par une simple encoche épidermique. Chez l'adulte, d'après les figures de Murie, toute trace de cette partie semble avoir disparu. L'ongle rudimentaire a l'aspect d'un bourrelet arrondi, entouré d'une légère dépression du tégument. Les modifications qui se passent dans la région unguéale des pinnipèdes, et en particulier du morse et de l'otarie sont donc simplement dues à l'adaptation à la vie aquatique, nécessitant la transformation des extrémités en nageoires étalées en surface et allongées à leur extrémité. Cet allongement a porté surtout sur les

(1) *Murie*, loc. cit. Anat. of the Sea Lion, p. 533.

(2) *R. Zander*.—Die frühesten Stadien der Nagelentwickelung—Arch. f. Anat. und Entwick. 1884, p. 103.

parties situées du côté palmaire de la région unguéale (pulpe du doigt), lesquelles en progressant dans le sens distal, ont produit l'atrophie de toute la région unguéale (*Sohlenhorn* et ongle proprement dit). C'est par un processus morphologique semblable que se fait chez l'homme la réduction du *Sohlenhorn* bien que le but à atteindre soit totalement différent, puisqu' il s'agit ici du développement de la pulpe des doigts comme appareil tactile. Les considérations générales émises à ce sujet par GEGENBAUR [1] sont donc également applicables aux pinnipèdes. On arrive ainsi, en passant par les ongles des primates, à rattacher la forme primitive de la griffe à l'ongle rudimentaire de l'otarie adulte.

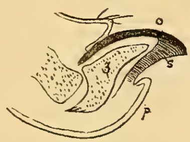


FIG. I.

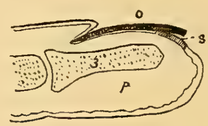


FIG. II.

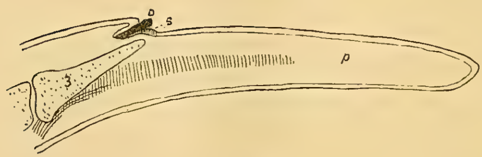


FIG. III.

Fig. I.—Griffe de carnassier (chien) d'aprés Gegenbaur.
Fig. II.—Doigt humain.
Fig. III.—Doigt d'otarie.

Les 3 figures schématiques portent les mêmes indications :

o. ongle.
s. *Sohlenhorn* (encoche épidermique sous-unguéale).
p. pulpe du doigt (avec axe fibreux chez l'otarie).
3. phalange distale.

Il est important de remarquer que l'allongement des doigts, quelque considérable qu'il soit, laisse absolument intacte la constitution typique du squelette. Les phalanges s'allongent, mais le nombre n'est pas dépassé. L'allongement relatif des phalanges s'observe très bien dans le développement ontogénique. En examinant un doigt de deux fœtus de phoque à des âges différents, on peut voir que l'allongement porte surtout sur les phalanges terminales. En prenant comme points de repère la longueur relative du premier métacarpien et de la phalange unguéale du pouce on voit que chez le plus petit fœtus, celui de $0^{m.}$ $05^{c.}$ la phalange n'a que la moitié de la longueur du métacarpien, tandis que chez celui de $0^{m.}$ $10^{c.}$, la phalange

[1] *Gegenbaur.*—Zur Morphologie des Nagels. Morpholog. Jahrb. X. 1885, pg. 476.

égale le métacarpien en longueur. Vient ensuite l'allongement de la pulpe des doigts peu considérable chez le phoque, mais qui joue un rôle important chez le morse et l'otarie.

Un naturaliste Américain, RYDER [1] a cru voir dans cet allongement des doigts des pinnipèdes le premier degré de la transformation qui aboutit à l'hyperphalangie des cétacés. Je ne puis pas admettre cette manière de voir, quelque bien fondée que puisse paraître l'hypothèse de RYDER à laquelle se sont ralliés des anatomistes aussi compétents que BAUR et M. WEBER. Il est certain qu' au point de vue fonctionnel, tout le squelette du doigt, portion osseuse et prolongement fibreux, remplit le même rôle, mais au point de vue morphologique il y a une différence fondamentale à établir entre le squelette typique et l'axe fibreux de la pulpe du doigt. Chez les cétacés, on ne peut, à aucune époque du développement, établir une distinction morphologique entre les deux ou trois phalanges proximales et les distales. L'apparition des points d'ossification marche d'une manière graduelle et régulière à partir de la première phalange, sans que dans ce processus aussi il soit possible, comme RYDER croit l'avoir observé, de voir un arrêt entre l'ossification de la troisième phalange et celle des autres. L'argumentation repose du reste sur une base inexacte. On a généralement admis que les phalanges surnuméraires des cétacés étaient une formation secondaire et que le nombre en était si peu limité qu' il s'en formait de nouvelles pendant le développement de l'individu de sorte qu' on en rencontrait plus chez l'adulte que chez le fœtus. J'ai trouvé tout au contraire sur les divers fœtus de cétacés que j'ai examinés, et dont plusieurs provenaient des collections de Dundee, le nombre de phalanges supérieur à celui de l'adulte ; dans le développement on voit les phalanges distales se réduire, et ce que l'on pourrait prendre pour des phalanges en voie de formation à l'extrémité distale des doigts chez l'adulte, ne sont que des phalanges fœtales devenues rudimentaires. J'ai publié une courte note sur ces recherches dans : *Anatomischer Anzeiger*, 1887, pag. 202 ; je compte y revenir ultérieurement dans un travail plus détaillé.

Je m'écarterais du plan que je me suis tracé en développant ici les motifs pour lesquels je considère l'hyperphalangie des cétacés comme une disposition héréditaire, j'ai du reste insisté sur ce point dans un autre travail. [2] Il me suffit d'avoir fait ressortir toute la distance qui sépare la nageoire atavique des cétacés, de l'extrémité transformée en nageoire par adaptation chez les pinnipèdes.

[1] *J. A. Ryder.*—On the genesis of the extra terminal phalanges in the Cetacea.—The American Naturalist, Oct. 1885, p. 1013.

[2] *H. Leboucq.*—Ueber das Fingerskelett der Pinnipedier und der Cetaceen.—Anatom. Anzeiger, 1888, p. 530.

EXPLICATION DES FIGURES.

Indications communes aux figures 1, 2 et 5.

R, radius ; *c*, cubitus.
r i c—radio-intermedio-centrale ;
u, ulnare ; *pi*, pisiforme.
1 à 5 carpiens de la deuxième rangée.
I. à V. métacarpiens.

Fig. 1.—Section transversale du carpe de fœtus de *Phoca grönlandica*, lg. $0^{m.}$ 05, × 15 diam.

Fig. 2.—Section transversale du carpe d'un fœtus de *Trichechus rosmarus*, × 15 diam.

Fig. 3.—Main droite du fœtus de morse précédent, vue de la face dorsale—$^1/_1$; doigts numérotés à partir du pouce.

Fig. 4.—Main gauche de morse adulte vue de la face dorsale (reproduction réduite de moitié de la fig. 8, pl. 53 de Murie, laquelle est aux $\frac{3}{10}$ de grandeur naturelle) ; les doigts numérotés comme précédemment.

Fig. 5.—Squelette du carpe d'un jeune *Phoca vitulina*, $^1/_1$.

Indications communes aux figs. 6 à 9.

a. phalange distale.
b. ongle.
c. encoche sous-unguéale (*Sohlenhorn*).
d. axe fibreux de la pulpe du doigt.
e. tendon extenseur.
f. tendon fléchisseur.
p. poil.

Fig. 6.—Section dorso-palmaire de l'extrémité du pouce du précédent fœtus de morse, × 25 diam.

Fig. 7.—Section dorso-palmaire de l'extrémité du 4^e doigt d'un fœtus d' *Otaria jubata*, lg. $0^{m.}$ 43 × 10 diam.

Fig. 8.—Section semblable à la précédente mais agrandie (Hartn. oc. 2 Syst. 4).

Fig. 9.—Coupe à travers l'appendice fibreux d'un doigt d'otarie. Squelette desséché (Hartn. oc. 2, Syst. 4).

Fig. 1.

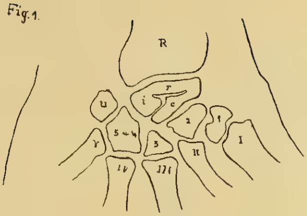
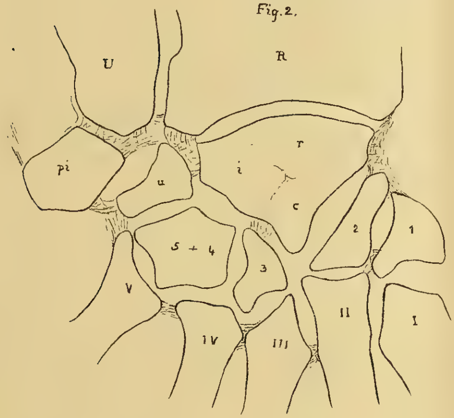


Fig. 3.

Fig. 4

Fig. 2.



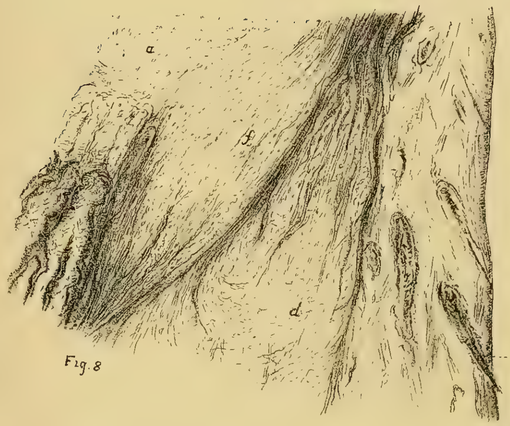


Fig. 8

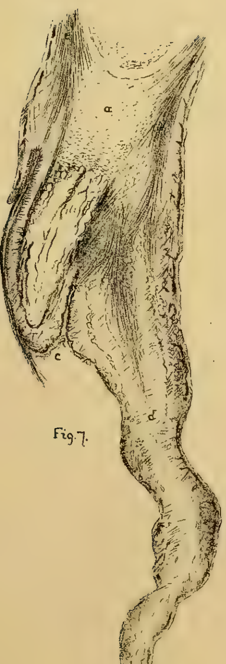


Fig. 7.

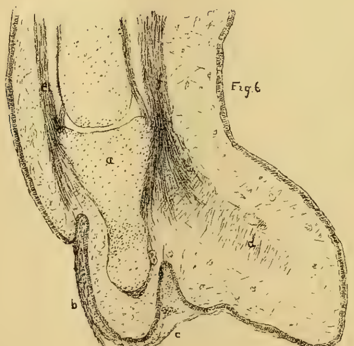


Fig. 6

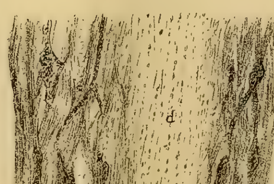


Fig. 9.

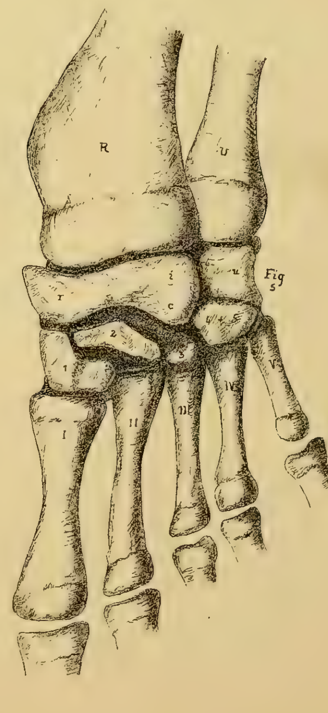


Fig. 5

Vol. I. No. 3.

Studies from the Museum of Zoology

IN UNIVERSITY COLLEGE, DUNDEE.

EDITED BY

D'ARCY W. THOMPSON,

Professor.

III. ON THE LARYNX AND HYOID OF MONOTREMATA.

BY

MARY L. WALKER.

DUNDEE:

Printed for the Museum.

January, 1889.

III. *On the Larynx and Hyoid of Echidna and Ornithorhynchus.*

By Mary L. Walker, *University College, Dundee.*

Great interest attaches to the monotreme larynx, not only on account of its obvious peculiarities, but also because it forms the basis of Dubois' remarkable theory of the morphology of the thyroid cartilage. According to Dubois the mammalian larynx is a composite structure. While the cricoid and arytaenoids are derived from the trachea, the thyroid cartilage is a derivation of the visceral skeleton, and is constituted out of two pair of post-hyoid visceral arches, *i.e.*, the fourth and fifth visceral arches, with their copula. In Amphibia and Reptilia these have not yet entered into the composition of the larynx at all: in Ornithorhynchus they still remain as separate arches: in higher mammalia the thyroid gives frequent indications of its primitive constitution, as for instance in the bifurcation dorsally into anterior and posterior cornua, or in the presence of a thyroid foramen which is a relic of the original separation of the two arches.

Of the few available descriptions, the older ones, for instance that in Todd's Cyclopædia, are unsatisfactory and inadequate. Of more recent accounts, the most complete is Dubois' paper,* dealing with the larynx of Ornithorhynchus, and it is in points at variance with the account given by Wiedersheim† of the larynx of Echidna.

Our specimen of Ornithorhynchus was not in very good preservation, and the laryngeal muscles were imperfectly studied. Rough sketches and notes were, however, taken of them some time ago, when the larynx was prepared for our Museum. The Echidna's larynx was furnished us by Professor Charles Stewart, and the dissected preparation is now in the Hunterian Museum. It had been removed from the body, together with a portion of the pharynx, and accordingly the extrinsic laryngeal and the pharyngeal muscles could not be properly investigated.

The Hyoid Bone.

In Echidna and Ornithorhynchus, the hyoid consists of a body and two pair of arches or cornua, which remain permanently separate from it.

In Echidna, the body of the hyoid is well ossified, large, and transversely elongated: its anterior margin presents two concave facets, separated by an interspace, for articulation with the anterior cornua; the postero-lateral angles are

* Dubois, *Zur Morphologie des Larynx.* Anat. Anzeiger, I. Jahrg., Nos. 8, 9, Sept. Oct., 1886.

† Lehrbuch d. vergl. Anatomie, 1st edit., p. 658.

truncated to form somewhat large concave facets for the attachment of the posterior cornua. The anterior cornua consist (so far as they could be examined) of three ossified segments, but they had been cut short, and their cranial extremities could not be studied. The first or proximal segment passes almost directly forwards. The posterior cornua passes outwards and backwards from its articulation with the body of the hyoid. It forms a broad osseous plate, which runs parallel for rather more than half its length with the anterior portion of the thyroid, and then more posteriorly becoming cartilaginous, fuses with it. From the anterior margin of the cornua a rounded process projects forwards, whose outer edge slopes directly backwards, to be continuous with the outer margin of the anterior thyroid horn.

In Ornithorhynchus, the body of the hyoid is much smaller, and transversely fusiform. The articular surfaces for the cornua are not well defined upon it, and, owing to its small size, the anterior and posterior cornua articulate with one another outside its lateral angles to a greater extent than with it. The anterior cornua are slender. Their proximal segments pass forwards parallel with one another, and are slightly ossified; distally the cornua curve outwards and backwards, and are unossified. The posterior cornua pass outwards and backwards, as rather broad strips of imperfectly ossified cartilage: for two-thirds of their length a wide space separates them from the anterior edge of the thyroids, but close to this origin from the body of the horn they are for a short space in contact with the thyroids, with which they again come into relation at their outer ends, an oblique line of fissure in the cartilage separating the one from the other. At the antero-lateral angle, a process more square and definite in outline than in Echidna passes forward from the posterior cornua.

The Thyroid Cartilages.

It is impossible to doubt that the elements above described represent the body or copula in the two pair of cornua of the hyoid in higher forms; and it is equally impossible to avoid recognizing, as Dubois has already shown, that the structures next to be described correspond to the thyroid cartilage of more ordinary types.

In Echidna, a median cartilaginous element, rectangular, narrow, and elongated from before backwards, articulates with the body of the hyoid. In relation with it are two pair of cornua. Together, these cornua with their median piece or copula represent the thyroid cartilage. The anterior cornua articulate with the copula to a very slight extent; to a greater extent they come in contact with the posterior margin of the body of the hyoid. Passing outwards and broadening as they go, they lie parallel with and separate from the posterior hyoid cornua for about half their length; after which they fuse with the latter, as has been already described, and extend backwards till each terminates in two short processes at its posterior angle. The posterior cornua are separate from and overlapped by the anterior.

Their inner margins articulate with, but posteriorly extend beyond, the copula. Broad at first, they narrow as they proceed backwards, and, embracing the cricoid, terminate underneath the more internal of the posterior processes of the anterior cornua.

In Ornithorhynchus, the copula of the thyroid is smaller and narrower. Its anterior cornua come into contact, to a very slight extent, with the body of the hyoid, and to a greater extent proportionately than in Echidna with their own copula. Their anterior margins, at first in contact with the posterior hyoid cornua for a short distance, are next separated from them by an ovoid space occupied by membrane, and again, as we pass outwards, come into close contact and union with them. In this region the thyroid cornua, narrow anteriorly, expand into a broad plate in whose posterior margin a semicircular notch leaves two square posteriorly-directed processes. A strong ridge passes backwards from the line of junction with the hyoid cornua to a point internal to the inner process. The posterior thyroid cornua, attached to the copula by a narrower origin, corresponds in its other relations to the same part in Echidna.

The Cricoid Cartilage.

In Echidna, the cricoid forms an imperfect ring of considerable breadth, and of the same diameter as the trachea. The anterior rings of the trachea are imperfectly defined, and are incomplete dorsally; a broad notch of equal breadth is cut out of the dorsal aspect of the cricoid. The surface of the cricoid is marked by parallel transverse grooves, which do not meet in the middle lines. Anteriorly, close to the arytenoids, this broad notch is continued into a narrow slit. Two small procricoid cartilages are present in Echidna. The posterior one lies over the narrow anterior part of the notch in the cricoid, and broadens in front where it lies partly over the arytenoids. The anterior procricoid is a T-shaped piece, lying transversely across the anterior end of the posterior.

In Ornithorhynchus, the upper rings of the trachea are also imperfect, but their ends are separated by a narrower interval. The notch in the cricoid is broader than the interspace between the ends of the tracheal rings, and does not extend to the anterior border of the cricoid. We did not detect procricoid cartilages similar to those in Echidna, but two small paired cartilages, evidently separated off from the arytenoids, lie dorsally between the latter and the anterior border of the cricoid.

Nothing remarkable, save their large size, is to be found in the arytenoid cartilages of either form.

Our specimen of Ornithorhynchus (an adult female) differs according to the above description from that figured by Dubois. In his specimen the two procricoids were distinct, the body of the hyoid was larger and broader, and the anterior thyroid cornua was in closer relation with the posterior arch of the hyoid. Possibly a sexual character may be at the bottom of these differences, in all of which DUBOIS' specimen approaches our figure of Echidna.

Muscles connected with the Hyoid.

For the reasons already mentioned, the extrinsic muscles in Echidna and the muscles generally in Ornithorhynchus were imperfectly studied. It was noted that the sterno-hyoid muscle was wanting in Ornithorhynchus, a fact to which DUBOIS has called attention. The sterno-hyoid and sterno-thyroid are both present in Echidna.

The *inter-hyoid* (*i.h.*) in Echidna is a large thick muscle, composed of several layers. It arises from the outer angle and adjacent portion of the anterior border of the posterior cornua of the hyoid, and is inserted into the posterior border of the anterior cornua in its two inferior segments. It is present in Ornithorhynchus.

The *inter-thyroid* (*i.th.*) consists of short fibres passing obliquely forwards between the cornua of the thyroid. The more internal (median) fibres pass obliquely outwards, the more external slightly inwards. In Ornithorhynchus the muscle is present, but very small.

The *thyro-hyoid* (*t.h.*) is similarly placed between the anterior cornua of the thyroid and the posterior cornua of the hyoid. Its fibres are very short, and are, to a great extent, replaced by ligament.

In Ornithorhynchus the thyro-hyoid is better developed, and in this animal we also noticed a curious slender strip of muscle passing directly from the external process of the anterior thyroid arch to the outer part of the anterior arch of the hyoid.

Intrinsic Muscles of the Larynx.

The *crico-thyroid* (*c.t.*) in Echidna appears to arise from the free end of the first ring of the trachea. It unites partly with its fellow of the opposite side in an aponeurosis, which plays over the anterior part of the cricoid cartilage, and is in part inserted into the internal end and adjacent lower border of the posterior thyroid cornua. The nerve to this muscle appeared to be a branch of the recurrent laryngeal. According to DUBOIS the crico-thyroid is absent in Ornithorhynchus, but in our specimen there was a small muscle apparently corresponding to the description given above, but much smaller.

The *posterior thyro-arytenoid* and *crico-arytenoid* (*p.*) together form one muscle, called by DUBOIS *kerato-crico-arytenoideus*, and represent the dilator of the larynx. The fibres arise from the extremity of the posterior cornua of the thyroid, and form the edge of the great notch on the dorsal aspect of the cricoid. Passing forwards over the cricoid cartilage, the external fibres, diverging as they go, are inserted into the external angle, the dorsal surface and its posterior border of the arytenoid. The remaining fibres, including most of those from the cricoid origin and a portion also of those from the thyroid cornua, are inserted into the anterior procricoid.

A small but distinct *aryteno-procricoid* (*a.p.*) lies concealed for the most part below the fibres of the posterior thyro-arytenoid, and, owing to the great development of the procricoid cartilage, takes the place of the more usual inter-arytenoid muscle.

The *lateral thyro-arytenoid* and *lateral crico-arytenoid* form a continuous sheet of muscle, called by DUBOIS *thyreo-ary-cricoideus*, and represent the constrictor of the larynx. The anterior fibres arise from the inner aspect of the body of the thyroid, and the adjacent portion of its inferior cornua; a few fibres arise more posteriorly from a line on the lateral and ventral aspect of the cricoid, close to its anterior border. Converging from these two origins, the muscle is inserted into the external border and outer side of the arytenoid cartilage. This muscle is found in both Echidna and Ornithorhynchus, and in both a few of the anterior fibres pass into the epiglottis, forming an *aryteno-epiglottidean* muscle.

Of these intrinsic muscles all, except the aryteno-procricoid, were recognized in Ornithorhynchus.

It will be seen that the above account, so far as it goes, gives abundant support to DUBOIS' theory based upon one of the two types here considered. The two pair of hyoid and two pair of thyroid cornua form together a system of four post-mandibular visceral arches; and the remarkable series of inter-thyroid, thyro-hyoid, and inter-hyoid muscles symmetrically connect them.

The simple condition of the constrictor and dilator muscles of the larynx is also noteworthy.

As regards the skeletal differences in this region between the two types, the greater size and ossification of the body of the hyoid, the better developed body of the thyroid, the robuster anterior hyoid cornua, the incomplete cricoid, and the better developed (?) procricoidea mark out Echidna as the more primitive form of the two, in respect to this as to so many other anatomical regions.

A point of considerable interest, which appears to have remained unnoticed, may be mentioned here. By means of an extraordinary prolongation of the soft palate, the elongated pharynx is divided into two passages. The dorsal one, a continuation of the posterior nares, is directly continuous with the gullet. The ventral one, continuous with the mouth, seems in a state of rest to be shut off from the other posteriorly, the broad semicircular epiglottis standing upright and coming in contact by its margin with the crescentic thickened posterior margin of the soft palate. From such a condition as this the transition is equally easy to the ordinary condition of the epiglottis and to the intranarial epiglottis of young Marsupials, of

Cetacea, the Mole, Hedgehog, Horse, and other forms.* Immediately below the larynx two thick rounded processes project downwards from the lateral walls of the œsophagus, and behind each there is a deep sinus. The purpose of these last structures is not apparent.

In Ornithorhynchus the epiglottis is thick, broad, pointed above, and cartilaginous.

* Cf. HOWES. *On a Rabbit with an intranarial epiglottis.* Journ. of Anat. and Phys., Jan. 1889, which paper reached us when this was in proof.

DESCRIPTION OF THE PLATE.

H. Body or copula of the Hyoid. H^1. Anterior hyoid cornua. H^2. Posterior cornua.

θ. Body or copula of the Thyroid. θ^1. Anterior thyroid cornua. θ^2. Posterior cornua.

C. Cricoid cartilage. A. Arytenoid; *n*, its accessory nodules in Ornithorhynchus. Pc. Procricoid cartilages in Echidna. Tr. Trachea. E. Epiglottis.

i.h. interhyoid muscle, *i.t.* interthyroid, *t.h.* thyro-hyoid, *c.t.* crico-thyroid, *p.* posterior thyro-arytenoid, and crico-arytenoid, *l.* lateral thyro-arytenoid and crico-arytenoid, *a.* aryteno-procricoid.

Fig. 1. Larynx and hyoid of Echidna, ventral view.
Fig. 2. Larynx and hyoid of Echidna, lateral view.
Fig. 3. Larynx of Ornithorhynchus, ventral view.
Fig. 4. Larynx of Ornithorhynchus, lateral view.
Fig. 5. Larynx of Echidna, dorsal aspect, after removal of the thyroid cartilages.
Fig. 6. Larynx of Ornithorhynchus.
Fig. 7. Diagram of muscles in Echidna, lateral aspect.
Fig. 8. Diagram of posterior thyro-arytenoid, posterior crico-arytenoid, and procrico-arytenoid in Echidna.
Fig. 9. Diagram of lateral thyro-arytenoid and lateral crico-arytenoid in Echidna.
Fig. 9*a*. View of glottis in Echidna, exposed by opening up the posterior wall of the pharynx. G. tongue. *dp.* placed upon the soft palate, lies in the posterior nares. *fp.* (at the base of the tongue), points towards the food-passage on the ventral side of the soft palate. E. epiglottis. *pr.* processes projecting from the œsophageal wall.
Fig. 10. Epiglottis of Ornithorhynchus.

Fig. 9.D

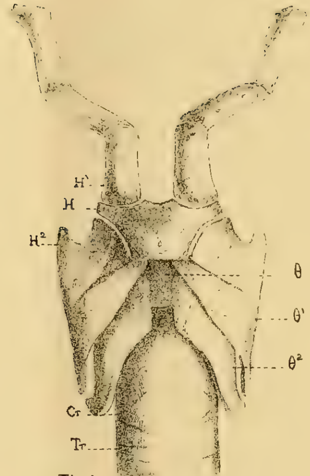


Fig. 1.

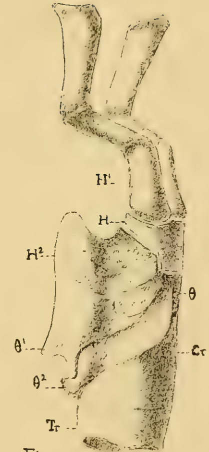


Fig 2

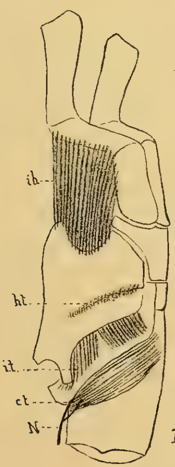


Fig. 7

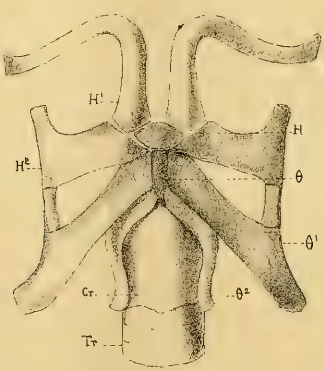


Fig. 3

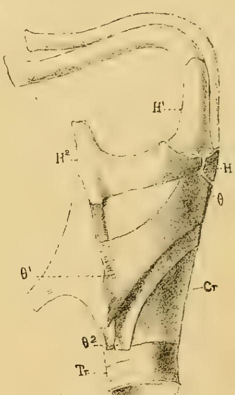


Fig. 4

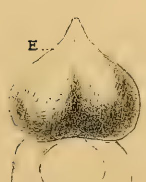


Fig. 10.

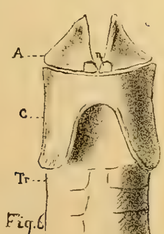


Fig. 6

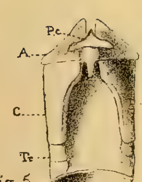


Fig. 5.

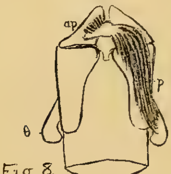


Fig. 8.

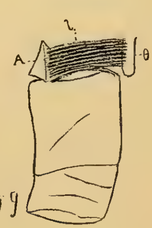


Fig. 9

Vol. I. No. 4.

Studies from the Museum of Zoology

IN UNIVERSITY COLLEGE, DUNDEE.

EDITED BY

D'ARCY W. THOMPSON,

Professor.

IV. ON THE AUDITORY LABYRINTH OF ORTHAGORISCUS.

BY

D'ARCY W. THOMPSON.

DUNDEE:

Printed for the Museum.

JANUARY, 1889.

IV. *On the Auditory Labyrinth of Orthagoriscus Mola L.**

By Professor D'Arcy W. Thompson.

A large Sunfish, caught in the Firth of Forth, came lately into my possession. It measured from snout to tail 1.35 m., and from the tip of the dorsal to that of the ventral fin 1.73 m. The anatomy of the fish is for the most part well known, but the auditory organ seems to have escaped critical examination; and Retzius in his great work notes with regret his inability to obtain a specimen.

Excluding one or two cursory notices, the only account of the organ that I know of, is that by Harting:† but Harting enters into no details whatever regarding the structure of the vestibule, merely describing the position of the labyrinth in the auditory capsule, and giving some of its dimensions, and also calling attention to the presence of three semicircular canals, instead of two, as had formerly been described.

The auditory labyrinth of Orthagoriscus is very peculiar, and differs more or less from that of all other Teleostean fishes. It hangs suspended by webs of delicate connective tissue within a wide space, continuous with the brain-cavity, very much as in Chimaera, according to Retzius' description. A single vertical pillar of cartilage passes down across this space, within the arc of the horizontal canal. (In Harting's specimen another passed within the arc of the anterior vertical canal.) After removal of the membranous labyrinth no distinct grooves or impressions remain in the cartilage capsule to indicate the former position of the parts within it.

Fig. 1.

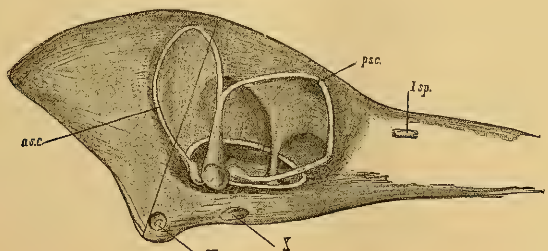


Fig. 1. Auditory labyrinth of Orthagoriscus Mola within its cavity. The connective tissue filaments are omitted. *a.s.c.*, *p.s.c.*, anterior and posterior semicircular canals. VII., X., I *sp.*, nerve foramina.

* Reprinted from the *Anatomischer Anzeiger*. III. Jahrgang, Nr. 4 und 5, 1888.

† "Sur *l'Orthagoriscus Ozodura*," Kon. Ak. Wet. Amsterdam, XI., 1868.

In the membranous labyrinth of Orthagoriscus the following parts are distinguishable: *Utriculus* with *Sinus superior; Recessus utriculi;* the three semicircular canals with their corresponding ampullæ; and the *Sacculus* and *Lagena* hardly separated from one another or from the Utriculus. Six nerve-endings are visible, three cristæ ampullarum, macula recessus utriculi, maculæ sacculi and lagenæ; but I sought in vain for the macula neglecta. The *Utriculus* is a roundish sac, passing gradually in its upper part into the thin-walled conical *Sinus superior,* which terminates by bifurcating into the anterior and posterior canals, without extending into any free "apex" between them. Anteriorly it opens into the wide recessus utriculi from which it is marked off by a scarcely notable constriction: at the base of the latter cavity is a well-marked and rather large macula recessus, opposite which is a little pouched diverticulum. The recessus is connected above with the ampula anterior and externally with the ampulla externa, which both open

Fig. 2.

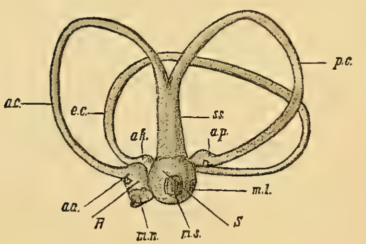


Fig. 3.

