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## EMBRYONIC BIRD SKELETONS FROM THE LATE CRETACEOUS OF MONGOLIA

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Seven specimens (two incomplete skeletons and five smaller fragments) are described as the remnants of highly advanced embryos, which belong in all probability to *Gobipteryx minuta* ELŻANOWSKI, 1974. Both the skull and the postcranial skeleton clearly show avian features although some traits are not known to occur in birds. The humerus displays closer similarities to *Wyleyia valdensis* HARRISON and WALKER, 1973. The forelimb skeleton and the shoulder region are suggestive of an advanced flight ability; these parts are almost completely ossified and give evidence of an extremely precocial development. The fusion of neural spines of two cervicodorsal vertebrae is thought to be either flight or hatching adaptation.

**Key words:** Cretaceous birds, bird development, ossification, flight, hatching, avian skeleton, *Gobipteryx*, *Wyleyia*.

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**Streszczenie.** — Opisano kopalne embriony, najprawdopodobniej należące do *Gobipteryx minuta* ELŻANOWSKI, 1974, na podstawie siedmiu okazów pochodzących z osadów górnokredowych pustyni Gobi, w tym dwóch niekompletnych szkieletów i pięciu mniejszych fragmentów. Obydwa szkielety zachowały embrionalne położenie z czaszką na stronie brzusznej skierowaną ku tyłowi; położenie takie można również wywnioskować dla dwóch mniejszych fragmentów. W większości okazy zachowane były z fragmentami skorupy, które zawsze skierowane były wklęsłą, wewnętrzną stroną do kości. Zarówno czaszka jak i szkielet pozaczaszkowy wykazują wiele cech typowo ptasich, przy czym proporcje i budowa szkieletu kończyny piersiowej oraz okolicy barkowej wskazują na posługiwanie się aktywnym lotem; dlatego kończyna ta może być uznana za skrzydło. Występują jednak również cechy, które wydają się prymitywne i nawiązują do Theropoda. Jedyną formą, która wykazuje bliższe podobieństwo z opisanymi szkieletami zarodkowymi jest *Wyleyia valdensis* HARRISON i WALKER, 1973 opisana na podstawie kości ramiennej z dolnokredowych osadów wealdu Anglii i zaliczona do ptaków. Na podstawie względnej długości skrzydła oraz stopnia skostnienia jego szkieletu, obręczy barkowej i sąsiadujących kręgów można wnosić, że młode zdolne były do lotu wkrótce po wylęgu i wykazywały skrajnie zagniazdowniczy rozwój.

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## INTRODUCTION

Embryonic skeletons are certainly among the rarest of fossils. ANDREWS (1932) reported "delicate skeletons of dinosaur embryos" contained in two broken eggs found in the beds of the Djadokhta Formation, in the locality Bayn Dzak (formerly Sabarakh Usu) by the 1928 Central Asiatic Expedition of the American Museum of Natural History. GRANGER (1936) referred more cautiously to these specimens as "what appears to be traces of highly developed embryos". The discovery has often been mentioned in the popular publications yet never confirmed neither by BROWN and SCHLAIKJER (1940) nor by any other authority. The American Museum of Natural History is unable to give any information on the alleged embryonic bones (dr E. GAFFNEY — pers. comm.) so the early reports appear to be mistaken. The only pre-quaternary remains of an embryo are the fragments of long bones (?metatarsals) adhering to the inner side of the dinosaurian egg-shell (SOCHAVA 1972); the specimen was found in Senonian of the eastern Gobi.

The embryonic remains described in the present paper were found by members of the 1971 Polish-Mongolian Palaeontological Expedition to the Gobi Desert (KIELAN-JAWOROWSKA and BARSBOLD 1972) in Khermeen Tsav I. The red beds of Khermeen Tsav are regarded as stratigraphical equivalent of the Barun Goyot Formation (see GRADZIŃSKI and JERZYKIEWICZ 1974, and GRADZIŃSKI *et al.* 1977) and are presumably of ?Middle Campanian age.

The only other bird-like fossils described from the Cretaceous of Central Asia are two skulls of *Gobipteryx minuta* (see ELŻANOWSKI 1977).

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## MATERIAL

Seven specimens i.e. two skeletons ZPAL MgR-I/33—34 and five smaller fragments ZPAL MgR-I/88—91, all including the egg-shell pieces; for the preserved parts see Table 1. All the specimens were found in the same place in the locality Khermeen Tsav I, Gobi Desert, red beds of Khermeen Tsav, ?Middle Campanian. All are housed in Warsaw in the Institute of Palaeobiology of the Polish Academy of Sciences, abbreviated as ZPAL. For the sake of brevity only the last terms of the long specimen numbers are used throughout descriptions, e.g. no. 33 instead of ZPAL MgR-I/33.

Table 1

Synopsis of the identified parts, with the most destroyed marked in parantheses

L — left side, R — right side

	ZPAL MgR-I/33		ZPAL MgR-I/34		ZPAL MgR-I/88		ZPAL MgR-I/89		ZPAL MgR-I/90		ZPAL MgR-I/91		ZPAL MgR-I/92	
	L	R	L	R	L	R	L	R	L	R	L	R	L	R
<b>Skull:</b>														
calvarium	+		(+)		+		-		-		(+)		-	
mandible	+	-	+	-	+	+	-		-		-		-	
<b>Vertebrae:</b>														
cervicals	8		10+(3)		-		-		-		-		-	
dorsals	6		1+(1)		-		3		-		-		-	
<b>Ribs</b>	(3)	(1)	(3)	(2)	-		-		-		-		-	
Scapula	+	+	+	+	-		-		-		-		-	
Coracoid	-	+	+	+	-		-		-		-		(?)	
Clavicle	-	-	+	(?)	-		-		-		-		-	
Humerus	+	(+)	+	(+)	-		(+)		-		(+)		(+)	
Radius	+	-	+	-	-		(+)		-		(+)		-	
Ulna	+	-	+	(?)	-		(+)		-		(+)		-	
<b>Metacarpals</b>														
II and III	+	-	+	+	-		+		-		+		(?)	
<b>Phalanges</b>														
of the pollex	-	-	2	1	-		-		-		-		-	
Femur	+	-	-	-	-		-		-		-		-	
Tibia	+	-	-	-	-		-		(?)		-		-	
<b>Phalanges</b>														
of the toes	+		-		+		-		+		-		-	

**ZPAL MgR-I/33** (pl. 42; fig. 2). — The bones appear to have been little calcified at the time of death and thus some of them may be disformed or artificially fused, this applies especially to the skull. The cervical vertebrae are totally disarrayed, forming an obscure lump associated with a displaced fragment of the right humerus. The skull is badly damaged and remains in the original position on the ventral side. The mandible adheres to the body and the palatal side is directed dorsally, while the culmen faces ventrally. The mandibular articulation lies between the forearm and metacarpals, the former partially covering the mandible, the latter adhering to the quadrate and squamosal. The rostral part of the skull extends to the posterior

end of the specimen, at least 3 mm behind the elbow joint of the completely folded wing. The postnasal bar is partially covered by the knee joint. In the left wing skeleton, the radius and ulna are so strongly appressed on the humerus that the three bones give the impression of being united. The elbow joint lies close to the shaft of the femur. The femur remains articulated with the tibia, which is strongly flexed. The knee joint, as preserved, is 3–4 mm anterior to the elbow joint. The specimen ends at the level of sixth dorsal vertebra.

