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SKULLS OF *GOBIPTERYX* (AVES) FROM THE UPPER CRETACEOUS OF MONGOLIA

(plate 3)

Abstract. — The discovery of a second skull of *Gobipteryx minuta* (ELŻANOWSKI 1974) establishes this to be a palaeognathous bird, showing the typical pattern of the palate as well as the features directly related to ratite rhynchokinesis. Some palatal characters of *Gobipteryx* are closely similar to those of the cassowary. *Gobipteryx* skulls are described and new partial reconstructions are given. Previously erected taxa are rediagnosed.

INTRODUCTION

After the description of the first *Gobipteryx* skull had been published (ELŻANOWSKI 1974), a second skull was found among other small fossils collected by the 1971 Polish-Mongolian Palaeontological Expedition to the Gobi Desert (KIELAN-JAWOROWSKA & BARSBOLD 1972). Both *Gobipteryx* specimens were found in the same locality (Khulsan), in beds of the Barun Goyot Formation, recognized by KIELAN-JAWOROWSKA (1974) as ? Middle Campanian. Both specimens are housed in the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw, abbreviated as ZPAL.

Although examination of the new skull has fully confirmed the palaeognathine affinities of *Gobipteryx*, there are many misinterpretations in the author's preliminary description that are corrected in the present paper. *Gobipteryx* is the oldest form which can be assigned to the Palaeognathae, other earliest records (*Opisthodactylus patagonicus* Ameghino, *Eleutherornis helveticus* SCHAUUB and *Eremopezus eocaenus* ANDREWS) being from Eocene (FISHER 1967). The only ratite fossils hitherto known from Asia are Neogene and Quaternary struthious remains (BURCHAK-ABRAMOVICH 1962) and the Miocene and, possibly, Eocene egg-shells of a separate "aepyornithid type" (SAUER 1972).

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DESCRIPTIONS

Order **Gobipterygiformes**, ELŻANOWSKI 1974

Revised diagnosis. — Mandibular articulation of the quadrate bipartite. Skull of palaeognathous type, approaching the cassowary conditions: (a) vomers fused far anteriorly, gradually diverging backwards to articulate suturally with pterygoids, (b) pterygoids widens posteriorly, (c) palatine supported mostly by the pterygoid, (d) ascending process of the maxilla present. Basal part of the palatine enclosed in the lateral sinus of the pterygoid.

Family **Gobipterygidae**, ELŻANOWSKI 1974Genus *Gobipteryx*, ELŻANOWSKI 1974*Gobipteryx minuta*, ELŻANOWSKI 1974

(pl. 37, text-fig. 1)

1974 *Gobipteryx minuta* n.g., n.sp.; A. ELŻANOWSKI, pp. 104—108, pls 32—33.

Material. — Two specimens, both from Khulsan, Gobi Desert, Mongolia, Barun Goyot Formation: the holotype ZPAL MgR I/12 and the second skull (ZPAL MgR-I/32), with the calvarium and the mandible, in the second specimen preserved in the anterior two thirds only and somewhat compressed laterally.

Revised diagnosis. — Culmen straight near its rostral end. No distinct grooves on the outer surface of the terminal part of the beak. Lateral contacting margins of the premaxilla and dentary flat in the terminal part of the beak (but behind the very tip) and well delimited from the middle depression. Mandible in postarticular region smooth ventrally (with no cristae). Upper mandibular margin well elevated above the level of the external mandibular process.

Dimensions. — See table 1.

Holotype skull (ZPAL MgR-I/12). See ELŻANOWSKI (1974). Two pairs of rows of nutrient foramina—two medial and two lateral—can be distinguished on the dorsal side of the premaxilla, although the bone surface is much weathered and not all the foramina preserved. The maxillary processes of the premaxilla begin some 2 mm anterior to the rostral extremity of the nasal opening. Despite previous interpretation, the transverse slit across the premaxilla appears now to be a simple fracture. In ventral view, many details of the palate have to be reinterpreted. Anteriorly, on the right side of the skull, a poor vestige of the bony ridge, converging antero-mesiad, which was described as the vomer, appears to be a remnant of the medial maxillopalatine margin. Its spurious symmetrical left counterpart seems to be a true vestige of the left vomer, lying medial to the left maxillo-palatine. Medial to the right maxillopalatine there is an obscure elevation probably representing the right vomer.

The left pterygoid, or rather its outer edge, is represented by a tongue-shaped fragment extending caudally from the left vomer vestige. The piece was formerly described as a part of the palatine. Posteriorly, the external pterygoid margin curves laterad and then forward forming the lateral sinus. Here the pterygoid becomes much wider. The right pterygoid begins as an elevation covered by a bony lamina, nearly at the same level as the left counterpart. The lateral sinus surrounding the palatine base is very obscure and immediately posteriorly there is a secondarily refilled break which supposedly represents the longitudinal overlap with the pterygoid bar. It follows that the prequadrate part of the pterygoid was probably longer than preserved. On the posterior part of the right pterygoid, behind the break, two articular sockets are exposed, the outer for the quadrate, the inner for the basipterygoid process. Just behind, or even across the sockets, the posteriormost part of the pterygoid is broken off. Some pieces of this seem to be crushed against the orbital process of the quadrate. A small terminal fragment of some