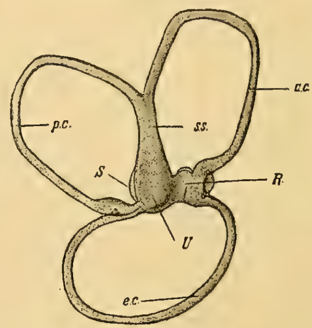


Fig. 2. Right auditory labyrinth, inner side.

Fig. 3. Right auditory labyrinth, outer side.

U. utriculus, *S.* sacculus, *L.* lagena, *rec.* recessus utriculi; *a.s.c.*, *p.s.c.*, *h.s.c.*, anterior, posterior, and horizontal semicircular canals; *a.a.*, *a.p.*, *a.h.*, their ampullæ; *s.s.*, sinus superior; *m.r.*, *m.s.*, *m.l.*, macula recessus, mac. sacculi, and mac. lagenæ.

somewhat widely into it. The ampulla posterior, rather more perfectly formed, opens by a narrow neck into the hinder part of the utriculus, just above the entrance into it of the horizontal canal. The *sacculus* and *lagena* form a single common cavity, and are only entitled to the retention of their names by still possessing their separate nerve-endings. They are neither separated from one another nor from the utriculus, of which they simply form a slightly bulging expansion on its inner side.*

Fig. 4.

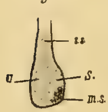


Fig. 4. Diagrammatic transverse section through vestibule.

* In a smaller specimen which I had an opportunity of dissecting last July in M. De Lacaze Duthiers' Laboratory at Roscoff, the sacculus was separated from the utriculus by a slightly more marked constriction.

The inner or median wall of the sacculus bears near its lower part a rather large roundish macula ; posterior to which is a smaller vertically elongated nerve-ending, corresponding to the *papilla lagenæ.* I could not find a trace of the ductus endolymphaticus.

No otoliths of the kind usual in Teleosteans exist, but instead the maculæ are furnished with numerous small white rounded otoconia, aggregated together. Of these a very few have a cubical crystalloidal form, like those of Acanthias, but the majority are rounded or oval, rough on the surface, and concentrically striated within.

The fish was unfortunately not fresh enough for histological study; nor am I able to describe the course of the auditory nerve, which was cut short in removing the brain.

The following are the dimensions of the parts :—

Auditory cavity, ant. post. diam., - - - - -	4.5 cm.
„ „ vertical „ - - - - -	3.5 „
„ „ transverse „ - - - - -	3.0 „
Utriculus, including recessus, length, - - - - -	0.8 „
Sinus superior, length vertically, - - - - -	1.2 „
Canalis ant., length incl. ampulla, - - - - -	5.7 „
„ post., „ „ „ - - - - -	5.5 „
„ ext., „ „ „ - - - - -	6.7 „
Ampulla anterior, length, - - - - - - -	0.4 „

It is difficult to measure the semicircular canals accurately, and the anterior and posterior canals probably do not differ in length. Together with the sinus superior they practically equal the horizontal canal.

The following features then are remarkable in the membranous labyrinth of this fish :—

I. In the complete conjunction of utriculus and sacculus, that is to say, in the absence of any distinction of *pars superior* and *inferior*, it differs from all other fishes (putting out of account the Cyclostomata) except the Lophobranchii.*

II. But in the lack of separation between sacculus and lagena, it is of simpler construction even than the two Lophobranchiate genera whose auditory organ has been studied. In this respect it is approached, though not equalled, by its close allies Ostracion and Tetrodon, in both of which according to RETZIUS (though not in the Lophobranchii) the communication between sacculus and lagena is wide and open instead of being by a narrow foramen or duct.

* See RETZIUS on *Siphonostoma* and *Hippocampus*, Gehörorg. d. Wirbeltiere, I., 1881, pp. 98–100.

III. It agrees with the four genera above mentioned, and differs from other Teleostei in the absence of a *macula neglecta.*

IV. The general proportions of the labyrinth are unusual, the semicircular canals being disproportionately long, and the vestibule very small.

V. Orthagoriscus is also exceptional among Teleosteans in lacking the usual solid otoliths, and in possessing instead numerous small otoconia, compacted together, but still distinct even to the naked eye, as in Elasmobranchs.

Vol. I. No. 5.

Studies from the Museum of Zoology

IN UNIVERSITY COLLEGE, DUNDEE.

EDITED BY

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V. ON THE MORPHOLOGY OF THE EXTENSOR MUSCLES.

BY

H. St. JOHN BROOKS, M.D.

DUNDEE:

Printed for the Museum.

February, 1889.

V. *On the Morphology of the Muscles on the Extensor Aspect of the Middle and Distal Segments of the Limbs: with an Account of the various Paths which are adopted by the Nerve-Trunks in these Segments.*

By H. St. John Brooks, M.D., *Chief Demonstrator of Anatomy in the University of Dublin.*

Part I.—On the Extensor Muscles in certain Amphibians, Reptiles, and Mammals.

This paper forms the first or introductory part of a systematic study of the extensor muscles in the groups of Vertebrata above fishes. In the succeeding part I hope to take up, one by one, the various individual muscles, and to trace the anatomy of each through a series of types upwards from the Amphibia, and, in fact, to discuss the history of the whole group of muscles. In this preliminary paper I offer a revised account of the muscles of this region in the three remarkable forms—Hatteria, Menobranchus, and Ornithorhynchus, of which specimens were furnished me for the purpose by Professor D'Arcy Thompson.

Hatteria.

In the forelimb of Hatteria, a superficial stratum of extensor muscles arises from the radial condyle of the humerus as an unsegmented mass, from which the triceps is completely separate. Passing downwards, this divides longitudinally into three sectors—a radial, an ulnar, and an intermediate. The radial sector presents (1) a tolerably distinct fasciculus (Fig. 9, *ex. c.r.*) inserted into the radial carpal bone, and obviously corresponding to the *ext. carpi radialis longior et brevior* of Mammals; and (2) a larger mass (*s*) which clothes the whole posterior and outer aspects of the shaft of the radius, and represents the *supinator longus et brevis.* The ulnar sector is partly inserted into the upper part of the shaft of the ulna, constituting an *anconeus** (*a*); and partly into the base of the fifth metacarpal *(ext. carpi ulnaris)* by a short tendon, from which an aponeurotic slip is given off to the fifth belly of the extensor brevis digitorum. The *extensor longus digitorum (ex. c.d.)* constitutes the intermediate sector, and is situated partly superficial to the other two. It passes at the wrist into an aponeurotic tendon, dividing into four slips, each of which is inserted in the bases of two adjacent metacarpal bones,

* The anconeus is usually regarded as a part of the triceps. In Hatteria the triceps is perfectly segmented from all the muscles in the forearm, including the anconeus. I shall give reasons, in the second part of this Paper, which will show, I believe conclusively, that the anconeus of Human Anatomy is to be associated with the *extensor carpi ulnaris*, and not with the triceps.

thus, the first slip into the bases of the first and second, and the remaining slips into the second and third, third and fourth, and fourth and fifth respectively: aponeurotic slips are prolonged also to the five bellies of the short extensor.

Taking origin from the middle and distal segments of the limb is a deep stratum, including two sets of muscles: (1) a sheet of fibres, arising partly from the ulna and partly from the carpus (Fig. 9, *ab. p. l.* and *ex. b.*); and (2) a series of muscular slips, arising from the dorsum and sides of the metacarpal bones. The former, or *proximal part of the short extensor*, divides below into six slips. Of these, the first *(ext. ossis metacarpi pollicis)* arises from the lower half of the ulna, and is inserted into the radial side of the base of the first metacarpal. The second *(ext. sec. internodii pollicis)*, arising below the preceding, passes to the terminal phalanx of the thumb. The third *(ext. indicis)* arises chiefly from the carpus, and is inserted into all the phalanges of the second digit. The fourth and fifth arise from the carpus, and supply the middle and ring fingers. The sixth *(ext. minimi digiti)* arises from the ulnar carpal bone and from the distal end of the ulna, and is inserted into the phalanges of the fifth digit.

The *metacarpal heads of the short extensor*,* partly overlapped by the proximal part of the muscle, arise in pairs from the dorsum and sides of the metacarpal bones. The first pair (Fig. 9, 1) joins the tendon of the *ext. sec. int. pollicis;* the second, third, and fourth join correspondingly the *ext. indicis, medii,* and *annularis.* In the fifth digit, the ulnar part of the metacarpal head is wanting, and the muscle is represented by a single fasciculus (Fig. 9, 5) joining the radial side of the tendon of the *ext. minimi digiti.*

The *musculo-spiral* nerve takes its usual course through the fibres of the triceps at the back of the humerus, and having reached the outer side of the arm, it passes through a foramen in the humerus immediately above the external condyle; it then bends backwards and pierces the supinator mass, and is continued as the posterior interosseous nerve. While passing behind the arm the musculo-spiral gives off a nerve of considerable size (Figs. 9 and 10, x) which passes through the fibres of the triceps to reach the interval between the external condyle and the olecranon. Here it becomes superficial for a short distance, and then passes under cover of the anconeus, which it supplies. It then supplies the extensor carpi ulnaris, gives a twig to the supinator mass, and finally becomes incorporated with the posterior interosseous nerve. This nerve obviously corresponds to the "nerve to the anconeus" of Human Anatomy, but it is relatively much larger in Hatteria than in Man, and takes a considerable share in the innervation of the muscles on

* These accessory heads are very generally confounded with interossei dorsales. Their innervation, however, among other important considerations, shows that they are quite distinct from "interossei." These accessory heads attain their maximum development in Lizards. I find them very similarly disposed in Varanus. Fürbringer, Mivart, and Sanders describe them as equally well-developed muscles (but under the name of *interossei*) in *Iguana*, *Platydactylus*, and *Liolepis*. In the Alligator (Fig. 16) they are more feebly represented.

the extensor aspect of the forearm. The trunk formed by the union of the posterior interosseous and the "nerve to the anconeus" gives off the nerve of supply to the extensor longus digitorum, and is joined a little lower down by a communicating twig* from the median nerve. It then passes under cover of the extensor ossis metacarpi pollicis, supplies every part of the deep stratum, including the metacarpal heads of the short extensor, and gives cutaneous branches to the digits.

According to the above account, the muscles of this region in Hatteria form an exceedingly symmetrical plan, and suggest a very primitive condition. The deviations from an almost ideal symmetry are slight, and include (1) the development from the *ext. brevis digitorum* of an *ext. ossis metacarpi pollicis:* (2) the unequal extension upwards of the origins of the slips of the short extensor: (3) the abortion of the ulnar metacarpal head of the short extensor of the fifth digit: (4) the absence of the aponeurotic slip from the *ext. carpi radialis* to the short extensor, which is present on the ulnar side. More noteworthy are the complete segmentation of the triceps from the muscles on the extensor aspect of the forearm, and the unsymmetrical condition of those portions of the radial and ulnar sectors which are inserted into the forearm—the supinator mass being very much larger than the anconeus.

The muscles in the two limbs are very similar to one another. In the superficial stratum of the hind limb the three sectors are distinctly segmented. The *tibial sector (tibialis anticus)* arises from the upper part of the anterior surface of the shaft of the tibia, and also from the outer border, and, to a certain extent, from the posterior surface of the same bone. It ends in a tendon which is inserted into the tibial side of the base of the first metatarsal bone, and sends a slip (*Fig.* 11, 1) to the base of the proximal phalanx of the hallux. The *fibular sector (peroneus)* arises from the middle three-fifths of the shaft of the fibula. It terminates in a short tendon which is inserted into the base of the fifth metatarsal bone, and gives off a very distinct slip *(peroneus quinti digiti)* which joins that division of the short extensor which is inserted into the little toe. The *intermediate sector (extensor longus digitorum)* arises by a rounded tendon from the fibular condyle of the femur. It forms a fleshy belly which terminates in two tendons. The *first* of these is inserted into the bases of the second and third metatarsal bones; the *second* into the base of the fourth metatarsal bone. The division of the extensor brevis, which is inserted into the third toe, passes between the two tendons of the long extensor.

The deep stratum consists of a proximal part and of a set of metatarsal heads. It shows a great similarity to the corresponding stratum in the fore limb.

* This twig passes downwards and backwards between the radius and the ulna to reach the posterior interosseous nerve. In Varanus it forms the chief nerve on the back of the forearm.

* Günther's account (*Phil. Trans.* 1867) differs materially from mine. He appears to have overlooked the greater part of the deep stratum, merely describing the *ext. ossis metacarpi pollicis*, and not mentioning the *ext. brevis digitorum*. He also describes the whole of the ulnar sector as inserted into the ulna.

The *first* division of the *proximal part, extensor ossis metatarsi hallucis (Fig. 11, ab.h.l.)*, arises exclusively from the fibula. It is inserted into the tibial side of the shaft of the first metatarsal bone. The *second* division, *extensor proprius hallucis*, arises partly from the fibula and partly from the tarsus, and is inserted into the phalanges of the hallux. The four remaining divisions are exclusively tarsal in origin, and end in moderately long tendons which pass to the four outer toes. Two other muscular slips are found in this situation, which are evidently segmented off from the short extensor, viz., a small fasciculus of muscle which passes from the lower end of the fibula to the tarsus, and a few fibres which arise from the tarsus and are inserted into the base of the fourth metatarsal bone.*

The *metatarsal heads* are represented by three pairs of muscles which arise from the dorsum and sides of the second, third, and fourth metatarsal bones respectively, and by a muscle arising from the dorsum and tibial side of the metatarsal bone of the hallux. The mode of insertion is precisely similar to the insertion of the metacarpal heads of the short extensor in the fore limb. The fibular head of the hallucial pair and both heads of the pair appertaining to the minimus are either aborted or absorbed into the proximal parts of the muscle.

The *peroneal nerve* passes forwards from the back of the thigh and winds round the neck of the fibula lying on the uppermost fibres of origin of the outer sector. It then passes under cover of the intermediate sector, and gives off nerves of supply to all three sectors. Lower down, it receives a communicating twig from the posterior tibial nerve, and then runs under cover of the extensor ossis metatarsi hallucis, supplies that muscle, gives twigs to the five bellies of the extensor brevis digitorum, including the metatarsal heads, and terminates in cutaneous branches to the toes.

The chief difference between the two limbs lies in the fact that, whereas in the fore limb the superficial stratum arises wholly from the *radial* condyle of the humerus (though completely segmented off from the triceps), in the hind limb the lateral sectors arise from the bones of the middle segment, and the intermediate sector, taking origin from the femur, does so from the *fibular (i.e., ulnar)* condyle. In both of these respects, Hatteria foreshadows the condition in Mammals. The intermediate sector shows a reduction in the number of its tendons. On the other hand, the *tibialis anticus* approaches the symmetrical form more nearly than does the *ext. carpi radialis*, by virtue of its insertion into the metatarsus, and more particularly by the presence of the tendinous slip (*Fig.* 11, 1) which reaches the proximal phalanx.

* Ecker *(Der Frosch)* describes two muscles in the frog which appear to correspond to these slips. One of these, "*m. flexor tarsi posterior*," arises from the outer side of the tibia, and is inserted into the dorsal surface of the astragalus (p. 134). The other, "*m. extensor dig. V. longus*," arises from the calcaneum, and is inserted into the fifth metatarsal bone. An inspection of his figure (*Fig.* 93) shows that these muscles are on the same plane as the *extensor brevis digitorum* (a muscle which Ecker regards as *extensor longus digitorum*).

The nervous arrangements in the fore and hind limbs show a very marked similarity, especially in regard to the innervation of the short extensor and the nerve-supply of the skin of the foot. In two respects, however, considerable difference exists: (1) The musculo-spiral (peroneal) nerve in the hind limb winds round the *fibula;* whereas in the fore limb it enters the forearm on the *radial* side. The objections which might be raised on this ground against the homologies of the two nerves appear to me to be completely met by the following remarks by Professor HUMPHRY. He says:—"The differences between the musculo-spirals in the two limbs, that is, between the peroneal and the radial, are dependent chiefly or entirely upon the difference in the direction of the rotation in the two limbs, causing a variation in the direction best adapted for the nerve course. . . . For the same reason, the nerves to the *quadriceps* pass in front of the pelvis as *anterior crural,* while those to the *triceps* pass behind the shoulder-girdle bound up in the *radial.*"* (2) In the fore limb there is a nerve which enters the forearm behind the external condyle, and takes part in the innervation of the extensor muscles situated below the elbow, viz., the "nerve to the anconeus." This nerve is not represented in the hind limb in Hatteria, and it appears to be absent in the hind limbs of the great majority of Vertebrate animals. It is, however, probably represented by a nerve which was first described by RUGE in Ornithorhynchus.† In this Ornithodelph, a branch of the anterior crural nerve passes through the fibres of the quadriceps, and makes its way downwards between the patella and the shovel-shaped process of the fibula. In this course it lies on the fibular condyle of the femur, and ends in tibialis anticus muscle. Among the objections which may be raised against the above view of the homology of this nerve, the following is perhaps the most prominent:—The "nerve to the anconeus" passes over the *radial* condyle of the humerus, while RUGE's nerve crosses the *fibular* condyle of the femur. Broadly speaking, however, the two nerves are serially homologous, as each may be described as *a nerve from the trunk which supplies the extensor muscles of the middle segment, prolonged to the extensors situated below the knee (or elbow) joints.*

Menobranchus.

I have chosen to consider Hatteria first, because it presents such a combination of low and high characters, that, while presenting itself as a primitive type, it is not difficult to deal with in the light of the highest. We reach a lower grade in passing to the great perennibranchiate amphibia.

* *J. of Anat. and Phys.*, Vol. VI., p. 53.

† RUGE (*Morph. Jahrb.* IV., 1878, p. 597) apparently does not regard this nerve as serially homologous to the "nerve of the anconeus." I had no difficulty in verifying RUGE's description in the Ornithorhynchus I dissected (see Fig. 7, *a.cr.*), but I have not met with this nerve in any other of the Vertebrate types I have examined.

In the fore limb of Menobranchus the *superficial stratum* is segmented, as in Hatteria, into three sectors. The *extensor communis digitorum longus* (*Fig.* 2, *i.s.*) arises from the external condyle of the humerus, and passes downwards to the carpus, overlapping the radial and ulnar sectors to a certain extent. At the wrist it divides into four slips. The *first* slip is inserted into the bases of the index and middle metacarpal bones ; the *second* slip into the middle and ring; the *third* into the ring and little metacarpal bones. The *fourth* slip ends in a tendon which is inserted into the phalanges of the little finger. This part is joined by a slip from the flexor carpi ulnaris, which passes from the palmar to the dorsal aspect. The *radial sector* arises from the external condyle and from the ridge immediately above. It is an unsegmented mass inserted into the whole length of the posterior surface and outer border of the radius, and sending a strong slip to the radial side of the carpus. The *ulnar sector* arises from the external condyle, and is inserted into almost the whole length of the inner border of the ulna, but does not reach the carpus. It represents the anconeus, and the extensor carpi ulnaris is therefore unrepresented. In Menopoma and Cryptobranchus this sector has a slight carpal insertion.

Deep layer.—The *extensor ossis metacarpi pollicis* arises from the extreme lower end of the ulna and from the carpus. It is inserted into the radial side of the base of the index metacarpal (the thumb being wanting) and into the adjacent part of the carpus. Its direction is nearly transverse. The *extensor brevis digitorum* consists of three small slips, which arise from the distal row of carpal bones and from the dorsum of the index, middle and ring metacarpal bones. The *first* slip is closely associated at its origin with the *extensor ossis metacarpi pollicis,* and passes with the latter muscle between the radial and intermediate sectors. It ends in a tendon, which is inserted into the phalanges of the index digit. The *second* and *third* slips pass between the divisions of the intermediate sector, and are inserted into the middle and ring digits.

The *musculo-spiral nerve* escapes from under cover of the triceps in the usual situation, and divides into a radial and a posterior interosseus branch. The *radial* runs downwards under the integument to the outer side of the hand. The *posterior interosseus* nerve plunges into the unsegmented radial sector in which it ends. The "*nerve to the anconeus*" *(Fig.* 2, *n.a.)* escapes through the fibres of the triceps close to the elbow joint, and passes between the external condyle and the olecranon. In this situation it gives off a twig, which is distributed to the integument on the ulnar border of the hand. It then passes under cover of the anconeus, supplies that muscle and the *extensor longus digitorum,* and runs nearly vertically down the fore-arm. At the wrist, it gives off the nerves of supply to the *extensor ossis metacarpi pollicis* and *extensor brevis digitorum,* and ends in cutaneous branches to the digits. It is therefore the main nerve, both muscular and cutaneous, to the back of the forearm.

I have not met with any description of the nerves of Menobranchus in the literature of the subject. The account given by MIVART of the muscles differs in several respects from the condition which I observed in my specimen. He appears not to have observed the ulnar sector at all; he represents the *extensor longus digitorum* as inserted into the digits, and he describes the *extensor brevis digitorum* in the following words :—" This is a very small muscle, which arises from the radial side of the distal end of ulna, and, passing obliquely downwards and outwards, goes mainly, if not exclusively, to the most radial digit."* It is evident, however, that HUMPHRY found a similar condition in Menobranchus to the arrangement in my specimen, for he says :—" In Menobranch and Saurians it *(extensor digitorum sublimis)* stops, like its homologue in the hind limb of those animals and of Aï, at the metacarpus, being inserted there in three portions; and small muscles arising from the metacarpus, close to its insertions, constitute the only extensors of the digits, and pass to the terminal phalanges."†

In the *lower limb*, the *superficial stratum* arises in part from the lower end of the femur, and is in part continuous with portions of the quadriceps extensor (*Fig.* 1, *ext.* 1 and *ext.* 2).‡ The *intermediate sector (extensor longus digitorum)* arises by fleshy fibres from the lower end of the femur immediately above the notch between the two condyles, and is also directly continuous, by means of a flattened tendon, with the muscle *ext.* 1. It passes downwards in front of and between the tibial and fibular sectors, and ends in three slips which are inserted into the bases of the second and third, the third and fourth, and fourth and fifth metatarsal bones respectively. The *tibial sector* is continuous by an aponeurotic tendon with the muscle *ext.* 2. Its chief origin, however, is by fleshy fibres from the anterior surface of the lower extremity of the femur under cover of, and partly internal to, the *extensor longus digitorum.* It is inserted into the whole length of the inner border of the tibia, a small slip passing on to the tarsus. The *fibular sector* arises from the front of the external condyle of the femur, and is inserted into the entire length of the outer border of the fibula, sending a distinct fleshy slip to the fibular side of the tarsus.

Deep stratum.—The *extensor ossis metatarsi hallucis* arises by a few fibres from the extreme lower end of the fibula, but chiefly from the tarsus, and is inserted into the tibial side of the base of the index metatarsal bone. The *extensor brevis*

* MIVART. *Proc. Zool. Soc.*, 1869., p. 461.

† HUMPHRY. *Jour. of Anat. and Phys.*, Vol. VI., p. 41, footnote.

‡ It is foreign to the subject of this paper to discuss the exact morphology of these two muscles. They correspond in position to the muscles which are described and figured by MIVART (*op cit. Fig.* 9, p. 463) under the names of *gluteus maximus* and *rector femoris.* These muscles are said, however, to be inserted into the bones of the middle segment, which was not the case in the specimen I dissected. The point of interest about the muscles is that they are both, very evidently, portions of the extensor mass on the extensor aspect of the proximal segment *which are in uninterrupted continuity with the extensors which are situated below the knee-joint.*

digitorum consists of four fleshy slips, which arise from the tarsus and from the dorsum of the metatarsal bones. The *first* slip passes through the interval between the tibial and intermediate sectors of the superficial stratum, and is inserted into the phalanges of the index digit. The *second* and *third* slips pass between the divisions of the intermediate sector and proceed to the third and fourth digits. The *fourth* slip makes its way between the intermediate and fibular sectors, and is inserted into the fifth digit.

The *peroneal nerve* passes forwards from the back of the thigh, and winds round the neck of the fibula to pass under cover of the fibular sector. It runs almost vertically down the leg under cover of the superficial stratum of muscles, supplies both the superficial and deep stratum, and ends in cutaneous branches to the digits.

MIVART does not notice the continuation of the muscles on the extensor aspect of the proximal segment into the intermediate and tibial sectors and the middle segment; and he describes the *extensor ossis metatarsi hallucis* (under the name of *extensor hallucis*) as the only representative of the *extensor brevis digitorum.**

In this description the following points are noteworthy :—

1. The great development of the *anconeus*, which is here represented by the whole ulnar sector in the fore-limb, and whose insertion corresponds in extent to that of the supinator longus on the radial side.
2. The almost equally slight differentiation of the radial sector, from which the *ext. carpi radialis* is not separated off.
3. The more distal origin than in Hatteria of the deep layer of muscles, and the absence of any separate metacarpal heads.
4. The important distribution of the nerve to the anconeus.
5. In the lower limb, the imperfect separation of the superficial stratum from the quadricips extensor, and its origin to a greater extent than in Hatteria from the lower end of the femur.
6. The insertion of the tibial and fibular sectors chiefly into the bones of the middle segment, and their consequent great resemblance to the radial and ulnar sectors in the fore limb.

Ornithorhynchus.

In the fore limb the *intermediate sector* is represented by a well-developed *ext. communis digitorum*, which arises from the external condyle of the humerus between the *ext. carpi ulnaris* and *ext. carpi radialis brevior*, and is separate from these muscles almost up to its origin. It passes into a tendon which becomes broad and flat on the dorsum of the hand, and then divides into five tendons inserted into the terminal phalanges of the digits. The tendon to the thumb is weaker than the

* *Op. cit.*, p. 466.

others. The *ulnar sector* is divided, as usual, into the *ext. carpi ulnaris* and the *anconeus.* The former arises, as in Man, from the external condyle of the humerus, but does not receive any fibres from the ulna. Its tendon passes through the same compartment in the annular ligament as the tendon of the ext. minimi digiti, and then divides into two parts. The *deeper part* is joined by a tendinous slip from the abductor minimi digiti, and is then inserted into the base of the proximal phalanx of the little finger. The *superficial part* (represented in the figure as drawn outwards by a pin) joins the other two extensor tendons of the little finger, and thus reaches the ungual phalanx of that digit. The normal insertion of the ext. carpi ulnaris has therefore disappeared, and the entire muscle is converted into an *ulnaris quinti digiti.* The *anconeus* is very deeply placed. It arises in common with the ext. carpi ulnaris from the external condyle, and is inserted into the upper third of the shaft of the ulna. It is covered at its insertion by the ext. indicis et pollicis. *Radial sector.*—The *ext. carpi radialis brevior* is a large and well-developed muscle. It arises from the external condyle and from the supra-condyloid ridge, and is covered at its origin by the triceps. Its tendon passes through the posterior annular ligament in the usual situation, and divides into three strong slips which are inserted into the bases of the second, third, and fourth metacarpal bones. The *ext. carpi radialis longior* is about one-fifth the size of the preceding muscle, by which it is concealed for the greater part of its extent. It arises from the external supra-condyloid ridge of the humerus, anterior to the uppermost fibres of the ext. carpi radialis brevior. It is continued into a slender tendon, which is inserted into the base of the first metacarpal bone, and also gives off a fibrous expansion which blends with the ligamentous structures on the back of the carpus. The *supinator brevis* arises from the external condyle and from the ridge immediately above the condyle, in common with the ext. carpi radialis brevior. It is inserted into the upper third of the external border, and slightly into the anterior surface of the radius. The *supinator longus* is entirely wanting.

Deep layer.—The *ext. ossis metacarpi pollicis* (*Fig.* 6, *ab. p. l.*) arises from the upper third of the posterior surface of the shaft of the ulna, and is covered from above downwards by the anconeus, the ext. indicis et pollicis and the ext. communis digitorum. Its tendon crosses the radial extensors of the carpus in the usual way, and passes through the outermost compartment of the annular ligament to be inserted into the metacarpal bone of the thumb. It is joined, close to its insertion, by a remarkable tendinous structure *(Fig.* 6, *r).* This tendinous slip arises from the ulnar side of the carpus, and lies under cover of all the extensor tendons, except the ext. carpi radialis longior. It may perhaps represent a remnant of the primitive carpal origin of the ext. ossis metacarpi pollicis. The *ext. indicis et pollicis** arises from the upper half of the posterior surface of the shaft of the ulna, extending

* This muscle probably represents the *ext. secundi internodii pollicis,* the *ext. indicis,* and the occasional *ext. medii* of Man.

upwards nearly to the tip of the olecranon (*Fig.* 6, *ex.* 1, 2, *and* 3). The muscle is subcutaneous for the upper three-fourths of its extent. The lower part of the muscle is placed under cover of the ext. carpi ulnaris and ext. minimi digiti, and is continued into a tendon which traverses the same compartment of the annular ligament as the tendon of the common extensor. It divides in the hand into three tendons, which proceed to the thumb and to the index and middle fingers, and are inserted into the deep surface of the corresponding tendons of the common extensor. The *ext. minimi digiti* is a slender muscle, which is deeply placed in the upper part of the forearm, and first becomes superficial near the wrist *(Fig.* 6, *ex.m.d.).* It arises from the external condyle under cover of the ext. carpi ulnaris, and forms a small ribbon-like band of muscle, which is compressed between the ext. carpi ulnaris and the ext. communis digitorum. In *Fig.* 5 it is exposed by the reflection of the ext. carpi ulnaris, and is seen in its natural position lying against the deeper fibres of the ext. communis digitorum. Its tendon accompanies the tendon of the ext. carpi ulnaris through the annular ligament, and divides in the hand into two slips. One of these blends with the fifth division of the common extensor and with the longer of the two portions of the tendon of the ext. carpi ulnaris to the extensor tendon of the little finger. The other slip *(ext. annularis)* crosses under cover of the fifth division of the tendon of the common extensor, and joins the ulnar side of the fourth or annular division of the same tendon.

The *posterior annular ligament* is divided into four compartments, which transmit the extensor tendons in the following order, commencing on the radial side :—(1) *Ext. ossis metacarpi pollicis;* (2) *Ext. carpi radiales longior et brevior;* (3) *Ext. communis digitorum* and *ext. indicis et pollicis;* (4) *Ext. minimi digiti* and *ext. carpi ulnaris.*

The *musculo-spiral nerve* divides at the elbow-joint into a radial and a posterior interoseous branch. The *radial* passes downwards on the back of the forearm under cover of the integument to the dorsum of the hand; here it divides into a number of large branches which communicate in a plexiform manner, and end in branches to all the digits. The *posterior interosseous nerve* has essentially the same course and relations as in Man. It supplies all the above described muscles, with the exception of the anconeus. I could not follow it further than the wrist. The *nerve to the anconeus* escapes through the fibres of the triceps, and passes between the external condyle and the olecranon process to end in the anconeus muscle. On account of the great development of the external condyle, this nerve is more deeply placed than in Man.

Meckel has noticed the phalangeal insertion of the *ext. carpi ulnaris* in the Ornithorhynchus, and Gruber has traced the tendon of the same muscle to the ungual phalanx in the Echidna.*

* I have unfortunately not been able to consult the text of Meckel's *Ornithorhynchi paradoxi descriptio anatomica,* but I have seen one of the plates which accompany this work. I extract the

Lower Limb.—Superficial stratum. Tibial sector. The *tibialis anticus* is divided into two parts. The *inner part* (Fig 7, t.a.)* arises from the upper part of the shaft of the tibia, from the ligamentum patellæ, from the patella, and from the large "shovel-shaped"† process of the fibula. Between the fibular and patellar origins some fibres are continued directly into the quadriceps extensor. The muscle ends in a tendon which is inserted into the internal cuneiform bone. The *outer part‡ ($t.a^1$.)* arises in common with the inner part from the shovel-shaped process and derives a few additional fibres of origin from the shaft of the fibula below the process. Its tendon (represented as drawn outwards by a pin in the figure) joins the hallucial division of the tendon of the ext. brevis digitorum. *Fibular sector.*—The *peroneus longus* arises from the upper and outer part of the shovel-shaped process of the fibula. It lies superficial to the peroneus brevis, and terminates in a tendon which crosses in front§ of the inferior extremity of the fibula. It then passes into the *planta pedis,* and is inserted partly into the bases of the fourth and fifth metatarsal and partly into the base of the first metatarsal.‖ The *peroneus*

following from GRUBER:—"Unter den Säugethieren setzt sich beim Ornithorhynchus nach J. FR. MECKEL der Musculus ulnaris externus an die I. Phlange des 5. Finger. Bei Echidna hystrix erstreckt sich der ganze Musculus ulnaris externus constant auf den 5. Finger, ist somit in seiner Gänze ein Extensor digiti V. Der Muskel inserirt sich nach GEORGE MURIE an die äussere Seite des 5. Fingers und erreicht nach meinen Untersuchungen an zwei vor mir liegenden Exemplaren dieses Thiers bestimmt die Nagelphalange.—Bei den Monotremata vielleicht überhaupt, sicher bei dem Genus 'Echidna,' existirt nicht nur, wie beim Menschen ausnahmsweise neben dem Ulnaris externus auch ein Ulnaris digiti V., sondern der Ulnaris externus selbst als Ulnaris digit V." (*Beobachtungen aus der Mensch. u. vergleich. Anat.* Heft V., 1884, p. 24.)

