PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

On the Ear Region of Certain of the Chrysochloridae

C. Forster Cooper

Phil. Trans. R. Soc. Lond. B 1928 **216**, 265-283
doi: 10.1098/rstb.1928.0005

V. *On the Ear Region of Certain of the Chrysochloridæ.*

By C. Forster Cooper, M.A., *Superintendent of the University Museum of Zoology, Cambridge.*

Communicated by Prof. J. T. Wilson, *F.R.S.*

(Received July 22, 1927,—Read February 2, 1928.)

(Plates 15–17.)

Introduction.

That the structure of the ear bones of some members of the family of Chrysochloridæ is unusual has long been known. The first to note any peculiarity was Hyrtl,* who, in 1845, pointed out that in *Chrysochloris capensis* the head of the malleus was much enlarged.

Doran,† in 1878, in his comprehensive work on the ossicula auditus, gave a description and figures of the ear bones of a *Chrysochloris*, but without giving any specific name. It is, however, clear, on comparing his figures with those of Hyrtl, as well as from evidence given in this present paper, that he was also using *C.* "*capensis*"‡ for his main description. He also examined *C. trevelyani*, in which species he stated that there is "a small tubercular processus muscularis in the neck of the manubrium of *C. trevelyani*, where the head does not form so great a prominence in the temporal fossa." It is curious that, having got so far, he did not note the great difference between the ear bones of this species and the one that he was using for his general description.

Dobson, writing in 1882, quoted Doran's work but added very little to our knowledge of the ear bones, and his work is chiefly of use for its classification of the group as far as it was then known. In 1905 Van Kampen quoted and commented on these authors' work, and himself added to our understanding of the problem. His own results are considered later on in this paper. Leche, in 1907, noted that *C. hottentota* had ossicles more nearly approaching the normal.

Finally Broom in 1916 described in some detail the conditions shown in the skull of a newly-born specimen of *C. hottentota*. In this account he does not lay great stress on the ear bones, which he mentions only as being "relatively large." His account,

* References to authors will be found in the list on page 281.

† Doran mentions Otto and Rudolphi as two observers earlier than Hyrtl. It appears, however, from his statement that their work may be neglected, except from the historical point of view.

‡ = *C. asiatica* = *C. aurea*.

 [Published March 21, 1928.

however, is in other respects most useful, since it contains a description and figures of the sutures of the skull bones. These close very early in life, and young specimens still showing them are, as BROOM himself points out, extremely rare and, from the retiring habits of the Golden Moles, very difficult to obtain.

It seems, then, that investigations of the ear bones of these animals have been made by comparatively few workers, and have been confined to the two species C. *capensis* and *C. hottentota*. Observations on other species, described in the present paper, reveal an unexpected range of variation in the conformation of these organs.

MATERIAL AVAILABLE FOR THE PRESENT INVESTIGATION AND ACKNOWLEDGMENTS

Several specimens were fortunately procurable for dissection, viz., *C. trevelyani*, one young and one old individual, one *C. rutilans*, three *C. villosa* and, probably belonging to *C. asiatica*, one fœtus. In addition, I have been able to examine the external features and to some extent, by means of X-ray photographs, the condition of the ear ossicles in a number of other species from the collection of the British Museum.

Some of these specimens were in the collection of the Cambridge University Museum of Zoology; for others I am indebted to Dr. H. GADOW and Prof. D. M. S. WATSON, and for the privilege of examining the British Museum Specimens to the Keeper of the Zoological Department and Mr. M. A. C. HINTON.

I am especially indebted to Prof. J. T. WILSON, in whose Department of Anatomy the sections of the embryo were cut and mounted for me, for the loan of certain instruments as well as for much technical advice; also to Dr. APPLETON, of the same department, with whom I have discussed certain questions. Dr. FF. ROBERTS most kindly undertook the X-ray photography.

As a result of the examination of this material it is shown that there is an extraordinary range of variation in size and shape of the ear ossicles, from a condition almost "normal" to one of extreme hypertrophy, accompanied by certain consequent changes in the external features of the head.

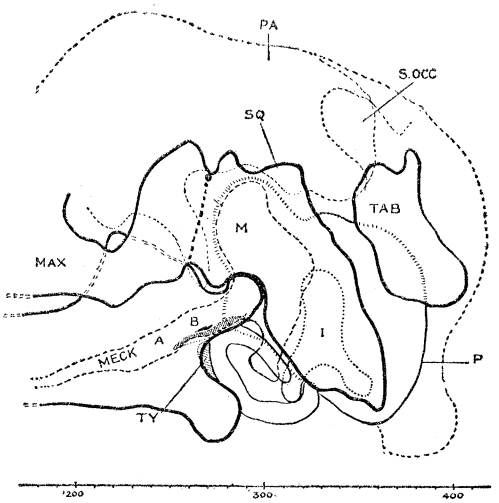
THE EAR REGION IN AN EMBRYO.

This specimen, which I owe to the kindness of Dr. GADOW, was of large size, and presumably ready to be born. Many parts of the skull are still cartilaginous, though a considerable amount of ossification is present. The external auditory meatus is not yet open, but the ear bones may be supposed to have reached nearly to their full development.

In detail the ossicles present the following characters as seen in sections and by reconstruction*:—The malleus in a lateral external aspect appears as a tall and somewhat

* The specimen was not sectioned exactly at right angles to the longitudinal plane, and there may be some slight distortion in the figure. The diagram was reconstructed from a mean of the two sides, and is probably not misleading in its general characters.

pear-shaped bone (text-fig. 1), from which, near the middle of the anterior border, springs the stout Meckel's cartilage. This cartilage, at its origin from the malleus, is supported underneath by a small gutter-like ossification which, without much doubt, represents the pre-articular. Attached to the inner side of this ossification is another one, very much smaller, which may possibly represent the sur-angular.

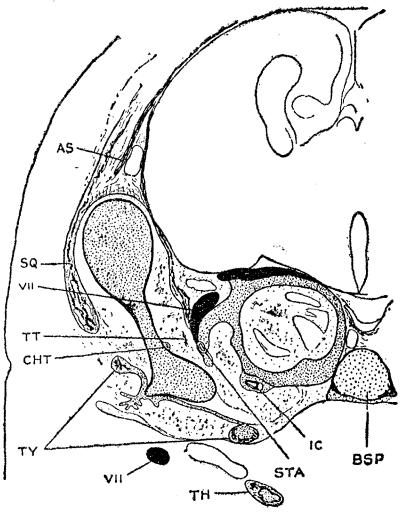


TEXT-FIG. 1.—Diagram of a reconstruction of the head of an embryo of Chrysochloris sp. TAB., *Tabular*. S.OCC., *Supra-occipital*. The line points to a cartilaginous extension which runs forward under the parietal. PA., *Parietal*. MAX., *Maxilla*. The ossification, at this stage, has proceeded no further backwards than to a point just in front of the coronoid process of the lower jaw. From this point there is an unossified tract as far as the dotted line which marks the ossified anterior border of the squamosal. SQ., *Squamosal*. M., *Malleus*. I., *Incus*. P., The outline of the cavity of the middle ear, the line is shown as broken when it passes under other structures. TY., *Tympanic ring*. The ring is as yet not closed. The line points to the forwardly-directed flange. MECK., *Meckel's cartilage*. A., The *pre-articular*. B., The "*sur-angular*." The latter is drawn displaced upwards: actually its position is at the same level and on the inner side of the pre-articular.

From the region of Meckel's cartilage the malleus narrows down to a rather small manubrium. In section at right angles to the longitudinal plane it is seen (text-fig. 2) to be somewhat like an hour-glass in shape, with the head end rather larger than the lower end. This lower part is, however, of considerable size in the transverse direction owing to the blunt rounded internal process shown in the figure.

The attachment to the tympanum takes the form of a short ridge which, in section, appears as a point. The front part of this ridge represents a small and rather blunt *processus brevis*. Apart from the attachment to the tympanic membrane and, of course, the articulation with the incus, the malleus seems to have little support. There is no trace or sign of a superior ligament and the *tensor tympani* is very weakly developed and, in this stage of development at all events, consists only of a small bundle of fibres running near the *canalis facialis* which are not in any way attached to the malleus. Whether they are so eventually or are vestigial cannot be told. This absence of ligaments

no doubt accounts for the fact that in dried skulls the malleus is always loose, and rattles when the skull is shaken. Its comparative great size and weight is sufficient for any small shock to loosen it from the dried tympanum.



TEXT-FIG. 2.—Section (No. 302) showing the malleus at the point where the manubrium, with its internal process, is attached to the tympanum. Cartilage is closely dotted. The embryonic "jelly" which at this stage fills most of the middle ear, except below the manubrium, is sparsely dotted. Ossification, *e.g.*, in the squamosal, tympanic ring and elsewhere, is shown by irregular black lines. Nerves are black. AS., *Alisphenoid*. SQ., *Squamosal*. VII., Branches of the seventh nerve. TT., Small bundles of fibres representing the vestige of the *tensor tympani*. CHT., *Chorda tympani*. TY., *Tympanic ring*. The ring is ossified: between it stretches the beginning of the tympanum. The digitate body just outside the junction of the manubrium and the tympanic membrane is the tract, as yet unopened, of the external auditory meatus. TH., *Tympano-hyal*, above which is a large vein. STA., *Stapedial artery*. IC., *Internal carotid*. BSP., *Basisphenoid*. The small notch in the external outline marks the future opening of the external auditory meatus.

DORAN'S description of the malleus of an adult *Chrysochloris* runs as follows: "The head is extremely elongated, so as to be over a quarter of an inch in length . . . pyriform, although, being rather thick and cylindrical at its root, convex behind, and slightly concave in front, it may be better compared in shape to a grenadier's bearskin . . . the neck is long, stout and cylindrical, and a small depression on it extends towards the root of the head, and probably represents the site of the lamina, the ridge of bone below it being the root of the *processus gracilis*. I have found the ossicle slightly adherent to the tympanic bone at that ridge, and have reason to believe that part of the *processus gracilis* is modified and enlarged, and assists in forming a portion of the process chiefly developed from the head. The manubrium is very short, being hardly the length of the neck; it bears a very prominent *processus brevis*, and is scarcely dilated at the extremity. HYRTL does not appear to recognise either neck or *processus brevis* in the Golden Mole."

A comparison of this account of a dried skull of an adult with the diagrammatic reconstruction here given of an embryo (text-fig. 1) shows that in general configuration there is considerable resemblance. Further comparison with an actual specimen of *C. asiatica* (= *C. aurea* = *C. capensis*) also shows that DORAN's unnamed specimen, as well as the embryo now described, belong either to this species or to one of a limited number of others. For, as will be seen from the figures, given further on, the tall pear-shaped form of malleus is characteristic of a certain number of the Chrysochloridæ only. DORAN's quotation that HYRTL found no neck, or *processus brevis*, suggests that he had some other species to examine.

The incus is an unusually large element, which, in side view, is tri-radiate with the radii approximately equal (text-fig. 1). The head pointing directly above is rather the larger, and is as broad as the head of the malleus, with whose inner and hinder face it articulates. The anterior lower radius, the *processus longus*, runs downwards and forwards, and bends round inwards to articulate with the stapes. The posterior radius or *processus brevis* is rather the longer, and runs downwards and backwards to end in a well-defined ligament, which runs from it below the cartilage (as yet unossified) of the petrosal. The stapes is of the usual stirrup shape, and has a well-developed stapedial muscle. The stapedial artery runs through the stapes protected by a cartilage canal which, as can be seen in other forms, becomes ossified, as it does in many of the Insectivora.

