6. On the Representatives of the Malleus and the Incus of the *Mammalia* in the other *Vertebrata*. By T. H. Huxley, F.R.S.

In the course of the last two years, Professor Peters has contributed to the 'Monatsberichte' of the Berlin Academy a series of papers in which he advocates what I may term, for brevity's sake, the "Okenian" doctrine of the homologies of the *ossicula auditûs* of Mammals and of the quadrate bone of the other *Vertebrata*. According to this view, the *ossicula auditûs* of *Mammalia* are completely represented by the auditory *columella* in other *Vertebrata*, while the tympanic is the homologue of the quadrate bone. In supporting it, Professor Peters necessarily argues against the doctrine originally put forward by Reichert, and subsequently adopted by myself, that the auditory *columella* of the lower *Vertebrata* does not answer to all the *ossicula auditûs* of the *Mammalia*, but only to the *stapes*—the *incus* being represented by the quadrate bone, the *malleus* by the articular; while the homologue of the tympanic is only to be found occasionally, in ossifications of the fibrous frame of the tympanic membrane.

In the first two papers of the series, Prof. Peters bases his argumentation upon the anatomical relations of the lower jaw and the tympanic bone in the *Marsupialia* and *Monotremata*; but as these facts are, undoubtedly, capable of being interpreted as well upon the Reichertian as upon the Okenian hypothesis, I did not conceive it necessary to enter, at present, upon any discussion of them.

On the 19th November, 1868, however, Prof. Peters made a third communication to the Berlin Academy, "Upon the Auditory Ossicles and the Meckelian Cartilage in Crocodiles," which was followed on the 7th January, 1869, by a fourth, "Upon the Auditory Ossicles of Chelonia, Lizards, and Ophidia, as well as upon the cavities of the Lower Jaw of the Crocodile," which seemed to me to demand immediate attention; for the quadrate bone of the Crocodile cannot possibly represent either the incus, or the malleus, if the statement of anatomical facts made by Prof. Peters is correct.

I therefore proceeded to the verification of his descriptions with much interest and a little anxiety; but after dissecting the skulls of several young Crocodiles with great care, I must declare my conviction that Prof. Peters is in error as to the facts, and, therefore, that the argument he bases upon them falls to the ground.

The able anatomist Stannius first drew attention to the pneumaticity of the lower jaw in the Crocodile, in the following terms:—

"The *os articulare* of the lower jaw is distinguished by its pneumaticity; its great hollow cells communicate, by a canal which lies at the back of the *os tympanicum* [quadratum], with the air-chambers of the cranial bones. The lowest part of the canal in question forms a groove in the dry skull. This, in the fresh skull, is converted into a soft tube; and a free membranous tube leads into a hole placed on the inner side of the surface of the *os articulare*." (Stannius, 'Handbuch d. Zootomie,' Zweiter Theil. Amphibien, p. 58, 1856.)

Prof. Peters adds to this account of the matter the following statements (Monatsberichte, 1869, pp. 593, 594) :—

That Meckel's cartilage, which persists throughout life in the Crocodile, becomes very slender posteriorly, and passes through the hole in the *os articulare*; that this slender cartilage then ascends upon the posterior and upper face of the quadrate bone enclosed in a membranous sheath; that, having reached the posterior edge of the membrana tympani, "it becomes connected with a cartilaginous plate, the narrow middle part of which is bent inwards towards the *columella auris*, with the external end of which it is connected by a joint. The broadest part of this cartilaginous plate is shaped like an axe-head, is directed perpendicularly against the *membrana tympani*, and forms, at the anterior end of its convex outer edge, a little plate which lies in the middle of the *membrana tympani*. It causes this region of the membrane to project slightly outwards, in the adult as well as in the young, and gives attachment to a filiform tendon which proceeds from the posterior boundary of the tympanic cavity. The other part of the cartilaginous plate bends away at an obtuse angle from the former, and has also the form of an axe-head, the convex edge of which, however, is narrower, and is applied below the posterior and inner part of the tympanic membrane to the cartilaginous margin of the tympanum." Prof. Peters considers that the last mentioned triangular cartilage is the homologue of the *malleus*.

In another embryo 20½ centimetres long, Prof. Peters finds (*l. c.* p. 594) a "little, short, cylindrical, intermediate cartilage," which connects the columella [*stapes*] and this so-called malleus, and which he compares to the *incus*, or the *os lenticulare*.

In a subsequent communication (7th January, 1869, Monatsberichte, pp. 6–8) "On the cavities of the Lower Jaw in the Crocodile," Prof. Peters repeats the assertion that his so-called "*malleus*" is connected by a cartilaginous cord with the posterior end of Meckel's cartilage, and states that he is unable to find the duct by which (as Stannius states) the pneumatic cavity of the *os articulare* is placed in communication with that of the quadrate bone.

Nevertheless the description given by Stannius is perfectly correct, and I am puzzled to comprehend how the pneumatic duct, which places the air-cavities of the quadrate and articular bones in communication, can be confounded with a cartilaginous rod surrounded by a membranous sheath. The fact is that there is no direct connexion between the posterior part of Meckel's cartilage and the so-called "*malleus*;" and thus, I cannot but think, the whole foundation of Prof. Peters's argument collapses.

Before particularly describing the very curious and instructive character of the outer extremity of the stapes (or so-called *columella auris*) and of the parts connected with it in the Crocodile according to my own observations, it is proper to remark that both Cuvier and Windischmann observed, though they did not quite rightly interpret, its structure.

Cuvier (Ossemens Fossiles, ix. p. 177) states of the stapes of the Crocodile, that "it consists of a long narrow elliptical plate, attached to the *fenestra ovalis*, from which passes a long and slender stem, which goes, becoming a little softer, to attach itself to the tympanic membrane; it then bends back and follows it, being fixedly attached thereto and taking a cartilaginous consistency, as far as its posterior margin. From the posterior wall of the tympanum a muscular filament proceeds and becomes attached to the stem of the bone at about a third of its length [from the tympanic membrane]; and a fold of the internal lining of the tympanum forms a triangular ligament which extends to the same point, and thus contributes to fix the stem to its recurved and tympanic portion."

Windischmann observes, "Ossiculum auditorium Scarpa delineavit, fere quatuor lineas longum, operculo triangulari instructum. In altera extremitate in cartilaginem tripartitam desinit, cujus una pars, ut dixi, in membrana media tympani adhæret, aliæ duæ in falce membranam hancce excipiunt." (Windischmann, De penitiori auris in Amphibiis structura. 1831.)

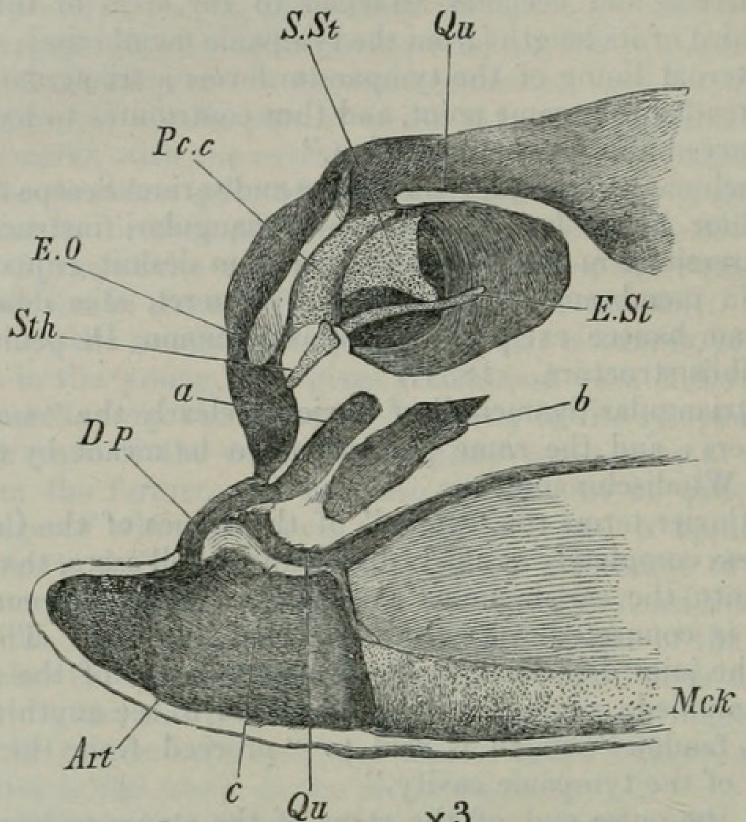
The "triangular ligament" of Cuvier is clearly the "*malleus*" of Prof. Peters; and the same part seems to be meant by the "aliæ duæ" of Windischmann.