* "Tibialis anticus," RUGE. Untersuchung über die Extensorengruppe am Unterschenkel u. Fuss. *Morph. Jahrb.* Bd. IV., 1878, p. 595.

† "Schaufelförmiger Fortsatz," RUGE. (*Op. cit.*, p. 593.)

‡ "Extensor longus hallucis," RUGE. (*Op. cit.*, p. 595.)

§ On account of the non-development of the external malleolus, the tendons of the peroneal group pass in front of the lower end of the fibula, and are on the same plane as the tendons of the anterior group of muscles. In this respect the Monotremes approach the Reptilia and depart widely from other Mammalia. RUGE was fully aware of the importance of this observation, but does not appear to have remarked the reptilian affinity—"Alle Sehnen der Muskeln aus der Peroneusgruppe verlaufen über die Vorderfläche der Fibula, ein Malleolus externus ist in der Art nicht vorhanden, dass hinter ihm etwa wie beim Menschen, Muskeln verliefen." (*Op. cit.*, p. 600.)

‖ RUGE describes the insertion of this muscle as follows:—"Sie heftet sich sowohl an die laterale Fläche des Os cuboides und, wohl mit der Hälfte ihrer Fasern, an die Basis des Metatarsale V., als auch an die Plantarfläche der Basis des Metatarsale I fest. Im queren Verlaufe der Sehne durch die Planta pedis liegt dieselbe nicht frei in einer Scheide, sondern es lösen sich von ihr leichte membranartige Zügen ab, welche, ähnlich wie auch MECKEL es angibt, sich zu den Keilbeinen begeben. Durch die Anheftung von Sehnenfasern an das Os cuboides und das Metatarsale V. ist die Scheide des Peroneus longus am lateralen Fussrande in zwei Abtheilungen getheilt, von denen die eine in der Planta, die andere am Fussrande und Fussrücken gelegen ist." (*Op. cit.*, p. 594.) RUGE considers that this condition may perhaps be explained by the hypothesis that the peroneus longus was originally inserted into the external side of the foot (fifth metatarsal), and generally extended its insertion across the sole to the inner side of the foot (p. 598.) An examination of the Reptilia (cf. Hatteria) confirms RUGE's hypothesis in a remarkable way.

*brevis** arises from the fibula immediately below and under cover of the preceding muscle. Its tendon divides in the foot into two slips. One slip is inserted into the base of the proximal phalanx of the little toe. The other and longer slip joins the division of the tendon of the common extensor which is inserted into the little toe. The close correspondence of this insertion to the insertion of the *ext. carpi ulnaris* in the hand of the same animal is very noteworthy.

Intermediate sector.—The *ext. communis digitorum* is placed rather more deeply than the muscles belonging to the tibial and fibular sectors. It arises from the lower part of the shovel-shaped process and from the upper part of the shaft of the fibula, and is divided longitudinally into two parts.† The tendons from these two parts, however, keep close together and divide to be inserted into the four outer toes. The tendon of the inner part passes exclusively to the index digit. The tendon of the outer part is distributed chiefly to the three outer digits, but sends a slip to the index also.

Deep stratum.—The *ext. brevis digitorum* is represented by a large and elongated muscle, which arises from the shovel-shaped process of the fibula under cover of the peronei. It ends in a strong tendon, which becomes flattened and expanded on the tarsus. This expanded tendon divides into five slips which pass to the five digits. The *first* slip joins the tendon of the outer division of the tibialis anticus, and is inserted into the ungual phalanx of the hallux. The *second, third,* and *fourth* slips join the deep surface and outer side of the tendons of the common extensor which are inserted into the second, third, and fourth toes. The *fifth* slip is inserted into base of the proximal phalanx of the fifth toe, under cover of the tendon of the superficial extensor.

The *external popliteal nerve* passes from behind forwards, winds round the shovel-shaped process of the fibula, and divides into a superficial and a deep branch. The *superficial* branch passes downwards towards the integument to the dorsum of the foot, where it divides into a number of large branches, which unite in a plexiform manner with the ramifications of the internal saphenus branch of the anterior crural.‡ The *deep* branch passes under cover of the peroneal muscles, and supplies

* "Extensor brevis digiti quinti," Ruge. (*Op. cit.*, p. 594.)

† These two parts appear like two distinct muscles in Meckel's plate, *op. cit.*

‡ This arrangement is exceedingly well seen in Ruge's figure *(op cit. Taf.* XXXII. *Fig.* 3*)*. In this respect the foot of Ornithorhynchus departs more widely from Reptiles than the majority of Mammals, for the deeper or muscular division of the peroneal nerve (anterior tibial) does not supply the integument of the foot at all, whereas in other Mammals it takes a more or less considerable share in the innervation of the toes. In *Ateles* (Ruge, *Fig.* 38) it gives branches to all the toes. The same abrupt departure from the reptilian condition is seen in the forelimb of Ornithorhynchus. The posterior interosseus nerve (which supplies the integument of the dorsum of the hand and digits in Hatteria and Alligator) ends above the wrist, and the radial nerve constitutes the sole supply of the back of the hand. In a Gibbon (Hylobates agilis) I found the posterior interosseus nerve supplying the integument on the dorsum of the ulnar half of the index finger, the middle finger, and the radial half of the ring finger. Sir William Turner has recorded a somewhat similar condition occurring as a variety in the human subject, viz., a branch of the posterior interosseus nerve dividing to supply the contiguous sides of the index and middle fingers. *(Journ. of Anat. and Phys.,* Vol. VI., p. 105.)

peroneus longus and brevis, ext. brevis digitorum and ext. longus digitorum. Its terminal twigs could be followed with some difficulty to the tarsus. A branch from the anterior crural nerve *(Fig. 7, a.cr.)* passes through the fibres of the quadriceps and crosses in front of the external condyle to end in the two divisions of the tibialis anticus muscle.*

The following points stand out prominently from this description :—

1. In both fore and hind limbs the three sectors of the superficial stratum are now completely separate.
2. The superficial stratum in the hind limb has not retained any origin from the femur.
3. The deep stratum in the fore limb, and still more remarkably in the hind limb, arises from a more proximal point in the limb than in the lower forms already considered.
4. The metacarpal heads of the short extensor are wanting.

The Extensor Muscles in the Forearm and Leg of Man.

A brief account may now be given of the changes which have probably occurred by which a condition resembling Hatteria has attained to the condition which is present in Man. The history of each muscle will be considered separately in the second part of this paper.

Fore limb.—In the *superficial stratum* the following changes have taken place : —The *ulnar sector* has retained very much the same connections as in Hatteria. The anconeus, however, has become more segmented from the ext. carpi ulnaris, and shows a tendency to unite with the triceps. The tendinous slip from the ext. carpi ulnaris to the phalanges of the fifth digit is not normally developed, but sometimes appears as an ulnaris quinti digiti. *Radial sector.*—The supinator mass is completely segmented into supinator longus and supinator brevis, and the ext. carpi radialis has divided into two muscles, longior and brevior ; moreover, the tendons of these muscles have wandered towards the ulnar side, and are inserted into the second and third metacarpal bones. *Intermediate sector.*—The ext. longus digitorum has no longer any hold on the metacarpal bones, but is inserted exclusively into the phalanges of the digits.

* This nerve is described in the following words by RUGE :—"Der Muskelast des Plexus cruralis begibt sich auf der Vorderfläche des Oberschenkels vom Stamme des Nervus cruralis am medialen Rande des zur Patella verlaufenden Extensor cruris in die Tiefe, durchbohrt die lateralen Oberschenkelmuskeln, um im distalwärts gewendeten Verlaufe schliesslich lateral von der Patella frei über den Condylus externus femoris und das Kniegelenk, zwischen der Fibula und Tibia, auf den Unterschenkel überzugehen. Wir finden den Nerven auf Figur 1 u. 2 in der Gegend der Tibiofibularverbindung. Er spaltet sich in mehrere Aeste, welche sich im M. tib. ant. sowohl als auch im Ext. hall. long. auflösen." *(op. cit.,* p. 597). I may add to this description that as the nerve passes through the substance of the quadriceps it gives off twigs to the muscular substance, reminding us of the manner in which the "nerve to the anconeous" gives twigs to the triceps.

Deep layer.—The ext. brevis digitorum appears, at first sight, to be wanting. We find, however, an ext. ossis metacarpi pollicis and an ext. secundi internodii pollicis, which differ from the muscles which I have described under these names in Hatteria only by being situated a little higher up in the forearm, and possessing relatively longer tendons. A third member of the group (ext. indicis) which is partly ulnar and partly carpal in origin in Hatteria, arises in Man entirely from the ulna. Occasionally, an ext. medii digiti is found arising from the ulna immediately below the preceding. It appears, therefore, that these four muscles have ascended from the carpus to the forearm bones, the most radially placed (ext. oss. met. poll) having ascended first, and the others followed in their order from the radial to the ulnar side.* It appears probable that when this stage is reached all the available space on the back of the forearm bones is taken up, and when the time comes for the bellies of the ext. brevis which appertain to the ring and little fingers to ascend in their turn, they creep upwards on the aponeurotic covering of the four radially placed muscles, and seek a bony origin from the external condyle of the humerus. Being here greatly compressed by the superjacent ext. communis digitorum and ext. carpi ulnaris they are forced to the surface between these two muscles and become the ext. minimi digiti of Human Anatomy, a muscle which, occasionally in Man and normally in many of the Mammalia, gives off two tendons, one for the little finger and one for the ring finger. This muscle has been almost universally regarded as belonging to the superficial stratum. I shall give (in Part II.) a summary of my reasons for classing it with the deep stratum. I may mention here, however, that although in most cases the muscular part appears to be quite superficial, the *annular tendon* (when developed) always crosses on the *deep* surface of the tendons of the common extensor, thus retaining, in the hand, a trace of its primitive position as a member of the deep extensor stratum.

The *metacarpal heads* of the short extensor are not represented in the normal human subject. They appear, however, as varieties, and have been described under the name of ext. brevis digitorum manus. It is generally implied that this muscle is homologous to the ext. brevis digitorum pedis, and this is expressly stated to be the case by MACALISTER.† A comparison with Hatteria and other reptilian and amphibian forms shows, however, that the ext. brevis digitorum of the human foot is serially homologous to the deep layer of muscles in the forearm, which have vacated their primitive position on the carpus and ascended to the middle segment of the limb. The ext. brevis digitorum manus corresponds to the metacarpal heads

* This ascent has already commenced in Hatteria, but the greater part of the deep extensor is still carpal in origin in that reptile. In many Amphibia (Menopoma, Cryptobranchus) the muscle is placed at a much more distal point of the limb, and arises almost entirely from the carpus. For the sake of simplicity, the *ext. primi internodii pollicis* is omitted from the above account—it is merely a slip of the *ext. ossis metacarpi pollicis.*

† MACALISTER. *Annals and Mag. of Nat. Hist.* Vol. I.—Fourth Ser., 1868., p. 315.

of the short extensor of reptiles; its position, connections, and innervation show this to be the case.

Hind Limb.—We have seen that in Hatteria the *intermediate sector* of the *superficial stratum* has retained its hold on the fibular condyle of the femur, and that the tibial and fibular sectors arise from the bones of the middle segment. A very similar condition is retained in some of the Mammalia, *e.g.*, *Hyxax capensis.** In Man, as in Ornithorhynchus, all three sectors have lost their hold on the femur. *Fibular sector.*—The undivided peroneus of Hatteria has split into *peroneus longus* and *brevis.* The tendon of the former has wandered across the sole to the inner side of the foot.† The peroneus brevis has retained the primitive attachment to the base of the fifth metatarsal bone, and not infrequently sends a tendon to the phalanges of the minimus (peroneus quinti digiti). This tendinous slip, in rare cases, becomes continuous with a fifth belly of the ext. brevis digitorum, and thus a condition greatly resembling the disposition in Hatteria becomes developed (see *Fig.* 11, *p.q.dig.*). *Tibial sector.*—The tibialis anticus is essentially similar to the muscle thus named in Hatteria. It is inserted into the internal cuneiform and into the base of the first metacarpal bone, and in rare cases it sends forward a slip to the paroximal phalanx of the hallux,‡ presenting a condition evidently homologous to the slip from the tibial sector to the hallux in Hatteria (*Fig.* 11, 1). *Intermediate sector.*—The ext. longus digitorum occupies a very much more distal position than in Hatteria. It arises slightly from the tibia and from almost the entire length of the fibula. It is inserted into the phalanges of the four other toes. A fifth tendon (peroneus tertius) is inserted into the metatarsal bone of the little toe. This, probably, represents a reversion to the more primitive metatarsal attachment.

Deep stratum.—The extensor brevis digitorum very obviously corresponds to the muscle thus named in Hatteria. The belly which supplies the little toe, however, is absent in the great majority of cases in the human subject; it may, however, appear as a variety.§ The extensor ossis metatarsi hallucis, which is so well represented in the upper limb of Man, has completely disappeared as a normal arrangement in the lower limb, but appears in rare cases as a variety.|| The extensor proprius hallucis has divided into two parts. One portion has extended its origin further up the leg than in Hatteria, and has become the extensor longus hallucis.

* MIVART and MURIE. *Proc. Zool. Soc.*, 1865, p. 349.

† RUGE has traced this migration of the tendon of the *peroneus longus.* (*Op. cit.*, pp. 594 and 598.)

‡ MACALISTER. *Trans. Roy. Irish Acad.*, Vol., XXV.—Science; p. 124.

§ MACALISTER. *Op. cit.*, p. 126. TESTUT. *Les Anomalies Musculaires chez l'Homme.* Paris, 1884, p. 724.

|| MACALISTER. *Op. cit.*, p. 123. TESTUT. *op. cit.*, p. 730.

The other portion has remained on the foot, and is represented by the first belly of the extensor brevis digitorum.

The *metatarsal heads* of the short extensor are represented by some deeply placed slips of the extensor brevis, which were first described by RUGE. These slips vary greatly in their attachment.

EXPLANATION OF PLATES.

The following letters have the same signification in all the figures :—

ab.h.l., Extensor ossis metatarsi hallucis.
ab.p.l., Extensor ossis metacarpi pollicis.
ex.b. 1 to 5, Extensor brevis digitorum, 1 to 5.
ex.c.d., Extensor communis digitorum.
ex.c.u., Extensor carpi ulnaris.
ex.m.d., Extensor minimi digiti.
ol., Olecranon process of ulna.
p.b., Peroneus brevis.
p.i.n., Posterior interosseous nerve.
p.l., Peroneus longus.
t., Triceps.
u.n., Ulnar nerve.

Fig. 1.—Leg of Menobranchus. (5) *ext.* 1., *ext.* 2, portions of quadriceps extensor which are continuous with the intermediate and tibial sectors, *i.s.* and *t.s.* *f.s.*, fibular sector. *e.p.n.*, peroneal nerve. *e.b.d.* 2 to 5, extensor brevis digitorum.

Fig. 2.—Hand of Menobranchus. (5) *m.sp.*, musculo-spiral nerve. *n.a.*, "nerve to anconeus." *e.c.*, external condyle of humerus. *u.s.*, *i.s.*, and *r.s.*, ulnar, intermediate, and radial sectors. *ep.a.*, epitrochleo-anconeous. *ex.b.d.m.*, extensor brevis digitorum manus.

Fig. 3.—Deep dissection of hand of Varanus. (2¼) The extensor carpi ulnaris is cut short and fixed by a hook, and its tendon, *ex.c.u.*, is seen to give slips to the palmar surface of the carpus and to the fifth and fourth metacarpal bones. *p.*, pisiform bone.

Fig. 4.—Forearm of Varanus viewed from the ulnar side. (2) *ep.a.*, epitrochleo-anconeus. *f.c.u.*, flexor carpi ulnaris. *abd.*^{5}, abductor minimi digiti. The tendon of the extensor carpi ulnaris (under which a pin has been placed) is shown passing into the palm under cover of this muscle.

Fig. 5.—A dissection of the forearm of Ornithorhynchus, showing the deep position of the extensor minimi digiti. (5) The extensor carpi ulnaris, *ex.c.u.*, has been reflected. *e.c.*, external condyle. *a.*, anconeus. *ex.* 1, 2, and 3, extensor pollicis, indicis et medii. *ex.c.r.*, extensor carpi radialis brevior.

Fig. 6.—Forearm of Ornithorhynchus. (2¼). *m.sp.*, musculo-spiral nerve.

Fig. 7.—Leg of Ornithorhynchus. (2). *f.*, "shovel-shaped" process of fibula. *p.*, patella. 1 and 2, branches of the peroneal nerve to peroneus longus and brevis. *a.cr.*, branch of anterior crural nerve supplying the two portions of tibialis anticus, *t.a.* and *t.a.*^{1} *e.b.d.*, extensor brevis digitorum.

Fig. 8.—Forearm of Myrmecophaga tamandua. (Nat. size.) *a.*, anconeus. *ex.c.r.*, extensor carpi radialis (in copying the drawing, the lithographer has made the tendon of this muscle appear as if it were the continuation of the supinator longus, *s.l.*). The extensor indicis is seen passing from under cover of the ext. minimi digiti and dividing into tendons for the three radial digits. *ex.b.d.m.*, extensor brevis digitorum manus.

Fig. 9.—Forearm of Hatteria. ($2\frac{1}{2}$) *a.*, anconeus. *x.*, "nerve to the anconeus." *ex.c.r.*, extensor carpi radialis. *s.*, supinator longus and brevis. 1 and 2, metacarpal heads of deep extensor, corresponding to the thumb and index finger. 5, metacarpal head inserted into the fifth digit.

Fig. 10.—Diagram of the nerves in the preceding figure. The three roots of the posterior interosseous nerve are shown.

Fig. 11.—Leg of Hatteria. ($2\frac{3}{4}$) *q.ex.cr.*, quadriceps extensor cruris. *ext.c.*, external condyle of femur. *p.n.*, peroneal nerve. *p.t.n.*, posterior tibial nerve. *p.*, peroneus muscle. *p.q.dig.*, peroneus quinti digiti. *t.a.*, tibialis anticus. 1, tendinous slip from tibialis anticus to phalanx of hallux. 2, metatarsal heads of deep extensor corresponding to index digit. 3, abductor quarti digiti (which can be seen to be plantar in position to the metatarsal heads of the deep extensor).

Fig. 12.—Diagram of Type Scheme. (1) line of articulation between the humerus or femur and the forearm or leg bones. (2) wrist or ankle joint. (3) articulation of carpus or tarsus with metacarpus or metatarsus. (4) articulation of metacarpus or metatarsus with phalanges. *a.*, triceps or quadriceps. *b.* and *d.*, ulnar or fibular sector. *f.*, intermediate sector. *c.* and *e.*, radial or tibial sector. I. to V., tendons of the extensor brevis digitorum. (The superficial muscles are shown in *red*, the tendons in *blue*, and the deeper muscles in *black*. The metacarpal or metatarsal heads are of a darker shade than the rest of the deep extensor.

Fig. 13.—Forearm of Capybara. (Nat. size.)

Fig. 14.—Leg of Varanus. ($1\frac{1}{3}$) *q.ex.cr.*, quadriceps extensor cruris. *p.n.*, peroneal nerve. *t.a.*, tibialis anticus. 1, slip from tibialis anticus to phalanx of hallux. 2, tibial metatarsal head of *ext.br.* 2. 3, fibular metatarsal head of *ext.br.* 4. 4, abductor quarti digiti.

Fig. 15.—Forearm of Ornithorhynchus showing the epitrochleo-anconeus. *ept.a.* ($2\frac{1}{4}$) *m.n.*, median nerve. *int.c.*, internal condyle of humerus. *fl.c.u.*, humeral head of flexor carpi ulnaris. *fl.c.u*[1]., ulnar head. *fl.d.*, flexor digitorum.

Fig. 16.—Forearm of Alligator. (Nat. size.) *ex.c.d.*, nerve to extensor communis digitorum cut short. *x.*, "nerve to anconeus." *ul.sect.*, ulnar sector (anconeus) reflected. *ext.c.*, external condyle of humerus. (The other letters are explained in the text.)

Fig. 17.—This figure is copied from Macalister (*Trans. Roy. Irish Acad.*, Vol. XXV.—Science, Pl. XXVI.; Fig. 5), the following description is given in the original:—*a.* Extensor digitorum longus. *b.* Tibialis anticus. *c.* Extensor hallucis longus. *d.* Extensor indicis longus. *e.* Extensor digitorum brevis. *f.* Fifth toe slip to last muscle *(e)*.

Note.—Certain of the above figures refer to the second part of this Paper.

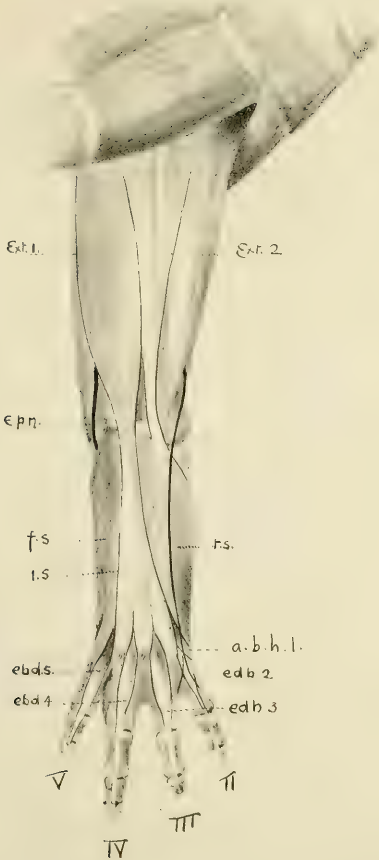

Fig 1

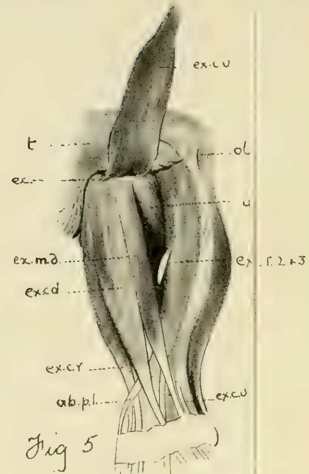

Fig 5

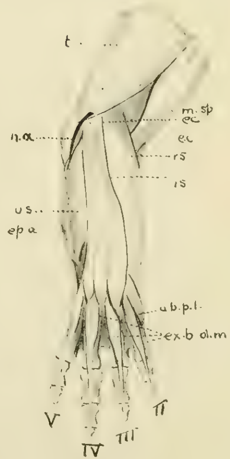

Fig 2

Fig 4

Fig 3

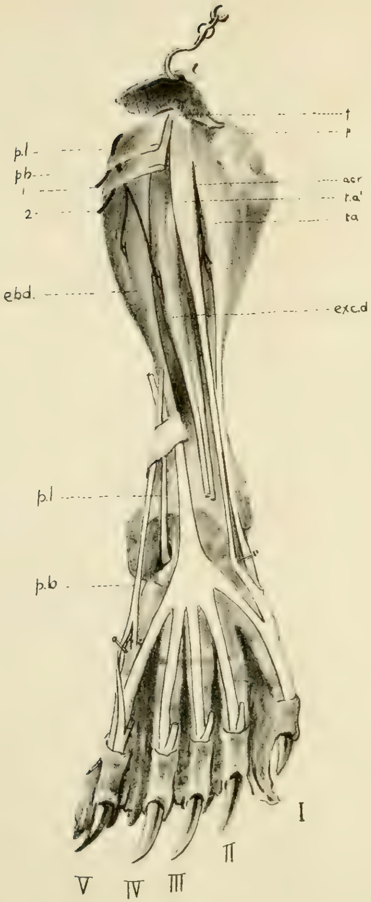

Fig. 7

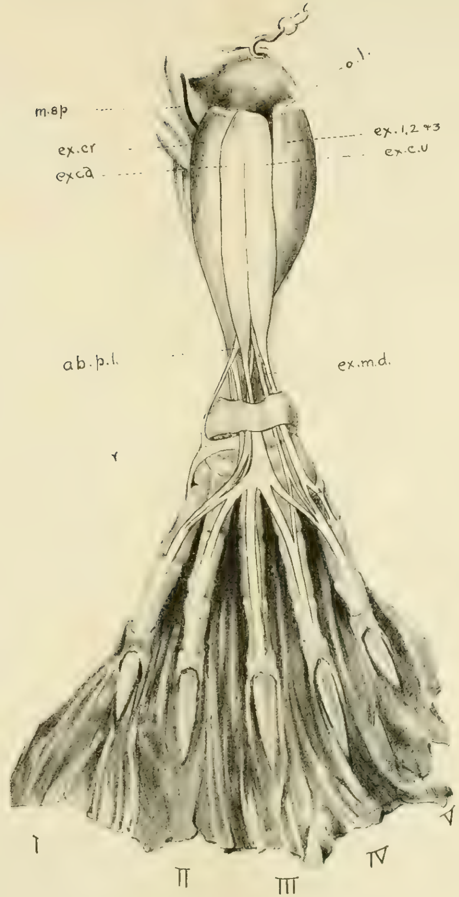

Fig 6.

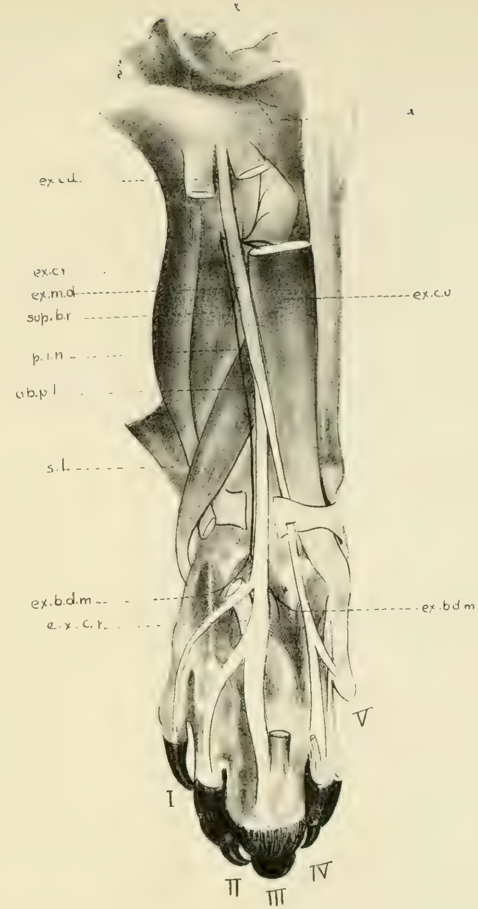

Fig 5


10
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13.
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11.
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12
17
15.
dig.5 dig.3 dig.1
dig.4 dig.2
ex.c.d
ex.m.d
abpl
ex.cr.br
ex.cr.l
fl.c.u'
ms.p.n
un
m.n
ol.
fl.c.u
fl.d.
q.ex.cr
ex.b.1
ex.b.2
ex.b.5

Vol. I. No. 6.

Studies from the Museum of Zoology

IN UNIVERSITY COLLEGE, DUNDEE.

EDITED BY

D'ARCY W. THOMPSON,

Professor.

VI. ON THE STRUCTURE OF TRACHYPTERUS ARCTICUS

(THE NORTHERN RIBBON-FISH).

BY

ALEXANDER MEEK.

DUNDEE:

Printed for the Museum.

February, 1890.

VI. *On the Structure of Trachypterus arcticus (the Northern Ribbon-Fish).*

By Alexander Meek, *University College, Dundee.*

In the year 1872 a very splendid specimen of the Ribbon-Fish came ashore near the town of Montrose. The specimen—nearly six feet long—was partially described and figured by Dr Howden, of Montrose,* and served, moreover, as the subject for a well-known figure in Day's "British Fishes." Unfortunately, the specimen was neglected, and having fallen to pieces, was sent us, that, if possible, it might yet be repaired and set up as a skeleton. The task was becoming hopelessly difficult, when we received, by the great kindness of Professor Lütken, of Copenhagen, two smaller examples of the same fish, in sufficiently good preservation for osteological research, and for the examination of a few of the viscera. From one of these the following results have been chiefly drawn. The dimensions of this specimen were as follows:—Length, $3\frac{1}{2}$ feet; greatest depth, $6\frac{1}{2}$ inches (in region of anus). The thickness varies from $1\frac{3}{4}$ inches in the cranial region, to an extreme tenuity between the interspinous bones.

No minute account of the osteology of *Trachypterus* has been published heretofore, but Professor T. J. Parker's monograph on *Regalecus argenteus*,† has furnished us with a basis for the following description, and, indeed, the recent thorough examination of this closely-allied genus helped to add interest to a closer study of our Northern Ribbon-Fish. It will be seen that numerous minor structural differences exist between these two much modified and in general very similar forms. The external characters of the fish are sufficiently well known. Such points, specific in general, as remain uncertain or deserve particular attention, have been discussed by Lütken,‡ Emery,§ and others: on these points, for instance—the character of the ventral fins, the anterior portion of the dorsal or nuchal fin, etc., our specimens throw no new light. And we are accordingly confined to an anatomical description, principally of the skeleton.

The Skull. (Plate I.)

The skull of *Trachypterus* is remarkably modified, on the same lines as in *Regalecus*, in consequence of the great lateral compression of the whole fish. We

* *Rep. Montrose Nat. Hist. and Antiq. Soc.*, 1872.

† T.Z.S., Vol. XII., Pt. I., 1886.

‡ C. Lütken. *Trachypterus arcticus og Gymnetrus Banksii.* Vidensk. Meddel. fra den naturh. Foren. i Kjobenhaen. 1881. *Nogle Bemærkninger om Vaagmæren.* Oversigt over K. D. Vidensk. Selsk. Forhandl. 1882.

§ Emery. *Contribuzioni all' Ittiologia.* Atti d. r. Acad. d. Lincei, Roma. 1880.

can, however, trace in it all, or almost all, the elements usually present in a Teleostean skull.

The parts originally preformed in cartilage still retain in the adult a large amount of this cartilage unossified; the membrane bones are for the most part greatly expanded, are characteristically sculptured, and those of them which lie superficially are covered by so thin a layer of silvery skin as to be easily recognizable in the undissected fish.

The cranium or brain-case is relatively very small in proportion to the general bulk of the fish, and to the great size of the jaws, and of the hyoid and opercular regions. Posteriorly the cranium is elevated in a high supra-occipital crest, which in *Regalecus* is flat and smoothed away; while below the foramen magnum a descending crest or keel, not quite so conspicuous as in *Regalecus*, is formed principally by the basioccipital and prootic bones. The orbit is immensely large, and the inter-orbital region very incomplete: the alisphenoids and orbitosphenoids meet together below the floor of the anterior part of the brain-case, in which the basisphenoid takes no part, while the presphenoid is altogether absent. The ethmoidal region is bent abruptly downwards, and the parasphenoid coming into relation with it anteriorly and with the basioccipital keel behind, forms a bridge even more than usually distant from the true base of the cranial cavity.

The roof of the skull, in front of the supra-occipital, constitutes a deep groove, in which long processes from the premaxillæ slide in the act of protrusion and retraction. This groove is mainly formed by a cartilaginous roof or *tegmen cranii*, in which is developed the large mesethmoid. The frontals are thus separated from one another to form great part of the walls of the groove, above which they rise in high ridges, nearly on a level with the supra-occipital posteriorly, but declining to a point in front.

