CASQUE AND BILL OF RHINOPLAX VIGIL (FORST.) IN CONNECTION WITH THE ARCHITECTURE OF THE SKULL

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INTRODUCTION

The occasion for this investigation was the donation by Dr. W. H. LEVEND of the University Hospital at Leyden to the Zoological Laboratory of Leyden University of a skull of an adult specimen of *Rhinoplax vigil*, so that an object was available, which we were allowed to saw through in the sagittal plane.

Form and structure of the bill and especially of the casque of *Rhinoplax vigil* proved to be very divergent – externally as well as internally – from those of other Bucerotidae. The investigation was therefore focussed upon the influence of these peculiarities upon the architecture of the skull. Special attention in this respect was paid to kinesis.

Moreover, an attempt was made to establish what modifications in function are related with these divergent structures. Starting points were on the one hand the architecture of the skull and on the other hand the functions of bill and casque of *Rhinoplax vigil*, as far as could be concluded from what is known about its external appearance, behaviour and way of living. A special aspect in this connection is the shifting of some functions from the bill to the casque, which has occurred in *Rhinoplax vigil* and the influence this has exercised on the architecture of the skull as a whole.

MATERIAL

Eight skulls of *Rhinoplax vigil* (Forst.) were available. The Zoological Laboratory at Leyden possesses one complete skull, which had been sawed through just beside the mediosagittal plane.

Out of the collection of the Rijksmuseum van Natuurlijke Historie (the national State Museum of Natural History) at Leyden through the good offices of Dr. G. C. A. JUNGE were put at our disposal: one complete skull; a second incomplete skull from which the part behind the orbita was wanting, and a third slightly damaged skull of a juvenile specimen.

The Zoological Museum at Amsterdam, by courtesy of Prof. Dr. K. H. VOOUS, provided one skull, which had been rather roughly prepared and to which part of the skin of the head was still adhering. After an exhaustive inquiry of the build of this skull, it was permitted to incorporate the detached elements in the anatomical collection of the Zoological Laboratory of Leyden University.

Of several foreign institutes of whom cooperation had been asked only the Smithsonian Institution of the U.S. National Museum, Washington was able to help by the courtesy of Dr. H. FRIEDMANN, with three skulls: one undamaged specimen which we were allowed to prepare, one from which the lower jaw was wanting and one belonging to a small, presumably female specimen.

Probably the rarity of this bird and the fact that it is protected by law can account for the fact that none of the collections included a head complete with the soft parts.

The specific properties of the skull of *Rhinoplax vigil* are determined a.o. by the same principles found in a number of other Bucerotidae. Therefore, these properties form a very suitable basis for investigation and called for comparative study of these Bucerotidae. Dry skulls were used of a number of representatives of the family Bucerotidae from the collection of the Rijksmuseum van Natuurlijke Historie at Leyden, among which must be mentioned:

Aceros plicatus (Forst.)
Aceros undulatus (Shaw)
Anthracoceros malayanus (Raffl.)
Buceros rhinoceros silvestris Vieill.
Tockus spec.

The soft parts of the head could be studied from a specimen preserved in alcohol of *Aceros plicatus* (Forst.) procured from the collection of the Zoological Laboratory Leyden. From this the position of the muscles and the situation of their points and areas of attachment could be studied.

TECHNIQUE OF THE INVESTIGATION

The observation of details of various components of the skull and the preparation were done with the aid of a binocular microscope at a magnification of 16 ×.

Previous to the preparation the head of *Aceros plicatus* was taken out of the alcohol and put into water for some days to soften.

In order to render the ligaments and articular capsules supple and flexible again the dry skulls were put into an aqueous solution of lactid acid 0.5–1 % for from half a day to a fortnight. Care had to be taken that the acid should not corrode the bone by dissolving too much of the Ca-salts. After this the flexible skulls could be stored in a mixture of 40 % alcohol, 40 % glycerine and 20 % water.

An aqueous solution of 0.5–1 % KOH (potassium hydroxide) was used to attack the mummified connective tissue so that the components of the skull could be isolated.

In order to measure on photographs the movements of the quadrata relative to the neurocranium, the two ventral condyli of the quadratum-articulare joint were marked with black dots; the neurocranium was mounted in a fixed position and the ventral view of the skull was photographed with the quadrata in various positions.

X-ray photographs were taken at the Department of Röntgenology of the Academisch Ziekenhuis (Academic Hospital) at Leyden with the cooperation of Dr. A. C. DE WILDE of the Anatomical Laboratory at Leyden; 43 kv and 118 m.a. were used. In the case of the skull with muscles of *Aceros plicatus* the exposure was timed at 0.75 sec. and in the case of the heavy dry skull of *Rhinoplax vigil* at 0.90 sec. The drawings after these photographs were made by tracing the outlines of the relevant parts on transparent paper upon a table with a white translucent glass top, illuminated by a light underneath it.

When röntgenograms of the head of *Aceros plicatus* had to be taken the upper bill was fixed with long pins on a block of cork, the rest of the head hanging freely, so that movements were not hampered.

The bill was opened wider and wider by putting successively longer and longer pieces of wood between upper and lower bill.

The sagittal sections through the skulls were made with a bandsaw.

Preparations of horn and bone ground thin for microscopic slides were made by Mr. J. J. F. HOFSTRA, technical assistant at the Rijksmuseum van Geologie en Mineralogie (State Museum of Geology and Mineralogy) at Leyden. To this end a section of 2 mm thickness was sawed from the bone or horn under investigation. This section was ground with carborundum on one side and this side was glued with Canada balsam on a microscopic slide; then the free surface was further ground by hand with carborundum till the section was transparent enough to be examined under the microscope.

To ascertain the specific gravity of horn, bone and pneumatic bone the weight and volume of the skull or part of the skull under consideration were determined. The volume was found as follows: The parts concerned are put into a receptacle, which subsequently is filled to the brim with sand. After removing the object under investigation, the volume of sand is determined which is needed to replenish the vessel to the brim again. Previous to the determination of the volume the apertures leading into the internal cavities of the pneumatic bone were sealed up with pieces of adhesive tape or with paraffine which could be removed afterwards by dissolving with xylol. This method is not particularly accurate owing to the tendency of sand to set, but it suffices for the purpose especially if the receptacle is tapped before each measurement. In this way the specific gravity of a skull expressed in gr./cm^3 was calculated by dividing the total weight of the skull by the total volume (*i.e.* of the pneumatic bone).

The centre of gravity of the various skulls is situated in the median plane owing to their bilateral symmetry. Its situation can be determined approximately by suspending the sagitally halved skull freely by a piece of string successively from a few different points of the circumference of the sagittal plane. A plumbline was suspended parallel to this string in a plane at right angles to the sagittal plane and passing through the point of suspension of the skull.

The centre of gravity is situated in the point of intersection of the projections of the plumbline in its different positions on the sagittal plane of the skull.

Thanks to the ready cooperation of the Dutch zoological gardens

Natura Artis Magistra at Amsterdam and Blijdorp at Rotterdam and the Dierenpark Oud Wassenaar at Wassenaar I had the opportunity of seeing several living Bucerotidae at close range and observing the natural movements of their heads.

I. STRUCTURE AND MECHANISM OF THE MOVEMENTS IN THE ADULT SKULLS

A. Shape and structure of the skull in external view

A superficial observation of the skull of *Rhinoplax vigil* already reveals that it is very divergent from that of the other Bucerotidae treated in this investigation; different as to the mutual relations of the components of the skull, as to weight and the massiveness of its build.

Three complexes can be distinguished in the skull of the Bucerotidae

1st the bill, consisting of the upper and lower bill, of which the upper bill is joined to the rostral and ventral part of the neurocranium, while the lower bill is situated ventrally of the upper bill
2nd the casque
3rd the neurocranium, to the ventral side of which are joined the separate paired bones, which will be treated in conjunction with the neurocranium: quadratum, pterygoid and jugale.

1) *The bill*

The bill in *Rhinoplax vigil* (figs. 1, 2, 4) in contrast with that of the other Bucerotidae mentioned, is particularly short and very slightly curved. Its shape approximates that of a high straight threesided pyramid, the base of which (the vertical tangent plane with the rostral border of the orbita) coincides roughly with the base of the bill. Its perpendicular is the straight line, *i.e.*, the projection on the sagittal plane of the imaginary line which can be drawn through the most dorsal point of the upper border of the lower bill and the tip of the bill. The rostral half of the bill is somewhat curved, so that its tip is situated about 2 cm below the longitudinal axis of the bill. One of the upright edges of the pyramid is not a sharp line but a curved plane like the surface of a cone; it is the dorsal side of the bill. Halfway its length – that is at the steep rostral border of the casque – the bill is about twice as high as it is broad, from this point in the rostral direction it tapers rapidly, so that the tip is shaped like a high, narrow wedge. On the ventral side of the bill a wedgelike segment is cut off from the caudal half of the pyramid by a horizontal triangular plane, the top of which is situated on the level of the rostral surface of the casque. From the tip of the bill to the top of this triangular plane both halves of the lower bill are fused; from this point the bony halves of the lower jaw diverge in the caudal direction (fig. 4). In the remaining Bucerotidae the bill is extremely strongly developed and very large in relation to the neurocranium. The bills are narrow in comparison to their height, in which upper and lower bill have an equal share. They are rather strongly curved. In general the rule holds good: the longer the bill, the stronger the curve, while a long bill appears to coincide with a large casque.

2) *The casque*

The casque in *Rhinoplax* (figs. 1, 2) is very large relative to the bill, especially when compared with that of other Bucerotidae having also a slightly curved bill, for as mentioned above the casque is generally small in these cases. In *Rhinoplax* it extends from half way the length of the bill to the middle of the dorsal border of the orbitae. The casque has roughly the shape of a cylinder, the dorsal side of which is semicircular in cross section, while the adjoining sides are flatter and high and find their continuation in the lateral sides of the bill. The rostral plane of the casque is high and slightly convex in a lateral direction but much more so in a dorso-ventral direction. Consequently, the most dorsal point is situated caudally of the level where this rostral plane rises steeply from the bill. The dorsal side slants a little downward in a caudal direction, making an acute angle with the horizontal axis.

The caudal plane of the casque is low and only slightly curved and it joins the neurocranium nearly at right angles. Hence, the casque is extensive in rostro-caudal, lateral and dorsal directions, but not ventrally: it does not extend beyond the plane of attachment on the upper bill.

In the other investigated Bucerotidae the casque extends rostralwards from the middle of the dorsal border of the orbitae to a third or half the length of the upper bill. The casque is very divergent in shape and size in the various species investigated.

When we arrange the Bucerotidae according to the size of their casques this series begins with *Tockus*, in which the casque is totally wanting, and runs via birds like *Aceros*, in which it consists of a small longish oval elevation with transverse "folds", to *Buceros*, in which the casque is a huge narrow and high "superstructure", which ends rostro-dorsally in a high caudalward-curved tip. In the larger casques in species belonging to this series the back wall slants in a dorso-caudal direction, and consequently, the base of the casque, where attached to the upper bill, is shorter than the horizontal section on a more dorsal level. The nostrils are situated on the caudo-lateral sides of the casque somewhat rostrally of the point where the casque meets the neurocranium in the dorsal median line (fig. 1).

3) *The neurocranium etc.*

The complex of neurocranium plus jugalia, quadrata and pterygoidea, together with the caudal half of the lower bill in *Rhinoplax* is much more strongly built than in the other Bucerotidae. In describing this part of the skull we will not enter too much into detail and we refer to figs. 1, 2, 3.

This complex of the neurocranium plus the caudal half of the lower bill in *Rhinoplax* can be compared with a rectangular parallelepipedon with a quadrangular base. The two parallel upright sides of this quadrangular base lie in the lateral surface of both halves of the lower bill and of the neurocranium. The ventral side is formed by a line through the ventral borders of the caudal part of both halves of the lower bill. The dorsal surface of the neurocranium is laterally curved like a cylinder.

The dorsal surface of the neurocranium and especially its lateral part, exhibits a great number of small round pits of 3 mm diameter lying closely side by side. In these pits small muscles are attached running to the base of the calami of feathers on the head, which will be raised by the contraction of these muscles.

The dorsal surface of the neurocranium in *Rhinoplax* is not curved caudally as in the other Bucerotidae: but from the median line it extends on both sides caudo-ventro-laterally as the caudo-lateral crista, which is broad and high, while its cross section is a quarter of a circle. At both sides the free end lies on a level with the ventral end of the caudal border of the orbitae. This crista is the caudal border of a deep fossa (the fossa temporalis) for the musculus adductor mandibulae. The free edge *i.e.* the upper surface of this caudo-lateral crista is flat and rough and extends from the dorsal median in a lateral direction to half the total height of the caudal complex of the skull *i.e.* the neurocranium plus the lower bill.

The fossa temporalis has a vertical direction in its dorsal part, and – like the caudo-lateral crista – then curves in a ventro-lateral direction, while it increases in width and depth; finally it ends at the caudal border of the orbita.

The orbitae, which enclose a cupshaped space, the diameter of which equals half the total breadth of the neurocranium, are separated from each other by a strong, solid septum interorbitale. The orbitae in *Rhinoplax* are small in relation to the neurocranium when compared with those of the other Bucerotidae. Rostrally they extend as far as the base of the bill; ventro-laterally they are separated from the mouth slit by the jugale. The caudo-lateral border of the orbita is constituted by the processus postorbitalis, a broad and elongated flat continuation of the lateral part of the rostral wall of the fossa temporalis. Medially of this processus, the medial part of the fossa temporalis extends as far as the orbita. In contrast with the other Bucerotidae, the processus postorbitalis extends as far as the jugale, which it meets at an angle of 120° rostrally.

The caudo-ventral border of the fossa temporalis is prolonged into a short, narrow, sharply tapering, rostro-ventrally directed process, the processus zygomaticus squamosi, which projects medially of the processus postorbitalis into the caudal side of the orbita.

Ventrally of the point of attachment of the processus zygomaticus squamosi to the wall of the fossa temporalis the quadratum is suspended. The ventral side of the quadratum articulates with the lower jaw. The jugale joins the quadratum latero-dorsally of this articulation.

On the caudal wall of the orbita occurs another short, broad, rostro-ventrally-directed processus – a processus which is situated so far medialward as to allow the passage of the musculus adductor mandibulae. The latter originates in the fossa temporalis and, running in a rostro-ventral direction, ends on the tuber externum mandibulae of the lower jaw. Dorsally of where the surface of the septum interorbitale curves to join the caudal wall of the orbita lies the round foramen opticum.

In caudal view the circumference of the neurocranium is roughly a circle, from which, however, a segment is lacking on the ventral side. Ventro-laterally the quadratum is situated together with the adjoining lower jaw, which in this caudal view tapers wedgelike ventrally. Quadratum and lower jaw occupy in this place a third of the total height. Medially on the caudal wall from the point where the caudo-lateral cristae meet – but far less strongly developed – runs the crista caudalis which towards the ventral side decreases in height and breadth. This caudal crista ends in a short, broad ventrally directed process in the centre of the caudal surface. In a sunk area rostrally and ventrally of this processus lies the large, round foramen occipitale with, on its ventral side, the strong, broad, reniform condylus occipitalis.

The caudal parts of both halves of the lower jaw run parallel to each other (fig. 4). The caudo-ventral wall of the neurocranium lies a little caudally of their ends (figs. 1, 2).

In ventral view (fig. 3) the neurocranium is shaped like an equilateral triangle. Two of the angular points of this triangle coincide with the ventral ends of the latero-caudal cristae on the neurocranium. A cup-shaped, walled in space – open in a ventro-latero-rostral direction – is situated medio-rostrally of each of these angular points and latero-rostrally of the condylus occipitalis. Within this cup are situated, on the medial side, the aperture of the auditory organ and on the lateral side the articulation of the quadratum with the neurocranium.

The basisphenoid lies in the rostral part of the above mentioned triangle. The top is prolonged into the keel-shaped ventral edge of the bony septum interorbitale. There is also a rudiment of the basipterygoid articulation: a narrow spineshaped, rostrally directed processus half way the rostro-lateral side of the basisphenoid.

The septum interorbitale itself rostrally joins the shortest of the two parallel sides of the trapeziform rostral part of the primary upper jaw between the rostral ends of the pterygoidea. Caudally the pterygoidea articulate with the ventro-medial side of the quadrata. The palatina, which enclose the choanae, rostrally border on the base of a low isosceles triangular area sunk into the roof of the mouth in the upper bill. This area, the rostrally directed top of which bears on either side two small apertures, extends in a lateral direction almost to the lateral side of the upper bill. To the caudal side of it each half of the upper bill – in ventral view – ends in a narrow rectangle to which the jugale is joined. Owing to the slanting position of the processus postorbitalis and the broad fossa temporalis running parallel to it and to the caudo-lateral extension of the surface of the skull with the enormous latero-caudal cristae, the neurocranium of *Rhinoplax vigil* suggests that its shape might have been achieved originally by protracting the shape of the neurocranium in the other Bucerotidae investigated in a dorso-caudal direction.

In the other investigated Bucerotidae the neurocrania plus quadrata, jugalia and pterygoidea are very much alike, and so are the joints of the jaws. The neurocranium in the other Bucerotidae is relatively very small and consists of an oval, slightly bulging case around the brain which is either not at all or only very slightly higher and broader than the caudal part of the upper bill. The caudal side is surrounded by a protruding ridge. The orbitae are very spacious and round. They extend from the base of the upper bill to about half way up the neurocranium in a dorsal and caudal direction and they are separated from each other by a membranaceous septum interorbitale. Ventro-laterally the orbitae are bounded by the narrow oblong jugale, which is the continuation of the lateral side of the upper bill. Laterally the caudal border of the orbitae is formed by the processus postorbitalis, which passes halfway down this caudal wall of the orbita into the ligamentum squamoso-mandibulare; this processus is perpendicular to the jugale and parallel to the ridge round the caudal wall of the neurocranium.

B. Internal structure of the skull

The skull of *Rhinoplax vigil* is extremely heavy. This fact is accentuated by the marked difference from that of the other investigated Bucerotidae, in which even the skulls with voluminous casques are very light. The heaviness in *Rhinoplax* can be explained only in part by the relatively larger volume of the bones of the skull. The main cause is the difference in massiveness of the skull (fig. 2).

In *Rhinoplax* the layer of horn on the rostral side of the casque is exceedingly thick (fig. 2).

The lower and upper bill and the casque in *Rhinoplax* are covered by a layer of horn (fig. 2), which can be pulled from the bony core in dry skulls. Within the mouth cavity this layer of horn is only 0.5 mm thick. On the inside of the upper bill it extends caudally as far as the palatinum and on the inside of the lower bill as far as the point, where both halves of the lower bill diverge from each other. On the lateral surface of the bill the layer of horn is 2 mm thick, which increases to 5 mm rostrally of the casque. Over the entire rostral surface of the casque the thickness amounts to 25 mm. On the dorsal and lateral surfaces of the casque, as on the lateral surfaces of the caudal part of the bill the thickness is only 1 mm, while it terminates thinner still at the base of the bill where the casque curves in caudal direction.