**ZPAL MgR-I/34** (pls. 40–41, fig. 1). — The cervical vertebrae surround the anterior end of the trunk and reach the ventral side of the skeleton where scattered fragments of the completely destroyed skull are present. The mandible lies between the forearm and metacarpals, the latter covering the region of the mandibular articulation. The specimen ends at the level of the second dorsal vertebra. Detailed similarities to no. 33 are seen in the morphology of the anterior end of the scapula, vertebrae 12–16 and metacarpals.

**ZPAL MgR-I/88** (pl. 41, fig. 4). — The specimen consists of the rostral part of the skull, together with the mandibles, and the fragment of the pes, represented by two phalanges, the penultimate and the ungual, located near the rostral end of the skull. In relation to the skull, the ungual points dorsally, with the plantar side directed rostrally. This design clearly suggests the rolled posture with the head in ventral position. Thus, the specimen represents the ventral and probably the posterior part of the skeleton. The shape and proportions of the beak as well as the detailed morphology of the premaxillae and nasals are the same as in no. 33.

**ZPAL MgR-I/89** (pl. 45: 1). — Diaphyseal fragments of the forelimb bones (?humerus, ?radius, ?ulna, 2 metacarpals in articulation) and neural arches of 3 dorsal vertebrae showing detailed similarity of size and shape to those of no. 33.

**ZPAL MgR-I/90** (pl. 45: 2). — Fragments of the hindlimb skeleton: ?tibia and phalanx ungualis, the latter showing detailed similarity of size and shape to that of no. 33.

**ZPAL MgR-I/91** (pl. 44: 2). — Fragments of the forelimb bones (humerus, radius, ulna, 2 metacarpals) and a piece of the postorbital region of the skull, adhering to the metacarpals. The size (width) ratios of the bones are the same as in the specimens no. 33 and no. 34.

**ZPAL MgR-I/92** (pl. 44: 1). — Fragments of the forelimb bones (?humerus, metacarpal II, ?coracoid) and (separately) fragments of two digital phalanges of the foot.

Detailed similarities of size and shape of different bones allow to recognize all the specimens to be unquestionably congeneric. Since they were found in the same place they are most probably also conspecific. All differences are explained (see below) as resulting from different stages of ossification.

Skeletons no. 33 and no. 34 are both laterally compressed and show the same bone arrangement. The dorsal side is marked by an interscapular series of the posterior cervical and dorsal vertebrae, the scapulae and the arm bones. The forelimbs are folded like bird wings (this pattern is shown also by no. 91). The humerus is directed backwards and the forearm bones forwards, parallel to the humerus; the metacarpus is folded only partially. The skull fragments lie on the ventral side. The humerus and forearm bones are appressed on the shoulder girdle and the thorax, while the acropodium closely adheres to the postorbital region of the skull (the last condition also occurs in no. 91). Preorbital region of the skull is associated with the leg bones in the specimens no. 33 and 88.

The egg-shell pieces of all the specimens have their inner (concave) surfaces oriented toward the bones. The external surface of the shell is smooth (without sculpture). Preliminary studies (G. MIERZEJEWSKA — pers. comm.) of no. 33 show that the shell is double (pl. 42: 1h). The largest (16 × 23 mm) preserved piece of the shell (no. 33, pl. 42: 1a, 1b) represents a near-equatorial (not polar) part of the egg. The external surface is convex along the lesser diameter but quite straight along the greater diameter. This implies an oblong shape of the egg, known in many reptiles such as the crocodiles or *Protoceratops*. The radius of curvature is about 1 cm so the lesser diameter is approximated as 2 cm. The greater diameter is expected to have exceeded 4 cm, as inferred from two estimates: (a) length of the thorax (glenoideum-acetabulum),

may be estimated as 20 mm, basing on the approximate position of the acetabulum in no. 33 (see below), (b) length of the embryo may be estimated as twice that of the thorax alone, as it is the case in the prehatching stage of the chicken (pers. obs.).

The sediment inside the egg shells does not differ from the surrounding sandstone and consists of rather coarse grains. Therefore, the eggs had been broken before consolidation of the sediment.

## DESCRIPTIONS

Three specimens no. 33, no. 34 and no. 88 are described in detail. The remaining ones, consisting of small fragments, are referred to only if they give additional information.

### SKULL

Major skull fragments are preserved in specimens no. 33 and no. 88 the latter being ossified much better. The common features shared by both specimens, are:

- toothless jaws forming a robust beak;
- straight culmen rising at an angle of about 30° in relation to the palate;
- unpaired premaxilla with the short maxillary process pointing caudally;
- long and loose overlap of the nasal by the premaxilla, the former being exposed at the surface only laterally;
- large nasal opening, rounded anteriorly.

**ZPAL MgR-I/88** (pl. 41: 3; fig. 4).— The rostral end of the premaxilla (somewhat damaged) had been rounded originally. The nasal process of the premaxilla, 5–6 mm long and lying loose on the nasal, extends to the level of the anterior margin of the orbit; the maxillary process appears to be short (1.1 mm). The nasal splints, overlapped by the premaxilla, extend to the anterior margin of the nasal opening. Posteriorly, the nasal expands laterally and somewhat ventrally, emerging from under the premaxilla (fig. 4A); further backwards the nasal overlaps the frontal. The maxilla has the dorsal edge projecting dorsomedially and forming a rounded eminence; this elevation may represent the ascending process that would mark the boundary between the nasal and the antorbital opening. Posteriorly, the labial bar is broken.

A perpendicular lamina of vestigially fossilized bone remains beneath the frontal and probably represent the anterior part of the antorbital septum i.e. the mesethmoid (fig. 4A, et). The lamina had originally (before preparation) the anterior outline convex and the posterior one concave. Anteriorly, there is still another vestige, preserved in the same way and joining the nasal dorsally; this vestige may represent a part of the ectethmoid.

The mandibles (fig. 4B, m) are quite free, with no symphysis, although they contact each other at the symphyseal region, having the rostral extremities much widened inwards. Externally, a shallow depression extends along each mandible beginning some 5 mm posterior to the rostral end where the dentary bifurcates into the dorsal and the ventral process. The dorsal edge of the right mandible is clearly elevated near the posterior broken end of the fragment. The lower edge is very thick and gently curved (concave). No sutures could be recognized with certainty except for the posterior bifurcation of the dentary.