The region of the auditory capsule is prominent, but is destitute of marked ridges or angles. Thus even the pterotic, usually salient, here forms only a small rough patch on a level with the surrounding bones.

The long processes of the premaxillæ, further elongated by a continuation backwards in cartilage, are attached to a loose fold of integument, which posteriorly is attached chiefly to the pre-orbital bones. In this fold the processes of the premaxillæ (and of the maxillæ which are attached to them) can be thrust backwards till the end of their cartilage continuation reaches the supra-occipital: in the protracted state it is on a level with the anterior end of the frontal. This whole mechanism is automatically pulled forwards as the mandible revolves upon its articulation with the quadrate, and is further depressed and withdrawn by movements of rotation at the palato-ethmoid and hyomandibular articulations. Its mouth, which, when closed, was situated at the extreme anterior and upper angle of the head, and was scarcely noticeable there, becomes when open a long, narrow vertical slit.

We may consider the skull in detail under the several headings of (1) the cranium; (2) the jaws, and (3) their suspensorial apparatus; (4) the hyoid and branchial arches; and (5) the opercular series.

The Cranium. (Plate I., *Figs.* 1, 3, 4. II., *Figs.* 5, 6.*)*

The *supra-occipital* is a cone-shaped bone, with oval base and rounded apex. The base forms part of the inner wall of the brain-case, and is traversed by large cavities which open inwards. The posterior and lateral margins of the base are articulated by slight cartilaginous intervention with the frontal and with the

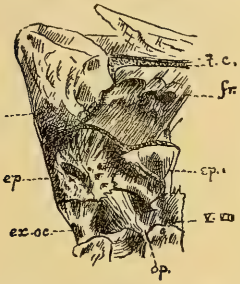


Fig. 1. INTERNAL VIEW OF CRANIUM.

ep., epiotic; *ex.-oc.*, ex-occipital; *fr.*, frontal; *op.*, prootic; *s.oc.*, supra-occipital (in this specimen, smaller and less prominent than in the other); *sp.*, sphenotic; *t.c.*, *tegmen cranii*; V., VII., foramen for the fifth and seventh nerves.

epiotic, the latter bone providing a shelf-like ridge for its reception. The parietal articulates with the lateral margin of the base, also, just external to the frontal and under cover of the epiotic. Anteriorly the bone articulates with the cartilaginous *tegmen cranii.* Thus the supra-occipital is here, as in *Regalecus*, displaced from its proper connection with the exoccipitals, owing to the great development of the epiotics, but it is a larger and much higher bone. The rounded apex forms the posterior dorsal angle of the skull.

The *ex-occipitals* are irregular in shape, but each may be described as consisting of a body, a wing, and an anterior process. The body, in each case, presents a notch which together form the foramen magnum, below which the two bones meet in the middle line, and above which they are only separated by a median cartilage. The body of the bone forms the dorso-lateral facet of the occipital condyle, below which is a foramen for the vagus nerve. The wing is a shell-like expansion which lies over the epiotic, and helps to form the pit for the lodgment of the post-temporal. Its lower border articulates with the lower portion of the pterotic. The anterior process articulates with the prootic. Internally it is excavated to form, together with the prootic and the epiotic, a pit which probably lodges the horizontal semi-circular canal.

Basi-occipital.—As has already been pointed out, this bone does not enter into the formation of the foramen magnum. It presents a surface posteriorly which joins with the ex-occipitals in forming the occipital condyle. Below it sends down two lateral processes which enclose a median vertical groove for the reception of the parasphenoid. Each process articulates by its anterior edge with the descending process of the prootic. Above, the basi-occipital sends upwards a median keel which projects between the ex-occipitals and separates those bones, except posteriorly in the region of the condyle. The basi-occipital enters into the formation of a pit-like hollow in the floor of the brain-case, and here also it is joined by that median cartilage which unites the prootics.

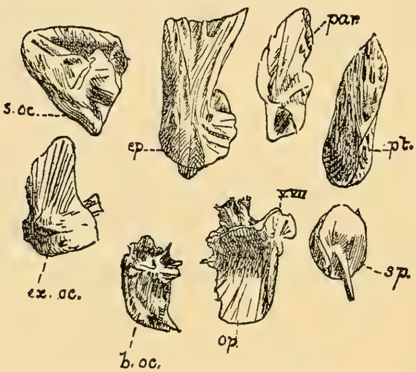


Fig. 2. The Occipital and Otic Bones.

b.-oc., basi-occipital; *ep.*, epiotic; *ex-oc.*, ex-occipital; *op.*, prootic; *p.sp.*, parasphenoid; *par.*, parietal; *pt.*, pterotic; *s.-oc.*, supra-occipital; *sp.*, sphenotic; V., VII., foramen for these nerves.

Epiotics.—The epiotics are very large, the largest of the otic series, and form the greater part of the back of the skull. They meet above the foramen magnum along a vertical line, an inch long, by a slight cartilaginous intervention which expands below to form the dorsal boundary of the foramen magnum. Internally the bone presents a regular curved ridge looking upwards, traversing the bone at its lower third. This ridge is capped by cartilage, and forms an articulation for the supra-occipital and for the frontal, both of which bones, therefore, the epiotic overlaps. Below the ridge the bone is thick and deeply pitted, and ends in a thick base, the outer portion of which is capped by cartilage, and is received within the great wing of the ex-occipital. Externally the epiotic articulates with the parietal and the pterotic; anteriorly there arises from the cranial surface of the bone a slight process, which uniting with a similar but larger process of the prootic, forms a strong pillar on the internal wall of the skull. The epiotic comes also into relation, to a slight extent, with the sphenotic.

The *pterotics* form the greater part of the ridge between the orbits and the posterior wall of the skull. This ridge is sharp and keel-like below, and passes up into a broad face above. From the surface the bone passes inwards like a wedge. The posterior face of the wedge is covered by the post-temporal, the pit for which it enters largely into the formation of. Below and internally this same face presents a rough articular surface which receives the outer lower portion of the wing of the ex-occipital; above this the pterotic articulates with the epiotic and the parietal.

The anterior face is covered above by the sphenotic; below, it is exposed and articulates with the prootic. The two faces meet in a rounded edge, which articulates anteriorly with the alisphenoid, and above with the frontal. The latter bone shuts it out from the internal surface of the brain-case above. A small portion, together with the intervening cartilage, serves to complete round the pillar formed by the epiotic and prootic the canal which seems to lodge the horizontal canal of the ear.

The *sphenotics* are rounded elements which present a smooth outer surface, slightly hollowed in the middle, and a deeply pitted internal surface. From the outer surface a thin splinter descends and meets a corresponding upgrowth from the parasphenoid, thus forming the post-orbital pillar. The sphenotic articulates by a large surface with the pterotic, and the posterior edge of that surface articulates with the epiotic; anteriorly it articulates with the alisphenoid, below with the prootic, above with the frontal.

Prootics.—In the figures accompanying this paper we have represented this bone under the letters *op.*, believing it to be the opisthotic. It is figured and described in *Regalecus* under the latter name by PARKER, who saw sufficient cause for his identification in the presence of a small separate prootic, imperfectly ossified, which is not present in *Trachypterus.* However that may be, and whether or no a true opisthotic be incorporated with it, the bone under consideration here can only be identified with the *prootic* on account of its large size, its union with its fellow in the middle line, its relation to the fifth and seventh nerves, and to the representative of the canal for the ocular muscles. It consists of a body from which diverge numerous processes, as follows:—(1) A process, stout and rounded, ascending to meet a corresponding process from the epiotic *(Pl.* II., *Fig.* 5*)*; (2) a process, outwardly directed, which meets the sphenotic; (3) a flat process which articulates with the lower margin of the alisphenoids, it is directed forwards, and contains the foramen for the fifth and for the seventh nerves—the first division of the fifth nerve passes internal to the post-orbital pillar, the second and third divisions and the seventh nerve emerging posterior to it; (4) a thin descending lamina, which is continued round on to the posterior end of the bone, and articulates by cartilaginous intervention with the corresponding descending process of the basi-occipital, below with the parasphenoid, and above with the anterior process of the ex-occipital, it is also continued behind the epiotic process, and articulates with the pterotic; (5) a horizontal process which stands inwards and meets its fellow to form part of the floor of the brain-case. This last is bony above and cartilaginous below, and is attached behind to the basi-occipital. This process in each case articulates also anteriorly with one of the forks of the basi-sphenoid.

Parietals.—The parietal is not seen in the complete skull until the post-temporal is removed; it forms the upper part of the floor of the pit for that bone. It articulates externally with the pterotic; posteriorly with the supra-occipital and epiotic—the latter slightly overlapping it; below with the epiotic; above with the frontal. It is prevented from entering into the formation of the inner surface of the skull-wall by the frontal, which sends a flat plate internal to it for articulation with the supra-occipital. Thus the parietals, overshadowed by the great size of the epiotics, and covered over by the post-temporals, form no longitudinal crest on the surface of the skull, as they do even in *Regalecus*.

The *frontals* are very large bones. Each presents a large triangular outer surface which is subcutaneous, and rises posteriorly into a high crest to a level with the supra-occipital. The inferior surface of the bone, which makes a sharp supra-orbital ridge at its junction with the preceding, constitutes the roof of the orbit. The inner face forms in its upper portion the side-wall of the great groove in which slide the pre-maxillary processes, and in its lower portion is excavated to receive the great cartilage of the *tegmen cranii* which forms the floor of the said groove. The supra-orbital plate of the frontal articulates in succession with the mesethmoid, the orbitosphenoid, and the alisphenoid. The anterior narrow end of the bone articulates with the parethmoid. Posteriorly the frontal articulates with the sphenotic, the pterotic, the parietal, the epiotic, and the supra-occipital.

The *nasals* are small, flat, thin, rectangular bones, and lie freely over the nostrils, attached by ligament to the frontals.

The *sub-orbital scutes* are reduced to two in the anterior region on each side. The upper one, the lachrymal of Teleosteans, is much the larger. It is nearly rectangular in outline. Its outer surface is deeply grooved. Its inner surface is rounded. The lower one is flat, thin, and very small. The two bones are in contact with one another; both are sub-cutaneous.

The *basisphenoid* is said by Parker to be entirely wanting in *Regalecus*, as also is the *presphenoid*. The latter bone is not to be found in *Trachypterus*, but the basisphenoid is well developed, though somewhat remarkably modified. This element, placed slightly anterior to the post-orbital pillars, rests below in a groove of the parasphenoid, and rises up as a sort of columella to join by its forked head the two prootics close to the alisphenoids, and immediately below a larger anterior cranial foramen. Anomalous as is the appearance of this bone, it is plainly the basisphenoid, displaced and elongated by the same causes which have led to the separation of the parasphenoid from its ordinary position in the base of the skull.

The *alisphenoids* are thin, flat, squarish bones, articulating in front with the orbito-sphenoids, above with the frontals, behind with the prootics and sphenotics. Below they are in contact with one another in the ventral middle line anteriorly, and diverge posteriorly to bound the anterior portion of the anterior cranial foramen.

Each *orbito-sphenoid* is also a thin, flat bone of similar appearance to the preceding. It also meets its neighbour in the middle line. It gives distinct evidence of a cartilaginous origin—the upper part of the bone being a wedge of cartilage encased in a thin shell of bone. It articulates behind with the alisphenoid, above or outside with the frontal, and in front with the mesethmoid. It is much smaller than in *Regalecus*.

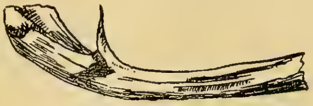


Fig. 3. THE PARASPHENOID.

The *parasphenoid*, as regards its remarkable displacement (as in *Regalecus*) far below the level of the *basis cranii*, has already been referred to in general terms. It is a long bone, straighter than in *Regalecus*, keeled below, receiving in front the pointed posterior end of the vomer beneath the pre-nasal cartilage, and appearing to a very slight extent in the posterior view of the skull, beneath the basi-occipital. In this latter region it does not present the strong ventral keel seen in *Regalecus*. Posteriorly the parasphenoid comes into relation with numerous bones. On the upper surface in the middle line is a prominent median ridge, which is received between the descending processes of the basi-occipital, which fit into grooves on either side of the said ridge. The anterior ends of the ridge and groove likewise articulate with the descending process of each prootic. The sides of the parasphenoid are raised into two outstanding processes, which take their origin opposite the anterior end of the ridge. These meet corresponding processes of the sphenotics and form the post-orbital pillars. Each is supported by coming into relation with the border of the prootic. Lastly, between these post-orbital processes, the ridge is replaced by a groove in which rests the basi-sphenoid.

The *vomer* is a hollow wedge, with thin bony walls, within which fits the pre-nasal cartilage; the latter is further clamped there by two ascending wings, which run upwards to articulate with the parethmoids. The lower surface of the vomer is keeled, and passes backwards into a deep excavation in front of the parasphenoid. The inferior keel of the vomer bears anteriorly three teeth, two large and a smaller one between.

The *mesethmoid* is a shield-shaped bone interposed between the great cartilage of the *tegmen cranii* and the pre-nasal cartilage (*Pl.* I., *Fig.* 3), and forming the anterior part of the groove for the pre-maxillary processes. It is much larger than in *Regalecus*, and articulates anteriorly and laterally with the parethmoids, posteriorly, to a small extent, with the frontals. Below it is somewhat keeled, and behind articulates with the orbito-sphenoids. In front it is excavated to form a small hollow pit, the mesonasal cavity (*cf.* PARKER, *loc. cit.*).

The *parethmoids* are flat bones, sculptured deeply above and very slightly below, to a great extent superficial. Each present a notch on the upper border, which is made into a foramen by the anterior process of the mesethmoid, and transmits the first division of the fifth nerve. Anteriorly it articulates with the vomer, posteriorly with the frontal, internally with the mesethmoid.

The Suspensorium and the Jaws (Plate I.*).*

The *hyomandibular* is very long and rod-shaped, presenting a broad end above, capped by cartilage, for articulation with the region of the auditory capsule ; below it is pointed, and articulates with the inter-hyal. The bone, as a whole, presents an anterior and an internal face, and posteriorly a groove formed by their sides, which is replaced near the head of the bone by a rounded surface merging into the inner side. Below this rounded surface, and just internal to the top of the groove, the operculum is definitely articulated. More than the upper half of the anterior edge of the preoperculum is lodged in the groove. Between the anterior and inner faces is a sharp angle, which below comes into relation with the metapterygoid. The pointed inferior extremity is articulated to the nodule of cartilage which caps the inter-hyal, and this nodule separates it from the symplectic. It gives support to the pseudo-branch or opercular gill *(Pl.* I., *Fig.* 2*).*

The *quadrate* is a triangular flattened bone. At the lower corner it is transversely thickened to form a horizontal condyle for the articular : the lower border is a flat one, enclosing a groove on the inner side of the bone for the lodgment of the symplectic. The anterior edge underlies the pterygoid. The upper border articulates with the mesopterygoid anteriorly : in this region, between the quadrate, mesopterygoid, and metapterygoid, are copious remains, as PARKER has pointed out in *Regalecus*, of the embryonic palato-pterygoid cartilage.

The *symplectic* reposes in a hollow on the inner side of the quadrate, beyond the posterior border of which it only slightly projects. It is a narrow bone, tapering as it passes into the quadrate.

The *pterygoid* is a narrow, flat bone, with pointed lower extremity. It articulates by its upper edge with the palatine, and by its posterior edge with the mesopterygoid and the quadrate.

The *mesopterygoid* is the largest of the series. It is irregularly four-sided in outline. Its outer surface is divided into an upper and lower half by a ridge-like horizontal fold. It articulates in front with the palatine and pterygoid, below with the quadrate, and posteriorly with the metapterygoid.

The *metapterygoid* is an excessively thin element, of a triangular shape. It articulates with the mesopterygoid, and below comes into relation with the common cartilage, uniting the quadrate and symplectic to the mesopterygoid and inter-hyal.

The *palatine* is a flat, rounded bone, with a well-developed head for articulation with the parethmoid and the pre-nasal cartilage. Below it is closely attached by membrane to the pterygoid, and it overlaps the mesopterygoid posteriorly.

The *articular* is a very large triangular bone, fitting into the dentary anteriorly, and forming about one-half the skeleton of the mandible. The upper border is straight and thickened, and presents posteriorly a large concavity for the articular end of the quadrate. From a conspicuous prominence on the inner surface, near the proximal end, a slender MECKEL'S cartilage is continued forward as far as the anterior extremity of the bone.

The *dentary* is also triangular, the posterior edge presenting a wide indentation to receive the anterior portion of the articular. The anterior extremity of the dentary is much thickened, and in the fibrous tissue forming the mandibular symphysis two small separate ossified nodules were found. The upper border of the dentary bears four or five small teeth anteriorly.

The *angular* is a small triangular flat bone, which lies on the inner face of the articular at its lower angle.

Each *pre-maxilla* is composed of a vertical portion which bounds the gape, it becomes horizontal above, to approach its fellow in the middle line, and is thence continued backwards as a long pointed "nasal" process. The latter is rounded and smooth externally, but its inner face is flat and applied to that of its neighbour. Anterior to the middle of this process, on the under side of the bone, is a slight projection directed downwards, which articulates with the internal process of the maxilla. Below, the processes are attached strongly to a median cartilage, which is large posteriorly, and is continued backwards beyond the processes a little distance. At the posterior end of the projection just mentioned, it suddenly is reduced to a thin median strip, which extends forwards to a point rather more than half-an-inch from the anterior end of the pre-maxilla. This cartilage is found in other Teleosteans, *e.g.*, the Cod (*c.f.* PARKER), but is here greatly developed to form a smooth surface which slides over the *tegmen cranii*. The smooth outer surface of the process is continued on to the vertical process or body as a ridge separating two shallow grooved fossæ. The posterior one receives the anterior edge of the maxilla. The anterior is sub-cutaneous (*Pl.* I., *Fig.* 1). Near the anterior end, and near the middle line are a series of small teeth, four or five in number.

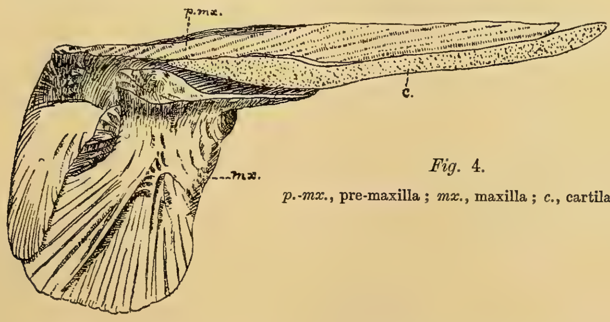


Fig. 4.
p.-mx., pre-maxilla ; *mx.*, maxilla ; *c.*, cartilage.

The *maxillæ* are situated external to and under the pre-maxillæ. Each consists of a flat sculptured sub-cutaneous plate, of an irregularly oval shape, and an inwardly-directed process, meeting its fellow below the pre-maxilla, and sending backwards a process like that of the pre-maxilla, but much shorter. The maxilla bears no teeth.

The Hyoid Arch (Pl. I., *Fig.* 2*).*

The constituents of the hyoid form a small but stout arch. Of the six branchiostegal rays, two are attached by cartilage to the epi-hyal, and four to the cerato-hyal. The rays are long, curved, and hollow, ending in the edge of the branchiostegal membrane.

The *inter-hyal* is a very short rod, possessing a nodule of cartilage at each end, and connects, in the usual way, the cartilage between the hyomandibular and symplectic with the epi-hyal.

The *epi-hyal* is a rather large, flat, and thickish bone, with a rounded and prominent posterior border.

The *cerato-hyal* is large and flat, constricted in the middle, much expanded at the top, slightly so below. The anterior and upper angle is very prominent, overhanging the larger of the two hypo-hyals. The cartilage between this and the preceding element diverges posteriorly, and supports four of the branchiostegal rays. The lower edge is rounded, and is capped by cartilage which contains the two hypo-hyals.

Of the two *hypo-hyals*, the upper one is much the larger: it is attached in its whole length to the anterior border of the cerato-hyal. The smaller hypo-hyal is a little crescent of bone, with a free inferior edge, from which a short ligament proceeds to join its fellow from the opposite side, and thus give attachment to the uro-hyal.

The *uro-hyal* is a large vertically flattened, median bone, with a somewhat pointed anterior end, from which strong ridges radiate backwards.

The Branchial Arches (Plate II., *Figs.* 7 *and* 8*).*

There are five pairs of branchial arches, which, in their general arrangement, the mode of their segmentation, and the disposition of their ventral median series of *copulæ,* agree for the most part, but not altogether, with those of *Regalecus.* All bear gills, with the usual exception of the fifth, and the gill-slits are all surrounded by a row of *gill-rakers.*

The first four arches contain each the usual four elements, viz., *hypo-branchial, cerato-branchial, epi-branchial,* and *pharyngo-branchial;* the fifth is, as usual, unsegmented, constituting the pair of so-called *hypo-pharyngeal bones.*

The *first arch* is the longest. Its hypo-branchial is a long three-sided rod, attached below to the cartilaginous third median element. The cerato-branchial is broad, and deeply grooved posteriorly for the branchial vessels. The epi-branchial, also grooved posteriorly, is a flattened bone, narrow at its articulation with the cerato-branchial, but broad and rounded at its proximal end; here is attached to it the long needle-shaped and rudimentary *pharyngo-branchial*, which lies over and in front of the succeeding pharyngo-branchials; the cartilaginous continuation or epiphysis, which PARKER describes in *Regalecus* under the name of *para-branchial*, is not to be detected.

In the three succeeding arches the cerato-branchials call for no remark. The hypo-branchial in the second arch resembles that of the first, but is much smaller; in the third, the hypo-branchials are thrust forwards, and appear as free projecting points of bone, attached *posteriorly* to a mass of cartilage, close to, but below the copula, which receives the corresponding cerato-branchials; in the fourth arch, the hypo-branchials are represented only by minute rudiments. The epi-branchial is, in the second arch, a short rod, on which a small projection is noticeable posteriorly; in the third and fourth arches, the epi-branchials are forked above, the anterior limb of the fork being the articular process for the pharyngo-branchial, the posterior limbs being applied to one another and united by ligament. The pharyngo-branchials are of peculiar form. The two which belong to the second and third arches are long bones, broad posteriorly, at which end they bear several sharp, curved teeth, and narrow anteriorly, where they are attached in common to a pointed cartilaginous epiphysis. Each is rounded above and grooved below, and articulates by a tubercle below with the corresponding epi-branchial. The fourth pharyngo-branchial also bears teeth, but is a shorter and relatively broader bone. The teeth on these three pharyngo-branchials are four, five, and six in number respectively. The fifth arch consists of a pair of long and very slender cerato-branchials, tipped at each end with cartilage.

The *copulæ* or median elements are very numerous. The first of these *(b.hy.)* the *basi-hyal* or *glosso-hyal*, is cartilaginous, and forms the supporting skeleton of the short, blunt tongue. The second *($b.br.^1$)* is large, well ossified, and produced into a deep keel below. It answers to W. K. PARKER'S *first basi-branchial*. Behind this we have—third, a cartilaginous inter-space, to which is attached the first branchial arch; a small centre of ossification is present in it. Fourth, a distinct ossified element *($b.br.^2$)*, flat and sculptured above and grooved below—the second basi-branchial. Fifth, a cartilage attaching the second arch: two small centres of ossifications are present in it, side-by-side. Sixth, a long, rod-like, rounded bone *($b.br^3.$)*, slightly narrowed in the middle—the third basi-branchial. Seventh, a cartilage with one nodule of ossification; just below this, the cartilage uniting the hypo-branchials and cerato-branchials of the third arch meet in the middle line. Eighth, a cartilaginous element, with an irregular centre of ossification *($b.br^4.$)*. The two cartilages representing the hypo-branchials of the fourth arch, each with a nodulary ossification, meet below $b.br^4$. Ninth, a small, but long and thin, laterally compressed cartilage *($b.br^5.$)*, devoid of ossification. Succeeding this are two round nodules of cartilage belonging to the fifth arch.

It is perfectly clear from this description that, as T. J. PARKER has pointed out in *Regalecus*, the median elements known, and described above, as basi-branchials, are really *inter-branchials*, the branchial arches articulating not with them but with the cartilaginous and imperfectly ossified elements which alternate with them.

Gill-rakers are present in two rows on each of the four anterior arches, in one on the fifth. They differ in the details of their arrangement from those of *Regalecus*. The first row of gill-rakers stand in a membrane which is attached to the inner border of the first arch. In the middle of the series, they are long and irregularly grooved; the lower ones are blunt, and stand free in the membrane without being attached to the arch itself *(Pl.* II., *Fig.* 7*)*. They are thirteen in number, and all bear on their inner edge small bristly denticles.

The rakers of the second row alternate with those of the first row, and are attached to the posterior face of the arch near to their inner edge. They are stronger, shorter, and blunter, and are likewise provided with small sharp teeth, which in this case are at the point. They also are thirteen in number.

On the *second arch* in the first row, a small raker leads from the second row of the first arch and appears on the basal element. All the rakers are attached to the arch. They are smaller than the corresponding row of the first arch, but bear small teeth, like them, on the inner edge. The first row consists of thirteen rakers, the second of ten alternating with the former.

The *third arch* has likewise thirteen rakers in the anterior and ten in the posterior row. The *fourth* has nine anteriorly, and posteriorly six only, which latter are confined to the cerato-branchial element. The *fifth arch* possesses eight or nine small tooth-like rakers in its anterior and only row. The lower ones are sharp and curved.

The alternation of large and small rakers in each series, which is characteristic of *Regalecus*, is thus not seen in *Trachypterus*. The immensely long rakers of the first arch in *Regalecus* are not developed, nor do the rakers extend on to the pharyngo-branchials of this or of the succeeding arches.

The Opercular Bones.

The *preoperculum* is a simple flat bone, with a three-sided *contour*, marked with radiating ridges or grooves, thin and papery posteriorly where it overlaps the operculum and inter-operculum, comparatively strong in front where it enters into the usual relations with the hyomandibular and quadrate.

The *operculum* is a much smaller bone, and more vertical in position than in *Regalecus*. It is of an irregular ovoid form, narrower and more solid at the top, where it articulates with the hyomandibular, broad and thin below where it overlaps the sub-operculum and inter-operculum.

The *sub-operculum* is small, and extremely thin : but appears to be somewhat larger and especially broader than in *Regalecus*.

The *inter-operculum* is remarkable for its great length and rectangular shape. It ends in front on a level with the preoperculum.

The Vertebral Column (Pl. II., *Fig.* 10*).*

The vertebral column consists of 101 slender and excessively fragile vertebræ, eight more, that is to say, than are present, according to Parker, in *Regalecus argenteus.* The vertebræ agree in general with, but differ in points of detail from, those of that genus. Each centrum is deeply amphicœlus, consisting as it were of two delicate cones, placed apex to apex, where in most cases a small aperture places the invertebral substance of the two sides in communication. The outer surface of the centrum presents a series of parallel radiating lamellæ, arranged like the slats of a water-wheel, and binding the two cones together. On the dorsal aspect of the centrum two somewhat similar but modified lamellæ arise. Each of these is elevated anteriorly and posteriorly into a pointed triangular *zygapophysis,* while between these arises a more delicate *neural process,* which meets its fellow of the other side to form a neural arch, from which arises the long slender *neural spine.*

The neural process is usually approximated to the anterior zygapophysis: and the two anterior zygapophyses are usually somewhat near together, and fit in between the posterior zygapophyses of the preceding vertebra.

From the under side of the centrum two *haemal* or transverse *processes* project downwards, enclosing between them one, two, or more lamellæ. Each haemal process is expanded at the base, especially on its anterior aspect, and each is strengthened by a ridge on its outer surface which is paralleled by a similar but weaker ridge at the base of the neural arch and spine. The first forty-three haemal processes are free, but the remaining ones unite to form *haemal arches* and haemal spines, which are not present in any part of the body of *Regalecus.*

Parker calls attention to the remarkable increase in length of the vertebral centra in *Regalecus,* from the anterior to the posterior end of the series. A similar increase is traceable in *Trachypterus,* but only as far as the ninety-second vertebra, beyond which the centra diminish again; and the vertebræ nowhere exhibit such an extraordinary length of centrum as *Regalecus* displays in the posterior half or third of its body.

Fig. 5. Anterior Aspect of atlas, dorsal and caudal Vertebræ.
(The neural spines of the two latter are broken off.)

In *Trachypterus* the first centrum is a thin curved disc; that of the second is much larger and wedge-shaped, being about one-eighth of an inch in length above and one-twelfth below. The third centrum is also wedge-shaped, but slightly: below, it measures three-sixteenths of an inch; and above, one-eighth (it appears more wedge-shaped in one of our specimens than in the other). From the third to the ninety-second there is a gradual increase in length of centrum; and the applied faces are now parallel. The fourth is very nearly one-fourth of an inch in length; the fifth is slightly more than one-fourth of an inch; the eighth is nearly five-sixteenths; the seventeenth is over five-sixteenths; the thirty-ninth is three-eighths; the seventy-eighth is five-eighths; and the ninety-second is thirteen-sixteenths. Beyond the ninety-second there is a gradual decrease. The ninety-seventh is nine-sixteenths; the ninety-eighth, seven-sixteenths; the ninety-ninth, nearly three-eighths; the one-hundredth, nearly five-sixteenths; and the last one, three-sixteenths of an inch, not including the terminal cartilage.

Ribs are either altogether absent, or are so very minute as to have escaped our notice.

The *first* vertebra, in spite of the thin discoidal centrum already referred to, is in respect of its neural arch and spine the strongest of the series. The centrum is firmly attached by ligament on the one hand to the occipital condyle, and on the other to the second vertebra. It is opisthocœlus, and presents near the middle of the rounded disc the foramen found in all. The centrum is oval, with the short diameter vertical, and half as long as the longer diameter. The arch is flattened anterior-posteriorly. The spine is club-shaped; there are no articular nor transverse processes, though the latter are, by a rare anomaly, present in *Regalecus.*

The *second vertebra* has a spine nearly as strong as that of the first. The wedge-shaped centrum is amphicœlous, but the cup is much shallower in front than behind; it is in section oval rather than circular, and has the typical structure otherwise of two opposed cones with strengthening lamellæ. The posterior zygapophyses are slightly developed, the anterior are still absent.

In the *third vertebra* the anterior zygapophysis is developed, and the posterior is now large and typical. The spine in this and in the succeeding vertebra is still flattened and club-shaped, but less strong than in the first and second.

The transverse process is present for the first time in the *fourth vertebra.* On the ventral surface, between the two transverse processes, are in one of our specimens four, in the other eight, of the longitudinal lamellæ; the eight in the one case showing signs of origin from the splitting of an original four.

The spine in one specimen is club-shaped like the preceding ones, but in the other it is almost reduced to the slender rod found in the succeeding vertebræ. It ought to be mentioned here that the neural arch of this vertebra, along with the preceding ones, bridges two fossæ, and not one as in the typical vertebræ. The median ridge which divides these fossæ gets gradually absorbed in the next one or two succeeding vertebræ.

The *fifth* to the *fortieth* have all a structure which answers to the typical description given above. The neural spine is very slender, being only ·0013 to ·0015 inch in thickness. Near the arch it is a flattened band of this thickness. The spines gradually increase in length. This increase may be seen in *Fig.* 10, *Pl.* II. At first they are curved backwards, but become gradually straighter and more erect as we pass back. The centra likewise show the gradual increase in length already referred to. The hæmal processes have the typical structure, the external ridge and anterior expansion, and are seen to increase in length up to the eighteenth, and then decrease in the succeeding two or three to a size which remains pretty constant in the group we are considering (*Pl.* II., *Fig.* 10). The first hæmal process (in the fourth vertebra) is directed downwards and obliquely backwards; the succeeding ones are reflected more and more downwards.

In the *forty-first* vertebra the hæmal process is found to be directed much more backwards, and at the same time greatly lengthened, and the extremities approximated. The latter meet and fuse in the *forty-fourth* and the following ones, that is to say, behind the ureter. The inner edges meet and are produced together into a hæmal spine, in which the individuality of the two transverse processes remains distinct for some way. The hæmal arches are directed gradually more and more backwards.

The *sixty-fifth* vertebra lies over the end of the body cavity. The centrum is now half-an-inch long. The neural spine reaches its maximum in this region, being about three and a-half inches long, and so does the hæmal spine, which is two inches long. The centrum presents fewer strengthening lamellæ. The spines are comparatively strong—nearly one-twentieth of an inch in diameter. The neural plate is long, corresponding to the increase of length of the centrum. It has remained of a nearly constant height throughout.

