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On the Modifications of the First and Second Visceral Arches, with Especial Reference to the Homologies of the Auditory Ossicles

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XVII. *On the Modifications of the First and Second Visceral Arches, with especial reference to the Homologies of the Auditory Ossicles.*

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[PLATES 71–74.]

AN ample material of rare Elasmobranch forms, especially *Heptanchus*, *Hexanchus*, *Centrophorus*, *Myliobates*, and *Trygon*, which I had collected during the last summer on the South Coast of Portugal, and several fresh specimens of *Hatteria*, have induced me to submit the question of the modifications of the two first visceral arches to a reconsideration.

The homologies of the auditory ossicles have not hitherto been settled beyond dispute, and only recently this question has again been taken up by ALBRECHT, DOLLO, BAUER, and GRADENIGO. The most important of these latest contributions has been made by ALBRECHT, who, chiefly for theoretical reasons, advocates that the whole of the auditory chain in all the Amphibia and Amniota is homologous with the hyomandibula of the Fishes.

However, since one of his premisses is highly disputable (quadrate = processus tympanicus of the os squamosum), and considering that one of his principal conclusions leads to a complete and absolutely unjustified reversion of the views which are generally accepted regarding the morphology of the visceral arches, his conclusions as to the homologies of the auditory ossicles have never met with any favour. I trust, therefore, that my attempt to reconsider the whole question on the broadest basis will not be superfluous.

Nearly all the preparations figured in this essay are in the Cambridge University Museum of Zoology and Comparative Anatomy.

Heptanchus cinereus.—The second visceral, or hyoidean, arch consists of a hyomandibular bar, a hyoid bar, and the copula. The whole arch is very slender, especially the level of the masticatory joint, and is almost completely hidden from a side view by the first visceral arch.

The connexion of the hyomandibula with the cranium is not effected by articulation, but by distinct and strong ligaments. One of these ligaments arises from the labyrinth region of the cranium, above and slightly in front of the exits of the facial and glossopharyngeal nerves; it is attached to the upper, or proximal, and anterior end of the hyomandibula. The second ligament is much longer, a strong, white, roundish band, which arises somewhat more forward from the lateriventral aspect of the vestibular process of the labyrinth region, and is attached to the anterior margin of the hyomandibula, somewhat above its middle. Between this ligament and the hyomandibula passes out to the posterior side of the arch the hyoidean division of the facial nerve.

The proximal end of the hyomandibula is connected also by one ligament with the upper corner of the ceratobranchial or second segment of the third visceral arch (first branchial arch), and by a similar ligament with the outside of the middle of the epibranchial of the same arch.

Whilst in *Heptanchus* there is hardly any articular facet on the proximal end of the hyomandibula, and only a very slight depression on the corresponding surface of the cranium, there is in *Hexanchus* a more distinct indication of a primitive articulation, although, owing to the intervention of the ligaments described, no absolute contact seems to take place.

The hyomandibula of *Heptanchus* passes down the median side of the very massive quadrato-palatine bar, is partly lodged in a slight excavation of this bar, and passes into the likewise very slender proximal end of the hyoid bar. The junction between these two elements is just as primitive as those between the various segments of the branchial arches. The second visceral arch is partly lodged in slight excavations of the quadrato-palatine and mandibular bars; the hyoid-hyomandibular junction rests against the hinder surface of a prominent knob, which forms the medial or inner quadrato-mandibular articulation. The only direct connexion between the first and second visceral arches is formed by a ligament which arises from the inner side of that mandibular knob, and is attached to the anterior brim of the end of the proximal third of the hyoid (fig. 1A, Plate 71).

The quadrato-mandibular junction exhibits some very important points. There are two articulations, separated by an empty space. Both articulations belong to the cup and ball type. On the outer or posterior articulation the ball is formed by a broad knob of the quadrato-palatine bar, fitting into a slight concavity of the posterior and outer end of the mandible. The inner, or anterior, articulation is formed by a roundish protuberance of the mandible which fits into a concavity of a corresponding process of the quadrate portion. This latter articulation is, so to speak, not yet completely finished, because in the angle between quadrate and mandible both these segments go over into each other by a thick portion of hyaline cartilage (fig. 1B*). Unless we assume that this continuation was once a ligament, which was later on converted into cartilage, we have to conclude that the quadrato-mandibular joint, this oldest of visceral joints, is not yet completed, and still partly represents, by the continuation of its two component segments, the primitive stage which we have to assign to the originally unbroken visceral arches.

Oxyrhina gomphodon (fig. 3).—This Selachian shows a great step in advance towards higher Elasmobranch conditions, and exhibits far less primitive conditions than the Notidanidæ. The quadrato-palatine bar no longer articulates by a broad and long concave facet with a post-orbital process of the cranium, so conspicuous a part in the cranium of *Notidanus*, but has lost this cranial connexion entirely. It is connected with, and is supported entirely by, the mandible. There are likewise an outer and an inner articulation, but, instead of the hyaline cartilaginous continuation of quadrate and mandible, there are now two partly fibro-cartilaginous ligaments, which cross each other—one, ligamentum quadrato-mandibulare internum superficiale; and the other, lig. quad.-mand. int. profundum. The great points of interest which mark the step in advance towards higher conditions are the formation of two distinct articulations of the mandible with the hyoid, and the formation of four new ligaments, by which an intimate morphological and physiological connexion between the first and second visceral arches is effected.

The two articulations between the mandible and the hyoid are these:—The mandibular knob on the inner quadrato-mandibular articulation, against which in *Heptanchus* leans the proximal end of the hyoid, is in *Oxyrhina* greatly enlarged into a medially and upwards directed thick process, against which leans firmly the anterior surface of the top end of the hyoid; there is developed even a distinct glenoid surface. On to this mandibular knob is attached, moreover, a weak ligament, which comes from the connective tissue which surrounds the hyomandibular-hyoid junction; most of the fibres of this ligament come, however, from the inner side of the lower end of the thick and blunt hyomandibula. This ligament is therefore a lig. hyomandibulo-mandibulare.

The second articulation between mandible and hyoid is effected by the posterior surface of the outer mandibular process of the quadrato-mandibular articulation; a slight depression on the mandible receives a knob of the hyoid, as is shown in fig. 3*b*. Above and below this primitive articulation are three strong and short ligaments, to be distinguished as lig. hyoideo-mandibulare laterale inferius, lig. hd.-mand. lat. superius, and lig. hyoideo-mandibulare mediale. The latter ligament is attached to the inner aspect of the mandible near the brim of its broad rounded-off portio angularis, and comes from the lower side of the articulatio hyoideo-mandibularis externa, just described. From this point of attachment to the hyoid, it is, however, continued around and over the inner surface of the hyoid, and splits up into two strong strands, one of which is attached to the posterior edge of the hyomandibula, a little below its middle, whilst the other strand passes on the medial side of the hyomandibula to the under surface of the cranium, far in front of the articulation of the hyomandibula with the cranium. Thus a connexion between the hyoid and the cranium, and, although indirectly, of the latter with the mandible, is effected. The sole ligament which connected the hyoid with the mandible in *Heptanchus* is absent in *Oxyrhina*.

The hyomandibula is attached to the cranium and to the first branchial arch by the same three ligaments, as in *Heptanchus*; but, in addition to them, it articulates with the cranium by a well-developed cup-and-ball joint.

Lastly, we observe that the second visceral arch, which, besides still carrying a gill, has assumed the function of suspending or carrying the first arch, is very strong and thick; its two principal components, the hyomandibula and the hyoid, articulate with each other, behind by two knobs, and in front by two concave facets, between which is placed a round piece of fibrous cartilage, held in its place by, and partly imbedded in, connective tissue (fig. 3 *c*.). The suspensorium in *Oxyrhina* is consequently formed chiefly by the hyoid.

Sphyrna zygæna (fig. 4).—The first visceral arch is comparatively weak; the palato-quadrate bar is, in fact, several times thinner than it is in *Oxyrhina*, and still weaker than in *Heptanchus*. The second arch is very strong. The thick and long hyomandibula articulates with the skull, and has the same ligaments (cranial and branchial) as have the two previous types. The long ligament from the under surface of the cranium, connecting the latter in *Oxyrhina* with the hyoid and mandible, after having received a band from the hyomandibular, is likewise present in *Sphyrna*, but, as the drawing shows, the direction of the angles formed by these ligaments with the parts to which they are attached is reversed.

The lig. mandib. hyoid. internum, absent in *Oxyrhina*, is present in *Sphyrna*, as in *Heptanchus*.

The inner big knob of the mandible, near the inner or median quadrato-mandibular articulation, articulates with its slightly rounded anterior surface against a distinct concavity of the posterior surface of the proximal end of the hyoid. The lig. hyomandibulo-mandibulare is, as in *Oxyrhina*, attached to the sustentaculum of the mandible, but it is very strong in *Sphyrna*, and arises chiefly, or almost entirely, from the hyomandibula itself. A new and strong ligament, hitherto not observed, connects the posterior side of the hyomandibula with the outer and anterior surface of the quadrate. From this point of attachment arises a long ligament which crosses all the others in going to the inner surface of the neck of the mandible: it is a lig. quadrato-mandibulare internum.

There are in *Sphyrna* none of the three ligg. hyoideo-mandibularia described in *Oxyrhina*.

Centrophorus (fig. 2).—In half-ripe embryos the hyomandibula articulates by a rather shallow facet with the cranium, and the whole second arch is considerably less bulky than the first arch, the quadrate region of which no longer articulates with the cranium. In the adult the second arch has become more bulky than the first arch, and the hyomandibula has formed a roundish big knob, which is received into a deep cavity of the labyrinth region; it is there connected with the cranium by loose ligamentous tissue, which surrounds the whole of the articulation. There are no distinct ligaments connecting the hyomandibula with the ventrilateral surface of the cranium, or with the first branchial arch. There is, however, a ligament which connects the posterior border of the proximal end of the hyoid with the posterior border of the middle of the hyomandibula, whence ligamentous tracts, together with the perichondral sheath, can easily be traced upwards to the cranium, near the posterior brim of the articulation. Thus, this tract corresponds with the posterior hyomandibular-hyoidean ligament of *Oxyrhina* and *Sphyrna*, and, to a certain extent, with the ligamentous cranio-hyoidean connexion of the same types.

From the anterior knob of the distal end of the hyomandibula goes a strong fibro-cartilaginous ligament to the sustentaculum of the mandible, and from this sustentacular or hyomandibulo-mandibular ligament goes a weak, ligamentous string to the neighbouring surface of the hyoid. This string, which we will call the *lig. intermedium*, corresponds with one of the ligg. hyoideo-mandibularia interna of other Selachians. Another lig. hyoid.-mandib., more distal, and somewhat stronger, is likewise present. The quadrate articulates with the mandible only by one (lateral) facet; the inner knob of the mandible is used for the articulation of the mandible with the hyomandibula and the hyoid. This articulation is, however, not a direct one, because the sustentacular knob of the mandible is separated from the two elements of the second arch by the cross-ligaments, as seen in fig. 2. Lastly, there is a long and strong lig. quadrato-mandibulare internum.

The suspensorial apparatus of *Centrophorus* presents, therefore, features which in many points are less advanced than those of either *Oxyrhina* or *Sphyrna*, although, as in these, the autostylic condition of the Notidanidæ has already been superseded by a hyostylic arrangement, with the additional suspension of the palatine bar from the cranium by a broad and strong, but loose, ethmo-palatine ligament.

Concerning *other Selachians*, I may be permitted to refer to some of GEGENBAUR's observations. The ligament which extends from the cranium along the anterior margin of the hyomandibula, and attaches itself to the anterior and inner surface of the mandibular process of this cartilage, is very strongly developed in *Mustelus* and *Galeus*. Of other ligaments, we find in the same genera and also in *Scyllium* the lig. hyomandibulare posterius, exactly as we have described it in *Centrophorus*, and, with modifications, in *Oxyrhina*. As in the latter form, this ligament is in *Mustelus* and *Scyllium* continued on to the mandible (our lig. hyoideo-mandibulare mediale; GEGENBAUR's äusseres Hyomandibularband, p. 169). His inneres Hyomandibularband is our lig. hyomand. mand. internum, *s.* lig. sustentaculi. Besides these, he describes a lig. hyomand. hyoideum anterius, which connects the lateral surface of the distal hyomandibula with the anterior proximal surface of the hyoid; it prevents the hyoid from contact articulation with the sustentacular knob of the mandible.

Whilst, therefore, in *Mustelus* and *Scyllium* there exists no immediate articulation between the hyomandibula and the mandible, GEGENBAUR found that in *Acanthias* the sustentacular or inner hyomandibular ligament sends a broad fibro-cartilaginous process to the sustentaculum, which process then acts as an interarticular cartilage disk between the mandible and hyomand. This arrangement is carried further in *Galeus* (sp. ?). The mandible articulates with the hyomandibula, and in the articular cavity is placed a pure cartilaginous disk, which is held in its place by a capsular ligament.

In *Scymnus* and *Cestracion* the hyomandibula articulates directly with the mandibular sustentacular knob, without the interference of cartilage, although the same ligaments as in *Mustelus* are present, but in a modified form.

Torpedo (fig. 6).—The quadrato-palatine and the mandibular bars are both very slender, and exhibit no processes whatever by which these elements in the Selachians are eventually connected with either cranium or hyoid.

The hyomandibula is an enormously broadened-out plate of a more or less triangular shape. Its basis is straight and articulates throughout its length with the cranium. There are no special ligaments developed. On the anterior irregular margin of the hyomandibula rest, and are loosely connected with it, two spiracular cartilages. That, and how, these elements—which originally belonged to and were carried by the palato-quadrate bar—gradually give up their original connexion and become attached to either the cranium or to the hyomandibula, has been fully explained by GEGENBAUR ('Kopfskelet,' pp. 197–205).

The posterior proximal end of the hyomandibula articulates with the proximal end of the first branchial arch. The hyoid articulates with the middle of the posterior margin of the hyomandibula. The distal end of the latter is connected by a thick and strong fibrous ligament with the sustentacular end of the mandible. Inside this ligament is enclosed an irregularly-shaped nodule of fibrous cartilage. This nodule is not circumscript, but passes gradually into the surrounding fibrous tissue of the ligament, after the manner of a sesamoid bone. The quadrate articulates with the mandible by a well-formed double joint, but there are no distinct ligaments. In fact, the strong hyomandibulo-mandibular ligament is the only one to be noticed.

Trygon (fig. 5).—In comparison with *Torpedo*, we find in *Trygon* a more complicated arrangement, which combines certain higher advanced features with the unmistakably retrograded, and therefore simpler, structures of the former type. The hyomandibula is by far less broadened out, and preserves the shape it has in most Selachians. It is placed in an almost horizontal position. Its proximal end articulates with the cranium and sends out a process towards the exit of the glossopharyngeal nerve; this process is likewise used for the cranial articulation. Immediately behind this process, leans on to it, and at the same time with a facet on to the cranium, the very slender hyoid bar. Special ligaments, connecting the hyoid with the hyomandibula, no longer exist, nor is the hyoid, now so far removed from the first visceral arch, in any way connected with the latter.

This cranial attachment of the hyoid behind the hyomandibula is of great importance concerning our investigations. This cranial connexion of the hyoid, going hand-in-hand with an absolute removal from the first visceral arch, is, as GEGENBAUR has shown, not owing to a migration of the hyoid upwards towards the cranium, but, firstly, to an arrest or retrogressive development of the proximal end of the hyomandibula, and, secondly, to considerable development of the sustentacular portion of the distal half of the hyomandibula. The longer this sustentacular portion becomes, the more the upper end of the hyoid bar will appear removed from the neighbourhood of the quadrato-mandibular and hyomandibulo-mandibular articulations; the ligaments which in previous types connected the hyoid with the first arch will gradually be given up, and a stage will be reached in which, as in *Torpedo*, the hyoid appears attached to the hyomandibula half-way between the masticatory joint and the cranium. In a further stage the cranial or upper portion of the hyomandibula will be still less developed, and the hyoid almost touches the cranium. GEGENBAUR mentions these important facts ('Kopfskelet,' p. 173): "The separation of the hyoid from the hyomandibula is completed in the other Rays (except in *Torpedo*). The hyomandibula there retains only its relation to the mandible; it becomes the bearer of the jaw-apparatus, whilst the hyoid henceforth behaves as the branchial arches. It is, in this case, either still attached to the cranium, as in *Rhyncobatus*, *Trygon*, and *Myliobates*, or it has become free, as in *Raja*. In either case its features are those of a branchial bar. The separation of the hyoid from the hyomandibula is, however, not quite complete even in these cases, because there is still a ligamentous connexion, which is traceable even in *Raja*. In *Rhyncobatus* and *Pristis* I find an articulation, close to the cranium, between the hyomandibula and that part of the hyoid which is attached to the cranium."