Dimensions (in mm):

Total length of the skull . . . . .	25 est.
Length of the preserved skull fragment . . . . .	14
Mandible: length . . . . .	(12+)
greatest width at the symphyseal region	2.0
greatest postsymphyseal width . . . . .	1.7

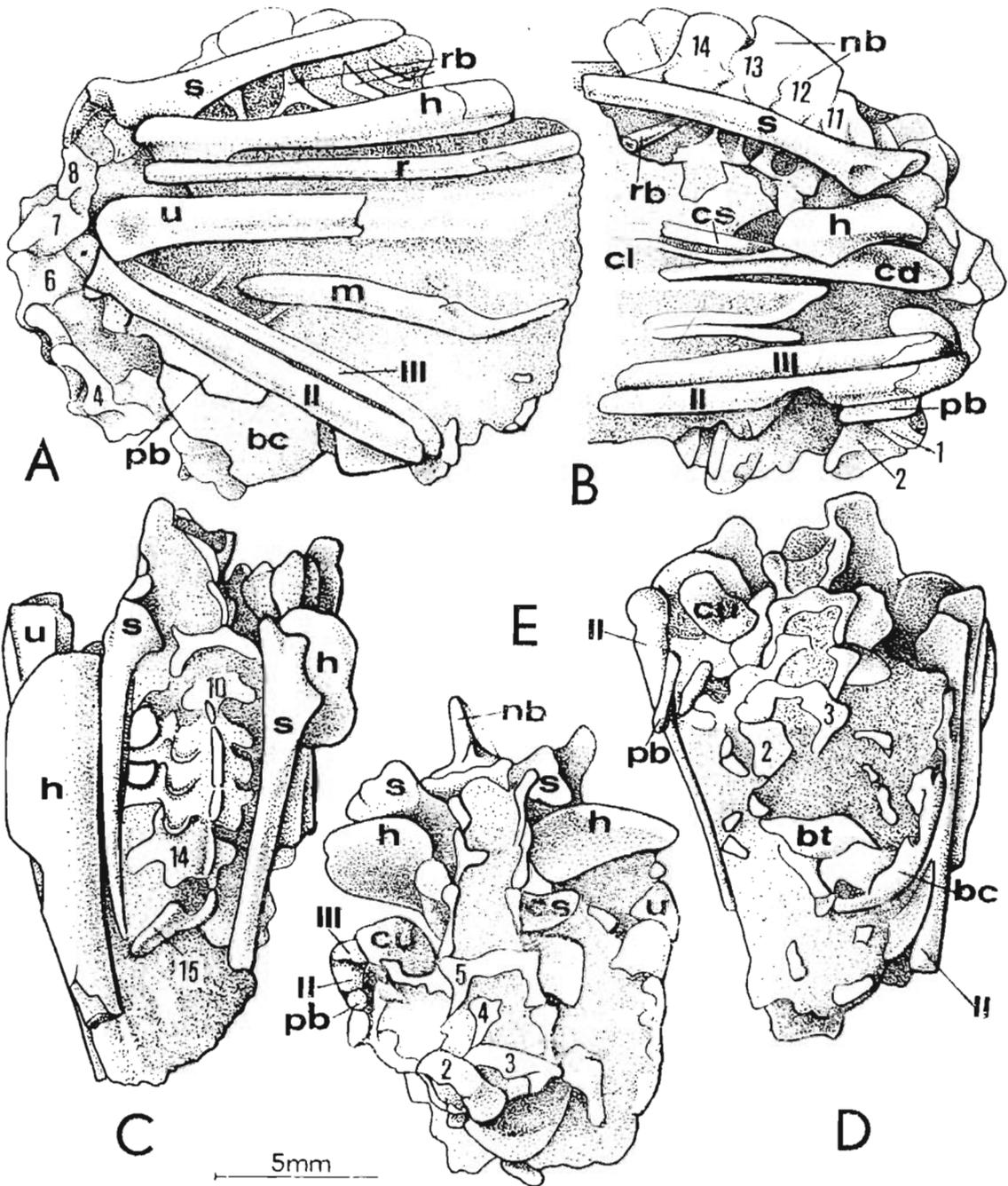


Fig. 1

Embryonic skeleton ZPAL MgR-I/34, *A* — left lateral view, *B* — right lateral view, *C* — dorsal view, *D* — ventral view, *E* — anterior view. Abbreviations: *a* acromion, *bc* roofing bones of the braincase, *bt* ?basitemporal, *ca* coracoid articulation of the scapula, *cd* right coracoid, *ce* external condyle of the ulna, *cl* clavicle, *cs* left coracoid, *cu* ?ulnar carpal, *h* humerus, *ha* hook-shaped process of the acromion, *lg* labrum of the scapular glenoid, *m* mandible, *nb* nuchal blade, *pb* pollex, *r* radius, *rb* rib(s), *s* scapula, *u* ulna, II, III metacarpals II and III, 1–15 tentative numbers of vertebrae.

**ZPAL MgR-I/33** (pls. 42–43, figs. 2, 3). — The total length of the skull is approximated as 20 mm. The premaxilla is damaged anteriorly (fig. 3 A). The nasal process of the premaxilla is 0.9 mm wide and extends well behind the posterior rim of the nasal opening. The maxillary processes of the premaxilla are short, extending no more than 1 mm behind the anterior rim of the nasal opening and seem to overlap the maxilla from the outside. The nasal openings are