Between the *sixty-fifth* and *ninety-second* vertebræ we find the increase in length of the centra gradually culminating at the same time that they become reduced vertically. At first four *radiating lamellæ* are found between the neural and hæmal processes, but these become reduced to three in the first few vertebræ of this group, and this number remains fairly constant till about the eightieth, when only two are found. Moreover, the double fossa enclosed by the hæmal arch gets replaced by one in about the first six of this group—the median ridge having disappeared. The neural and hæmal spines gradually decrease in size, and towards the end of the group become inclined more and more backwards; both remain of a pretty uniform thickness throughout. The neural plate also becomes reduced in height gradually.

The articular processes in the sixty-fifth are perfectly normal, but as we trace the series backwards we find that the anterior is gradually rounded off, while the posterior zygapophysis remains prominent, but in the last four or so of the group the latter also become reduced.

The neural spines now arise further back, behind the middle of the neural plate, and the hæmal processes originate further back still. The hæmal process is now seen to originate from two lamellæ, of which the upper gives origin to the external ridge, and projects beyond the general surface.

From the *ninety-second* to the *one-hundredth*, the vertebræ get smaller and smaller. The centra up to the ninety-fourth show two supporting ridges, and these go to support also the external ridges of both neural and hæmal arches. These are reduced in the next two, and disappear in the remaining ones, and are replaced by irregular and slightly marked ridges. The centrum of the second last vertebra—the one-hundredth—is bent upwards at the middle, so that the base of one of the cones is inclined to that of the other. Both neural and hæmal arches get gradually bent backwards, till the latter almost lie parallel to the axis of the vertebral column, each extending beyond the length of the following vertebra up to the ninety-sixth.

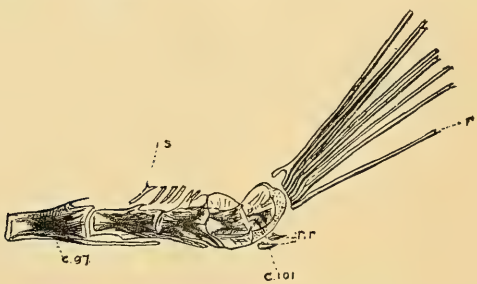


Fig. 6. THE LAST FIVE VERTEBRÆ AND THE RAYS OF THE CAUDAL FIN.

r., rays of caudal fin ; *r.r.*, rudimentary rays ; *s.*, neural spine ; *c.* 97, the centrum of the 97th vertebra ; *c.* 101, the centrum of the 101st vertebra. (Behind and below the last vertebra is the cartilage which supports the caudal fin.)

In the following vertebræ it becomes shorter. In the ninety-eighth it is slightly expanded lengthwise ; in the ninety-ninth, more so ; and in the one-hundredth it forms a longitudinal plate beneath the latter end of the vertebra, forming at the same time a long tunnel beneath the vertebra. The neural spine becomes reduced in a similar manner, but much more so in the last two or three. In the ninety-third it is an inch long ; in the ninety-eighth it is a short spine, one-fourth of an inch long ; in the next two it is only represented. The neural plate has also undergone a slight reduction. The articular processes dwindle away, and finally disappear between the ninety-second and ninety-sixth vertebræ.

The *last* vertebra is little more than half a centrum. It consists of a cone with a couple of parallel ridges extending along it from base to apex in the vertical plane. These are evidently modified from the neural plates and the hæmal processes. They form a groove, filled with cartilage in the recent state, which supports the rays of the caudal fin.

The Interspinous Bones and Dorsal Fin Rays.

The interspinous bones are about 173 in number, and have a similar structure from beginning to end, consisting of a stem, of varying length, which divides at the upper extremity into two little branches *(Pl.* II., *Fig.* 10, *i.b.).* The posterior process of one approximates to the anterior process of the interspinous bone behind it, and forms with it a support for the fin ray *(f.r.).* The stem and processes are hollow, the latter being cup-shaped, with an irregular sub-rectangular margin. Both are winged in four places in two planes, transverse and longitudinal. On each side of the stem, in the longitudinal plane, and a little below the fork, a broad wing occurs, which may be traced upwards on to the process where it becomes reduced, and down on to the stem where it dwindles away. Similarly, two wings occur in the same part of the stem, but in the transverse plane. Each forks above to go to the two processes, and each below runs downwards to form a ridge upon the stem.

The supporting arms undergo very little modification except in the rudimentary ones near the posterior extremity *(Fig.* 6*).* Anteriorly the arms are very short, and consist simply of two little cups set at an angle to each other. Passing back they get larger and more distinct. Posteriorly they are not so strong, but the processes are even better developed than in the middle of the body. Anteriorly the arms are about the same size, but the posterior gradually get larger than the anterior as we follow the series backwards. Near the tail the posterior process and the stem are in the same line, and the anterior arm is borne as a branch.

For the most part, the interspinous bones alternate with the neurapophyses. It is only near the head and the tail that the former exceed the latter. The first eighteen interspinous bones correspond with the first eleven or twelve vertebræ—sometimes two and even three being enclosed between two neural spines.

The longest interspinous bones lie near the middle of the body, and get smaller anteriorly and posteriorly; near the tail, the merest traces are got. The anterior ones do not suffer the same reduction—the shortest being over an inch long.

Dorsal Fin Rays.—The dorsal fin is supported by light hollow, unbranched rays, expanded cup-like at the bottom, and split, as in *Regalecus,* in the median vertical plane of the fish into right and left halves. This cup, along with those described for the interspinous bones, receives a nodule of cartilage, such as PARKER describes in *Regalecus,* but smaller *(loc. cit., p.* 24*).*

The length of the fin rays reaches a maximum in the middle of the body and a minimum at each extremity. The greatest length seems to be over four inches at least, but the rays are so easily broken that none remain perfect.

The Shoulder-girdle and Pectoral Fin (Pl. II., *Fig.* 9*).*

The shoulder-girdle of *Trachypterus* resembles, to a certain extent, that of *Regalecus,* but shows a still greater degree of modification in the points where both differ from the ordinary Teleostean type. The post-temporal is equally simple, the supra-clavicle and clavicle are narrower, straighter, and longer; the coracoid smaller and narrower, the scapula almost equally, and the brachials still more minute and rudimentary.

The *post-temporal* is firmly attached to the back of the skull. It lies in a recess covering the parietal, and bounded internally by the epiotic and exoccipital, externally by the frontal and pterotic *(Pl.* I., *Fig.* 4*)*. It is an elongated, flattened bone, slightly hollow on the anterior face, which is applied closely to the skull, and convex on the posterior or external face. It is pointed anteriorly, and has longitudinal grooves and ridges running down its length. Below it is thickened, and presents an articular surface at its base for the head of the supra-clavicle.

The *supra-clavicle* is a long straight bone, articulating above by a rounded, thickened head with the post-temporal, and applied below by a long splint-like surface to the outer face of the clavicle. The bone is broadest in the middle and pointed below; it is longitudinally grooved on the outer surface, and is somewhat hollowed within where it fits on to the clavicle.

The *clavicle* is a long, slender, curved bone. The upper end is pointed, and continued downwards from it are two grooves on the posterior side, separated by a sharp ridge or keel; the outer of these grooves receives the supra-clavicle, the inner one is longer, and extends to the angle of the bone. The lower extremity is also pointed, and meets its fellow in the middle line.

The *post-clavicle* is a long slender bone, which extends backwards and downwards from the clavicle, and is firmly attached by ligament to the inner of the two grooves on the posterior surface of that bone. The post-clavicle is about two and one-fourth inches long, much shorter, that is to say, than in *Regalecus*.

The *coracoid* is a flat triangular bone, slightly twisted, with an uneven sculptured surface. Its base is partly hidden by the cartilage uniting it with the scapula and brachials. It is not united, as in *Regalecus*, by its anterior border to the clavicle, but ends below in an elongated spine, which is attached by ligament to the extremity of the former bone.

The *scapula* lies in the cartilage already mentioned. It is a very small, flattened nodule, with rounded corners, and bearing a foramen a little anterior to its centre.

The *brachials* are three very small, thin, flattened bones. Between the first or anterior and the second two small foramina exist in the cartilage: the second and third are in close contact. The first is much the smallest. They seem to be rather smaller than in *Regalecus*, and contrast more with the scapula than in that genus.

The *pectoral fin* consists of twelve unjointed rays. Of these, the first three articulate with the scapula, and only the last with the third or posterior brachial.

The *pelvic fin*.—Between the coracoid and post-clavicle on each side we found a number of elongated, hollow ossifications. These were about one-sixteenth of an inch in diameter, but broken in both our specimens. A comparison with *Regalecus* leads us to the belief that these are all that represent the pelvic girdle and fin. According to LUTKEN, it is always rudimentary or absent.

Internal Anatomy.

Neither of our spirit specimens was in a condition to admit of detailed anatomical research. In both the brain was shrivelled up, the cranial nerves torn, and the muscles soft and pulpy. We can at best only describe and figure a few of the viscera.

Alimentary Canal.—The wide œsophagus, laterally compressed in relation to the narrow slit-like form of the body-cavity, merges insensibly by the development of thickened muscular walls with large, thin mucous folds or ridges, in the first or cardial portion of the stomach. The latter runs straight backwards, and terminates in a tapering cæcal pouch, closely bound down to the underlying intestine, about six inches from the anus.

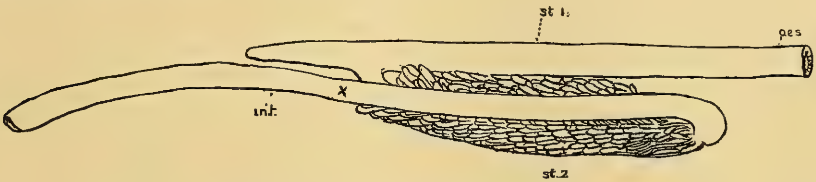


Fig. 7. Diagram of Alimentary Canal ($\times \frac{1}{4}$).

œs., œsophagus; *st.* 1, first chamber of stomach; *st.* 2, second chamber of stomach, with pyloric cæca; *int.*, intestine; ×, position of intestinal valve.

About three inches in front of the cæcal end, a wide orifice on the ventral side leads into the second or pyloric chamber. This is bent sharply on the former portion, and runs parallel to and below it to near the anterior extremity of the body-cavity. The pyloric chamber is about seven and a-half inches long. Through the orifice before referred to, about seven of the mucous folds pass for about three-fourths of an inch into the pyloric chamber; at the point where they end the lumen suddenly widens, and the internal surface becomes honeycombed in appearance, by reason of the numerous orifices of the pyloric cæcal appendages. These cæca surround the pyloric chamber in its whole length, and are more numerous above and below than laterally; they are simple unbranched tubes, on the average about an inch in length, and number altogether nearly 500.

At the anterior end of the pyloric chamber a small aperture, set in a valvular papilla, leads into the intestine, which, bending upwards for a very short distance, turns sharply back, and runs backward on the right side of the stomach, to which it is closely attached by mesentery. The intestine is divided into an anterior and a shorter posterior portion by a valve, which occurs on a level with the cardio-pyloric orifice. At this point in the intestine the mucous membrane is reflected into a single valvular partition, with a slightly projecting median aperture, whose lips point backwards. The intestine in general is excessively thin-walled. Its mucous membrane is thrown into delicate folds set in a reticular manner with longitudinal meshes. The lining membrane is of similar character, but with coarser meshes, posterior to the intestinal valve. The anus is near the middle of the body, on a level with the sixty-fifth vertebra.

Female Generative Organs.—Anteriorly the ovaries are two long bands closely applied medianly, uniting at about one-third from their anterior ends to form a single organ. The whole extends forwards into the body-cavity for two-thirds of its length. The left branch ovary is three-fourths of an inch longer than the right. The length of the whole to the end of the larger band is twelve and one-fourth inches, and to the shorter eleven and one-half inches. The whole structure is hollow, the small ova being budded off from its side. The ovary in other words is *cystoarian.*

Kidneys.—A median ureter, wide near the external opening and gradually narrowing as we follow it upwards and forwards, leads to near the middle of the body-cavity, and passes there into the posterior end of the kidney. The kidney runs forwards from this point beneath the centra of the vertebral column, and protected by the transverse processes, and expands beneath the clavicles into the head kidney. The latter are separate and very distinct, and pass gradually, after uniting medianly, into the middle kidney. The latter is a single organ, though it gives evidence, by a median furrow above and below, of its paired nature. It is laterally compressed, and is broader at its ventral border, sloping imperceptibly

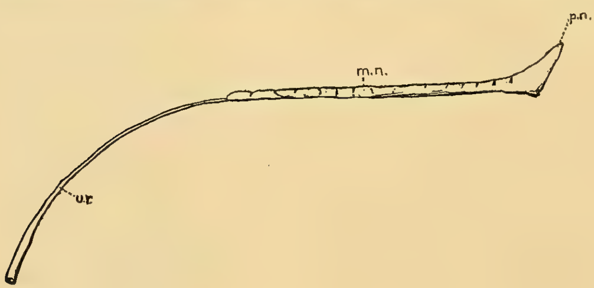


Fig. 8.

URINARY ORGAN ($\times \frac{1}{4}$).

p.n., pronephros, or head kidney; *m.n.*, mesonephros, or middle kidney; *ur.*, ureter.

upwards on each side to the dorsal edge. Near to the head kidney the lower border passes into a distinct face, while the upper border retains its sharp edge. Here then a section gives almost the figure of an equilateral triangle. The head kidney is directed upwards from the plane of the middle kidney—the upper edge passing on in a gentle curve, the lower going forwards and forming an angle. At the corner the lower aspect of each head kidney becomes reduced to a rounded border, but it expands again into a flat face, which is retained to the pointed extremity. The upper edge has the character already described for the rest of the kidney. There is no trace of a hind kidney.

The Heart.—The pericardial sac lies just behind and below the gills, in front of the pectoral arch, the large median urohyal element bounding it in front and below. The heart nearly fills the cavity. It is comparatively small, and shares in the extreme lateral compression which affects the whole fish. From base to apex it measures about one inch and an eighth. The sinus venosus, very small and thin-walled, lies entirely dorsal to the auricle, and receives, as usually, the ducts of Cuvier and the hepatic veins. Between the openings of the latter a slight membranous partition extends into the cavity. The sinus venosus opens into the auricle by an aperture guarded by a thin, transparent, membranous valve, consisting of two flaps. These flaps are lateral in position, and each is tied down to the auricle by two membranous cords, those on the right side reaching to the base of the auricle, the

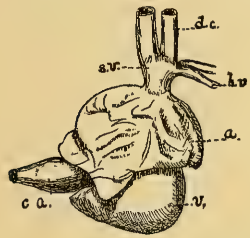


Fig. 9. The Heart (× 1).

a., auricle; *c.a.*, conus arteriosus; *d.c.*, ductus Cuvierii; *h.v.*, hepatic veins; *s.v.*, sinus venosus; *v.*, ventricle.

left-hand ones being attached near the valve. The cords are attached throughout their length, and apparently are the result of a strengthening fold accompanying the expansion of the internal lining which form the valve. The auricle is a flattened cone, lying over the ventricle and conus anteriorus. From each side a small auricular appendix projects downwards to partially embrace the ventricle.

A simple, membranous, two-flapped valve guards the auriculo-venticular aperture. Its two flaps are anterior and posterior. The ventricle is small, elongated, and rounded below. In front, very close to the auriculo-ventricular orifice, it passes directly into the conus arteriosus, by a two-flapped semilunar valve, whose two deep pockets are situated laterally. The bulbus arteriosus has a wide lumen, with extremely thin, almost membranous walls.

SUMMARY.

The principal facts in regard to the skeleton that admit of being further summarized are as follows:—

1. The enormous orbit is correlated with the development of a *sub-cranial crest* or keel, less extensive, however, than in *Regalecus.*

2. The supra-occipital crest is small, though larger than in *Regalecus,* and is separated widely from the ex-occipital and from the foramen magnum by the immense epiotics.

3. The lateral ridges usually formed by the pterotics, epiotics, and parietals are slight or absent.

4. One element only is present in place of the prootic and opisthotic; it agrees with the bone named opisthotic by T. J. PARKER, but is rather to be identified with the prootic.

5. The sphenotics send descending processes to meet the parasphenoid, and form post-orbital pillars as in *Regalecus*.

6. The ex-occipitals are united below, excluding the basi-occipital from the foramen magnum, though not from the floor of the brain-case.

7. The orbitosphenoids and alisphenoids are large bones, and meet in the middle line ventrally as in *Regalecus*. The basi-sphenoid, absent in *Regalecus*, is here well developed.

8. The roof of the skull is largely composed of cartilage, by which the frontals are separated from one another, and a groove is formed in which processes of the pre-maxillæ work back and forward.

9. The parietals are small. They do not appear on the outer surface of the skull, being covered over by the post-temporal; nor do they appear on the inner surface of the skull-wall, being shut out by the frontal passing in to articulate with the supra-occipital.

10. The mesethmoid is very large.

11. The vomer clasps the pre-nasal cartilage and meets the parethmoids.

12. The premaxillæ, the vomer, and the dentaries bear teeth.

13. The nasal processes of the premaxillæ and the general mechanism for the retraction and protrusion of the jaw is similar to that in *Regalecus*. The mandible is short and high, but is much larger relatively than in *Regalecus*.

14. The nasals are loosely attached, and are very small indeed, smaller even than in *Regalecus*.

15. There are two pre-orbital bones, of which the upper and anterior bounds the nostril below, as in *Regalecus*.

16. The branchial arches bear denticulated gill-rakers, smaller and more simply arranged than in *Regalecus*.

17. The copulæ or medio-ventral elements of the branchial skeleton are at least *nine* in number.

18. The vertebral column consists of 101 vertebræ, whose neural arches support about 173 interspinous bones:—a greater number of vertebræ, and a less number of interspinous bones than in *Regalecus*.

19. Ribs are absent or very minute.

20. The post-temporal, as in *Regalecus*, is simple and not forked.

LIST OF THE ABBREVIATIONS.

al.sph.	alisphenoid.
ang.	angular.
art.	articular.
a.zy.	anterior zygapophysis.
b.br.^{1}—*b.br.*^{5}	basi-branchials.
b.hy.	basi-hyal.
b.oc.	basi-occipital.
br.	brachials.
br.^{1}—*br.*^{5}	branchial arches.
br.r.	branchiostegal ray.
b.s.	basi-sphenoid.
c.^{1}—*c.*^{92}	centra of vertebræ.
c.br.^{1}—*c.br.*^{5}	cerato-branchials.
c.hy.	cerato-hyal.
cl.	clavicle.
cor.	coracoid.
d.	dentary.
e.br.^{1}—*e.br.*^{4}	epi-branchials.
e.hy.	epi-hyal.
ep.ot.	epiotic.
ex.oc.	ex-occipital.
f.	foramina in scapula and between the branchials of the pectoral girdle.
fr.	frontal.
f.r.	fin ray of the dorsal fin.
h.br.^{1}—*h.br.*^{4}	hypo-branchials.
h.hy.	hypo-hyal.
h.m.	hyomandibular.
i.b.	interspinous bone.
i.hy.	inter-hyal.
i.op.	inter-operculum.
ligt.	ligament uniting hypo- with uro-hyal.
mek.	Meckel's cartilage.
ms.eth.	mesethmoid.
ms.eth.^{1}	prenasal cartilage.
ms.pt.	mesopterygoid.
mt.pt.	metapterygoid.
mx.	maxilla.
na.	nasal.
n.s.	neural spine.
oes.	oesophagus.
op.	operculum.
op.ot.	prootic.
op.ot.^{1}	downward process of prootic.
orb. sph.	orbito-sphenoid.
pal.	palatine.
par.	parietal.
pa.sph.	parasphenoid.
p.cl.	post-clavicle.
p.eth.	parethmoid.
ph.br.^{1}—*ph.br.*^{4}	pharyngo-branchials.
p.mx.	premaxilla.
p.op.	pre-operculum.
p.orb.	post-orbital pillar.
pr.orb.	pre-orbital bones.
psd.br.	pseudobranch.
pt.	pterygoid.
p.tm.	post-temporal.
pt.ot.	pterotic.
p.zy.	posterior zygapophysis
r.	rays of pectoral fin.
s.cl.	supra-clavicle.
scp.	scapula.
s.oc.	supra-occipital.
s.op.	sub-operculum.
s.op.^{1}	ridge on the epiotic for articulation with the supra-occipital
sp.ot.	sphenotic.
sym.	symplectic.
tr.p.	transverse process.
u.hy.	uro-hyal.
V.^{1}	foramen for the first division of the fifth nerve.
vo.	vomer.

EXPLANATION OF THE PLATES.

All the Figures are Natural Size.

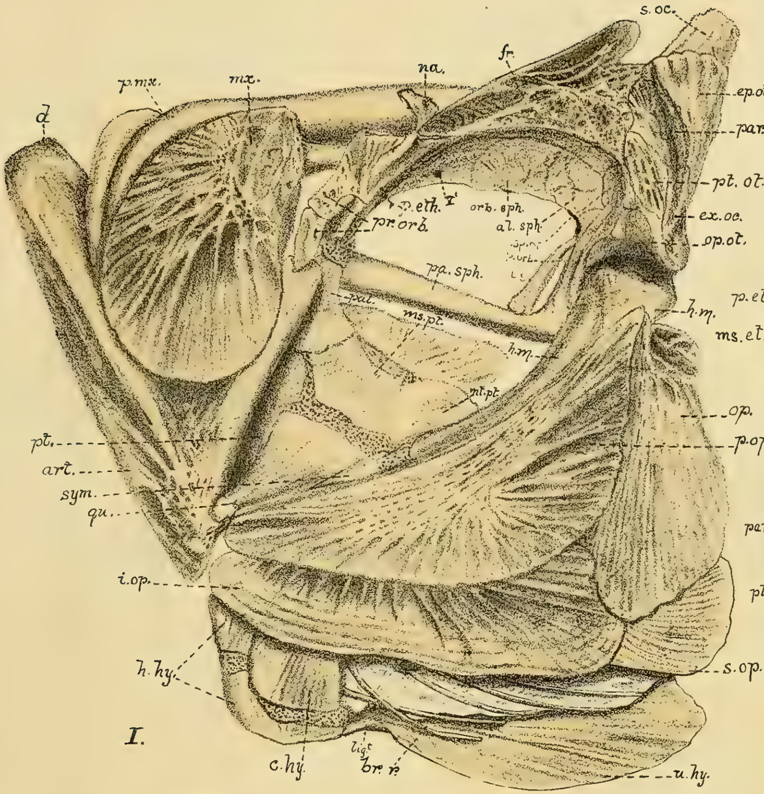
PLATE I.

Fig. 1. Side view of the skull.
Fig. 2. The lower jaw, suspensorial, opercular, and hyoid apparatus, seen from within.
Fig. 3. The cranium, from above.
Fig. 4. The cranium, from behind.

PLATE II.

Fig. 5. Longitudinal vertical section of the cranium. The supra-occipital and the frontal have been removed.
Fig. 6. The ethmoid region, and vomer.
Fig. 7. The branchial region, showing the arches on one side separated from their attachment below the cranium, and spread out horizontally.
Fig. 8. The bony elements of the branchial arches, laid out horizontally.
Fig. 9. The right shoulder girdle and pectoral fin.
Fig. 10. A series of vertebræ. The centra are numbered. Over the seventy-eighth are placed the corresponding interspinous bones and fin ray.

PLATE I.



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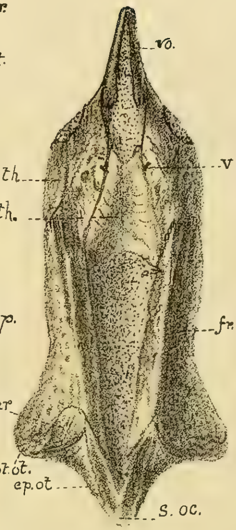

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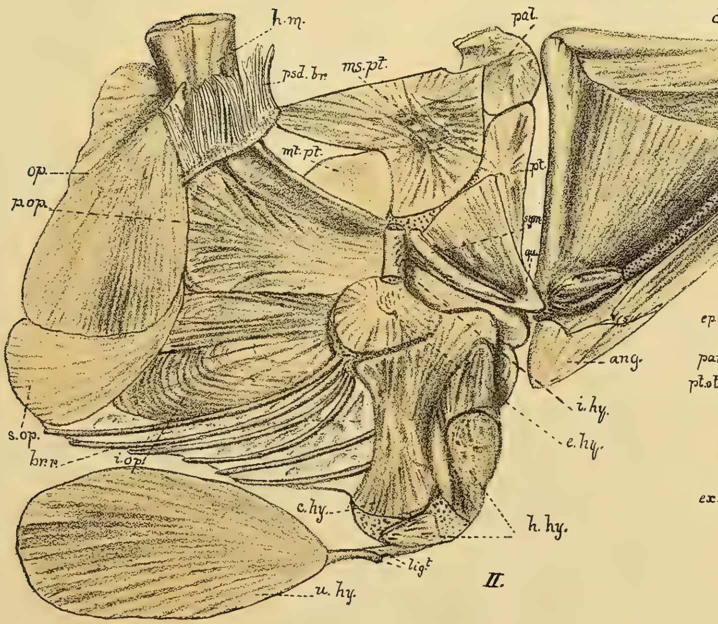

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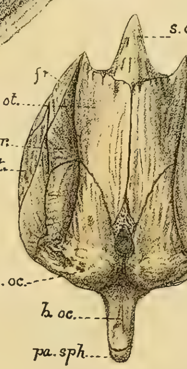

IV.

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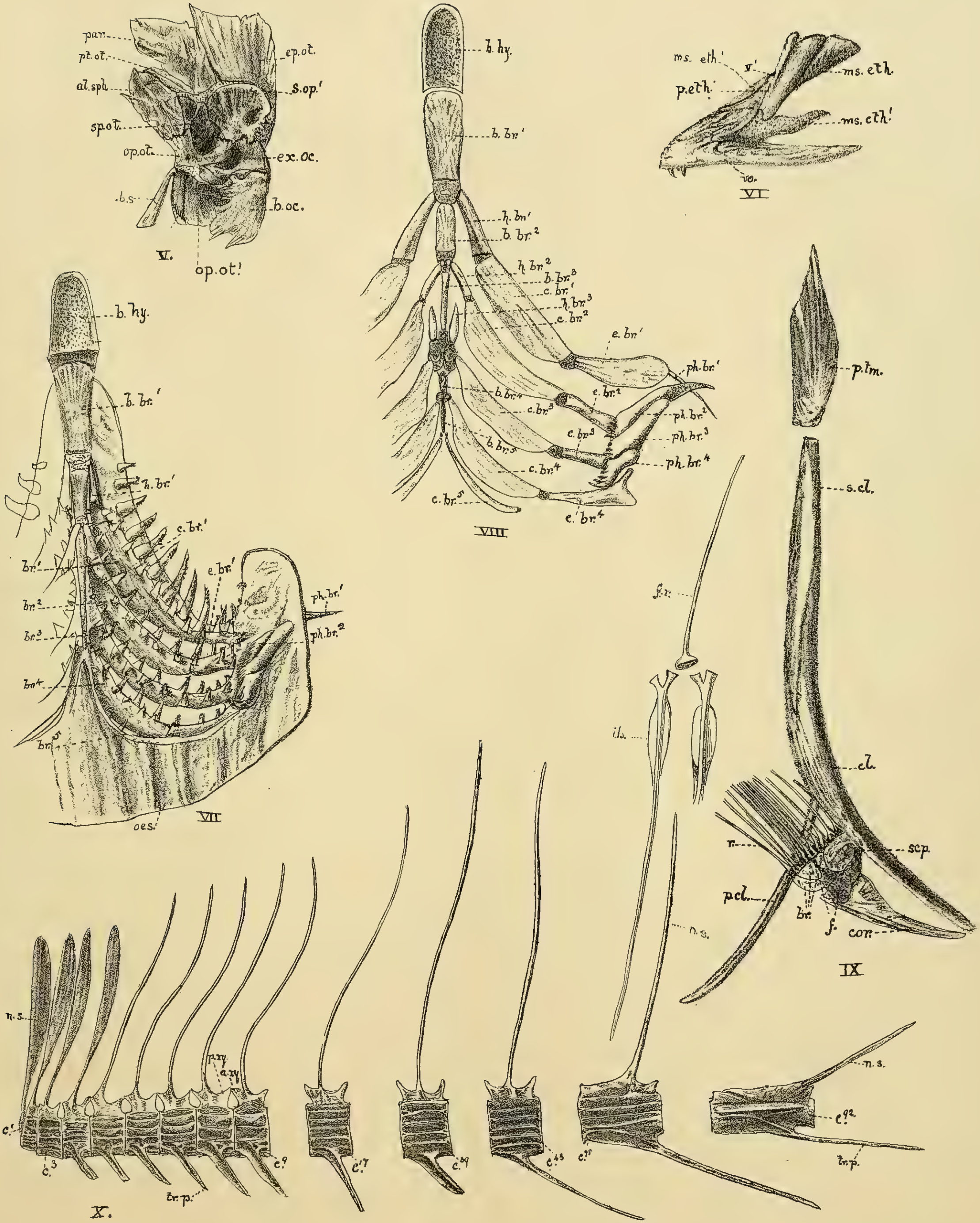

A.M. del.

Trachypterus arcticus.

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Studies from the Museum of Zoology

IN UNIVERSITY COLLEGE, DUNDEE.

EDITED BY

D'ARCY W. THOMPSON,

Professor.

VII. ON THE SKULL OF TARSIPES ROSTRATUS.

By Professor W. K. PARKER, F.R.S.

VIII. NOTE ON THE VISCERA OF TARSIPES.

By Professor D'ARCY W. THOMPSON.

DUNDEE:

Printed for the Museum.

April, 1890.

VII. *On the Skull of Tarsipes rostratus.*

By Professor W. K. PARKER, F.R.S.

[*Received March* 28, 1889.]

THIS paper contains the description of a scarcely-adult skull of *Tarsipes*, belonging to the Museum of University College, Dundee, and placed in my hands by Professor D'ARCY W. THOMPSON.* The account of the skull of Tarsipes given by GERVAIS and VERREAUX, by WATERHOUSE, and others, and the short notes thereon in manuals and catalogues by, for instance, FLOWER and OLDFIELD THOMAS, are very incomplete, and the figures scanty. This tiny and somewhat aberrant skull seemed, accordingly, to deserve a special description.

In the general aspect of the skull, we are struck by the relatively small size and extreme slenderness of the whole naso-maxillary region, by the imperfect definition of the orbits, and by the great expansion of the cranial region, all the parts behind the exit of the optic nerve being swollen and large.

The superficial cranial bones are extremely thin, glassy laminæ; the parieto-frontal fontanelle persists, doubtless owing to the specimen being not quite full-grown, and a large post-orbital fontanelle also exists between the orbital plate of the frontal above and the orbitosphenoid and alisphenoid below; this last is due to arrest of growth in the orbital plate, as well as to the exceedingly minute size of the orbitosphenoid bone.

The *nasal bones* are very narrow anteriorly, and are nearly twice as long as the frontals; on their posterior and outer border they come into relation in a very curious way with the lachrymals.

The *frontals* are, as is usually the case in Marsupials, comparatively small, being not much more than half as broad as the parietals. Anteriorly they are excluded by the lachrymals from articulation with the maxillary.

The narrow inter-orbital "waist" is just one-fourth the width of the middle of the parietal region. Laterally, the frontals send down inside the orbit an extremely thin orbital plate, which is deficient behind, and in front is so thin where it walls in the nasal labyrinth that the turbinals shine through (*Fig.* 1).

Behind the great vaulted *parietals* is a very large oblong *inter-parietal*, which in size and shape recalls that of the half-grown Mole. Its sinuous outer border articulates with the mastoid.

* The specimen, a male, was obtained, together with other scarce Marsupials, from MR HENRY WARD, Rochester, N.Y.

In the *occipital* region, the supra-occipital is rather small and rounded; the sutures are apparent between the various occipital elements; the foramen magnum is very large; the condyles are small, lateral, and far apart.