The voluminous casques of the other investigated Bucerotidae consist of a horny bladder, which for the greater part is empty.

The bill and the casque in these Bucerotidae are covered by a thin layer of horn which is extremely thin in the mouth cavity, and reaches its greatest thickness on the upper bill (*Buceros* 2 mm) while it is only half as thick on the casque. Here a generalisation may be made: the larger the casque the thicker the horn covering. This seems logical, because as the surface increases proportionally stronger structures are necessary to maintain the required solidity.

In *Rhinoplax* the entire space in the casque is occupied by thickwalled coarse spongy bone with strong trabeculae (fig. 2) while a firm, solid bony septum separates the orbitae and a median bony partition divides the rostral part of the brain case.

The bony core of the casque and bill in *Rhinoplax* fits exactly into the horn layer and so it duplicates – though inwardly – the outward surface. There is no hollow vesicular part, as we found in the voluminous casques of the other Bucerotidae.

In the rostral part of the upper bill the rather thin trabeculae are directed perpendicularly to its ventral wall and constitute a number of parallel small partitions. The trabeculae arise from the ventral bony wall with short forked ramifications, so that the wall is covered by a fine meshwork. In *Rhinoplax* the trabeculae in the casque and the caudal part of the bill are considerably thicker and more solid; they lie closely side by side. Only the bony filling of the most caudo-dorsal part of the casque and of the palatinum have a fine spongy character.

The neurocranium is exceedingly thick-walled; the wall has an average thickness of 8 mm, which increases to even 15 mm at the place where the caudo-lateral crista arises. Only in the fossa temporalis is it reduced to a thinner wall of massive bone. Two solid bony layers constitute the inner and outer surfaces of the neurocranium and the space between is filled with thick-walled coarse spongy bone in which the trabeculae form a distinctly criss-cross structure. The condylus occipitalis is large and consists of compact bone.

The septum interorbitale, which rostrally borders on the nasal cavity, is bony. Both lateral surfaces are slightly concave, so that this septum is thinnest in the centre. Moreover, it consists of compact bone here. Towards the borders it runs parallel to the curve of the eye ball and consequently it is thicker there. It is no longer compact here and a number of firm trabeculae are visible. In the ventral part of the orbita these arise perpendicularly from the rostral wall of the orbita and run to the condylus occipitalis (fig. 2).

A strong compact bony septum divides the rostral part of the cavity containing the telencephalon. Both these skull cavities which communicate in their dorsal parts, are egg-shaped with the pointed end directed rostrally; they are about 3 cm long and 2 cm deep. The cavity containing the cerebellum joins on ventro-caudally; dorsally the latter reaches half as high and caudally it extends as far as the foramen occipitale. This cavity has the shape of a quarter of a sphere with a radius of 1 cm.

Ventrally of the caudal part of the brain cavity for the telencephalon is found a practically round cavity of 1 cm diameter, in which we can safely assume that the lobi optici are situated.

The foramen opticum lies rostrally of the last mentioned cavity, a little beside the sagittal plane. All these cavities in the neurocranium of *Rhinoplax* eventually open into the cylindrical space containing the medulla oblongata which terminates with the foramen occipitale at an angle of 45° to a horizontal plane.

In the orientation of the bony trabeculae of the casque and the neurocranium in *Rhinoplax* different directions can clearly be distinguished. Figs. 2b and 12 show the course of the trabeculae diagrammatically. By far the greater number and the strongest thickest trabeculae are directed perpendicularly to the rostral wall of the casque and, converging caudally, run towards the bony septum in the cavity for the brain. They are attached to the wall of the casque with a great number of practically contiguous forked ramifications, which merge into thicker trabeculae; these in turn divide again here and there and thereafter fuse with other trabeculae. Sometimes even a kind of bony septa which are situated in parasagittal planes, are formed in this way, so that a firmly interconnected network results. The most ventral of these trabeculae are caudally not directed towards the bony septum in the cavum cranii because the nasal cavity is in their way. Instead they run ventro-caudally towards the palatinum.

The orientation of a second, much smaller group of trabeculae, which are directed from ventro-rostral to dorso-caudal, is far less evident. This does not refer to continuous trabeculae, but rather to a great number of short rods, being in direct line with the other and interconnecting the above mentioned trabeculae. The rostral ends of these trabeculae arise at the place where the upper bill joins the casque and ventrally of this area, on the roof of the mouth. Their course follows curved lines more or less parallel to the rostral surface of the casque, towards the dorso-caudal end of the casque, or in less curved lines to the rostro-dorsal area of the neurocranium.

A third, least distinct direction can be discerned in the trabeculae, which curve dorso-caudalward from the ventral to the rostro-dorsal part of casque and neurocranium. Some of them lie in the upper bill ventrally of the place where this passes into the casque; the others run from the palatinum along the rostral wall of the nasal cavity to the dorso-rostral part of the casque.

The structure of the bone in the lower bill closely resembles that of the upper bill, with this difference that in the former horizontal rods parallel to the outer surface occur as well.

In the other Bucerotidae investigated only about a fourth of the caudal part of the casque is filled with spongy bone. Only small casques as in *Aceros* are entirely filled with spongy bone. The bill also is filled with spongy bone and the same holds for the other bones of the skull, except the massive condylus occipitalis. Where the fine-meshed spongy bone of the casque rostro-ventrally joins that of the upper bill, it has a firmer and more solid structure of horizontal trabeculae. In the upper and lower bill the trabeculae are directed vertically.

The thick roof of the skull in the other Bucerotidae consists of two thin bony lamellae between which very fine-meshed spongy bone is situated. The trabeculae in this spongy bone, however, are very thin.

The paired part of the nasal cavity, divided in two by a median connective tissue membrane, is situated in *Rhinoplax* halfway between the bony rostral wall of the casque and the foramen occipitale. The nasal cavity from the choanae in the roof of the mouth first curves slightly in rostro-dorsal direction and then vertically upwards to half the total height of the casque plus upper bill. At this point both halves diverge with a rostro-lateral curve and via half a spiral coil, end in the nostril, situated near the latero-caudal base of the casque (figs. 1 and 2).

In the medially sectioned skulls of the other Bucerotidae it can be observed that the nasal cavities, to which the choanae ventrally give entrance, are at first directed vertically as far as two thirds of the height of the bill and then via a horizontal spiral coil they end at the external nostril. This cavity, surrounded by a thin bony wall, lies embedded in fine-meshed spongy bone, which passes into the spongy bone occupying the space in the upper bill.

C. Lower jaw, quadratum, jugale and pterygoid and their movability in the skull

1) *Lower jaw*

The lower jaw of *Rhinoplax vigil* consists of a single bone, which shows no suture even in the median (figs. 1 and 4). The left and right halves rostrally are fused as far as half their length and constitute a dorsally open gutter, which deepens in caudal direction and forms the floor of the mouth cavity. The height of the lower jaw gradually increases from the rostral tip towards the point where the two halves of the jaw diverge from each other, and then decreases caudalward again to 2 cm. At the caudal ends the distance between left and right lower jaw amounts to 3 cm.

The horny covering of the lower jaw extends ventrally as far as the point, where the two halves diverge from each other, but dorsally and laterally it extends as far as half the distance from this point to the caudal end of the lower jaw. Slightly rostrally of the caudal ends are situated the articular cavities for the condyli of the quadrata. Caudally of the border of the horny layer the dorsal surface increases in breadth in a medial direction from 0.5 cm to nearly 2 cm; this greatest breadth is reached at the place, where the articular cavities are situated. In a ventral direction this part of the lower jaw gradually decreases in breadth again and becomes the keel-shaped ventral edge.

Half way between the articular cavity and the caudal border of the horny covering on the dorsal surface of the lower jaw is situated a mushroom-shaped process, occupying half of the breadth on the medial side: the processus mandibulae internus (a). This process consists of a short, thick medio-caudo-dorsally directed stalk crowned by an oval concave upper surface with its long axis perpendicular to the longitudinal axis of the lower jaw.

Caudally it passes into another process (b) with a triangular upper surface and only half the height of the first. To these processes the adductor muscles of the lower jaw were probably attached by their aponeuroses.

Between this process (b) and the articular cavity, on the medial surface, a little below the dorsal plane, runs a short spina, directed medially and slightly dorsally (c). Just rostrally of the articular cavity, on the lateral surface, projecting a little beyond the lateral and dorsal surfaces, lies a latero-caudo-dorsally directed narrow and short protuberance: the tuberculum externum mandibulae (d).

The area round the articular cavity is roughly square in dorsal view, with sides of 1.8 cm. The angles are rounded.

The caudo-lateral and especially the medio-rostral angle lie ventrally deeper than the surrounding edge of the articular cavity (cavitas glenoidea). These two angles are connected by a broad fossa (f), which originates caudo-laterally where it forms an articular facies covered by a narrow strip of cartilage (e). The fossa first runs medio-rostro-ventralwards and reaches its deepest point in the centre of the square. Then the fossa is continued upwards – without reaching the height of the other side – in a medio-rostro-dorsal direction, while it ends again in a smooth surface covered by cartilage (g). The first mentioned strip of cartilage (e) continues from the latero-caudal angle in a rostral direction, curving slightly lateralwards, along the dorsal surface as far as a little beyond the latero-rostral angle. Mid-way this strip of cartilage (e) has a dorsal vaulting. Medio-caudo-ventrally from the latero-rostral angle lies a shallow cup-shaped pit (h). The medio-caudal angle is situated high in the dorsal direction. The medial brim is broadly rounded in its caudal part – with the highest point somewhat rostro-laterally. It then runs steeply ventralward forming the medio-rostral ending of the fossa (f).

2) *Quadratum*

The quadratum is situated ventrally from the caudo-lateral angle of the neurocranium (fig. 1). The quadratum is situated in a plane, which is directed from latero-caudal to medio-rostral. Viewed perpendicularly to this plane the circumference of the quadratum is rectangular (fig. 5). The ventral condylus (j) articulating with the lower jaw is one of the four angular points. Medio-rostro-dorsally of it the narrow, high and long processus orbitalis just out into the caudo-ventral angle of the orbita, and constitutes the second angular point (l). The third angular point is the rostro-latero-dorsal articular condylus (m) by which the quadratum articulates with the neurocranium. The fourth angular point finally is the caudal knob (i″) of the lateral facies, articulating (i) with the lower jaw.

Rostrally from this caudal knob of the lateral articular facies, lies a thick spoon-shaped process, which ventrally bears the rostral part (i′) of the lateral articular surface for the lower jaw and dorsally the lateral articular cavity (p) for the jugale. This articular cavity is conical, with the axis directed from rostro-lateral to caudo-medial.

At a third of the distance between the angular points (j) and (l) a small slightly convex articular condylus (q) with a smooth surface is situated at the medio-rostral side of a medio-dorsally projecting elevation. This articulates with the concave caudal end of the pterygoid.

For the articulation with the lower jaw the quadratum has corresponding articular facies, the shape of which are rather intricate (figs. 1, 3 and 5).

The articular surface of the jaw joint on the quadratum consists of two facets (i and j) which in a ventral view constitute respectively the base and top of an isosceles triangle. The base (i) lies in a plane, which is the continuation of the lateral surface of the upper bill and caudally it curves slightly in the medial direction (fig. 3). The articular facies of the base forms a narrow strip with a smooth surface in a horizontal plane. A dorsally directed depression in the middle of the ventral surface divides the base in a rostral part (i′) and a caudal part (i″). The caudal part (i″) curves caudally and forms a spherical surface directed from rostro-lateral to medio-ventral. This surface covers the caudal part of a rostro-ventro-medially directed cylindrical bony ridge (k) which medio-ventrally bears the second convex surface of articulation (facies glenoidea) (j). This last mentioned surface has a long tongue-like projection on the medial side in a dorsal direction.

3) *The quadrato-cranial joint and its movability*

The articulation with the neurocranium is establised by two articular condyli: *viz.* the already mentioned condylus (m) and medio-caudally of it a second condylus (n) which reaches less far dorsalward. The connecting line between (m) and (n) is nearly perpendicular to the general plane of the quadratum. The axis of the first mentioned condylus (m) is directed from latero-rostral to medio-caudal; it bears dorsally a half-cylindrical smooth surface: the facies glenoidalis. This fits into a corresponding cavity of the neurocranium between the processus zygomaticus squamosi and the ventral end of the caudo-lateral crista (see text p. 10, fig. 1). The axis of this articular cavity has the same direction as that of the first condylus (m). The axis of the second condylus is also directed from latero-rostral to medio-caudal; the facies is very slightly convex and constitutes the smooth upper surface of a mushroom-shaped condylus directed medio-dorso-caudally. This condylus fits into an articular cavity, situated laterally in the sunk and walled in – but ventro-latero-rostrally open – area of the ventral surface of the neurocranium (see text p. 11); this cavity for the condylus (n) lies a little medio-ventro-caudally of the first mentioned cavity. Between the two cavities a firm tooth-shaped projection of the neurocranium juts out, fitting into a shallow groove (o) on the latero-caudal surface of the quadratum between the condyli (m) and (n). As the axes of both condyli (m) and (n) are directed from latero-rostral to medio-caudal a rotation of the dorsal part of the quadratum about these axes, can only result in a movement in a plane directed from latero-caudal to medio-rostral; at the same time the ventral part of the quadratum will move a little dorsalwards, at least with the medio-rostral movement. For the tooth-shaped process blocks any movement in a latero-caudal direction. The presence of the second condylus (n) prevents medio-caudal movements and increases the area of contact with the neurocranium.

4) *The quadratum-lower jaw joint and its movability*

When the bill is closed the lateral articular facies (i) of the quadratum rests on the facies (e) of the lower jaw and the convexities of the former fit into the concavities of the latter along a wavy line (fig. 1). Movements in a rostral direction on a horizontal plane are prevented a.o. by this device. The medial condylus of the quadratum (j) rests in this position on the deepest point of the fossa (f) of the lower jaw. Both these articulations (i–e) and (j–f) are not situated in one and the same transverse axis of the skull. If the elements of the articulation (i) and (e) fit directly together and if (j) fits into the deepest part of the fossa (f), and the bill is opened by a rotation of the lower jaw round the quadratum as a hinge, the rostral condylus (i′) and the medial condylus (j) of the quadratum will be lifted out of their cavities which would result in an unstable condition and this is very unlikely.

When the bill is opened the condyli will in the new position remain surrounded by their cavities and continue to function as such, only when the caudal part of the lateral condylus (i″) of the quadratum can sink into the medio-rostro-ventrally directed part of the fossa (f) of the lower jaw. At the same time the medio-rostral condylus (j), which is connected with it by the bony ridge (k), will shift forwards in the medio-rostro-dorsally directed part of the fossa (f).

The mutual distance between corresponding points of the right and left fossa (f) is caudally greater than rostrally because of the rostro-medial direction of the fossae. So during this shifting, either the glenoid cavities of the lower jaw must be able to move away from each other – in case the distance between the quadrata remains the same – or the quadrata must be able to approach each other – in case the distance between the caudal ends of the lower jaw is constant. As both halves of the lower jaw, because of the absence of a suture or movable symphysis and because of the presence of a rostral horn covering and because of its solidity cannot possibly move away from each other the only remaining mechanism is that the quadrata approach each other.

The mutual movability of quadratum, jugale and pterygoid will be dealt with later on.

5) *Jugale and its movability*

The jugale in *Rhinoplax*, constituting the latero-ventral bridge between quadratum and upper bill, is a rod-like bone, the longitudinal axis of which lies horizontally. It is about twice as high as broad (figs. 1, 3 and 6). Rostrally it is fixed by means of a sutural connection a little dorsally of the caudo-ventral end of the upper bill. This rostral end forms a triangular plane of connection, which is covered with irregular small pits and knobs which fit together with those on the connecting plane on the skull, so as to leave a slight possibility of movement.

One side of the triangle is the end of the lateral surface of the jugale and coincides with the lateral surface of the skull.

The height of the jugale is least in the middle just under the orbita. Ventrally of the processus postorbitalis it is higher and caudally it ends in a conical condylus with a smooth surface. This condylus, the horizontal axis of which is directed caudo-medially, fits into the articular cavity (p) of the quadratum so that jugale and quadratum can rotate mutually round a horizontal axis directed from rostro-lateral to caudo-medial.

6) *Pterygoid and its movability*

The pterygoid, the ventral, more medially situated connection between the quadratum and palatinum (figs. 3 and 7) is somewhat shorter and thinner than the jugale. The axis is directed from medio-rostral to latero-caudal. The pterygoid is cylindrical and in cross section oval with the long axis directed vertically. Rostrally it broadens and is connected with the palatinum by a suture (t) which resembles that of the jugale. This connecting plane (t), shaped like a dorso-ventrally directed oval, just beside the median, joins the shortest of the two parallel sides of the – in a ventral view – trapeziform projecting rostral part of the primary upper jaw. Caudally, where the pterygoid broadens somewhat, it bears a shallow articular cavity (v) in which the medial condylus (q) of the quadratum fits. On the medio-dorsal surface, a little caudally of the middle, is situated a small elevation, a rudiment of the processus basalis pterygoidei of the basipterygoid joint.

D. Kinesis of the skull

1) *Introduction*

From the above anatomical description the following conclusions can be drawn concerning *Rhinoplax vigil*:

1) By moving the lower bill the mouth can only be opened, when the quadrata are able to rotate in a direction with a medial component.
2) The structure of the articulations of the quadratum with the neurocranium allows of a medio-rostral movement of the quadratum.

But this implies for the movements of jugale and pterygoid besides a medial component, which their connections with the bones of the skull (neurocranium) will allow, also a rostral component. The latter can only be realized, when the upper bill (consisting of new upper jaw, to the caudo-ventral side of which pterygoid and – via palatinum – jugale are attached), and on the other hand the neurocranium are not immovably joined together. If these conclusions are correct there must exist also in *Rhinoplax vigil* some form of kinesis.

The build of the skull and the structure of the casque at first sight seem to make kinesis rather improbable, at least in the manner in which it generally occurs in birds.

In order to ascertain the way in which and the place where upper bill and neurocranium are movably joined to each other, a thin section was made of the area dorsally of the paired part of the nasal cavity, where the casque passes into the neurocranium (for technique see p. 7; fig. 2). Herein the fissura cranio-facialis is visible as an irregular boundary. In this section the fissura cranio-facialis runs from the caudo-dorsal part of the paired nasal cavity dorsalwards with a caudal "hairpin turn" (w) (fig. 8) to the point where the caudal wall of the casque rises dorsally on the neurocranium. This borderline intersects the caudally directed horizontal bony trabeculae at about right angles. The trabeculae on either side of the borderline fit so exactly together that in the medial section no dividing line is discernible with the naked eye.

An attempt to make a few dry skulls movable again by a special treatment was successful (for technique see p. 6). It appeared that kinesis occurs along this fissura cranio-facialis. While the upper bill and the neurocranium move away from each other ventrally along the dorsal side of the nasal cavity, the "hairpin turn" of the fissura cranio-facialis dorsally functions as a hinge. During this kinetic movement the quadratum can shift in a medio-rostral direction as the lower bill rotates in opening the mouth (see text p. 18).