The articulation of the hyomandibula with the two jaws is, in *Trygon*, effected in the following way:—(1.) A complete articulation of the hyomandibula with the posterior border of the upper jaw; above this joint is found a small cartilage. (2.) A less complete articulation between the hyomandibula and the mandible. (3.) Articulation of the hyomandibula with the under jaw, not directly, but interfered with by the following ligaments:—

A strong lig. hyomandibulo-mandibulare. This encloses a piece of cartilage, like that in *Torpedo*. From this strong fibro-cartilaginous ligament goes a thinner one to the middle of the anterior or upper margin of the under jaw. It likewise contains a piece of cartilage. The quadrate bears a distinct convex knob, which fits into a facet borne by the inner mandibular articular process. In opposition to *Centrophorus*, there is in *Trygon* an inner, and not a lateral, jaw articulation of the two jaws, and whilst in *Centrophorus* the inner or sustentacular knob is used for the direct contact articulation with the hyomandibula and hyoid, the hyomandibula in *Trygon* comes into contact with the mandible only behind the sustentacular ligament.

I. In summing up with respect to the Elasmobranchs, we find that the first and second arches do not at all articulate with each other in the Notidanidæ, that a suspensorial arrangement is found in all the others, but that this does not lead to a direct contact articulation in *Centrophorus*, *Mustelus*, and *Acanthias*. Again, in *Oxyrhina* and in *Sphyrna* the hyoid and mandible have developed articular facets for contact, whilst the hyomandibula does not do so. Contact between the hyomandibula and the mandible takes place in *Galeus*, *Scymnus*, *Cestracion* and *Trygon*. Lastly, in *Trygon* we have contact also between the hyomandibula and the quadrate portion of the first arch.

II. With regard to the hyoid bar, this becomes more and more removed from the jaws until it reaches the cranium, and lastly is firmly attached to it, behind the hyomandibula, in certain Rajidæ, notably in *Raja*, *Myliobates*, and *Trygon*. The hyomandibula is invariably attached to the labyrinthic region of the cranium and articulates with it.

III. With regard to ligaments, we find that with the exception of capsular ligaments at the masticatory joint, the only constant one is the lig. hyomandib. mandibulare internum, *s.* lig. sustentaculi. This is phylogenetically very early developed; it is, in fact, found in all the cartilaginous Fishes above the Notidanidæ. This ligament, moreover, frequently contains fibrous and even hyaline cartilage, *e.g.*, in *Galeus*, *Trygon*, *Torpedo*.

There exists not unfrequently a ligamentous connexion between the labyrinthic region of the cranium and the proximal end of the hyoid element, *e.g.*, in *Oxyrhina*, *Centrophorus*, *Sphyrna*, *Trygon*, *Raja*; and these ligaments are certainly not the remnants of cranio-hyoidean muscles, although they sometimes (*Oxyrhina*) do serve as additional supporters of muscular fibres.

Ceratodus.—The massive first visceral arch is divided into three parts, the upper bar being differentiated into a palatine and a quadrate element. The latter is fused with the cranium by its proximal broad end, and therefore resembles the conditions met with in other holostylic skulls, as, *e.g.*, in *Cestracion* and *Chimæra*. The distal end of the quadrate articulates by a concave surface with a convex knob of the mandible. There is no contact or articulation of the lower jaw with the second visceral arch. The hyomandibula is represented by a small irregularly shaped cartilage, which is attached to the labyrinthic region of the cranium and to the neighbouring quadrate. It sends a small conical process outwards and downwards. In this process we recognise the suspensorial portion of the Elasmobranch hyomandibula, and Huxley compared it with the symplectic element of Teleostean Fishes.

The outer surface of this hyomandibular remnant is loosely connected with the small cartilaginous operculum, which we know to be the result by fusion of the branchiostegal rays, carried by the hyomandibula.

Of ligaments the following are important:—

1. Lig. hyomandibulo-hyoideum = Huxley's hyosuspensorial ligament. It arises with a broad basis from the lower surface of the hyomandibula and the cranium, and is attached to the broad top end of the club-shaped hyoid. Imbedded in this ligament

is the conical process mentioned above. The whole ligament represents undoubtedly the anterior and posterior hyomandibular-hyoidean ligaments of Elasmobranchs, and it has still preserved the cranio-hyoidean connexion.

2. Lig. hyoideo-mandibulare. A strong and round ligament, which connects the anterior proximal surface of the hyoid with the posterior proximal end of the mandible, closely behind its articulation with the quadrate. Owing to the fusion of the quadrate with the cranium, and owing to the large downward extension of the quadrate, the second visceral arch in *Ceratodus* is dispensed with as a suspensor of the jaws, and the existing few, but strong, ligaments connecting the two arches mainly serve the purpose of holding the hyoid in its place, instead of, as in most Elasmobranchs, holding and supporting the first arch.

The hyomandibula has lost its important function, and persists now as a degenerated piece of cartilage, which is, so to speak, shoved into a dead corner by its overgrowing neighbour, the quadrate. However, it still preserves its original connexion with its distal paramere, the hyoid.

We are not permitted to look upon the arrangement of the arches of *Ceratodus* as more primitive than those of any Elasmobranch; on the contrary, we have to derive it from an amphistylic, and this, of course, from a simple autostylic, form.

It is highly probable that in the ancestral *Dipnoi* the hyomandibula was much larger, and that it was already, as in Teleosteans, broken up into a proximal cranial persisting part, and into a distal or symplectic element, which later on, when the hyostylic support of the jaws was superseded, either persisted (*Proteus*, &c.), or ultimately became lost (*Ceratodus*, *Salamandrina*).

Urodela.—In *Siren* and *Menopoma*, the hyomandibula is about as much, or rather as little, developed as in *Ceratodus*, and it is partly confluent with the periotic and quadrate cartilage. In *Proteus* there is besides a "stapes" (see fig. 8), a large piece of cartilage which is with its extended top attached to the lower edge of a large fascia. This fascia runs along from the upper part of the "suspensorium," behind and beneath the stapes, and is attached to the inferolateral face of the epiotic (PARKER). This broad ligament (PARKER'S suspensorio-stapedial ligament) is the same as that in *Menobranchus*. There is also a ligament which runs from the hyomandibula and upper end of the hyoid to the quadrate; this ligament corresponds with the two in *Menobranchus*; lastly, there is the usual hyoideo-mandibular ligament. Whilst PARKER calls the broad piece of cartilage of *Proteus*, which, according to him is absent in *Seironota perspicillata*, and probably is absent also in *Siredon* and in *Amblystoma*, the hyomandibula proper, and thinks ('Urodela,' p. 554) that the "stapes is cut out from the preformed cartilage of the ear-capsule," it seems to me more probable that PARKER'S hyomandibula of *Proteus* and of other Perennibranchiata is the distal segment of the hyomandibula, comparable to a symplectic, whilst the "stapes" is the proximal portion of the original hyomandibula, which is now broken up into two pieces. If this symplectic or distal cartilage disappeared in *Proteus*, this creature would present almost exactly the same features as *Menobranchus*. That we are justified in postulating the disappearance of the distal part of the original hyomandibula, is shown by *Siren* and *Menopoma*, in which this same cartilage is scarcely one-fourth the size of that of *Proteus*, and is moreover confluent with the quadrate. Lastly, such a cartilage appears no longer in *Seironota perspicillata* (PARKER).

This conception of the hyomandibula is strengthened by the fact that PARKER himself is not clear about the origin of the whole "stapes." His first suggestion that the stem of the stapes in *Menopoma* is equal to the annulus tympanicus of the Frog is to be found in his work on the Urodela, p. 559, foot-note. On p. 587 he says :— "By the time the tail has disappeared in the Frog, the primary otic process has become a free trifoliate 'spiracular cartilage'; this becomes the cartilaginous annulus tympanicus; it is always, at any stage, above the portio dura nerve. In certain Urodela (*Menopoma*, *Spelerpes*, *Desmognathus*), the two latter being Caducibranchs, this cartilage grows to the stapes, and generally fits its narrow posterior end into a cup-shaped process of the stapedial bony centre; in some it is independently ossified and free. These two specialisations of that peculiar Selachian spiracular cartilage are of great interest, suggesting the possibility of many curious transformations of ichthyic elements in the higher classes."

Now the very circumstance that this otic process is always situated above, *i.e.*, dorsally from and anterior to the facial nerve, shows that it cannot become the stem of the stapes, because the ossicular chain is invariably situated behind and inwards from that nerve. On the contrary, the long outgrowth of the otic process gives rise to the long suprastapedial element of certain Anura; the base of this element forms the annulus tympanicus, whilst its distal end is attached to the lateral end of the ossicular chain, and can in time become fused with it.

Menobranchus (fig. 7).—The first visceral arch, with the addition of a well-developed squamosal bone, and the hyoid bar resemble that of *Ceratodus*.

The hyomandibula is removed from contact with the quadrate; it is much smaller than it is in *Ceratodus*, and, moreover, its base is broadened out into a round disk, which is firmly wedged into a corresponding foramen of the otic region. This foramen corresponds with the fenestra ovalis, and the hyomandibula itself has assumed a stapes-like form. It has entered a new service, namely, that of the whole auditory apparatus.

Of ligaments there are four, which it is easy to compare with those of the Dipnoi and Elasmobranchs, provided we take into account the changes which must have been produced by the development of a long and independent quadrate, together with a corresponding withdrawal and reduction of the hyomandibula.

Ligaments :—1. Most medially placed is a broad fibrous ligamentous connexion of the proximal end of the hyoid with the quadrate, and with the whole brim of the cranium from the distal end of the quadrate to the base of the hyomandibula.

2. A lig. quadrato-hyoideum = HUXLEY's hyosuspensorial ligament, arising from the posterior side of the middle of the quadrate and the adjoining part of the cranium.

3. A strong fibrous bundle from the lower surface of the hyomandibula, and with a few fibres from the cranium to the middle of the quadrate. The hyoid branch of the facial nerve passes above this hyomandibulo-quadrate ligament, *i.e.*, in front of the hyomandibula and behind the quadrate. This ligament is, therefore, in the same relative position to other parts as is the anterior cranio-hyomand. lig. of many Selachians, and this comparison becomes still more obvious if we look upon the 2nd and 3rd ligaments of *Menobranchus* as equivalent to the ligamentous connexion between the cranium, hyomandibula, and mandibula in *Oxyrhina*, and with the quadrate region in *Sphyrna*. At any rate, the broad medially-situated 1st ligament contains potentially all the possible connexions between the cranium, hyomandibula, quadrate, and hyoid. Ligaments 2 and 3 are to be looked upon as differentiations of the lateral tracts of a hyomandibulo-hyoidean connexion which, because of the reduction and withdrawal of the hyomandibula, have obtained a hold upon the quadrate, and this has led to the formation of two apparently new ligaments.

4. A lig. hyoideo-mandibulare.

Anura.—The larva of *Pseudis paradoxa*, described and figured by PARKER, exhibits an arrangement almost the same as that in *Menobranchus*. The symplectic half is absent. The stapes, with a pillar-like extension, the "columella," turns towards a tympanum, which, like the tympanic ring and the whole auditory capsule, is highly developed. The auditory cartilages are not connected with either quadrate or hyoid. The hyoid bar itself does not reach the cranium, but is fastened to the posterior side of the quadrate by a broad ligament.

In most of the Anura, however, this connexion is given up, and, instead of this, the proximal end of the hyoid is attached to the cranium, either by short ligaments, or it may even be fused with the cranium, as in the adult of *Pelobates* or in *Bufo*. The hyoid in these cases resembles that of the Rajidæ. The fact that the point of the cranial attachment of this "stylohyal" varies, indicates that it is a feature which was acquired after its separation from the hyomandibula or ossicular chain had taken place inside the Anurous group. We can, therefore, not be astonished to find the stylohyal end attached to any of the neighbouring cartilages or bones, which lend it the support required. The auditory chain of *Pelobates* and *Otilophus* (fig. 9B) is very simple; it is let into the fenestra ovalis by a stapedial disk; this passes into a straight or a curved slender rod (mediostapedial), the outer end of which is bent downwards (extrastapedial), and is attached to the middle of the tympanum. There is no attachment of the fenestri-tympanal elements with either mandible, quadrate, or hyoid. ALBRECHT's "figure schématique," in which he represents the Amphibian ossicular chain as connected with the mandible, is not supported by facts (*cf.* his paper on the Eustachian tube, fig. 10, p. 22).

Just as the hyomandibula of Fishes can break up into two parts, this fenestri-tympanal cartilage can become jointed at various places. The most frequent joint is that between the basal or fenestral disk and the stem or rest of the rod; the latter is then conveniently spoken of as the columella auris; or this columella may break up again, and form an inter-, medio-, and extra-stapedial piece. ALBRECHT therefore distinguishes between "Amphibiens columellifères" and "Amphibiens ossiculifères"—*e.g.*, *Rana pipiens* (fig. 9A), *R. halecina*, *R. pygmæa*, according to PARKER. These Anura show frequently a further complication by the possession of a suprastapedial element. This I consider as originally not belonging to the interfenestral chain. It is, as, for instance, in *R. pipiens* (fig. 9A), very long, turned back, and attached to the auditory capsule, and has nothing to do with the stylohayl.

Summing-up of the Dipnous and Amphibian Features in comparison with those of the Fishes.—1. The gradual, and lastly absolute, estrangement of the hyomandibular-hyoid arch from the palato-quadrato-mandibular arch, which leads eventually to the loss of ligamentous connexions, and to the final attachment of the hyoid to the cranium.

2. The complete separation of the hyoid from the hyomandibula (analogous to that observed in certain Rays).

3. The same setting free of the hyomandibula, which would have become completely aborted unless it had assumed new—namely, auditory—functions, by becoming connected with a tympanum; *i.e.*, a cavity formed out of the Piscine first visceral cleft.*

4. The breaking up of the hyomandibula into two and more pieces, as an ossicular chain.

5. The loss of the old piscine ligamentous, and sometimes even cartilaginous, connexion between the hyomandibula and the mandible, so that the Amphibia have returned to an absolutely autostylic condition.

6. The gradual loss, in the Urodelous group, of a piece of cartilage (PARKER's hyomandibula of *Menopoma* and *Proteus*), which piece is comparable with either a symplectic or with an opercular element.

7. The connexion of the tympanal end of the auditory chain or rod with the cranium by a suprastapedial element of probably periotic origin.

8. The reduction of the quadrate to a small cartilage, wedged in between the elongated pterygoid and squamosal bones. This elongation of the pterygo-quadrate bar, or the transposition of the masticatory joint far outwards, away from the cranium, has caused, or has at any rate facilitated, the separation of the hyoid from the hyomandibula.

Chelonia (Plate 74).—The broad quadrate is fused with the skull. PETERS has drawn attention to the following difference between the various families. In the Trionychidæ and in the Land Tortoises the quadrate bone forms a closed canal, through

* HOWES' discovery of a tympanum in *Raja* is most important; it shows, although perhaps by analogy only, how the approach of the hyoid to the cranium is correlated with the change of function of the first cleft.

which passes the columellar rod. In the other Water Tortoises and in the Turtles, however, the quadrate forms only an imperfect canal, which is open behind and below, rendering the whole columella visible from below.

In all Chelonians the interfenestral apparatus consists of two pieces. A long bony rod, or columella proper, fits into the fenestra ovalis; to its outer end is attached a broadened-out cartilaginous plate, which is firmly attached by connective tissue to the small tympanum. We can scarcely speak of a tympanum proper, because its place is covered over by the ordinary skin of the sides of the head. I found in a half-grown *Chelone imbricata*, after removal of the skin, a small globule of fibrous and partly ossified cartilage, of the size and shape of half a pea. Its convex middle was attached to the columella, and the plane disk fitted exactly and firmly, like a plug, into the small tympanic part of the auditory meatus. There are no special ligaments which connect this plug or the columella with either cranium, quadrate, mandible, or hyoid.

The latter is frequently either absent or is a mere bit of bone or cartilage, attached to the basilingual plate—*e.g.*, in *Emys*. All between this remnant and the cranium has disappeared, not even traces of a stylohyal or craniohyal ligament being left. The pair of long bony bars, which acts as hyoid, is in reality the third visceral or first branchial pair.

Crocodilia.—The auditory apparatus is very complicated. It was first accurately described by PETERS, who discovered and figured the connexion of the outer columellar element with the mandible. The following is a description of the arrangement which I have found in a young *Alligator mississippiensis*, whose skull is 15 cm. in length.

In order to make the preparation which is figured (fig. 14, Plate 72), the bones, after removal of the skin and the masticatory muscles, were gradually filed down in a plane parallel with the long axis of the quadrate bone.