What Cuvier terms the "stem" of the stapes of the Crocodile is more or less completely ossified; but I find, in all cases, that it passes directly into the cartilaginous axehead-like plate, the convex edge of which is connected with the *membrana tympani*. There is no trace of the joint described by Prof. Peters in any of the specimens I have examined; neither have I been able to see anything of the "filiform tendon" which is said to "proceed from the posterior boundary of the tympanic cavity."

Where the outer end of the stem of the stapes widens out into this process for the tympanic membrane, which I shall call the "*extrastapedial*" cartilage (fig. 1, *E.St*), it gives off, upwards and backwards, a slender cartilaginous prolongation, which expands and becomes the second "axehead-like" process, called "*malleus*" by Prof. Peters (*S.St*); but I have not been able to detect any trace of what Prof. Peters calls "a little short cylindrical intermediate cartilage" between this and the stem of the stapes. In all the specimens I have examined there is complete cartilaginous continuity between the two.

What Prof. Peters terms the "cartilaginous margin of the tympanum" is a backward prolongation of the cartilage of the periotic region of the skull, which corresponds in part, if not wholly, with the *tegmen tympani* of a mammal. It may be called the "parotic process" (fig. 1, *Pc.c*); and in the adult it is converted, in great measure, into a slender and curiously curved process of the pro-otic, and, in part, into a process of the so-called exoccipital bone. Muscular fibres, which represent the *stapedius* muscle (fig. 2, *Stp*), proceed from this cartilaginous margin, or the corresponding bones, to the margin and outer face of the cartilage called "*malleus*" by Prof. Peters, but which I shall term the "*suprastapedial*" cartilage (*S.St*). The inner surface of the posterior edge of the supra-stapedial cartilage is thus closely connected with the posterior part of the parotic process of the skull, while its anterior end comes into contact with the quadrate bone, which is connected with the front part of the same process.

Fig. 1.



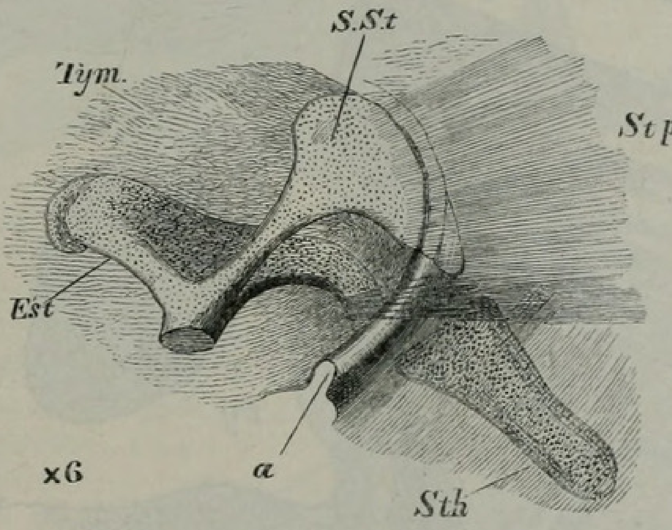
Side view of the right side of the hinder part of the skull of a young *Crocodilus biporcatus*. The squamosal, the postfrontal, and the tympanic membrane are removed, and the quadrate (*Qu*) is, in part, indicated only by an outline.

E.O. Exoccipital. *Pc.c.* Cartilaginous termination of the parotic process of the skull. *E.St.* Extrastapedial process of the stapes. *S.St.* Its suprastapedial process. *Sth.* The stylo-hyal cartilage supposed to be seen through the quadrate bone. *a, b.* Air-chambers of the quadrate. *D.p.* Pneumatic duct, leading from the posterior of these (*a*) to *c*, the air-chamber of the articulare (*Art*). *Mck.* Meckel's cartilage.

In the natural position of the parts, and when the head is horizontal (fig. 1), the plane of the extrastapedial cartilage is also nearly horizontal. The long axis of the suprastapedial cartilage is inclined at an angle of 45° to that of the extrastapedial cartilage; and the posterior ends of the two cartilages approach one another very closely. In close proximity to both lies the upper and broader end of a small and short rod of cartilage (*Sth*) which tapers below to a free rounded extremity. It lies upon the upper and posterior face of the quadrate bone; and its lower extremity terminates some distance above the upper end of the pneumatic duct (*D.p*), the fibrous wall of which is continuous with the sheath of connective tissue which envelopes the cartilaginous rod in question. It is this relation of the parts which, I am disposed to imagine, has deceived Prof. Peters, who seems to have taken the pneumatic duct and this cartilage for one continuous cartilaginous rod. In front, this minute cartilaginous style is in relation, as I have said, with the quadrate bone; behind, the *portio-dura* nerve passes down close to and parallel with it, and the digastric muscle covers it; above, it abuts against the lower and posterior walls of the tympanic cavity. Can there be any doubt, therefore, that it answers to the styloid cartilage, or proximal end of the hyoidean arch, in a mammal?

A fold of the lining membrane of the tympanum (*a*, fig. 2) somewhat obscures the junction of the extrastapedial and suprastapedial cartilages with the styloid cartilage; but by detaching the parts and saturating them with glycerine and caustic soda, it is plainly demonstrable that the styloid cartilage is only connected by fibrous tissue, and, indirectly, by the *stapedius*, with the *stapes*.

Fig. 2.



Inner view of the tympanic membrane (*Tym*) of a young *Crocodilus biporcatus*, with the attached stapedial cartilages (*S.St*, *E.St*), the fold (*a*), the styloid cartilage (*Sth*), and the stapedius muscle (*Stp*). The stem of the stapes is cut through just where it begins to ossify.