As regards the boundaries of the region of the middle ear, the most noticeable character is, of course, the enlargement of the ear space to house the hypertrophied head of the malleus. There has been some difference of opinion as to the elements which take part in the formation of this epitympanic cavity. According to HYRTL it is formed by a divergence of the wings of the sphenoid, and the squamosal takes no part in it. VAN KAMPEN, on the other hand, considers it to be bounded by the squamosal, and the cavity to lie "as usual between the squamosal and the periotic." That VAN KAMPEN, in spite of the fact that he had only dried adult skulls to examine, was the more correct is shown clearly enough by the sections (text-figs. 2 and 3) of this embryo. The greater part of the roof of the epitympanic cavity, however, is formed not so much by the squamosal, as VAN KAMPEN states, as by a wing which runs upwards from the vestibular end of the petrosal and curves round the head of the malleus, following its outline pretty closely. This part of the roof, after passing over the head, joins the squamosal, which bounds the lateral parts of the malleus and extends backwards over the larger part of the ear region (diagram, text-fig. 1). In a young skull of *C. trevelyani* (Plate 15, fig. 3) this part, seen from the inner face, shows the junction between the petrosal flange and the squamosal as a clearly-defined ridge.

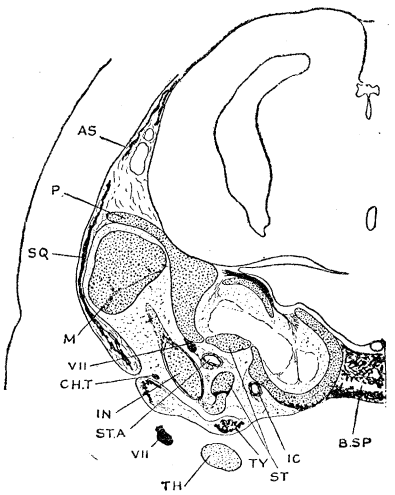
Certain other structures seen in the embryo may be mentioned briefly. The tympanic ring is still open towards the outer side, and on its front border there is a small shelf of bone running towards the angle of the jaw. The squamosal is a somewhat elongated bone running to a point below; at this stage it is ossified up to a line a little in front of the glenoid cavity, and as far as the head of the malleus. Beyond

this point there is a tract of unossified tissue which runs directly to the ossified process of the maxilla, which is growing backward to join the squamosal. No trace is present of any ossification in this tract, which could be called the jugal. Behind the squamosal there is a separate ossified tabular, similar to that described by BROOM for *C. hottentota*.

THE ALLEGED COMMUNICATION BETWEEN THE MIDDLE EAR REGIONS.

It is convenient here to interpolate a remark on HYRTL'S statement, which is quoted also by VAN KAMPEN, that it is a peculiarity of *Chrysochloris* that the two ear cavities communicate with one another. HYRTL says that "in a careful study of the ear cavities after taking away the bullæ, one is convinced that each cavity is in connection with the sinus of the sphenoid through an easily-found opening towards the front inner side, and thus constitutes a connection between the two cavities."

The embryo now being described does not altogether bear out this statement. It is true that the sphenoid is much honey-combed, and that in the diploe a considerable sinus system is present (text-fig. 3). This is filled with ramifications of the venous system in the complicated lacunæ of the sphenoid.



TEXT-FIG. 3.—Section (No. 319) through the posterior part of the head of the malleus, middle of the incus and the stapes. P., The extension of the upper part of the *periotic* over the head of the malleus, forming the inner wall of the epitympanic cavity. ST., *Stapes*. The section passes through both plate and the upper part of the stirrup which joins the incus. M., The line points to the junction of the malleus (above) and the incus (the lower portion). IN., The superior limb of the incus. B.SP., The *basisphenoid*, showing the lacunæ of a transverse vein. Other lettering as in fig. 2.

In a dried skull these lacunæ might easily appear as a true connection between the two ear regions, but I am not able to convince myself that there is any true intercommunication in life. A median longitudinal section of an adult skull of *C. villosa*, confirmed by a transverse section through the sphenoidal region in another skull (Plate 15, fig. 7), also failed to demonstrate any interconnection.

Hyrtl was, however, so careful and so skilled an investigator that one hesitates before making a definite statement contrary to his, especially as the Chrysochlorids are shown to vary so much in the details of their ear structures. Moreover, a specimen of *C. tenuis* (Plate 15, fig. 6) in the collection of the British Museum happens to have the side of the skull broken away sufficiently to afford a view of this particular region in section. Here the appearance of the sphenoid is very different; it is blown up into a much larger diploe and there is an extra large sinus system. In this there is a large hole which, in the dried skull, gives every appearance of forming an intercommunication between the two sides. A bristle could be passed through, but it is a question whether, in doing so, it would not break a false passage through the extremely thin bony trabeculæ.

To this condition an intermediate one can be seen in *C. obtusirostris** (Plate 15, fig. 5), where the sinus system is greater than in *C. villosa* and less than in *C. tenuis*. Here also there is, on each side, as seen in a transverse section, a well-marked opening in the anterior part of the bulla on its medial surface. This opening leads into the ramifications of the sinus, but no direct communication in the sphenoid between the two openings can be traced.

The point can only be settled finally by the examination of serial sections of an animal in the flesh. As far as the present evidence goes it is probable that in life the space is entirely filled with blood vessels, and that the intercommunication for which the dried skull of certain species gives some evidence is more apparent than real.

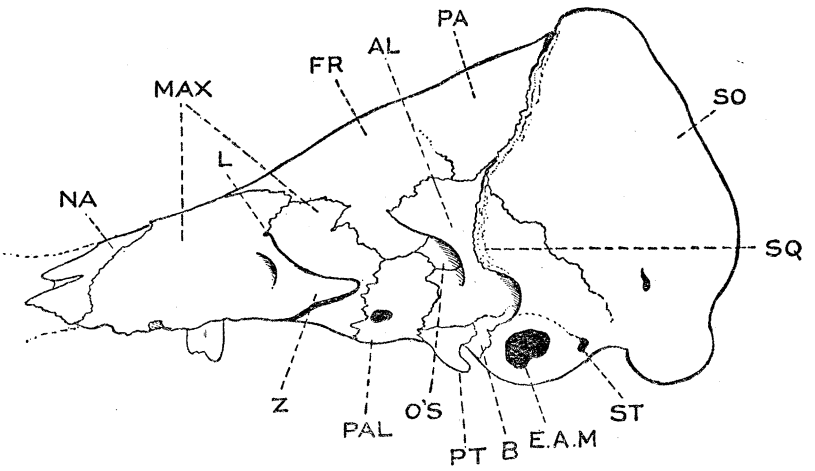
It has not been possible to examine more than a very few skulls in respect of this point, so that the correlation of the condition of the sphenoid with the shape of the ear ossicles cannot be made. At present the evidence seems to show that there is none, because *C. villosa* and *C. trevelyani*, forms with the largest round malleus, have the least expanded sphenoidal sinus; *C. obtusirostris*, with a small "normal" malleus, is intermediate, and *C. tenuis*, with a large pear-shaped malleus, has a large sinus system.

The Skull of a Young Specimen of *C. trevelyani*.

Gunther has already briefly described the adult skull. To his description may now be added further details, that can be seen better in a young animal in which the sutures are, many of them, still present and visible. In side view (text-fig. 4) the contour of the squamosal can be made out fairly clearly. In this stage it has not a very large expanse when compared with the area occupied by the bones of the occipital region. This is because the broad projecting flange, so noticeable a feature in the adult, is not yet developed and is marked only by a roughened line. The upper limit of the bone is shown by a suture line which starts behind, close to, and at the level of, the occipital condyle, whence it runs forwards and diagonally upwards to end as a sharp point. From here the anterior edge, the part which will eventually join the zygomatic process, runs sharply down to the glenoid cavity.

* A dried skull in the University collection without history which appears to be this species.

The inner side of this area, from the level of the external auditory meatus up to the top of the squamosal, is joined by the alisphenoid, which thus abuts on, but takes a very small part in, the formation of the bulla itself. The suture between the squamosal and tympanic is already obliterated. This specimen also upholds the view mentioned by Broom as well as by Leche and Gregory, that the jugal is absent, since the maxilla ends as a sharp point, the intervening tract not being as yet ossified, as has already been



Text-Fig. 4.—Skull of a young *C. trevelyani*, showing some of the sutures still persistent. The pre-maxillæ are lost. NA., *Nasal*. MAX., *Maxilla*. L., *Lachrymal foramen*. FR., *Frontal*, and PA., *Parietal*, still partially divided. AL., *Alisphenoid*. OS., *Orbitosphenoid*. Z., Growing *zygomatic process* of maxilla. PAL., *Palatine*. PT., *Pterygoid*. B., *Basioccipital*. E.A.M., *External auditory meatus*. ST., *Stylomastoid foramen*. SO., *Supra-occipital*. SQ., *Squamosal*. The line points to the (dotted) growing border of the flange. The foramen below the line is the *post-squamosal*.

shown in the fœtal specimen. Gregory's view that the zygomatic arch of the Chrysochloridæ is entirely secondary, being derived from an ancestral form that had already lost the primary arch, the new arch being formed by the backward growth of the maxilla to join the squamosal, is strongly supported.

Although the head of the malleus is so large, it gives rise to no " vesicle " in the space between the crest formed by the squamosal flange and the alisphenoid, and practically no " blister " on the lateral face of the squamosal.*

The alisphenoid has a large upper wing which joins the squamosal posteriorly, its anterior edge having a hollowed outline, which covers a collection of openings that represent the optic foramen, foramen rotundum and sphenoidal fissure. A separate

* I retain the term " vesicle " as used by Dobson for the swelling which is directed forwards, and which lies on the inner side of the zygomatic arch. The term " blister " is used to denote the swelling on the lateral face of the squamosal caused by the head of the malleus. These two swellings occur in some species and not in others, and are strictly conditioned by the shape of the malleus, which can thus be foretold with some accuracy by an inspection of the surface of the skull.

optic foramen, which LECHE states to be present, was not externally visible; this point is referred to again in the description of the foramina in the skull of *C. villosa*.

The orbitosphenoid is a small bone, as are the pterygoids, which appear to be without the ascending process, its place being taken by an expansion of the palatine on the side of the face.

Posteriorly the skull shows no sutures remaining between the various occipital bones. The tabular, which BROOM figures as a clearly separate element in a much younger skull of *C. hottentota*, has likewise lost all trace of its identity.

In a ventral view the only structures that call for comment are those which bear some relation to the ear region. Between the exoccipitals and basioccipital, and between the basioccipital and the basisphenoid, all sutures are obliterated, nor in the ear region proper can any clear distinction be made between the tympanic and the petrosal. This mass is supported on its inner side at the front by a vertical plate of the basisphenoid, which also forms a part of the inner boundary of the bony eustachian tube. At the posterior end the petrosal sends out a lateral wing which abuts on the exoccipital, its posterior margin being marked by the fissure of the foramen lacerum posterius. Above and in front this wing fuses, without remaining sutures, to the squamosal, so that the exact amount of mastoid exposure cannot be stated. The tympanic bulla is somewhat flat, and in general has the appearance of that described later for *C. villosa*, where also are noted the foramina of this skull.

On opening the ear region from the exterior lateral side of the skull, by removal of the squamosal, the auditory ossicles are brought into view (Plate 15, fig. 4), and their extraordinary size and shape are at once apparent, as is also the relatively small part played by the tympanic portion of the bulla when compared with the epitympanic part. The malleus, seen thus in side view, is a large mass with a pea-shaped head, which is rounded above and rather flattened below. The neck is well-defined, and marks the beginning of the manubrium, and from its whole extent springs a flat lamina of bone which is acutely triangular, and is directed straight forwards to end in a sharp point lodged in a recess in the anterior part of the bulla. The anterior upper edge of this lamina runs on to the lower part of the head of the malleus. From its position this lamina must be recognised as a very well-ossified *processus gracilis*. It was found well developed in *C. villosa*, but is apparently a variable vestige, even within the limits of a single species, for one adult of *C. trevelyani* at least does not show it. Unfortunately it has not been feasible to dissect more than a very small number of skulls, and photography by X-rays does not sufficiently demonstrate the presence or absence of this very thin lamina of bone.