2) *Fissura cranio-facialis*

When a dry skull, which is made movable again, is carefully prepared so that the component parts are isolated, it appears that the upper bill bearing the casque and the neurocranium are two separate bony complexes, which are only dorsally attached to each other by connective tissue and not by bone.

The boundary lies along the fissura cranio-facialis, which appears to extend in a rostrally convex half cylindrical plane, the longitudinal axis of which is perpendicular to the median plane. The fissura lies along the caudal wall of the vertical part of the nasal cavity and laterally of it a little rostral of the orbitae, so that rostrally the orbitae possess a double wall (fig. 2).

On the outer surface of the skull the line of demarcation is visible as a suture between the complex of upper bill plus casque and the neurocranium. In the dorsal median this fissura lies slightly caudally of the place where the caudal wall of the casque rises steeply above the level of the roof of the neurocranium. In the dorsal median and also a little laterally of it this fissura (y) passes into a slot, above which the caudal wall of the casque and the dorso-rostral side of the neurocranium approach each other very closely (fig. 1).

From this point (y) of the slot the fissura on the surface leads towards a point (x) near the rostro-dorso-lateral angle of the bony wall of the orbita, just below the horny covering of the upper bill. From this point (x) the line of demarcation runs rostralwards along the rostral wall of the orbita, at a little distance from the lateral border (figs. 9 and 10). Dorsally of the suture (r) between jugale and upper bill, it curves with a wide round bend along the bony process (z) in the rostral wall of the orbita medialwards to end in the median plane on the level of the nasal cavity.

This fissura is situated between a segment of the skull lying rostrally of it and one caudally of it which respectively furnish the rostral and the caudal walls of the fissura.

3) *Rostral wall of the fissura cranio-facialis*

The rostral wall of the fissura is formed by the complex of upper bill plus casque. In caudal view it has roughly the shape of a pentagon (fig. 9). The round dorsal edge of the casque constitutes the top angle; the rostro-dorso-lateral-angles of the orbitae near point (x) are the next two corners; while the connecting planes (r) with the jugale represent the basal angles.

The dorsal and the lateral sides of the casque consist of a compact layer of bone; they are covered by a tapering extension of the horny layer; the caudal bony wall, however, does not consist of such firm compact bone. A low long crista (aa) runs from the dorso-lateral corner (x) along the latero-dorsal side of the upper jaw; midway the top of the pentagon it makes a slight curve medialward to proceed from there in a horizontal direction. In the median, dorsally (bb) as well as ventrally (cc) of the crista (aa), is situated an unpaired, shallow more or less conical depression. The surface of the crista and of these depressions bear irregular knobs and pits, the axes of which are perpendicular to the plane of the crista, they are arranged in small groups with the longitudinal axes directed vertically, while the groups are separated by small dorso-ventral grooves. A slightly sunk area with the shape of an equilateral triangle (dd) adjoins dorsally with its base the edge of the crista (aa) along half its horizontal length. A little latero-ventrally of the top of this triangle, thus on the right and on the left half of the skull, lies a small spina (ee). Ventrally of the top of the triangle the two halves of the paired nasal cavity – separated by a membranaceous septum running in the median plane – diverge from each other. Both halves pass with a latero-rostral curve into the upper bill and via half a spiral coil end at the oval (external) nostril in the caudo-lateral side of the casque (fig. 1).

On the dorso-lateral surface the nasal cavity bears on the right and the left, a vertically suspended very thin bony pennon-shaped process (gg). This is attached by its dorsal scallop-like part, continues narrowing ventrally and ends in a flat triangular surface.

The slightly concave lateral part of the rostral wall of the fissura cranio-facialis constitutes at the same time the rostro-lateral wall of the orbita (see text p. 21). Half way the height of this wall of the "orbita" and a little medially lies the beginning of a shallow horizontal groove (hh), which gradually deepens medialwards. Because medialwards the dorsal edge covers it more and more this groove ends as a nearly closed tube (hh), which with a slight ventral curve leads into the vertical nasal cavity (ff). This groove (hh) must enclose the lachrymal duct.

At the level of this groove (hh) in the rostral wall of the nasal cavity is situated the round aperture (ii) of a tube which ramifies into the bill, and through which nerves and blood vessels can enter into the bill. The triangle of the pennon-shaped process (gg) probably serves as support during kinesis of the rami of nerves and blood vessels, which lead from the rostro-ventral surface of the bony interorbital septum.

Ventrally of the horizontal groove (hh) the nasal cavity (ff) narrows to a deep vertical groove which, half way the distance to the roof of the mouth in the upper bill, disappears into the palatinum and ends in the choana in the roof of the mouth (fig. 3).

The palatinum is shaped like a truncated pyramid and projects ventro-caudally. The surface in the roof of the mouth is trapeziform. At the caudal side of this trapezium and on the truncated top are situated the irregular oval surfaces (t) of the sutural connection with the pterygoid. A shallow small groove (jj) leads from the point, where the nasal cavity disappears ventrally behind the pyramidal, ventro-caudally projecting palatinum, along the full length of the caudo-ventrally directed upright surface of this pyramid. Between the triangular lateral upright surfaces of this same pyramid and the triangular connecting facet (r) with the jugale, is situated a cup-shaped hollow (kk), which dorsally extends as far as the ventral border of the rostral wall of the orbita.

4) *Caudal wall of the fissura cranio-facialis*

The caudal wall of the fissura cranio-facialis is formed by the caudal segment of the skull. Its general form also approximates a pentagon, of which, however, the height is considerably less than that of the rostral wall described above (fig. 10). The wall of the caudal segment of the skull closely fits in shape and structure against the wall of the rostral segment of the skull. This caudal wall is produced into a thin bony lamella rostral of the orbita.

A hemispherical elevation on the rostro-dorsal surface of the skull in and beside the median at the point (y) in the fissura constitutes the top. This elevation fits into a corresponding slight depression of the caudal side of the casque and reaches as far as half way the distance between the top and the crista (aa). Ventrally of this hemispherical elevation and closely dorsal of the sulcus (a′a′), lies the spina (b′b′).

The next angles again are the rostro-dorso-lateral angles (x) of the orbita in the fissura. Opposite the crista (aa) lies a shallow sulcus (a′a′) with the same course and a similar relief. In the median dorsally and ventrally of this sulcus are situated the above mentioned dorsal spina (b′b′) with a ventro-rostrally directed upper edge and a ventral spina (c′c′) with a dorso-rostrally directed top. These spinae fit into the pits (bb and cc) dorsally and ventrally of the crista (aa) and so they hold the crista (aa) in their grip as a pair of pincers.

The rotating movement of the kinesis, during which the fissura cranio-facialis widens ventrally, so that the distance between the two segments of the skull increases ventrally, occurs round the horizontal part of the sulcus (a′a′) as hinge line. The crista (aa) remains firmly settled in the sulcus (a′a′), because the uneven surfaces of knobs and pits of both sides fit closely into each other. Moreover, the spinae (b′b′ and c′c′), which grip the crista (aa) as in a pair of pincers and fit into the corresponding cavities (bb and cc), ensure a further consolidation of the casque articulation. In the median section of the skull the hairpin turn (w) is the cross section of this pincer construction (figs. 2 and 8). During kinesis the rostro-dorso-lateral angles of the wall of the orbita near point (x) and a caudal angle of the wall of the bill—which both have a flat vertical facet, move slightly away from each other.

Ventrally of the sulcus (a′a′) a somewhat raised triangular area (d′d′) adjoins, which fits into a corresponding—but sunk—area (dd) of the rostral segment of the skull. Latero-ventrally of the top of this triangle is situated a conical cavity (e′e′), its floor bearing a kidney-shaped aperture. From the position of this aperture and the comparison with the other investigated Bucerotidae it may be concluded that this is the foramen nervi olfactorii. The spina (ee) on the rostral segment of the skull occupies the dorsal part of this conical cavity (e′e′) in such a way, that space remains for the passage of the nerve. The nervus olfactorius which no doubt enters the orbita dorsally of the foramen nervi optici (fig. 1a) follows the interorbital septum in a horizontal direction. On the dorsal side of the septum interorbitale a shallow horizontal groove for this nerve is visible. The nerve supposedly continues over the scallop-shaped dorsal part of the process (gg) into the nasal cavity – both in the rostral segment of the skull.

Ventrally of the top of the triangle (d'd') in the median is situated a broad groove (f'f') which constitutes the caudal wall of the paired nasal cavity (ff). This groove is divided longitudinally in two by the median bony ridge of attachment of the membranaceous nasal septum. Ventrally this groove ends at the rostral free edge (j'j') of the most ventral part of the bony interorbital septum. The edge (j'j') of this septum is directed ventrally and a little caudally and when the fissura cranio-facialis is ventrally widened it slides along the small groove (jj) in the caudal-ventral side of the palatinum in a caudo-ventral direction.

The last two of the five angles of the caudal wall of the fissura cranio-facialis are the spade-shaped latero-ventral ends (z) of the rostral wall of the orbita. Dorsally of these angles the lateral side has a shallow medial incision so that the entrance of the groove (hh) on the wall of the upper bill – containing the lachrymal duct – is free.

On the wall of the neurocranium medially of the incision lies a shallow horizontal groove (h'h') which constitutes the caudal wall of this duct. As the rostral wall of the orbita is concave, the spade-shaped ends (z), which rest against the wall of the upper bill dorsally of the place of attachment of the jugale, are situated in a plane directed from rostro-dorsal to caudo-ventral. The ventral border of the spade-shaped process follows the concave dorsal circumference of the cup-shaped cavity (kk) in the rostral segment of the skull.

5) *The fitting together of the two walls of the fissura cranio-facialis*

As appears from the above, the rostral and the caudal wall of the fissura cranio-facialis are of such a shape, that they fit closely together with the general curves of their surfaces and their local projections, deepenings and undulations. Consequently the two walls are in all directions firmly fixed relatively to each other, as long as the bill remains closed.

During kinesis the fissura cranio-facialis widens ventrally and the connection is more or less loosened in a rostro-caudal direction, but remains firm in a lateral direction, because the ridge of the interorbital septum remains enclosed by the groove (j'j') of the palatinum during its movement. On the other hand the fixation becomes firmer during kinesis, because the parts lying dorsally of the crista (aa) are pressed together. At first the groove (y) between the rostro-dorsal elevation of the neurocranium and the caudal wall of the casque, narrows. During this narrowing the elevation of the neurocranium is pressed closer against the wall of the casque, which, because it consists at that place of thin spongy bone, will be able to yield.

Besides the greater areas dovetailing into each other, there is a second kind of surface structures on the opposite walls that lock closely together. These are best described as "buffers". They are flat surfaces, round or oval or more intricately shaped, generally surrounded by a depression accentuating that they project a little above their surroundings. In the several specimens they are rather variable in position, size and number. From parasagittal sections through the skull it appears that they are situated at the ends of bony trabeculae abutting on the walls of the fissura cranio-facialis between upper bill with casque on the one side and the neurocranium on the other side. When the fissura is closed the trabeculae of both segments of the skull fit so exactly onto each other as to make the impression of a single uninterrupted rod and the facets fitting together, function like the buffers of a train.

Especially in the median and along the lateral walls of the nasal cavity the buffer surfaces are well developed. We will describe their position on the rostral segment of the skull *i.e.* the rostral wall of the fissura cranio-facialis. Here the buffer surfaces (ll) are situated ventrally of the crista (aa) along and inside the sunk triangle (dd); there are buffer surfaces (nn) along the lateral sides of the nasal cavity (ff) and finally a few very large round buffer surfaces (oo) between the groove (hh) containing the lachrymal duct and the ventral cup-shaped cavity (kk). On the caudal segment of the skull the buffer surfaces (n′n′) are found on the ventral side of the conical cavity (e′e′) bearing the foramen nervi olfactorii.

Besides these a great number of small surfaces fitting together occur scattered over the entire area ventrally of the crista (aa), where the fissura cranio-facialis possesses a rostral and a caudal bony wall. Such surfaces also occur in the area rostrally of the orbita, but trabeculae fitting dorsally upon them are of course wanting.

The exact fitting together of the corresponding flat smooth surfaces of the "buffer" mechanism which by themselves do not constitute a fixed connection is achieved – besides by the fixation of the large areas of both walls engaging in each other – by connective tissue between the buffer surfaces.

6) *Degree of movability of the complexes of the skull*

Now that shape and position of the various complexes of the skull have been described the manner in which and the degree to which their movements take place can be considered more in detail (figs. 1, 3, 4).

From a skull made flexible again the lower jaw was removed and the neurocranium mounted in a fixed position. Kinesis then could be achieved by moving the upper bill dorsalwards. The accompanying displacements of upper bill, pterygoidea, jugalia and quadrata could be observed and measured (figs. 11a and b; for technique see p. 6).

In the investigated skull the width of the fissura cranio-facialis ventrally increases with 2.5 mm (as measured in the increase from 56.5 mm to

59 mm of the distance from the rostral border of the choana to the caudal border of the condylus occipitalis). Hence the skull is capable of only slight kinesis, though of course it must be kept in mind that in the living animal it may be greater owing to greater elasticity of joints and ligaments.

When the centre of the caudal part (i″) of the lateral condylus (i) of the quadratum is called A and the medio-rostral condylus (j) B, it appears, that the angle between the production of AB and the median increases by 8°, *i.e.* from 32° to 40° (see figs. 11a and 11b). In other words the quadratum performs a rotating movement with a considerable medial component. At the same time the distance from A to the median decreases by 1 mm (*i.e.* from 28 mm to 27 mm) and that from B to the median by 2.5 mm (*i.e.* from 21.5 mm to 19 mm), from which it follows that the pivot of the movement must be situated nearer to A than to B. Finally the distance between the projection of A on the median plane and the caudal border of the condylus occipitalis increases by 3 mm (*i.e.* from 10.5 mm to 13.5 mm). This rostro-medial displacement of the quadratum corresponds to an increase in width of 2.5 mm (*i.e.* from 56.5 mm to 59 mm measured between rostral side of the choana and caudal side of the condylus occipitalis) of the fissura cranio-facialis for which the rostral component is responsible.

During kinesis the quadratum indeed rotates round the axis of the quadrato-cranial-articulation – directed from medio-caudal to latero-rostral – as a pivot.

Because of the medial component of this movement the caudal part (i″) of the lateral condylus (i) is brought in front of the entrance of the groove in the articular cavity of the lower jaw, in which it can sink because of the rostral component in a medio-rostral direction. At the same time the part of the lower jaw situated caudally of it rotates dorsalwards because of the contraction of the musculus depressor mandibulae, which will insert on this part. Hereby the part rostrally of the condylus rotates ventralwards and the bill is opened. By the movement of the rostro-medial condylus (j) of the quadratum, which has a greater medial but also a small dorsal component, this condylus, which lies in the centre of the fossa, slides along the medio-rostral articular plane (g). Eventually, when the bill is opened very wide, this condylus may slide out of the fossa; its supporting function is then taken over by the bony ridge (k) which connects this condylus (j) with the caudal part (i″) of the lateral condylus. At the same time the rostral part (i′) of the lateral condylus (i) shifts into the latero-rostral shallow articular cavity (h) of the lower jaw. As the imaginary axis of the rotation of the lower jaw lies dorsally of this part (i′) of this condylus, the displacement of the quadratum will mainly result in a change of orientation of this part (i′) of this condylus in the lower jaw.

The movement of the quadratum, which is most clearly visible in its rostral part, can be resolved into a dorso-ventral, a latero-medial and a caudo-rostral component. In this triaxial movement the caudal ends of jugale and pterygoid are involved. These two elements which are not fused with the quadratum – but remain separate bones – are joined to the quadratum by a ball and socket joint. The rostral ends of jugale and pterygoid are joined by connective tissue in a suture-like connection to the skeletal upper jaw and here the movability is at least in so far restricted that the distance to the medial plane remains the same. This loose connective tissue only permits of a slight turning, which indeed is the only movement that takes place.

7) *The rudimentary basipterygoid articulation*

Functioning basipterygoid articulations are not present in *Rhinoplax*. The rudiments of it are rather variable in size in the different skulls.

In one very robust specimen, however, they were still functioning as an articulation. The basisphenoid in this specimen possessed a small rostro-laterally directed columnar process, bearing a flat oval surface extending in a rostro-medial direction. This corresponded with a similar – though shorter – medio-dorsal process at a third of the length counted from the caudal end of the pterygoid. During the medio-rostral displacement of the pterygoid relative to the basisphenoid, the processes slide along each other with their flat upper surfaces, so that the pterygoid is given extra support. The fact, that the articulations were small and weak in relation to the robust skull, while they are totally wanting in other specimens demonstrates the insignificance of their function.

E. Ligaments of the skull

1) *Structure and course of the ligaments*

The ligaments of the joint of the jaw were present still in a fairly undamaged condition in one of the available skulls of *Rhinoplax* (fig. 1).

On the lateral side of the joint of the jaw is situated as the most lateral ligament, a broad, flat ligament directed from caudo-dorsal to rostro-ventral, the ligamentum jugo-mandibulare externum. This connects the latero-ventral side of an oval knob on the caudal parts of the lateral side of the jugale with the tuberculum externum mandibulae (d). This well developed ligament, which is also present in *Buceros* and *Rhytidoceros* (Starck, 1940, p. 608) is wanting in most Bucerotidae.

Medially of the ligamentum jugo-mandibulare externum is situated a similar band, the ligamentum squamoso-mandibulare, leading from the ventro-caudal side of the processus postorbitalis in a ventral direction also toward the tuberculum externum mandibulae (d).

The jugale and the most ventral point of the processus postorbitalis are connected by the ligamentum squamoso-jugale, which in *Rhinoplax* is extremely short in comparison with that of the other Bucerotidae, owing to the fact, that in this species the processus postorbitalis extends much farther ventralwards.

In lateral view the ligamentum jugo-mandibulare-articulare is only partially visible. It arises on the jugale ventro-medially of the ligamentum jugo-mandibulare externum and runs horizontally along the caudal part of the lateral articular facet of the quadratum, along the articular cavity of the lower jaw and inserts on the caudo-medial angle of the edge round the glenoid cavity of the lower jaw.

Finally the ligamentum quadrato-mandibulare is situated between a part of the quadratum medially of the quadrato-jugal articulation and the lower jaw, just rostrally of the medio-rostral glenoid cavity. This ligament runs parallel to the ligamentum jugo-mandibulare externum. In *Rhinoplax* it is oval in cross section. STARCK already mentioned this ligament in the other Bucerotidae.

2) *Functions of the ligaments*

The ligaments consist of elastic material. In *Rhinoplax* they are exceptionally well developed, which can be understood in connection with their function, which consists of the consolidation of the connection between the elements of the joint of the jaw and anchorage of the – in this case so much heavier – bones of the skull in the joint of the jaw. At the same time the ligaments have a function in the opening and closing mechanism of the bill.

When the lower jaw rotates around the quadratum articulation it can be seen that the imaginary axis of the movement is situated at about the level of the quadrato-jugale articulation.