The air cavities of the os articulare of the under jaw stand in connexion with the middle ear or tympanic cavity by the fibrous and partly cartilaginous siphonium. This is situated at the hinder corner of the quadrato-mandibular articulation.

To the same part of the os articulare, immediately behind the siphonium, is attached a cartilaginous and partly ligamentous string, which extends upwards along the hinder surface of the quadrate; this bone forms a slight semi-canal, which in its proximal posterior region becomes a complete wide canal. Through this passes the cartilaginous rod or ligament, and, where it enters the tympanic cavity, it is attached to the cartilaginous lower process of the distal element of the columella. This distal columellar cartilage consists of a short stem, which articulates with the columella proper, and of three irregularly-shaped processes. The lower one is connected with the mandible as described above, the anterior or most lateral one is attached to the middle of the tympanum, whilst the third is fixed on to the hinder upper corner of the tympanum. To the anterior or most lateral (HUXLEY's extrastapedial), not to the "suprastapedial" process, is attached the tendon of a tiny muscle which arises from the anterior cartilaginous brim of the tympanic cavity; it is a m. tensor tympani. The same periotic region is connected by thin ligamentous tracts with the upper, posterior process. The extracolumellar-mandibular connexion is subject to many variations. According to HUXLEY, the cartilage which is attached to the "infrastapedial" process, and which he calls the styloid cartilage, lies in his young *Crocodilus acutus* "upon the upper and posterior face of the quadrate bone; its lower extremity terminates some distance above the upper end of the pneumatic duct, the fibrous wall of which is continuous with the sheath of connective tissue which envelopes the cartilaginous rod in question." This latter tapers below to a free rounded extremity.

PETERS found (1868) in an embryo of the same species of 20·5 cm. in length "a small and short cylindrical cartilaginous piece between the distal end of the columella proper and the trifid malleolar cartilage"; he compares it with either the os lenticulare or with the incus of the Mammalia. In a still younger embryo of *Crocodilus vulgaris* he found the transition of the lower extracolumellar process into MECKEL'S cartilage very plain and obvious. In his paper on the pneumatic duct of Crocodiles (1870) he describes and figures a whole series of modifications of the parts in question. The principal results of his investigation, which also agree with the specimens examined by myself, are the following (see fig. 19, and PARKER'S illustrations, figs. 15–18):—

1. The outer end of the columella proper possesses a concave facet by which it articulates with the short basal stem of the trifid extracolumellar cartilage, or malleus.

2. The lower process of this trifid piece passes into a long cartilage (HUXLEY'S styloid), which is continued into the swollen cartilage of MECKEL at the posterior and upper articular corner of the mandible.

3. The siphonium connects the air cavities of the os articulare directly with the tympanic cavity, but not with the air cavities of the os quadratum; the latter are, however, in direct communication with the tympanic cavity.

4. Siphonium and mandibulo-extracolumellar connexion are independent formations, although the fibrocartilaginous siphonium is continued upwards into the connective tissue which partly lines the bony canal of the quadrate, through which passes the mandibulo-extracolumellar string; the siphonium is, therefore, "continuous with the sheath of connective tissue which envelopes the cartilaginous rod in question," as HUXLEY describes it.

5. This whole string is originally entirely cartilaginous. Fig. 19 shows the gradual transformation into connective tissue of the cartilage at the distal end of the lower process of the trifid piece and at the mandibular end; this leads sometimes to the reduction of the cartilaginous rod to a very small cartilage, which remains as a pulley-like arrangement in the region of the complete tympano-quadrate canal. See fig. 14 (*Allig. mississ.*).

6. There is a musculus mallei, *s.* tensor tympani, but not a m. stapedius nor a m. incudis.

The lingual skeletal parts of the Crocodilia are much more reduced in number than those of the Chelonia. There is, besides the broad shield-shaped unpaired basilingual piece, only a pair of thyrohyals or ceratobranchials, which, of course, are homologous with the third pair of visceral arches. The second, or hyoid, pair has entirely disappeared as far as ceratohyal and stylohyal pieces are concerned.

It is obvious that the system of cartilages and ligaments extending from the fenestra ovalis to the mandible is at least analogous with the cranio-mandibular or suspensorial connexion, *i.e.*, the hyomandibulo-symplectic elements, of the Fishes.

PARKER, the latest worker on the Crocodilian ossicular chain, gives in his essay (Plate 68) a series of beautiful figures of embryonic Alligators and Crocodiles (see figs. 15–18), which demonstrate the correctness of PETERS's observations and conclusions. Whilst in the earlier stages there is a continuous rod of cartilage passing from the tympanal region down and behind the quadrate into the portio articularis of MECKEL's cartilage, this cartilaginous continuation is, in the 5th stage embryos (of $4\frac{1}{2}$ inches total length), near the siphonium, reduced to a ligamentous one. PARKER (p. 272 and p. 281) compares the mediostapedial shaft of the columella with part of a pharyngohyal element, which is equal to the hyomandibula of Fishes; "the unossified proximal end is always a separate cartilage (stapes) in the Amphibia." All the rest outwards from the lateral end of the columella down to the mandible he compares with the hyoid bar proper. His nomenclature of the whole second visceral arch, as given on p. 272 of his work, and reproduced in fig. 16 of this essay, is this :—

1. Columella = hyomandibula.

2. The "suprastapedial" is a special hyoid element not found in normal branchial arches, and restricted as a separate piece to the Crocodilia.

3. The "epihyal," already ligamentous in later, nearly ripe stages like those of PETERS.

4. The main bar or ceratohyal. It "lessens downwards, becoming terete, and is thoroughly fused below with the mandible, close behind the articulation with the quadrate, in embryos of *Alligator mississ.* (of $1\frac{1}{2}$ inch total length). The rest of this arch at present is merely a median hyobranchial tract, the hyoid part of which lies in front of the first ceratobranchials or paired thyrohyals."

PARKER assumes consequently the absolute fusion of the distal end of the ceratobranchial with MECKEL's cartilage, and the disappearance of the original connexion which must have existed between the ceratohyal and the hypohyal, "which latter is not distinct from the common basi-hyo-branchial plate" (our basilingual cartilage). This view is wrong. We do not know in either Elasmobranchs, Dipnoi, or Amphibia of any ligamentous connexion of the mandible with the distal, or even with the middle, portion of the hyoid bar, but only and occasionally with the proximal end of the hyoid; a ligament which could possibly lead to a cartilaginous junction between hyoid and mandible. On the other hand, the possibility of a cartilaginous connexion between the distal end of the hyomandibula and MECKEL'S cartilage is demonstrated by Elasmobranchs.

Hatteria (fig. 11).—This very primitive Reptile has been used both by HUXLEY and PETERS to prove their views with regard to the morphological value of the auditory ossicles.

HUXLEY'S description has to be given in full. He says (1869, p. 396):—"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 mandible to the anterior margin of the anterior corner of the hyoid, 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 in the form of a little scroll with a backward concavity. 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 outer end of the tympanic cavity; when it is removed, the proximal end of the corner 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. There can be no doubt, therefore, that it corresponds with the extrastapedial cartilage of the Crocodile. What answers to the axe-head-shaped suprastapedial cartilage of the Crocodile is the upper process of the cartilaginous part of the stapes, which, however, passes into the extrastapedial cartilage externally and above, so as to enclose the foramen *a*. On the left side, the suprastapedial process was fibrous at the point *b*. Superiorly, the suprastapedial cartilage is directly continued into the cartilaginous termination of the parotic process of the skull, 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."

HUXLEY assumes the absolute continuation of the hyoid into the stapes, whilst the proximal end of the hyoid projects on to the parotic cartilage. PETERS (1874) does not deny this ligamentous connexion, nor even the partial coalescence of the hyoid with the malleus, but he looks upon it as secondarily acquired. He observed that "the fibres of the hyoid are softer and have a different direction to those of the harder fibres of the malleus, the two sorts of fibres crossing each other." The swelling of the hyoid, when it is apposed to the extrastapedial cartilage (malleus), does not owe its existence to the cartilage itself, but to connective tissue. Moreover, the hyoid is not connected with the inner or lower process of the malleus, but it passes above it without being attached to it, so that the open space, figured in HUXLEY's and in PETERS's specimens, is not a foramen, formed by junction of the hyoid with the two processes, but is only a notch. Undoubtedly, PETERS continues, the mandible was formerly connected with this inner axe-shaped process.

The proximal end of the hyoid is connected, as in HUXLEY's specimen, with the cartilaginous parotic styloid process. It is jammed in between the quadrate, parietal, and exoccipital or mastoid bone. This position of the proximal end of the hyoid above, and slightly in front of, the auditory ossicles is satisfactorily explained by PETERS by the peculiarly slight development of the proximal part of the quadrate bone and its firm connexion with the mastoid, so that the latter is removed from its original position.

BAUR mentions only that in three specimens of *Hatteria* the cartilages in question were partly coalesced, but that "series of sections showed that the hyoid arch was free from the malleus proper," and "that these conditions were less clear than he expected."

My own investigations were made on five adult and half adult specimens. The tympanic cavity is represented by a large pharyngeal recessus. The membranous walls of this recessus are attached as follows:—The anterior wall lines the whole of the posterior aspect of the broad quadrate, and it closes the space between the inner brim of the quadrate, the pterygoid, and the anterior ventral sharp edge of the exoccipital bone. This wall lies consequently in front of the columellar rod. The posterior wall of the recessus is spanned out between the sharp lateral brim of the conjoint exoccipital bone and the basisphenoidal lateral process; thence it extends to the posterior angle of the mandible, and to the posterior inner surface of the hyoid up to the quadrato-exoccipital junction. This wall lies consequently behind the columella. There is no auditory opening visible externally, the outer skin covering the whole region, but underneath the skin we find the space between quadrate, mandible, and hyoid closed by strong fibrous connective tissue, which represents an imperfect tympanum (see fig. of specimens A and B).

Specimen A, apparently adult.—The extracolumellar cartilage has no foramen whatever, nor is it attached to the cranium directly, except by a strong ligament, which arises from the parotic corner and attaches itself to the extracolumellar cartilage on its outer margin, after having passed over the greater part of the cartilage. The more superficial fibres pass on and diverge to the outer brim of the quadrato-mandibular articulation and to the mandible alone. In other words, there is a cranio-quadrato-mandibular ligamentous tract = cranio-extracolumellar + extracolumellar-quadrato-mandibular tract.

There is, further, a thin membrane of thin elastic tissue between the whole lower and anterior convex margin of the extracolumellar cartilage and the quadrate, mandible, and hyoid, as shown in fig. A. This membrane is situated internally to the other tracts.

The long "infrastapedial" process is jointed to the top end of the slender hyoid cartilage. The proximal third of this hyoid is connected with the posterior inner knob of the mandible by sharply-defined tendinous fibres, which gradually form a distinct and strong hyoideo-mandibular ligament.

Specimen B.—The formation of the imperfect tympanum by means of a tendinous fan-shaped connexion between the parotic corner of the cranium and the quadrate, mandible, and hyoid, with the important feature of the extracolumellar cartilage being attached to the middle of this tympanum, shows some modifications (fig. 11). As in specimen A, the extracolumellar cartilage does not touch the cranium, but its "infrastapedial" process passes without a break into the hyoid, and the fibres of the triangular hyoideo-mandibular ligament do not arise from the hyoid alone, but also from the "infrastapedial" process.

Specimen C is of the greatest importance. The slender hyoid is continued as a curved "scroll" along the anterior and lower margin of the extracolumellar cartilage upwards to the parotic corner, where it does not fuse with, although it directly touches, the cranial cartilage. Moreover, there is a foramen, although far smaller than that of HUXLEY's and PETERS's specimens, it being of the size of a pin-hole only. This foramen, which is absent in specimens A and B, and the circumstance that in specimen C as well as in HUXLEY's and PETERS's specimens the hyoid is continued up to the cranium, strengthen PETERS's view that this foramen is formed by the hyoid and by the extracolumellar processes. The hyoid is fused with the margin of the extracolumellar cartilage, and causes a thickening of its margin. Stained microscopical sections show this fusion to be a secondary one. The cartilaginous cells of the thick margin run in the same direction as the whole hyoid, whilst those of the extracolumellar plate run at right angles to them; moreover, in another specimen, which likewise possessed the cranio-hyoid connexion, the cells showed the arrangement represented in fig. 11 *C.* 1. Similar sections through specimens like A and B show only a uniform arrangement of the cells from the stem of the extracolumellar piece to its margin.

Another important point in specimen C is that the hyoid does not form the continuation of the lower or infrastapedial process itself, but that this latter is free, it being situated somewhat more inwards, as shown in fig. 11 *C.* 2, and from the distal end of it starts the lig. hm. m.

We conclude, therefore—

1. That the fusion of the hyoid with the extracolumellar cartilage is a feature acquired secondarily and owing to juxtaposition.

2. That the proximal end of the hyoid was originally connected with the parotic cartilage of the cranium; and that

3. This contact-connexion disappeared (specimens A, B, D), whilst the hyoid portion from *s* to *i* either remained—be it fused or not fused with the extra columella—or disappeared (specimens A and D).

4. There are occasional traces of a ligamentous connexion between the distal end of the "infrastapedial" process and the mandible, notably in specimen C, besides a hyoideo-mandibular ligament.

Nobody can assume that this hyoideo-mandibular ligament is homologous with a continuation of MECKEL's cartilage into the upper half of the ceratohyal, as PARKER suggested for the Crocodilia. Such an idea is to be discarded because of the entire preservation of the ceratohyal portion in *Hatteria*, and because of the important circumstance that the strong ligament *l.h.m.e.* is attached to the posterior corner of the mandible, whilst the thin infrastapedial + hyoideo-mandibular tracts are attached to the inner articular knob of the articular part of the mandible.

We can recognise in this small inner ligament the last trace, now nearly aborted, of the infrastapedial-mandibular tract of the Crocodiles. Moreover, the Crocodilian "suprastapedial" recognised by PARKER as part of the hyoid is possibly contained in the strong parotic-extracolumellar ligament of *Hatteria*, and it is not beyond the limits of possibility to assume that a Crocodilian free "suprastapedial" of PARKER would result from the reduction of the part *e–i* of the hyoid.

Uromastix spinipes.—PETERS found an articulation between the columella and the extracolumellar cartilage; from this latter, near its articulation, descends a process downwards, which changes gradually into a ligamentous or tendinous thread; it descends on the inner side of the quadrate, passes through between the quadrate and the hinder end of the pterygoid bone, and passes lastly into the mandible in front of the inner margin of the articulation with the quadrate. He naturally looks upon this thread as the continuation of the extracolumella into MECKEL's cartilage. The following descriptions refer to my own observations.

Psammosaurus scincus (fig. 12).—In this North African Lizard all the points in question are easily examined after the severing of the head from the neck. The whole pharynx and part of the tympanic recessus are pigmented black, except the anterior wall of the recessus and the tympanum itself. The tympanum is complete and visible from without. The long hyoid bars are far removed from the skull. The hinder body of the tympanum itself is formed by a strong yellow tendinous tract, which extends from the outer exoccipital corner to the upturned angle of the mandible. The extracolumellar cartilage articulates with the columella. Its shape and its connexion with the tympanum are best explained by the figures (12). There is a short and strong ligament from the parotic corner to the uppermost short process of the auditory cartilage. As in *Uromastix*, there is a long basal process; it is continued into a round fibrous thread, which squeezes itself in between the quadrate and pterygoid bones. After the end of the pterygoid has been broken off the thread is seen to be attached to the inner side of the distal part of the quadrate, some tendinous fibres being continued towards its distal end, but not to the mandible.

From the mandible, immediately behind its articulation with the quadrate, MECKEL's cartilage is continued upwards as a round string of fibrous tendinous tissue, but this string attaches itself to the exoccipital parotic region, and sends hardly any fibres to the stem of the extracolumella, while it passes to the inside of it.

Hydrosaurus salvator, from Australia, shows the same arrangement as that represented in fig. 12.

Teju (fig. 13).—Large specimen of five feet in length. The columella articulates with the extracolumella by a complete joint. A strong yellow tendinous ligament connects the parotic corner, between the exoccipital, squamosal, and quadrate, with the two tympanic processes of the extracolumella, and is then continued as an indistinct ligament to the mandible. The ligamentous thread from the inner lower process is lost between the pterygoid and quadrate bones. There is no extramandibular continuation of MECKEL's cartilage. The hyoid is long, and far removed from the skull.

Gecko mauritanicus, adult (fig. 10).—The long hyoid bar is attached to the cranium by a strong ligament, but there is no connexion whatever of the hyoid with the extracolumellar cartilage. The upper short process of the latter is, as in some other Saurians and in the Crocodiles, connected with the skull by a short "suprastapedial" ligament. Mandibular connexions are absent. BAUR makes a statement which I have not been able to corroborate, viz., that the "infrastapedial" process is connected with the mandible by a fine thread. This thread he homologises with the extramandibular part of MECKEL's cartilage. On the other hand, I find PETERS's remark correct (1869, page 6), that a fine semicartilaginous thread from the infrastapedial loses itself between pterygoid and quadrate.