Almost the whole of the malleus is lodged in the enlarged epitympanic recess, the manubrium only and the remaining ossicles being in the tympanic cavity proper. The inner surface of the epitympanic recess is somewhat roughened by a deposit of nodular bone, which in some other species has been observed to be present to a very considerable degree, so much so that it appears that movement of the malleus within the chamber would be much curtailed.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The incus is a stout tri-radiate bone which articulates with a prominent process of the malleus; its proportions are similar to those already described in the embryo. The stapes (Plate 15, fig. 1) is stirrup-shaped, and is held in place by a bony canal through which runs the stapedial artery. This canal has a foramen on its upper side, at a point almost in the middle of its course (Plate 15, fig. 2), which is said to transmit a small vessel, though in the embryo none could be traced, and it is often entirely absent.

If, now, we examine a similar preparation in yet another species, *C. obtusirostris* (Plate 15, fig. 5), a smaller animal than *C. trevelyani* but with a rounded and more inflated bulla, we find that a totally different condition occurs. Instead of a large epitympanic cavity there is a very much smaller one, whose roof does not reach the level of the lower border of the zygomatic arch, whereas in *C. trevelyani* more than half the recess lies above it. Instead of a rather flat tympanic bulla there is, on the other hand, a large and rounded one. The auditory ossicles show the widest difference from those described above. They are quite small, and might be described in this respect as "normal," and, as LECHE has already pointed out in the case of *C. hottentota*, more nearly approach the condition found in other Insectivora.

It is clear, then, that there is a great range in size of the ear ossicles in members of the family of Chrysochloridæ, especially in the size of the malleus.

ON CERTAIN FORAMINA OF THE SKULL (Plate 16).

There has been some difference of opinion as to some of the foramina of the skull, so that it may be serviceable here to give an account of the foramina in *C. villosa*,* together with notes of such variations as have been observed in other species.

The Post-Squamosal Foramen.—This is a large hole on each side, just above the level of the top of the occipital condyles. In some species, *e.g.*, *C. stuhlmanni*, a form in which the bone in this part of the skull is very thin, this foramen is clearly seen to be a "foramen lacerum," a space, that is to say, left between the upper part of the exoccipital wing and the mastoid, where the sutures have not closed. The sutures of the mastoid with the tympanic and petrosal bones are obliterated. The upper border of the foramen is very likely made by the lower edge of the tabular, but here again all sutures between this bone and its neighbours are lost. The foramen leads, on the inner side of the skull, to a groove which runs forward on the wall of the cranial cavity in the region above the head of the large pea-shaped malleus. It then enters a canal in the skull wall which opens above the front of the malleus between the zygomatic flange and the parieto-frontal wall of the skull. This foramen, which may be accompanied by one or two more variable ones, is the supra-squamosal. Other species show varying conditions from one large to three small foramina.

* This species has been chosen as a standard only because there were several skulls at my disposal which could be cut up and examined in greater detail than others.

While the post-squamosal foramen is fairly constant, in some species it seems to close up, in adult life at all events, *e.g.*, *C. sclateri*.

The Condylar Foramen.—It has been disputed whether there are two condylar foramina present or one. MIVART speaks of "small double pre-condyloid foramina"; DOBSON also states that there are two. This LECHE denies, saying that DOBSON "has considered the foramen lacerum posterius as a second condylar foramen, and that *Chrysochloris* has, as have all other Insectivores, only one such foramen." In certain respects each of these divergent views is correct. The condyle is pierced by two canals whose foramina lie in a common crater, placed right under the lower anterior lip of the condyle, so as almost to be hidden when the basicranium is viewed directly from above. On tipping up the skull it can be seen that what appears as a single condylar foramen, in reality contains the foramina of the two canals. Of these foramina the larger belongs to a short canal which runs straight through the condyle, almost at right angles to the basicranial axis, to open in the cranial cavity on the front border of the condyle. The other smaller foramen lies in the common crater, a little to the outer side of the larger one, and leads to a longer canal which runs upwards through the condyle, to open half-way up on its odontoid face.

In *Chrysochloris*, then, there are certainly two "condylar foramina," but not in the sense of a double foramen for the XIIth nerve. This nerve with a vein runs through the larger of the two foramina, which is the condylar foramen *sensu stricto*. Judging from the conditions shown by the sections of the embryo, the smaller canal transmits a vein, which branches off from the jugular, passes through the condyle, and rejoins the jugular again. This small canal is curiously constant in all the species of *Chrysochloris* that have been examined. It has not been found to occur in any other of the Insectivora (*e.g.*, *Hemicentetes*, *Centetes*, *Microgale*, *Erinaceus*, *Talpa* or *Macroscelides*; though two specimens of *Tupaia* examined and one of *Rhynchocyon* appear to have a somewhat similar condition).

The Foramen Lacerum Posterius.—When looking straight down on the basi-cranium this foramen lies directly under the crater of the condylar foramen. It is placed in a pit whose posterior and median borders are made by the exoccipital and basioccipital bones, which overhang and to some degree hide the foramen. On the outer side the pit shallows out over the mastoid. On the front median side lies the carotid foramen, and at the same level on its outer side is another small foramen, of whose function I am at present ignorant.

Foramen X.—In *C. villosa* there is on each side an unusual foramen which pierces the basioccipital at the level of the carotid foramen, but more towards the median plane, and which is not included in the same pit (Plate 16, fig. 3—B).* A bristle being passed through enters a canal which runs through the basisphenoid and appears on the floor of the cranial cavity in front of the clinoid plate and close to the middle line. In *C. villosa*

* The manuscript B on the figure itself

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

this foramen is separate and exceptionally clear. *C. trevelyani* appears to approach it fairly closely in that there is a similar canal. The foramen, however, is not separate, but lies within the crater of the carotid foramen. *Chrysochloris bayoni* (Plate 16, fig. 2) also has a very noticeable foramen, lying rather more anteriorly than that in *C. villosa*, and, instead of piercing the basioccipital, lying between it and the bulla. It is further emphasised by a deep, clearly-marked gutter, which leads to the condylar foramen. This foramen and gutter must have the same function as that of *C. villosa*. What this function is, whether it transmits a vein or artery, must remain uncertain until one of these species has been examined in the flesh. The embryo, which does not belong to any of these forms, throws no light, and the majority of other Chrysochlorids examined do not show either the foramen or canal in external view. WORTMAN illustrates, in the skull of *Nyctipithecus felinus*, a foramen similar in position under the name of the "accessory carotid canal," and states that in this species, as also in *Hapale*, "the main artery pierces the bulla in the usual position, but it apparently gives off a considerable branch which enters the cranial chamber through a canal between the bulla and the basioccipital." It is possible that certain of the Chrysochloridæ also show this feature.

The Stylomastoid Foramen and Tympanohyal Pit.—In *C. villosa* these lie in a depressed triangular area on the posterior side of the tympanic bulla, a little way behind the external auditory meatus. The inner and hinder borders of this area are sharply marked off by an overhanging shelf of bone formed by the mastoid wing of the ear region. The foramen and pit are separated by a pointed and forwardly-directed tongue of bone arising from the mastoid at a deeper level than the shelf (Plate 16, fig. 3).

In *C. trevelyani* the condition is a little different. The stylomastoid foramen lies at the inner end of a transverse slit-like fissure, which runs right up to the opening of the external auditory meatus and marks the division of the tympanic and mastoid areas. The tympanohyal pit lies posterior to the foramen. In other species, especially those with rounded or inflated bullæ, the stylomastoid foramen is a round hole on the smooth surface of the bulla. The fissure is not present, and the pit is not distinguishable.

The Foramen ovale, Foramen rotundum and Foramen lacerum anterius.—These present no features requiring particular comment. The foramen ovale varies somewhat in size in different species, and is separated from the conjoined foramina rotundum and lacerum anterius by a bridge of bone of greater or lesser extent.

The Optic Foramen.—The presence of a separate optic foramen has been denied. LECHE, however, is undoubtedly right in his statement that it is present, though it is usually not easily visible in external view. In a sectioned skull, seen from the inside, a large opening lying in front of the malleus is at once apparent.

Following this outward, it leads into a chamber with a bridge of bone dividing it into two external openings, which are the foramen ovale and foramen lacerum. Well above this single inner opening is another smaller one which leads down into the chamber, where it opens just inside and at the top of the bridge. This is the separate optic foramen, and in this the Chrysochloridæ come into line with others of the Insectivora.

There is yet another small foramen above the optic foramen, which forms the exit of a system of venous canals which skirt round the cribriform plate.

Other Foramina.—There is a number of foramina which are less constant in their appearance and of less importance. A glenoid foramen was seen only in a young specimen of *C. trevelyani;* it appears to have a temporary use only. In some cases the region round the eustachian opening is pierced by foramina, notably in *C. trevelyani*, where there is one at all events constant on the outer side of the eustachian cover, to be mentioned presently. There is often also a small foramen on the lower lip of the external auditory meatus. In one case only, *C. obtusirostris*, there was a pair of post-palatine foramina.

The Eustachian Cover.—Gunther first described this very curious feature in *C. trevelyani*, where it occurs as a well-marked semi-lunate little bone, which lies as a flat cover over the opening of the eustachian tube. The occurrence of a loose bony cover of this sort is not confined to this one species, but in the forms examined has been found also in *C. corriæ*, *C. duthiæ*, *C. chrysillus*, and *C. namaquensis*. It occurs therefore in forms with small as well as with large auditory ossicles. It may be that it is present in some of the other species and has been lost in the cleaning of the skull, but general appearances are against this view, and it is certain that in *C. villosa* it is not present as a separate bone. In this species the bone of the edge of the eustachian tube turns in and blocks the entrance, but does so only partially, so that the tube is not entirely closed. When a cover is present the groove leading from the eustachian tube is not clearly marked; in many of the other species in which no cover was observed there is a very clearly-defined groove, which lends support to the view that a cover was not formed and that its absence is not due to accident.

The Shape of the Tympanic Bulla.—Three main forms of the shape of the bulla are here illustrated (Plate 16, figs. 1, 2, 3). In *C. villosa* (fig. 3) (and also in *C. trevelyani*) the surface of the bulla is divided into two areas by a ridge which runs from the external auditory meatus, at first straight towards the median line of the skull and then bends round and runs forwards to the inner side of the eustachian tube. The posterior area is somewhat rounded, the anterior, which includes the region from the external auditory meatus to the eustachian, is flat or even hollow. In *C. bayoni* (fig. 2), a species with an elongated pear-shaped malleus and pronounced vesicle, the bulla is more rounded and is not so clearly divided into areas, though there is still a slight indentation just above the eustachian tube. In *C. obtusirostris* (fig. 1) with small ossicles the bulla is large, smooth and inflated.

The Shape of the Ossicles in Various Species of the Chrysochloridæ.

Altogether some twenty species and sub-species of the family have been described, and, in addition to the family and generic name of *Chrysochloris*, other generic names have at various times been proposed. The earliest division of the family into genera was proposed in 1848 by Pomel, who made the genus *Amblysomus* for the forms which had, by loss of the third molars, only 36 teeth instead of 40, and which, in addition, were

without any enlargement of the temporal fossa.* Mivart, in 1867, made the genus *Calcochloris* for "species with a reduced number of teeth," which is the same as *Amblysomus*, a name which therefore has the priority.

In 1884 Gill placed *C. villosa* and *C. trevelyani* in a separate genus, which he called *Chrysospalax*, using as generic characters "the upraised zygomatic processes covering the sides of the skull like a high collar or hood," and in addition the presence of 40 teeth and absence of a vesicle. Cope, in 1892, made yet another generic name, *Bematiscus*, using the presence or absence of a talon on the lower molars to divide those forms which lack a talon, as *Chrysochloris*, from those with it. This remainder he divided into the genera *Bematiscus* (*C. villosa* and *C. trevelyani*), with 40 teeth, and *Amblysomus*, with 36 teeth.