longer bone was obviously dislocated above the left pterygoid. It was previously supposed to be a part of the quadratojugal, certainly false. The piece is boot-shaped and consists of two parts that meet at right angle. In the corner, the edges of both perpendicular parts are flat and so their contact is precisely rectangular. The elongated "sole" is regularly rounded on the „underside" and suggestive of some articular connection. A minute, circular excavation is present on the very tip. On one side of the other part, directly broken off from the whole, there is a (pneumatic?) foramen and a slight ridge descending to the sole. The opposite side is not preserved. The fragment is supposed to be the posterior end of the pterygoid, the sole possibly abuted the quadrate medially, well above the internal condyle. The pneumatic foramen near the comparable ridge is present in the cassowary. Although hardly identifiable, the right palatine seems to be preserved. Its lateral, thickened edge can be observed prolonging the outer pterygoid margin rostrally. The anterior part of the left palatine, fused with the maxillopalatine, may also be present. On the left side, the palatine can be clearly seen only near to anterior fusion with the maxillopalatine, where the vertically oriented bar passes anteriorly into the horizontal blade of the maxillopalatine.

The disarticulated quadrate is preserved in a quite artificial position, its mandibular articular surface facing forwards and the otic process projecting ventrally. Only the basal part of the orbital process is fairly distinct and can be seen to descend from the otic process up to a point a little above the internal condyle. The remaining part of the orbital process is crushed against the braincase. The process was formerly called "the pterygoid process of the quadrate" (see discussion). Between the ventral base of the orbital process and the inner mandibular condyle of the quadrate, there is a minute tubercle, obviously for articulation with the pterygoid. Unfortunately, further details of the pterygoid-quadrates articulation can not be reconstructed with sufficient reliability, since both the posterior end of the pterygoid and the orbital process are incomplete. The mandibular articulation of the quadrate, as described before, is bicondylar. The lateral edge of the quadrate, in particular just above the outer condyle, is somewhat damaged, and the quadratojugal articulation is gone.

In dorsal view of the right mandible, two articular surfaces can be recognized. The outer surface, roughly circular (2.5 mm in diameter) extends laterally on the external process of the mandible. Anteromedially there is a small, somewhat excavated area where the posterior adductor commonly inserts. Posteromedial to the outer surface there is a large pit, whose antero-lateral wall, the only preserved part of the inner articular surface, evidently articulated with the inner quadrate condyle. The latter slanted some 2 mm below the outer surface of the mandible. Just behind the external mandibular process there is a small tubercle, behind which the upper edge of the mandible curves gently downwards and then, still further backwards, rises in the elevated upper edge of the retroarticular process.

In external view of the right mandible, some 12 mm from the rostral tip, the dentary bifurcates into the dorsolateral and ventrolateral processes with the longitudinal groove in between, extending about 8 mm posteriorly. No definable suture between the dorsolateral process of the dentary and the supraangular can be recognized. Beginning from the posterior end of the longitudinal groove, the upper margin of the ventrolateral process of the dentary curves downwards, and the process ends as a narrow, acute tongue, wedged between the supraangular and the angular. The supraangular, forming the whole coronoid elevation, is convex below and seems to continue in the groove between the dentary processes. Posteriorly, the bone extends the whole length of the retroarticular process forming the upper half of its height at the caudal end. The lower half is formed by the angular, which tapers gradually anteriorly and disappears to be replaced by the dentary on the lower edge of the mandible. The whole postdentary region of the left side is gone and no new details were noticed on the preserved part except that at the point of divergence of the lateral dentary processes there is a particularly well marked depression corresponding to the anterior mandibular fenestra.

In internal view of the mandible, the splenials seem to be absent (see discussion) and the