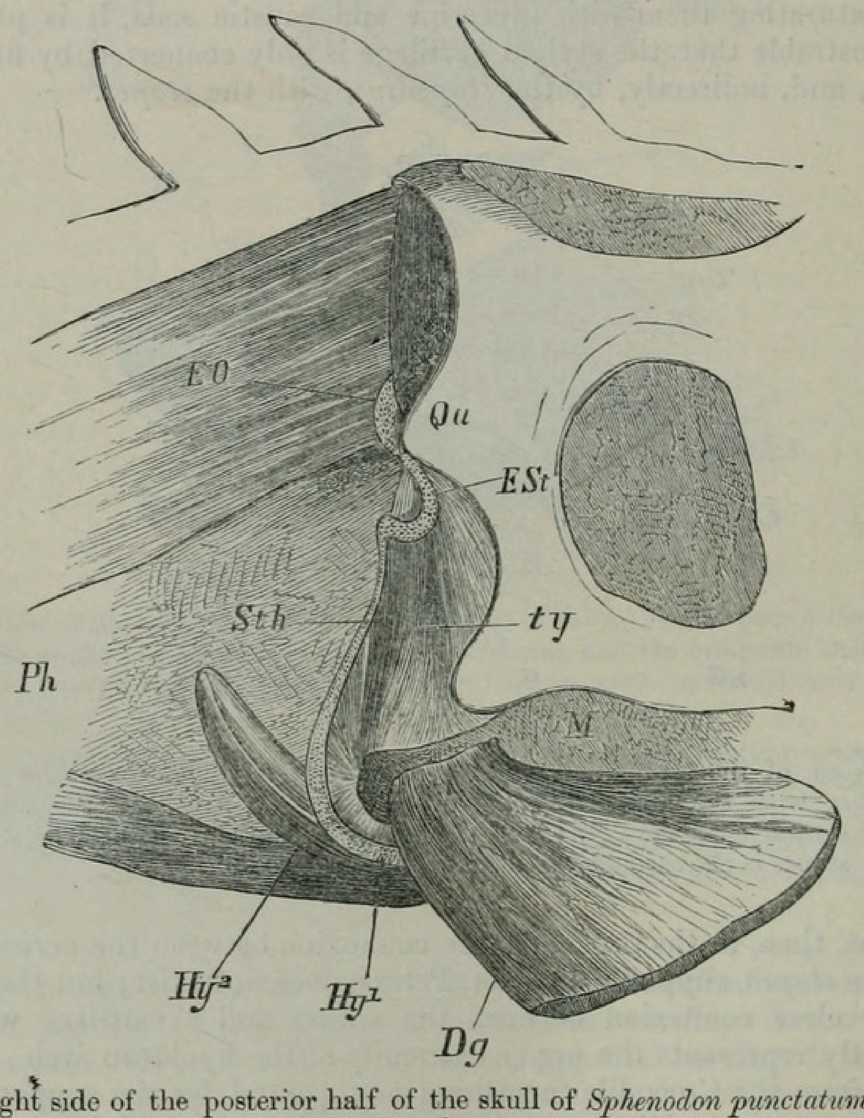
Thus, then, in the Crocodile, the connexion between the *articulare* and the *stapes*, supposed by Prof. Peters, does not exist; but there is a very close connexion between the *stapes* and a cartilage which distinctly represents the upper extremity of the hyoidean arch; and, so far from the Crocodile furnishing any ground for the supposition that the *stapes* and its appendages are modifications of the skeleton of the first visceral arch, as is suggested by Prof. Peters, the facts observed strongly suggest that these parts are modifications of the skeleton of the second visceral arch.

This suggestion is converted into a certainty when that remarkable Lizard *Sphenodon punctatum* (=*Hatteria*) is examined. Dr.

Günther's statement (Phil. Trans. 1867, p. 620), that, in this Lizard, the stapes is "attached by a fibro-cartilaginous ligament" to the anterior cornu of the hyoid, strongly attracted my attention when I read his valuable memoir on this reptile; and having had an opportunity, thanks to him, of examining into the question for myself, I can fully confirm his assertion.

Nothing can be more instructive than the arrangements represented in Fig. 3. *Sphenodon* has no externally visible tympanic membrane; but on removing the integument which lies over the aural region and the anterior portion of the digastric muscle, the fibres of a strong aponeurotic expansion, which takes its place, are seen to pass from the posterior edge of the quadrate bone and from the angle of the

Fig. 3.



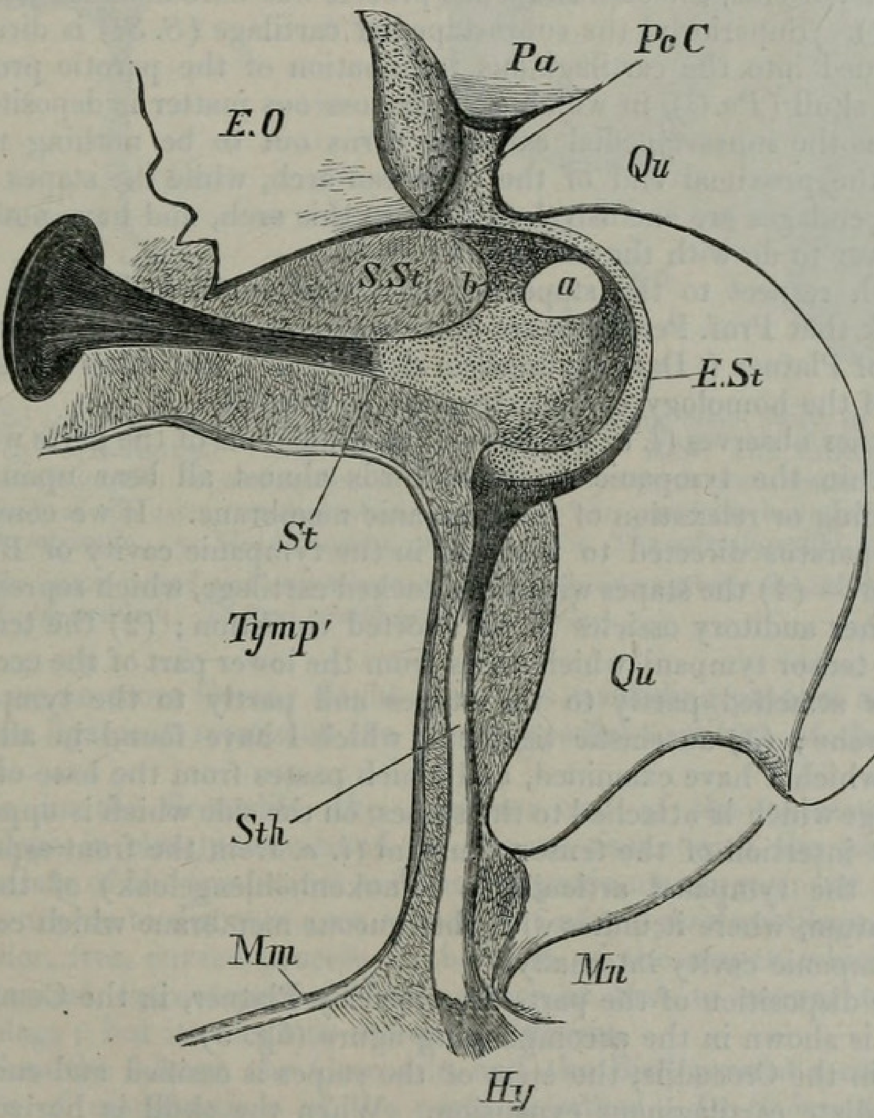
The right side of the posterior half of the skull of *Sphenodon punctatum*, twice the size of nature.

The integument is taken away and the digastric muscle (*Dg*) detached from its origin. *E O.* Exoccipital. *Qu.* Quadrate. *M.* Mandible. *Hy*¹, *Hy*². Anterior and posterior cornua of the hyoid. *Sth.* "Stylo-hyal" part of the anterior cornu. *E St.* Extrastapedial cartilage. *Ph.* The membranous wall of the pharynx, attached, in front, to the hyoidean cornua, and then continued into the aponeurotic outer wall of the tympanic cavity, *ty*.

mandible, to the anterior margin of the anterior cornu of the hyoid (Hy^1), the upper part of which is entirely cartilaginous. The hyoidean cartilage ascends behind the quadrate bone, with a slight backward convexity, until it has nearly reached the skull, and then appears to be suddenly bent into the form of a little scroll with a backward concavity (fig. 3, *E St*). The upper end of the scroll becomes connected with the skull; the concavity is filled up by aponeurotic fibres.

The aponeurotic expansion which has been mentioned covers the

Fig. 4.



The tympanic cavity and the adjacent parts laid open from behind, and the aponeurotic expansion removed, in *Sphenodon punctatum*. Five times the size of nature.