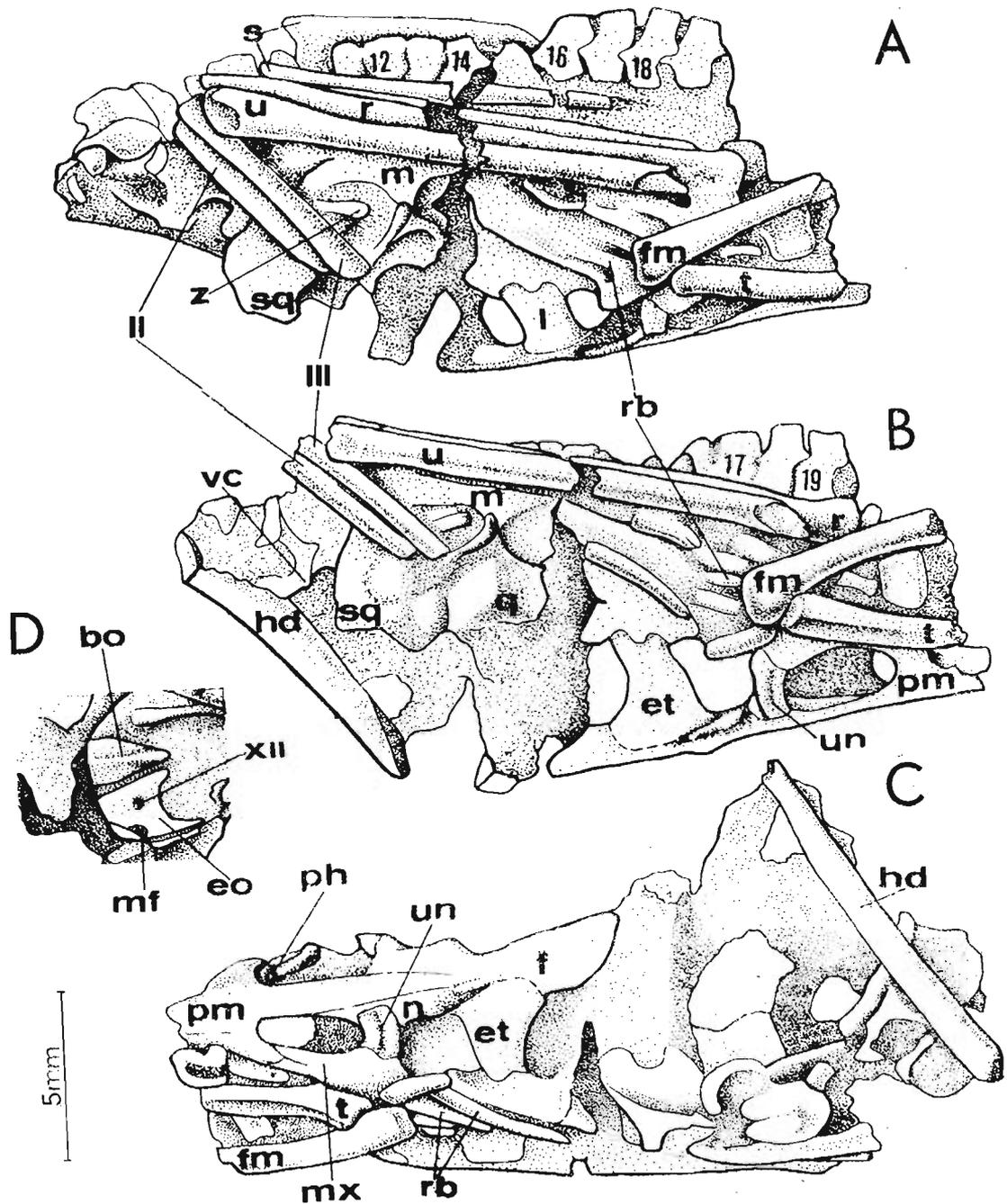


Fig. 2

Embryonic skeleton ZPAL MgR-1/33, *A* — left lateral view, *B* — left ventrolateral view, *C* — ventral view, *D* — occipital region in dorsal (internal) view. Abbreviations: *bo* basioccipital, *eo* exoccipital, *et* ?mesethmoid, *f* frontal, *fm* femur, *hd* right humerus, *hs* left humerus, *m* mandible, *mx* maxilla, *mf* metotic foramen, *n* nasal, *ph* phalanx, *pm* premaxilla, *q* quadrate, *r* radius, *rb* ?ribs, *s* scapulae, *sq* ?squamosal, *t* tibia, *u* ulna, *un* ungual, *vc* cervical vertebra, *z* ?zygomatic process, II, III metacarpals II and III, XII foramen for the hypoglossus, 1–19 tentative numbers of vertebrae.

elongate; the left one is closed posteriorly by what appears to be an ungual appressed on the skull. On the right side, the postnarial region is strongly damaged. Thus, the boundary between the nasal and the antorbital opening remains obscure; it is possibly marked by a slight ventral expansion of the nasal.

The postnarial and antorbital region is damaged and extremely obscured, most probably

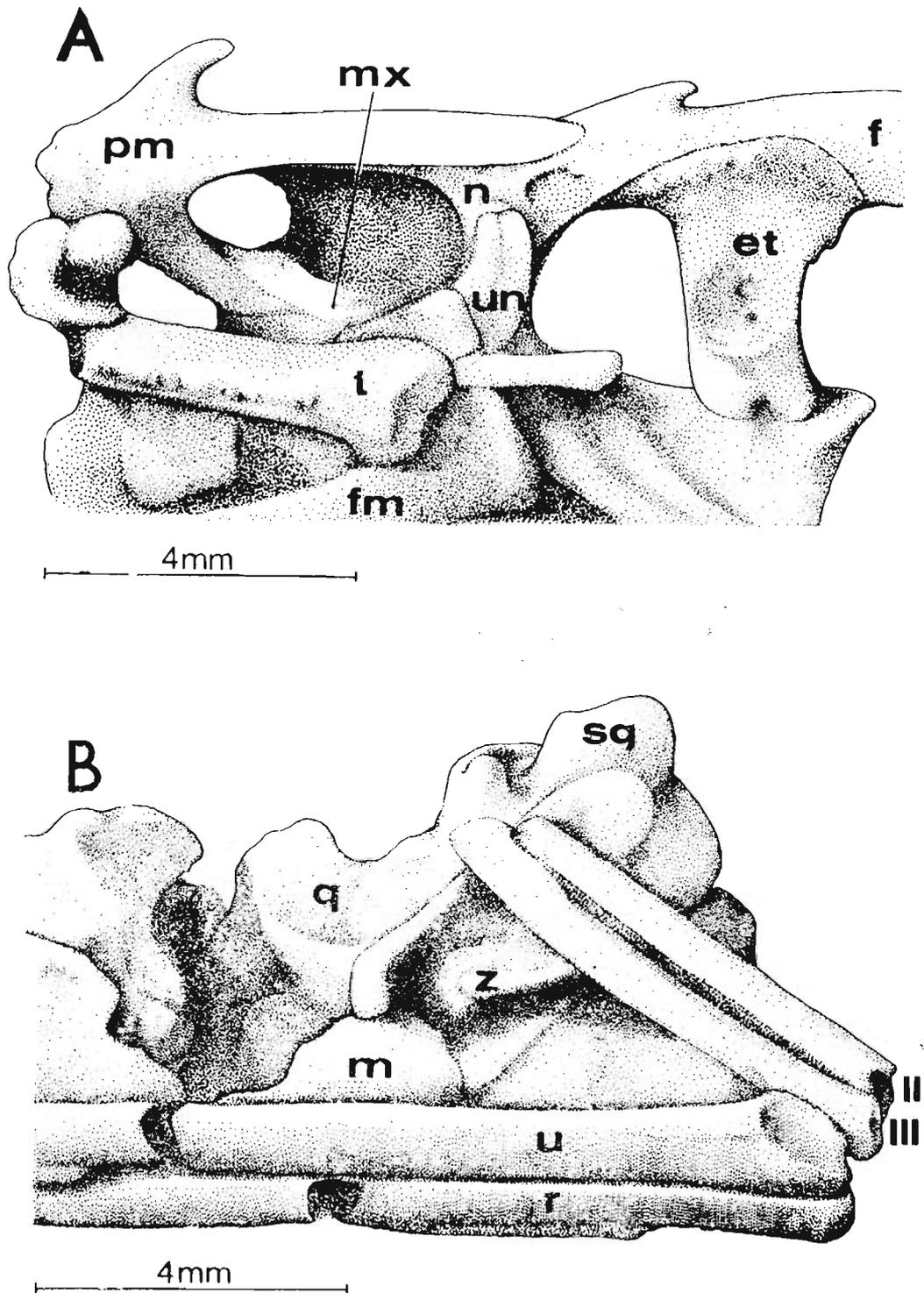


Fig. 3

The cranial fragment of the embryonic skeleton ZPAL MgR-1/33, *A* — rostral part in dorsal view, *B* — posterior part in left lateral view. Abbreviations: see fig. 2.

as the result of dislocation. A wide lacrimal-like plate (fig. 3A, et), supporting the frontal probably represents the mesethmoid dislocated to the left.