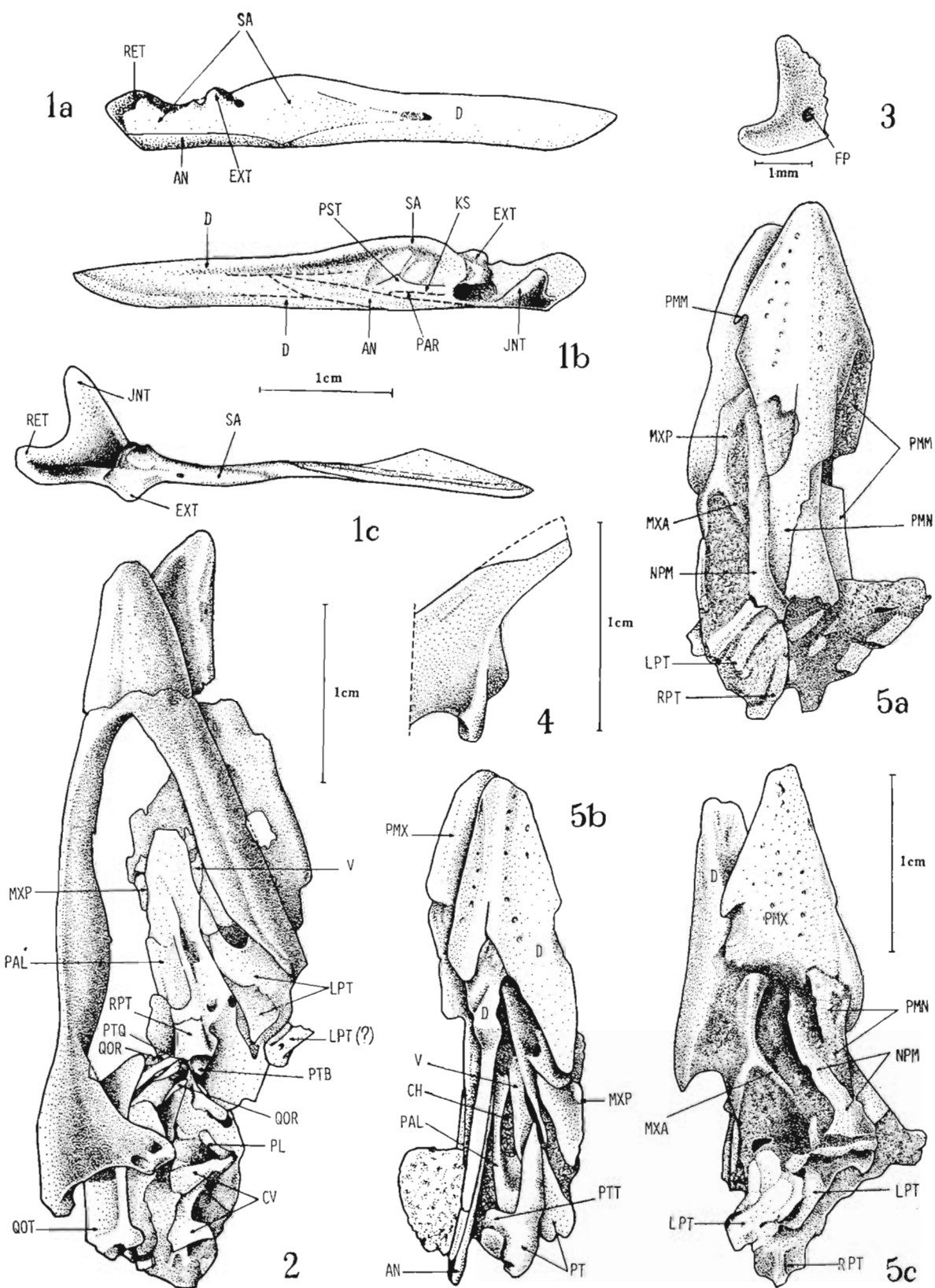


Table 1

Comparison of some cranial dimensions of two *Gobiptyerx* specimens (in mm). Paranthetic values are of fragments

	First specimen ZPAL MgR-I/12	Second specimen ZPAL MgR-I/32
Skull length	est. 45	(27+)
Length of the rostral part of the lower edge of premaxilla, to the level of the anteriormost margin of the nasal opening	8	8
Width of premaxilla at the base of the maxillary processes	7	7
Premaxillary height at the base of the maxillary processes	4	4
Vomer length (in ventral view):		
laterally	—	9
medially	—	7
Pterygoid length (in ventral view)	est. 12	(7+6)
Mandible length	38	(29+)
Mandibular symphysis length	9	9
Mandible height at the level of the anterior foramen	4	4

anterior, ascending part of the angular is exposed. On the only complete right mandible, the sutures are secondarily obliterated and their courses very difficult to establish. The coronoid elevation, inflected inwards, is composed mostly of the supraangular which also closes the posterior fossa. The diagonal ridge dividing the fossa is met by a small pseudotemporal process (MÜLLER, 1963) projecting upwards and a little backwards from a rod of bone extending from the articular region. This rod of bone appears to be the ossified part of the MECKEL's cartilage or Knochenstab (MÜLLER, 1963). Only the upper edge of the Knochenstab is exposed for it is covered below by the narrow prearticular lamina running forwards and upwards from the articular. Below the prearticular, the angular appears in the medial side of the mandible and forms its lower edge up to the level of the anterior end of the fossa, where the angular is replaced by the dentary. Then the angular ascends and tapers gradually reaching the dorsomedial process of the dentary above. In the anteriormost region of the right mandible there is a loose fragment of the bony lamina which may be a remnant of the splenial. In medial view of the only well preserved anterior part of the left mandible, the ascending part of the angular is very distinct. A break occurs at the point where the angular has just left the lower margin of the mandible. Some very poor fragments of the posterior part of the left mandible were dislocated forwards and attached to the outer side of the anterior part. Only the pseudotemporal process could be distinguished clearly among these pieces.