The *premaxillæ* are moderately large, but their ascending processes, which never in Marsupials reach the frontals, go here a very short way indeed. The slender, delicate *jugal* extends backwards as in other Marsupials to the glenoid region. The facial plate of the lachrymal, usually large in Marsupials, is here very markedly so, coming into relation with the frontal, nasal, maxillary, and jugal bones. The lachrymal canal is, as usual, external to the orbit. Neither zygoma nor frontal bones bear any trace of post-orbital processes.

The hard palate is formed in front for a short distance by the *premaxillæ*, which send inwards and backwards long slender palatine processes (always large in Marsupials), between which the septum nasi appears for a short distance in front. Posteriorly their pointed ends slightly overlap the palatine plates of the *maxillaries*, which are deeply notched, to form the *anterior palatine foramina;* these last, above which lie the large Jacobson's organs, are extremely large, as long as the whole premaxillary bones. The palatine plates of the maxillaries are again deeply notched behind, and into these notches fit the *palatine* bones. The latter are thin, sub-convex, spatulate plates, which become very thin and narrow posteriorly. The wide space between them is in part occupied by two independent bones, thin and slender, the *inter-palatines;* these may possibly have become separate by absorption, but I have noted their presence and independent origin in certain Phalangistidæ.

The *pterygoids* are less than half the length of the palatines; they reach from the posterior extremity of the palatines to far back below the squamosal, and possess a *hamular process* in the form of a very delicate hook. Just behind the pterygoids, on the inner side of a narrow isthmus connecting the main portion of the alisphenoid with the tympanic bulla, is a rounded notch for the Eustachian tube. On removing the inter-palatines, the posterior end of the narrow *vomer* comes into view.

The *squamosal* is very large, and, thrust downwards by the great parietal, is visible to as great an extent upon the floor as on the side-wall of the skull. The zygomatic process is very short and pointed. Between the upper border of the squamosal and parietal is a narrow lanceolate fontanelle, in the hinder part of which lies a small intercalary ossicle such as I have figured in *Microgale (Phil. Trans.* 1885, *pl.* 35*)*, and have there ventured to call a *supratemporal.* This hollow shell of the squamosal abuts behind upon the auditory meatus, and forms in front of and above that passage a large oblique crescent, vaulted and pneumatic within, mimetic of, and ancillary to, the true tympanic ring which lies below.

Behind the auditory meatus a large portion of the squamosal appears externally as a broad surface of bone between the parietal, the interparietal, the occipital, and the tympanic bulla. The large vaulted tympanic bulla is constituted of several bones. Under the crescentic outgrowth of the squamosal, fits the crescent of the *tympanic bone*, with its concavity looking forwards, opposite to the other, and with a rounded convex rim posteriorly, behind which the seventh nerve emerges. This tympanic bone is not only firmly articulated with the surrounding bones, but is in part anchylosed both with the posterior part of the squamosal and with the hindermost *os bullæ*. This is a very rare condition in Marsupials. The inner and inferior portion of the bulla is formed by two shells of bone, which remain, so far, distinct from one another. The anterior ($o.b.^1$) is continuous* in the neighbourhood of the Eustachian tube with the alisphenoid, and the posterior ($o.b.^2$) already mentioned unites with the mastoid and partly with the true tympanic.

The great bullate structure thus constituted differs from that of a Carnivore, for instance the Cat, by the absence of a *septum*, by the *ossa bullæ* being apparently not preformed in cartilage, by these being double, and by the connection of the anterior with the alisphenoid. Owing to the great size of these *ossa bullæ*, the cochlea is not indicated on the basal aspect of the skull as it is, for instance, in Kangaroos and Opossums.

The basis cranii is long and becomes very slender in front. The presphenoid, a very slender rod, is distinct from the basisphenoid; the latter is longer but narrower than the basioccipital. From the ossified mesethmoid a long cartilaginous septum nasi runs forwards.

The exoccipitals are large, the paroccipital processes small and short. The alisphenoids are very large and swollen, and lie entirely behind the orbitosphenoids, not overlapping them. The latter are very small bones, whose posterior margin is notched for the passage of the optic nerve.

In the olfactory region, the turbinals are of simple form and ossified; long recurrent cartilages, forming the capsules of Jacobson's organs, lie over the long palatine process of the premaxillaries.

The *mandible* is as slender and delicate as in *Echidna* or *Myrmecophaga*. There is the very slightest possible coronoid elevation, and no angular process whatever; the articular condyle is small, convex, and oval, with its height greater than its breadth. The dentary foramen is a long narrow groove, extending from the condyle along one-third the length of the bone.

The *malleus* is rather large; its processes gracilis, once the continuation of Meckel's cartilage, has become thin and leafy by absorption. The incus is normal; the perforation in the stapes is small and triangular. The *tensor tympani* muscle is very large, and in its tendon I find a small oval nodule of bone ($o.t.$) which I have not detected in any other mammal; the stapedius is also comparatively a very large muscle.

* The original distinctness of these elements has been traced by me in several species of Marsupials. It is a mistake to suppose that this anterior *os bulla* is only a backward *process* of the alisphenoid; though such it appears to be in its even greater development in adult skulls of the Koala and the *Hypsiprymni*.

The dental formula of Tarsipes has been stated differently by different observers, and apparently varies in different individuals. In this specimen the formula appears to be—

$$i. \frac{2}{1},\ c. \frac{1}{0},\ pm.\ (?)\frac{1}{0},\ m. \frac{2}{2}$$

being less by an upper and lower molar than that usually received. The lower incisors are long, lanceolate, and in a straight line with the fuble mandibular ramus; the other teeth are all small, and the canines and molars have blunt rounded crowns.*

The whole skull is 21·5 mm. long, and 9 mm. in its greatest breadth. The greatest height of the mandible is ·8 mm., its average height is ·6 mm.; the condyle is 1 mm. long by ·6 mm. wide; the whole mandibular ramus is 13·8 mm. long, beyond which the incisor tooth projects 2·6 mm.

In my paper on the Development of the Skull in the Insectivora (*Phil. Trans.*, 1885), I have discussed at length the general characters of the Marsupial skull, and it is interesting to note how fully these characters are maintained in the skull of Tarsipes, reduced and to some extent degenerate as it is. Thus we see in Tarsipes (1) the small size of the frontals compared with the nasals and parietals, and the relatively enormous development of the squamosals; (2) the large lachrymals with their greatly developed facial plates; (3) the imperfect, as it were *schizognathous* palate, with accessory *interpalatine* bones; (4) the small pterygoids and vomer; (5) the long jugal, coming into relation with the lachrymal in front, and with the glenoid cavity behind; (6) the small nasal labyrinth, and the small squarish cribriform plate; (7) the small orbitosphenoids, flush with the alisphenoids, and with a notch instead of a complete foramen for the optic nerve; (8) the relation of the alisphenoids to the drum-cavity; (9) the perforation of the basisphenoid by the carotids, and the imperfect development of the pituitary fossa and clinoid processes; (10) the small perforation in the stapes. Almost the only aberrant points to be noted in Tarsipes are the partial anchylosis of the tympanic, the absence of the inflected angle in the mandible, and the circumstance that the lachrymal excludes the maxillary from articulation with the frontal. The brain-cavity is comparatively large, but this is usually the case in the smaller members of any group. But, on the other hand, the special characters of the skull in Tarsipes give us little if any help in seeking its relations among neighbouring genera. In the general form of the skull, the absence of any postorbital processes, the shape of the mandible as well as in the characters of the dentition, Tarsipes differs from all the other Phalangistidæ.

* That the animal is at least partly insectivorous appears to be proved (*vide* Gould, *Austr. Mamm.*, *pt.* 1, and Thomas, *Brit. Mus. Cat. of Marsup.*, 1888, *p.* 134); but the stomach of our specimen was quite full of honey and pollen. The large lower incisors are evidently functional, and perhaps find their use in piercing or tearing asunder the parts of the flower.

EXPLANATION OF THE PLATE.

The Roman Numerals indicate Nerves or their Foramina.

al.n. alinasal.
al.s. alisphenoid.
a.p.f. anterior palatine foramen.
ar.c. articular cartilage.
a.s.c. anterior semi-circular canal.
a.ty. annulus tympanicus.

b.o. basi-occipital.
b.s. basi-sphenoid.

ch.l. cochlea.
cr.g. crista galli.

d. dentary.

e.n. external nostril.
e.o. ex-occipital.
eu. Eustachian passage.

f. frontal.
f.m. foramen magnum.

gl.c. glenoid cavity.

i. incus.
i.c. internal carotid.
i.p. inter-parietal.
i.pa. inter-palatine.

j. jugal.

l. lachrymal.
l c. lachrymal canal.

m.b. manubrium mallei.
m.eth. mesethmoid.
ml. malleus.
m.ty. membrana tympani.
mx. maxillary.

n. nasal.
n.p. nasal passage.

o.b. os bulla.
oc.c. occipital condyle.
o.s. os tensoris tympanici.

p. parietal.
pa. palatine.
pg. pterygoid.
p.gr. processus gracilis.
p.oc. paroccipital.
p.px. palatine process of premaxillary.
p.s.c. posterior semi-circular canal.
px. premaxillary.

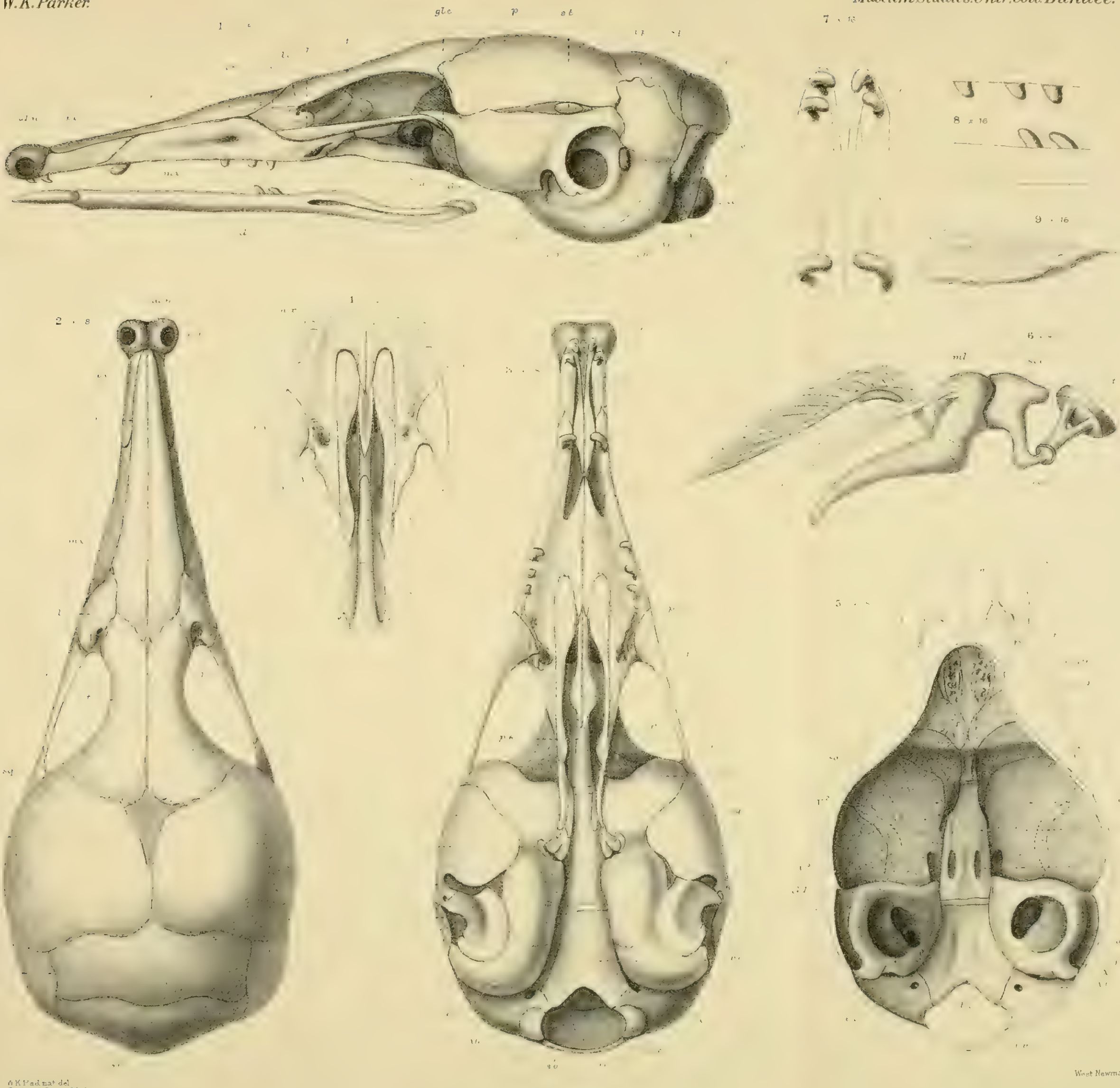
rc.f. recessus flocculi.

s.c.i. short crus of incus.
s.o. supra-occipital.
sq. squamosal.
st. stapes.
s.t. supra-temporal.

t.ty. tensor tympani.

W. K. Parker.

Museum Studies. Univ. Coll. Dundee.



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VIII. *Note on the Viscera of Tarsipes.*

By Professor D'Arcy W. Thompson.

My friend, Dr Leche of Stockholm, told me recently that he had collected a number of specimens of this rare Marsupial, in order to study its anatomy in detail; and, accordingly, we gave up the attempt to dissect fully our single, somewhat ill-preserved specimen. Nevertheless, one or two organs of which we have made preparations may in the meantime be figured here, especially as one of them, the stomach, is very peculiar.

The stomach of Tarsipes is quite unlike that of any other Marsupial. It is a compound stomach, with two main divisions, and certain small diverticula. The narrow œsophagus enters a globular chamber, into which opens the pylorus also. Nearly opposite to the pyloric valve, below and a little ventral to the œsophageal orifice, a short tubular passage, in width about equal to the duodenum, leads to another chamber somewhat larger than the first, which in our specimen was filled with a mass of honey and pollen-grains. To the left side of the second paunch-like chamber is applied the spleen, which, as is usually the case in Marsupials, is small and trilobed. From this chamber project three short cæcal pouches, of which two are anterior, close to the anterior extremity of the spleen, and one is placed more posteriorly on the left side.

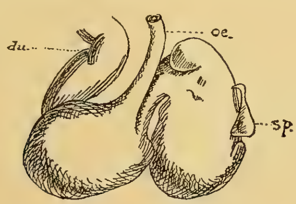

Fig. 1. Stomach of Tarsipes (× 3).
oe., œsophagus; *du.*, duodenum; *sp.*, spleen.

This stomach shows as it were an exaggeration of the tendency to form a cardiac prolongation, found in so many Marsupials as well as in other families. Such an elongated fundus occurs in *Phascogale*, *Antechinomys*,* &c., among the Dasyuridæ, and still more markedly, as is well known, in *Macropus* and *Halmaturus*. Were the immensely elongated cardiac end of the stomach in *Halmaturus* to become constricted close to the œsophagus, it would lead to a kind of stomach not unlike that here described in *Tarsipes*. Unfortunately, we possess very little information concerning the stomach in the many genera of the smaller *Phalangistidæ;* but in some at any rate, *e.g.*, *Belideus*, a cardiac prolongation,

* Alston. *P.Z.S.*, 1880, p. 458.

though of no great size, is to be found. Though there is perhaps not yet sufficient reason for constituting *Tarsipes* the type of a separate family, yet the characters of the stomach further strengthen the reasons already known (of which the most important perhaps is the absence of a cæcum) for separating it in a sub-family from the other genera of Phalangeridæ.

The *liver* is deeply cleft, and the left lobe is much the smaller of the two. The

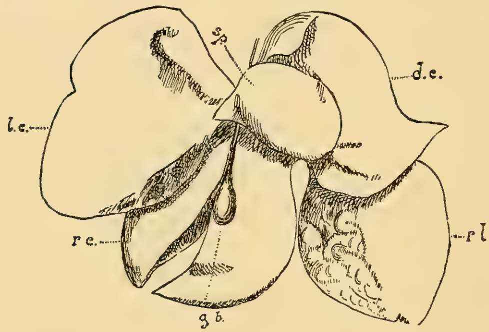

Fig. 2. LIVER OF TARSIPES ($\times$ 3).

d.c., caudate lobe; *sp.*, Spigelian lobe; *l.c.*, left central lobe; *r.c.*, right central; *r.l.*, right lateral; *g.b.*, gall-bladder.

left lobe is not divided, or at most by a mere rudiment of a fissure. The right central lobe is divided by a great cleft and furrow, which lodge the gall-bladder in its upper part. The Spigelian lobe and caudate lobe, especially the latter, are extremely large. In *Phalangista vulpina*, on the other hand, the left lobe is very

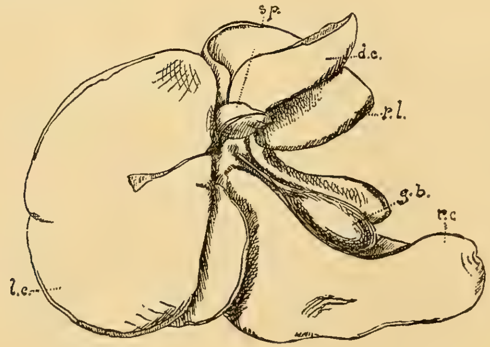

Fig. 3. LIVER OF PHALANGISTA VULPINA ($\times$ 1).

large, and divided into a left central and a left lateral lobe; the gall-bladder is relatively much larger, and the left half of the right central lobe has increased greatly at the expense of the other; the Spigelian lobe is very small indeed, and the caudate lobe small, narrow, and elongated. The liver is so variable in its details of form among the Marsupials that its minor characters have little value in classification. For instance, among the Phalangistinæ, *Cuscus** has a liver in which, as in Phalangista, the left lobe is very large and divided, and the right lateral lobe is small; but in which, on the other hand, the Spigelian lobe is large and trilobed, and the caudate lobe, in comparison, very small.

The long pointed tongue bears three circumvallate papillæ, the posterior very

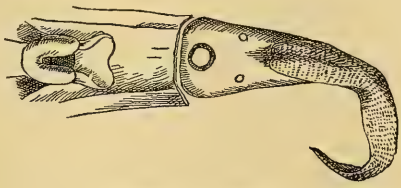

Fig. 4. TONGUE OF TARSIPES *(magnified).*

large, and all three circular and symmetrical. The angle formed by the posterior with the two anterior papillæ is acute. Unlike the tongues of the Phalangistidæ described by POULTON,† the anterior as well as the posterior papillæ are radially symmetrical. The greater part of the dorsum of the tongue, within the limits shown in the figure, is covered with very long compound filiform papillæ of the "coronate" type, now well known through POULTON's researches as characteristic of the Marsupialia. I have sought for the lateral organ and cannot find it. Its apparent absence may be due only to the state of the specimen; but I am sure that if it be present at all, it will be found to be small or rudimentary.

* CUNNINGHAM. *Challenger Rep.*, V. p. 162.

† *P.Z.S.*, 1883, p. 599, *et seq.*

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Studies from the Museum of Zoology

IN UNIVERSITY COLLEGE, DUNDEE.

EDITED BY

D'ARCY W. THOMPSON,

Professor.

IX. ON THE SYSTEMATIC POSITION OF ZEUGLODON.

BY

Professor D'ARCY W. THOMPSON.

DUNDEE:

Printed for the Museum.

June, 1890.

IX. *On the Systematic Position of Zeuglodon.**

By Professor D'Arcy W. Thompson.

In another essay I hope to discuss fully, before long, the systematic position of the Cetacea. Those authors are, I am convinced, in the right, who from time to time have asserted the wholly anomalous position of this order among the Mammalia, and the impossibility of sustaining their derivation from either the Ungulates or the Carnivores in consonance with generally accepted views. To such a conclusion we are led, it seems to me, by almost every characteristic feature of the Cetacean anatomy: by the characters of the vertebræ, the carpus, the auditory ossicles, the larynx, the stomach, the mammary glands, the numerous phalanges, the numerous, similar, equi-distant, single-rooted teeth, the great development of the pterygoid in comparison with the palatine bones, and the simple and primitive characters of the placentation; while the wide morphological differences present within the limits of the order, are in themselves no slight evidence of great antiquity.

But however this may be, very obvious difficulties at once arise before us, in connection, namely, with the Zeuglodonts and the Squalodonts, both of which groups offer numerous exceptions to the foregoing generalisations. The case of the Squalodonts is much the simpler of the two, though presenting certain special difficulties of its own; there can be, at least, no doubt as to their Cetacean nature. But as to the Zeuglodonts, which alone I propose to discuss here, it soon becomes manifest that if they be associated with the Cetacea, the problem of the origin of these latter becomes a thousand times more difficult: that then our definitions of the order become complicated by a crowd of exceptions, and that the theory of a primitive place for the Cetacea amongst the Mammalia falls to the ground.

Briefly stated, my thesis in the present paper is simply this, that the Zeuglodonts have no direct affinities with the Cetacea, but have, on the other hand, the closest possible relation with the Pinnipedes; and, accordingly, that we may leave them out of account henceforth in our discussion of the classificatory position of the Cetacea.

It is neither needful nor indeed possible to recount in detail here the innumerable views that have been put forward regarding the affinities of these strange enormous animals. But it may be said that, since Owen first demonstrated that

* The substance of this paper was communicated to the *Congrés internationale de Zoologie* in Paris in August, 1889, and is printed in the *Compte-rendu* of the Congress, under the title "*Faut-il associer les Zeuglodontes aux Cétacés?*

the tooth of the so-called *Basilosaurus* belonged to a mammal, and since JOHANNES MÜLLER published his great work upon the group,* naturalists have, almost without exception, connected them in some way or other with the Cetacea; some, like BRANDT, placing them definitely within the Cetacean order; others, like HUXLEY and LEIDY, seeing in them a transition towards the Carnivores. One or two exceptions only may be cited to the general rule: for instance, GIEBEL (in the *Fauna der Vorwelt*, p. 220) and JOURDAN (*Comptes rendus*, 1861, p. 962) insist upon their affinities with the Pinnipedes; and MM. P. J. VAN BENEDEN and P. GERVAIS, in the *Ostéographie des Cétacés*, though not in their preceding works, leave the Zeuglodonts outside of the order Cetacea, without, however, assigning to them a definite position. But in England I know of no such exception: in our text-books, in the galleries and the catalogues of the British Museum, in the articles in the *Encyclopædia Britannica*, everywhere we find the Zeuglodonts intercalated among the Cetacea.†

Naturally, the resemblance of the molar teeth of Zeuglodon to those of the Seals was recognized almost from the very first. We are all familiar with the typical molar of Zeuglodon, and I may simply call attention to the fact that its resemblance is a very superficial one even to that of Squalodon, which alone approaches it among the Cetacea. The canine and incisor teeth of Zeuglodon have no less definite resemblance to those of Seals, while the dental formula of Zeuglodon, according to CARUS, FLOWER, and others, is $i\,\frac{3}{3}$, $c\,\frac{1}{1}$, $m\,\frac{5}{5}$, the identical dental formula of Otaria. Even those who most warmly upheld the Cetacean nature of Zeuglodon have admitted these facts: and I may quote the following passage from BURMEISTER‡ in illustration thereof:—" Mit diesem Gebiss, und zwar besonders mit dem der ächten Phocæ, scheint nun der Zahnbau von Zeuglodon in allen Hauptpunkten übereinzustimmen. Uebersehen wir die bei Phoca stets einfach kegelförmige Schneidezähne, weil dieselben von Zeuglodon mir nicht bekannt sind, so ist, zuvörderst die Formähnlichkeit der Eckzähne total." And as to the characters here referred to of the incisor teeth, their inadequacy is remedied and the resemblance confirmed by a figure in MÜLLER'S Monograph (Pl. XXVI.), where the incisors are shown to be, as in the Seals, of simple conical form.

But leaving then in the dentition what is at least a suggestion of affinity to the Seals, with a special hint of likeness to *Stenorhynchus* and perhaps also to Otaria, let us examine the rest of the skeleton, seeking resemblances with the Pinnipedes.

* *Ueber die fossilen Reste der Zeuglodonten von Nord-Amerika.* Fol. Berlin, 1849.

† There remains one exception to cite, and that a very important one. The day before I communicated this paper to the Congress in Paris, M. PAUL FISCHER showed me in the galleries of Comparative Anatomy of the *Muséum d'histoire naturelle*, Zeuglodont remains arranged in a cabinet devoted to the Pinnipedia.

‡ *Bemerk. ü. Zeuglodon Cetoides.* 4to. Halle, 1847.

In the imperfect skull figured by JOHANNES MÜLLER (Pl. I.), and of which a sketch is here reproduced, we remark the following characters. The large,

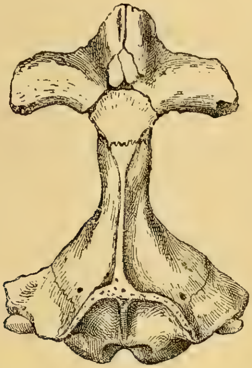

Fig. 1. SKULL OF ZEUGLODON.
(*After* JOHANNES MÜLLER.)

broad nasal bones, and the narrow, pinched parietal region are absolutely different from anything to be seen among the Cetacea. Nothing *overlaps;* the parietal is wholly in front of the occipital, the frontal of the parietal. Nothing, as it seems to me, save perhaps the lateral expansion of the frontals, could suggest the idea of a resemblance to the Cetacea. But on the contrary, the resemblance to certain of the Pinnipedia is really striking. If one compare the skull of Zeuglodon with that of an Arctocephalus or an Otaria, one can show to demonstration how, line for line, the narrow parietal region, the parietal and occipital crests, the vertical occiput, even the configuration of the fronto-nasal sutures all agree in these several skulls. The lateral frontal expansions appear to me to be nothing more than an exaggeration of apophyses, which, absent in the Common Seal, attain a great development in, for example, the Otarias.

Examining the skull on its posterior face the triangular outline of the occipital

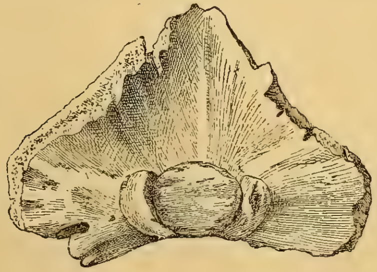

Fig. 2. OCCIPITAL REGION OF ZEUGLODON.
(*After* J. MÜLLER.)

agrees precisely with that of the Eared Seals. The occipital condyles are small, prominent, vertical, lateral, and widely separate from one another below, as in

Otaria and the Bears: while in the Cetacea the condyles are large, flat, closely approximated to one another, and are situated as much or more below than at the sides of the foramen magnum.

In the view of the palatal region given by Müller (Pl. IV. 2), one may detect the pterygoid, represented as a short, blunt, hooked, process, as in, for instance, the Carnivores, and totally different from the flattened plate in the Cetacea, which has always seemed to me one of the most important and archaic features in the skull of that order. Even so minute a point as the cochlea seems to help us, for Johannes Müller has shown that it possesses in Zeuglodon two and a-half turns, one more than in Cetacea.

On the lower jaw much argument has rested, and many naturalists have found Cetacean resemblances in its narrow elongated form, its small or deficient coronoid and angular processes, and its large alveolar foramen. But even if all this be true, the figure, such as that which I copy from Koch's memoir,* shows, surely, that the

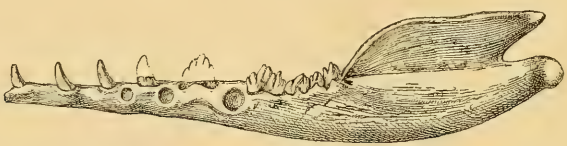

Fig. 3. Lower Jaw of Zeuglodon. (*After* Koch.)

jaw though narrow is not nearly so narrow and straight as in a Dolphin, that the coronoid process is far too high, and that the foramen alveolare, though large, is nothing like the gigantic cavity which represents it in the Dolphins. And noting that it is the angular process which is here deficient, it is to the Seals that we must again turn for a parallel case. In the common *P. vitulina*, still better perhaps in Macrorhinus, we find a jaw which, in the absence of an angular process and even in the form of the coronoid, recalls the jaw of Zeuglodon, if we only suppose the latter to be shortened down a little. In fact, the Dolphin has a rudimentary coronoid and a fairly well-marked angular process, while in Zeuglodon and in the Seals the case is just the reverse.

The two mandibles are united by synostosis, according to Müller, and therein lies another difference from the Cetacea.

The cervical vertebræ are distinct and unanchylosed, for which reason Huxley† and Flower, holding the Cetacean theory, have sought to find a special approximation to *Inia* and *Platanista*, in which the neck vertebræ are in the same condition.

* Dr A. Koch. Das Skelet des Z. Macrospondylus. *Versamml. Fr. Wiss.* Wien, 1850.

† "The cervical vertebræ are distinct and unanchylosed, nearly resembling those of the Rhynchoceti."—Huxley, *Vertebrates*, p. 349.

But if we sketch a cervical vertebra of Zeuglodon, as figured by MÜLLER, we

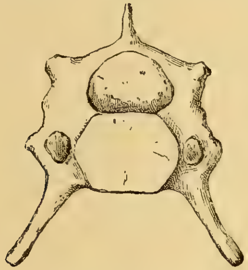

Fig. 4. CERVICAL VERTEBRA OF ZEUGLODON.
(*After* J. MÜLLER.)

find it quite unlike the cervical vertebra of any Cetacean, even of Platanista: the transverse processes, the lateral foramina, the shape of the neural canal are totally different, but agree almost line for line with the cervical vertebra of our common *Phoca vitulina.*

The characters of the atlas and axis need not be recited in detail. It may be simply said that the axis with its distinct odontoid process is quite unlike a Cetacean's; and that the atlas is entirely Seal-like in its broad transverse processes, pierced by a foramen, the semilunar form of its odontoid space, and in the shape of the glenoid cavities which agree with the condylar surfaces above described. DAMES, in a recent paper,* shows that the odontoid has on each side near the point a long oval groove with a narrow smooth ridge below, and that below the articular surface for the third cervical vertebra is a median excavation, all of which characters are minutely reproduced in the Pinnipedia.

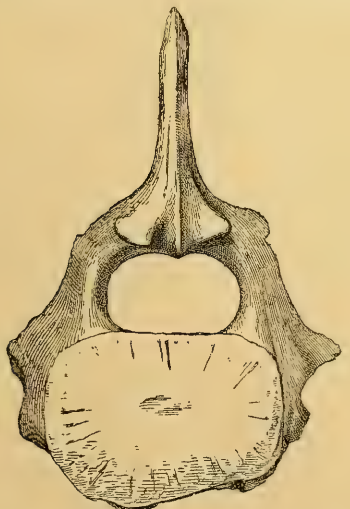

Fig. 5. DORSAL VERTEBRA OF ZEUGLODON *(posterior view).*
(*After* J. MÜLLER.)

* W. DAMES. *Sitzungsber. K. Akad. Wissensch.* Berlin, 1883. p. 129

The dorsal vertebræ are also like those of the Seal. The transverse processes are very short, and the distinct posterior zygapophyses, horizontally placed, are characters which do not occur in the Cetacea.

In the vertebra next represented, the laterally expanded neural canal and the

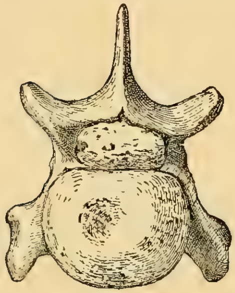

Fig. 6. Vertebra from the Posterior Dorsal Region *(front view).* (*After* J. Müller.)

position of the costal facet are just as in the posterior dorsal vertebræ of a common Seal.

As regards the remarkable elongation of the vertebral bodies in Zeuglodon, I may simply say that in the Seals the bodies are certainly somewhat long, and that the epiphyses are slow of ossifying, even though these characters do not attain in recent Seals their remarkable prominence in the Zeuglodon.

In the next place, there is here copied Müller's figure of a lumbar vertebra of his Zeuglodon. We note in it the transverse processes placed low down on the body

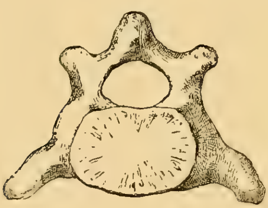

Fig. 7. Lumbar Vertebra of Zeuglodon. (*After* J. Müller.)