The large quadrate is 5.1 mm long or high what equals about one quarter of the total skull length. The ventral mandibular part, about 2 mm wide, remains in articulation with the

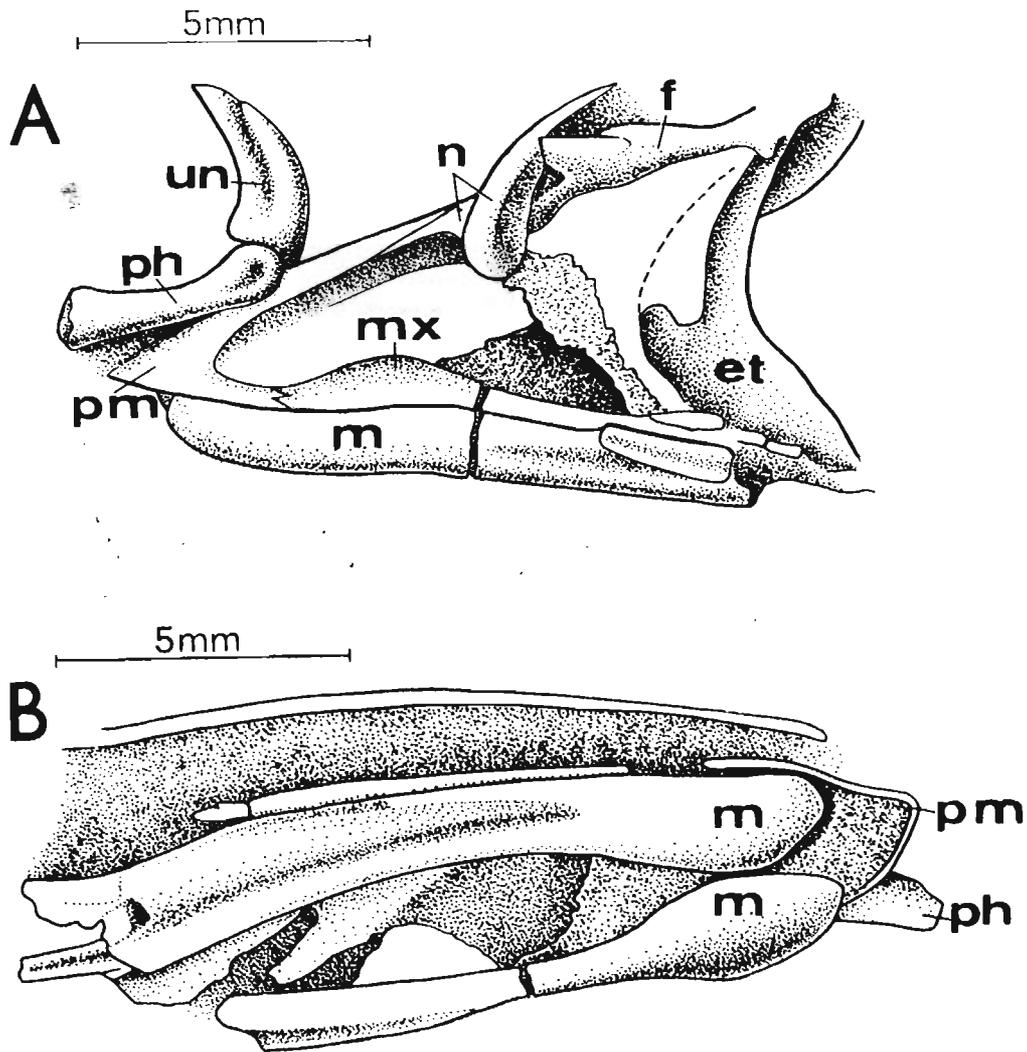


Fig. 4

Fragmentary specimen ZPAL MgR-I/88, with the skull in left lateral (A) and ventral (B) view. Abbreviations: see fig. 2.

mandible. Externally, just above the mandibular articulation, there is a ridge ascending to the otic process. The otic process is partly covered by the left metacarpals and emerges above them, in close connection with a remnant of the braincase which appears to be the squamosal. Medially, the obscure orbital process seems to project in ventralmost position. A rod of bone descending to the level just above the mandibular articulation, is reminiscent of a zygomatic process.

The two occipital bones (fig. 2D) are very distinct in dorsal (internal) view. The basioccipital is symmetrical plate, 1.3 mm wide in the anterior rectangular part and 2 mm long, with a low median ridge. The bone narrows in the posterior triangular part with the margins converging toward the condylar end. On the left side, the basioccipital is adjacent to (but not fused with) the basal part of the exoccipital, perforated by the foramen for the nerve XII medially and the metotic foramen laterally. The posterior margin of the basal part of the exoccipital is concave with two processes projecting from the medial and lateral corners. The medial, rounded process, suggesting a contribution to the occipital condyle, approaches the condylar part of the basioccipital. The posterior margins of the exoccipitals and the condylar part of the basioccipital form the ventral and lateral parts of the rim of the foramen magnum. Laterally, the otic part of the exoccipital extends upwards and seems to be thickened in the dorsal part. Anterior to the otic part of the exoccipital there are poor vestiges of the prootic.

Only a small area of the articular part of the left mandible may be seen. The retroarticular process extends for at least 2 mm. The dorsal margin of the retroarticular part is concave with the posterior end rising upwards.

**ZPAL MgR-I/34** (pl. 43: 2a; fig. 1A, D). — Among the extremely scattered skull bones (fig. 1D), the only complete, symmetrical element is interpreted as the basiparasphenoid (basitemporal plate). The bone (pl. 43: 2a) is very similar, though more bulbous, to the basitemporal of *Stercorarius skua* (MAILLARD 1948). It may be described as having a body with a strongly convex ventral surface, and two lateral, horn-shaped processes having tips spaced ca 4.5 mm and directed somewhat posteriorly. The anterior margin of the body is convex, the posterior margin is concave. The ventral surface of the basiparasphenoid faces mostly anteriorly somewhat ventrally and to the left. Thus, the orientation of the basiparasphenoid would suggest that the skull was crushed in the reversed position, with the ventral side directed externally. A small fragment lies close to the anterior margin of the basiparasphenoid. Possibly, it represents the articular surface of the quadrate with the adjacent remnant of the pterygoid. The basiparasphenoid, with associated pieces, is enclosed by the unidentifiable bones of the braincase.

A fragment of the mandible (fig. 1A) located between the metacarpals and forearm, is 10 mm long and 1.7 mm high. The external side is exposed. It is broken at both extremities, the posterior break appearing to be just anterior to the articulation. The anterior end tapers into a "beak" and is reminiscent of the anterodorsal extremity of the surangular that, in all probability, covered the main part of the external surface of the fragment. No suture could be recognized with certainty, although the surface is not uniform. The bones are apparently fused.