Fig. 1

Gobiptyerx minuta ELŻANOWSKI 1974: 1. Partial reconstructions of the mandible, *a* — in lateral view, *b* — in medial view, *c* — in dorsal view. 2. Skull of the type specimen (ZPAL MgR-I/12) in ventral view. 3. Fragment of the type specimen, unidentified, possibly posteriormost ending of the pterygoid. 4. Partial reconstruction of the quadrate in medial view. 5. Skull of the second specimen (ZPAL MgR-I/32), *a* — in dorsal view, *b* — in ventral view, *c* — in left lateral view. Abbreviations: *AN* — angular, *AR* — articular, *CH* — internal naris, *CV* — cervical vertebra, *D* — dentary, *EXT* — external process of the mandible, *FP* — pneumatic foramen, *INT* — internal process of the mandible, *KS* — Knochenstab, *LPT* — left pterygoid, *LV* — left vomer, *MXA* — ascending process of the maxillopalatine, *MXP* — maxillopalatine, *NPM* — premaxillary process of the nasal, *N* — nasal, *PAL* — palatine, *PL* — pleurapophysis of the cervical vertebra, *PAR* — prearticular, *PST* — pseudotemporal process, *PMM* — maxillary process of the premaxilla, *PMN* — nasal process of the premaxilla, *PT* — pterygoid, *PTB* — basiptyergoid articulation of the pterygoid, *PTQ* — quadrate articulation of the pterygoid, *PTT* — outer tine of the pterygoid, *RPT* — right pterygoid, *RV* — right vomer, *QOR* — orbital process of the quadrate, *QOT* — otic process of the quadrate, *RET* — retroarticular process of the mandible, *SA* — surangular.

Second skull (ZPAL MgR-I/32). Only the rostral part of the skull is preserved. In the region of the anterior orbital rim, the bones are broken and partially dislocated, the fracture crossing the nasals and pterygoids. The skull is compressed laterally to some extent. The premaxilla is wide, its rostral tip is rounded and the lateral edges converge, their prolongations meet at the relatively great angle of about 40° . This all suggests a short, robust beak. Dorsally, the premaxilla is strongly domed with many nutrient foramina, the majority of them arranged in four rows: two medial and two lateral, the last running just above the premaxillary edges. There are about 7 foramina in each medial and about 5 in each lateral row. At the rostral tip of the premaxilla, the medial rows begin with the vestigial grooves.

Nasal openings extend far anteriorly. Below and, unexpectedly, a little (approximately 2 mm) forwards, the maxillary processes of the premaxilla originate as separate projections. The broken anterior part of the maxillary process is preserved only on the right side. The nasal processes, strongly tapering posteriorly, extend 22 mm from the rostral end of the premaxilla, and fit between the premaxillary processes of the nasals. The last extend to the anterior rim of the nasal opening and are overlapped, as the thin laminae, by the nasal processes of the premaxillae. On the better preserved, left side of the specimen, the corresponding nasal and premaxillary processes are disarticulated, the nasal process of the premaxilla having been lifted off the premaxillary process of the nasal. Such a condition suggests a loose and movable connection between these bones. Beneath the right nasal, part of the jugal bar is preserved. It appears to consist mostly of the caudal prolongation of the maxillary process of the premaxilla. The lateral edge of the maxilla is represented by only a small medial fragment, other maxillary parts were identified are the maxillopalatines (see below). Neither the jugal nor the quadratojugal could be identified.

The middle part of the palate, with vomers, palatines and pterygoids arranged in typical palaeognathous pattern, is fairly well preserved in ventral view, with some dislocation resulting in slight asymmetry in the hind part of the specimen. The vomers are fused anteriorly and begin 13–14 mm from the premaxillary rostral end. About 4 mm posteriorly they diverge (at 20° to the lateral edges) and run 5 mm further caudally to be suturally overlapped by the pterygoids. The separate parts of the vomers are inclined in such a way that the lateral edges are more ventral than the medial edges. The vomeropterygoid suture is oblique (about 25° to the sagittal plane) and 3 mm long, while the vomeropterygoid bar is little more than 1 mm wide at this level. From the vomeropterygoid suture the pterygoids widen gradually toward the palatine suture posteriorly. The pterygoid laminae are inclined in accordance with the vomers position. In the palatine region the right pterygoid becomes horizontal and, just behind this, an outer wing projects laterally. The lateral pterygoid margin curves outwards and then forwards to project as a terminal outer tine and thus encloses the posterior edge of the palatine in the rostrally open lateral sinus. The outer tine of the pterygoid projects slightly beyond the adjacent external palatine margin. The pterygoid achieves the greatest width of nearly 3.5 mm at the level of the outer tine, where the medial pterygoid margin curves gently posterolaterally.

The right pterygoid is broken just behind the palatine base and the remaining part is gone. The left pterygoid is dislocated to the midline so that the shape and size of the interpterygoid vacuity cannot be established directly. The bone is broken at a more anterior position than its right counterpart; only a part of the lateral sinus remains. The remaining, posterior part of the left pterygoid is dislocated on the dorsal side so that its posterior end, appearing to be boot-shaped, touches the left nasal. The right palatine is based in the pterygoid sinus posteriorly. Medially, the contact with the pterygoid extends to the vomeropterygoid suture anteriorly. The lateral margin of the palatine is much thicker than the inner lamina and projects somewhat ventrally as a ridge which continues forwards as the lateral rim of the internal naris. The indistinct maxillopalatine-palatine suture seems to cross the choanal rim at the level of the vomeropterygoid suture. Anteriorly the ridge disappears and the medial margin of the right maxillopalatine curves to the vomer enclosing the internal naris anteriorly. A small part of the

left maxillopalatine is visible in dorsal view. Posteriorly it sends out the ascending or nasal process with the free end projecting dorsoposteriorly and partially separating the nasal and the antorbital openings. In ventral view, only the posterior part of the left maxillopalatine is visible as a shelf fused medially with the palatine without any definable suture and facing somewhat outwards, as in the cassowary.