During the dorsal movement of the caudal end of the lower jaw the ligamentum jugo-mandibulare-articulare slides in a dorsal direction along the round dorsal side of the caudal part (i″) of the lateral articular surface (i) of the quadratum. This condylus is thereby guided in its rostro-medial movement into the fossa of the glenoid cavity of the lower jaw, whereby at the same time the caudal end of the lower jaw is drawn dorsalward.

The dorso-caudal ends of the ligamentum jugo-mandibulare externum and of the ligamentum quadrato-mandibulare internum move, together with the quadratum, rostro-medialwards and a little dorsalwards; the ventro-rostral ends, however, ventralwards together with the lower jaw. The increase of the distance between the two places of attachment of each ligament entailed by this movement, is compensated because the elastic ligaments pull the quadratum firmly into the glenoid cavity of the lower jaw.

The dorsal attachment of the ligamentum squamoso-mandibulare is situated on the processus postorbitalis, and so remains fixed in relation to the neurocranium. If the bill were opened very wide, the distance between the places of attachment would have to increase. As the ligament does not allow of this, it acts as security against too extreme opening of the bill.

As the tension of the elastic ligaments increases somewhat during the opening of the bill, the quadratum will remain firmly pressed into the glenoid cavity of the lower jaw.

The question, whether in the case of *Rhinoplax* kinesis can occur independent of the rotation of the lower jaw relative to the upper jaw must in my opinion be answered in the negative, because of the action of the ligaments, even though the anatomy of the articulations would allow it.

For the occurrence of kinesis it must be assumed that the quadratum is moved in a rostro-medial direction and it must be taken into account that the tip of the upper bill will move dorsalward relative to the neurocranium. But by our assumption the lower bill should be able to remain in the same horizontal position in relation to the neurocranium. The lower bill should remain lying against the caudo-ventral end of the base of the upper bill, as this end makes a movement, which is only directed rostrally, while a dorsal component is absent, because the hinge (aa–a′a′) on which the upper bill rotates relatively to the neurocranium is situated dorsally of this end of the upper bill.

The quadratum, however, will move in a medio-rostral and a little in a dorsal direction relatively to the caudal end of the lower jaw. Hereby the condyli would be lifted out of their glenoid cavities in the lower jaw. However, the ligaments will keep the quadratum firmly pressed into the glenoid cavity of the lower jaw, because during the movement of the quadratum their tension increases. So the caudal end of the lower jaw will move upwards and consequently the rostral end of the lower jaw downwards. The movements of upper and lower jaw consequently can only occur simultaneously.

II. STRUCTURE AND MECHANISM OF MOVEMENT OF THE JUVENILE SKULL

A. The juvenile skull in outward view

Inspection of the juvenile skull of *Rhinoplax vigil* throws light upon the development of the divergent structure in this species of bird.

The juvenile skull investigated has a maximal height of 7 cm and a length of 18 cm, as against respectively 8.5 and 23 cm on an average in our adult specimens. The skull is very light in weight. Its specific weight (for technique see p. 7) of 0.13 gr/cm^3 equals that of *Buceros rhinoceros silvestris*, which has the specific lightest skull among the available material of Bucerotidae. The specific weight of an adult skull of *Rhinoplax* amounts to 0.51 gr/cm^3.

Not only in weight, but also in shape and structure the marked resemblance to skulls of the other Bucerotidae is striking.

Only the length and curvature of the bill and the position of the processus postorbitalis are already clearly typical of *Rhinoplax*. Orbita and nostril are large in comparison with those in an adult specimen; the bones of the skull are small and thin and the processus, cristae and spinae hardly developed.

The casque appears as a big globular elevation on the caudal part of the bill and the rostral part of the orbita. Dorso-caudally the casque slants towards the level of the neurocranium. The rostro-ventrally slanting side bears a narrow sharp crista, decreasing in height in the direction of the tip of the bill. The fissura cranio-facialis is very indistinctly visible from the outside as a small suture dorsally of the orbita. It extends as far as midway the distance to the median. From here it can be followed at the rostral side of a flat, oval area – sunk in relation to its surroundings – of very thin-walled bone, which in the median passes into a narrow open groove.

B. The internal structure of the juvenile skull

The parasagittal section, made of this skull, shows that the bony trabeculae in the casque are still totally wanting. The spongy bone in the rostral part of the upper bill, however, shows a vertical structure. The area of the casque rostrally of the nasal cavity is practically empty, only the walls are covered by a thin layer of spongy bone, stratified parallel to the surface. This finely meshed thin walled spongy bone rostrally joins that of the upper bill in a slight curve and fills the most caudal part of the casque and the space round the nasal cavity, as is the case with the other Bucerotidae having a large casque. The bones of the skull are thin walled and also filled with spongy bone. At the place, where in the adult skull a median bony septum divides the rostral part of the brain case, occupied by the telencephalon, only a narrow crista is present. The interorbital septum was damaged too much to allow of any conclusions concerning its structure and extension.

The horny covering is a thin layer on the bill and the casque. Only on the rostral side of the casque it has a greater thickness *i.e.* 5 mm.

Jugale and pterygoid appear to be connected with the upper bill by means of cartilage as in the other Bucerotidae. In specimens in which the soft parts had been preserved, cartilage was found in this connection.

At the place, where in the adult skull the part of the fissura cranio-facialis is situated ventrally of the horizontal crista (aa), the finely meshed spongy bone is locally thickened especially in the middle. One gets the impression that both walls of the fissura cranio-facialis are present separately, but that the hinge-like articulation is not yet functioning as such. The spongy bone by its flexibility appears to allow of kinesis.

III. ONTOGENY OF STRUCTURE AND MECHANISM OF MOVEMENT

On the strength of conditions in the juvenile specimen it is possible to form a conception of the development of the skull in the adult *Rhinoplax* with its divergent casque and architecture adapted to it.

The skull of the young animal will develop especially strongly in a caudo-dorsal direction. The bones of the skull increase in thickness and at the same time the internal structure of the bone develops. The cristae, especially the latero-caudal ones, on the neurocranium as well as the fossae, processus and spinae develop vigorously. The bill, however, lags behind in development. The spongy bone will spread until it fills the casque entirely. Proportionally to its increase in thickness the structure of the bony trabeculae will become more and more distinct and it will become thicker and more rigid. Simultaneously with this decreasing flexibility of the spongy bone in the area of the hinge-like articulation (aa–a'a') the walls of the fissura cranio-facialis will be thickened and reinforced so that the movement occurs less and less by flexure and more and more exclusively by actual rotation.

The connections between jugale, respectively pterygoid, and the upper bill become ossified to not quite immovable sutures. As the casque develops – especially in a dorso-caudal and dorso-rostral direction – horny layers will be deposited on the rostral surface until a thick parcel of horn has accumulated (fig. 2). The stratification visible at the rostro-ventral side on the outer surface of the casque will partly be due to the fact that the originally present rostro-ventral horny crista is rubbed off in a similar way as BARTELS (1956) observed in a young *Aceros plicatus.*

IV. DEDUCTION OF THE MECHANISM OF MOVEMENT IN THE SKULL OF RHINOPLAX FROM THAT IN BUCEROTIDAE IN GENERAL

The great differences in build between the skull of *Rhinoplax vigil* (Forst.) and those of the other Bucerotidae suggest that adaptive modifications in the mechanism of movement in the skull must follow. The same holds when the skulls of the commonest Bucerotidae are compared with those of most other birds.

A special property of the birds' skull is kinesis: the possibility of raising the maxillary segment, especially the upper bill relatively to the occipital segment, especially the neurocranium. A flexible zone in the prae-orbital part of the roof of the skull serves as pivot, there where it passes into the upper bill. Concerning the commonest Bucerotidae we will begin with the conclusion drawn by STARCK (1940, pp. 618, 622) in his investigations on the trigeminus musculature of the Bucerotidae, *i.e.* that kinesis is very strongly developed in the skull of the Bucerotidae. Also HOFER (1955, p. 120) in his observations on the head ornaments (cephalic ornaments) of the Bucerotidae calls the skull "hochkinetisch".

Inspection of the skull of a representative of the family of the Bucerotidae *e.g. Buceros rhinoceros* would not lead one to expect the possibility of kinesis to such a degree.

The casque which overlaps the rostro-dorsal part of the roof of the neurocranium and so constitutes a bridge between bill and neurocranium, seems a hindrance to independent raising of the upper bill. On a parasagittal section of a skull of *Buceros rhinoceros*, however, it is visible that a cleft, the fissura cranio-facialis, separates the neurocranium partly from the upper bill. This fissura begins ventrally between the caudal part of the palatinum and the edge – filled with spongy bone – which surrounds the membranaceous interorbital septum and continues between this edge and the vertical part of the nasal cavity. On close examination of this parasagittal section this fissura here also is discernible as a thick line through the light spongy bone which makes a similar "hairpin turn" as in *Rhinoplax.*

In one available head with muscles of *Aceros plicatus*, the mechanism of movement could be investigated.

Jugale and pterygoid in this case are rostrally connected by cartilage with the upper bill, caudally both articulate with the quadratum. The quadratum itself is joined dorsally to the ventro-caudal part of the neurocranium by a double articulation and ventrally to the lower jaw by a sliding articulation with two articular facies.

When the bird opens its bill the strong musculus depressor mandibulae contracts. This muscle inserts on the ventro-caudal side of the lower jaw and runs towards the dorso-caudal part of the neurocranium. Consequently the caudal end of the lower jaw is displaced dorsalwards and because the lower jaw rotates round the sliding articulation with the quadratum as pivot, the bill opens.

At the same time the ventral part of the quadratum is moved in a medio-rostral direction by the musculus protractor quadrati. For this muscle originates ventrally of the prooticum, passes caudalward and inserts ventrally on the medial side of the quadratum. The quadrato-cranial articulation acts as pivot of the movement. The sliding movement of the quadratum in the glenoid cavity of the lower jaw is enlarged by this.

Simultaneously, however, jugale and pterygoid will be displaced in a rostral direction. This is possible because the upper jaw is not fixedly connected by means of the casque to the neurocranium. The fissura cranio-facialis will increase in breadth ventrally while the spongy bone situated between casque and neurocranium on either side of the fissura cranio-facialis will act as elastic sponge, that is: yield and function as a hinge.

To close the bill strong muscles are required. The musculus pterygoideus, which arises ventrally on the pterygoid and inserts partly on the inner side and partly on the outer side of the lower jaw, plays a part, as also the musculus adductor mandibulae, which is attached with an aponeurosis to the processus mandibulae internus and runs towards the surfaces of the fossa temporalis.

So far the situation as observed in the specimen of *Aceros plicatus.* On account of the resemblance in the configuration of the fissura in *Rhinoplax* and the other Bucerotidae it seems probable that also in the latter a rotation occurs to some extent in the same way as in *Rhinoplax.* This would be contrary to the opinion of STARCK who holds that this is effected solely by flexion of the spongy bone and does not mention the existence of an open fissura. This requires further investigation.

In still another respect STARCK's opinion seems somewhat doubtful. He writes (1940, p. 615), "dass der Schädel der Bucerotidea ausserordentlich stark kinetisch ist und hierin dem Papegeienschädel kaum nachsteht". When a parrot is shelling a peanut the upper bill seems to be entirely loose from the neurocranium; so distinct and considerable are the movements which it is able to make. Bucerotidae in action do not show similar movements. As a matter of fact when the bill is opened wide, the head is thrown back. The muscles of the neck contract and the feathers on the neck will be raised, so that the casque seems to approach the neurocranium still more. On photographs of living birds this approaching, however, appears to be very slight. Unfortunately it proved impossible to make comparable Röntgenograms of one and the same living bird.

Röntgenograms were taken of the head with muscles of *Aceros plicatus* with the bill opened to different extents while the upper bill was mounted immovably (for technique see p. 7). Theoretically it makes no difference whether for these observations on different degrees of opening of the bill, the upper bill or the neurocranium is fixed immovably. But the first method proved more practicable.

When comparing a photograph of the skull of *Aceros* with the bill closed with one in which the bill is fully opened, it is confirmed, that the ventral side of the quadratum moves rostralwards and that the fissura craniofacialis is ventrally widened, so that the angle between casque and neurocranium decreases. But it also becomes clear that kinesis is only slight. It must be kept in mind that the material was not fresh, and so perhaps allowed of less extensive movements than the living animal.

We have seen that in the adult *Rhinoplax*, there is no question of flexibility any more, but only of rotation in a hinge-like articulation. This condition in the adult skull develops from a juvenile condition of the skull of *Rhinoplax*, which resembles that in the commonest Bucerotidae. The juvenile skull in *Rhinoplax* is not very different from that of the other Bucerotidae in the adult state, neither in shape, nor in build nor in weight.

V. FUNCTION OF BILL AND CASQUE IN CONNECTION WITH HABITUS AND MODE OF LIFE

A. Habitus and mode of life

Very little is known about the mode of life and behaviour of *Rhinoplax vigil* (Forst.) because of its great shyness and rareness (see for older literature: MARSHALL, 1911, pp. 186–188).

It is present on the Malay peninsula, on Sumatra and Borneo and lives in virgin forest with high trees up to great elevations.

This bird has been so intensively hunted because of its extraordinary casque, about the magic power of which all kinds of legends circulate and the "ivory" of which is used in handicraft by the aborigines that now it is protected by law. So it will hardly be found among the living inmates of zoological gardens and accordingly a living specimen is not readily accessible for investigation.

The total length of the male inclusive the two extremely long median rectrices of the tail is rather more than 1.05 m (3 feet 6 inches) or even 1.5 m. The wing is 0.5 m (19 inches). The female is somewhat smaller. The bill is yellow, brickred at its base. The casque is orange-red on its anterior half, brickred for the remainder. The colour of most feathers is brownish black, those on the head are black. The neck and a spot on the back are bare and brickred (ELLIOT, 1877, text to plate 10).

It is a shy bird living usually alone (HUME and DAVISON, 1878, p. 116; HARTERT, 1901/02, p. 179), "or in small parties rarely of more than four" (ROBINSON, 1928, p. 50).

Concerning its food HUME and DAVISON (1878, p. 115) mention, that a shot specimen "had eaten only a quantity of fruit". Further FORBES (1885, pp. 153, 154) reports that he observed a specimen of *Rhinoplax vigil* belabouring the branches of a large *Urostigma* tree full of fruit with "far-resounding thuds" of the casque. The animal moved with the greatest ease through the tops of the trees nothwithstanding its heavy casque. FORBES (1885, p. 154, fig. on p. 155) already looked for a connection with the structure of the casque, which was known to him from a median section.

Their flight is not different from that of the other Bucerotidae. During the flight also in *Rhinoplax* a "rattling sound" is heard "made by the air against the primaries".

The voice of *Rhinoplax* is striking and audible at great distances. "It commences with a series of whoops uttered at intervals of about half a minute for five or ten minutes; the bird ending up by going off into a harsh quacking laugh" (HUME and DAVISON, 1878, p. 115).

The manner of nestbuilding is not known with certainty. As *Rhinoplax vigil* differs little in behaviour from other large Bucerotidae – as far as is known – it is very probable that it also makes its nest in hollow tree-trunks.

To this may be added the facts known from literature concerning these points in other Bucerotidae. The known species of the Bucerotidae mutually differ little in mode of living and habits. A selection will be made from the data on their habitus and mode of life, that may be relevant for understanding the function of bill and casque.

Generally the Bucerotidae are large birds, which have a dark and rather uniform colour, except for a strikingly bright-coloured bill and casque and feathers on head and neck. All species live in couples, but often assemble into larger groups. The large flying species, to which *Rhinoplax* belongs, move with great ease among the treetops. With their strong wings they make a loud rustling noise during flight. The eyes, which are large, can be moved independently from each other. Their voice is striking and very loud and persistent. Sometimes it reminds one of a drum.

Their food is miscellaneous. They eat all kinds of fruit, but also insects are to their taste and even small birds and other small vertebrates are not despised.

The movements when eating, as I observed myself on animals in captivity, can be described as follows. With the tip of their long, curved bill they pick up a fruit or other piece of food, examine it by small biting movements between the tips of the bill and then – when it proves acceptable – the head is thrown back with a quick movement, while at the same time the piece is thrown up in a curve and the bill opened wide, so that the food can be caught in the back of the vertically raised open bill. The animals have in fact only a very short tongue. Larger objects as mice they dispatch step by step with small snapping movements towards their gullet. The tips of the bill are at first directed forward, but, as the food is shifted towards the gullet, the bill is each time opened wider and wider and raised more and more upwards.

I could also observe the peculiar manner in which the birds move among the branches of the trees. In the same way as *e.g.* parrots do, they catch hold of a branch with their curved strong bills. Next they swing their body from one branch on to the next one, suspended from their bills.

The mode of nest building, according to the literature, is characteristic of the Bucerotidae. The female during the time of incubation is completely walled off in a hollow tree. Only a narrow vertical slit remains open and the male proffers food through this slit. The female remains in this "goal", in which she meanwhile moults, till the young – generally two – are big enough to fly. The artificial wall is then broken down again.

The material of which the wall is built, consists of an at first pulpy but soon hardening mixture of "mainly excrements with small amounts of dung, applied in quick sidelong vibrations of the bill and then the bill moves along the surface. Later on dry peat-dust-like matter is applied by the same kind of movements interrupted as the bill – all the time vibrating – now slowly moves upwards and downwards, its tip constantly tapping sideways at the newly built layer, making it smooth and solid" (BARTELS, 1956 on *Aceros undulatus*; see also BARTELS, 1937, pp. 121/122, 142, 168, 169).

As to enemies: especially the large species among the Bucerotidae have few. The long mobile neck, the strong muscles of the neck, which can be deduced from their extensive surface of attachment caudally on the skull, and the enormous size of the bill, make this bill a dangerous weapon.

According to a personal communication of Mr. H. J. V. SODY 1) the

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1) H. J. V. SODY was at that time retired forester in the former Dutch East

development of the bill in the Bucerotidae would have no relation with their food, although as a rule there does exist a connection between the possession of large and strong bills and the eating of vertebrates. He believed, however, that a parallel can be drawn, especially in tropical birds, between the possession of large bills and the habit of nesting in hollow trees. The Bucerotidae have maximally developed bills and are also extremely specialized, as nestlers in hollow trees; the nesting hole is even walled up. The casque together with the bill would serve as defence during the period of incubation against predative enemies as *e.g.* the numerous arboreal lizards (Lacertilia), flying squirrels and bats which chase small birds from their nesting holes. Only birds with large or very large bills will be able to maintain themselves against these agressors. Sody leaves aside whether these bills will serve as means of defence or to deter (*e.g.* against monkeys). Though, according to him, it is conceivable that there should be a close connection between the development of the bill and the way of feeding, this seems very improbable with regard to the casque on the bill.

B. Function of bill and casque

From the data in literature on the mode of life of *Rhinoplax vigil* (Forst.) next to nothing can be learned with regard to the function of bill and casque.

Concerning the other Bucerotidae it is evident from the preceding that the tip of the strong bill serves for the acquisition of food, the middle part for locomotion among the branches of trees, while the sides are specially used as "trowel" when walling in.