#### VERTEBRAL COLUMN

The minimum number of presacral vertebrae is 19. The last 6 of these are qualified as dorsals on the basis of their narrow span of zygapophyses, wide diapophyses and movable ribs; most posterior dorsal vertebra(e) may be gone along with all the remaining posterior vertebrae which are absent in both skeletons. The first preserved cervical vertebra is hardly identifiable, so the numbering of vertebrae is tentative; 1 or 2 cervical vertebrae may have been lost and the numbers should then be shifted accordingly.

**ZPAL MgR-I/34** (pls. 40 and 43–44; figs. 1 and 5).—15 presacral vertebrae are preserved in their original sequence; there are also two displaced centra.

The atlas and axis could not be identified with certainty and may have been lost. The atlas is possibly represented by a poor remnant located between the pollex and the first cervical vertebra. It shows an U-shaped structure reminiscent of the cranial articulation of the atlas. Thus, the first unquestionable vertebra of the cervical series would represent the axis; its neural spine appears to have projected caudally.

The 3rd, 4th and 5th vertebrae are very similar (pl. 43: 2b; fig. 5J) and typical of the most anterior cervical vertebrae of birds and theropods. The prominent ridge, projecting laterally above the centrum, extends between prezygapophysis and postzygapophysis. The robust anapophyses are in caudalmost position and project behind the articular facet of the postzygapophysis. The best preserved anapophysis of the 3rd vertebra points caudolaterally. The articular facets of the postzygapophyses are oblique anteroposteriorly, i.e. tilted at an angle of 45° to the vertebral axis. The neural spines preserved on the 3rd and 5th vertebrae are in caudal position so that the posterior outline of the neural arch is convex; the neural spine of the 3rd vertebra points caudally.

The 6th vertebra is poorly preserved and similar in general proportions to the preceding cervicals, but has more slender postzygapophyses with the articular facets oriented horizontally.

The 7th and 8th vertebrae have long and slender postzygapophyses. Diapophyses and

parapophyses are present as small tubercles. The neural arches are mostly destroyed. The neurocentral sutures, somewhat arched dorsally, are fairly distinct.

The 9th and 19th vertebrae begin the well preserved interscapular series and are very similar having slender postzygapophyses but shorter than those of the 7th and 8th. The dorsal surface of the neural arches is smooth, with no trace of neural spines. The diapophysis of the 10th cervical has the articular facet for the tuberculum of the cervical rib in the ventral position. The centra of the 9th, 10th as well as this of the 11th vertebra are separated from the arches and remain below in original articulation (fig. 5).

The 11th and 12th vertebrae have transversally oblique zygapophyseal facets i.e. those of zygapophyses look somewhat inwards and those of postzygapophyses — outwards. The facets are tilted at an angle about 40° to the frontal plane. The diapophysis of the 11th vertebra is alike that of the 10th. An elongated convexity or ridge extends from the base of the diapophysis to the posteroventral corner of the neural arch. A quite similar design occurs in the posterior but not posteriormost cervicals of the 5 day chicken. The diapophysis of the 12th vertebra has the costal articulation located much more dorsally and pointing laterally, without ventral inclination. The neural spine of the 11th vertebra is low and narrow in comparison with the following vertebrae. The neural spine of the 12th vertebra is very high (1.3 mm) and long (0.9 mm) extending for the major part of length of the neural arch. The neural spine of the 13th vertebra is still larger being 2.5 mm high in the midlength and 1.1 mm long in the basal part; dorsally it is expanded in both the cranial and caudal direction which makes it much like the fan-shaped neural spine of the last free cervical preceding the notarium in the completely ossified chicken skeleton. The lateral surface of the neural spine of the 13th vertebra is clearly convex, the spine being the thickest in the midlength. The neural spines of the 12th and 13th vertebrae are almost completely fused with the exception of the most basal parts where a small foramen persists. In this way the neural spines of the 12th and 13th vertebrae form the highly projecting *nuchal blade* which is the greatest elevation of the vertebral column, with the dorsal edge strongly arched. The blade is 3 mm long. The postzygapophyses of the 13th vertebra are somewhat less divergent than those of the 12th. The 13th vertebra articulates with the first movable rib. The capitulum extends to the neurocentral suture so that it articulates with both the arch and the centrum. The capitular and tubercular articulations are connected by an elongated elevation or ridge. No such distinct ridge exists on the preceding 12th vertebra while in the 11th vertebra the lateral convexity (mentioned above) is quite different.

The 14th vertebra, recognized as the first dorsal, has the neural spine only slightly expanded dorsally (ventral length — 1.5 mm, dorsal length — 1.75 mm) and somewhat inclined cranialwards; the lateral surface of the spine is flat. The span of postzygapophyses is much smaller than in any preceding vertebra (Table 1) and the diapophysis is larger than that of the 13th.

The centra of the 12th, 13th and 14th vertebrae adhere to each other very closely and may have been initially fused. The centra of the 12th and 13th vertebrae are low and have small hypapophyses; distinct sutures separate them from the arches. The centrum of the 14th vertebra is much higher and has prominent hypapophysis at the anterior end.

The 15th vertebra is represented only by a fragment of the arch with the neural spine similar to that of the 14th.

**ZPAL MgR-I/33** (pl. 42: 2).—Only the interscapular series is preserved in the original order and the number of vertebrae represented in the specimen cannot be established directly. The neural arches appear to be generally preserved without the centra; several loose centra are present among smaller unidentifiable fragments.

The anterior cervicals are fragmented and haphazardly scattered. The only fairly well preserved neural arch has the posterior margin slightly convex, with the neural spine projecting caudally. Thus it represents one of the four anterior cervicals (atlas excepted) of specimen no. 34. Anterior to this vertebra there is an annular structure which may represent the atlas. The

vertebra that precedes the interscapular series has the neural arch mostly destroyed with the right postzygapophysis moderately long. This vertebra has been recognized as the 8th cervical by comparison with specimen no. 34.

Table 2

## Dimensions of the vertebrae (in mm)

No of vertebra	Length of centrum		Span of postzygapophyses	
	ZPAL MgR-I/34	ZPAL MgR-I/33	ZPAL MgR-I/34	ZPAL MgR-I/34
2	—	2.6	—	—
3	—	—	—	2.9
4	1.3	—	—	2.9
5	1.3	—	—	2.9
7	1.7	—	—	—
8	1.7	—	—	—
9	—	—	—	2.9
10	—	2.1	—	—
11	—	—	—	2.5
12	1.3	—	—	2.5
13	1.3	—	—	2.2
14	1.6	1.6	1.6	1.6
17	—	1.6	1.6	—
18	—	1.6	1.6	—

The 9th cervical, locked between the acromions (fig. 2), has fairly slender and widely spaced postzygapophyses. The dorsal surface of the neural arch is convex but without any trace of neural spine. The 10th vertebra is almost completely destroyed. The 11th, 12th and 13th vertebrae have distinct, elongate traces of the broken neural spines. The diapophysis of the 12th vertebra is much more dorsal than that of the 11th. The 13th vertebra remains in articulation with the rib.