The letters as in fig. 3, except:—*Pa.* Parietal. *Pc.C.* Parotic cartilage. *S.St.* suprastapedial cartilage. *b.* Origin of this cartilage from the stapes. *a.* Foramen included between it and the extrastapedial. *Mm.* The cut edge of the mucous membrane. *Tymp.* The pharyngeal recess which takes the place of the tympanic cavity. The exoccipital is supposed to be broken away to show the fenestral end of the stapes.

outer end of the tympanic cavity; when it is removed, the proximal end of the cornu of the hyoid is seen to expand, and becomes converted into a broad plate of cartilage, the curved margin of which gives rise to the "scroll." Internally the plate is continued into the stem of the stapes, and speedily becomes ossified (fig. 4). There can be no doubt, therefore, that it corresponds with the extrastapedial cartilage of the Crocodile.

What answers to the axehead-shaped suprastapedial cartilage of the Crocodile is the upper process of the cartilaginous part of the stapes (*S. St*), which, however, passes into the extrastapedial cartilage externally and above, so as to enclose the foramen, *a* (fig. 4). On the left side, the suprastapedial process was fibrous at the point *b* (fig. 4). Superiorly, the suprastapedial cartilage (*S. St*) is directly continued into the cartilaginous termination of the parotic process of the skull (*Pc.C*), in which granular osseous matter is deposited.

Thus the suprastapedial cartilage turns out to be nothing more than the proximal end of the hyoidean arch, while the stapes and its appendages are exclusively related to this arch, and have nothing whatever to do with the mandibular arch.

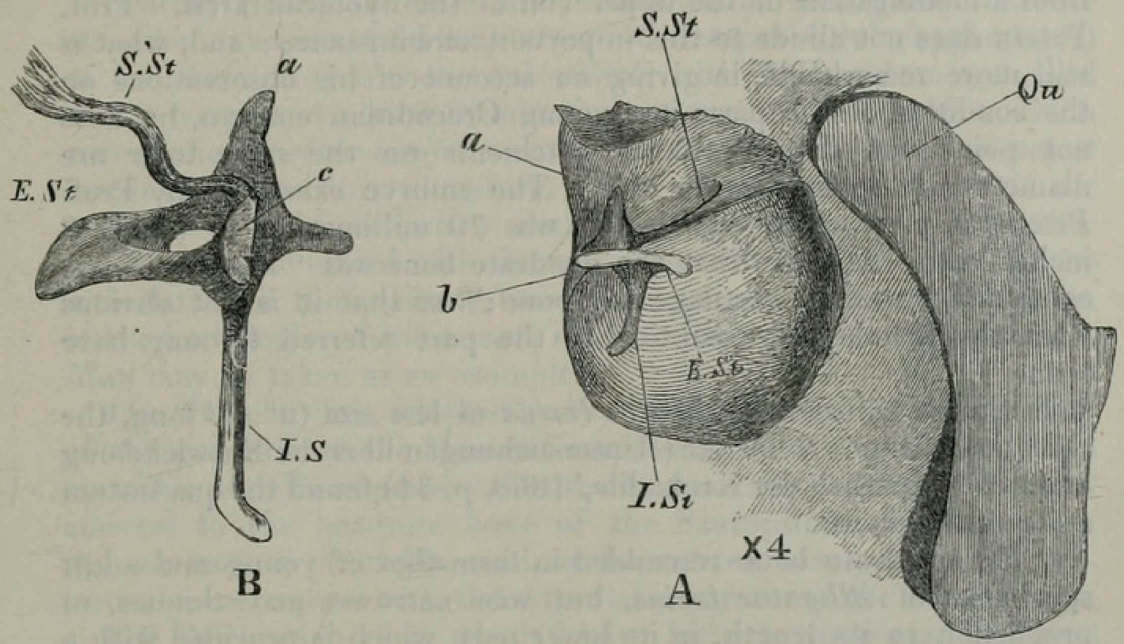
With respect to the stapes (or *columella auris*) in Birds, I may remark that Prof. Peters makes no reference to the careful investigations of Platner ('Das Quadratbein der Vögel'), who takes the same view of the homology of that structure as himself.

Platner observes (*l. c.* p. 16):—"The functions of the parts which lie within the tympanic cavity of birds almost all bear upon the tightening or relaxation of the tympanic membrane. If we consider the apparatus directed to this end in the tympanic cavity of Birds, we find:—(1) the stapes with the attached cartilage, which represents the other auditory ossicles in an aborted condition; (2) the tendon of the tensor tympani, which arises from the lower part of the cciput and is attached partly to the stapes and partly to the tympanic membrane; (3) an elastic ligament, which I have found in all the birds which I have examined, and which passes from the base of the cartilage which is attached to the stapes, on the side which is opposite to the insertion of the tensor tympani (*i. e.* from the front aspect), up to the tympanal articulation (Paukenhöhlengelenk) of the os quadratum, where it unites with the mucous membrane which covers the tympanic cavity internally."

The disposition of the parts described by Platner, in the Common Fowl, is shown in the accompanying figure (fig. 5).

As in the Crocodile, the stem of the stapes is ossified and ends in a triradiate cartilaginous expansion. When the skull is horizontal one ray of the expansion is represented by a horizontal triangular plate, the outer edge of which is fixed to the tympanic membrane. It represents the extrastapedial cartilage of the Crocodile, but differs therefrom in being perforated by a large hole. Where the stem of the stapes passes into this plate, it gives off a short vertical process upwards and a long slender curved process downwards. Both these lie free in the tympanic cavity. From the root of the upper process an elastic ligament arises and passes forwards to the outer wall of the periotic capsule, just behind the articulation of the quadrate bone.

Fig. 5.



A. The auditory region, the tympanic membrane being taken away, in a Fowl. *Qu.* Quadratum. *S.St.* Platner's ligament. *E.St.* The extrastapedial cartilage, the edge of which is fixed to the tympanic membrane. *b.* The end of the extrastapedial which is fixed to the posterior boundary of the tympanum. *c.* The ascending process. *I.St.* The infrastapedial process.

B. The outer end of the stapes separated from the stem where the latter begins to be ossified. Turned round and magnified.

I see no room for any doubt that this ascending process and the elastic ligament represent the suprastapedial cartilage of the Crocodile.

As in the Crocodile, the posterior end of the extrastapedial cartilage is closely connected by fibrous tissue with the posterior boundary of the tympanum and the tympanic membrane; but I have been unable to discover even a rudiment of a styloid cartilage. The inferior, free, curved process of the stem of the stapes, which may be termed *infrastapedial* (*I.St*) seems at first to answer to that cartilage; but its relations are quite different.

Thus the Lizard, the Crocodile, and the Bird present a complete series of modifications of the parts described. In *Sphenodon* the hyoidean arch is histologically continuous throughout its entire length; and in its upper part is a rod of cartilage which, at one point, passes into the *stapes*.

In the Crocodile, the upper part of the hyoidean cornu has no direct connexion with the lower, and the rudimentary styloid part is not histologically continuous with the stapedial part.

In the Bird the styloid part has vanished, and the suprastapedial is represented only by fibrous tissue.

Such developmental evidence as exists is entirely in accordance with the view of which these anatomical facts appear to me to afford a sufficient demonstration.

Rathke distinctly states that in *Coluber natrix* the *stapes* results from a modification of the upper end of the hyoidean arch. Prof. Peters does not allude to this important circumstance; and, what is still more remarkable, in giving an account of his observations on the condition of the parts in a young Crocodilian embryo, he does not point out that Rathke's statements on the same topic are diametrically opposed to his own. The embryo examined by Prof. Peters (*l. c.* p. 595, figs. 1, 1*a*) was 70 millimetres, or nearly 3 inches long. He says that the quadrate bone was "angelegt," but contained "neither cartilage nor bone;" so that it is not obvious what the histological condition of the part referred to may have been.

But in an embryo of *Aligator lucius* of less size (2″ 2‴ long, the skull measuring 7‴) Rathke ('Untersuchungen über die Entwickelung und den Körperbau der Krokodile,' 1863, p. 34) found the quadratum quite cartilaginous.