The casque, however, has no function as a tool in these Bucerotidae. This hollow, bladder-like structure which during life is indentable and elastic, over its entire surface and as a matter of fact often was indented or damaged with specimens from museum-collections, would be very unsuitable for this. On the contrary it seems very probable that the casque should be a threatening structure. The bright light colours of the feathers of head and neck and the imposing bill with casque, which in certain cases also has special markings, contrasting with the grey colour of the rest of the bird, attract full attention to this area. The casque will make the indeed dangerous bill look bigger still and thereby help to deter possible agressors. Probably the head is in these cases turned sideways so that the greatest surface is rendered visible to the opponent, a well known procedure with threatening postures. Undoubtedly the casque will also play a rôle during display as an "imposing structure". But which

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Indies. He had a great knowledge about the food of birds. After his death in January 1959 a manuscript was found on the food of Javanese birds, which will be published in the Zoologische Verhandelingen van het Rijksmuseum van Natuurlijke Historie te Leiden.

rôle and whether the males when fighting each other charge upon the casque, I found nowhere mentioned in literature.

Because of its negligible weight the casque may in some species develop into an enormous structure apparently without any inconvenience for the bird.

The Bucerotidae are able to produce powerful sounds. It seems plausible, that there exists a relation between volume and likeness to a drum of the produced sound and the casque. The hollow space in the casque seems an excellent soundboard intensifying the sound by resonance. The sound might be conveyed from the syrinx via the gullet and the choanae to the nasal cavity covered by thin walled bone, which runs with half a spiral coil along the caudal part of the casque.

C. Discussion of a possible function of bill and casque founded on their structure

1) *Structure of the bony trabeculae*

As the data on the mode of life of *Rhinoplax vigil* are too scanty to deduce much from them on a possible specific function of the exceptional casque, we will investigate whether anything with regard to this can be deduced from its internal structure.

Pauwels (1954a, 1954b), by means of model experiments and observations on the structure of the trabeculae in the human femur – in a case of ankylosis of the knee joint and of a normal femur – concludes, that the thickness and the density ("Dichte"; perhaps the number of trabeculae per unit of cross section; see Pauwels, 1954b, pp. 35, 53) and the number of trabeculae – thus the distribution of the mass – at each place is proportional to the magnitude of the tensions acting on them and that also the individual elements of the spongiosa are situated in the direction of the trajectories of the compressive and tensile stresses. This kind of bony construction after Pauwels (1954b, p. 54) represents a flexion free network, built after the principle of greatest economy in material.

Applying this principle to interpret the structure of the casque of *Rhinoplax vigil*, it can be concluded that the entire architecture suggests, suitability to receive stresses of pressure and bending on the tip of the bill and above all on the rostral side of the casque (fig. 2 and pp. 13, 14).

The bony trabeculae in the rostral part of the casque function as supports. They strengthen the roof and floor of the bill against bending – and tensile stresses, which occur, when pressure is applied to the tip of the bill tending to bend the rostral part round an axis or area directed from left to right.

On the casque a force may be expected perpendicularly to the thickened horny layer on the rostral surface. This horny layer fits upon the rostral side of the bony core of the casque. From here robust mutually firmly connected bony trabeculae lead towards the bony wall of the cavity in the skull (cavum cranii) situated caudo-ventrally of it (fig. 2b). (N.B. the rather thin walled spongy bone situated in the small caudo-dorsal part of the casque, lies outside the area of pressure).

A possible pressure will be received locally on the massive horny layer, which in its entirety will press upon the tips of the bony trabeculae ending closely side by side caudally of the horn layer. These trabeculae will transmit the pressure caudalwards passing along the nasal cavity to the bony septum in the brain cavity in the skull on which they abut. They converge slightly in caudal direction. The pressure is further transmitted by the thick walls of the neurocranium, which themselves are reinforced by firm crosswise trabeculae, to the condylus occipitalis and thence to the spinal column. The bony interorbital septum functions as a bridge between the base of the upper bill on one hand and the ventral part of the bony wall of the cavity in the skull for the brain on the other hand. Laterally of the median nasal cavity the trabeculae are stronger – as appears from a Röntgenogram – so that the extra pressure developed along these walls can be transmitted to the adjoining rostral wall of the orbitae, which converges caudally into the massive interorbital septum. Pressure upon the ventral part of the casque is transmitted by a few bony trabeculae in a caudo-ventral direction to the palatinum. Thence it is passed on by way of the jugale and the pterygoid to the quadratum or directly to the interorbital septum and from there through the basisphenoid to the condylus occipitalis again.

In the casque lies a second much less numerous group of bony trabeculae, which is directed from ventro-rostral to dorso-caudal; it firmly interconnects the first group of bony trabeculae and also forms a bridge between the dorsal side of the base of the upper bill and the bony wall of the cavity of the skull for the brain. These trabeculae help in the first place to counteract bending stresses developed during pressure on the rostral side of the casque; in the second place they transmit the pressure applied to the horny tip of the bill, along the dorsal side of the bill to the neurocranium.

Finally the bony trabeculae which arise from the caudal part of the roof of the mouth and curve dorso-rostralwards will act as support between the ventral side of the base of the upper bill and the dorso-rostral part of the casque. Hereby bending stresses can be received and diverted from the nasal cavity.

The occurrence of two larger empty spaces ventrally of the casque in the upper bill can be explained by the principle of economy in material, as no stresses occur in this area.

The considerations regarding the manner in which the pressure may be conducted from the horny layer to the bony wall of the cavity in the skull for the brain, can be applied to pressure in the opposite direction. The construction of bony trabeculae also receives pressure exerted by the dead weight of the neurocranium when a forward directed blow is suddenly checked by resistance against the rostral side of the casque.

The construction will only be suitable to intercept rostral pressure as long as the fissura cranio-facialis remains closed so that no kinesis occurs. As soon as the fissura widens ventrally, the bony trabeculae are interrupted except in the area of the crista (aa) where their density is greatest.

The significance of the buffer mechanism (see text p. 25) now becomes evident. As long as no kinesis occurs the bony trabeculae on either side of the fissura cranio-facialis, constitute uninterrupted rods, in which the pressure can be transmitted by way of the buffering planes perpendicular to the direction of the pressure. The very fact that the buffers project somewhat above their surroundings results in the rest of the wall remaining practically unaffected by the pressure. So the pressure is transmitted by these reinforced places only.

During kinesis the possibility to transmit pressure is very much reduced. Ventrally of the crista the fissura cranio-facialis opens. In the area dorsally of the crista continuous bony trabeculae are absent. Hence the possibility of transmitting pressure remains only in the crista. This is because the bony trabeculae of the casque – though now at an angle with their prolongations in the thick wall of the neurocranium – abut against a very much fortified area of the bony septum.

Because of the presence of the fissura cranio-facialis the bony trabeculae passing from the casque into the wall of the neurocranium are not calculated to withstand tensile stress. The connection between the horny layer and the bone is even very weak. So it can be concluded with certainty that these bony trabeculae are only fit to transmit pressure.

Moreover, because of the presence of the fissura cranio-facialis the structure of bony trabeculae will only be able to transmit pressure as long as the bill is closed and no kinesis occurs.

2) *Horny layer*

The horny layer covering casque and upper and lower bill is massive and represents a considerable weight.

The dorsal and lateral sides of the casque are coloured brickred and so is the adjoining lateral side of the upper bill. Rostrally the casque and bill are light yellow but according to some authors the colour in the living animal is brighter owing to a pigment secreted by an oilgland at the coccyx. While on the bill the yellow gradually changes via orange into red caudalwards, the transition on the casque is abrupt.

The surface of the horny layer is smooth except for a horizontal ridge extending on the lateral side of the casque from the dorso-lateral angle of the orbita rostralwards (fig. 1). Ventrally of this ridge the surface of the lateral as well as of the rostral side show a layered structure due to the scaling off of the upper layers of horn beginning at the ventral border.

On a medial section after polishing a stratified texture of the horn layer appeared (fig. 2). The thin layers, varying in thickness between

0.2 and 0.1 mm and directed parallel to the surface of the bony casque, are mutually distinct, because their colour is slightly different. This is probably due to periodical growth. During each period of growth the uppermost cells of the stratum Malpighii in the skin between bone and horn, deposit a subsequent homogeneous layer of horn, whilst the previously formed layer lying upon it will shift towards the periphery.

On the rostral side of the casque each of these thin layers has a constant thickness over a considerable area, but at the transitions to the flat dorsal surface and rostro-ventrally it decreases very much in thickness. Evidently the matrix deposits more cornificated cells per unit of time on the surface of the casque than on the upper bill. The regular mechanical stresses are perhaps also in this case the stimulus for depositing horn on the irritated spot.

The outermost layers of horn scale off on the rostral side of the casque and the more so the more ventrally they are situated so that here deeper lying layers come to the surface. Perhaps this can be explained partially by wear, partially by the casting off of the horny crista which was present here during the juvenile stage (see text p. 31). The red layer of horn covering the lateral and dorsal sides of the casque is only thin. This layer extends also over the thickness of the yellow rostral horn layer with which it has been simultaneously deposited rostro-dorsally so as to form a single unit.

Thin sections were made through this area; one in the plane of the medial section and one in a plane perpendicular to the median plane and to the rostral surface of the casque. It appears that the cornificated cells are very much flattened in a direction perpendicular to the stratum Malpighii. The fibres deposited between the cells follow the direction of stratification. In the transitional region between the yellow and the red zone the cells are oriented from rostro-ventral gradually to caudo-dorsal, and finally in the red layer they are parallel to the dorsal surface.

Obviously the horny layer also has the dimensions, position and structure suggesting the function of intercepting rostral pressure.

3) *Specific gravity of horn, compact bone and spongy bone*

To ascertain the relations between the weights of horn and bone in the skull of *Rhinoplax*, the specific weights were determined (for technique see p. 7).

The average density of horn was determined at 1.6, that of compact bone at 1.9. So bone has a higher specific gravity than horn. Horn can constitute a thicker construction for equal weight. The thick horn layer, however, is compact, so it will represent more weight per cubic centimetre than the construction of bony trabeculae. Horn is more elastic than bone a.o. because of a greater percentage of organic matter.

The specific gravity of the skulls was determined in order to gain an insight into the difference in density between the skulls of a number of

species of Bucerotidae and that of *Rhinoplax vigil*, in which the light filling of spongy bone in the bill and the largely hollow casque have been replaced by a much more compact construction of bony trabeculae. The following values for the specific gravity of the skulls were obtained:
Tockus spec. 0.22
Aceros undulatus (Shaw) 0.26
Anthracoceros malayanis (Raffl.) 0.21
Buceros rhinoceros silvestris Vieill. 0.13
Rhinoplax vigil (Forst.) 0.51
,, ,, ,, skull without horn 0.35
,, ,, ,, neurocranium with jugalia, pterygoidea and quadrata 0.55
,, ,, ,, bill with casque without horn 0.29.

These data have been arranged after the increasing size of the casque. Leaving out of account *Tockus* in which the casque is wanting and the so divergent *Rhinoplax*, we find: the bigger the casque the smaller the specific gravity. For in this series an ever increasing part of the total volume is occupied by the hollow casque, which more than compensates for the effect of the slightly increasing weight of the horny layer. *Rhinoplax vigil*, which according to the size of its casque should be placed at the bottom of the list, on the contrary has the highest specific gravity, *i.e.* four times that of the bearers of the biggest casques among the Bucerotidae.

The measurements of parts of the skull of *Rhinoplax*, show that the neurocranium plus the loose bones are far more robustly built than the bill plus casque, notwithstanding the fact that the casque is filled with bony trabeculae.

4) *Position of the centre of gravity*

In a number of skulls of *Rhinoplax vigil* as well as of other Bucerotidae the position of the centre of gravity was determined in order to gain insight into the relations in *Rhinoplax* between the influence of the horny layer and the massiveness of the casque on the one hand and the strengthening of the neurocranium on the other hand (for technique see p. 7).

As the determinations had to be carried out on dry skulls so that no account could be taken of the muscles, which as a matter of fact are concentrated on the caudal part of the skull, the position of the centre of gravity will lie more caudalward in the living animal. However, the deviation will be much smaller in *Rhinoplax* than in the relatively so much lighter skulls of the other Bucerotidae.

The centre of gravity in *Rhinoplax* is situated on the imaginary line connecting the rostral tip of the upper bill and the dorso-medial point of the fissura cranio-facialis at 8/11 *i.e.* nearly $^3/_4$ of this distance from the tip of the bill (fig. 2b). In general the rule in Bucerotidae holds: the larger the casque, the more dorsal the position of the centre of gravity. However, as the weight of the casques is small, it affects the position of the centre of gravity only slightly. In *Tockus* spec., where the casque is wanting, it lies between upper and lower jaw. In *Buceros rhinoceros silvestris* Vieill. with its huge casque, it has shifted to $^1/_3$ of the height of the upper jaw, which is very little in comparison to the place in *Rhinoplax vigil* mentioned above.

5) *Places of attachment for the muscles*

The elongation in a dorso-caudal direction of the caudal part of the neurocranium with its exceedingly heavy, broad latero-caudal cristae and broad, deep fossa temporalis with its irregular surface, results in a considerable increase of the surface for the attachment of the muscles of the jaw and neck. This points to a very strongly developed muscular system and this is understandable on account of the weight of the skull, the centre of gravity of which moreover is situated far rostrally of the condylus occipitalis with which the skull rests on the spinal column.

6) *Conclusions on the function of bill and casque*

It is evident that the bill of *Rhinoplax vigil* (Forst.), as in the other Bucerotidae, will serve to take in food in such a manner that the morsel is thrown up with the tip. The height to which the morsel is thrown up depends upon the acceleration given to it and on its mass. The acceleration depends again on the length of the bill assuming that the morsel is held by the bill near its tip, and on the action of the muscles between skull and neck that impart a certain angular acceleration. It might be worthwhile to make an investigation on the relation between the weight of the food particles, the height to which they are tossed up, the length of the bill and the development of the muscles between skull and neck in different Bucerotidae.

As the bill has no curvature worth mentioning it will be less suited for gripping tree branches in locomotion. The groove for the musculus adductor mandibulae, however, is very deep and the processus mandibulae internus is big, which indicates very strong closing muscles for the lower jaw. Perhaps these powerful muscles compensate the lack of curvature, so that the grasping function is not impaired.

The heavy head of *Rhinoplax* might be compared with the head of a hammer, whereby the neck functions as the handle. Or more precisely the massive casque in relation to the bill might be considered as the rear side of an axehead in relation to the sharp side. The weight serves to add to the force of the blow. In this way the lack of length and curvature of the short straight bill with its firm horny point—which in itself will have less weight than the long curved bills of the other Bucerotidae—will be compensated amply. The function of the bony trabeculae then might be to connect the horny layer firmly with the neurocranium. However, this function alone seems an inadequate explanation for the development of such an intricate heavy structure of bony trabeculae.

When considering besides the weight of the casque also the structure of the horn and the position of the bony trabeculae, the conclusion appears to be warranted that the casque serves to take up pressure on its rostral side. This will be the case when the animal receives blows with its casque as with a shield or when it actively uses the casque as a hammer.

The former will be the case when the animal is assaulted. It is a common phenomenon that shy animals are very aggressive when cornered.

Rhinoplax vigil is shy and the fact that it is mostly found by itself and not in large groups already indicates possibly a certain aggressivity. Also the distribution of its colouring might point in this direction. Bill, casque and their adjoining parts are of a brightly hue; the remainder of the bird is gray-black. The roused aggressivity of the opponent will be directed against that highly coloured area and thrusts and blows from the assailant will probably be warded off with the casque as a shield. So the casque would have acquired an active defensive function beside its being a threatening and imposing structure.

The animal itself uses the casque as a hammer a.o. when it beats the trees with the casque as FORBES (1885, p. 154) describes. Possibly it acts thus to get at the bark itself or at insects hiding in it, or perhaps to shake off fruit. Another possibility is that it cracks nuts with the casque or knocks open other kinds of fruit, to which the broad flat rostral side of the casque by its larger surface indeed seems better suited than the tip of the bill. When the condylus occipitalis is perpendicularly above the tip of the bill, the centre of gravity in *Rhinoplax* contrary to that of other Bucerotidae lies in front of the line connecting these two points (fig. 2). So the head, because it has a loose connection with the neck in the condylus occipitalis articulation, would tend to tip over in the theoretical situation of muscle relaxation at that place, until the casque and the point of the bill rest together on the same horizontal plane. The casque now touches this horizontal plane at a point situated rather far dorsally of the rostral side, that is to say not in the centre of the reinforced area. This centre, which seems the most suited place to intercept blows, lies at the intersection of the line through the condylus occipitalis and the centre of gravity with the rostral surface of the casque. As the tangent plane through this point of intersection with the casque meets the bill, the conclusion might be drawn that the bird hammers with the casque in a favourable position on round surfaces as fruits or branches of trees. For in these cases the tip of the bill can project freely below the point of impact with fruit or branch.

Other Bucerotidae use the lateral side of the bill as "trowel" when the female is immured during the breeding time. The bill of *Rhinoplax*, however, is much narrower and shorter and rostrally of the casque its lateral side is convex. Therefore the bill is far less suited to be used for that purpose than the large high bills of the other Bucerotidae with their flat lateral surfaces. But the caudal part of the lateral surface of the bill is flat indeed and it forms one continuous surface of considerable size with the high lateral side of the casque. This surface as well as the flat rostral surface of the casque appear to be very well suited for trowel.

The supposition that the casque might serve as soundboard to reinforce the voice of the Bucerotidae is based on the hollowness and thin wall of the large casques. Though *Rhinoplax* also is able to produce powerful sounds, the fact that the casque is for the greater part filled with spongy bone, so that little space is left, leads to the supposition that the casque in this case will contribute much less to the reinforcement of sound.

All these possibilities are mainly hypothetical in character and constitute working hypotheses for observations on the behaviour of the living animals.

7) *Significance of the kinesis*

Notwithstanding the deduced new functions of the casque, which demand a very strong and solid construction of the neurocranium, so that the architecture was radically altered, kinesis could be maintained by the development of a new articulation between the upper bill and the neurocranium. This raises the question what significance kinesis can have for birds in general and for *Rhinoplax* in particular.

It has been demonstrated that in *Rhinoplax* the bill can be opened only when the quadrata move rostro-medialward, which is only possible when kinesis occurs. The bill of a bird possesses a kind of lock. As long as the quadrata retain the same position the bill remains automatically closed. In the case of *Rhinoplax vigil* this is very important, because the skull is a solid construction suited for the function of the casque as a hammer or shield only as long as kinesis does not occur. The very fact that the ligaments are constituted in such a way that they keep the bill closed even when the muscles of the jaw do not actively cooperate, ensures that the bill cannot fall open by the deadweight of the lower jaw.

When only the dorsalward displacement caused by kinesis is considered, by which the increase of the width to which the bill can be opened is relatively small, it seems improbable that this slight gain should constitute the significance of the kinesis for most birds (and not only for Bucerotidae), as VERSLUYS (1912a, pp. 605, 681, 682, 683, 684, 689, 690; 1912b, p. 501) assumed in the case of Reptiles. In parrots and *Phalacrocorax* and the like the significance of the kinesis is another one.