In 1907 Broom, who has had the opportunity of examining a large number of different species, without using generic distinctions divided the family into two categories with 40 and 36 teeth, and subdivided these into further groups according to the index of skull breadth and length and other characters.

In 1912, however, he showed that in *C. namaquensis* the species varied in its tooth formula from 36 to 40, a fact which he considered to vitiate the classification into genera.

While it is conceivable that a survey of a much larger number of individuals might still show a general cleavage of forms into those with 36 and 40 teeth, a reference to the table on p. 280, which shows the distribution of the various characters, suggests, from the way in which they are mixed up, that Dobson and, later, Broom were correct in declining to accept generic distributions. Following them, and for similar reasons, the single generic name *Chrysochloris* has been used throughout this paper.

While the shape of the auditory ossicles does not afford any help to support or define the different genera alluded to above, its variation in different species is of considerable interest from the evolutionary and physiological point of view, although an explanation of the varying conditions found has yet to be discovered.

It has not been possible to extract and describe minutely the ossicles of the species now to be described, but by means of X-rays (a method useful when dissection of the skull is not allowed, but which does not yield all the information that is desirable) the shape of the malleus and its size can be least be demonstrated.

By this method it becomes evident that the malleus occurs in three main forms. One is a very large pea-shaped ossicle, another has an elongated pyriform shape, while the third type is small and, as already stated, may be described as normal. These three types are not absolute, in that there are forms transitional both in size and in shape from the small ossicles to the large pea and pear-shapes, respectively. *C. granti*, for instance (Plate 17, fig. 3), may be cited as a form intermediate between the pea and pear types, *C. sclateri* as a small form on the way to the pear type, and so on.

* Dobson (1882) was clearly aware of these differences, but did not accept the genus *Amblysomus* as valid. He noted that certain species with 40 teeth also lacked the enlargement of the fossa, and in his synopsis says that the characters "of the single genus are those of the family."

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

As the figures give all the required information better than a verbal description can, it will be sufficient to show in tabular form as follows a list of the species examined, with the condition of the malleus in each case, together with such details as number of teeth, presence or absence of talon on lower molars, and such other characters as have been used to found generic distinctions. The order of species is here arranged according to the size and shape of the malleus.

Broom, in the various papers quoted on page 281, has given an opinion as to the specific relationships of certain species as follows: *C. obtusirostris* and *C. chrysillus* are closely allied, *C. corriæ*, *C. rutilans* and *C. hottentota* form another allied group, and *C. tenuis* and *C. namaquensis* a third. It is interesting to note that the shape of the auditory ossicles in each case supports the correctness of Broom's views, which were formed from the observation of other characters.

Summary.

It has now been shown that the ear region in certain species of the Chrysochloridæ is very unusual, but that it is by no means so in all of them. The malleus in those forms that have an abnormally large one may be either round in shape or oblong. What the function is in such cases is very difficult to explain. All Chrysochlorids are nocturnal burrowing animals, and it is perhaps natural to jump to the conclusion that there is here some adaptation to habit. On the other hand, there is apparently no great difference of habit in the various species of the family, many of which, perhaps the majority, have quite small ear ossicles.

Equally good burrowers, such as *Talpa*, *Notoryctes* and others, have undergone no special adaptations in this particular respect, so that, even if there is any correlation between structure and function, it is not an essential one. Nor is it a sexual character, as when the enlarged malleus occurs it does so in both sexes. Fossil members of the group are not known, or only doubtfully, and so give no information on the point. In a family, moreover, in which the component species are in most other respects so homogeneous, it is not likely that this particular evolution of the ear ossicles can have had a very long past history.

Certain structures of the ear region have a considerable interest, as yet unexplained, from the physiological point of view. The absence, for instance, of the tensor tympani (which, however, requires confirmation from a study of the adult), of ligaments to the malleus, and the common presence of a bony cover over the eustachian tube, all point to some unusual method of hearing. It would seem that a malleus of unusual mass would be capable of taking up heavy vibrations only, but that this would be any advantage is not clear. It is possible that we are dealing with one of those instances, rare but not unknown, of evolution along in-adaptive lines, and that the enlarged ossicles, so far from having any adaptation to function, might eventually, from a change of environment, cause the extinction of those species which suffer from them.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Species.	Sex.	Malleus.	Number of teeth.	Talon of lower molars.	Anterior cusps of second upper incisors.	Shape of bulla.	Vesicle.	Blister.	Zygomatic crest.
*C. villosa** (4 specs.) ...	♂ ♀	Very large pea	40	Talon ...	Shorter	Flat to concave ...	Very small ...	Large ...	High.
C. trevelyani (3 specs.)	—	Large pea ...	40	Talon ...	Shorter	Flat to concave ...	None	Large ...	Very high.
C. granti	—	Round pear ...	40	—	—	—	None	Small ...	Low.
C. asiatica	♀	Long pear ...	40	No talon ...	Cusps equal ...	—	Very prominent	None ...	Low.
C. namaquensis ...	—	Long pear ...	40	—	—	Smooth, rather inflated	Very prominent	None ...	Low.
C. bayoni	—	Long pear ...	40	No talon ...	Shorter	Moderately inflated ...	Prominent ...	None ...	Low.
C. tenuis	—	Long pear ...	—	—	—	Inflated	Prominent ...	None ...	Low.
C. stuhlmanni... ...	♂	Long pear ...	40	Small talon	No anterior cusp	Inflated	Prominent ...	None ...	Low.
C. sclateri	—	Small pear ...	40	Very small...	No anterior cusp	Moderately inflated ...	Moderately prominent	None ...	Low.
C. duthieæ	—	Small pear ...	40	No talon ...	Shorter	Large smooth	None	None ...	Low.
C. congicus	—	"Normal" ...	40	—	Longer	Large smooth	None	None ...	Low.
C. obtusirostris ...	—	These forms have all small malleus, but with some variation in size.	36	No talon ...	Shorter	Rounded, much cancellous bone on median side	None of these forms has either blister or vesicle, and the zygomatic crest is always low.		
C. hottentota	♂ ♀								
C. hottentota longiceps			36	Talon ...	No anterior cusp	Inflated			
C. hottentota pendoliæ									
C. azis	♀		36	Talon ...	Shorter	Inflated			
C. rutilans	♂		36	Talon ...	Shorter	Flat			
C. Corriæ	♀		36	Talon ...	Very short ...	Rather inflated... ...			
C. chrysillus	—		36	No talon ...	No anterior cusp	Large smooth			

* In proportion to skull size, *C. villosa* has the largest malleus of all.

A blank line signifies that the specimens examined were defective, or no information was available.

WORKS CITED.

1845. Hyrtl, "Vergleich Anat. Untersuch. über das innere Gehörorgan." Prague.

1848. Pomel, 'Arch. d. Sci. Phys. et Nat.,' vol. 9.

1867–8. Mivart, "The Osteology of the Insectivora," 'Journ. Anat. Phys.,' vol. 2 (2nd series, vol. 1), p. 117.

1876. Gunther, 'Ann. Mag. Nat. Hist.,' 4, vol. 17, p. 347, Plate XX. *Chrysochloris trevelyani*.

1878. Doran, "The Mammalian Ossicula Auditus," 'Trans. Linn. Soc.,' Series II, Zoology, vol. 1, Part VII.

1882–90. Dobson, 'Monograph of the Insectivora.' London.

1884. Gill, 'Standard Natural History,' vol. 5, Mammals (*Chrysospalax*).

1892. Cope, 'American Naturalist,' p. 127. (Makes the genus *Bematiscus*.)

1902. Tandley, "Entwicklungsgeschichte der Kopfarterien" (Arterial circulation of the head), 'Morph. Jahrb.,' vol. 30, p. 2.

1903. Wortman, "Studies of Eocene Mammalia—Primates," 'Amer. Journ. Sci.,' vol. 15.

1905. Van Kampen, "Die Tympanalgegend des Säugetierschädels," 'Morph. Jahrb.,' vol. 34, Parts III and IV.

1907. Leche, "Zahnsystems der Säugetiere" (Contains a description of the teeth of Chrysochlorids and notes on the skull structure), 'Zoologica,' vol. 20, Heft 49, Part II.

1907. Broom, 'Ann. Mag. Nat. Hist.,' 7, vol. 19, p. 262. Description of new species: *C. sclateri*, *C. wintoni*, *C. granti*, *C. namaquensis*, *C. tenuis*.

1908. Broom, 'Ann. Transvaal Museum,' vol. 1, p. 14. Description of new species: *C. gunningi*.

1909. Broom, 'Ann. Natal Govt. Museum,' vol. 2, p. 129. "On the Teeth of *Chrysochloris*."

1910. Gregory, "The Orders of Mammals," 'Bull. Amer. Mus. Nat. Hist.,' vol. 27.

1912. Broom, 'Trans. Roy. Soc. S. Africa,' vol. 2, p. 41. "Variation in the tooth formula of *C. namaquensis*."

1913. Broom, 'Proc. Zool. Soc.' (abstract), vol. 2, p. 547. "Description of *C.* (*Bematiscus*) *transvaaliensis*."

Broom, 'Trans. S. African Phil. Soc.,' vol. 18, p. 283. "A contribution to the knowledge of the Cape golden moles—Description of new species, *C. duthieæ*."

1914. Broom, 'Proc. Zool. Soc.,' vol. 2, p. 1071. "Dental variations in mammalian skulls."

1915. Broom, 'Proc. Zool. Soc.,' p. 156. "Exhibition of a skull of *Chrysochloris asiatica*, with four upper molars on each side."

1916. Broom, 'Proc. Zool. Soc.,' p. 451, Plates I, II. "On the structure of the skull in *Chrysochloris* (*C. hottentota*)."

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

DESCRIPTION OF PLATES.

Plate 15.

EAM.	... ...	Auditory meatus, external.
IAM.	... ...	Auditory meatus, internal.
C.	... ...	Condyle.
CC.	... ...	Carotid canal.
CF.	... ...	Condylar foramen.
ETY.	... ...	Epitympanic chamber.
FF.	... ...	Floccular fossa.
G.	... ...	Glenoid cavity.
I.	... ...	Incus.
M.	... ...	Malleus.
S.	... ...	Stapes.
S.C.	... ...	Stapedial canal.
SPH.	... ...	Diploe in sphenoid region.
TY.	... ...	Tympanic chamber.
X. (fig. 1)	...	A bristle passing through the stapedial canal.
Y. (fig. 1)	...	A bristle passing through the carotid canal. (Both bristles enter by the carotid foramen.)
Z. (fig. 1)	...	A short bristle entering a venous foramen.
SQ.P. (fig. 3)	...	The line of junction between the squamosal and petrosal over the head of the malleus,
XX. (fig. 7)	...	The tympanic region on this side is opened up. That on the opposite side is intact, except that the eustachian opening is somewhat enlarged.

Fig. 1.—*Chrysochloris trevelyani*. Dissection of the skull of an immature specimen showing part of the cranial cavity seen from above. The long black bristle passes through the canal for the stapedial artery. The shorter bristle passes through the canal for the internal carotid. The canal shows as a white line, to the left of which the stapes can be seen. The epitympanic cover is broken away to show the enlarged malleus. A venous foramen shows at the anterior border of the malleus. × 3.

Fig. 2.—Much enlarged view of the stapes of the same specimen, showing the transverse bony canal with its foramen.

Fig. 3.—Lateral internal view of the same specimen as fig. 1, showing the groove at the junction of the periotic cover of the malleus with the squamosal. × 4 (approx.).

Fig. 4.—Lateral external view of the same specimen, showing the malleus and incus in position after removal of the squamosal. × 3 (approx.).

Fig. 5.—*Chrysochloris obtusirostris* skull with the tympanic chamber opened up. The chamber of the bulla is marked by two foramina, the small epitympanic chamber lies above.