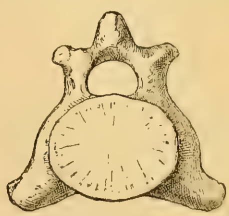

Fig. 8. Lumbar Vertebra of *Phoca vitulina.*

of the vertebra, and the muscular apophyses high up on the arch. The adjacent figure shows the lumbar vertebra of a common Seal: the two are almost identical. Contrast them with the lumbar vertebra of a Dolphin—the enormous transverse processes, set high up on the body of the vertebra, the long dorsal spine, the tiny neural canal.

Regarding the limbs, I have but a word to say. Of the scapula a fragment only is known. It shows a distinct spine, a long, curved acromion, and no coracoid process. The latter is absent or rudimentary in the Seals also. How different from the scapula of a Dolphin, even, for example, Inia, with no spine, with a vertical acromion, and an enormous coracoid.

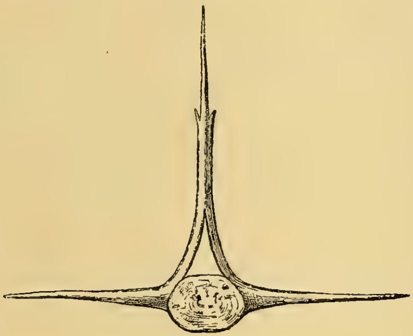

Fig. 9. Lumbar Vertebra of *Delphinus delphis.*

The elbow joint seems to have been freely movable, and the carpal bones to have possessed distinct articular facets.

The digital phalanges are little known. They are described, but not figured, by Burmeister (*loc. cit.* p. 23), who could scarcely believe that they really belonged to Zeuglodon, "was wohl nicht bezweifelt darf." According to him they are short and broad, with a broad basal epiphysis, and a distal extremity somewhat dilated and partially divided into two heads. He admits that they have no resemblance to a Cetacean limb, in the following words, "Denn mehr als irgend ein anderer Theil des Knochengerüstes scheinen diese Zehenbeine *gegen die Cetaceeennatur* des Zeuglodon zu sprechen, und dadurch das Räthselhafte seines Baues nur zu vermehren."

The ribs are curiously expanded towards their distal extremity. The same

Fig. 10. Rib of Zeuglodon.

(*After* J. Müller.)

condition is seen to a considerable extent in the common Seal.

There remain many other points to which reference might be made, and from which arguments consonant with the foregoing might be adduced. Suffice it to say that, in my opinion and so far as my knowledge goes, all that has been done, the researches of M. GERVAIS* on the brain-cavity of Zeuglodon, all the other bones that various authors have figured, all these various researches contain no facts which deserve to be chronicled as opposing the conclusion at which I have arrived.

But, it may be asked, if the case be really so clear as from the foregoing considerations it appears to me, how comes it that so many eminent anatomists have all along supported a contrary opinion? I fancy that this arises mainly from the circumstance that fifty years ago, when the Zeuglodons were discovered and much was written regarding them, the notions concerning the Cetacea were vague and incomplete. That order not only included the Sirenia, but was in many minds closely linked with, if it did not comprise, the Pinnipedes as well: that, in short, when JOHANNES MÜLLER called the Zeuglodons *Cetacea*, he used the word in a very different sense to ours.† And, finally, that since that time few discoveries, comparatively speaking, of Zeuglodont remains have been made to call fresh attention to the group.

* GERVAIS. Formes cérébrales propres aux Thalassothériens. *J. de Zool.* III., p. 570. 1879.

† Compare, for instance, the following passage from BRANDT (*Symbolæ sirenologicæ*, III., p. 333): "Formerly I was of opinion that the Zeuglodons formed *a separate order* of the Cetacea, *equivalent to the Sirenia* and to the Delphinoidea together with the Balænoidea; and were rather intermediate between Cetacea and Sirenia, than between Phocidæ and Cetacea. Later researches induced me to unite the Zeuglodontia with the Delphinoidea," *et seq.* And similarly JOHANNES MÜLLER says (*loc. cit.* pp. 5 and 31), that "the Zeuglodons are intermediate between the Seals and Cetacea, but *within the order of the Cetacea*."

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Studies from the Museum of Zoology

IN UNIVERSITY COLLEGE, DUNDEE.

EDITED BY

D'ARCY W. THOMPSON,

Professor.

X. ON THE SYSTEMATIC POSITION OF HESPERORNIS.

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DUNDEE:

Printed for the Museum.

August, 1890.

X. *On the Systematic Position of Hesperornis.*

By Professor D'Arcy W. Thompson.

For some years past I have been accustomed in my laboratory teaching to consider the group of Toothed Birds, or *Odontornithes* of Marsh, as an unreal and illusory one, and to believe that in the first place these birds had not the Ratite affinities which Marsh claimed for them, and that in the second they were by no means very closely related to one another; that it would be as unreasonable to unite the toothed birds on account of the persistence of their teeth as to group together the edentulous mammals for their loss of them; and that the apparent general structural resemblances, for instance of *Hesperornis* to the Grebes and Divers, or of *Ichthyornis* to the Terns, have a true classificatory value which Marsh denied them.

Such an opinion has been long held by several naturalists, especially by Cope,* and one of my pupils has propounded it before in connection with a subordinate anatomical point.† Fürbringer, in his "*Morphologie und Systematik der Vögel,*" discusses the affinities of these birds at great length. He admits the existence of a wide difference between *Hesperornis* and *Ichthyornis:* and, breaking up Marsh's group of the Odontornithes, he relegates the latter genus to the Carinatæ, while following Marsh so far as to advocate the Struthious affinities of Hesperornis; ‡ and he considers Hesperornis to possess undoubted affinities both towards the Enaliornithidæ, Colymbidæ, and Podicipidæ, at the same time that he is content to class it as a "toothed, swimming Ostrich." ||

* Vertebrata of the Cretaceous Formation of the West. Washington, 1875.

† Mary L. Walker. The Quadrate Bone in Birds. *Studies from Dundee Museum.* December, 1888.

‡ *Op. cit.*, p. 1475. Ich kann somit jenen Autoren nur zustimmen, welche die Subclasse der Odontornithes auflösten, und die eine Ordnung derselben (*Odontotormæ*, Marsh) den Carinaten, die andere (*Odontolcæ*, Marsh) den Ratiten, zurechneten.

Ibid., p. 1473. Die Hesperornithes bilden somit, nach der jetzigen Definition der Ratiten-gruppen, gewiss Vertreter dieser Abtheilung, und ich stimme Marsh, Vogt, Wiedersheim, und Newton vollkommen bei, wenn sie dieselben als schwimmende und bezahnte Strausse bezeichnen, oder mit den lebenden Ratiten in die gleiche Kategorie bringen.

|| *Op. cit.*, p. 1516. Früh, doch wie auf grund der morphologischen Configuration zu schliessen, erst nach den Struthionidæ und Rheidæ, mögen sich die Hesperornithes vom Vogelstamme abgezweigt haben, und zwar in der nächsten Nachbarschaft derjenigen Fasern welche die Enaliornithidæ, und wohl nach diesen die Colymbidæ und Podicipidæ zur Enstehung kommen liessen; die genealogische Relationen zu den Ahnen Dieser dürften als noch nähere aufzufassen sein als jene, welche Apteryx und Dinornis mit den frühen Vorfahren der Rallidæ und Crypturidæ verbinden.

SHUFELDT, in a recent paper,* saying nothing about Ratite affinities, declares, parenthetically, his conviction that "however widely separated now, our existing Loons and Grebes are derived from the same ancestral stock to which *Hesperornis regalis* belonged."

Professor NEWTON, in his article *Birds*, in the *Encyclopædia Britannica* (1875), said briefly that *Hesperornis* "seemed to have been related to the *Colymbidæ;* but in his later article, *Ornithology* (1885), he accepts MARSH's conclusions, and says with him that "it is probable that *Hesperornis* came off from the main 'Struthious' stem, and has left no descendants."

Mr LYDEKKER, in his new text-book of Vertebrate palæontology,† discarding the union of *Hesperornis* and *Ichthyornis* under MARSH's Order *Odontornithes*, states that "in its whole skeletal organisation *Hesperornis* conforms strictly to the existing Ratite type," and classifies it accordingly.

It is not necessary to quote further from recent literature. It is certain that the original view laid down by MARSH, of the independence of the Odontornithes and of their preponderant affinity with the Ratites, has taken deep root and holds its own in the modern text-books. And, further, that those authors who have supported the relationship of Hesperornis with the Divers and the Grebes have for the most part tried to advocate this view without abandoning the other: to make, in short, Hesperornis both an Ostrich and a Grebe!

It would carry us too far into the general question of the classification of birds to discuss the whole problem raised by the systematic position of Hesperornis. In the present paper we propose merely to institute a close comparison, bone for bone, of its osteological characters with those of *Colymbus*, to show that it must stand or fall by whatever classificatory position may be found acceptable for the latter, and that definite resemblances to a typical Ratite, for instance an Ostrich or a Rhea, are not to be found. A precisely similar comparison, perhaps less perfect in detail, might be instituted between Ichthyornis and the Terns.

As our type of the Colymbidæ, we have used throughout *Colymbus septentrionalis, L.*, the Red-throated Diver.

As regards the *general* resemblance in shape and structure between Hesperornis and the birds with which we propose to compare it, nothing need be said. It is obvious that the resemblance is marvellously close: and MARSH used the skeleton of Colymbus to aid his restoration of Hesperornis, though denying the actual *relationship* of the two.

* Contributions to the Comparative Osteology of Arctic and Sub-Arctic Water Birds. VI. *Journ. of Anat. and Phys.* January, 1890.

† ALLEYNE NICHOLSON and R. LYDEKKER. 1889. Vol. II., pp. 1222, etc.

The Skull.

The skull, says Professor Marsh (p. 6), "has a general resemblance to the skull of *Colymbus torquatus*, Brünnich; . . . but the likeness soon ceases, for the type of cranial structure is essentially different in the two genera. In its more important characters the skull of *Hesperornis* resembles that of the Ratitæ, or Struthious birds. . . . The base of the skull shows nearly all the cranial characters which Huxley, in his invaluable Memoir on the Classification of Birds, lays down to distinguish the Ratitæ, viz. :—

(1) The posterior ends of the palatines, and the anterior ends of the pterygoids, are very imperfectly, or not at all, articulated with the basi-sphenoid rostrum.

(2) Strong 'basi-pterygoid' processes, arising from the body of the basi-sphenoid, and not from the rostrum, articulate with facets which are situated nearer the posterior than the anterior ends of the inner edges of the pterygoid bones.

(3) The upper, or proximal, articular head of the quadrate bone is not divided into two distinct facets."

Now in regard to the first point, it is very remarkable that we are here face to face with a character in which the Grebes and Divers are exceptional too. In well-prepared skulls in our museum we find that in the Diver the posterior ends of the palatines articulate very little with the rostrum, and the anterior ends of the pterygoids scarcely, if at all. And in the Grebe the same extremities of the two bones meet their fellows of the other side below, and the rostrum plays freely in the groove formed by their upper surface. It is on this account that basipterygoid processes are, as is well known, entirely absent. But there is not in this any real relation with Ratite characters: and, moreover, we must note that Marsh has omitted one-half of Huxley's sentence, which should conclude with the words "being *usually* separated from it, and supported by the broad, cleft hinder end of the vomer." To the general statement the Ostrich itself is an exception, being remarkable for "the shortness of the vomer, which does not articulate with either palatines or pterygoids posteriorly." So that the character is a very uncertain one. It is not definitely displayed, and is not figured at all, in Marsh's account; and if it were, it would be very far from supporting his conclusion.

In the detailed account of the bones, Marsh states that the *palatine* resembles that of the Ostrich. But the palatine is a most variable bone among the Ratitæ; the long, slender palatine of the Ostrich has no resemblance whatever with the same bone, flat, broad, and foliaceous, in Rhea, the Cassowary, and the Emu; and, to my mind, the figure given of the palatine in Hesperornis is by no means unlike that of the Colymbidæ.

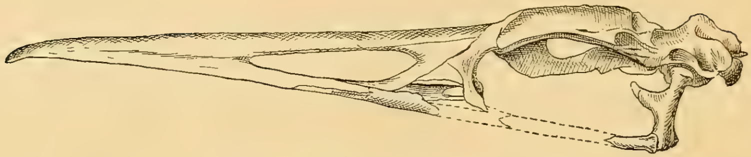

Fig. 1. Skull of Hesperornis regalis. (*After* Marsh.)

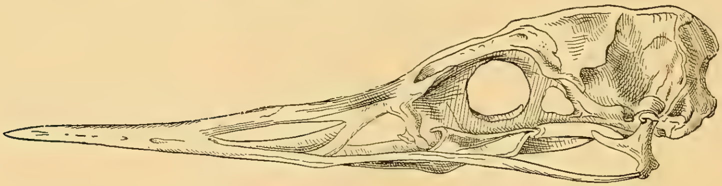

Fig. 2. Skull of Colymbus septentrionalis.

The vomer in Hesperornis is double. This is not the case in the Struthious birds; but in the Colymbidæ and Podicipidæ it is very deeply cleft behind, the two vomers being united for scarcely one-third of their length in Colymbus, while their posterior extremities are widely separate and help to keep the posterior ends of the palatines from contact with the basi-sphenoidal rostrum.

To pass to the second of these points, Marsh gives no description in his text of the "strong 'basi-pterygoid' processes," but they are figured (Pl. II.) in the posterior view of the skull. Now I know no bird's skull in which these processes are visible in the rear-view: the process figured is a tubercle on the basi-occipital, far behind the pterygoid and the quadrate, which is well marked in Colymbus and Podiceps, but much better in the Vultures, the Geese, and many other birds, and which serves for the attachment of the inner portion of the digastric muscle.

Fig. 3. Skull of Hesperornis.

Fig. 4. Skull of Colymbus.

(*Occipital view.*)

As regards the quadrate bone, we have shown elsewhere that it resembles in Marsh's figure the quadrate of the Grebe to a considerable extent: and that it differs from a Ratite quadrate in every important feature; in having, for instance, "a long, slender, well-formed shaft, a head whose two capitula are defined though not deeply cleft, a slender pointed (?) anterior process springing from the shaft at some distance from the head, a distinctly prominent pterygoid process, and a deep quadrato-jugal cup."

The posterior end only of the pterygoid bone is figured by MARSH, but this small portion is of great interest, for it shows besides the socket for the pterygoid process of the quadrate bone, another distinct, lateral, articular surface. Now the pterygo-quadrate articulation is remarkable in the Divers : for the pterygoid articulates with the quadrate not only by its head, but again a little way in front by its external surface, which comes in contact with the anterior process of the quadrate. This condition occurs to some extent in certain other Schizognathous birds, for instance the Fowls, but is quite absent in the Grebes. It is therefore one of the points in which we consider that Hesperornis resembles the Colymbidæ more definitely than the Podicipidæ.

Thus, in short, it appears to us that in the three most crucial regions of the skull where resemblances to Ratite characters have been sought, these resemblances break down ; but that in all three the real resemblances are with the Colymbidæ.

Passing to the other regions of the skull, the general shape, the narrow orbital "waist," the distinct sagittal and occipital crests, are quite similar in Colymbus and Hesperornis. The glandular supra-orbital depressions, so characteristic of the Colymbidæ as well as of the Alcidæ and Laridæ though nearly obsolete in the Grebes, are present in Hesperornis. None of these are Struthious characters. The inter-orbital fenestra, very small in the Ratites as in the Fowls, is here very large, as in Colymbus, though not so enormous as in Podiceps.

The nostrils are holorhinal, and the nasal bone is identical in form with that of Colymbus : in the Ratites it is as different as can be, for its external process is wanting altogether.*

The lachrymal bone of Hesperornis is imperfectly defined in MARSH's figure, but, if I understand it aright, it is by no means unlike that of Colymbus, and certainly very different from the large, flat, curved bone in the Ratitæ.

The description given of the premaxillaries† is not very diagnostic, but the two chief points noted, the posterior longitudinal fissure and the lateral excavation, are to be found in the Grebe and the Diver, but are distinctly not present in the Ratitæ.

The posterior view of the skull is very much like that of Colymbus, for example in the form of the foramen magnum, the cordate shape, large size, and great prominence of the occipital condyle, and in the characters of the ex-occipital region which does not form the broad descending process characteristic of the Ratites.

The great descending process of the squamosal, which in the Ratites overlaps the head and body of the quadrate, is entirely absent in Hesperornis.

* Cf. GARROD. Collected Papers, p. 129.

† "The premaxillaries are elongate and separate throughout their posterior two-thirds. Their extremities touched the frontals. Their sides are deeply excavated for the anterior nares, and in front they are ankylosed, and form a long pointed beak, the end of which is somewhat decurved." (MARSH, *loc. cit.*, p. 8.)

The union of the mandibles at the symphysis by ligament is a feature quite peculiar to Hesperornis : but the shape of the mandible, the character of its articular surface, and the oblique truncation of the posterior extremity are all as in Colymbus. In the Ratites the posterior extremity is truncated in the opposite direction, the angle being bevelled off instead of prolonged backwards.

To sum up as regards the skull, we have in Hesperornis, as it seems to me, no single Ratite character : but, on the other hand, in detail as well as in general form, particularly in the palatine region, the pterygoid, quadrate, squamosal, and nasal bones, in the supra-orbital depressions, in the inter-orbital septum, and in the articular extremity of the lower jaw, we have characters unknown in the Ratites, and in most cases identical with those of Colymbus.

The Vertebral Column.

The vertebræ of birds are so variable in number, that the large number present (forty-nine) in Hesperornis, cannot be made a point in classification ; greater than that in Colymbus, it is considerably less than in any Ratite except Apteryx.

The atlas vertebra is missing in the specimens described by Marsh.

The axis in the Ratitæ* has certain definite general characters. Though immensely larger than the atlas, it is small (except in Apteryx) compared with the third vertebra. The ridge between the anterior and posterior zygapophysis is perforated longitudinally by a canal or foramen ; and the ventral or hæmal process is either absent, or is short, rounded, and blunt. In Colymbus, as well as in Hesperornis, the axis is as large and as long as the third vertebra, and there are

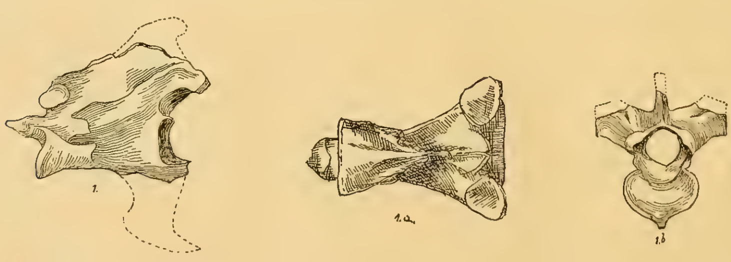

Fig. 5. Axis vertebra of Hesperornis.

1, Lateral. 1*a*, inferior. 1*b*, anterior view.

* Compare with what is here said about the vertebræ of the Ratites the description and figures of Mivart (*Trans. Zool. Soc.* VIII., pp. 385–451, 1874 ; and X., pp. 1–52, 1879).

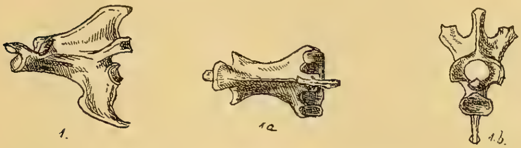

Fig. 6. Axis vertebra of Colymbus.

no lateral perforations; in Colymbus a thin, sharp hæmal spine runs downwards from the posterior half of the body of the vertebra, and the existence of this in a precisely similar position is indicated in Marsh's figures of Hesperornis.

The figures given above show how closely, in every detail of form, for instance in the notches above the posterior extremity of the vertebral body, in the ridge proceeding to the posterior zygaphysis, and in the character of the odontoid process, the two vertebræ agree.

The third vertebræ resemble one another in the two birds in great detail, except that the neural spine is absent, or possibly not preserved, in Hesperornis.

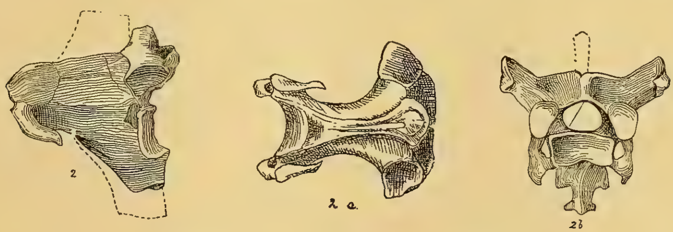

Fig. 7. Third cervical vertebra of Hesperornis.

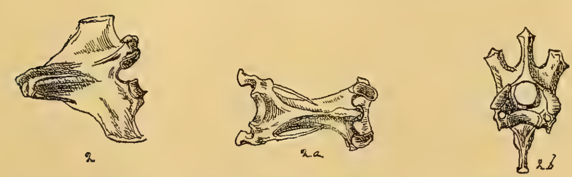

Fig. 8. Third cervical vertebra of Colymbus.

The great tubercles over the posterior zygapophysis (*hyperapophyses*, Mivart) are striking points of resemblance, and are wanting or rudimentary in the Ratites, and the posterior zygapophyses are set at the sides of the neural canal instead of above it as in the Ratites. The middle part of the vertebral body is much compressed from side to side, while it is broad and oblong in the Ratitæ.

The fifth cervical vertebræ are equally similar, so far as the known characters go, but the neural spine and the pleurapophyses are damaged in the specimens of

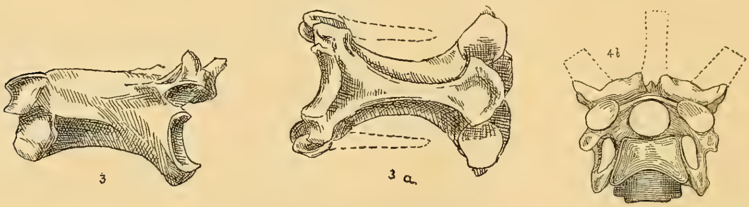

Fig. 9. Fifth cervical vertebra of Hesperornis.

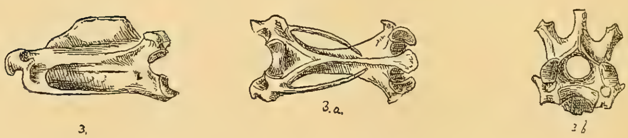

Fig. 10. Fifth cervical vertebra of Colymbus.

Hesperornis. They differ on precisely the same lines as the last from the same vertebra in the Ostrich or the Rhea.

The dorsal vertebræ of *Hesperornis* agree equally well with those of *Colymbus*, except that in the first dorsal the long hæmal process or hypapophysis is single instead of forked: the hæmal processes are broken in the remaining dorsal vertebræ figured by Marsh. No hæmal processes, or very rudimentary ones, exist in the Ratitæ. In other respects, in the shape of the articular surfaces of the centra, the position of the articular processes, the long transverse processes, and the long, high, and compressed neural spines, the agreement between *Colymbus* and *Hesperornis* is complete.

The ribs are nine in number in Hesperornis, the same number as in Colymbus: in Hesperornis the three first, in Colymbus one only, is without attachment to a sternal rib. They are in both birds flatter and broader than in the Ostrich, and the first is fairly well developed, instead of being very minute. The uncinate processes afford better characters. In the Ostrich and Rhea they are small and three in number only: in the other living Ratites they are rudimentary or absent. In Hesperornis and in Colymbus they are very large, flat, and long, directed upwards at an acute angle, and are borne by six ribs in both genera. In Hesperornis they are free and unanchylosed with the ribs; such is the case in four out of the six ribs in my most adult specimen of Colymbus.

The Shoulder-Girdle.

On the keelless sternum and other characters of the shoulder-girdle of Hesperornis, Marsh lays great stress in his advocacy of the bird's Ratite affinities. I believe that the real affinities here again are obviously with the Colymbidæ, and that the special features are all due to the degenerate condition of the wings.

In the first place, the sternum shows both in the figure of *H. regalis* (Marsh, Pl. vi., fig. 2), and to a less extent in that of *H. crassipes* (Pl. vii., fig. 3), undoubted traces of *a rudimentary keel.* The oblong, elongated shape, and the two notches in the posterior margin, are precisely as in Colymbus, and unlike anything in the Ratitæ; and the peculiar articulation with the coracoid, which latter bone fits into a deep notch on the ventral face of the sternum, is exactly paralleled in the Colymbidæ and Alcidæ.

The coracoid is remarkably short and broad, much shorter than in Colymbus, but its outline, allowing for the shortening up of the shaft, is not dissimilar: in particular, we may note the curious angular projection on the outer side of the sternal extremity (the *epicoracoid* of Parker), which is not represented, or very feebly indicated, in the Ratites.

The second point on the strength of which the Ratite affinities have been urged, is in the very obtuse angle between the scapula and the coracoid, "the long axis of the adjacent parts of the scapula and coracoid being parallel, or identical." Now it is certain that the angle between the coracoid and the scapula is in Hesperornis a very obtuse one, and much more obtuse than in Colymbus or any ordinary Carinate bird, though hardly so obtuse as the description above quoted would imply. From Marsh's figure (*loc. cit.*, p. 58) it would seem to be an angle of about 110°, or very nearly the same as in the Emu. But this is a point in which the Ratitæ differ very considerably among themselves, and I doubt whether it be not a feature too much dependent on function to be a safe classificatory guide. But if an apparent Ratite affinity be detected here, it is surely more than overthrown by the fact that in Hesperornis the scapula and coracoid are separate bones, while in all the known Ratites they are united. Not only is this a morphological character of greater importance, but it throws some doubt on the accurate measurement of the angle itself.

The clavicles in Hesperornis, though separate, meet in the middle line, and are thus better developed than in any Ratite. They resemble in form the clavicles of Colymbus, which are much thinned away at their junction, and meet without any interclavicular expansion.

A peculiarity in the proximal extremity of the clavicle in Colymbus, which passes beyond the head of the coracoid to articulate by a long tapering extension with the scapula, is not found in Hesperornis.

The Pelvic Girdle.

The very close resemblance in general shape of the pelvis of Hesperornis to that of Podiceps or Colymbus has been noted by Marsh. How close it is may be

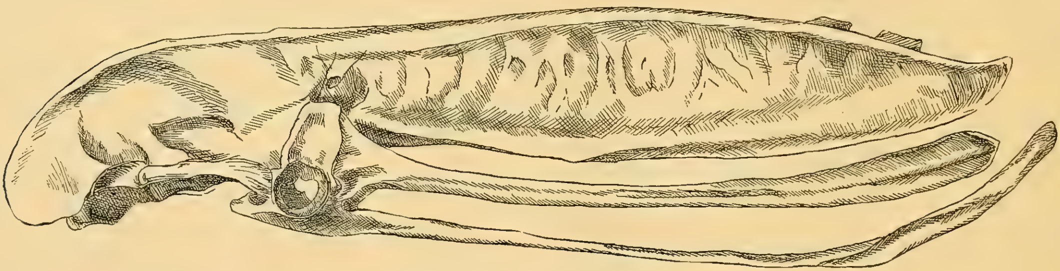

Fig. 11. Pelvis of Hesperornis.

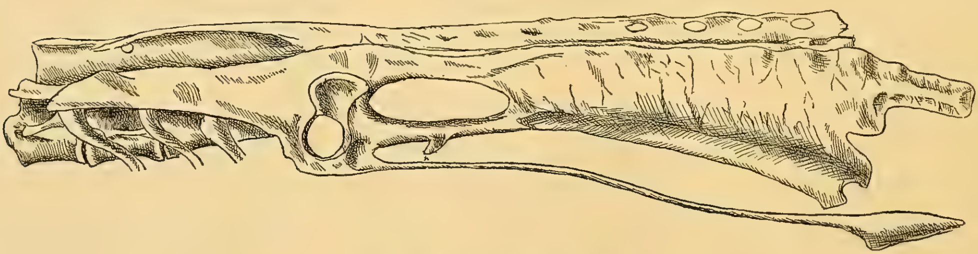

Fig. 12. Pelvis of Colymbus.

expressed by saying that Marsh's whole paragraph descriptive of the ilium of Hesperornis might be transferred to that of Colymbus, perhaps without the alteration of a word.

The most striking character in the pelvis of Hesperornis is the want of any union between the posterior extremities of the ilium, ischium, and pubis. This is a common but not universal character in the Ratites as well as in the Tinamous; at variance with it are the familiar facts of the pubic symphysis in *Struthio*, the ischial symphysis in *Rhea*, and the union between ilium and ischium in *Rhea* and *Casuarius galeatus.* But apart from this matter, the general proportions of the parts are very strikingly different. The Ratite pelvis is remarkable, in comparison with all other birds, for the great relative development of the pre-acetabular part of the ilium. The pre-acetabular portion is as long, or very nearly so, as the post-acetabular, and is always the stronger, higher, and bulkier: in Apteryx and Dinornis the post-acetabular part of the bone is almost rudimentary. In Hesperornis we go quite to an opposite extreme, the pre-acetabular part being thin or weak, and little more than one-fourth of the entire extent of the bone; a similar relation holds in

Colymbus, where the pre-acetabular part is even less in proportion. In short, except for the want of the union between the ilium and ischium in the fossil species, these two very striking pelves are practically identical.

The Hind-Limb.

The bones of the hind-limb in Hesperornis are so closely similar to those of the Colymbo-Podicipidæ that Marsh in describing them has throughout used Podiceps as the standard of comparison: and in no single point in connection with the hind-limb has Marsh been able to cite the existence of even apparent Ratite affinities. It is, therefore, not necessary to recapitulate in detail the characters of the bones, further perhaps than to call attention to two more or less striking points. Firstly, the extreme shortness of the femur is a very Colymbine feature: that bone is in

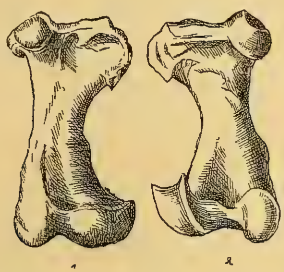

Fig. 13. Left Femur of Hesperornis.
1, anterior; 2, posterior view.

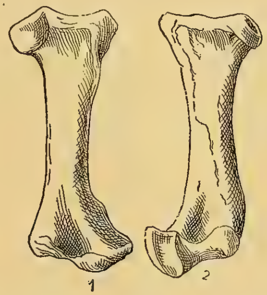

Fig. 14. Left Femur of Colymbus.

Colymbus and Hesperornis about one-quarter the length of the ilium; whereas in the Ratites, except in exceptional cases, such as *Dinornis elephantopus*, the two bones are nearly of equal length. Secondly, and of greater importance, the patella,

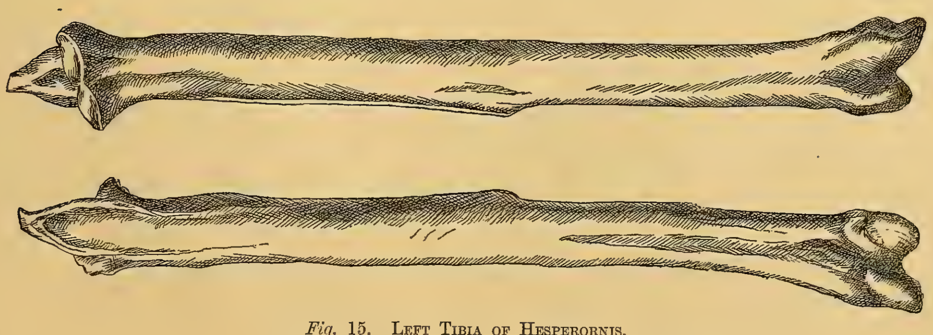

Fig. 15. Left Tibia of Hesperornis.