MARINELLI (1928, pp. 148, 151; 1936, pp. 810, 817, 834), with whom HOFER (1955, p. 135) agrees, assumes that kinesis of upper jaw *etc.* can occur independently of the movement of the lower jaw and according to him the significance of the kinesis does not lie in the possibility of opening the bill wider but on the contrary in closing it firmer. HOFER (1955, pp. 135/136) in this connection thinks of a lowering against a resistance *e.g.* in biting ("Senkung gegen einen Widerstand also im Biss") and also of an elastic securing of the whole system ("elastisch federnden Sicherung des ganzen Systems") especially in hacking birds like woodpeckers. HOFER (1955, p. 136) points out that in seed eating birds ("Körnerfresser") it is a matter of a sure catch with the tip of the bill ("einen sicheren Zugriff mit der Schnabelspitze").

I myself have not studied these phenomena in other birds, but to me it seems impossible that in *Rhinoplax* kinesis could occur independently of the movements of the lower jaw (see text p. 20). But it is conceivable that the elasticity of the ligaments allows of some play in the movement of the quadratum and therefore in that of the upper bill, so that *e.g.* a struggling prey remains fixed in a firm grip.

In Mammals, which masticate their food before swallowing it, the construction of the joint of the jaw is totally different from that in birds. Birds in general swallow their morsels of food whole as there are no teeth on the jaws. Perhaps kinesis must be understood in relation with this very divergent way of dealing with their food. As every position of the lower jaw corresponds to a definite attitude of the quadratum, the jaw will remain fixed as it were in a certain position as long as the quadratum does not shift. This makes the bill of birds especially suited as an instrument for gripping, which is stabilized in every required position according to the size of the morsel. This property will have its significance in the Bucerotidae also when they use their bill for gripping branches in locomotion. Perhaps this property of being a stabilized seizing instrument may stand in relation to the possibility of kinesis in the skull of birds.

VI. SUMMARY

In this investigation, the strikingly differently built skull of *Rhinoplax vigil* (Forst.) has been compared with those of the other Bucerotidae. An attempt was made to establish what modifications in function were related with these divergent structures.

For an understanding of the functioning of the mechanism of movement of the skull, knowledge of its shape, built and structure is necessary. Therefore a description in detail was given of its typical external shape with the short, straight bill, the large high, narrow casque and the robust neurocranium. Also described is its internal structure, with the tremendously thick hornlayer, which covers the casque, the spongy bone and intricate systems of trabeculae, that fill the casque, the bill and the wall of the neurocranium. Further description includes the shape of the loose bones: quadrata, pterygoidea, jugalia and the lower jaw with their mutual articulations. A comparison with the situation in the other Bucerotidae was made throughout the description.

To all appearances the bony trabeculae pass uninterrupted from the casque into the neurocranium. Therefore a flexible area at the root (inplantation) of the bill is wanting and moreover a basipterygoid connection does not exist. These facts notwithstanding, it could be concluded from the shape of the articulation of the jaw, that kinesis must be possible. This articulation shows that the mouth can only be opened by moving the lower jaw, when the quadrata are able to rotate in a mediorostral direction. This implies a rostral movement of jugale and pterygoid, which is possible only if the upper jaw is movable with respect to the neurocranium, in other words, if kinesis does exist. This inference could be confirmed by the discovery of continuing fissura cranio-facialis with dorsally a kind of "hinge"-articulation between casque and neurocranium. The most important groups of trabeculae are perpendicular to the rostral wall of the casque and converge towards the bony septum interorbitale. The largest concentration occurs in the "hinge", which itself consists of a ridge at the rostral side of the fissura cranio-facialis that remains enclosed by a groove at the dorsal side. The other trabeculae are interrupted by the fissura cranio-facialis at both sides of which they close on each other in the same way as buffers of a train. This means they are able to transmit pressure through the neurocranium via the condylus occipitalis to the spinal column, just as long as the fissura cranio-facialis remains closed.

The skull of an immature specimen shows that not in shape, built, structure nor in moving mechanism it is very different from the adult skull of the other Bucerotidae. With the aid of these, the development of the divergent adult skull could be reconstructed (mostly as a general ossification and hornification) and the adaptive modifications in the moving mechanism understood.

From the facts known about habitus, behaviour and mode of life, and on the basis of the architecture of the skull, the functions of the casque of the bill have been tentatively deduced.

In the Bucerotidae in general the large, curved, vigorously hacking and imposing bill serves to seize and master food, as a defence against enemies, and as a "trowel" for nestbuilding. No functions as an instrument can be attributed to the casque, only an ethological significance: the bill must seem greater still and help to overawe assailants and congeners. Besides the larger casques probably serve as a soundboard.

In *Rhinoplax* on the contrary the heavily reinforced casque with its thick rostral horn layer (which requires a solid construction of the rest of the skull and a strongly developed musculature) will be able, like the heavy head of a hammer, to add force to the blows of the smaller, short, straight and less imposing bill. The casque itself, built to intercept blows, will have been modified as to become an active instrument. It will serve as a hammer in the acquisition of food, as a shield for the defense against enemies (besides being merely a threatening and imposing structure) and as a "trowel" for building the wall of the nest. These alterations will have taken place at the expense of the function as soundboard.

Notwithstanding these alterations the fundamentally important kinesis of the bird's skull has been maintained, thanks to the development of a new articulation for the casque.

The assumption of transference of functions seems to give a plausible explanation for the progressive development of the casque and the attendant reduction in size of the bill of *Rhinoplax vigil* (Forst.).

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LIST OF FREQUENTLY USED ABBREVIATIONS IN THE FIGURES

ap. org. aud. = apertura of the organon auditus
basisph. = basisphenoid
cond. occ. = condylus occipitalis
cr. caud. = crista caudalis
cr. ca. l. = crista caudo-lateralis
fiss. cr. fac. = fissura cranio-facialis
f. n. olf. = foramen nervi olfactorii
f. n. opt. = foramen nervi optici
f. occ. = foramen occipitale
jug. = jugale
l. j. = lower jaw
palat. = palatinum
pr. orb. q. = processus orbitalis quadrati
pr. postorb. = processus postorbitalis
pr. z. sq. = processus zygomaticus squamosi
pr. α = processus α
pteryg. = pterygoid
quadr. = quadratum
sept. int. orb. = septum interorbitale
u. j. = upper jaw

EXPLANATION OF THE FIGURES ON THE PLATES

Fig. 1a. *Rhinoplax vigil* (Forst.). Zool. Lab. Univ. Leiden, no. 7104. Left half of the skull with lower jaw seen from the left side. From nature. 1 × nat. size. The three white spots in the orbita are indebted to the fact that this left half of the skull contains less than the exact half of the skull; the septum interorbitale has fallen out at the two white irregular rostral spots; the caudal white spot is the foramen nervi optici.

Fig. 1b. *Rhinoplax vigil* (Forst.). Zool. Lab. Univ. Leiden, no. 7104. Left half of the skull with lower jaw seen from the left side. Diagram. 1 × nat. size. Abbreviations: cerebr. sk. = cerebral skull; fossa temp. = fossa temporalis; horny cov. = horny covering; l. ju. ma. e. = ligamentum jugo-mandibulare externum; l. sq. j. = ligamentum squamoso-jugale; l. sq. ma. = ligamentum squamoso-mandibulare; pr. ma. i. = processus mandibularis internus; tuber ma. e. = tuber mandibulare externum. For x, y see text. For other abbreviations, see List of frequently used abbreviations.

Fig. 2a. *Rhinoplax vigil* (Forst.). Zool. Lab. Univ. Leiden, no. 7104. Right half of the skull with lower jaw seen from the left side. From nature. 1 × nat. size.

Fig. 2b. *Rhinoplax vigil* (Forst.). Zool. Lab. Univ. Leiden, no. 7104. Right half of the skull with lower jaw seen from the left side. Diagram. 1 × nat. size. The course of the bony trabeculae and the layers of the horny covering are diagrammatically shown. Sections of compact bone are shaded. Abbreviations: c.g. = centre of gravity; cav. cerebelli = cavity for the cerebellum in the skull; cav. cerebr. = cavity for the cerebrum in the skull; cav. nas. = cavitas nasalis; cav. oris = cavum oris; red horny cov. = red horny covering; sept. cav. brain = septum in the cavity, containing the brain, in the skull; yellow h. cov. = yellow horny covering. For gg, w see text. For other abbreviations, see List of frequently used abbreviations.

Fig. 3a. *Rhinoplax vigil* (Forst.). United States National Museum, Washington, no. 19476. Skull without lower jaw seen in ventral view. From nature. A little more than 1 × nat. size.

Fig. 3b. *Rhinoplax vigil* (Forst.). United States National Museum, Washington, no. 19476. Skull without lower jaw seen in ventral view. Diagram. A little more than 1 × nat. size. Abbreviations: pr. basipt. = processus basipterygoideus; sept. nasi = septum nasi. For i′, i″, j, k see text. For other abbreviations, see List of frequently used abbreviations.

Fig. 4a. *Rhinoplax vigil* (Forst.). Zool. Lab. Univ. Leiden, no. 7104. Left half of the lower jaw seen from the dorsal side. From nature. About 1 × nat. size.

Fig. 4b. *Rhinoplax vigil* (Forst.). Zool. Lab. Univ. Leiden, no. 7104. Left half of the lower jaw seen from the dorsal side. Diagram. About 1 × nat. size. Abbreviations: fossa mand. = fossa mandibularis. For a, b, c, d, e, f, g, h see text.

Fig. 5a & 5a′. *Rhinoplax vigil* (Forst.). Zool. Lab. Univ. Leiden, no. 7104. Left quadrate. a. Seen from the lateral side. a′. Seen from the medial side. From nature. 1 × nat. size.

Fig. 5b & 5b′. *Rhinoplax vigil* (Forst.). Zool. Lab. Univ. Leiden, no. 7104. Left quadrate. b. Seen from the lateral side. b′. Seen from the medial side. Diagram. 1 × nat. size. For i′, i″, j, k, l, m, n, o, p, q see text.

Fig. 6a & 6a′. *Rhinoplax vigil* (Forst.). Zool. Lab. Univ. Leiden, no. 7104. Left jugale. a. Seen from the lateral side. a′. Seen from the medial side. From nature. 1 × nat. size.

Fig. 6b & 6b′. *Rhinoplax vigil* (Forst.). Zool. Lab. Univ. Leiden, no. 7104. Left jugale. b. Seen from the lateral side. b′. Seen from the medial side. Diagram. 1 × nat. size. For r, s see text.

Fig. 7a & 7a′. *Rhinoplax vigil* (Forst.). Zool. Lab. Univ. Leiden, no. 7104. Left pterygoid. a. Seen from the lateral side. a′. Seen from the medial side. From nature. 1 × nat. size.

Fig. 7b & 7b′. *Rhinoplax vigil* (Forst.). Zool. Lab. Univ. Leiden, no. 7104. Left pterygoid. b. Seen from the lateral side. b′. Seen from the medial side. Diagram. 1 × nat. size. Abbreviations: pr. bas. pter. = processus basipterygoideus. For t, v see text.

Fig. 8a & 8b. *Rhinoplax vigil* (Forst.). Rijksmuseum van Natuurlijke Historie at Leiden, cat. b. Environment of the articulation between casque and cerebral skull. a. Seen in a transparent microscopic slide of the bone. Microphotography. b. Diagram of the surface of the "maxillary segment"; for w see text. . . . × nat. size.

Fig. 9a. *Rhinoplax vigil* (Forst.). Zool. Lab. Univ. Leiden, no. 7105. Left half of the rostral "segment" of the skull without lower jaw, seen in caudal view, being the rostral wall of the fissura cranio-facialis seen from behind. From nature. 1 × nat. size.

Fig. 9b. *Rhinoplax vigil* (Forst.). Zool. Lab. Univ. Leiden, no. 7105. Left half of the rostral "segment" of the skull without lower jaw, seen in caudal view, being the rostral wall of the fissura cranio-facialis seen from behind. Diagram. 1 × nat. size. For aa, bb, cc, dd, ee, ff, gg, hh, ii, jj, kk, ll, nn, oo, r, t, [x] see text. For other abbreviations, see List of frequently used abbreviations.

Fig. 10a. *Rhinoplax vigil* (Forst.). Zool. Lab. Univ. Leiden, no. 7105. Left half of the caudal "segment" of the skull without lower jaw, seen in front, being the caudal wall of the fissura cranio-facialis seen in front view. From nature. 1 × nat. size.

Fig. 10b. *Rhinoplax vigil* (Forst.). Zool. Lab. Univ. Leiden, no. 7105. Left half of the caudal "segment" of the skull without lower jaw, seen in front, being the caudal wall of the fissura cranio-facialis seen in front view. Diagram. 1 × nat. size. For a′a′, b′b′, c′c′, d′d′, e′e′, f′f′, h′h′, j′j′, l′l′, n′n′, o′o′, [x], [y], z see text. For other abbreviations, see List of frequently used abbreviations.

Fig. 11a & 11b. *Rhinoplax vigil* (Forst.). Zool. Lab. Univ. Leiden, no. 7105. Right half of the caudal part of the skull without lower jaw seen in ventral view, in two extreme positions (a and b) of kinesis. a. Mouth closed. b. Mouth opened. Diagram. 11 × nat. size. For A and B and for the distances and angles, indicated by numbers see the text.

Fig. 12. *Rhinoplax vigil* (Forst.). Zool. Lab. Univ. Leiden, no. 7104. Right half of the skull with lower jaw seen from the left side. Diagram of a röntgenogram, indicating the general course of the bony trabeculae. A little more than 1 × nat. size.