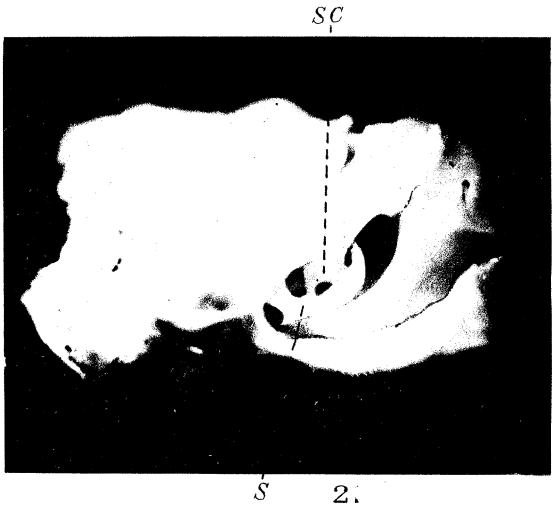
Above is the malleus (right) and incus (left) removed from the skull. These, as well as the skull, are enlarged to the same scale as fig. 4.

Fig. 6.—*Chrysochloris tenuis* skull with part of the cranial wall broken away. To the left of the black line is the cavity of the cranium, showing the epitympanic cover, which fits closely to the elongated malleus of the further side. To the right of the line is the tympanic chamber of the right side opened up, showing the large foramen into the basisphenoid. Below is the bulla of the left side. The skull is somewhat tilted up. × 3.

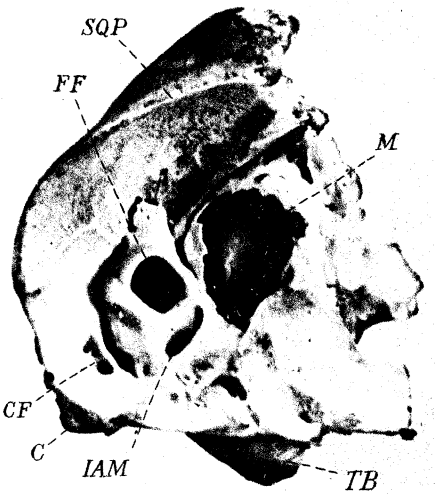
Fig. 7.—*Chrysochloris villosa*. Transverse section of skull through the basisphenoid, showing the diploe, and on each side a depression with small foramina. The tympanic bulla on the left (actual right) is more opened up than that of the opposite side, and shows the dark epitympanic cavity from which the malleus has been removed. × 3 (approx.).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

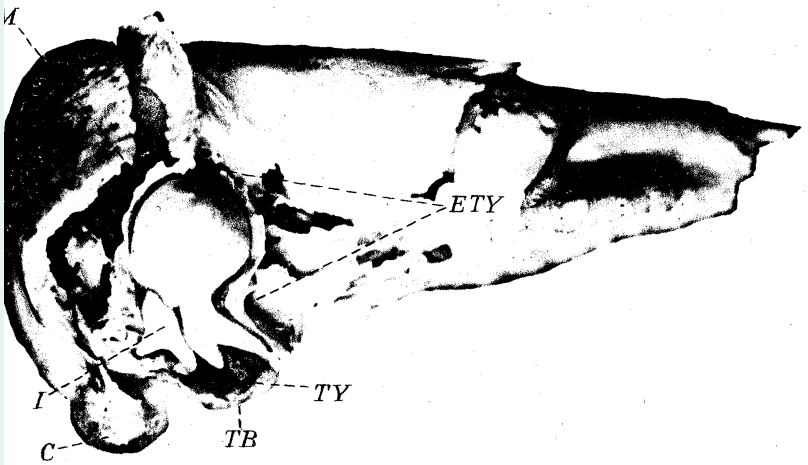
1.



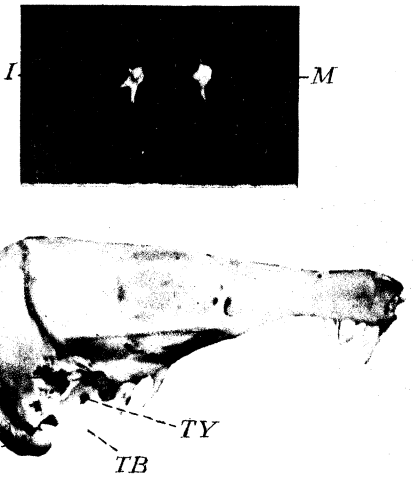
2.



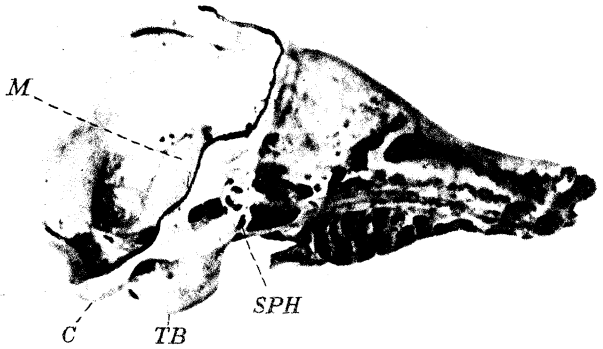
3.



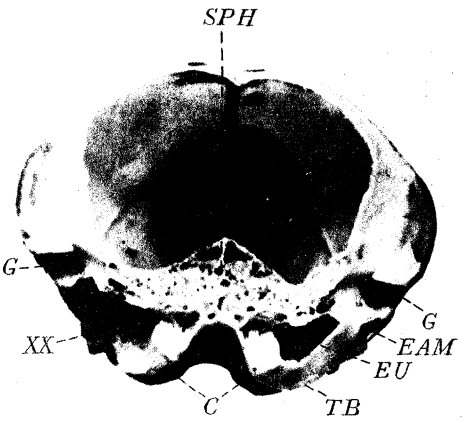
4.



5.

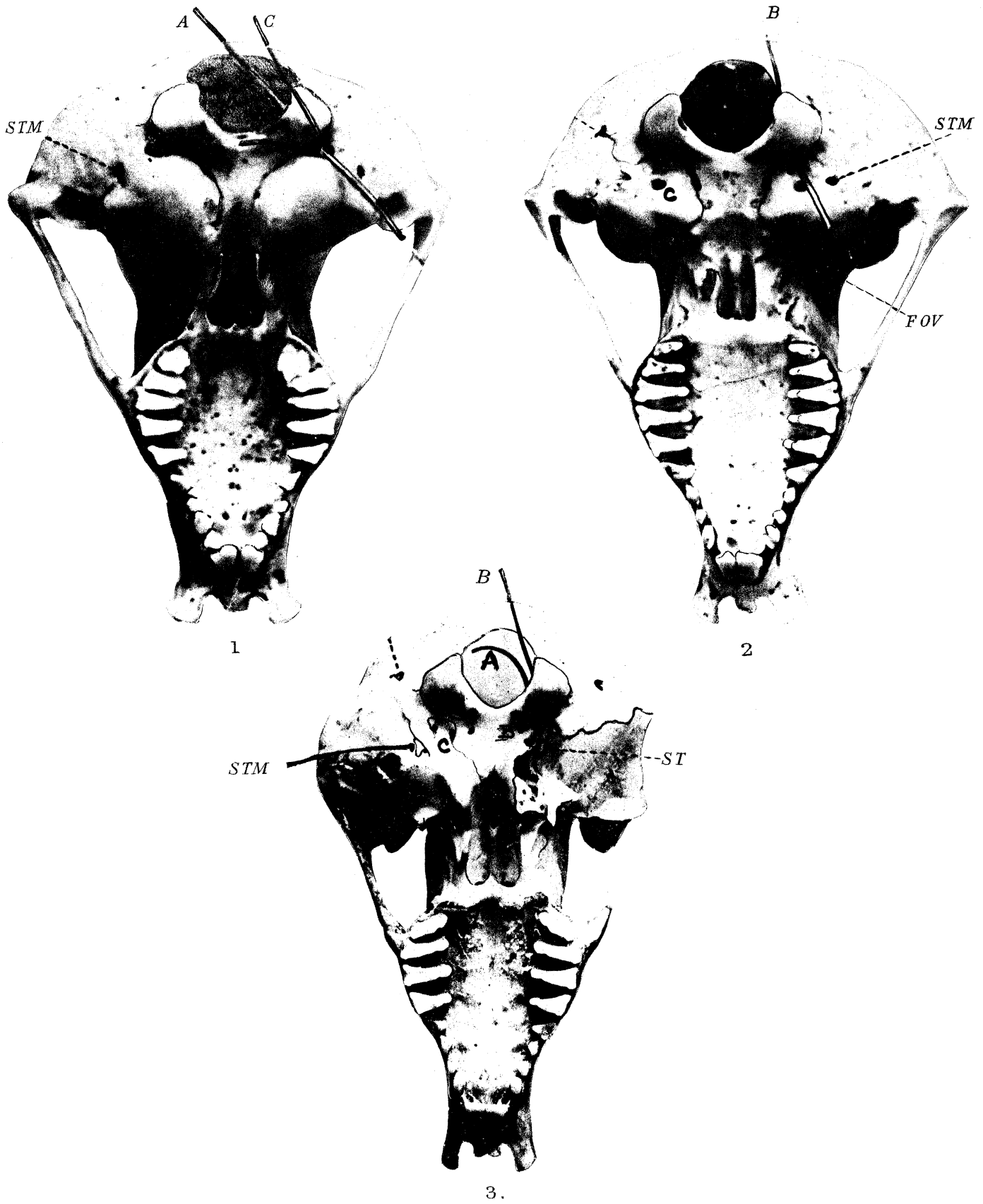


6.



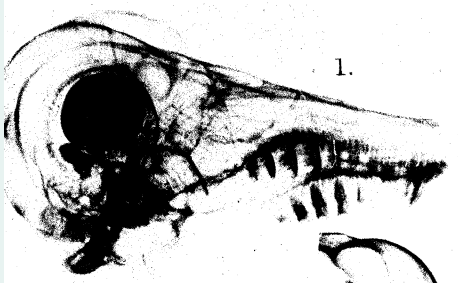
7.

Huth coll.



Huth coll.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES


1.


1a.


2.


3.

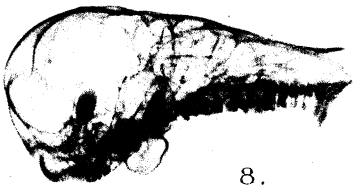

3a.


4.

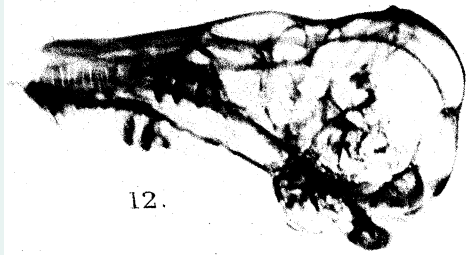

5.

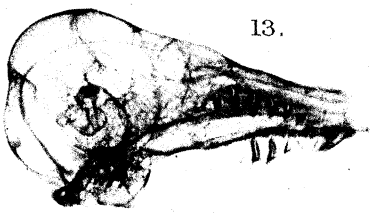

6.

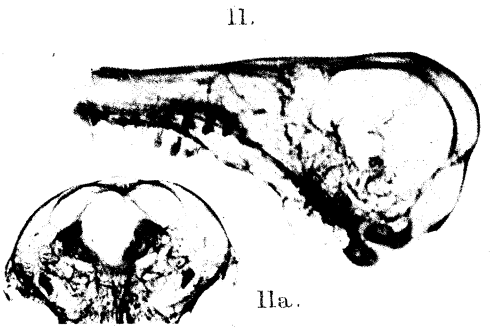

7.


8.

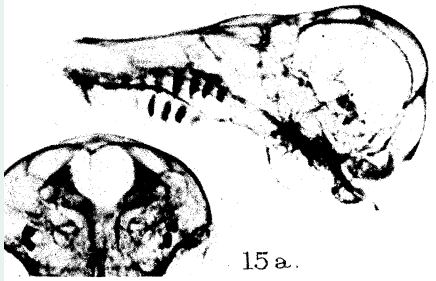

9.


12.


13.