The mandible has a long smooth symphysis. The rounded outline of the rostral tip is exactly the same as that of the premaxilla. In dorsal view the rostral parts of the lateral edges are also equally wide but quite flat with no concavity. In ventral view there is a very similar pattern of nutrient foramina as occurs on the upper jaw: a pair of medial rows beginning with the slight grooves on the very tip, and a pair of lateral rows. There are 9—10 foramina in each medial and 6 or more in each lateral row. Posteriorly, the mandible edges are damaged, so that some lateral foramina are probably gone. In the right mandible, the whole lower part of the dentary is present. The upper part is broken across the dorsolateral process. The whole post-dentary region of the mandible is missing. The preserved part of the right mandible is badly fractured, the rostral piece being overlaid by the posterior one — so, exact length measurements are not possible. From the external side, the posterior bifurcation of the dentary into upper and lower processes is fairly distinct. The posterior part of the dorsolateral process is absent. The ventral process tapers backwards, its upper margin descending gradually, to end as a narrow tongue. Behind this the lower edge of the mandible is formed by the angular. The dorsolateral process of the dentary forms a part of the dorsal edge of the mandible, the middle part of which is composed of the surangular. What I interpret to be also the surangular closes the space between the lateral dentary processes and, in this way, forms a bottom of the 8 mm long external depression, occurring at mid-height of the mandible. Behind this depression, the surangular becomes convex, just in front of the broken end of the mandible. In internal view the anterior part of the angular rises gradually exposing the ventral process of the dentary beneath. The splenial seems to be absent on the specimen. In the left mandible, only the anterior part of the dentary is preserved and no additional details were noticed.

Remarks. — An uncertain point on the reconstructed ventral view (text-fig. 2, 1a) is the pterygoid-quadrato articulation, which is complex and quite variable in palaeognathous birds. A posterodorsal process of the pterygoid occurs adjacent to the medial side of the quadrato in Ratitae (*Rhea*, *Struthio*, *Casuarus*, *Dromaius* — pers. obs.) and perhaps in *Gobipteryx* as the puzzling, boot-shaped fragment, that I suppose to be a caudal end of the pterygoid.

The lack of splenials on both specimens appears to be natural, for in all Ratitae the splenial is quite loosely connected with other bones. In view of the poor preservation of both skulls, it is highly probable that the splenials became disarticulated.

In the holotype skull, the orbital process, previously called "the pterygoid process of the quadrato", projects into the articular socket of the pterygoid. However, this position appears to be accidental and, thus, the commonly used term "the orbital process" is introduced here, although both names are sometimes used as synonyms.

Although the jaws of the two specimens are almost the only parts that can be compared, their detailed similarity together with identical measurements (table 1) indicates both *Gobipteryx* specimens to be conspecific. Striking similarity is conveyed by the terminal parts of the jaws, with their flat margins, slightly concave on the premaxilla, converging at the same angle of about 40°. The rostral part of the culmen is rectilinear, ascending from the tip at the angle of 32° to the rostromedial premaxillary edges (measured in the sagittal plane). A possible difference between the specimens is the number of nutrient foramina which seem to be fewer on the premaxilla of the first skull, although the bone surface is weathered, and smaller foramina could have been destroyed. The symphyseal surface of the holotype mandible is completely ground off, and no relevant details are observable.

Differences in the kind of food are commonly reflected in the bill structure, especially in ground-feeding birds (CODY, 1974: 35—39, and references therein). Therefore, the high degree

of similarity of the bill shape and dimensions of both *Gobipteryx* specimens would suggest closely similar food requirements. As far as the Gause's principle is still valid (CODY, 1974, p. 54), a persistent coexistence of two species with common food resources is less probable.

DISCUSSION

Gobipteryx provides new evidence in favour of the classic hypothesis of PYCRAFT (1900), who argued for the morphological and phylogenetic unity of palaeognathous birds. PYCRAFT's views have been challenged many times and therefore require some comments in the light of contemporary knowledge.

The main criticism was furnished by McDOWELL (1948), who claimed the impossibility of defining the palaeognathous palate. The principal characters used in the definition (the vomeropterygoid and the palatinopterygoid sutures as well as the lack of pterygoparasphenoidal contact) were shown not to be universal. In *Struthio* the small vomer does not contact the pterygoid, the latter touching the parasphenoid; the occurrence of the pterygoparasphenoidal contact is also mentioned for *Apteryx*, although it is not indicated in the description of the "apterygiform type"; lastly, the lack of contact between the palatine and the pterygoid in *Dromaius* is emphasized. Moreover, McDOWELL argued that many features thought to specify the palaeognathous condition occur in various neognathine groups, for example the backward position of basiptyergoid processes "can be matched by the Musophagidae and Turnicidae among the Neognathae".