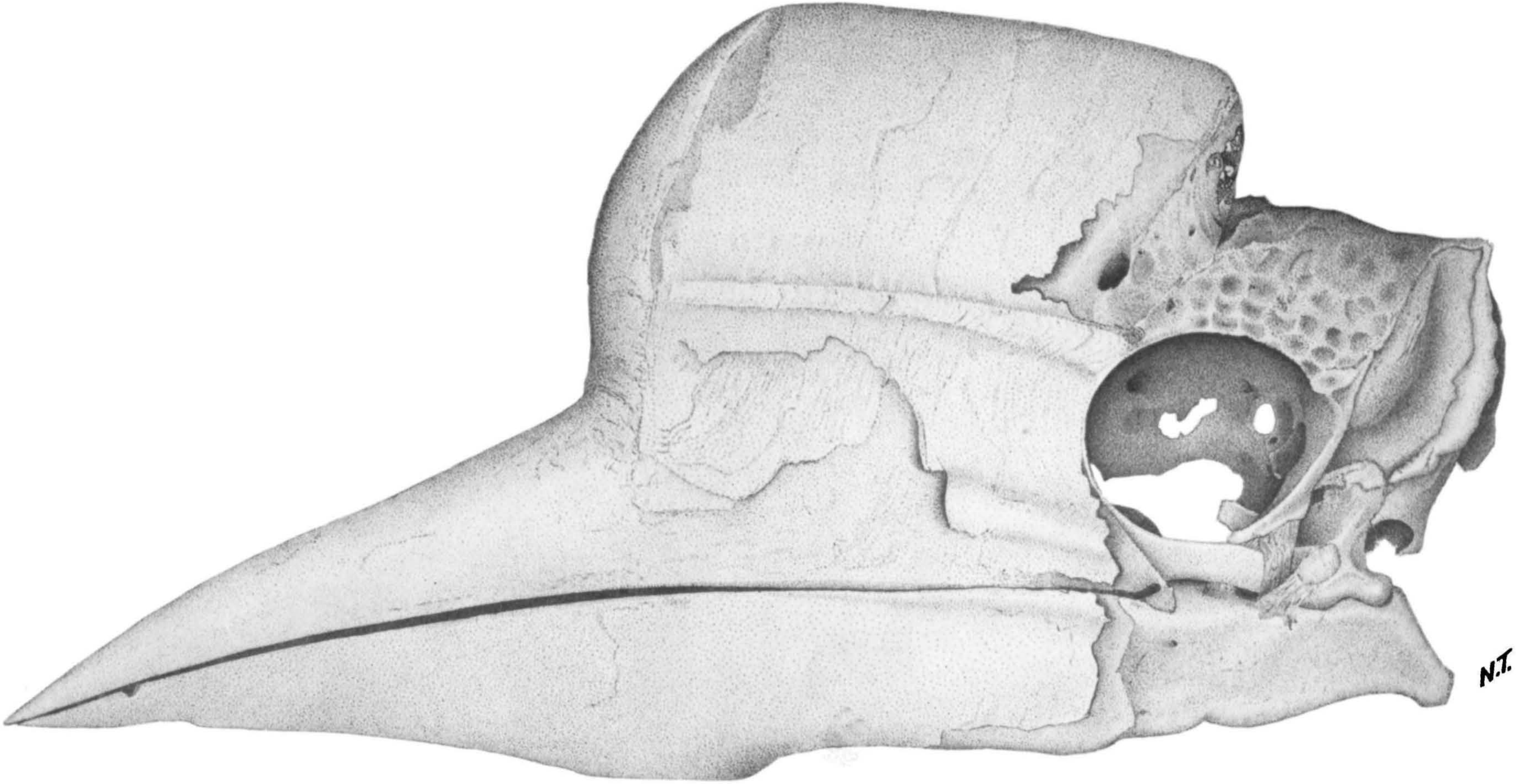


fig. 1a

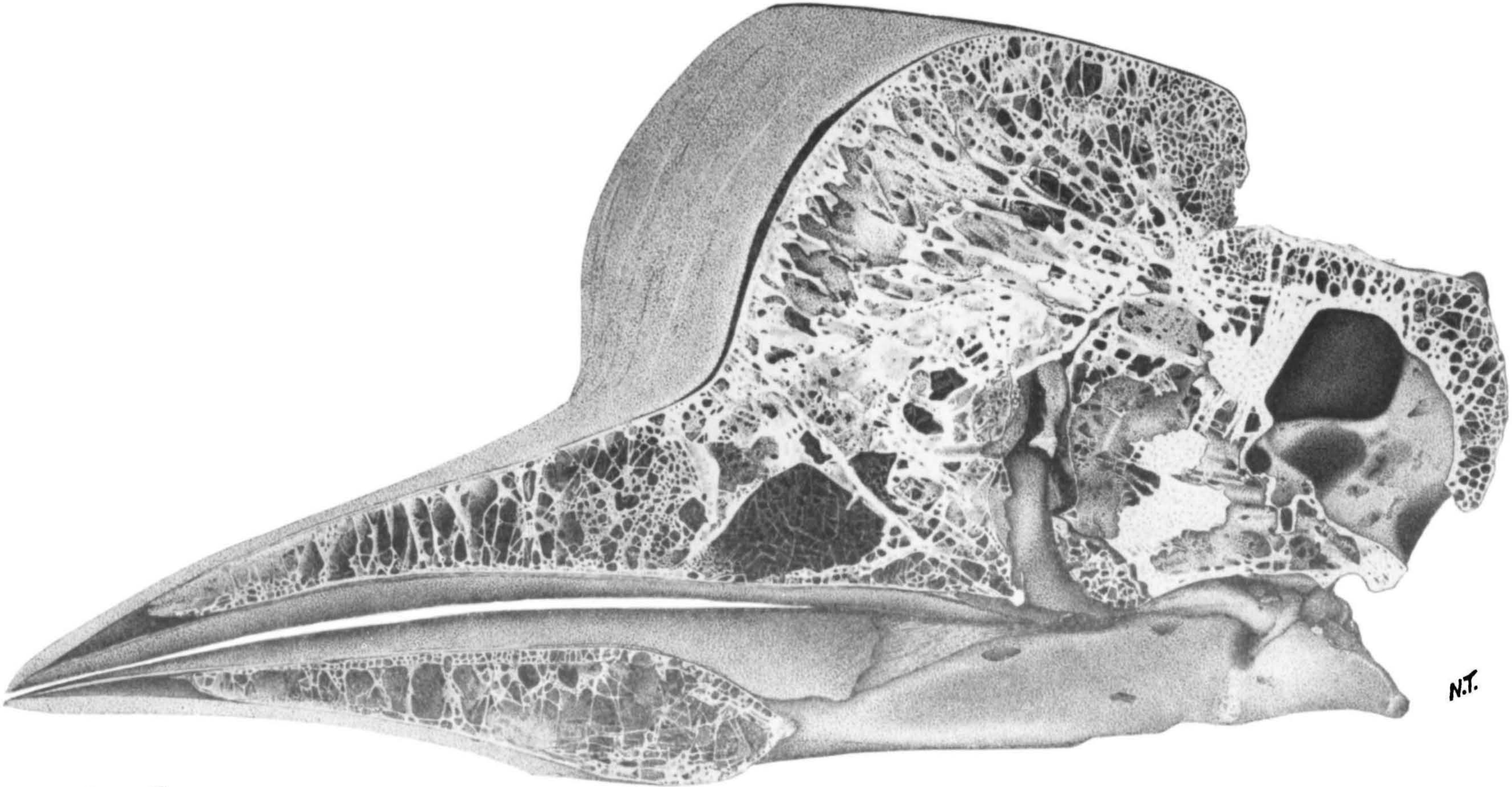
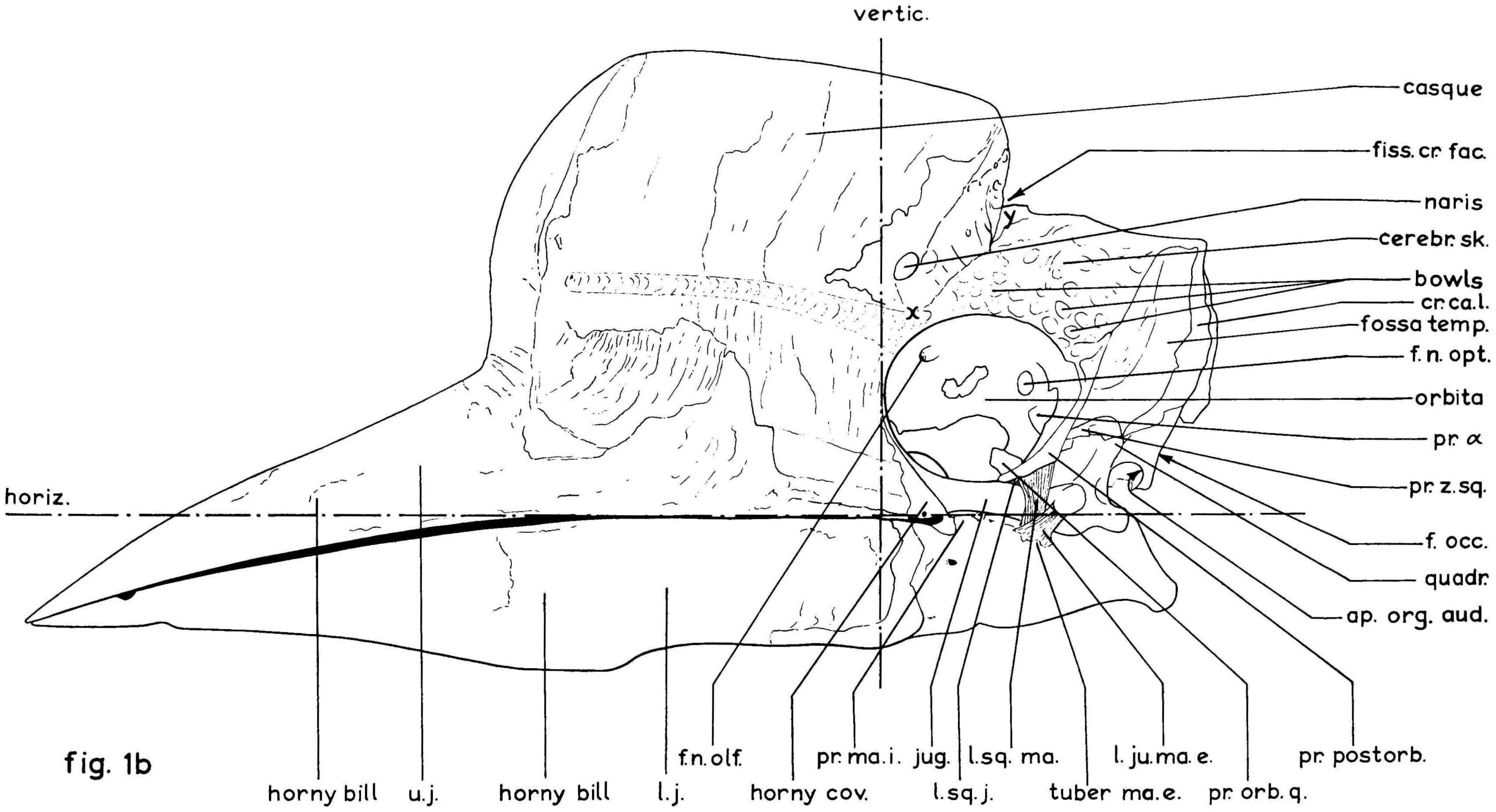


fig. 2a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naris
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cerebr. sk.
bowls
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orbita
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pr. z. sq.
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f. occ.
quadr.
ap. org. aud.
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pr. ma. i.
jug.
l. sq. ma.
l. ju. ma. e.
pr. postorb.
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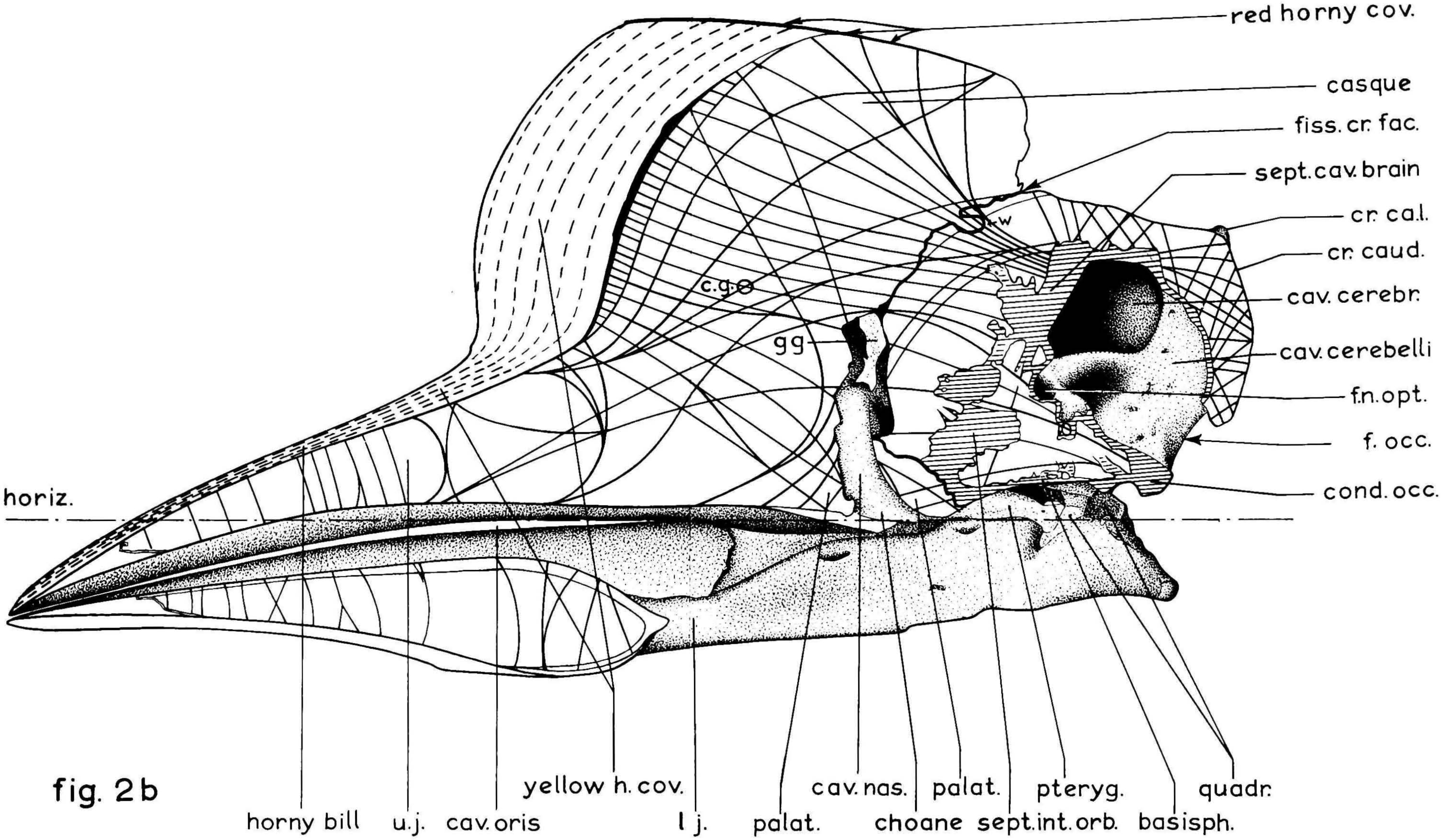
u. j.
horny bill
l. j.
horny cov.
l. sq. j.
tuber ma. e.
pr. orb. q.

fig. 1b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sept. cav. brain
cr. ca.l.
cr. caud.
cav. cerebr.
cav. cerebelli
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fig. 2b

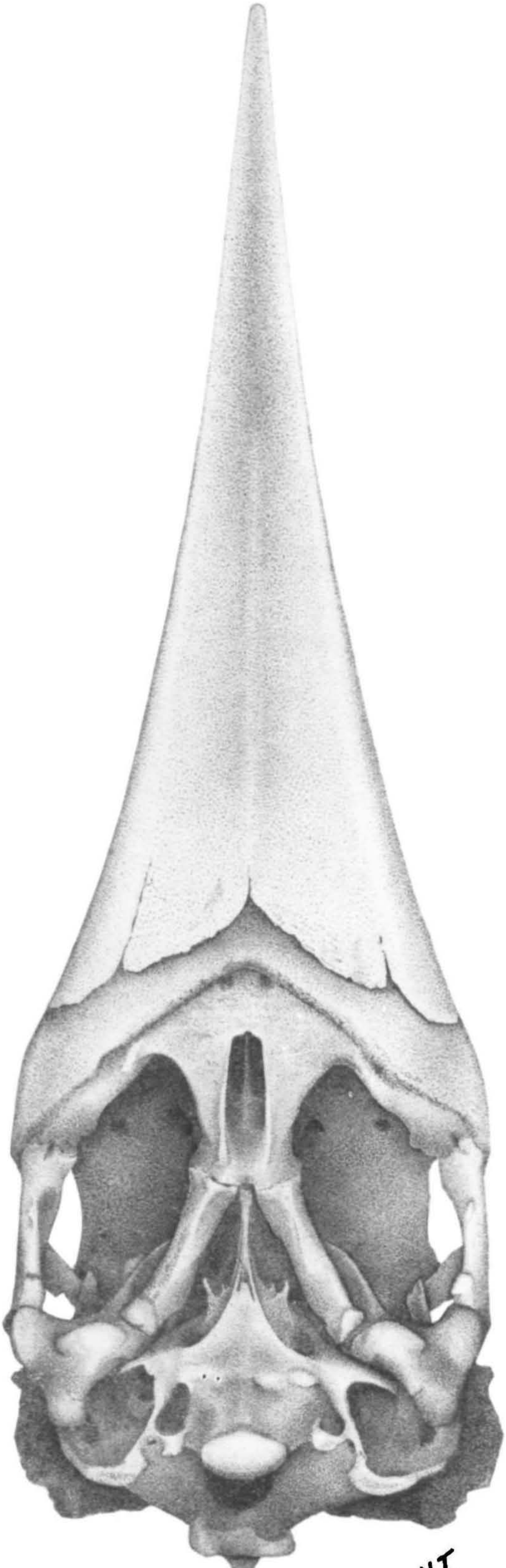
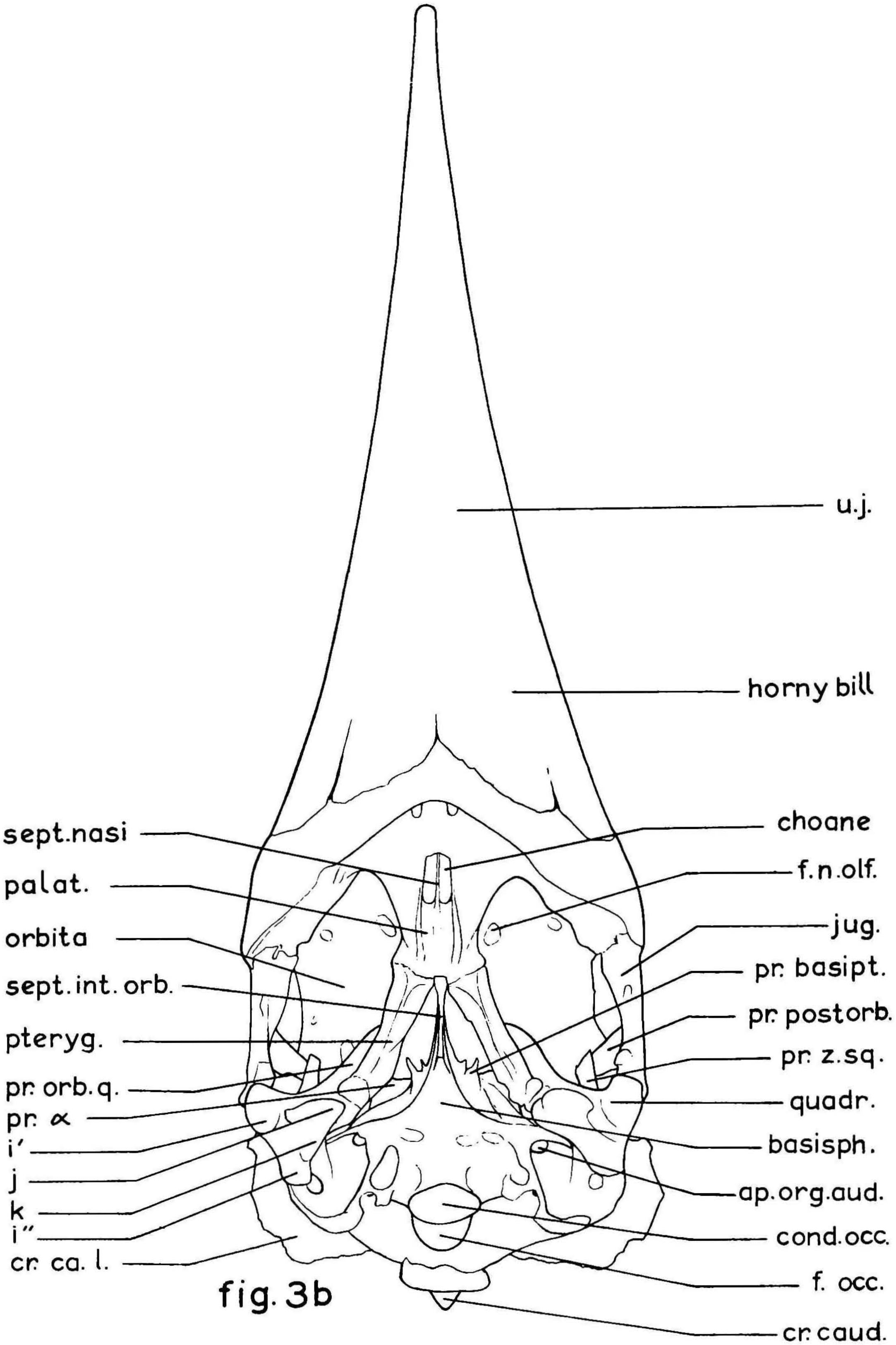


fig. 3a


u.j.
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orbita
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pr. orb.q.
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cr. caud.