The 14th vertebra is clearly intermediate between the cervicals and the dorsals: the postzygapophyses are much closer to the midline than are the prezygapophyses. The diapophysis is large. The neural spine is broken, but must have been prominent, as suggested by the strong basal part.

The 15th to 19th vertebrae are typical dorsals with the postzygapophyses short and narrowly spaced, and strong neural spines. The best preserved neural spine of the 18th vertebra is nearly as high (1.1 mm) as the remaining part of the neural arch. There is no trace of fusion between the neural spines although some of them are broken. Posteriorly the dorsals become more delicate, in particular the postzygapophyses are thinner than the bone of the last dorsals is almost transparent.

## RIBS

No more than three ribs are preserved in natural position. The first preserved rib articulates with the 13th vertebra and may represent the last cervical or false rib. It seems to be thinner than the next, possibly the first dorsal rib. The ventral articulations of the ribs are, as usual, bifurcate.

**ZPAL MgR-I/34** (pls. 43–44; figs. 1 and 5).—The prominent parts of the last cervical and first dorsal rib (fig. 1A, B) articulate on both sides with the 13th and 14th vertebrae. In the last cervical rib, the head is supported by a very slender stem and articulates with the anterior margin of the centrum; the tubercle is not preserved, only the basal part of its stem is present.

**ZPAL MgR-I/33** (pl. 42; fig. 2).—The proximal fragment of the last cervical rib articulates with the 13th vertebra on the right side. The more distal parts of the last cervical and two first dorsal ribs emerge on the left side, laterally to the scapula. Other rib fragments are possibly represented by the bony rods covering the jaw region of the skull.

#### SHOULDER GIRDLE

##### Scapula

In specimen no. 34 the scapulae are evidently better fossilized and considerably thicker (Table 3) than those of specimen no. 33.

**ZPAL MgR-I/34** (pls. 40–41 and 43–44; figs. 1 and 5).—The scapulae are preserved only in their anterior parts. The glenoid is perpendicular to the blade and faces laterally (without the dorsal tilt); posteriorly there is a prominent glenoid labrum. The strong acromion points rostrally and somewhat medially; it has a medioventral, hook-shaped process, (pl. 43: 2c; fig. 5G), pointing posteroventrally, which may have served as the insertion for a part of the ligament (lig. sterno-acromiale FÜRBRINGER 1888) that in modern birds forms the thickest string of the sternocoraco-clavicular membrane and goes to the sternum (pers. obs.). A distinct tubercle for the coracoid articulation is present (pl. 44: 3c–d; fig. 5H).

**ZPAL MgR-I/33** (pl. 42; fig. 2).—Both scapulae are nearly complete (only the right acromion is destroyed). The blades taper gradually backwards to end as quite thin rods of bone.

Table 3

#### Dimensions of the shoulder girdle (in mm) Paranthetic values of fragments

	ZPAL MgR-I/33		ZPAL MgR-I/34	
	left	right	left	right
Shoulder girdle				
Scapula:				
length	11.0	11.0	(10.0+)	(10.0+)
greatest width at the head (at the glenoid labrum)	—	1.4	2.0	2.0
width of the blade (6 mm behind the apex of the acromion)	—	0.6	1.1	1.1
Coracoid:				
length	—	—	(8.5+)	(8.5+)
greatest ventral width	—	—	—	1.7
Clavicle length	—	—	(6.5+)	—

##### Coracoid

**ZPAL MgR-I/34** (pls. 40–41 and 43; fig. 1).—The coracoids are ossified somewhat less than are the scapulae. The dorsal parts of both coracoids are separated from the scapulae and project on either side of the neck. Their horizontal orientation is rather exaggerated,