11.

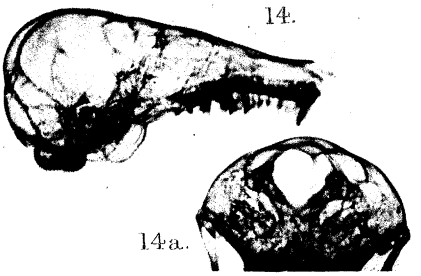
11a.


15.

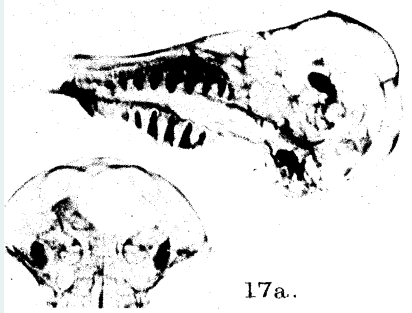
15a.


16.

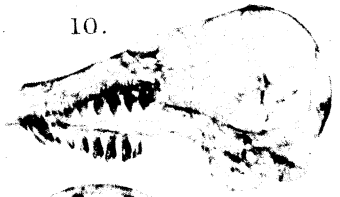

16a.


14.

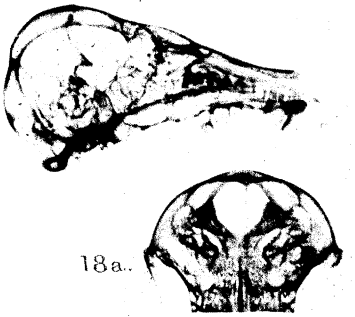
14a.


17.

17a.


10.


10a.


18.

18a.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PLATE 16.

FIG. 1.—*Chrysochloris obtusirostris.* FIG. 2.—*C. bayoni.* FIG. 3.—*C. villosa.*

These skulls have been enlarged to the same size for comparison. *C. villosa* is enlarged approximately three and a half times, the other two six times.

STM.—*Stylomastoid foramen.*

A.—Bristle through the *foramen lacerum posterius.* In fig. 3 this is passed on through the canal of the stapedial artery.

B.—In figs. 2 and 3 a bristle through the second "condylar foramen." This is twisted round and passed on through the foramen described as the "accessory carotid foramen" or "foramen X" in the text.

C.—In fig. 1 a bristle passed into the *carotid* foramen. In figs. 2 and 3 this foramen is marked with a C on the apparent left-hand side.

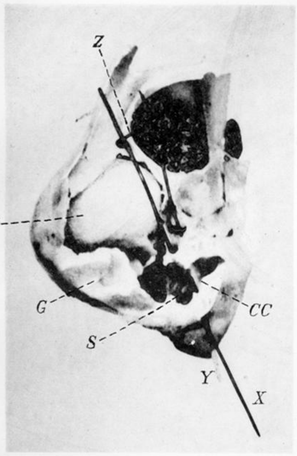
In fig. 2 the vesicle for the pear-shaped malleus shows in front of the bulla on each side. In the other two species no vesicle is present.

In fig. 3 the tympanic chamber on the apparent right side and the ossicles have been removed, except the stapes marked ST. The canal for the internal carotid shows as a white line on its median side. The smaller letter B on the skull marks the "foramen X." See page 275.

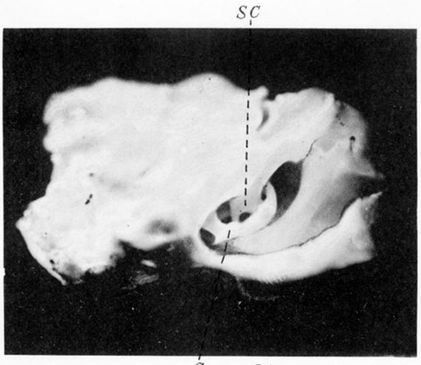
PLATE 17.

X-ray photographs of skulls of species of Chrysochloridæ, all approximately twice the natural size.

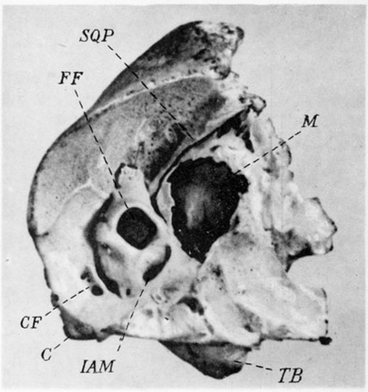
1. *Chrysochloris villosa.*	1*a*. Dorso-ventral view.
2. *C. trevelyani.*	
3. *C. granti.*	3*a*. Dorso-ventral view.
4. *C. bayoni.*	
5. *C. asiatica.*	
6. *C. namaquensis.*	
7. *C. sclateri.*	
8. *C. stuhlmanni.*	
9. *C. tenuis.*	
10. *C. congicus.*	10*a*. Dorso-ventral view.
11. *C. hottentota.*	11*a*. Dorso-ventral view.
12. *C. hottentota-longiceps.*	
13. *C. hottentota-pondoliæ.*	
14. *C. iris.*	14*a*. Dorso-ventral view.
15. *C. cozziæ.*	15*a*. Dorso-ventral view.
16. *C. chrysillus.*	16*a*. Dorso-ventral view.
17. *C. duthieæ.*	17*a*. Dorso-ventral view.
18. *C. congicus.*	18*a*. Dorso-ventral view.



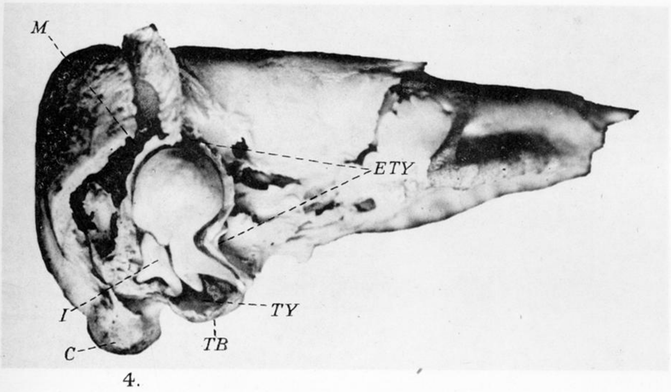
1.



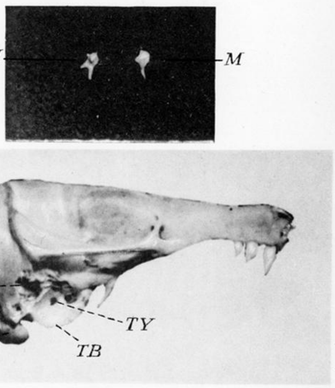
2.



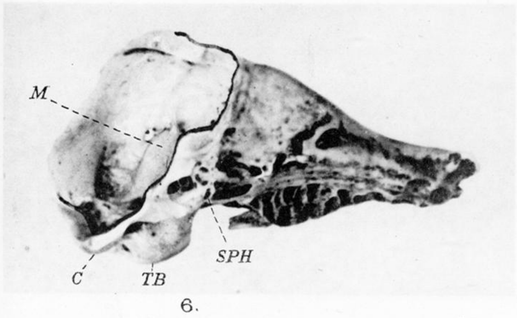
3.



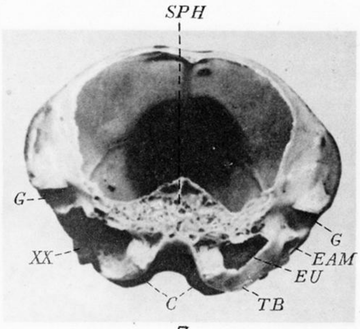
4.



5.



6.



7.

PLATE 15.

EAM.	... ...	Auditory meatus, external.
IAM.	... ...	Auditory meatus, internal.
C.	... ...	Condyle.
CC.	... ...	Carotid canal.
CF.	... ...	Condylar foramen.
ETY.	... ...	Epitympanic chamber.
FF.	... ...	Floccular fossa.
G.	... ...	Glenoid cavity.
I.	... ...	Incus.
M.	... ...	Malleus.
S.	... ...	Stapes.
S.C.	... ...	Stapedial canal.
SPH.	... ...	Diploe in sphenoid region.
TY.	... ...	Tympanic chamber.
X. (fig. 1)	...	A bristle passing through the stapedial canal.
Y. (fig. 1)	...	A bristle passing through the carotid canal. (Both bristles enter by the carotid foramen.)
Z. (fig. 1)	...	A short bristle entering a venous foramen.
SQ.P. (fig. 3)	...	The line of junction between the squamosal and petrosal over the head of the malleus.
XX. (fig. 7)	...	The tympanic region on this side is opened up. That on the opposite side is intact, except that the eustachian opening is somewhat enlarged.

FIG. 1.—*Chrysochloris trevelyani*. Dissection of the skull of an immature specimen showing part of the cranial cavity seen from above. The long black bristle passes through the canal for the stapedial artery. The shorter bristle passes through the canal for the internal carotid. The canal shows as a white line, to the left of which the stapes can be seen. The epitympanic cover is broken away to show the enlarged malleus. A venous foramen shows at the anterior border of the malleus. × 3.

FIG. 2.—Much enlarged view of the stapes of the same specimen, showing the transverse bony canal with its foramen.

FIG. 3.—Lateral internal view of the same specimen as fig. 1, showing the groove at the junction of the periotic cover of the malleus with the squamosal. × 4 (approx.).

FIG. 4.—Lateral external view of the same specimen, showing the malleus and incus in position after removal of the squamosal. × 3 (approx.).

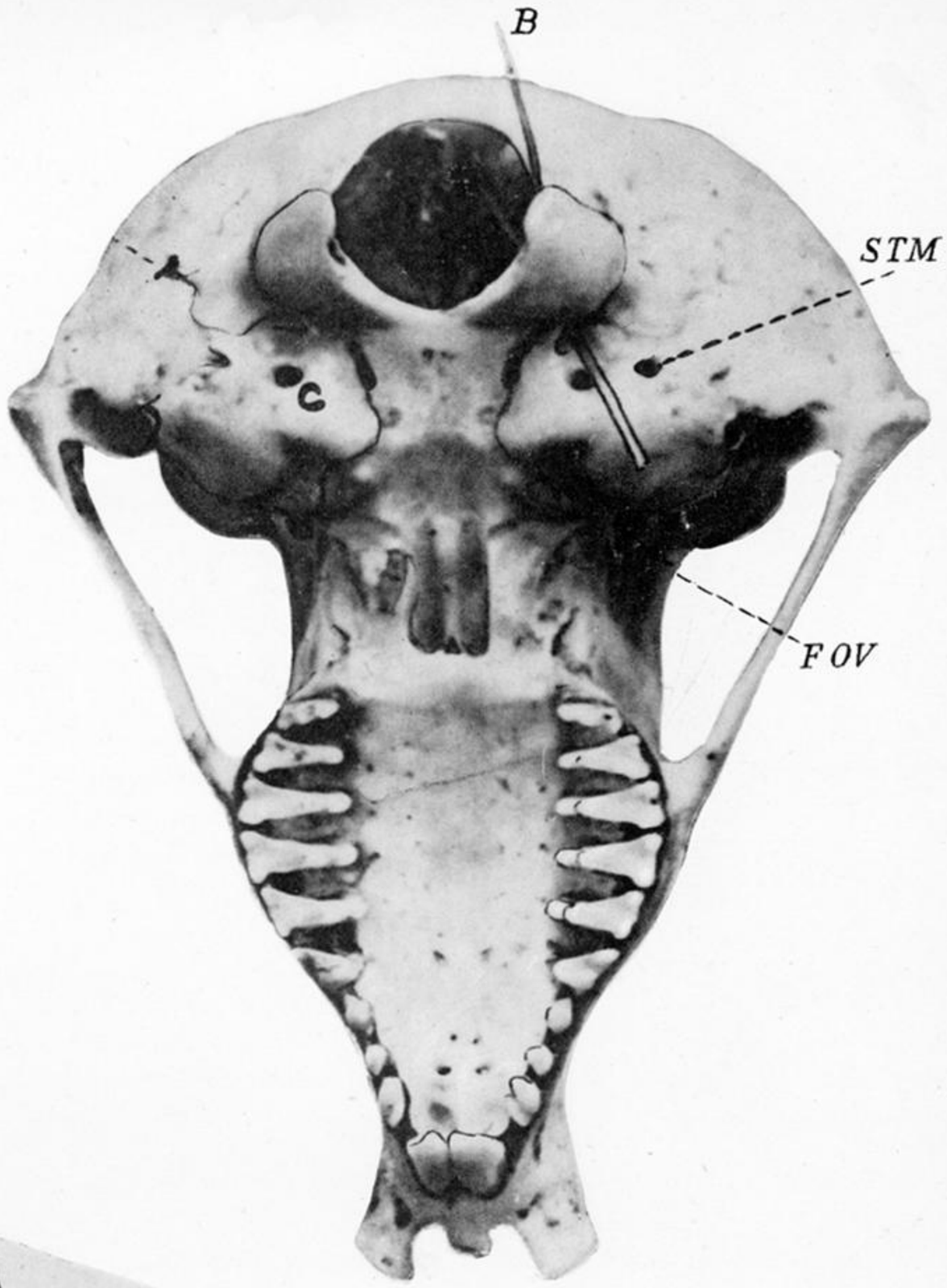
FIG. 5.—*Chrysochloris obtusirostris* skull with the tympanic chamber opened up. The chamber of the bulla is marked by two foramina, the small epitympanic chamber lies above.