fig. 3b

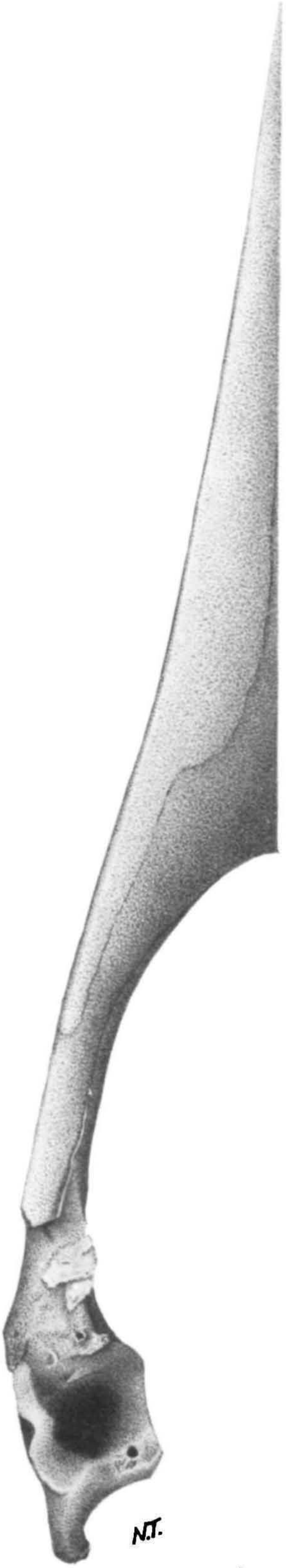

fig. 4a

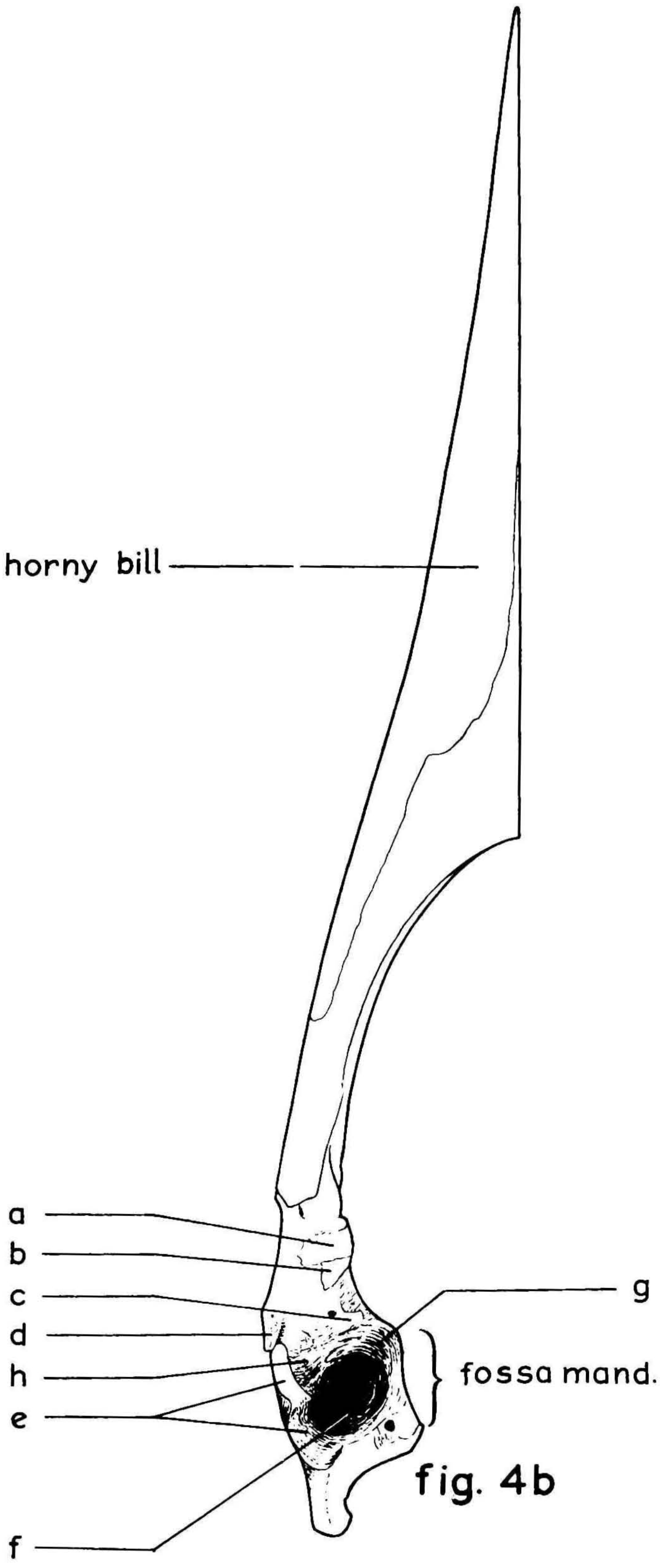

fig. 4b

fig. 5a

fig. 5a′

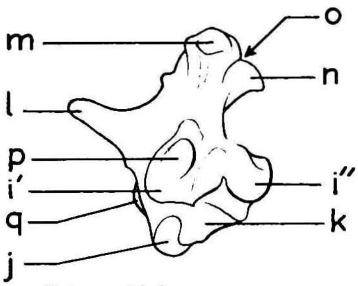

fig. 5b

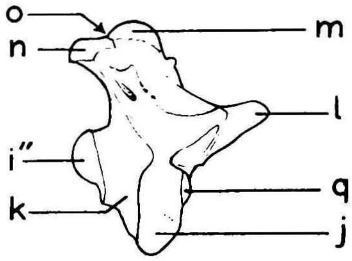

fig. 5b′

fig. 6a

fig. 6a′

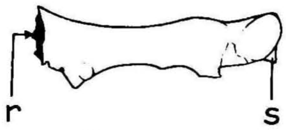

fig. 6b

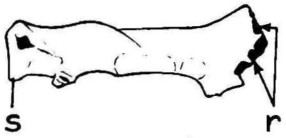

fig. 6b′

fig. 7a

fig. 7a′

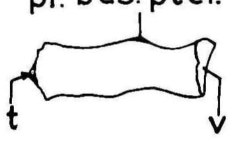

fig. 7b

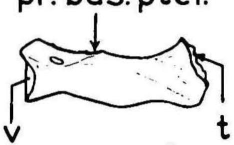

fig. 7b′

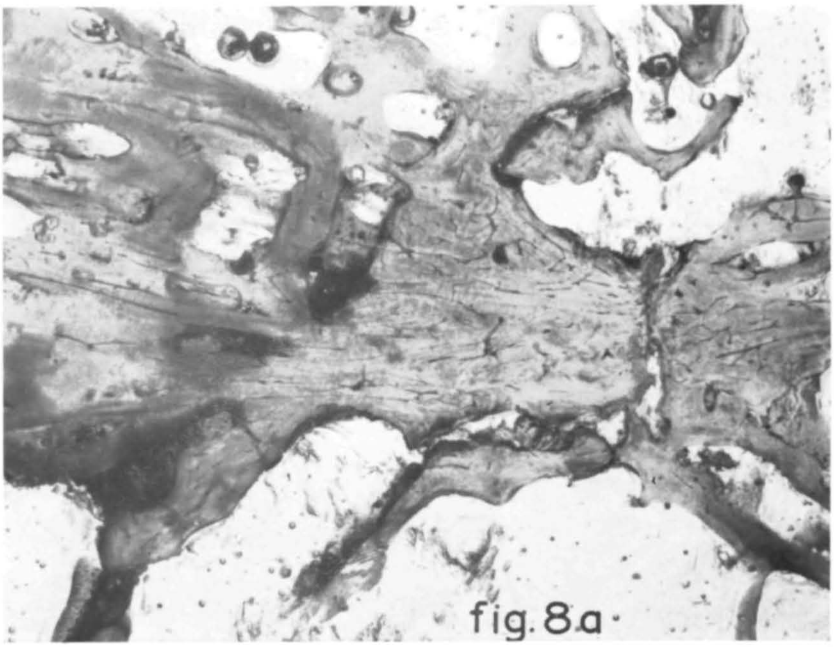

fig. 8a

fig. 8b

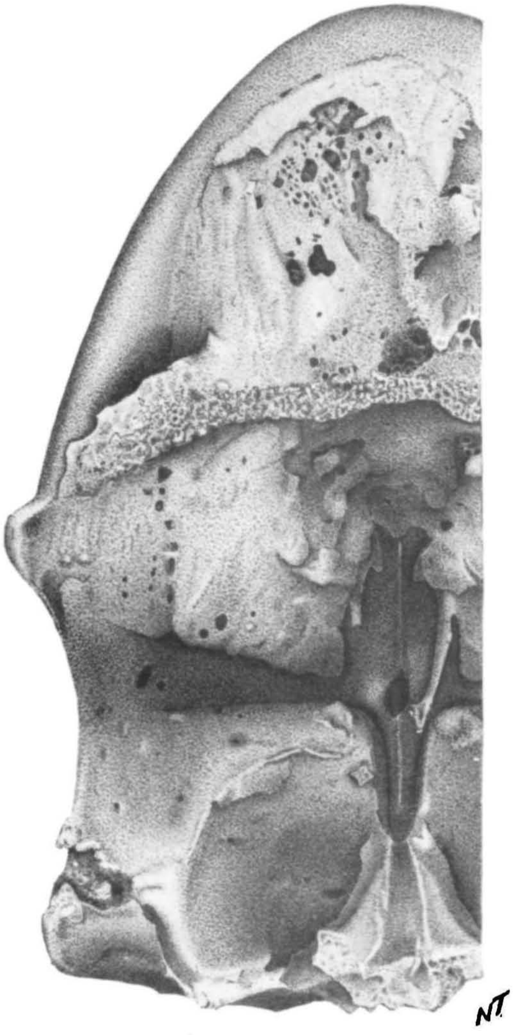

fig. 9a

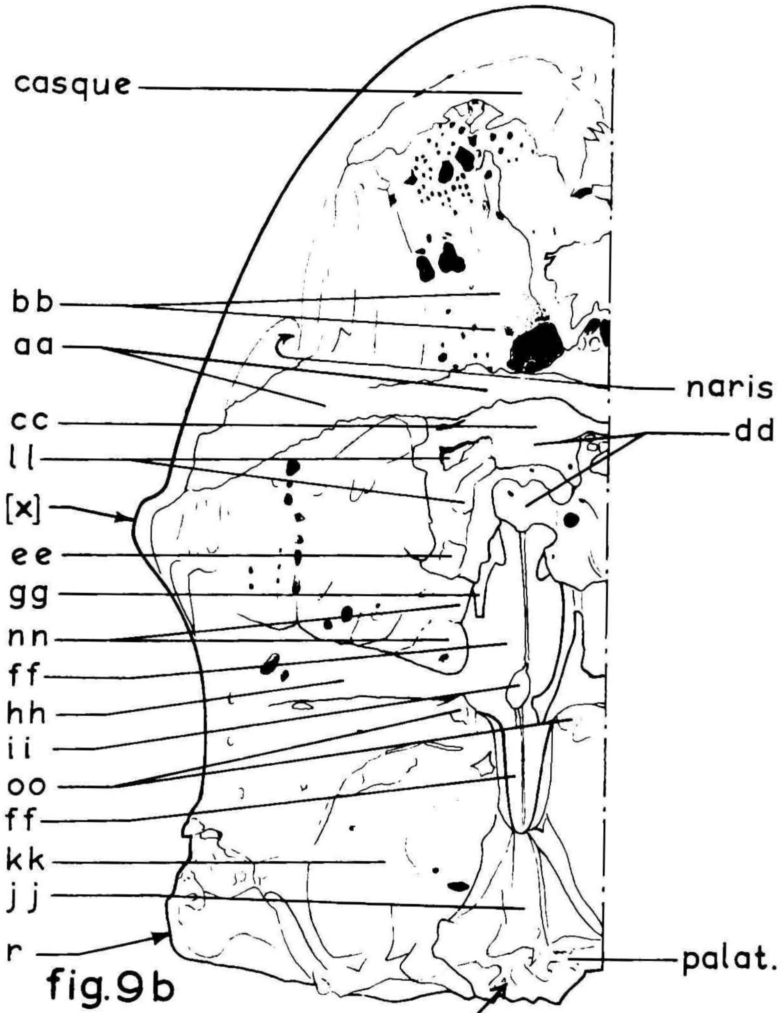

fig.9b

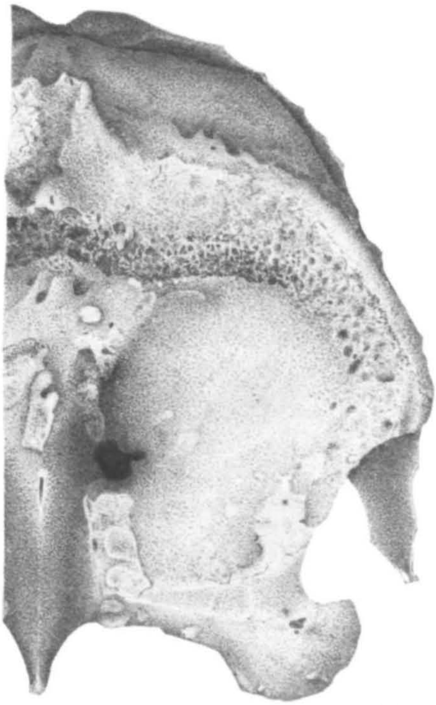

fig. 10 a

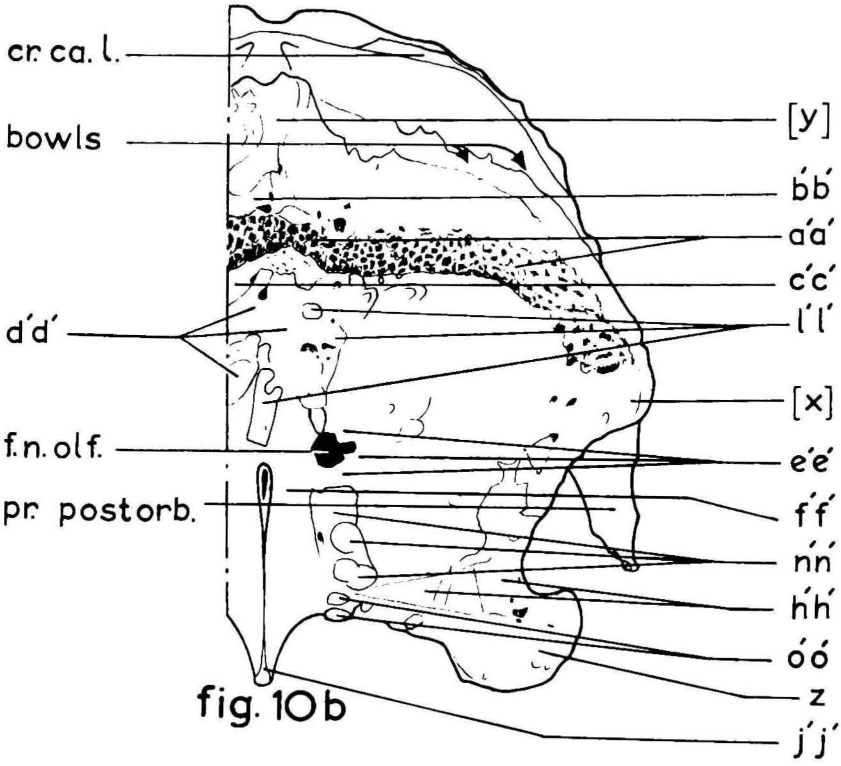

fig. 10b

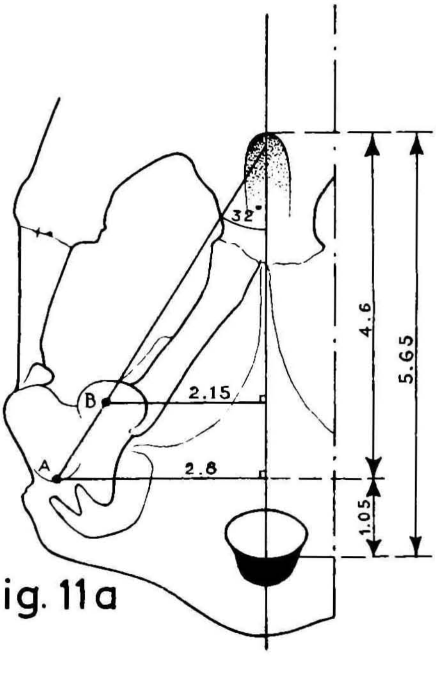

fig. 11a

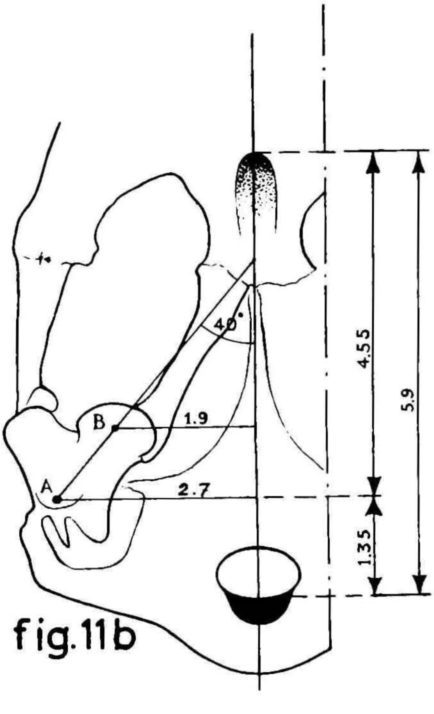

fig.11b

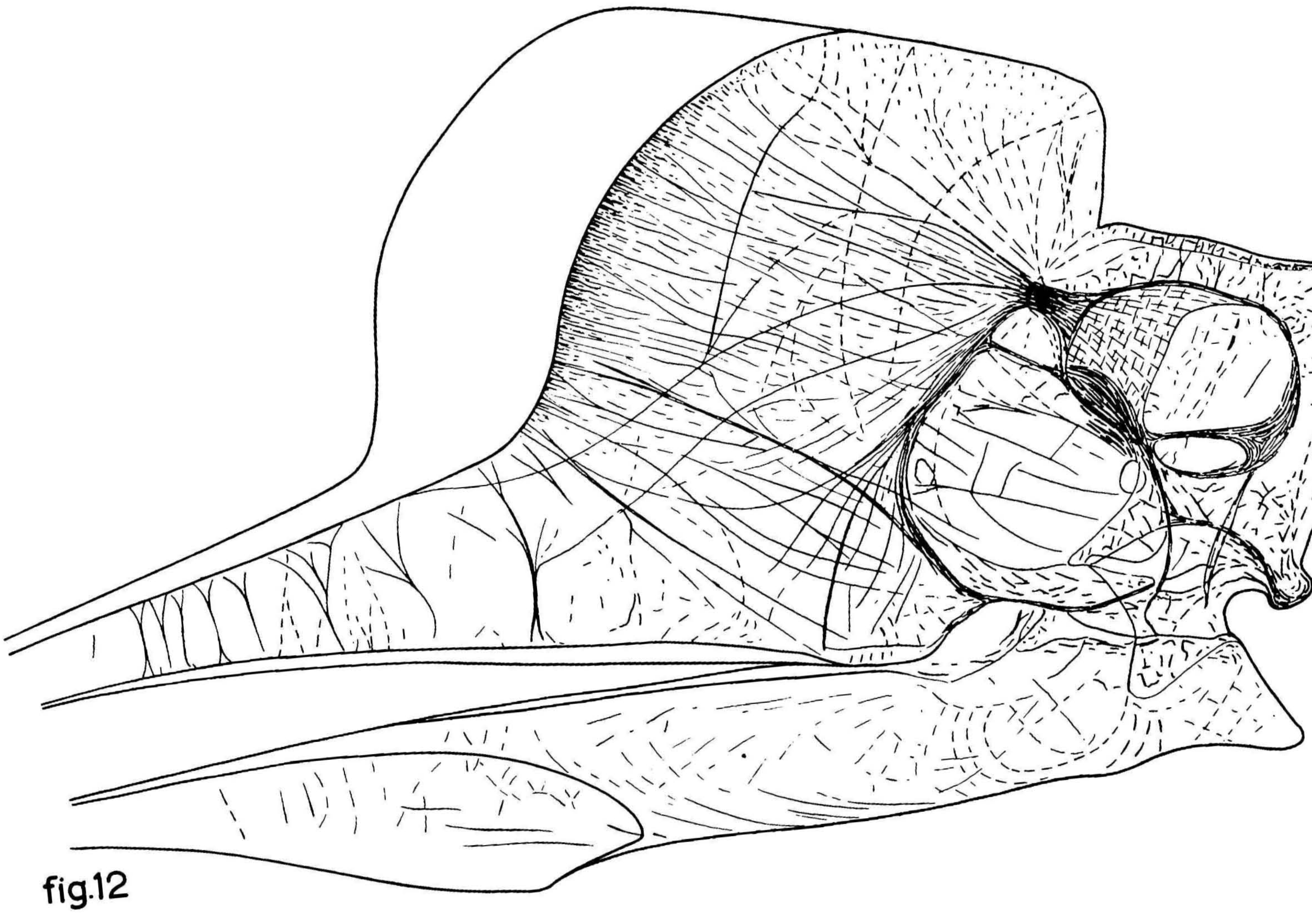

fig.12