Fig. 16. Patella of Hesperornis.

which, small and double in the Ostrich, is rudimentary or absent altogether in the other Ratites, is of immense size and peculiar shape in Hesperornis. In this bird it is a long trihedral pyramid, pointed at its superior extremity, concave on its outer surface, bearing at its lower extremity special and separate articular surfaces for the tibia and femur, and lying in a line with the long axis of the femur. Except that it is perforated for the tendon of the *ambiens* muscle (as in the Gannet), it is extremely like the patella of the Grebe, and practically identical with that of *Colymbus*, except that in this latter it is fused with the upper extremity of the tibia. The existence of a small additional sesamoid

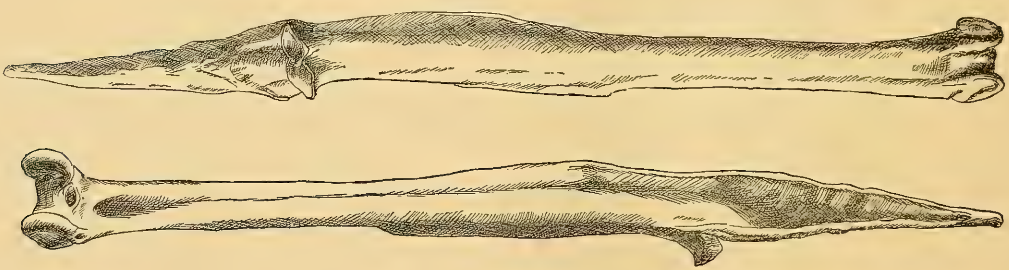

Fig. 17. Left Tibia, with co-ossified Patella of Colymbus.

in the knee-joint of Colymbus (Owen, *Comp. Anat.*, II., p. 83) does not invalidate the homology here adopted of the long "rotular process of the tibia" with the patella.

The resemblances and differences on which the whole preceding argument is based may be small points if taken separately, but the strength of the case must rest on their great number, and on their all, without exception, pointing the same way. Many of the points are not easily made clear with the means of illustration at our command. Such as they are, they may be recapitulated as follows:—

In the skull of Hesperornis

The sagittal and occipital crests are present as in Colymbus: but they are quite absent in the Ratites.

The supra-orbital glandular depressions are present as in Colymbus: but they are quite absent in the Ratites.

The inter-orbital fenestra is very large, as in Colymbus, not very small as in the Ratites.

The basi-pterygoid processes, which, arising from the body of the basi-sphenoid bone, are conspicuous in the Ratites, have not been demonstrated to exist in Hesperornis and are entirely absent in Colymbus.

The vomer is double in Hesperornis, and is so deeply cleft as to be nearly so in Colymbus; but it is short and single in the Ratites.

The pterygoid has two articular surfaces for contact with the quadrate as in Colymbus, not one only as in the Ratites.

The occipital condyle is large, cordate, and very prominent, as in Colymbus; not small and low as in the Ratites.

The ex-occipital region, as in Colymbus, sends down no broad descending process as it does in the Ratites.

The squamosal, as in Colymbus, sends down no descending process to overlap the quadrate as it does in the Ratites.

The lachrymal bone was apparently small, narrow, and bent, as in Colymbus; not large, flattened, and curved as in the Ratites.

The nostrils are holorhinal, as in Colymbus; but their character is quite different in the Ratites.

The premaxillaries are deeply excavated at their sides for the anterior nares, as in Colymbus; they are not excavated at all in the Ratites.

The mandible is prolonged backwards at its angle, as in Colymbus, not bevelled off or truncated as in the Ratites.

The quadrate has a head which is almost certainly divided into two capitula to as great an extent as in Colymbus: its anterior process is long and slender as in Colymbus, not short, thick, and truncated as in the Ratites: its quadrato-jugal cup is deep and well-defined as in Colymbus, not imperfect or rudimentary as in the Ratites: its pterygoid process is distinct and prominent as in Colymbus, and not ill-defined or absent as in the Ratites.

The axis vertebra in Hesperornis

Was as large as the third vertebra, as it is also in Colymbus, not small compared with it as in the Ratites.

It had, like Colymbus, no lateral foramen or canal, such as is present in the Ratites.

It appears to have had a thin, sharp hæmal spine, which in Colymbus also is thin, sharp, and long, but is absent or rudimentary in the Ratites.

The other characters drawn from the vertebral column need not be further recapitulated here.

The ribs are in Hesperornis

As in Colymbus, much flatter and broader than in the Ratites.

The uncinate processes are, as in Colymbus, large, long, and six in number; in the Ratites they are either small, rudimentary, or absent, and never exceed three.

In the shoulder-girdle of Hesperornis

The sternum shows distinct traces of having once possessed a keel. It is oblong and elongated in form as in Colymbus, not short and shield-shaped as in the Ratites. It bears, as in Colymbus, two deep notches on its posterior margin.

The coracoid bears a blunt, square "epicoracoid" process as in Colymbus, not possessed by the Ratites.

The coracoid and scapula are separate, not anchylosed as in the Ratites.

The clavicles meet in the middle line; they do not meet in any Ratite.

In the pelvic-girdle of Hesperornis

The ilium is, as in Colymbus, immensely elongated posteriorly to the acetabulum, and its pre-acetabular part is very short and small as in Colymbus, not long, high, and massive as in the Ratites.

In the hind-limb of Hesperornis

The femur is short, flattened, and thick as in Colymbus, not long and cylindrical as in the Ratites.

The patella is very long, trihedral, and pointed, as in Podiceps and as in Colymbus, except that in the latter it is anchylosed with the tibia: but it is small or absent altogether in the Ratites.

To sum up, it appears to me that from purely osteological characters, the wide difference between Hesperornis and any Ratite, and its close resemblance to Colymbus or to Podiceps is clear and patent. From these characters it is a Colymbine bird, of great size and prodigious swimming power, which, while losing its wings and sternal keel and otherwise somewhat modifying its shoulder-girdle as the faculty of flight degenerated, has retained in its brain-case, its palate, its mandibles, its vertebræ, its sternum, pelvis, and hind-limbs, resemblances almost amounting to identity with the existing Colymbi: resemblances as great as between *Strigops* and the other parrots, and much greater than between *Didus* and the ordinary pigeons.

There remain the two marked peculiarities of the teeth and the under-sized brain. As regards the former, when birds undoubtedly descend from toothed ancestors of some kind, and when every other great division of the vertebrates comprises toothed as well as toothless forms, I cannot see that this fact, however interesting, should be permitted to alter or to determine the great lines of ornithological classification.

While as to the small size of the brain, rather than make *Hesperornis* on this account a type ancestral to all existing birds two possible explanations suggest themselves. For bearing in mind the small size of the brain that Professor MARSH himself has demonstrated in so many of the great American fossil Mammalia, some of which are obviously very highly specialized and by no means primitive, we may judge either that immense structural specialization might and did go on without corresponding advance in cerebral development, or that the brain had actually a certain tendency to dwindle under the exceptional conditions of environment which conduced to the development of these huge extinct forms. And, lastly, we must not forget that the brain of very large animals is never quite as large in proportion, compared with smaller and closely allied forms.

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Studies from the Museum of Zoology

IN UNIVERSITY COLLEGE, DUNDEE.

EDITED BY

D'ARCY W. THOMPSON,

Professor.

XI. ON THE CETACEAN LARYNX.

By Professor D'ARCY W. THOMPSON.

XII. NOTE ON ERETHIZON DORSATUS.

By ALEXANDER MEEK.

DUNDEE:

Printed for the Museum.

August, 1890.

XI. *On the Cetacean Larynx.*

By Professor D'Arcy W. Thompson.

Some years ago Professor Howes* detected in the larynx of the Porpoise a division of the great so-called arytenoid cartilage into two imperfectly separate parts. He suggested that of these only the lower represented the true arytenoid of other mammals, and that the long upper horn was the equivalent of the Cartilage of Wrisberg or cuneiform cartilage of human anatomists. This observation has been confirmed by Professor Cleland† in regard to *Lagenorhynchus albirostris;* but in general it has not received the attention which it deserved; and various authors, including Max Weber and Dubois, Beauregard and Boulart, have since discussed the Cetacean larynx without referring to Howes' paper or rediscovering for themselves the condition which it describes.

It is plain that if only a part of the great Cetacean "arytenoid" be the true arytenoid, then into that part alone should pass the several arytenoid muscles. On investigating a series of Cetacean larynges to determine this point, I find it to be strictly the case.

The larynges that I have examined as yet belong all to the Delphinoidea, to wit, to the genera *Monodon*, *Beluga*, *Lagenorhynchus*, *Delphinus*, and *Globiocephalus:* but doubtless as regards the arytenoids the generalisation drawn for the Delphinoids applies to the Balænoidea also.

In the larynx of a foetal *Globiocephalus melas* (*Figs.* 1—6), 45 cm. long, the true arytenoids *(Ar)* are still completely separate from the arytenoid cornua, which will be henceforth referred to as the *supra-arytenoids.* The arytenoids exhibit a rounded or somewhat triangular posterior surface, a prominent external border, and an elongated triangular external surface: the whole arytenoid has the form of a three-sided pyramid, whose base is posterior, and whose lower surface runs for some distance parallel to the superior border of the cricoid. The two arytenoids are set far apart from one another upon the cricoid, near the angles of the posterior surface of the latter cartilage.

The form of the other cartilages is sufficiently shown in the figures. The *cricoid* is thick and massive posteriorly: it bears just at the posterior and inferior angle on each side an articular facet for the posterior horn of the thyroid: its own lateral horns curve downwards and forwards, and end freely in front near the middle line.

* *Journ. of Anat. and Phys.* Vol. XIV., p. 471. 1880.

† "I beg to verify the observation of Mr Howes that the cartilages which together with the epiglottis are so remarkably elongated in porpoises are not arytenoids, but articulate with them, and may be regarded as Cartilages of Wrisberg." *Journ. of Anat. and Phys.*, Vol. XVIII., p. 333. 1884.

The *thyroid* cartilage is somewhat broad in front, narrower laterally: the posterior horn is curved, and is very long and slender: the region of the anterior

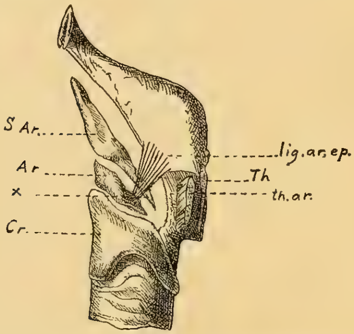


Fig. 1. Larynx of foetal Globiocephalus (*natural size*).

The right ala of the thyroid cartilage (*Th*) and part of the corresponding thyro-arytenoid muscle (*th.ar.*) have been cut away. *Cr.*, cricoid. *Ar.*, arytenoid. *S.Ar.*, supra-arytenoid. *lig.ar.ep.*, the aryteno-epiglottidean ligament. ×, the separate nodule at the extremity of the supra-arytenoid cartilage.

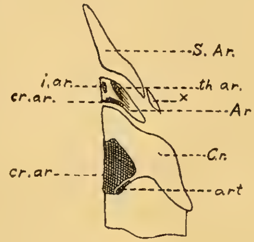


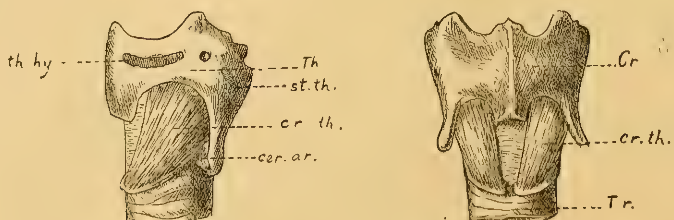
Fig. 2.

Part of the same larynx, showing diagrammatically the insertions of the muscles. *cr.ar.*, crico-arytenoid. *i.ar.*, inter-arytenoid. *th.ar.*, thyro-arytenoid. *art.*, articulation of the posterior thyroid cornu with the cricoid.

horn is obliquely truncated: the thyroid foramen for the superior laryngeal nerve and artery is present.

The supra-arytenoid cartilages are long and slender. Each of them sends forwards and downwards a long descending horn, which reaches as far as, or a little farther than, the anterior apex of the arytenoid: and sends upwards its superior horn parallel with its fellow and with the epiglottis, and somewhat overtopped by the latter.

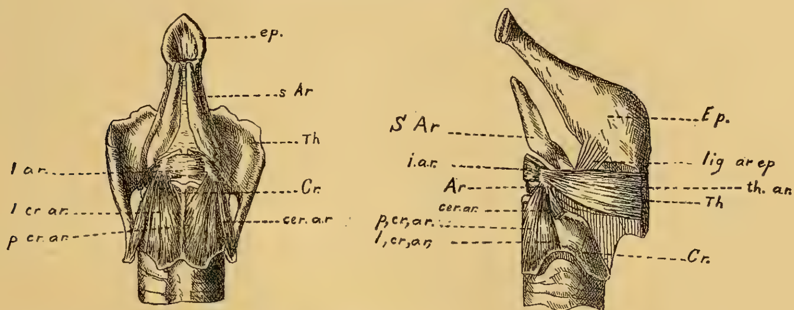
Muscles.—The *crico-thyroid* muscle springs from a narrow origin at the extremity of the horn of the cricoid cartilage, and, expanding fan-wise, goes to be inserted into an extended line on the inferior border of the thyroid and its posterior cornu.



Figs. 3 *and* 4.

Parts of the same larynx from the front and from the left side, chiefly to show the crico-thyroid muscle (*cr.th.*). *cer.ar.*, cerato-arytenoid muscle. *th.hy.*, origin of the thyro-hyoid muscle. *st.th.*, insertion of the sterno-thyroid muscle. *Tr.*, trachea.

The *crico-arytenoid*, rather indistinctly divided into posterior and lateral portions, arises from the posterior surface of the cricoid below the level of its lateral process or horn, and is inserted into the lower part of the posterior face of the arytenoid. Running parallel with this muscle, close to its outer border, and inserted together with it, is the *cerato-arytenoid*, arising from the inner face of the posterior thyroid cornu, near its articulation with the cricoid.



Figs. 5 *and* 6.

The same larynx from behind and from the right side. In *Fig.* 6 the right ala of the thyroid has been cut away. *l.cr.ar.*, lateral crico-arytenoid muscle. *p.cr.ar.*, posterior crico-arytenoid. The other letters as before.

The *inter-arytenoid* is a very narrow, straight muscle, uniting the two arytenoid cartilages.

The *thyro-arytenoid*, a thick, broad muscle, arises from the angle of the thyroid, and is inserted into the prominent external border of the arytenoid.

Thus the whole of the "arytenoid" muscles, without exception, pass to the three arytenoid cartilages, and the arytenoid horns, herein called the supra-arytenoids, are destitute of muscular connections.

After reflecting the ala of the thyroid, a very strong triangular ligamentous band, closely connected with the mucous membrane, is seen passing from the lower part of the epiglottis to the anterior process of the supra-arytenoid, and partly over the same to the true arytenoid: the extreme anterior part of the supra-arytenoid into which this is inserted is separated off as a cartilaginous nodule from the rest.

Now I am inclined to think that this condition explains at least two points. Firstly, the main portion of the supra-arytenoid is now shown quite conclusively to be independent of the true arytenoid, and must from its position be taken as the structure which our Cartilages of Santorini represent in the form of a very degenerate rudiment. Secondly, the other rudimentary cartilages in the larynx of higher mammals, namely, the Cartilages of Wrisberg, seem to be likewise explicable as being identical with the separate portion of the supra-arytenoid involved in the ligamentous fold connecting the arytenoid with the epiglottis. In short, the Cartilages of Santorini and of Wrisberg represent remnants of the superior and inferior (anterior) portions of a once large Cetacean-like supra-arytenoid.

This case in Globiocephalus illustrates sufficiently in itself all the main points of importance which the Delphinoid larynx presents us with. I figure certain additional specimens to illustrate or corroborate minor points.

The youngest fœtus in our collection is that of a Narwhal, whose total length was 8 centimetres.

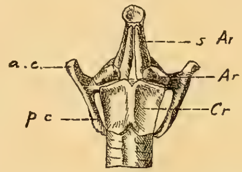
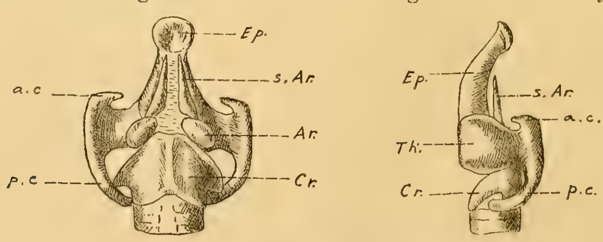


Fig. 7. LARYNX OF FOETAL ~~NARWHAL (× 3)~~. BELUGA
ac.pc., anterior and posterior thyroid cornu.

The arytenoids are here comparatively large, oval cartilages, set somewhat wide apart, above and a little to the side of the cricoid cartilage. The supra-arytenoids are very small and delicate: they rise upwards to a pointed apex overtopped by the epiglottis, from a broad base attached to the arytenoids: the anterior or inferior process running forwards over the arytenoids appears to be as yet undeveloped. The cricoid is peculiar: its anterior processes are rather short and stout, and beneath them the inferior angles of the cartilages, with which the posterior thyroid cornua articulate, project to a shorter distance laterally; so that the cricoid looks like a broad posterior plate from which two pairs of lateral processes project instead of one. The thyroid has the anterior and posterior cornua well developed: the former are reflexed, forming a deep notch which answers to an imperfect thyroid foramen. The epiglottis is already solid and cartilaginous, and is very firmly attached at its base to the anterior border of the thyroid.

In an older but still young fœtus of *Beluga*, about 20 cm. in length, the cricoid has attained nearly to the conformation of the adult. Its posterior surface is broad and massive, with a median longitudinal ridge: anteriorly (or ventrally) it is incomplete, as it remains in the adult; and all trace of the lateral extension of its posterior angles seen in the earlier stage has disappeared. The arytenoids are as distinct and separate as in the former case: they are still oval nodules of cartilage, lying somewhat closer together and with their long axes more nearly coincident,



Figs. 8 *and* 9. LARYNX OF FOETAL ~~BELUGA.~~ NARWHAL.
From behind and from the left side (× 3).

upon the upper border of the cricoid. The body of the thyroid is broad in the middle, very narrow laterally: the anterior cornu is short and blunt, the posterior narrow and long. The anterior extremity of the epiglottis overlaps but is closely united by membrane to the body of the hyoid.

In a fœtus of *Lagenorhynchus albirostris*, about two feet in length, the adult condition is more nearly approached. The arytenoids are now much enlarged, and elongated in an antero-posterior direction, lying, as shown in the annexed figure, along the superior border of the long decurved ventral horn of the cricoid. The

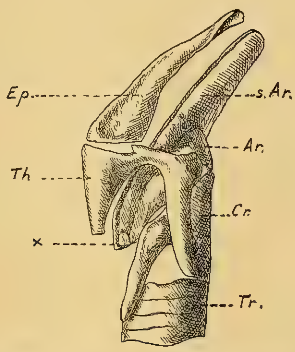


Fig. 10. LARYNX OF FOETAL LAGENORHYNCHUS *(natural size).*

arytenoid is enfolded by the supra-arytenoid, but no actual fusion has taken place. The separate nodule at the ventral extremity of the supra-arytenoid is very distinct. The anterior horn of the thyroid is rudimentary, the posterior very long: there is no thyroid foramen.

In a nearly adult *Delphinus delphis* (7 feet long), whose larynx is very like that of *Lagenorhynchus,* the supra-arytenoid is seen to have increased in size, when compared with the former figure, relatively to the arytenoid and to the cricoid: the arytenoid is still separate, though very intimately connected with the supra-arytenoid; and the nodule at the ventral extremity of the supra-arytenoid is distinct, and of irregular elongated form. The epiglottis has greatly increased in size and massiveness: the area of its attachment to the body of the thyroid has diminished, and its posterior angles embrace the arytenoids.

In a specimen of *Globiocephalus,* about 12 feet long, the arytenoid is still separate from its adjacent cartilages. The supra-arytenoid, at its original point of articulation with the arytenoid, articulates with the latter by a smooth cartilaginous facet; beyond, that is to say ventral to that point, it slightly overlaps, and no special surface of articulation is developed: but such a definite articular surface is again present where the arytenoid meets the terminal nodules of the supra-arytenoid. In older specimens of Globiocephalus the whole are fused.

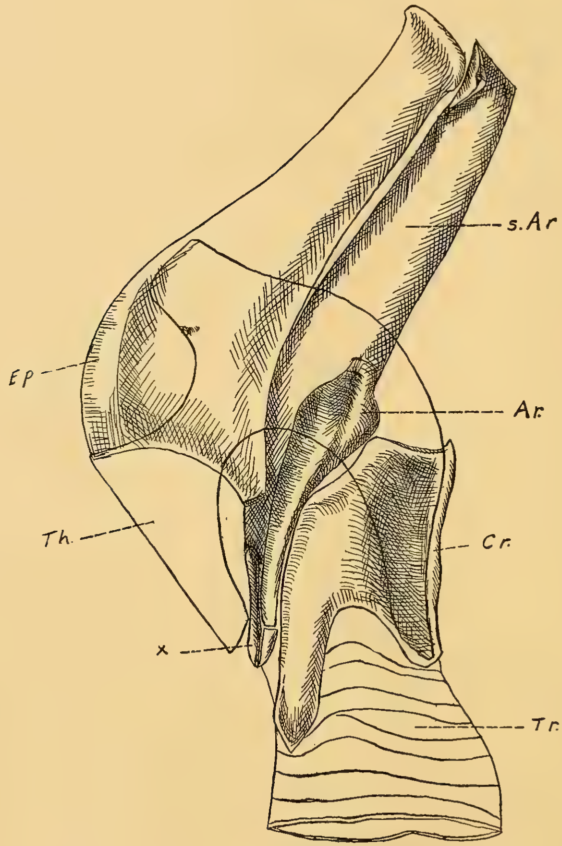


Fig. 11. Larynx of Delphinus delphis *(natural size).*
The thyroid cartilage is shown in outline only.

The larynx in *Orcella* and *Platanista* is very interesting, in as much as it appears in these two genera to retain in the adult state the precise conditions here described in the fœtus of other Delphinoidea. The descriptions given by Dr John Anderson* have not been quoted by recent writers on the Cetacean larynx; and Dr Anderson himself has not called attention to what seems to us the great morphological importance of the facts described. The following is the account given of the arytenoid cartilages and the structures connected with them in *Orcella*:—

"The body of the arytenoid cartilage of *Orcella* is a laterally compressed oval, with a sharp margin directed forwards and a rounded margin posteriorly, by the upper two-thirds of which it is articulated to

* Zoological Results of Expeditions to Western Yunnan. 4to. London, 1878. pp. 387, 455, pl. xxviii.

the cricoid by a synovial capsulated joint. The anterior horn is a long, laterally compressed and pointed structure in the upper half of its extent, but in the lower half of its surface is thickened and convex from side to side. It is connected to the arytenoid body by fibrous tissue, *so that it is freely moveable on it as is the case in Platanista.* The posterior horn is a downward prolongation of the anterior, and is a rounded bar of cartilage, and terminates abruptly in a flattened end at the lower portion of the penultimate sixth of the arytenoid body, where it is capped by two small cartilages applied to each other laterally, succeeded by another cartilage which is wedged in between them and the last sixth of the arytenoids, and curving forwards overlies them. *A great part of the attachment of the aryteno-epiglottidean ligament takes place from the outer border of these cartilages*" (*loc. cit.* p. 387).

Thus so far as this description goes, the muscles not being described, we have here the exact counterpart of the *foetal* larynx of *Globiocephalus.* We have, that is to say, a distinct arytenoid and supra-arytenoid ; and we have, segmented off from the inferior extremity of the latter, in close relation with the aryteno-epiglottidean ligament, a separate cartilage, comparable to the Cartilage of WRISBERG.

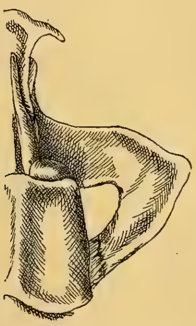


Fig. 12. LARYNX OF PLATANISTA. *Fig.* 13. LARYNX OF ORCELLA.

Posterior view. (*After* ANDERSON.)

To conclude, the so-called arytenoid cartilage of the Delphinoid Whales originates in two parts, of which one receives the whole of the arytenoid muscles, and is therefore proved to be the true *arytenoid:* the other may be called the supra-arytenoid. This supra-arytenoid itself tends to divide into two parts. Its inferior or ventral extremity becomes separated off, apparently owing to its implication in the great aryteno-epiglottidean ligament: it may therefore be considered homologous with the Cartilage of WRISBERG of human anatomy. The remaining superior and much larger portion of the supra-arytenoid is thus homologous with the Cartilage of SANTORINI.

The young stages of the larynx in the Balaenoidea are not known. In all probability, in them also the arytenoid is of double origin, its supra-arytenoid horn being relatively much smaller, and its basal or true arytenoid part being remarkably prolonged along the superior border of the cricoid.

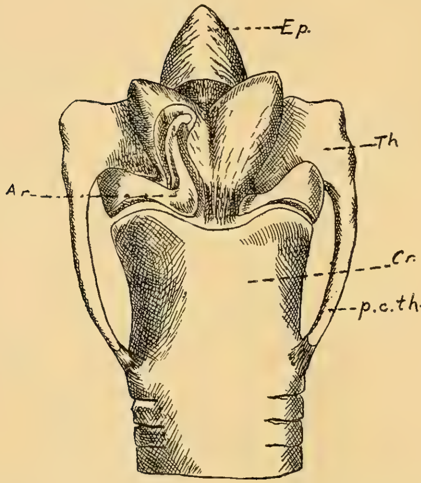


Fig. 14. LARYNX OF BALAENOPTERA MUSCULUS (× $\frac{1}{8}$). (*After* BEAUREGARD and BOULART.)
One of the great aryteno-epiglottidean folds is opened to show the horn of the arytenoid lying within.

In regard to other morphological points, the Cetacean larynx, so far as the above description goes, supports DUBOIS'S* view that the cricoids and arytenoids come from a different morphological origin to that of the thyroid; and that while the latter is derived from the visceral arches, they are modifications of the anterior rings of the trachea. If that be the case, our Cetacean larynges would suggest that the cricoid, the arytenoids, and the supra-arytenoids are formed out of *three* such tracheal rings. The shape of the arytenoids in the Balaenoidea and of the supra-arytenoids in the Delphinoidea appear to me to favour this view somewhat. But these larynges do not help us in regard to the thyroid cartilage, in settling, for instance, whether it arises from *two* visceral arches, as it appears evidently to do in the Monotremata. The origin of the epiglottis is a difficulty, and its form and structure in the Cetacea are not the least remarkable features in the group. Taking it as proven that the thyroid cartilage originates from the visceral skeleton in some such way as DUBOIS asserts, and considering the relations of the epiglottis to the thyroid in Cetacea, and in their young stages to the basi-hyal also, I am inclined to suspect that the cartilaginous epiglottis in Cetacea is a somewhat ancient type, and was really developed from the copula or basi-branchial skeleton uniting the thyroid and hyoid arches. But earlier stages than I possess would be required to support this inference.

* EUG. DUBOIS. Zur Morphologie des Larynx. *Anat. Anz.*, I., pp. 178, 225. 1886.

XII. *Note on the Female Organs of Erethizon dorsatus.*

By Alexander Meek, B.Sc., University College, Dundee.

About a year ago the Museum received from the Zoological Society an adult female Canadian Porcupine, *Erethizon dorsatus*. In making some Museum preparations of the animal's viscera, we were struck by the characters of the uro-genital organs, in connection with which remains of the Wolffian Body and its duct were unusually conspicuous.

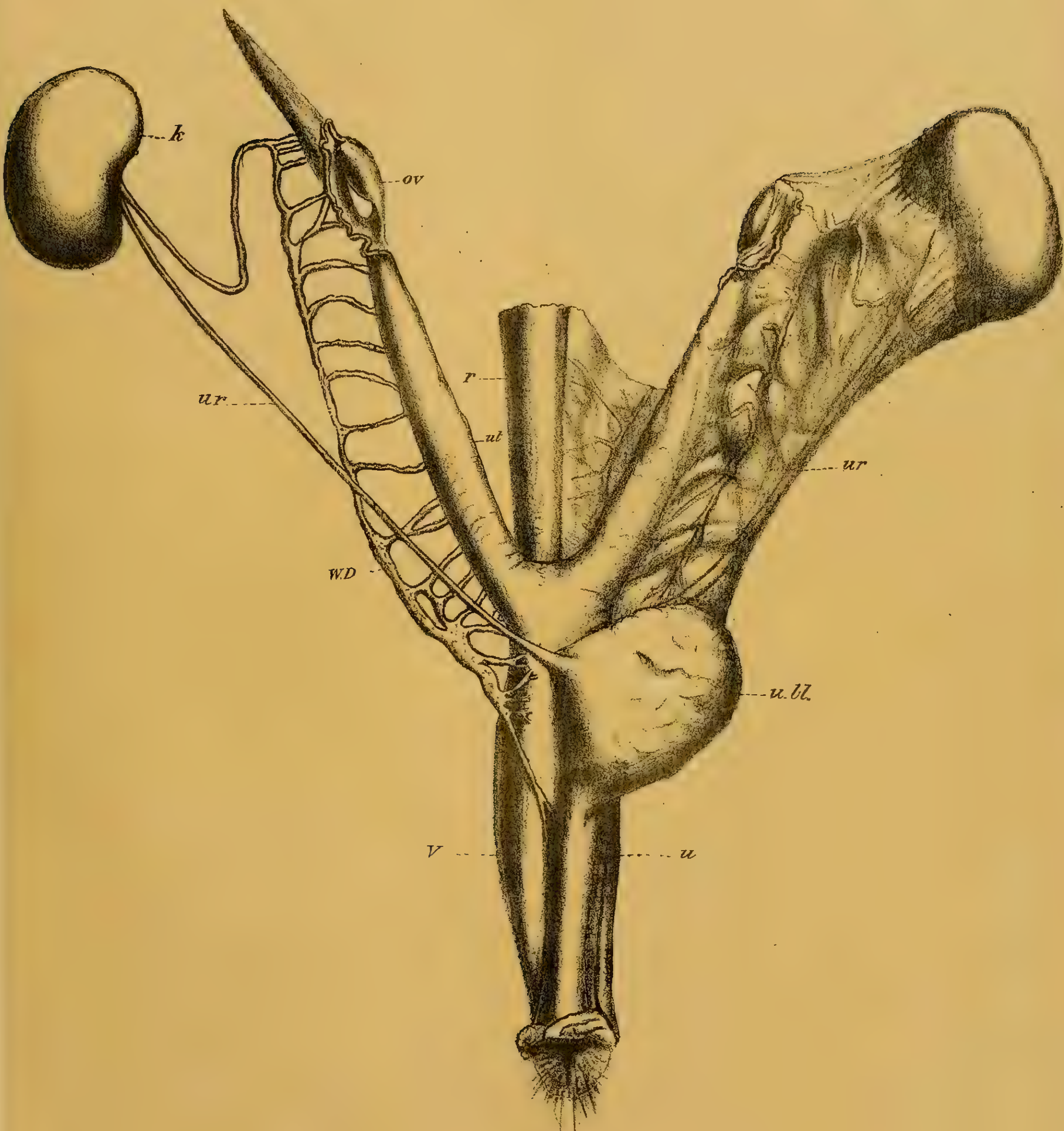
The annexed drawing scarcely requires description. The uteri are, as in the Rabbit, completely separate. Parallel to each, in the broad ligament of the uterus, runs a fine undulated tube, which thins away and is lost above on the hilus of the kidney and below on the wall of the urethra, close to the neck of the bladder. This tube is the duct of Gaertner, the persistent vestige of the Wolffian duct. With this duct, along the greater part of its course, are connected about twenty lateral diverticula, sometimes branching, sometimes slightly anastomosing with one another, but generally simple, whose distal ends lose themselves in the neighbourhood of the ovary, on the walls of the uterus, and on the upper portion of the vagina. These represent the segmental tubules of the Wolffian Body, not gathered together into an irregular clustered parovarium and paroophoron, but regularly arranged in a longitudinal and very primitive-looking series. The extension of the duct of Gaertner inferiorly on to the neck of the bladder is in accordance with the known embryological connection between the lower ends of the Wolffian duct and of the ureter; but its extension upwards to the hilus of the kidney is not to be explained so easily.

None of the other mammals, such as the Pig, the Guinea-pig, various Ruminants, Rodents, &c., in which the duct of Gaertner and its correlated structures have been described, shows, so far as is known to us, the parts in so complete and primitive a condition as here.

EXPLANATION OF THE PLATE.

k.	kidney.	*u.bl.*	urinary bladder.
ov.	ovary.	*ur.*	ureter.
r.	rectum.	*ut.*	uterus.
u.	urethra.	*v.*	vagina.

W.D. Wolffian duct, or duct of Gaertner.



A.M. Del.

J. Durham, Son & Kinnoch, Litho.