Chamæleo vulgaris (fig. 20).—There is no tympanum. The hyoid is far removed from the skull. The columella is a long, bony, and slender rod, which, according to PARKER ('Chameleon,' p. 96), is already in the young confluent with the oval stapedial plate which fits into the fenestra ovalis: "Where the bone ceases there the extrastapedial region begins; but any segmentation of the cartilage, which may have existed, is gone."

"The extrastapedial cartilage is attached to the inner side of the quadrate behind, in its normal ichthyic condition, for there is no drum cavity in this type, and therefore the extrastapedial does not ride over the edge of the quadrate. There is a fenestra in the proximal part of the cartilage, and above this space the thickened inner edge of the cartilage passes upwards as a short suprastapedial; this is finished above by an enlarging ligament, which is inserted on the inner face of the quadrate, close to the top."

The remarkable points of *Chamæleo* are therefore—first, the apposition and fusion with the inner aspect of the quadrate of those parts of the extracolumella which in other types would be attached to the tympanum; secondly, as a result from this fusion, the absence of an extrastapedial or central tympanal process; thirdly, the absence of a special connexion of the infrastapedial process with MECKEL's cartilage, owing to the fusion of the former with the quadrate. That cartilage which PARKER calls (*cf.* fig. 20B) the extrastapedial in *Chamæleo* I homologise with the infrastapedial = long process of the malleus, and assume the reduction of the true extrastapedial. The presence of the little fenestra is the last remnant of the rectangular space or niche between these two processes in other Lizards.

Ophidia. *Pelophilus madagascariensis*, adult (figs. 22, 23, Plate 73).—The columella is entirely bony, and is of nearly the same length as the long horizontally-placed squamosal bone. To the end of the columella is attached a small, peculiarly shaped moveable cartilage; this extracolumella has a concave smooth facet, which freely with a convex smooth facet of the quadrate, as shown in fig. 22B; around and articulates between this articulation lies a ring-shaped complete meniscus of hyaline cartilage; one end of this meniscus goes over into connective tissue, which is lost on the periost between the inner corner of the quadrate and pterygoid bones; the other end of the meniscus passes into similar connective tissue, which surrounds the whole columella like a sheath, and attaches itself with tendinous fibres to the cranium below and a little behind the proximal end of the columella. The little extracolumella has no connexion whatever with either the sheath or with any other parts except with the columella itself.

Crotalus durissus, adult (fig. 24).—The squamosal bone is very short and weak, the long and slender quadrate having almost entirely replaced it by position and function. The distal end of the pterygoid does not at all touch the quadrate, but is connected with it by a ligament, much longer than that in *Pelophilus.* One pair of hyoid-like, very thin cartilaginous arches runs down the sides of the trachea.

The columella and the extracolumellar cartilage are like those of the Boa. The cartilage articulates upon a sharpish ridge of the quadrate, but there is only half a meniscus on the inner side. The columellar sheath, which is strongest on the posterior and inner side of the bony rod, is continued as tendinous tissue to the fibrous quadrate-pterygoid ligament, and partly towards the end of the quadrate.

Parker gives a description and figures of the embryonic Snakes (fig. 21), which I cannot quite reconcile with his description of the ripe stage. He says (Embryos of 3rd stage), p. 398:—"the hyoid fold has cartilage only in its upper third; this is a rib-like piece, with a rounded capitulum, a solid tuberculum, and a sickle-shaped shaft, whose convexity is backwards. The hind edge below has a crest ready to separate from the main part. The capitulum is attached to the membrane of the fenestra ovalis (*st.*), which is beginning to chondrify continuously with the hyoid rib-like rod." On p. 406 (Ripe Embryos) he says: "the backward extension of the huge mandibular arch has thrust it past the hyoid rudiment; this is the cause of the very peculiar position of the stylohyal and columella on the inner face of the quadrate—notwithstanding the small size of the arrested hyoid arch, it has become segmented into two normal pieces; the columella (minus the stapedial plate) answering to the hyomandibula, whilst the stylohyal is the upper part of the familiar 'stylo-ceratohyal' bar. There is no distinct membrana or cavum tympani, and at present the stylohyal cleaves to the columella. This element is reniform (*st. h.*) and its middle and convex portion is covered with a scabrous ectosteal plate; this and the extrastapedial are jammed between the skull and quadrate. The terminal third of the columella is unossified = extrastapedial part, and it has no suprastapedial spur." In a foot-note, PARKER says :—"in every Ophidian skull examined by me there was to be seen a thin scale of bone adherent to or coalesced with the inside of the quadrate, above its middle. The arrested stylohyal is stowed away there, permanently faint and functionless."—"There is no cartilage in the distal part of the Snakes' hyoid or lingual region" (p. 407). "Of the hyoid arch remain in the adult only two rudiments; both have lost their independence; the antero-posterior or hyomandibular element is now the small columellar prickle on the oval stapedial plate; the postero-inferior piece is starved and useless, it is anchylosed to the quadrate, towards the back of the upper third (*st. h.*). There is no distal or lingual cartilage" (p. 415).

PARKER's reniform cartilage is the extracolumella of our nomenclature, and not the stylohyal, as PARKER was compelled to assume, since he homologised the terminal unossified third of the columella with the "extrastapedial part" (our extracolumella). The tract of connective tissue which, in his fig. of the 3rd stage, is shown to run forwards from his "hy" (my hyomandibula) may well represent the last trace of the aborted hyoid, as would be the case in *Hatteria*, specimen A, if the ceratohyal were no longer cartilaginous but reduced to connective tissue.

It is easy to connect the Ophidian arrangement with that of the Chameleons. Juxtaposition of the extracolumella and the quadrate bone leads to fusion of these two parts, and this dispenses with any extracolumellar-mandibular connexion. The occasional existence in the Lizards of a double connexion of the extracolumella, namely, with the quadrate and with the mandible, indicates that these Reptiles have retained more primitive features than either Chameleons or Snakes. These remind us of other highly specialised types, the Chelonia. These three types have all, although each through different causes, lost the tympanum and the tympanic cavity proper, the extracolumellar-mandibular connexion, and the greater part of the hyoid.

That neither of the extracolumellar connexions can contain ceratohyal elements is proved by the adjoined table, which shows that there is no interdependence between the parts tabulated.

	Extracolumella connected with—		Hyoid long, attached to cranium or to extra-columella.	Hyoid long and free.	Hyoid aborted.
	Quadrate.	Mandible (MECKEL's cartilage).			
Hatteria	+	+	+	—	—
Hydrosaurus, Psammosaurus, Teju	+	+	0	+	—
Chamæleo	+	0	0	+	—
Ophidia	+	0	0	0	+
Chelonia	+	0	0	—	+
Aves	0	+	In embryo columellar connexion	—	+
Mammalia	0	+	+	—	—
Anura	0	0	+	—	—
Urodela	+	0	—	+	—
Sphyrna	+	+	to hyomandibula	—	—
Oxyrhina	0	+	,,	—	—
Torpedo	0	+	,,	—	—
Trygon	0	+	to cranium	—	—
Hexanchus	0	0	,,	—	—

We have then amongst the Reptiles to look for types which have preserved more primitive conditions if we want to connect the Reptilian auditory ossicles or cartilages with those of the lower and higher classes. Such types are *Hatteria*, the Crocodiles, and most of the Lizards proper. These taken together show the following important features.

1. The connexion by tendinous, and partly by cartilaginous, tissue of the extracolumella with the quadrate and with MECKEL's cartilage.

If we put columella + extracolumella = hyomandibula, we recognise the hyomandibular-quadrate ligaments and the cranio-hyomandibulo-mandibular ligaments of Urodela and Pisces.

The apparent absence in the Urodela of a direct hyomandibulo-mandibular connexion is explicable by the disappearance of the loose "symplectic" cartilage. Moreover, in the Urodela both visceral arches are slanting forwards, so that the masticatory joint is placed far forwards from the otic region, and the anterior pterygo-quadrate-mandibular angle is frequently greater than 90°; in the Reptiles the reverse takes place, the angle is by far less than 90°, and its apex is placed in a level below and even far behind the otic region.

2. The existence of a cartilaginous and osseous severally-jointed connexion between the tympanum and the fenestra ovalis, as in Anura, Mammalia, and Aves.

3. The attachment of the proximal end of the hyoid to or near the periotic region of the cranium, as in the Anura, unless the hyoid has become free or has degenerated. For this latter condition we have no analogous cases in the Urodela, because in them the reduction of the hyoid to a slender rod has not yet taken place, nor has the hyoid lost its primitive feature as the distal complement of the whole original second arch.

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Aves.—The arrangement of the auditory ossicular apparatus is very similar to that of the Monitors, as is shown in Plate 74. HUXLEY draws attention to the absence of even a rudiment of a styloid cartilage, and to the elastic ligament discovered by PLATNER, which represents the "suprastapedial" cartilage of the Crocodile. A tensor tympani muscle arises from the lower part of the occiput, and is attached partly to the extracolumellar cartilage and partly to the tympanic membrane.

PETERS (1868, p. 597) makes the following correct observation:—In an embryo of *Struthio camelus*, whose head measured 3 cm. in length, the extracolumellar cartilage was continued into a very fine thread, which soon swelled into a thicker string of cartilage; this ran down behind the quadrate and passed into the inner articular knob of the mandible, exactly at the same place where, later on in the adult, is found the pneumatic foramen. PETERS mentions the same of the embryo of *Spermestes atricapilla*, a fringilline form.

Fig. 25A represents the conditions of the auditory chain in an adult specimen of *Rhea americana*. The preparation and the following up of the cartilaginous, and later on ligamentous, thread from the extracolumella to the inner angle of the mandible is rather difficult. The thread, where it passes over the anterior brim of the tympanic cavity, is overgrown and partly enclosed by bony scales of the alisphenoid. Close to the entrance of the thread into the mandible is a pneumatic foramen (*F.pn.*). The inner and posterior aspect of the stem of the quadrate is partly surrounded by a wing from the alisphenoid and by a similar extension from the zygomatic process of the squamosal.

In the adult bird the whole hyoid bar is absent, with the exception of a small cartilage, which constitutes one-half of the "os entoglossum." In the embryo there are, however, traces of the ceratohyal part, represented by a fine tract of connective tissue, which attaches itself to a process sent down from the distal end of the columella. (See PETERS, 1868, Pl. I., figs. 4 and 4*a*, and 1870, p. 18, foot-note, my diagram on Plate 74). This is undoubtedly a secondary connexion, analogous to that in *Hatteria*. What is, perhaps, the greatest resemblance to Teleostean features is thus produced by this hyoidean connexion with a point between the extracolumella = malleus = symplectic and the columella = rest of hyomandibula.

Mammalia.—In the embryo MECKEL'S cartilage is continued behind the quadrato-mandibular articulation upwards into the processus longus of the malleus (= proc. gracilis, *s.* pr. Folii). This connexion is soon reduced and disappears; threads of the vanished cartilage can occasionally be traced from the tip of the Folian process into GLASER'S fissure. It looks as if the approach of the mandible and of the annulus tympanicus to the squamosal bone had squeezed out and destroyed this connexion.

The ossicles of the ear are usually four in number. The malleus articulates with the incus, and sends a long process (manubrium) to the middle of the tympanum. The stapes becomes perforated near its basis by a branch from the internal carotid artery, as SALENSKY has shown. Between stapes and incus lies the small lenticular element, frequently remaining cartilaginous and imperfectly jointed, occasionally absent, *i.e.*, not developed.

The hyoid has no connexion with either mandible, palate, quadrate, or with the ossicular chain, but its upper end is fused with the cranium behind the tympanic ring.

The views which have been advocated concerning the homologies of the Mammalian ossicles of the ear are tabulated below; which of these views we shall have to follow can be settled only by the following considerations:—

TABULAR Arrangement of the Views held concerning the Homologies of the Auditory Ossicles of the Mammalia.

	Malleus.	Incus.	Lenticulare.	Stapes.	Quadratum.	Columella.
TIEDEMANN (1810)	..	..	..	..	Processus zygomaticus of squamosal.	Columella = whole ossicular chain of Mammalia.
REICHERT (1837)	Articulare.	Quadratum.	..	End of hyoid.	Incus.	Hyoid.
GEGENBAUR	Articulare.	Quadratum.	Symplectic.	Hyomandibula.	Incus.	Hyomandibula.
PETERS (1867)	All developed from MECKEL'S cartilage.				Os tympanicus	
HUXLEY (1867)	Quadratum.	Hyomandibular. (Suprastapedial.)	Hyomandibular.	Hyomandibular.	Malleus.	Hyomandibula.
PARKER, I.	Quadratum.	Hyomandibular. (Suprastapedial.)	Hyomandibular.	Auditory capsule.	Malleus.	Hyomandibula.
„ II.	Articulare.	Quadrate.	..	Auditory capsule.	Incus.	
SALENSKY (1880)	MECKEL'S cartilage.		..	Tissue around a ramus arteriæ mandibularis.		
FRASER (1882)	End of mandibular cartilage.	Proximal end of hyoid	..	Periarterial tissue.		
ALBRECHT (1883)	Hyomandibular.	Hyomandibular.	Hyomandibular.	Hyomandibular.	Forms the processus zygomaticus of the squamosal.	
GRADENIGO (1887)	MECKEL'S cartilage.		..	Hyomandibula and periotic cartilage.		

The all-important question is that of the homology of the quadrate bone. PETERS was the first to prove that the quadrate bone of the Sauropida has in the Mammalia become the tympanic bone or tympanic ring. This incomplete tympanic ring is situated below, behind, and in front of the tympanum, also in front of the tympanic canal and in front of, and laterally from, the ossicular chain, exactly like the quadrate of the Sauropida. Moreover, PETERS found in embryos of *Halmaturus bennetti*, of 8·5 cm. in length, the following remarkable conditions:—"The anterior part of the tympanic bone grasps round MECKEL'S extramandibular cartilage, and possesses on its lower surface a convexity which articulates with the medial side of the ramus ascendens of the under jaw; it also articulates by a smooth surface with a concave facet of the inward-curved angle of the under jaw. Somewhat older specimens of *Didelphys* showed similar conditions, but the tympanic bone was already separated from this second articulation by a thin layer of connective tissue."

Peters draws the conclusion that the inner or median process of the mandible, which acts as a temporary articular knob, corresponds with the permanent inner articular process of Birds, and, we can add, of Reptiles and certain Elasmobranchs (see there, and fig. 27 and Plate 74).

In a young *Tachyglossus hystrix* Peters found : The middle of the tympanic ring touches the pterygoid, and here it has a convexity for the inner articulation with the mandible. The processus longus of the malleus is extraordinarily developed, more than in any other Mammal; later on this process articulates with, and even fuses with, the pretympanic end of the tympanic ring, but there was still a small convex surface on the lower surface of the latter bone which indicated the former articulation with the mandible's inner concave facet. The incus was extremely small, and was first discovered in the Monotremata by Flower (fig. 26*i*). It fuses with one end with the malleus, and, later on, comes to be placed against the squamosal bone, near the hinder end of the os jugale. (Anchylosis between malleus and incus likewise occurs occasionally in many Rodentia.—Doran.)

The illustrations (figs. 26–30, Plate 73) taken from specimens in the Cambridge University Collection, show that Peters's observations are quite correct. The long process of the malleus is extraordinarily developed and ossified in *Echidna* (*Tachyglossus*), but owing to the degenerated condition of the under jaw in the adult it no longer reaches the inner angle of the latter. In a young *Orycteropus* I find the tympanic ring still connected with the squamosal bone, and, moreover, there is at the distal end of the pretympanic portion of this ring a distinct process or knob, which indicates the former articulation with the inner angle of the mandible. In *Phascolomys* the long process of the malleus is very strong, passes through a broad fissure between the tympanic ring and the periotic capsule, and even in the adult skull almost touches the typically developed inner angle of the under jaw.

Peters draws attention to the fact that the quadrate bone most frequently carries a considerable portion of the tympanum, and invariably so when the quadrate bone is immovably fixed to the skull, as in Chelonia and Crocodilia. We add the hardly less important fact that no animal possesses an os tympanicum besides a distinct quadrate bone.

This statement seems, perhaps, open to doubt, because of the existence of a tympanic ring in the Anura. This necessitates a consideration of the embryonic development of the tympanic ring.

According to Balfour ('Comp. Embryol.,' p. 483), "the metapterygoid region of the quadrate (in the Frog) gives rise to a posterior and dorsal process, the end of which is constricted off as the tympanic annulus, whilst the proximal part of the process remains as the otic (metapterygoid) process, articulating with the auditory cartilage."