"The quadrate bone resembled in form that of young and adult specimens of *Alligator lucius*, but was narrower and thinner, in proportion to its length, in its lower part, which is provided with a shallow articular excavation. It consisted of cartilage ensheathed in its middle third by a bone. By its broader and flatter upper half it was loosely attached to the outer surface of the cartilaginous auditory capsule, in front of and above the fenestra ovalis . . . . .

"With the quadrate bones articulated two long and, on the whole, slender Meckelian cartilages, which extended to the mandibular symphysis. For the greater part of their length they were cylindrical, and diminished in diameter very gradually from behind forwards; posteriorly, however, where they were connected with the quadrate bones, they were a good deal enlarged. An absolutely and relatively short, hook-like prolongation extended beyond the articulation. The thinner and longer cylindrical portion of each was loosely invested by five very thin, but completely ossified, plates, which enclosed it, as in a sheath, though they were separated by larger or smaller intervals. At a later period these plates grow and become closely united, thus giving rise, as in other Reptiles and in Birds, to the greater part of each ramus of the mandible. But of Meckel's cartilage only the enlarged part ossifies, and thus gives rise to the articular piece of the lower jaw."

How is this discrepancy to be accounted for? Unfortunately I have been able to procure no specimen of an embryonic Crocodile so small as either of those here described; but Prof. Peters's figures (Taf. i. figs. 1, 1*a*) leave very little doubt on my mind that the cartilage which he marks *m*, and imagines to be his "malleus" (the suprastapedial cartilage) is really the quadratum, the articulation of which with Meckel's cartilage takes place in the ordinary way, and that *i*, called the *columella* (or *stapes*), is neither more nor less than the pterygo-palatine cartilage. The most cursory glance is sufficient to prove that the inner extremity of *i* must needs lie beneath and internal to the eye, and cannot by any possibility come near the *fenestra ovalis*. It therefore seems to be impossible that *i* can be the *stapes*.

Bearing clearly in mind the demonstration now given that the *stapedial apparatus* (if I may so term the *stapes* with its appendages) of the *Sauropsida* is connected entirely with the hyoidean arch, and that it consists of a stem terminating, at one end, in the plate which covers the *fenestra ovalis*, and, at the other, in sundry processes of cartilaginous or fibrous texture, one of which is connected with the tympanic membrane (when that structure exists), while another passes up to be united with the otic region of the skull, close to the articulation of the quadrate bone, we may pass to the consideration of the homologies of these parts in the ordinary *Mammalia*, of which Man may be taken as an example.

The Okenian view, adopted by Prof. Peters, assumes that the *ramus* of the mandible of the Mammal answers to the whole *ramus* of the mandible of a Sauropsidan, that the tympanic bone of the Mammal answers to the quadrate bone of the Sauropsidan, and that the *ossicula auditûs* of the Mammal, or the *malleus*, *incus*, and *stapes*, collectively, correspond with the stapedial apparatus of the Sauropsidan.

The Reichertian view, which I have hitherto supported, assumes that the *ramus* of the mandible of the Mammal answers only to part of the *ramus* of the Sauropsidan, inasmuch as the articular piece of the Sauropsidan mandible answers to the *malleus* of the Mammal—that the quadrate bone of the Sauropsidan is the homologue of the *incus* of the Mammal—and, consequently, that the stapedial apparatus of the Sauropsidan is entirely represented by the *stapes* of the mammal. In the place of the tympanic bone of the mammal there are only the ossifications which are found in the membranous frame of the tympanic membrane in some *Sauropsida* (*e.g.* many birds) and *Amphibia*.

The arguments by which this view has been supported are briefly these:—

In the Sauropsidan embryo a rod of cartilage occupies the first visceral arch on each side, and meets its fellow in the middle line. The rod becomes jointed, and the part on the distal side of the joint is converted into Meckel's cartilage, while that on the proximal side of the joint is modelled into the rudiment of the quadrate bone, which is invariably, in its earliest state, cartilaginous. Soon, however, the quadrate cartilage ossifies, and a centre of ossification appears in that part of Meckel's cartilage which articulates with the quadratum. This gives rise to the articular element of the mandible. All the other constituents of the lower jaw are developed in the fibrous tissue which surrounds the rest of Meckel's cartilage, which structure either persists throughout life, or disappears.

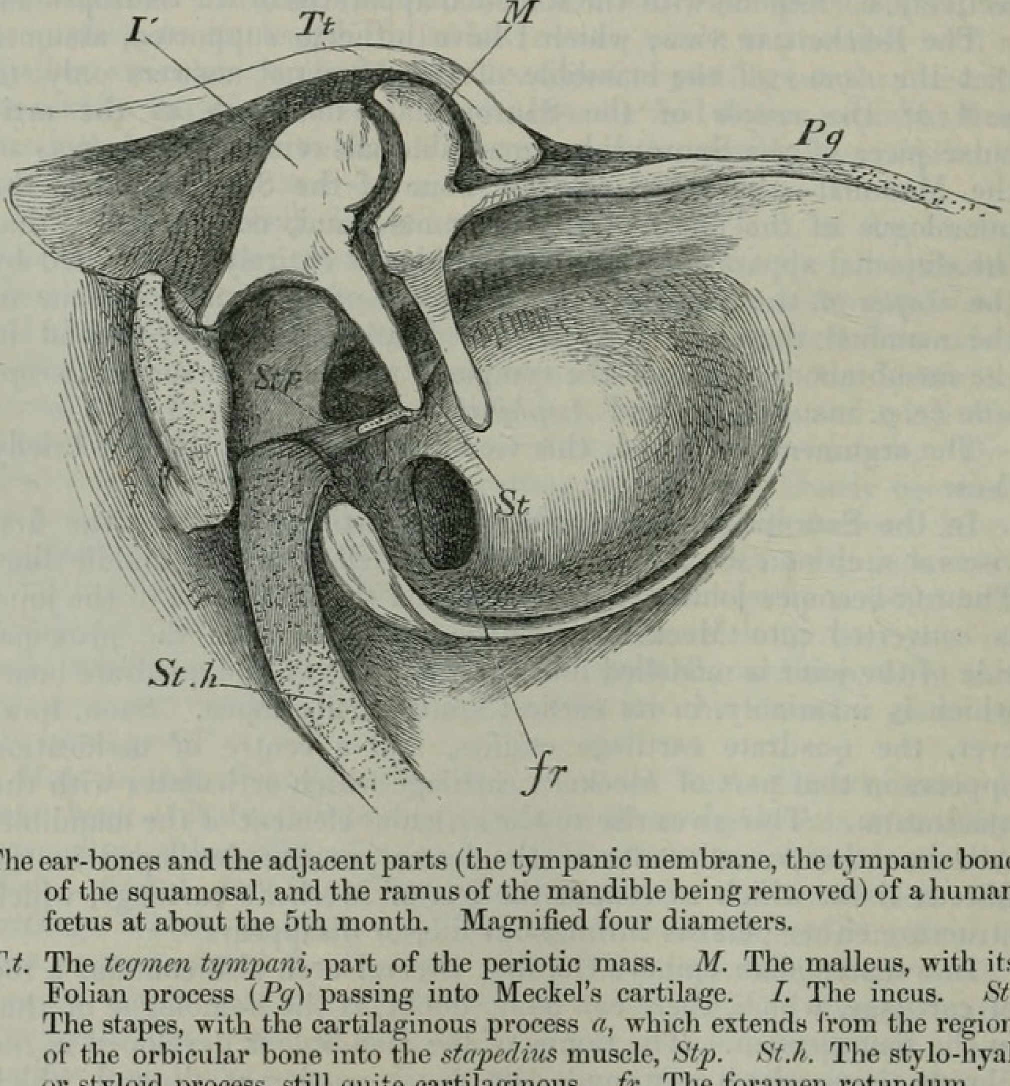
In a mammalian embryo the first visceral arch also contains a rod of cartilage, which, there can be no doubt, is the homologue of that in the Sauropsidan. The ramus of the mandible is developed in the fibrous tissue which surrounds the distal portion of the rod, which remains for a time, as Meckel's cartilage, but soon disappears. The ramus of the mandible of a Mammal, therefore, cannot contain any representative of the *os articulare* of the Sauropsidan, which takes its origin in the proximal end of Meckel's cartilage.