Above is the malleus (right) and incus (left) removed from the skull. These, as well as the skull, are enlarged to the same scale as fig. 4.

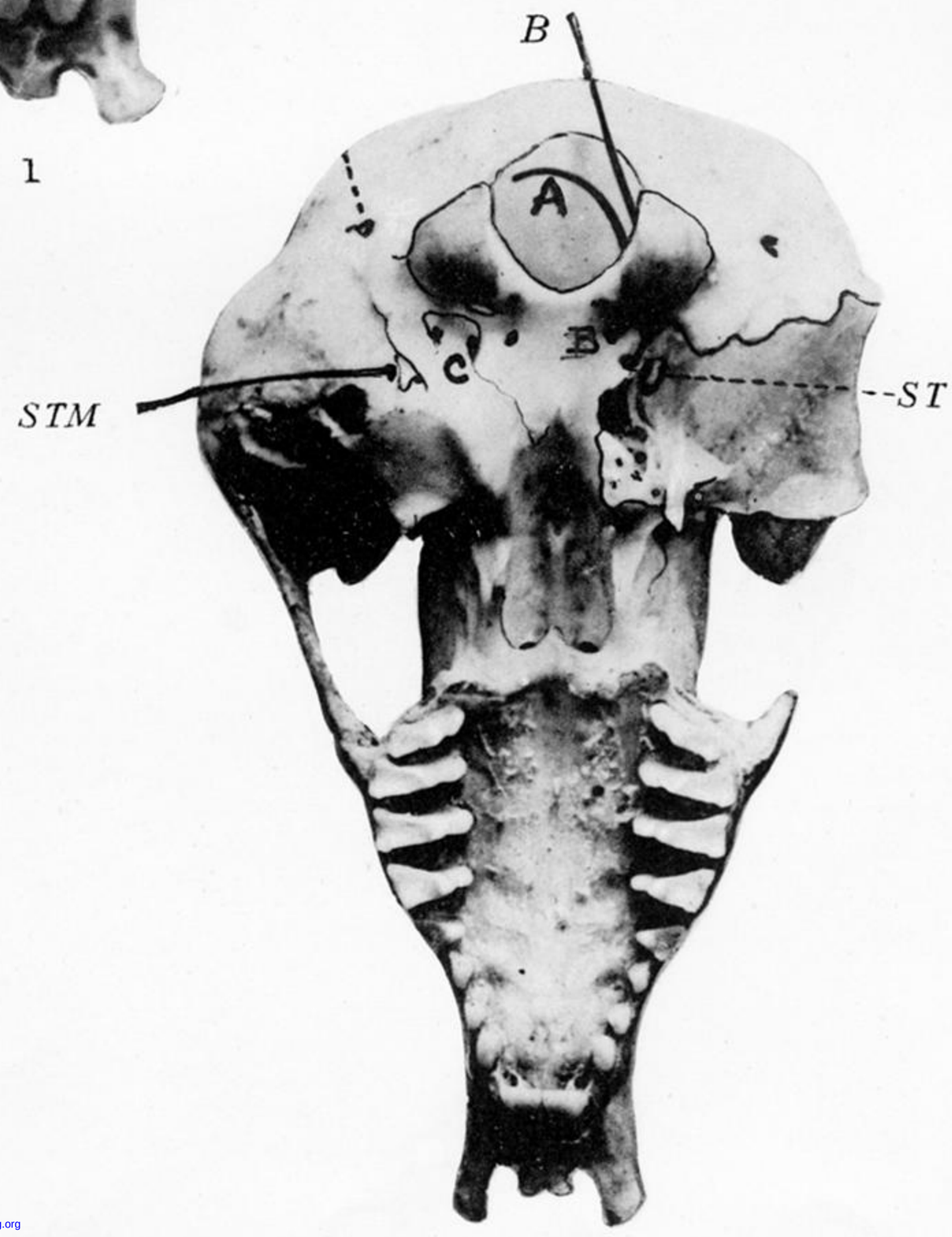
FIG. 6.—*Chrysochloris tenuis* skull with part of the cranial wall broken away. To the left of the black line is the cavity of the cranium, showing the epitympanic cover, which fits closely to the elongated malleus of the further side. To the right of the line is the tympanic chamber of the right side opened up, showing the large foramen into the basisphenoid. Below is the bulla of the left side. The skull is somewhat tilted up. × 3.

FIG. 7.—*Chrysochloris villosa*. Transverse section of skull through the basisphenoid, showing the diploe, and on each side a depression with small foramina. The tympanic bulla on the left (actual right) is more opened up than that of the opposite side, and shows the dark epitympanic cavity from which the malleus has been removed. × 3 (approx.).

1



2



3.

PLATE 16.

FIG. 1.—*Chrysochloris obtusirostris.* FIG. 2.—*C. bayoni.* FIG. 3.—*C. villosa.*

These skulls have been enlarged to the same size for comparison. *C. villosa* is enlarged approximately three and a half times, the other two six times.

STM.—*Stylomastoid foramen.*

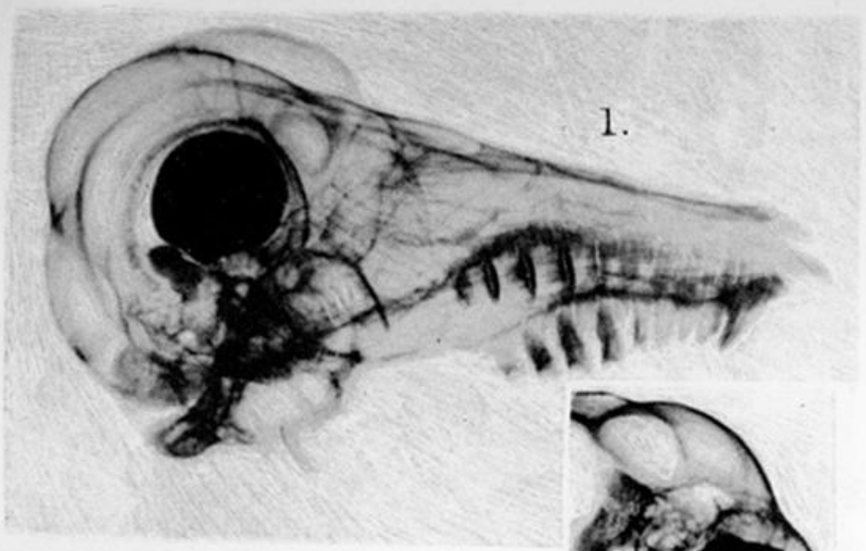
A.—Bristle through the *foramen lacerum posterius.* In fig. 3 this is passed on through the canal of the stapedial artery.

B.—In figs. 2 and 3 a bristle through the second "condylar foramen." This is twisted round and passed on through the foramen described as the "accessory carotid foramen" or "foramen X" in the text.

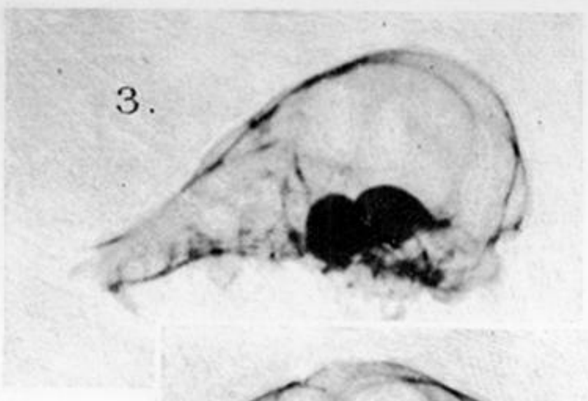
C.—In fig. 1 a bristle passed into the *carotid* foramen. In figs. 2 and 3 this foramen is marked with a C on the apparent left-hand side.

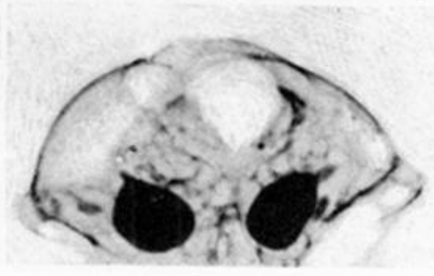
In fig. 2 the vesicle for the pear-shaped malleus shows in front of the bulla on each side. In the other two species no vesicle is present.

In fig. 3 the tympanic chamber on the apparent right side and the ossicles have been removed, except the stapes marked ST. The canal for the internal carotid shows as a white line on its median side. The smaller letter B on the skull marks the "foramen X." See page 275.

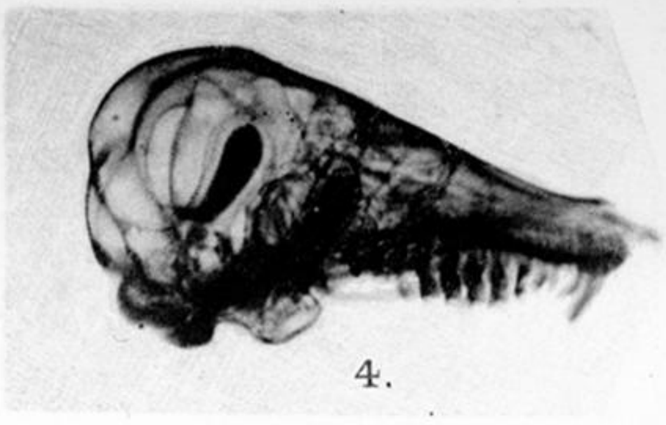


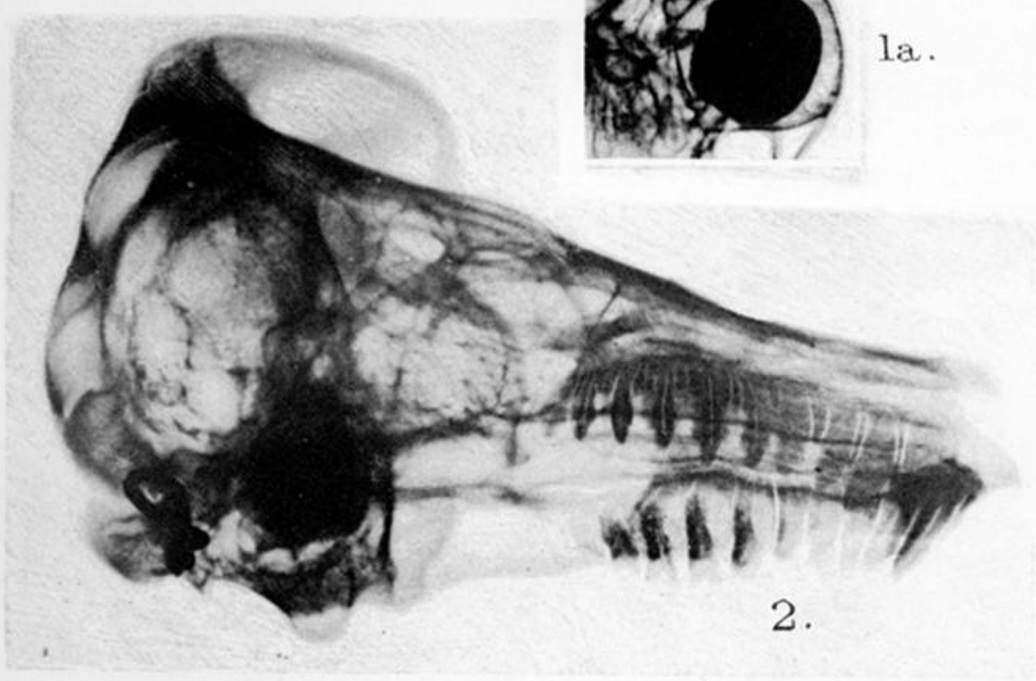
1a.