Parker ('Mammalia,' 1885), figures and describes the annulus tympanicus of the embryo of *Tatusia* as cartilaginous, with an osseous scale on its outer side. In higher

Mammalia this membrane bone becomes preponderant over the cartilage, and causes the whole or nearly the whole of the "os tympanicum" to be developed as a membrane bone, with little or no cartilaginous basis. This explains FLOWER's remark ('Osteology of Mammalia,' 3rd ed., p. 133), that "the inner part of the bulla in many Mammals is developed in a distinct cartilaginous lamella, interposed between the lower edge of the tympanic ring and the base of the skull." The inner and under surface of the tympanic bone is greatly expanded in Mammalia, and forms the auditory bulla. The usual statement (*e.g.*, HERTWIG's 'Embryologie,' p. 461), that the "os tympanicum" is a membrane bone, is applicable only to the higher Mammalia.

PARKER ('Batrachian Skull,' Part III., 1881) informs us that "the annulus tympanicus is the spiracular cartilage, which may chondrify with the otic process of the quadrate pedicle." See also the remarks on p. 460 of this essay.

We conclude that the os tympanicum of Mammals is equal to the quadrate + annulus tympanicus of the Anura = quadrate proper + its metapterygoid region, or that the metapterygoid process of the Anura = greater part of annulus tympanicus of Mammalia; the quadrate proper of Anura = that part of the annulus tympanicus, which, in the young of *Orycteropus*, Monotremata, and Marsupials, lies between the squamosal and the inner angle of the mandible. If, then, the quadrate has been converted into the Mammalian tympanic ring, the whole retrotympanic arm of the latter must be an outgrowth of that part of the quadrate to which, in Lizards and Snakes, is attached the extracolumellar cartilage. In *Pelophilus* there is already such an analogous, although still rudimentary, process.

The masticatory joint has undergone a complete change within the Amniota. In the Sauropida it is an articulatio quadrato-mandibularis, with an inner and an outer facet, both being concave on the mandible, convex on the quadrate. In the Monotremata there is developed a new articular or ascending process on the outer side of the articular region, by means of which the latter gains a new articulation, viz., with the squamosal, the convexity being carried by the mandible.

This alleviates the burden of the quadrate bone as a suspensorial element; it becomes reduced in bulk and gradually gives up its contact with the mandible; the malleus or outermost part of the extracolumella is attached to the quadrate, analogous to that similar attachment in Snakes and Chameleons.

In the Marsupials, traces only of the old suspensorial function of the quadrate remain; and, lastly, in the Monodelphic Mammals, the quadrate is entirely and solely devoted to the auditory service as principal carrier of the tympanic membrane. The masticatory joint has changed from a quadrato-mandibular into a squamoso-mandibular articulation.

Indications of the lessened importance of the quadrate, which is so powerfully developed in the Fishes and in the Urodela, are met with in the Anura, but there the quadrate is not rendered free, but, through its fusion with the squamosal, assumes conditions which at first sight seem strikingly like those which ALBRECHT assumes to exist in the Mammalia.* The cases are, however, analogous only, like other instances of the occurrence of Anurous features in the Mammalia, *e.g.*, the two condyles.

HUXLEY, in starting the view that the quadrate bone of Sauropida is transformed into the Mammalian malleus, logically assumed an articulation of the os articulare mandibulæ with the squamosal. He ignores the continuity of the long process of the malleus with MECKEL'S cartilage in the Mammalia, but lays stress upon the "continuity" of the auditory chain with the hyoid in certain Reptiles.

GEGENBAUR, and lately also PARKER, looks upon the malleus as the modified os articulare, because of its continuity with MECKEL'S cartilage, whilst they homologise the quadrate with the incus. They have therefore to assume that the incudo-malleolar articulation corresponds with the masticatory joint of the other Vertebrata. So far as the necessity of a newly-acquired formation of a mandibulo-squamosal articulation is concerned, these authors are right, and ALBRECHT is wrong, who upholds that the masticatory joint is an articulatio quadrato-articularis in all the Vertebrata. ALBRECHT'S great merit is, however, to have shown, by logical considerations, that the quadrate bone cannot in any case have become one of the elements of the inter-fenestral or auditory ossicular chain of the Mammalia. These reasons are:—The spiracle is homologous with the tympanic canal and the Eustachian tube. This canal is the cleft between the first and second visceral arches; it lies, therefore, behind the quadrate and in front of the hyomandibula. The cartilaginous auditory chain in the Anura, Sauropida, and Mammalia connects the same homologous parts, viz., the fenestra ovalis and the tympanum. It is universally admitted that at least the columella is a modification of the hyomandibula; therefore the columella lies behind the palato-quadrate-mandibular bar. The stapes-malleus chain (or columella + extra-columella) is situated behind the canalis tympanicus; the last remnant of the external opening, when not completely closed by the tympanum, is represented in Man by the occasional foramen Rivini. This defect I compare with the slit R in the imperfectly-closed tympanum of *Hatteria* and other Saurians (figs. 11, 12). Embryological development shows that the ossicular chain in Birds is originally placed closely against the hinder wall of the tympanic canal, and that it gradually severs itself from the latter, becomes free, and is then placed inside the tympanic canal. Consequently no pre-tympanic element like the quadrate can form part of the ossicular chain, unless

*ALBRECHT (with DUVERNOY, TIEDEMANN, PLATNER, and KOESTLIN) thinks that the Mammalian quadrate is fused with the squamosal, and is, in fact, the "processus zygomaticus." As proof of this hypothesis, he takes the highly pathological skull of a new-born child, in which the left zygomatic portion is partly separated by a suture from the rest of the squamosal. DUVERNOY mentions the same in a *Hydrochœrus* according to BAUR. The latter found the same on the right side of a still-born Tiger fœtus. He refers also to COPE'S remark upon the quadrate of the Permian Theromorphic *Clepsydra*. ". . . this horizontal ramus of the quadrate is nothing more than the zygomatic process of the squamosal bone of the Mammalia, forming with the malar bone the zygomatic arch." This may well be the case. Something very similar would occur after slight modification of that long horizontal anterior process of the quadrate, which is named *pt. c.* in PARKER'S fig. (16) of the Crocodile.

there be an element (incus or malleus) which lies in front of, whilst the rest of the chain is situated behind, the canal. But this is not the case, neither in any Reptile nor in any Mammal; in the latter the tympanic ring fulfils the topographic conditions required of a quadrate bone. Lastly, the lower branch of the n. facialis runs behind the spiracular cleft, in Elasmobranchi between the ligamentum cranio-hyomandibulare anterius and the hyomandibula (fig. 3), and behind the external auditory meatus in the Mammalia (see PARKER's fig. of Pig's embryo). The chorda tympani, a distal connexion between the hyoid branch of the facialis and the third branch of the trigeminus, passes behind and above the meatus, and in front of the ossicular chain.

But there are other reasons besides why the quadrate can be neither the incus nor the malleus of the Mammalia. Provided the malleus is the modified upper part of MECKEL's cartilage, then the incus cannot be the homologue of the quadrate, because of the impossibility of intercalating the quadrate as an incus into the ossicular chain, as a link between the stapes (hyomandibula) + lenticular (symplectic) and the malleus (os articulare). The Monotreme incus cannot be used as a support of such an hypothesis, because its connexion with the squamosal and its gradual abortion are not primitive features; moreover, this half-suppressed incus, and not the malleus, articulates typically with the stapedial part. PETERS correctly thought it highly improbable that the same element which, in the Monotremes, is reduced to a tiny rudiment, should, in the closely-allied Sauropida, still occur as an enormous bone, viz., as quadrate; this is all the more improbable, since the supposed conversion of the quadrate into the still large tympanic ring is so well supported.

HUXLEY (1863, p. 403) gives weighty reasons against this incus = quadrate view, in pleading for the "suprastapedial" part of the Crocodiles as the representative of the Mammalian incus.

The quadrate can likewise not be the Mammalian malleus, because in that case that part which, in Reptiles, Birds, and Anura, touches the tympanum, would have to be withdrawn from the tympanum to make room for the changed quadrate, the latter to be intercalated between the Sauropidan tympanum-bearing cartilage (henceforth to be incus) and the tympanum. We know of no intermediate stage which might indicate these enormous changes.

Lastly, the os articulare cannot have been converted into the malleus, because the latter is, like all the rest of the auditory chain, developed as cartilage; whilst the os articulare is ectochondral bone, like the other bony parts of the mandible. We shall not consider the enormous changes, wholly unsupported by observation, which would have had to be gone through by the ancestral Mammalia during the conversion of the old articulo-quadrate joint into an articulatio incudo-malleolaris, the loss of the quadrato-squamosal connexion, and the development of a new joint and break between the pars dentalis and the pars articularis of the mandible.

There is, then, nothing left but to assume that the distal part of the hyomandibula, analogous to a symplectic, has been converted into the tympanum-bearing malleus.

The continuity of the long process of the embryonic malleus with MECKEL's cartilage is explained by the conversion of the old lig. hyomandibulo-mandibulare into a cartilaginous connexion. That this can take place is indicated by Elasmobranchs. Here ALBRECHT errs. Instead of looking upon this connexion as secondarily acquired, he concludes that the hyomandibula forms the proximal half of the mandibular arch, his "costa mandibularis"; the next arch in front (the first of all) is then the palato-quadrate bar, his "costa palatina"; the original visceral cleft between these two arches is then the mouth + spiracle! His third arch is the hyoid alone ("costa hyoidea"). The second cleft is absent as an open one, although he calls it in his diagram a fissura mandibulo-hyoidea. From this follows that ALBRECHT looks upon the visceral arch arrangement of the Rajidæ as more primitive than that of the Notidanidæ. He reverses one of the most clearly and perfectly preserved series of phylogenetic development, as it has been worked out so admirably by GEGENBAUR in one of his most "Epoche machende Werke," and which I have tried to summarise in the first part of this essay.

We consider it as firmly established that the palato-quadrate bar, together with the mandible, forms the first arch. The discontinuity of cartilage between quadrate and mandible is explained by the extreme phylogenetic age of the joint (in *Heptanchus* the continuity of cartilage is still preserved). If we admit that the malleus is formed out of MECKEL's cartilage, we must admit also that the mandibular arch went through a stage similar to that represented in fig. 28, and that the extracolumellar connexion with the mandible in Reptiles is not homologous with MECKEL's cartilaginous continuation, because the latter must then be an articulo-dental connexion.

SUMMARY.

The phylogenetic development of the first visceral arches shows us some most interesting changes of function, which we can follow upwards from the lowest Selachians to the highest Mammals.

Originally entirely devoted to respiration as gill-bearing structures, the whole hyoidean arch becomes soon a factor in the alimentary system. Its proximal half forms the hinge of the masticatory apparatus; its distal half remains henceforth connected with the process of deglutition. Then this suspensorial arrangement is superseded by a new modification; the hyomandibula is set free and would disappear (it does nearly do so in Dipnoi and certain Urodela) unless it were made use of for a new function. With its having entered the service of the conduction of sound, it has entered upon a new departure, and it is saved from degeneration. The whole system of the one to four elements of the middle ear, which all have the same function as conductors of sound, is to be looked upon as *one* organ of *one* common origin, namely, as a modification of the hyomandibula, the primitive proximal paramere of the second visceral arch.

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Successive Modifications of the Mandibular and Hyoidean Visceral Arches.

I. Primitive condition. The palato-quadrate bar alone carries the mandible (Notidanidæ). The second arch is indifferent. Hyomandibula and quadrate (the palatine part is an outgrowth) are both attached to the cranium.

II. The hyomandibula gains a fibrocartilaginous connexion with the mandible; the masticating apparatus becomes amphistylic and occasionally hyostylic. (Rajidæ, most Selachians.)

The hyoid gains a cranial attachment (many Rajidæ).

III. The quadrate, or autostylic suspensorium, becomes preponderant; the hyomandibula is, as in Teleosteans, divided into a proximal and into a distal (symplectic) element. The proximal part is received into a fenestra of the otic capsule, and is converted into a stapes, whilst the distal half either remains (*Proteus*, *Siren*, *Menopoma*) or is lost (other Urodela). The whole hyomandibula would have been lost owing to its excalation from suspensorial functions, unless it had entered the auditory service.

IV. The autostylic arrangement prevails. The whole hyomandibula remains, gains an attachment on the "tympanum," and differentiates itself into several conjointed pieces, notably stapes, or columella proper, and extracolumella, or malleus.

The extracolumella gains connexion with the parotic cartilage; this connexion frequently remains, but in Anura alone it contains a special element of probably parotic origin.

The quadrate forms an important part of the tympanic frame.

IV.*a*. Collateral departure of the Anura. The connexion between the tympanal part of the hyomandibula with the mandible is lost.

V. The quadrate still forms the principal suspensorial part of the mandible. The extracolumella, or malleus, retains for a long time its previously-acquired connexion with Meckel's cartilage (Amniota).

V.*a*. The top end of the hyoid is attached to the cranium (*Gecko*, Mammalia), and is occasionally fused with the extracolumella (*Hatteria*).

V.*b*. Or the proximal portion of the hyoid is removed from the skull, and remains otherwise well developed (most Lizards), or its proximal portion becomes reduced and lost (Chelonia, Crocodilia, Ophidia, Aves).

V.*c*. The extracolumella gains an attachment to the quadrate, squamosal, or pterygoid, whilst its connexion with the mandible and the tympanum is lost (Ophidia, *Chamæleo*).

VI. The quadrate gradually loses its articulation with the mandible; the latter gains a new, outer, articulation with the squamosal; the quadrate acts entirely as a tympanic frame. Incus and malleus fuse sometimes with each other, and lean on to the parotic region. The masticating joint is doubly concavo-convex (Monotremata).

VII. The quadrate is converted into the principal part of the tympanic frame, viz., annulus tympanicus. The mandible has lost its articulation with the quadrate, and the masticatory joint is a single concave-convex one, the convexity belonging to the mandible (Monodelphia).

Modifications of the Visceral Arches.

	Amphibia.	Reptilia.	Aves.	Mammalia.
Ist arch. Palato-	quadrato-mandibul	ar arch.		
IInd arch. a. Hyomandibula.	Forms the cartila	ginous or osseous	apparatus of the	middle ear. [minus
b. Hyoid	Principal, hyoid arch	Small, anterior horn	Os entoglossum	Anterior horn, *s.* cornu = cerato + epi + stylo − } hyal
IIIrd arch (2nd branchial)	Remains in the adult Frog as the cornu thyroideum	Big, second horn	One only well-developed horn, wrongly called "hyoid"	Thyrohyal *s.* cornu posterius *s.* cornu majus
IVth arch (2nd branchial)		Often big, *e.g.*, in Chelonia	Disap	peared
V. VI. VII. Pre	sent in Tadpoles, p	artly permanent in	Perennibranchiata	.
VIII. Present on	ly in Heptanchus.			
Copula between II. and III. forms the	} Basihyal, *s.* cor	pus linguæ.	Basihyal, *s.* corpus	linguæ.
Copula between III. and IV. forms the			Urohyal	

Explanation of Plates.

The following abbreviations have been used throughout the figures

Als. Alisphenoid.
asc.p. Ascending process of quadrate.
A.ty. Annulus tympanicus, or tympanic bone.
Art. Os articulare mandibulæ.
Br.I. First branchial (= 3rd visceral) arch.
Cd. Condyle of occiput.
Cd.m. Condyle of mandible of Mammalia.
Col. Columella auris.
C.br. Ceratobranchial (of 3rd visceral arch).
ep. Epiotic bone or cartilage.
Ex.o. Exoccipital bone.
e.co. Extracolumella = extrastapedial + infra + suprastapedial of Huxley and Parker.
e.st. Extrastapedial process of Huxley and Parker = manubrium of malleus.

e.hy. Epihyal of PARKER.
F. Fenestra in extracolumella of *Hatteria* and *Chamæleo.*
Gl. Glenoid facet of squamosal.
l.h.m.m. Ligamentum hyoideo-mandibulare mediale.
l.h.m.l.i. „ „ „ laterale inferius.
l.h.m.l.s. „ „ „ „ superius.
l.hm.m. „ hyomandibulo-mandibulare.
l.hm.q. „ hyomandibulo-quadratum.
l.hm.h.p. „ hyomandibulo-hyoideum posterius.
l.m.h.i. „ mandibulo-hyoideum internum.
l.q.m.i. „ quadrato-mandibulare internum.
Hm. Hyomandibula = proximal part or paramere of 2nd or hyoid arch.
Hy. Hyoid or hyoid bar = distal „ „ „ „
I.A. Inner angle of mandible.
i.st. Infrastapedial process of HUXLEY and PARKER, frequently connected with MECKEL'S cartilage.
Md. Mandible.
men. Cartilaginous meniscus.
m.st. Mesostapedial of PARKER = principal part of columellar rod = stem of stapes.
Mk. MECKEL'S cartilage.
Par. Parotic corner of cranium.
Per. Periotic region.
Pt. Pterygoid.
p.gl. Postglenoid process of squamosal.
Q. Quadrate bone or cartilage.
Sq. Squamosal.
st. Stapes.
s.st. Suprastapedial of HUXLEY and PARKER.
Sp.c. Spiracular cartilage.
Siph. Siphonium of Crocodilia.
st. h. Stylohyal = epihyal of PARKER = proximal part of hyoid bar.