The tympanic bone of the Mammal is developed, quite independently of the cartilaginous axis of the first visceral arch, in the fibrous rim of the tympanic membrane. Therefore it cannot represent the Sauropsidan quadrate, which is preformed in cartilage, and is, in fact, the proximal end of the cartilaginous axis of the first visceral arch.

These arguments, to my mind, retain their full force, and have not been affected by the observations of Prof. Peters.

In the next place, it is not disputed that the *malleus* of the Mammal arises by the direct ossification of a part of the cartilage of the first visceral arch. But I have shown, in the present paper, that the suprastapedial of the Sauropsidan is the proximal end of the hyoidean, or second, arch. It is therefore impossible that the suprastapedial should be, as Prof. Peters supposes, the homologue of the *malleus*.

Fig. 6.



The ear-bones and the adjacent parts (the tympanic membrane, the tympanic bone of the squamosal, and the ramus of the mandible being removed) of a human fœtus at about the 5th month. Magnified four diameters.

T.t. The *tegmen tympani*, part of the periotic mass. *M.* The malleus, with its Folian process (*Pg*) passing into Meckel's cartilage. *I.* The incus. *St.* The stapes, with the cartilaginous process *a*, which extends from the region of the orbicular bone into the *stapedius* muscle, *Stp.* *St.h.* The stylo-hyal or styloid process, still quite cartilaginous. *fr.* The foramen rotundum.

Thus I find myself compelled to dissent from every one of Prof. Peters's conclusions; but, in working over the ground again, I have also been led to depart from the Reichertian view (which I have hitherto adopted) in one point, and that a very important one.

In a young mammalian fœtus, Meckel's cartilage passes, above, directly into the *malleus*; and at no time is any articulation developed between the *malleus* and the rest of the cartilage. Further, the *incus* articulates by a broad surface with the *malleus*, and its dimensions are such that its long axis appears to continue that of the malleus and Meckel's cartilage. In fact it appears exactly as if the *incus* were the proximal end of the cartilage of the first visceral arch. If so, the articular surface between the *incus* and the *malleus* must needs answer to that between the *quadratum* and the *articulare* of the Sauropsidan; and as the *incus* and the *malleus* ossify, nothing can seem closer than the resemblance which they bear to the *quadratum* and the *articulare* respectively. Hence Reichert conceived that the *quadratum* was the homologue of the *incus*, and the *malleus* that of the *articulare*, and I have followed him. But the study of *Sphenodon* and of the Crocodile has led me to believe that we have fallen into an error.

It is admitted, on all hands, and indeed cannot be disputed, that the stem and fenestral plate of the stapedial apparatus of the Sauropsidan answer to the crura and fenestral plate of the *stapes* of an ordinary mammal. But the *incus* of a mammal is related to the *stapes* on the one hand, and to the walls of the tympanic cavity on the other, nearly as the suprastapedial of a Crocodile is to the same parts; if the *incus* remained cartilaginous the resembance would be complete. On the other hand, in the human fœtus, the *stapes* has a cartilaginous prolongation which is embraced by the *stapedius* muscle, and contributes to reduce the interval between the *stapes* and the upper extremity of the cartilaginous styloid process (or upper end of the hyoidean arch) to a very small space.

Thus, in the Mammal, the proximal end of the hyoidean arch is in nearly the same condition as in the Crocodile, except that—

(1) There is a distinct articulation between the suprastapedial part and the stem of the *stapes*.

(2) The extrastapedial portion of the *stapes* is no longer distinguishable, and the *stapes* has lost its direct connexion with the tympanic membrane.

(3) The suprastapedial is ossified and converted into an *incus*. The *incus*, therefore, cannot be the homologue of the quadratum.

If this view be correct, it follows that as the *malleus* is the ossified proximal end of the cartilage of the first visceral arch, the *malleus* must represent the *quadratum*.

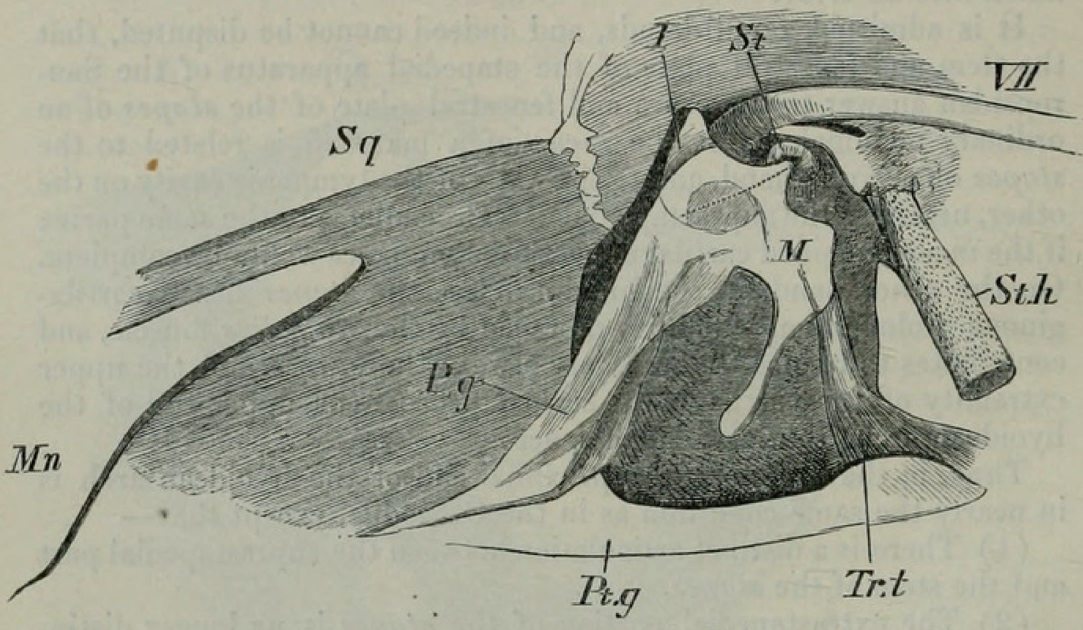
And thus the difference between the Sauropsidan and the Mammal will be, that in the latter the cartilage of the first visceral arch does not become jointed, and does not develope any representative of the *articulare*; while it gives off an extrastapedial process, which becomes connected with the middle of the tympanic membrane.

Thus, in principle the Reichertian doctrine still holds good; but in one matter of special homology it must be altered, and for *quaratum*=*incus* we must read *quadratum*=*malleus*.

The modification of Reichert's view which I now propose completely removes a difficulty which has often presented itself to my own mind, and which is urged with much force by Prof. Peters, in his first two papers. If the *incus* be the homologue of the *quadratum*, why does it become so small and insignificant in the Marsupials and Monotremes, which, in so many respects, approach the *Sauropsida*? This question I have always felt could only be met by another. Why, if the *ossicula auditûs* of the mammal do not represent bones of much more importance in the *Sauropsida*, does the *malleus* attain such a vast size in the *Monotremata*?

If the *malleus* is, as I have endeavoured to prove it to be, the homologue of the quadratum, the last question receives an obvious answer; and no less readily is it intelligible why the *incus* should be reduced, seeing that the suprastapedial is always insignificant in size, and may even become a mere fibrous band, in the *Sauropsida*.

Fig. 7.



The left tympanic cavity and the adjacent parts in *Echidna setosa*. Some portions of the squamosal and of the periotic bones, with the tympanic membrane, have been removed.