Meanwhile, a great deal of evidence (BOCK, 1963) in favour of monophyly of the palaeognathous birds accumulated since the time of publication of the McDOWELL's paper. Even if such a rigorous requirement of universality for every morphological criterion is justified, the factual basis of the McDOWELL's argument was shown to be dubious. In the case of struthious palate, vomers are extremely variable in shape and size and reach the pterygoid in some specimens (WEBB, 1957). In the kiwi, the pterygoparasphenoidal contact does not exist on the specimen of *Apteryx mantelli* examined by the present author. In most specimens of the emu, the palatine does articulate with the pterygoid (SIMONETTA, 1960).

PARKES and CLARK (1966) noticed a new feature linking the palaeognathine groups, which is a specific pattern of division of the rhamphotheca, distinct from that occurring in some other birds with a complex horn-sheath of the beak. Among other kinds of research, MEISE (1963) compared behavioral features and came to the conclusion that the Ratitae on one hand and tinamous on the other are sister groups. The arguments for palaeognathine monophyly have been recently summarized by CRACRAFT (1974).

The most convincing argument, especially in the present context, for the unity of the palaeognathous condition was given by BOCK (1963). If the whole complex of features, and not the single ones taken independently, is included in the definition, the palaeognathous pattern can be precisely defined even if one or another of these characters happens to occur in some neognathine group. Following (with some modifications) BOCK's (1963) important paper, the palaeognathous complex includes: (1) Relatively large vomer articulating with the premaxillae and maxillopalatines anteriorly and (*Struthio* excepted in most cases) with the pterygoids posteriorly; (2) Palatine articulating suturally with the vomeropterygoid bar, never with the parasphenoid (this criterion is universal for palaeognathous birds); (3) Large basiptyergoid processes articulating with the pterygoid close to the quadrate articulation; (4) Complex articulation between the pterygoid and quadrate, with a well developed articular surface on the orbital process and/or the posterodorsal process of the pterygoid ascending along and adhering medially to the base of the orbital process. This complex of characters is not simply an arbitrary assemblage chosen from many other possibilities. It is substantiated by the biomechanical interpretations (HOFER, 1945) of the palaeognathous skulls, further elaborated by BOCK (1963). HOFER showed, that the primary importance of the parasphenoid contact of the palatopterygoid

joint is for transmission of longitudinal forces to the basicranium, what is especially important in the case of shocks coming from the beak. Palaeognathous birds have neither such a middle palate joint nor a mesial support, so there is almost full transmission of the forces from the beak to the quadrate. It follows that shocks can not be reduced in this way and reach the quadrate, its articulations being the most critical points (HOFER, 1945). In palaeognathous birds, the shocks are possibly absorbed, instead, by another automatic device (ELŻANOWSKI, in press): when the pterygoid is pushed backwards, the quadrate rotates downwards and somewhat inwards, and at the same time, its orbital process presses the pterygoid against the basiptyergoid process. The entire mechanism would fail if the quadrate were not prevented from moving outwards by the zygomatic process of the squamosal. Thus, the general morphology of the anterior part of the palaeognathous palate can be correlated with the particular structure of the quadrate-ptyergoid articulation and the peculiar zygomatic process.

All palaeognathous birds are primarily rhynchokinetic, although their rhynchokinesis is of a special kind. The uniformity of their kinetic mechanism is the second major reason, by which the unity of this group should be recognized. The structural features related directly with the rhynchokinesis are: (1) Orbital septum continuous with the nasal septum; (2) Nasal openings extending far anteriorly; (3) Lack of continuous bony connection between the nasal and the maxilla. Moreover, ratite rhynchokinesis is not associated with any definable zone of bending in the bones roofing the beak, and in some ratites at least (Casuariformes, Dinornithiformes, Apterygiformes) the nasals are lifted off the premaxillae during the upward movement of the upper jaw (SIMONETTA 1960). In any case, in all the ratites and some tinamous at least (*Crypturus rufescens* and *Tinamotis elegans*) there is a loose premaxillary-nasal connection (pers. obs.).

From the preserved remains, the skulls of *Gobipteryx* appear to be palaeognathous in nearly all relevant features:

(1) In the palate, the pterygoids articulate suturally with the vomers anteriorly and with the palatines laterally. The posteriorly diverging vomers are relatively large and are approached by the maxillo-palatines anteriorly. The only obvious interpretation for the medial socket of the posterior part of the pterygoid in the first specimen is the existence of a basiptyergoid joint. Its caudal position would be also indicative of a palaeognathous condition.

(2) Among the features directly related with ratite rhynchokinesis, the forward extension of the nasal opening is clearly seen on both specimens. The lack of a bony connection between the nasal and the maxilla is evident on the second specimen in the free ending nasal process of the maxilla. Among birds such a process occurs only in some ratites (GADOW & SELENKA, 1891). The loose connection between the nasal and the premaxilla concurs with the other ratite rhynchokinetic characters. Hence, *Gobipteryx* gives a new piece of evidence of the correlation between palatal and directly rhynchokinetic features — all together they can be viewed as the "functional unit of characters" (BOCK, 1963). One of the features that has been thought typical of the palaeognathous skull (PARKES & CLARK, 1966) is lacking in *Gobipteryx*: on the outer surfaces of the premaxilla and dentary there are no distinct grooves, indicative of rhamphothecal division, only some dubious vestiges being present on the very tips of the bones. It must be noted that the grooves are also lacking in some recent tinamous (PARKES & CLARK, 1966).