PLATE 71.

Fig. 1A. *Heptanchus cinereus.* Mandibular and hyoid arch; left, inner view.
Fig. 1B. *Heptanchus cinereus.* Quadrato-mandibular articulation; left, posterior view.

* The cartilaginous connexion, unaffected by the joint.

L.Br.I. Ligaments to cerato- and epi-branchial.

Fig. 2A. *Centrophorus granulosus.* Embryo. Inner view of left mandibular and hyoid arches.

Fig. 2B. *Centrophorus granulosus.* Embryo. Outer view of left mandibular and hyoid arches.

l.i. = ligamentum intermedium.

Fig. 3. *Oxyrhina gomphodon.* Left side, outer view of mandibular, posterior view of hyoidean and anterior view of first branchial arch.

Fig. 4. *Sphyrna zygæna.* Right side, inner view; first branchial arch turned over.

Fig. 5. *Trygon.* Cranium with first and second visceral arches; outer view.

Fig. 6. *Torpedo marmorata.* First and second visceral arch; outer view.

Fig. 7. *Menobranchus lateralis.*

Fig. 8. *Proteus anguineus.* Diagrammatic, after W. K. PARKER.

Fig. 9A. *Rana pipiens.* Tadpole. Lateral view of auditory chain; part of tympanic ring cut away. After PARKER.

Fig. 9B. *Otilophus margaritifer.* Half adult. Posterior view. After PARKER.

PLATE 72.

Fig. 10. *Gecko mauritanicus.* Ventral view of left side; hyoid apparatus turned back.

Fig. 11. *Hatteria punctata.* All the figures refer to the left side and are somewhat enlarged, except *C.* 2, which is natural size, and represents the columella and hyoid as seen from the median side.

Specimen *D* represents a posterior view.

Fig. 12. *Psammodromus scincus.* Left ossicular chain; natural size and enlarged.

Fig. 13. *Teju* sp. Left ossicular chain, posterior view, enlarged; and right ossicular chain, natural size. *Par.* and *Md.* Attachment of the strong ligament which borders the tympanum, to the parotic corner and to the mandible.

Fig. 14. *Alligator mississippiensis.* Natural size.

Fig. 15. *Crocodilus palustris.* Embryo of 4th stage ($3\frac{1}{2}$ inches long). Obliquely external view.

Fig. 16. *Crocodilus palustris.* Embryo of PARKER's 3rd stage (nearly 2 inches in length); lateral view of right side. Nos. 15–18. After PARKER, with his denomination of the parts.

Fig. 17. *Alligator mississippiensis.* Embryo of 5th stage ($4\frac{1}{2}$ inches long). Inner view.

Fig. 18. *Crocodilus palustris.* Embryo of 5th stage; outer view of whole hyoidean arch.

Fig. 19. Three stages, to show the reduction of the cartilage between the extracolumella and the mandible; embryos of *Crocodilus palustris* and *Alligator mississippiensis*, 5, 3, and $1\frac{1}{2}$ times enlarged. After PETERS.

Fig. 20. *Chamæleo vulgaris.* Posterior views, enlarged, to show attachment of extracolumella to quadrate. After PARKER.

PLATE 73.

Fig. 21. *Tropidonotus natrix.* Embryo. A. PARKER'S 3rd stage } After PARKER.
B. ,, 4th ,, }

Fig. 22A. *Pelophilus madagascariensis.* Inner view of quadrato-mandibular region of the right side, with the muscles, and the extracolumella attached to the quadrate *in situ.* Natural size.

Fig. 22B. *Pelophilus madagascariensis.* Columella with its sheath and with the meniscus between the extracolumella and the quadrate.

Fig. 23. *Eunectes murinus.* Ventral view, right side. The cartilaginous extracolumella between columella and quadrate is taken away. Natural size.

Fig. 24. *Crotalus durissus.* Inner view of right pterygoid, quadrate, and columella with its sheath.

Fig. 25A. *Rhea americana.* Ventral view. Natural size.

Fig. 25B. *Rhea americana.* Dorsal view of articular region of left mandible.

1. Flat articular facet for inner articular process, or distal end, of quadrate.
2. Flat articular facet for lateral aspect of inner articular process of quadrate.
3. Concave articular facet for posterior outer process of quadrate.
4. ,, ,, ,, quadrato-jugal process of quadrate.

Fig. 26. *Echidna setosa.* Natural size.

Fig. 27. *Echidna brujni.* Natural size.

Fig. 28. *Orycteropus capensis.* Fœtus. Ventral view. Natural size. The tympanic ring is still connected with the squamosal. *a.m.* = remnant of the lost articulation with the (lost) inner angle of the mandible.

Fig. 29. *Thylacinus.* Juv. Natural size.

Fig. 30. *Phascolomys wombat.* Natural size.

PLATE 74.

The figures on Plate 74 represent diagrammatically some of the most important modifications of the first and second visceral arches.

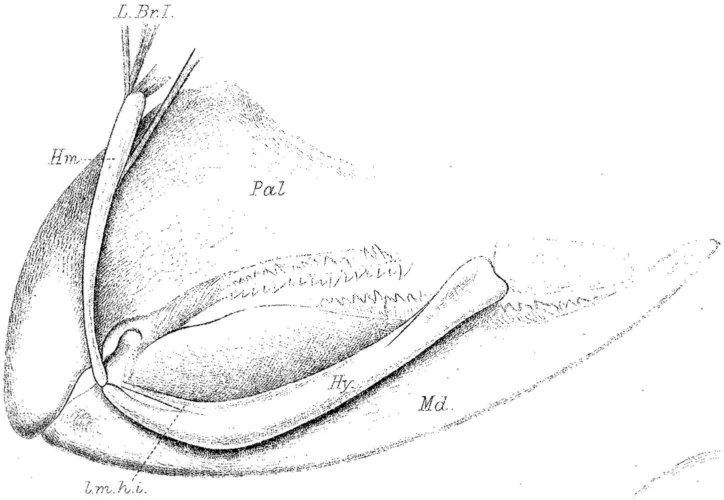


Fig 1.A.
Heptanchus-cinereus.
Left, Inner-view.

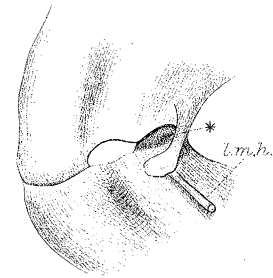
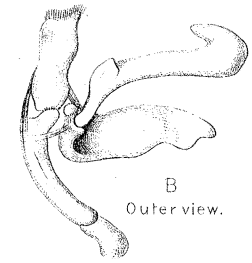


Fig 1.B.
Heptanchus.
Left, from behind.



Centrophorus-granulosus.
Embryo.

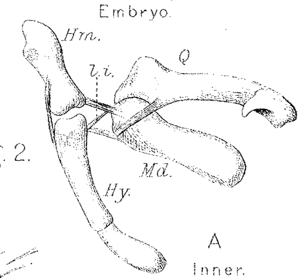


Fig. 2.

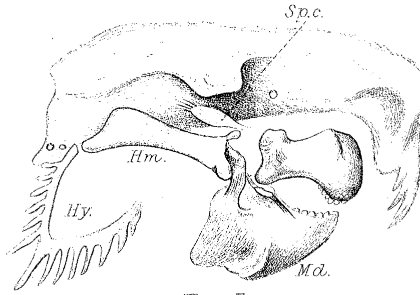


Fig. 5.
Trygon.

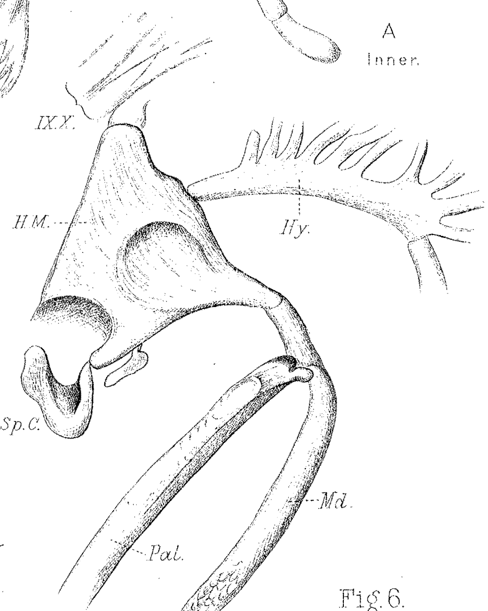


Fig 6.
Torpedo marmorata.
Left, dorsal-view.

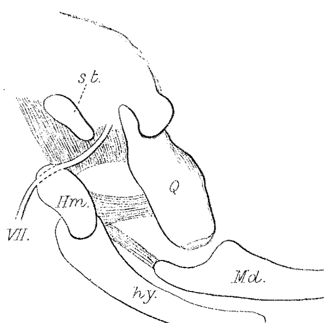


Fig 8.
Proteus.

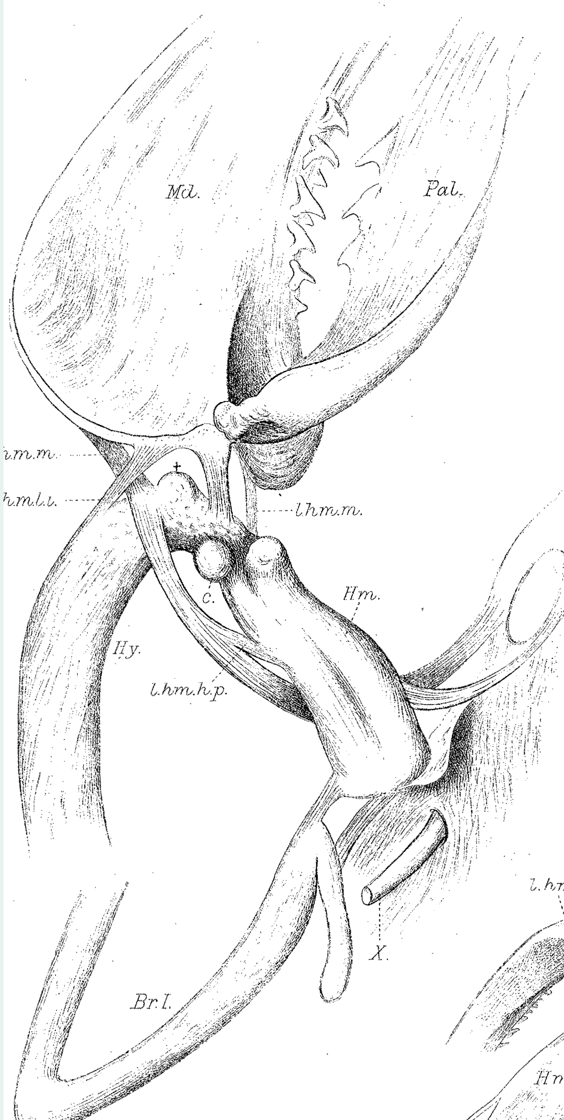


Fig 3.
Oxyrhina gomphodon.
Left, outer, backview.

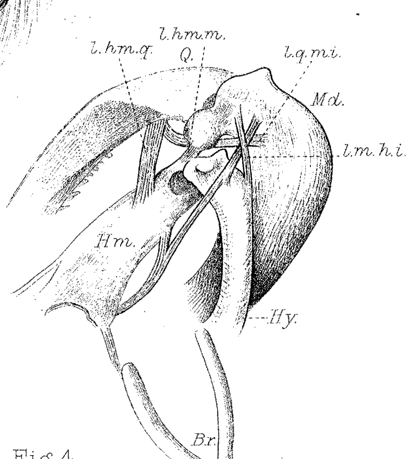


Fig 4.
Sphyrna zygaena.
Right, inner, view.

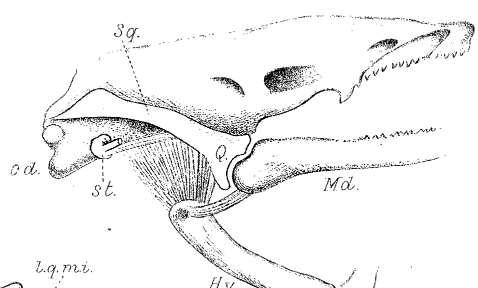


Fig 7.
Menobranchus.
Right side view.

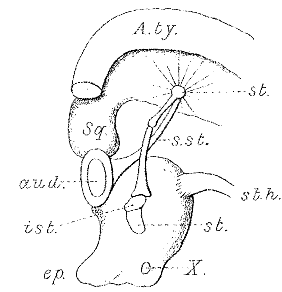


Fig 9.A.
Rana pipiens. Tadpole.

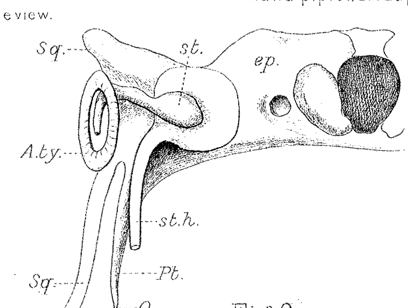


Fig 9.B.
Otilophus margaritifer. Half adult.

Gadow. del.

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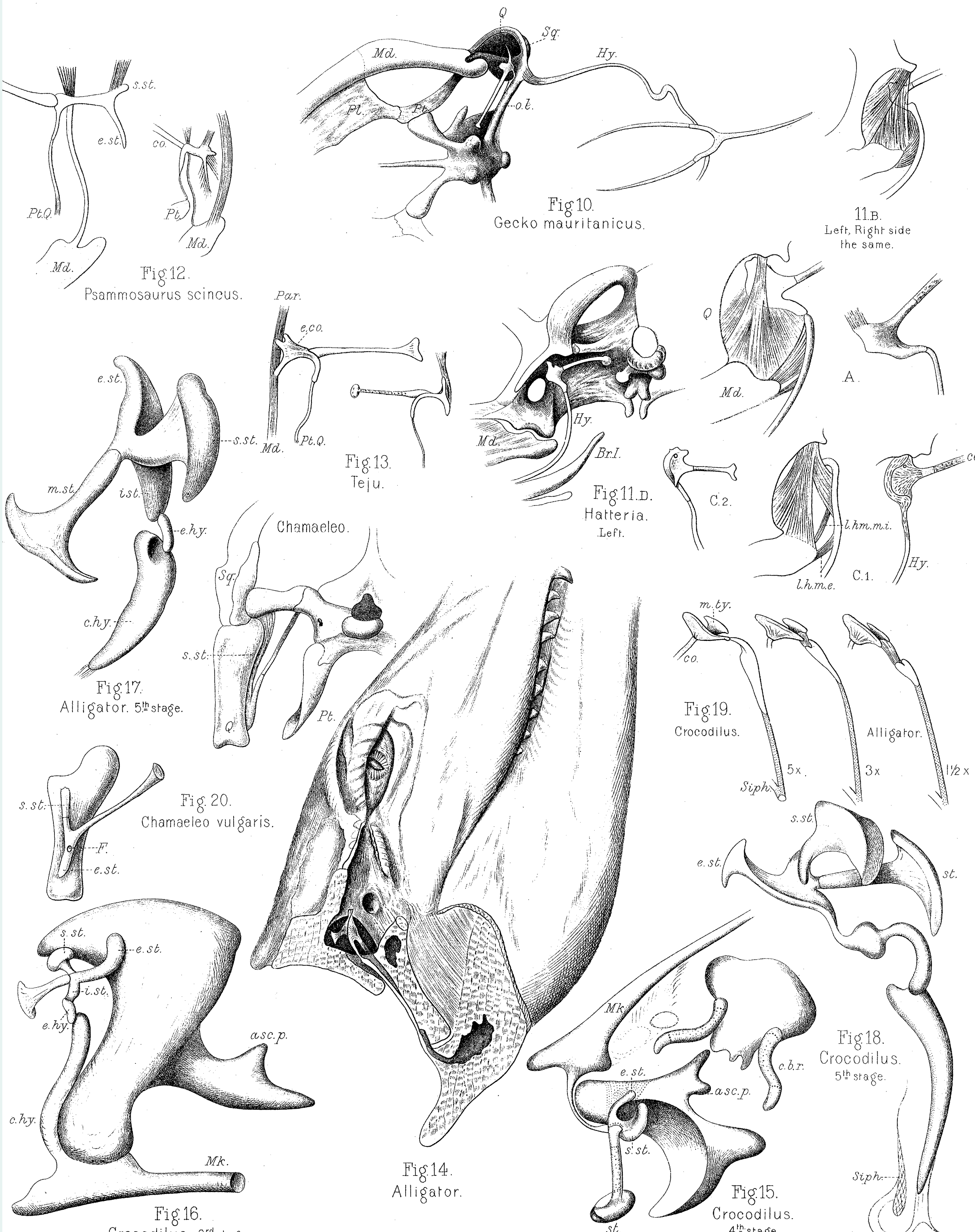


Fig 10. Gecko mauritanicus.