Mn. Mandible. *Sq*. Squamosal. *Pt.g*. The pterygoid. *St.h*. The stylo-hyal. *VII*. The portio dura. *St*. The stapes. *I*. The incus, the greater part of the contour of which is supposed to be seen through the malleus (*M*). *P.g*. Folian process of the malleus. *Tr.t*. The tensor tympani.

I may mention, incidentally, that *Echidna* presents other anomalies than those which have been described by Prof. Peters and others. The muscle which plays the part of the *tensor tympani* is very large and arises from the base of the skull, where it forms the roof of that posterior and inner region of the tympanic cavity which is bounded below by the pterygoid. The strong tendon of this muscle passes outwards, and is inserted into the upper aspect of that knee-like process of the *malleus* which is fixed to the tympanic membrane.

The cartilaginous " styloid " end of the hyoidean arch is fixed into the wall of the outer and posterior end of the tympanic cavity, very near the *incus* and *stapes*; but I can find neither a *stapedius* muscle, nor any ligament representing it.

It will be observed that the proximal end of the skeleton of the first visceral arch (whether it be osseous, cartilaginous, or fibrous), like that of the second, remains attached to one and the same part of the skull, viz. the outer and upper wall of the periotic mass, external to the vestibular sac, throughout the *Mammalia* and the *Sauropsida*. In Mammals the proximal skeletal elements of the arches (*malleus* and *incus*) are very generally equal, or the *incus* may be the smaller.

In the *Sauropsida*, the suprastapedial (=*incus*) is always smaller than the *quadratum* (=*malleus*).

In Teleostean and Ganoid fishes, and in the Sharks, the general relations of the two arches remain unchanged, but their proportions are reversed.

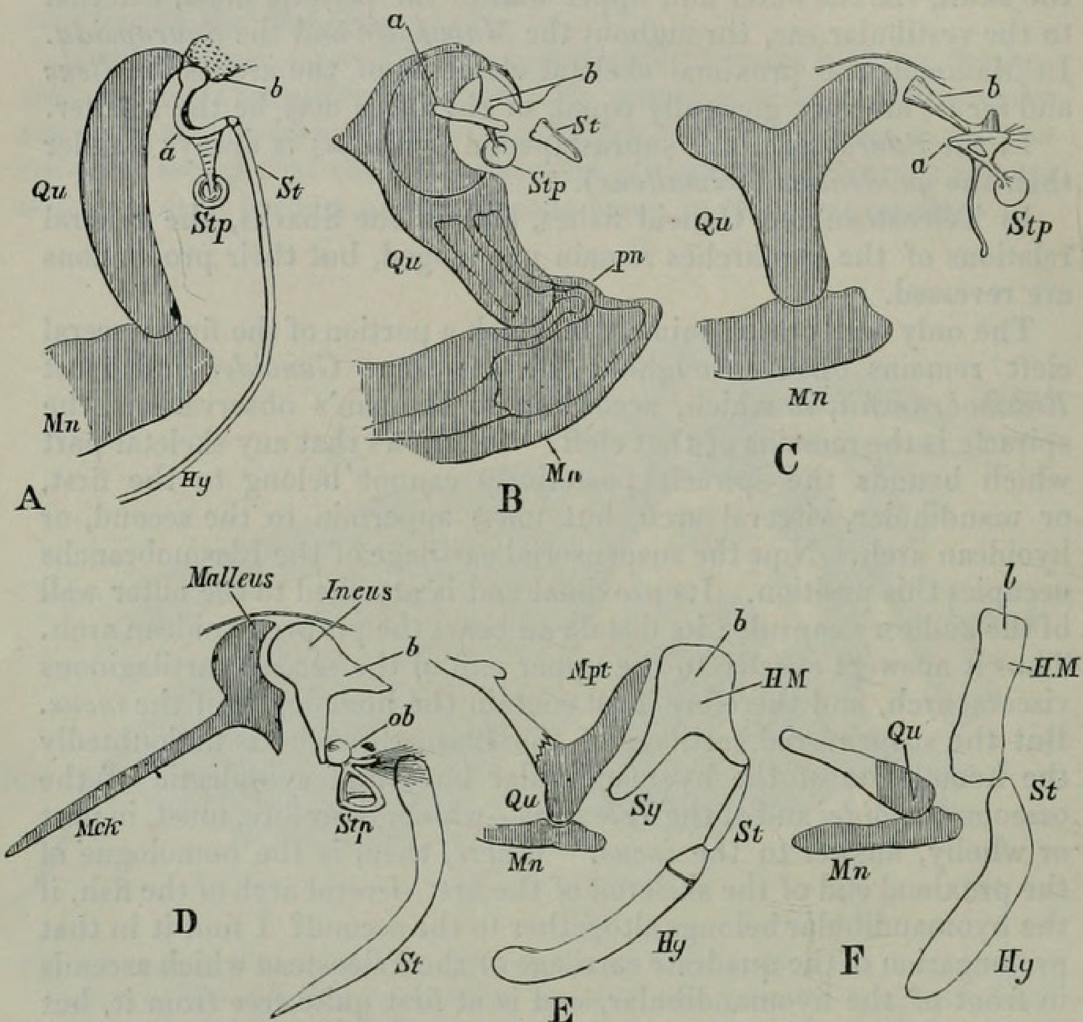
The only vertebrated animals in which a portion of the first visceral cleft remains open throughout life are some *Ganoidei* and most *Elasmobranchii*, in which, according to Wyman's observations, the spiracle is the remains of that cleft. It follows that any skeletal part which bounds the spiracle posteriorly cannot belong to the first, or mandibular, visceral arch, but must appertain to the second, or hyoidean arch. Now the suspensorial cartilage of the Elasmobranchs occupies this position. Its proximal end is attached to the outer wall of the auditory capsule; its distal end bears the proper hyoidean arch. Thus it answers exactly to the upper end of the second cartilaginous visceral arch, and therefore must contain the homologue of the *incus*. But the suspensorial cartilage of the Elasmobranchs is undoubtedly the homologue of the hyomandibular bone and symplectic of the osseous *Ganoidei* and of the *Teleostei*—which, therefore, must, in part or wholly, answer to the *incus*. Where, then, is the homologue of the proximal end of the skeleton of the first visceral arch of the fish, if the hyomandibular belongs altogether to the second? I find it in that prolongation of the quadrate cartilage of the Teleostean which ascends in front of the hyomandibular, and is at first quite free from it, but afterwards becomes surrounded and replaced by the metapterygoid, which eventually helps to bind it to the hyomandibular.

Thus the puzzling division between the mandibular and the hyoidean parts of the suspensorial apparatus in a fish becomes intelligible as the result of their primarily separate development.

In the osseous fishes the proximal end of the mandibular arch is arrested in its development and loses its direct connexion with the skull; but in the Sharks the ascending portion of the quadrate atrophies altogether, or is represented merely by pre-spiracular cartilages; and the quadrate itself forms only the posterior termination of the palato-quadrate arch, or so-called upper jaw.

In the *Chimæræ, Dipnoi,* and all *Amphibia,* the proximal ends of the cartilaginous first and second visceral arches become united together, at an early period, into a common plate, in which the malleal and incudal elements are not separately distinguishable. In the *Chimæræ, Dipnoi,* and the lower *Amphibia* they remain in this condition throughout life; but in the higher *Amphibia* changes of a most remarkable kind take place, of which I do not now propose to speak, as my friend Mr. Parker is engaged in working out that part of the subject.

Fig. 8.