The unusual structure of the mandibular articulation of the *Gobipteryx* quadrate, not known in the other Palaeognathae, raises a more serious problem. In all other Palaeognathae, as well as in the majority of the Neognathae, the mandibular articulation of the quadrate is roughly triradiate with one part projecting backwards, well behind a straight line between the inner condyle and the quadratojugal articulation. In *Apteryx* and tinamous, the mandibular articulation of the quadrate is rather bipartite with the outer part moved well backwards, leaving in front a bony shelf, seen in rostral view as a ridge extending from the base of the orbital process and supporting the quadratojugal articulation medially. In the remaining ratites, the part of the articulation projecting backwards is separated as the posterior condyle, the whole

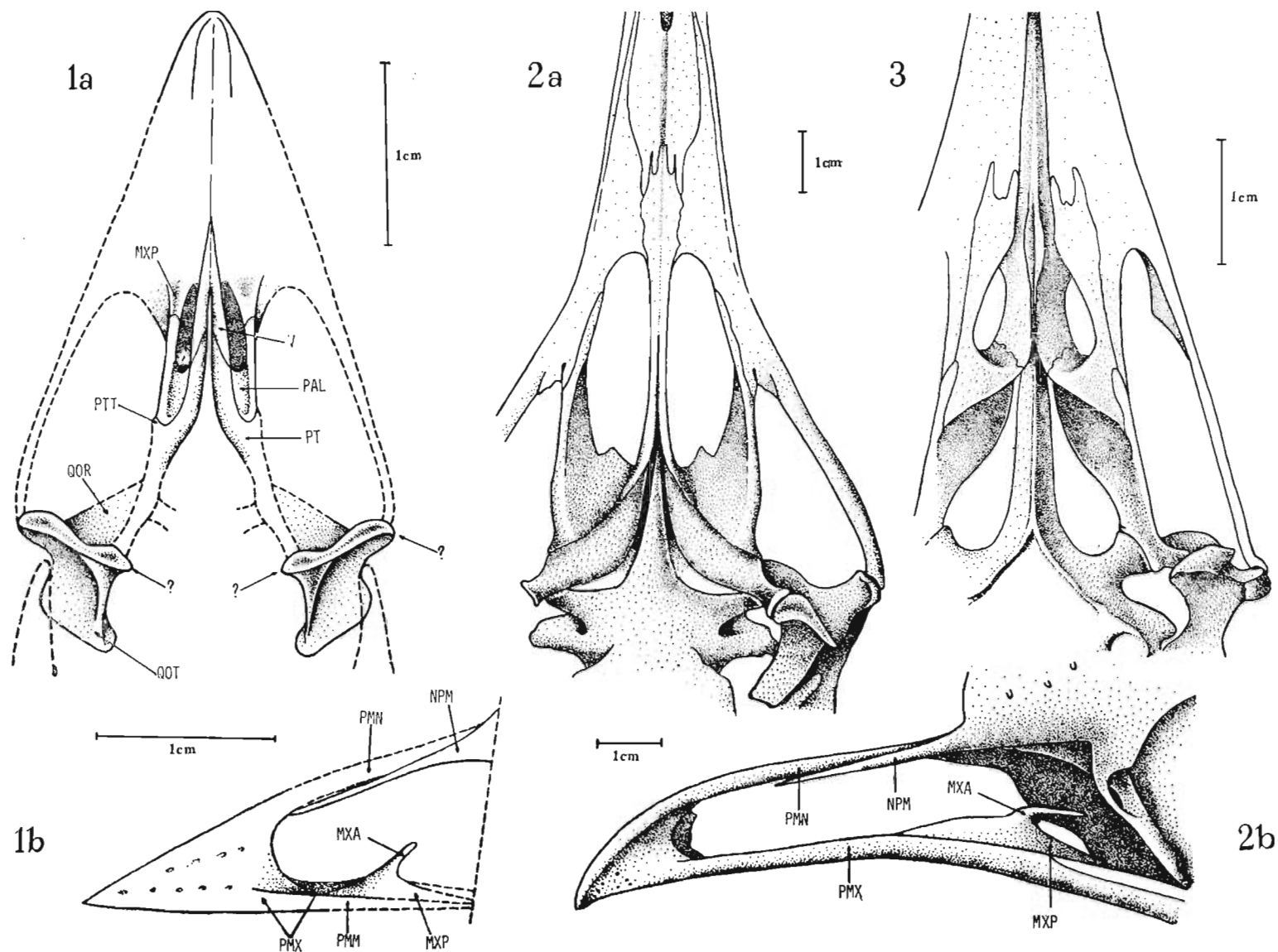


Fig. 2

1. *Gobiptyx minuta* ELŻANOWSKI, 1974, partial reconstructions of the skull, *a* — in ventral view, *b* — in lateral view (rostral part). 2. *Casuarius casuarius* (L.), palate. 3. *Apteryx mantelli*, BARTL., palate. Abbreviations as in text-fig. 1

being strictly comparable with the bipartite condition. In contrast, in the bipartite mandibular articulation of the *Gobipteryx* quadrate, no part is retracted behind the straight line connecting the inner condyle with the quadratojugal articulation. The lower part of the *Gobipteryx* quadrate is rather pigeon-like. Against the overwhelming evidence of the palaeognathine affinities of *Gobipteryx*, the difference in the structure of the mandibular articulation of the quadrate is quite isolated and seems to be of secondary importance for the relations between the major avian taxa. In *Platalea* the mandibular articulation of the quadrate lacks the posterior part, which occurs in other Ciconiiformes. Within the Palaeognathae, however, this feature appears to be fairly important (although its phylogenetic significance can not be understood until its biomechanical role is ascertained).