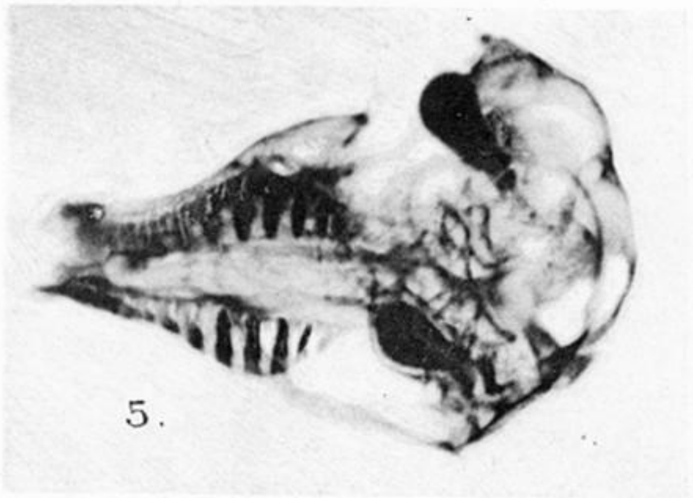


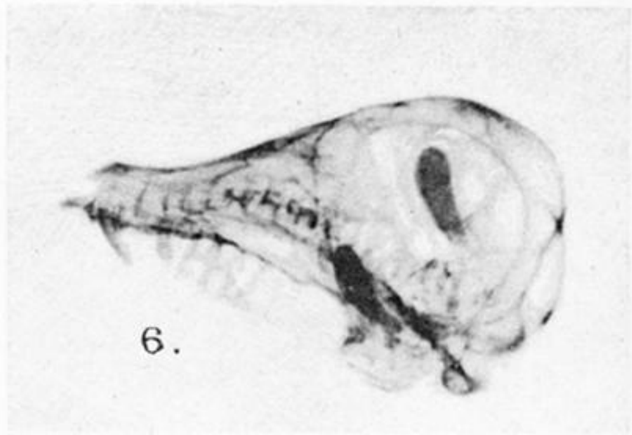
3a.



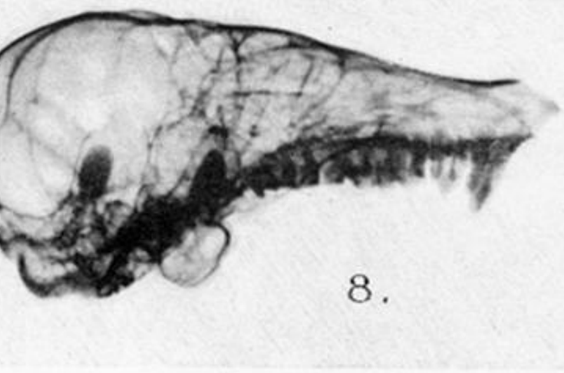


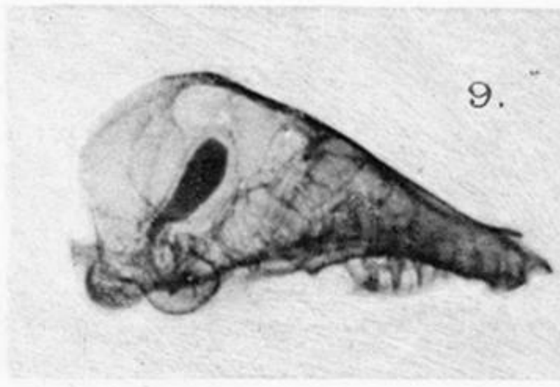
2.

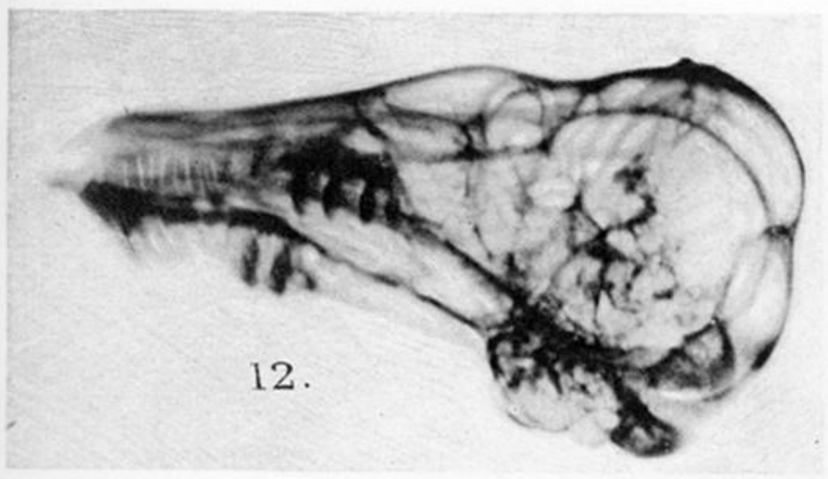




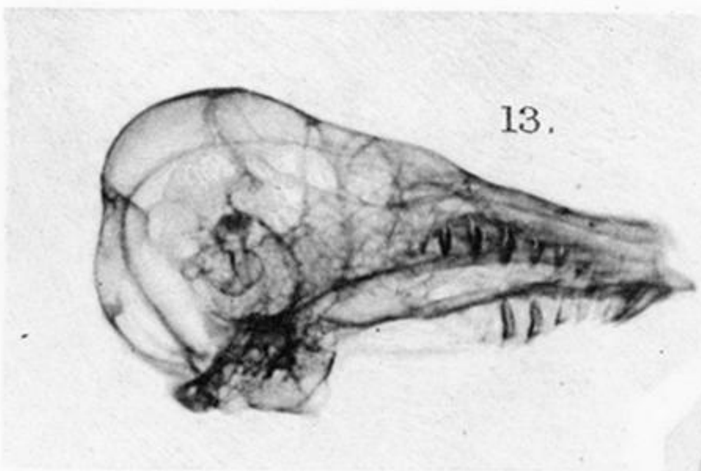
7.



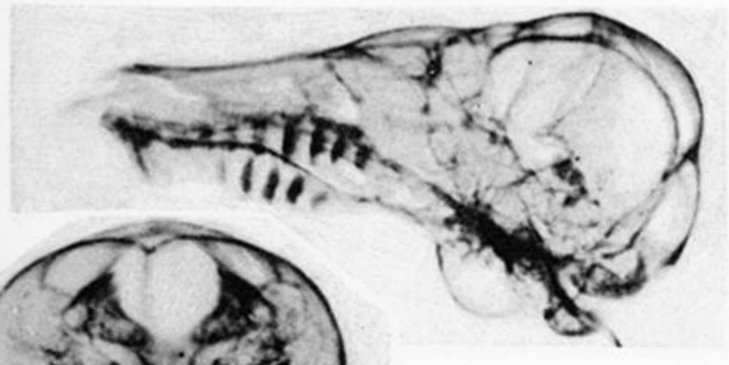




12.

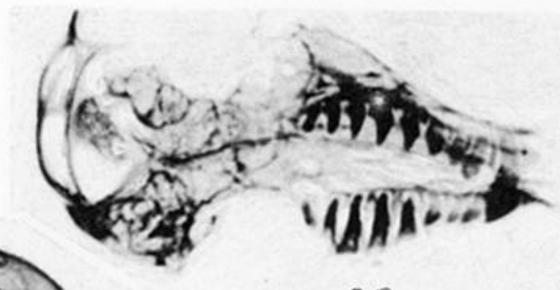


11a.

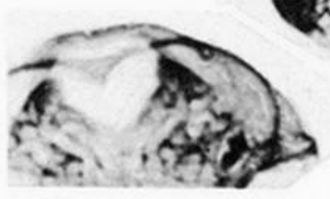


15.

15a.

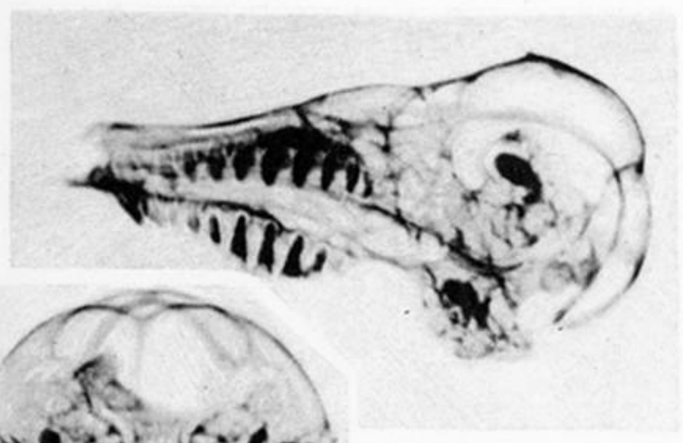


16.



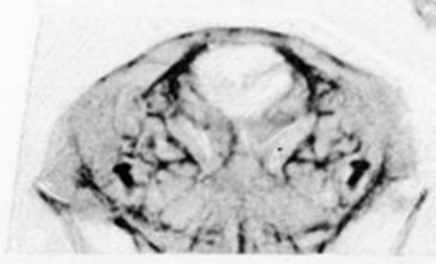
16a.

14a.

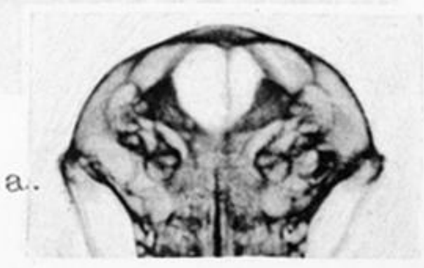


17.

17a.



10a.



18a.

Plate 17.

X-ray photographs of skulls of species of Chrysochloridæ, all approximately twice the natural size.

1. *Chrysochloris villosa.* — 1*a*. Dorso-ventral view.
2. *C. trevelyani.*
3. *C. granti.* — 3*a*. Dorso-ventral view.
4. *C. bayoni.*
5. *C. asiatica.*
6. *C. namaquensis.*
7. *C. sclateri.*
8. *C. stuhlmanni.*
9. *C. tenuis.*
10. *C. congicus.* — 10*a*. Dorso-ventral view.
11. *C. hottentota.* — 11*a*. Dorso-ventral view.
12. *C. hottentota-longiceps.*
13. *C. hottentota-pondoliæ.*
14. *C. iris.* — 14*a*. Dorso-ventral view.
15. *C. cozziæ.* — 15*a*. Dorso-ventral view.
16. *C. chrysillus.* — 16*a*. Dorso-ventral view.
17. *C. duthieæ.* — 17*a*. Dorso-ventral view.
18. *C. congicus.* — 18*a*. Dorso-ventral view.