11.B. Left, Right side the same.

Fig 12. Psammosaurus scincus.

Fig 13. Teju.

Fig 11.D. Hatteria. Left.

Fig 17. Alligator. 5th stage.

Fig 19. Crocodilus.

Fig 20. Chamaeleo vulgaris.

Fig 14. Alligator.

Fig 18. Crocodilus. 5th stage.

Fig 16. Crocodilus. 3rd stage.

Fig 15. Crocodilus. 4th stage.

Gadow. del

Lith & Imp. Camb. Sci Inst. Co.

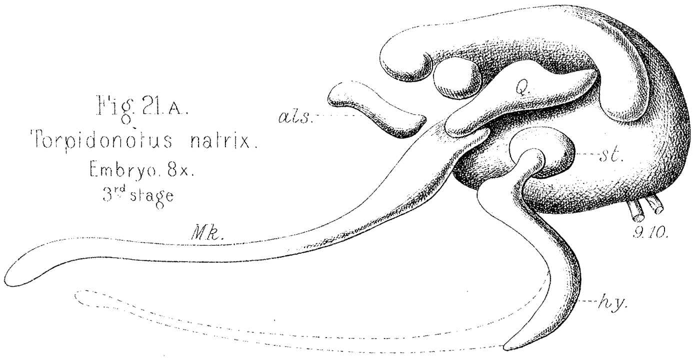


Fig. 21A.
Torpidonotus natrix.
Embryo. 8x.
3rd stage

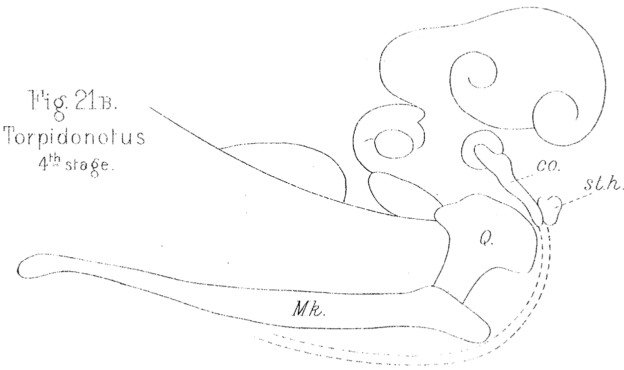


Fig. 21B.
Torpidonotus
4th stage.

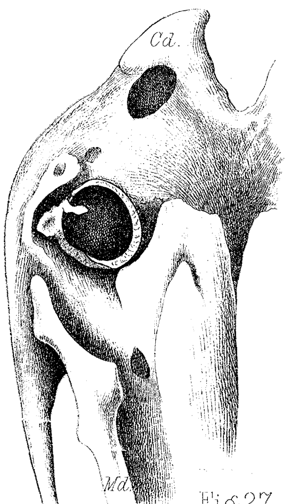


Fig. 27.
Echidna brujni.

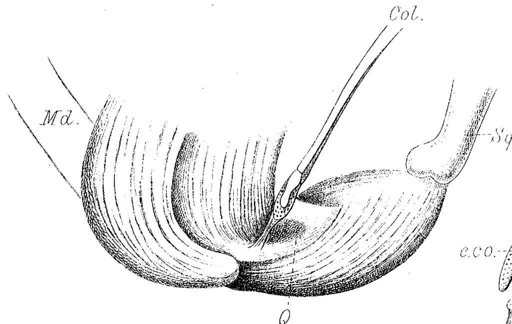


Fig. 22A.
Pelophilus.
Right, inner view.

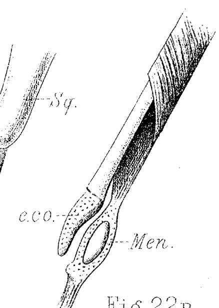


Fig. 22B.

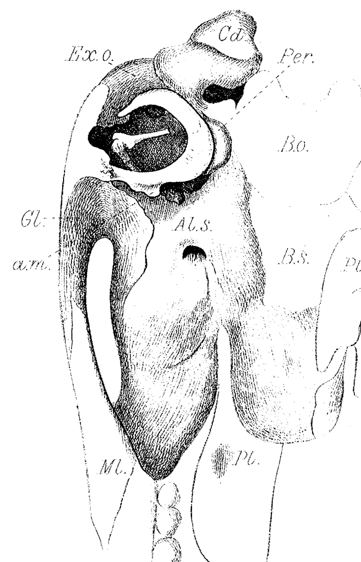


Fig. 28.
Orycteropus capensis.
Foetus.

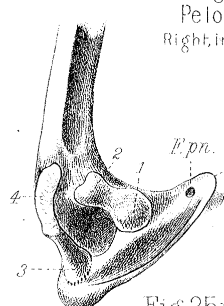


Fig. 25B.
Regio articularis of Left Mandible.
Dorsal view.

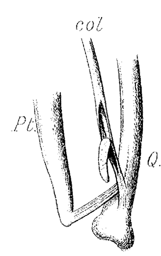


Fig. 24.
Crotalus.
Right side.

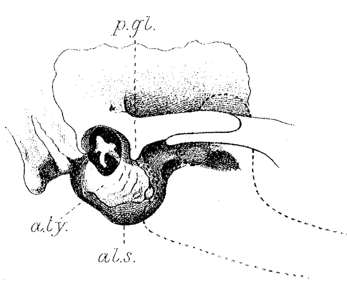


Fig. 29.
Thylacinus, juv.

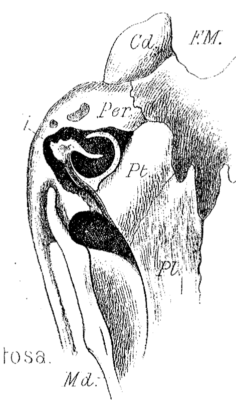


Fig. 26.
Echidna setosa.

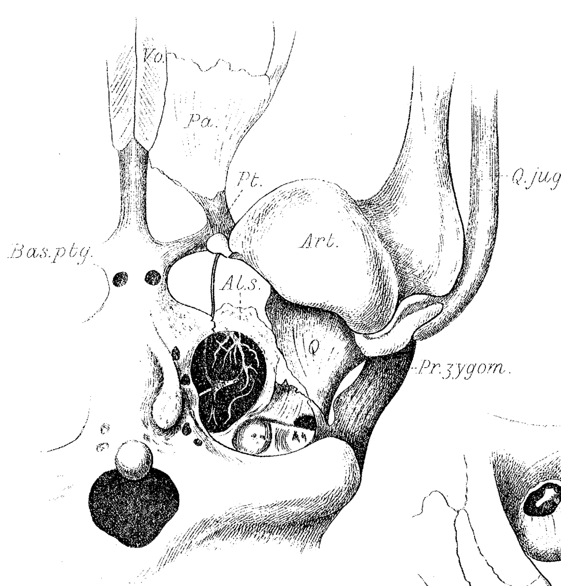


Fig. 25A.
Rhea americana.
Nat. size.
Ventral view.

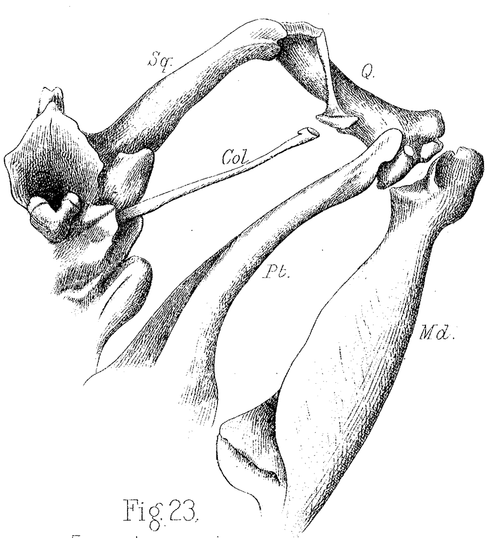


Fig. 23.
Eunectes murinus.

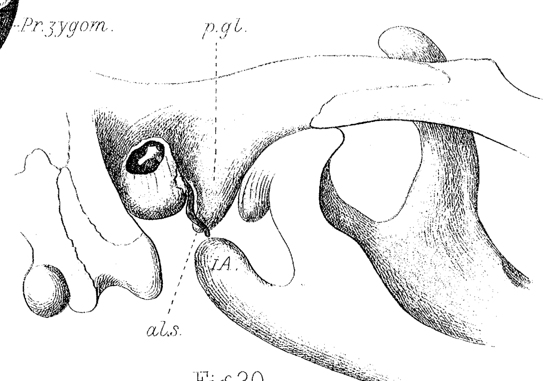
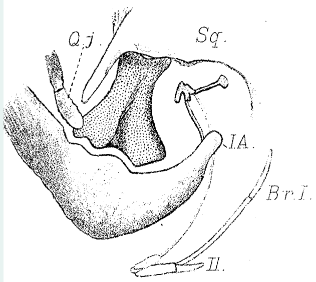
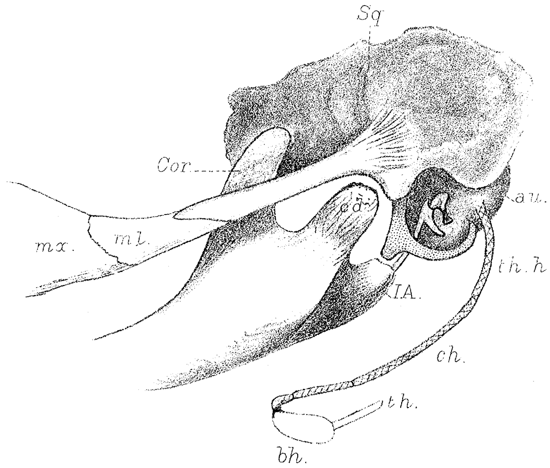


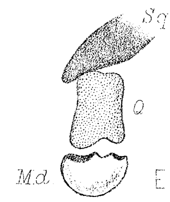
Fig. 30.
Phascolomys wombat.



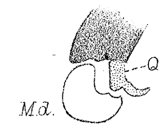
Aves.



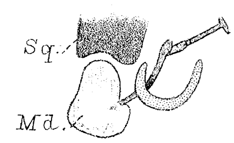
Combined diagram of Pro–Meta–and Eutheria.



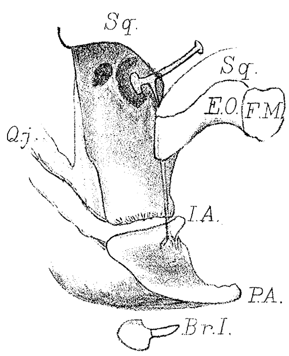
Ichthyopida.



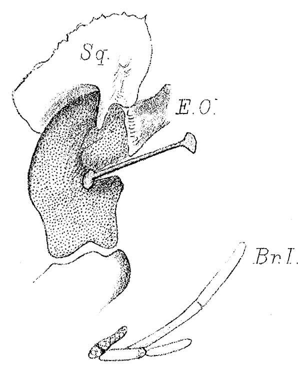
Embryonic Monotremes and Didelphia.



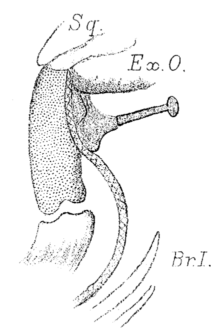
Mammalia.



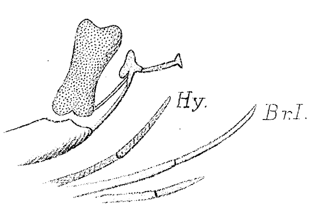
Crocodilia.



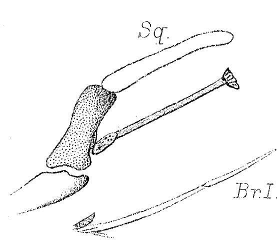
Chelonia.



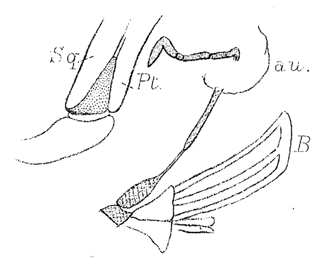
Hatteria.



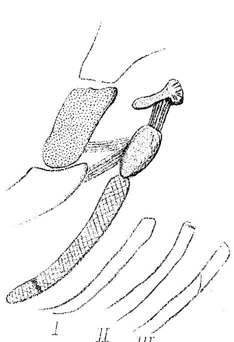
Sauria.



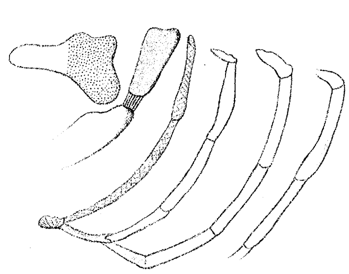
Ophidia.

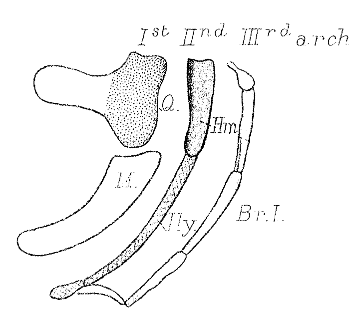


Anura.



Proteus.


Centrophorus.



Notidanidæ.

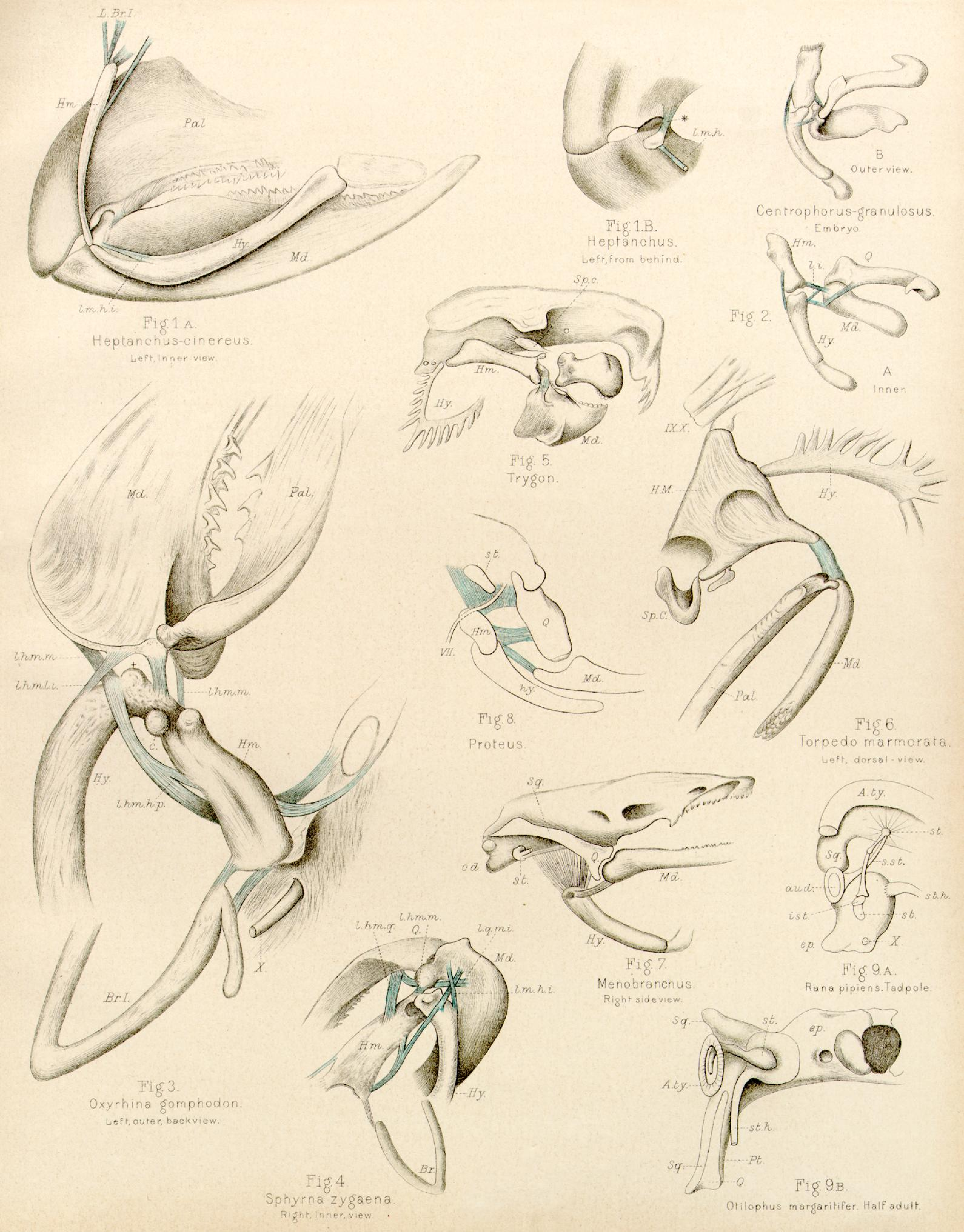


PLATE 71.