I have endeavoured to give visual expression to my interpretation of the modifications of the proximal ends of the mandibular and hyoidean arches in the series of diagrams A, B, C, D, E, F, displayed in fig. 8. In all these the mandibular arch is shaded with vertical lines, while the hyoidean arch is left unshaded or nearly so. The letters have the same signification throughout. In the mandibular arch:—*Qu.* Quadrate. *Mn.* Mandible or Meckel's cartilage. In the hyoidean arch:—*a.* Extrastapedial. *b.* Suprastapedial. *Stp.* Stapes. *St.* Stylo-hyal. *Hy.* The ventral moiety of the hyoidean cornu. A. *Sphenodon.* B. Crocodile. C. Bird. D. Mammal. E. Teleostean fish. F. Shark.

In D, *ob* stands for the *orbiculare*; in E, *Mpt* is the metapterygoid, and *Sy* the symplectic.

I subjoin a tabular view of the homologies of the parts under discussion in the *Mammalia*, *Sauropsida*, and Teleostean Fishes.

Mandibular arch :—

I. MAMMAL	*Malleus*	*Meckel's cartilage.*	
II. SAUROPSIDAN	*Quadratum*	*Articulare*	*Meckel's cartilage.*
III. TELEOSTEAN	*Metapterygoid* & *Quadratum*	*Articulare*	*Meckel's cartilage.*

Hyoidean arch :—

I. MAMMAL	*Incus*	*Stapes*	*Stapedius, Styloid, Hyoid cornu.*
II. SAUROPSIDAN	*Suprastapedial.*	*Columella auris*	*Hyoid cornu* (Sphenodon).
III. TELEOSTEAN	*Hyomandibular*		*Stylo-hyal, Hyoid.*

June 10, 1869.

George Busk, Esq., F.R.S., in the Chair.

The Secretary called the attention of the Meeting to the following noticeable additions to the Society's Menagerie during the month of May :—

1. Five Greenland Seals (*Phoca grœnlandica*), which had been brought from the north by one of the sealing-vessels into Peterhead, and purchased for the Menagerie on the 6th and 11th of May. This species of Seal had not been previously exhibited in the Society's Menagerie, and presented several interesting points of difference when compared with its allies. In particular it was noticeable for the use of its fore limbs in locomotion, instead of progressing by the action of the muscles of the belly as is the case with *Phoca vitulina* and *Phoca fœtida*.

On the 18th of May two additional specimens of the same species had been brought home in one of the Hudson's Bay Company's ships, and presented to the Society by Sir C. M. Lampson, Bart., F.Z.S.

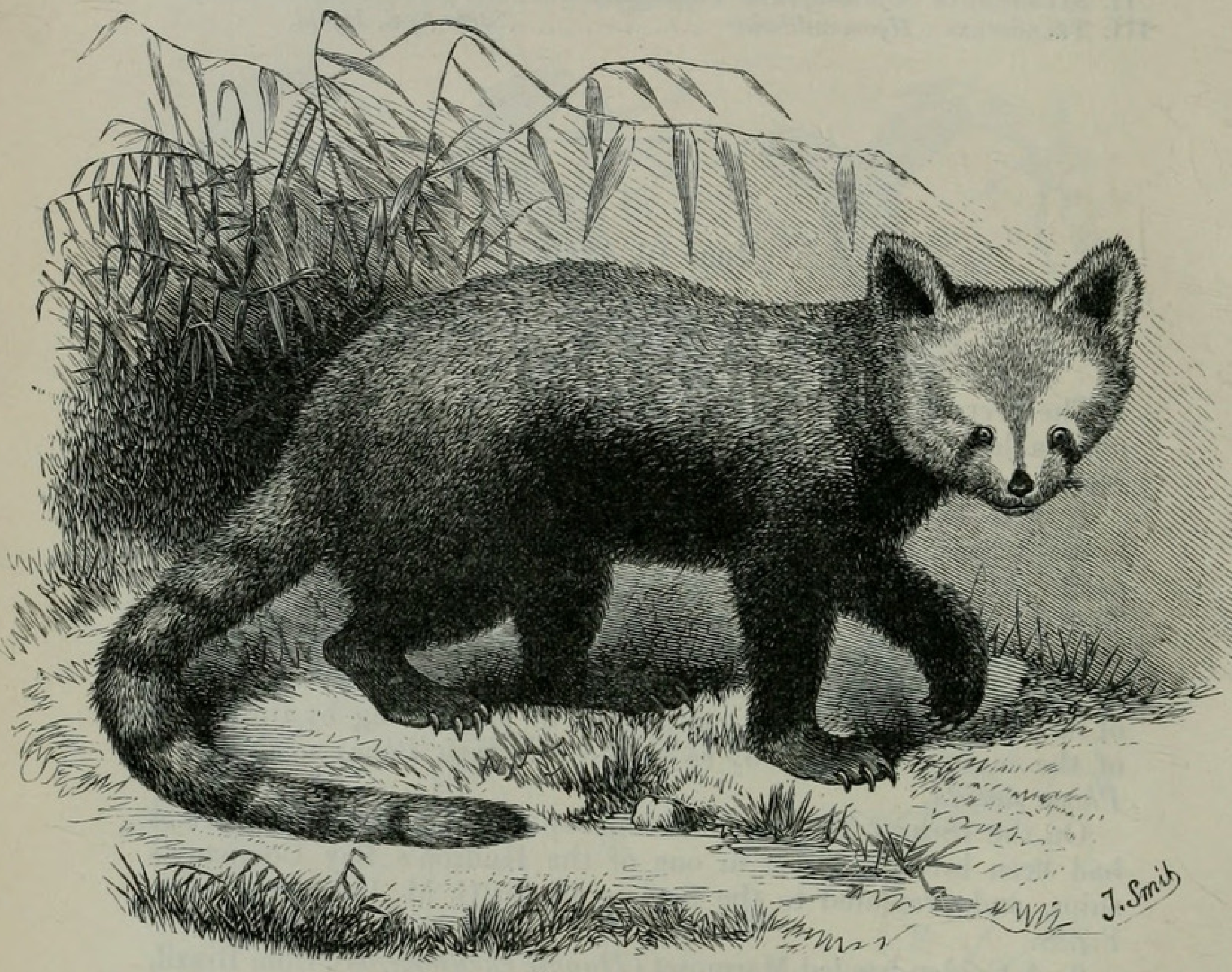
2. A Golden-headed Marmoset (*Hapale chrysomelas*), from Brazil, purchased May 14th, and believed to be the first example of this scarce species ever exhibited in the Society's collection.

3. Two additional specimens of the Aard-wolf of South Africa (*Proteles lalandii*), brought home by Captain Dixon on the 20th of May, and purchased for the Menagerie. These animals had been placed in the collection in company with the former specimen, purchased October 26th, 1868 (see P. Z. S. 1868, p. 530). All three of them appeared likely to thrive in captivity.

4. A fine example of the Vulturine Eagle (*Aquila vulturina*), brought home by Captain Dixon, on behalf of Mr. E. L. Layard, F.Z.S., by whom it had been presented to the Society's Menagerie.

The only example of this Eagle previously exhibited was believed to be the one acquired at the sale of Lord Derby's Knowsley collection in 1851.

5. An example of the Panda (*Ailurus fulgens*), presented by Dr. H. Simpson, May 22nd, being one of three specimens obtained in the neighbourhood of Darjeeling, as mentioned by the Secretary in a former communication to the Society (*anteà*, p. 278). Two of the animals of this species, with which Dr. Simpson had started from Calcutta, had unfortunately died upon the voyage; the third



Ailurus fulgens.

had reached the Gardens in a very exhausted state, but was gradually recovering under the care of the Superintendent. Its food appeared to be mainly of a vegetable nature.

6. A specimen of the West-Indian Brown Pelican (*Pelecanus fuscus*) in immature plumage, presented by Captain Dow, F.Z.S., of the Royal Pacific Steamship Company's ship 'Costa Rica,' and received May 30th. This bird had been captured by Captain Dow on Pedro Gonzalez Island, one of the group of Pearl Islands in the Bay of Panama, on the 4th of May.