Among the known palaeognathous birds, *Gobipteryx* displays the closest similarities to Casuariformes and especially *Casuarius*: (1) vomers diverging gradually with (2) the ventral edges of their laminae deflected laterally; (3) pterygoids much widening in the region of the palatine articulation; (4) palatines articulating mostly with the pterygoid; (5) outer margin of the palatine distinctly thicker and lying more ventrally than the inner blade; (5) ascending process of the maxillopalatine present. The last cassowary character was indicated by BOCK (1963, see fig. 4) and is clearly seen on the specimen at the author's disposal (text-fig. 2), yet not referred to by GADOW & SELENKA (1891, p. 31) and SIMONETTA (1960, see fig. 5). In *Casuarius*, the ascending process is much weaker than in *Rhea* and, as in *Dromaius*, it is developed as the posterior, terminal process of the "dorsal, arched lamina" (MCDOWELL 1948) of the maxillopalatine.

The vestigial, anterior bifurcation of the pterygoid of *Gobipteryx* seems to be intermediate between *Casuarius* and *Apteryx*. In *Casuarius* the entire posterior margin of the palatine is supported by the pterygoid. In *Gobipteryx*, the posterior palatine margin is surrounded by the pterygoid, which bears the small outer tine projecting anterolaterally. A similar outer tine is visible on the ventral side of the *Apteryx* palate as figured by MCDOWELL (1948, see text-fig. 5) and observed by the present author on a specimen of *A. mantelli*. In the figures given by BOCK (1963) and PARKER and HASWELL (1910), the outer tine is not indicated. In any case it does exist and can be seen in its entire extent in dorsal view of the palate, where it has been identified in the second specimen of *Gobipteryx*. The anterior pterygoid bifurcation in the kiwi was thought by MCDOWELL (1948) to be unique among birds and provided one of the principal criterions to distinguish the "apterygiform type" of the palate. In the light of the *Gobipteryx* palatal structure, the "casuariform" and "apterygiform" types are clearly linked. Therefore, *Gobipteryx* would also provide a direct evidence for the morphological and phylogenetic unity of the palaeognathous birds and, unless the structure of pterygoid-palatine articulation is a plesiomorphic feature, for closer relations between the Casuariformes and Apterygiformes. Thus, the old views of MIVART (1877) and PARKER (1895), adhered to by SIMONETTA¹ (1957, 1960) and PARKES and CLARK (1966), postulating closer affinities between emus and cassowaries on the one hand and kiwis and moas on the other, would be further confirmed. These hypotheses have recently been denied by CRACRAFT (1974), who approaches emus and cassowaries to the ostriches and rheas on the basis of the synapomorphic features of the postcranial skeleton.

Although the relationships between the birds assigned to Palaeognathae seem to be well substantiated, a taxonomic value of the sole palaeognathous condition of the palate appears to be questionable, this condition being "probably truly primitive in birds" (GINGERICH, 1973). In this light, the palaeognathous palate, which occurred in *Hesperornis* (GINGERICH, 1973), would designate only an early grade of the avian phylogeny. Thus, if the phylogenetic relationships are to be established, a great attention should be paid to differences rather than

¹ It should be noted, that the allocation of Casuariformes and Apterygiformes (together with Dinornithiformes) into one of three distinct palaeognathous groups has been claimed by SIMONETTA on the basis of the skull anatomy and kineism.

similarities of the basic pattern, and the aberrant structure of the *Gobipteryx* quadrate may be more important than assumed in the present study.

Palaeognathous birds are the prime avian example of southern dispersal and their present distribution is explained by the breakup of the Gondwanaland (CRACRAFT, 1974; RICH, 1975). Sauer (1972) pointed out, however, that their past distribution could be much wider than the present and this opinion is well corroborated by the *Gobipteryx* discovery.

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EXPLANATION OF PLATE

PLATE 37

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Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia

- 1a. Stereophotograph of the skull in dorsal view. ZPAL MgR-I/32; $\times 2.5$.
- 1b. Stereophotograph of the same in ventral and somewhat lateral view; $\times 2.5$.
- 1c. Stereophotograph of the same in right, lateral view; $\times 2.5$.
- 1d. Stereophotograph of the same in left lateral view; $\times 2.5$.
- 1e. Stereophotograph of the same in ventral view; $\times 2.5$.
- 1f. Stereophotograph of the same in rostral view; $\times 5$.
- 2a. Stereophotograph of the skull in rostral view. Type specimen, ZPAL MgR-I/12; $\times 5$.
- 2b. Stereophotograph of the mandible of the same specimen in medial view; $\times 6$.

Photo: E. Wyrzykowska