Fig. 1A. *Heptanchus cinereus.* Mandibular and hyoid arch; left, inner view.

Fig. 1B. *Heptanchus cinereus.* Quadrato-mandibular articulation; left, posterior view.

Fig. 2A. *Centrophorus granulosus.* Embryo. Inner view of left mandibular and hyoid arches.

Fig. 2B. *Centrophorus granulosus.* Embryo. Outer view of left mandibular and hyoid arches.

l.i. = ligamentum intermedium.

Fig. 3. *Oxyrhina gomphodon.* Left side, outer view of mandibular, posterior view of hyoidean and anterior view of first branchial arch.

Fig. 4. *Sphyrna zygæna.* Right side, inner view; first branchial arch turned over.

Fig. 5. *Trygon.* Cranium with first and second visceral arches; outer view.

Fig. 6. *Torpedo marmorata.* First and second visceral arch; outer view.

Fig. 7. *Menobranchus lateralis.*

Fig. 8. *Proteus anguineus.* Diagrammatic, after W. K. Parker.

Fig. 9A. *Rana pipiens.* Tadpole. Lateral view of auditory chain; part of tympanic ring cut away. After Parker.

Fig. 9B. *Otilophus margaritifer.* Half adult. Posterior view. After Parker.

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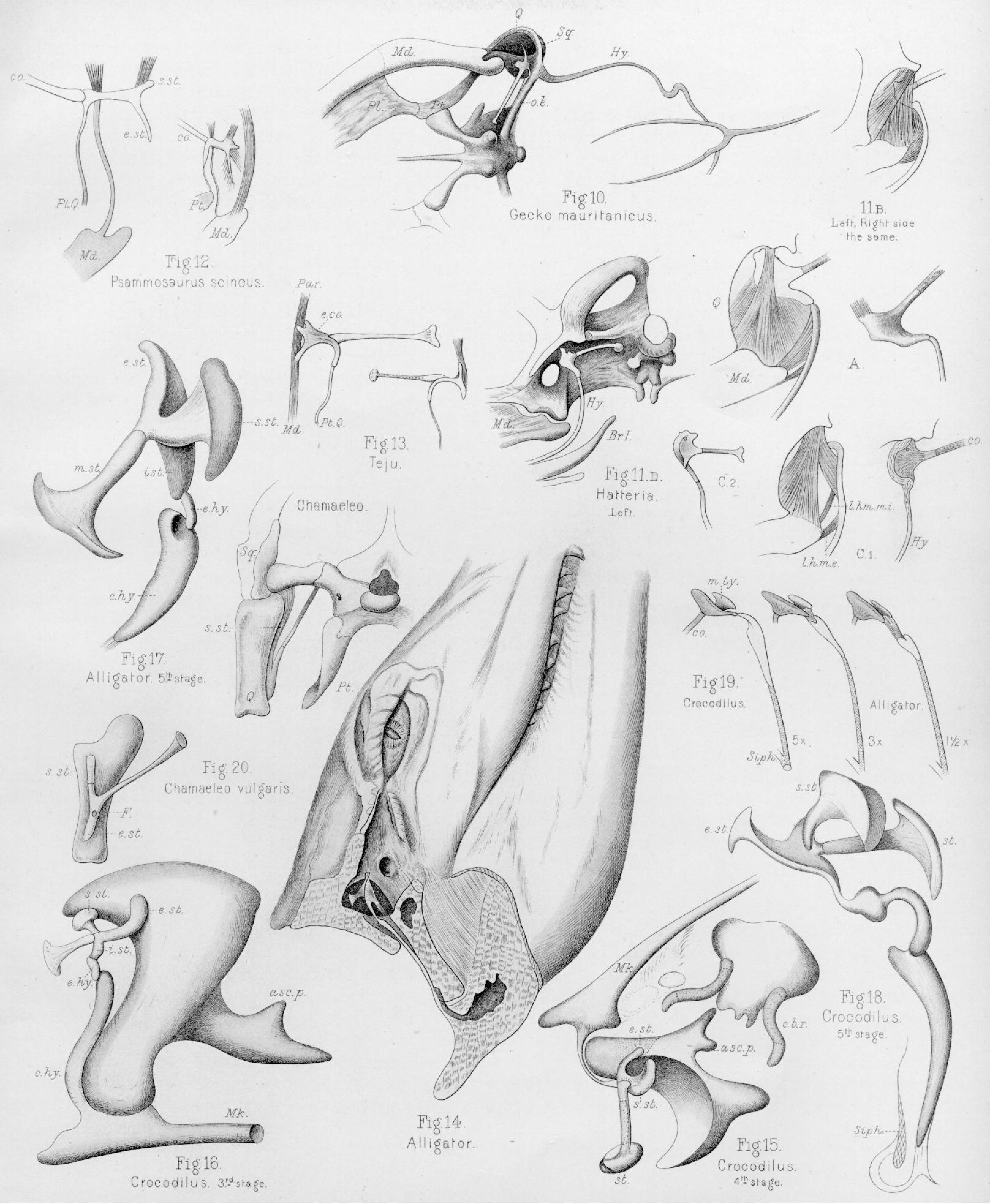

PLATE 72.

Fig. 10. *Gecko mauritanicus.* Ventral view of left side; hyoid apparatus turned back.

Fig. 11. *Hatteria punctata.* All the figures refer to the left side and are somewhat enlarged, except *C.* 2, which is natural size, and represents the columella and hyoid as seen from the median side.

Specimen *D* represents a posterior view.

Fig. 12. *Psammodromus scincus.* Left ossicular chain; natural size and enlarged.

Fig. 13. *Teju* sp. Left ossicular chain, posterior view, enlarged; and right ossicular chain, natural size. *Par.* and *Md.* Attachment of the strong ligament which borders the tympanum, to the parotic corner and to the mandible.

Fig. 14. *Alligator mississippiensis.* Natural size.

Fig. 15. *Crocodilus palustris.* Embryo of 4th stage (3½ inches long). Obliquely external view.

Fig. 16. *Crocodilus palustris.* Embryo of PARKER'S 3rd stage (nearly 2 inches in length); lateral view of right side. Nos. 15–18. After PARKER, with his denomination of the parts.

Fig. 17. *Alligator mississippiensis.* Embryo of 5th stage (4½ inches long). Inner view.

Fig. 18. *Crocodilus palustris.* Embryo of 5th stage; outer view of whole hyoidean arch.

Fig. 19. Three stages, to show the reduction of the cartilage between the extra-columella and the mandible; embryos of *Crocodilus palustris* and *Alligator mississippiensis*, 5, 3, and 1½ times enlarged. After PETERS.

Fig. 20. *Chamæleo vulgaris.* Posterior views, enlarged, to show attachment of extracolumella to quadrate. After PARKER.

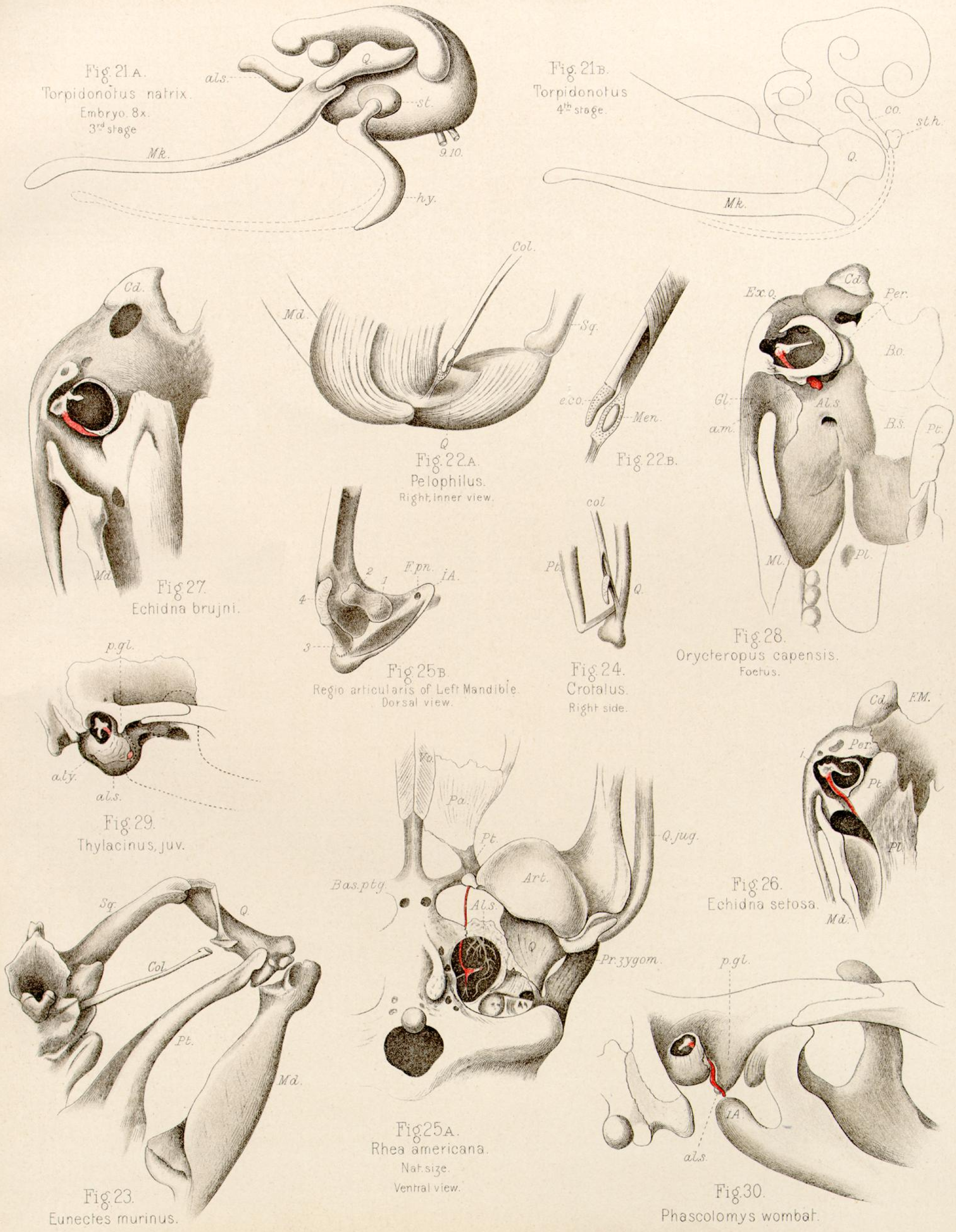

PLATE 73.

Fig. 21. *Tropidonotus natrix.* Embryo. A. PARKER's 3rd stage, B. ,, 4th ,, } After PARKER.

Fig. 22A. *Pelophilus madagascariensis.* Inner view of quadrato-mandibular region of the right side, with the muscles, and the extracolumella attached to the quadrate *in situ.* Natural size.

Fig. 22B. *Pelophilus madagascariensis.* Columella with its sheath and with the meniscus between the extracolumella and the quadrate.

Fig. 23. *Eunectes murinus.* Ventral view, right side. The cartilaginous extra-columella between columella and quadrate is taken away. Natural size.

Fig. 24. *Crotalus durissus.* Inner view of right pterygoid, quadrate, and columella with its sheath.

Fig. 25A. *Rhea americana.* Ventral view. Natural size.

Fig. 25B. *Rhea americana.* Dorsal view of articular region of left mandible.

1. Flat articular facet for inner articular process, or distal end, of quadrate.
2. Flat articular facet for lateral aspect of inner articular process of quadrate.
3. Concave articular facet for posterior outer process of quadrate.
4. ,, ,, ,, quadrato-jugal process of quadrate.

Fig. 26. *Echidna setosa.* Natural size.

Fig. 27. *Echidna brujni.* Natural size.

Fig. 28. *Orycteropus capensis.* Fœtus. Ventral view. Natural size. The tympanic ring is still connected with the squamosal. *a.m.* = remnant of the lost articulation with the (lost) inner angle of the mandible.

Fig. 29. *Thylacinus.* Juv. Natural size.

Fig. 30. *Phascolomys wombat.* Natural size.

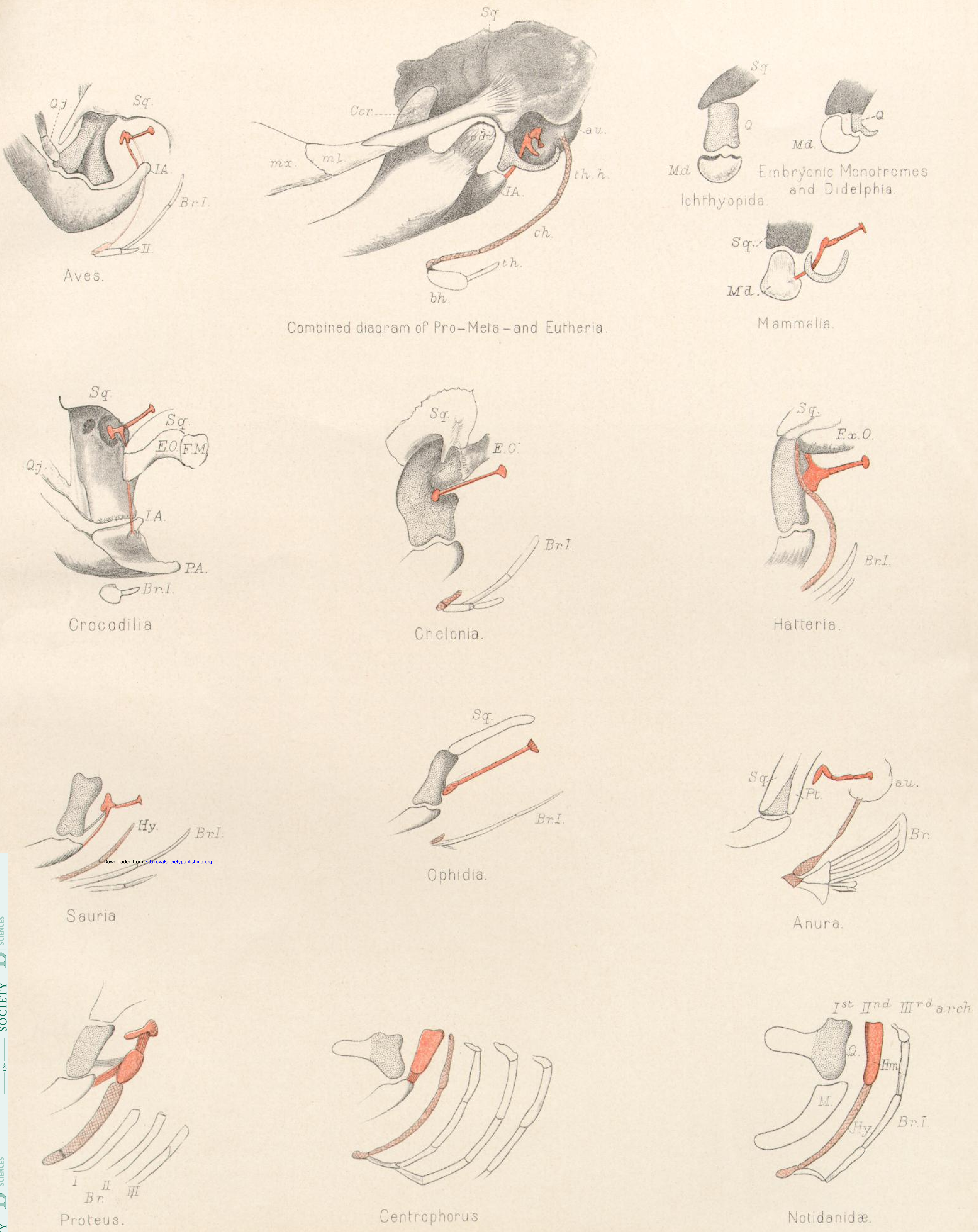

PLATE 74.

The figures on Plate 74 represent diagrammatically some of the most important modifications of the first and second visceral arches.