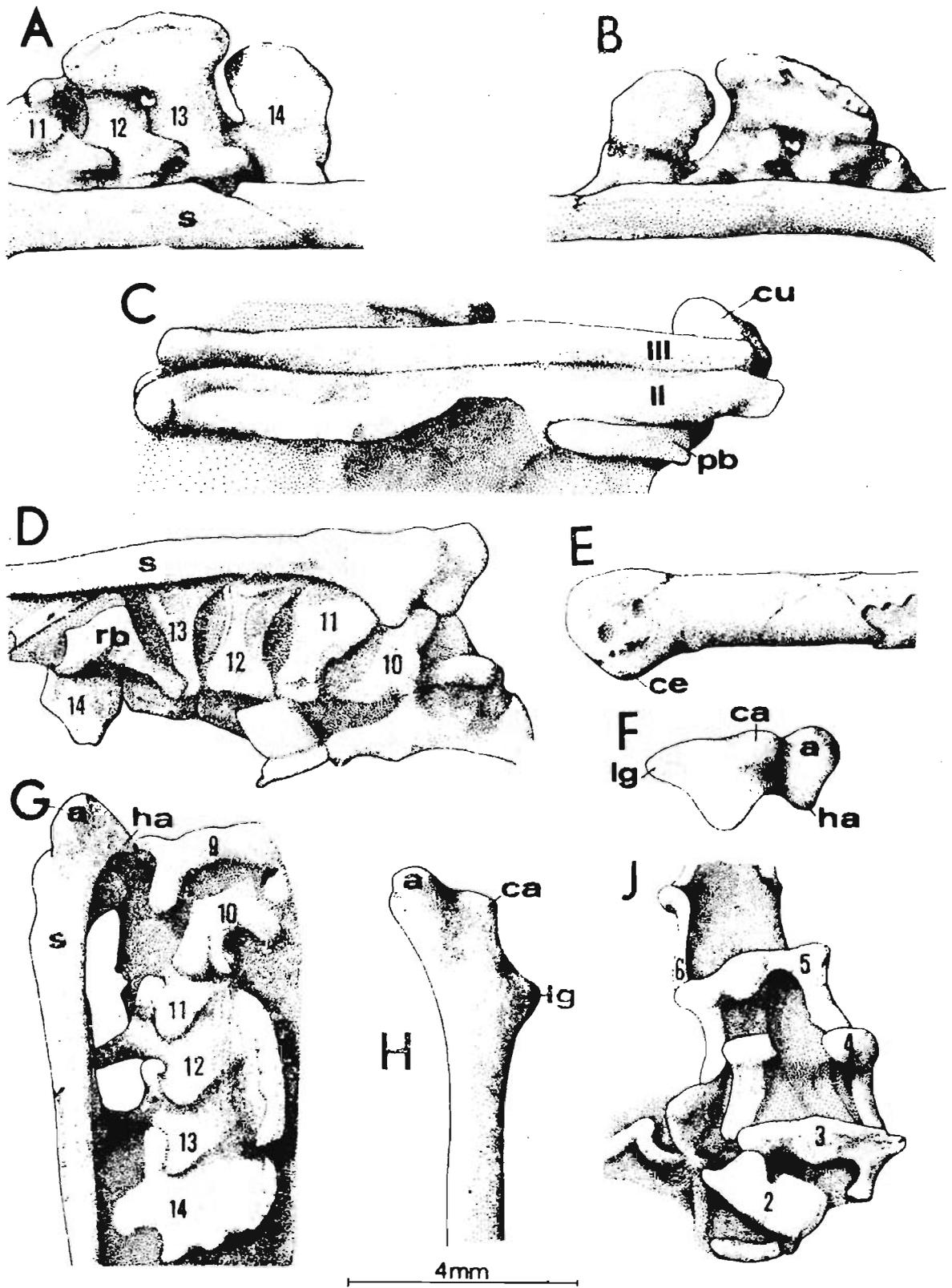


Fig. 5

Fragments of the embryonic skeleton ZPAL MgR-1/34, *A* — left lateral view of the nuchal blade, *B* — right lateral view of the same, *C* — distal bones of the right forelimb in right lateral view, *D* — vertebral column at the boundary between the cervical and dorsal vertebrae in right lateral view, *E* — distal extremity of the ulna in external view, *F* — cranial extremity of the right scapula in anterior view, *G* — the shoulder region with the vertebrae in dorsal view and the left scapula (rotated) in medial view, *H* — right scapula (anterior part) in dorsal (external) view, *J* — anterior cervical vertebrae in dorsal view (anterior view of the specimen). Abbreviations: see fig. 1.

resulting from the compression of the whole skeleton. The acrocoracoidal part (pl. 43: 2d) curves somewhat cranialwards so that the dorsal part of the coracoid is slightly concave anteriorly. There is no trace of the procoracoid process. The head of the right bone must have been post mortem twisted relative to the ventral part, since the glenoid, as preserved, looks inwards rather than outwards.

The remaining part of the left coracoid is hidden inside, beneath the wing bones. On the right side of the specimen the wing bones are mostly gone, and, owing to this, the inner side of the infraglenoid part of the right coracoid may be seen (fig. 1B). The ventral (sternal) end is lacking, the lateral margin is slightly concave and the medial margin is also concave ventrally but becomes convex below the glenoid. The sternocoracoidal fossa is of triangular shape with the dorsal corner extending far towards the glenoid. In the ventral part, the fossa is very deep with the bottom lamina inflated, like a sail, between two prominent marginal ridges, the lateral very thick and the medial much thinner. The bottom lamina is very thin, almost transparent and hardly preserved in several points. Medially, below the glenoid, in place of the supracoracoid foramen, there is a short and deep groove, situated very close and parallel to the medial margin of the coracoid.

**ZPAL MgR-I/33** (pl. 42).—The dorsal part of the right coracoid projects dorsolaterally as a slender rod separated from and anterior to the scapular head. Some remains of the left coracoid may also be present under the left wing and skull bones.

#### **Clavicle (ZPAL MgR-I/34, fig. 1B)**

The bone representing the clavicle originates in all probability from the left side and lies just medially and parallel to the left coracoid, being the most interior among the recorded elements. The ventral part of the bone may be seen in the right lateral view between the coracoids (fig. 1B). It is a brittle, narrow slat of bone, flattened throughout the preserved length. The ventral part is lacking, so that nothing can be said about the possible fusion of the clavicles. The dorsal extremity, which seems to be nearly complete, curves laterally, to the left side of the specimen. This appears to be the usual posterior curvature of the avian clavicle.

### FORELIMB

The forelimb bones are folded in the same way in three specimens: no. 33, no. 34 and no. 91. The humerus, directed caudally, is parallel to the forearm bones which are directed cranially. The humerus, radius and ulna closely adhere to each other in specimens no. 33 and no. 91. The metacarpus remains folded only partially, forming an angle of about 30° with the forearm; in all cases the metacarpus is preserved in this position (both sides of specimen no. 34, left side of no. 33 and no. 91).

The intramembral proportions may be observed directly only in the left forelimb of specimen no. 33. The forearm bones are significantly longer than the humerus; the long metacarpals suggest that the manus is also elongated. The relative length of the phalanges may be then safely expected to be at least that of *Archaeopteryx* and estimated as 0.4 of the length of the humerus; this ratio occurs among the modern poor fliers e.g. in the coot (*Fulica atra*). Thus, the total length of the forelimb skeleton would be 44 mm in the specimen no. 33 and 60 mm in specimen no. 34 assuming the same proportions for both specimens and 18.7 mm as estimated length of the humerus (see below).

#### **Humerus**

**ZPAL MgR-I/34** (pls. 40–41 and 45; figs. 1 and 6).—The proximal part of the left humerus is perfectly preserved with a nearly complete pectoral crest and head touching the posterior labrum of the scapular glenoid. The anconal surface of the bone is tilted dorsally, the palmar

surface overlies the distal part of the radius. The right humerus is represented only by a short proximal fragment including the head which was found in articulation with the coracoid but disarticulated from the scapular glenoid; the head is somewhat damaged and the pectoral crest is ground off.

The head is delimited from the shaft in palmar view by a shallow, transverse depression, which extends almost to the internal margin of the bone. In proximal view, the head is comma-shaped, with the anconal margin strongly convex and the palmar margin concave. The palmar concavity divides the articular surface into two unequal parts: the shorter internal and the longer external surface. The external surface includes what would correspond to the external tuberosity. The pectoral crest is large and robust; it extends for about 6 mm. The crest projects laterally i.e. does not roll up palmarly and the palmar surface of the crest is but slightly concave. This surface shows a small ridge along the margin of the crest, at least in its distal half-length; proximally the ridge becomes thinner and appears to have been ground off. Since the crest is thick, especially in the basal portion, its anconal surface slopes gradually from the shaft, like in the coot, i.e. there is no concavity that occurs when the crest becomes abruptly thinner than the shaft. The most prominent structure of the internal profile of humerus is the internal tuberosity which is roughly conical and has the apex strongly projecting anconally (but without any lateral extension). The tuberosity is separated from the head by a shallow capital groove. Distally to the tuberosity, the humerus has the internal profile evenly concave and the internal edge is rather rounded (transversally) so that the bicipital crest is evidently absent. Both pneumatic fossa and foramen are also missing.

Assuming the relative length of the pectoral crest to be the same as in the specimen no. 33 the total length of the humerus should be estimated as 18.7 mm.

**ZPAL MgR-I/33** (pl. 42; fig. 2).—The left humerus is strongly appressed on the body and scapula, and partly covered by the forearm bones. The anconal surface is directed medially. The distal part of the shaft is slightly curved (convex posteriorly) as usual in birds. The distal articular end is present. The pectoral crest is ground off; the scar allows to approximate its length as 4.5 mm i.e. somewhat less than one third of the total length of the bone.

### Forearm bones

**ZPAL MgR-I/34** (pls. 40–41 and 44; figs. 1 and 5).—The only preserved, distal parts of the forearm bones remain in articulation with one another and with the metacarpals. On the distal extremity of the ulna there is a large external condyle that passes proximally into the bony ridge of the ulnar shaft. A tendinal pit is present on the external surface of the external condyle. The internal condyle, seen in the anterior view of the specimen (the joint is open anteriorly) is rather robust and much shorter. The ulnar shaft is about twice as thick as the radial (Table 4). Assuming the same intramembral proportions as in no. 33, the total length of the ulna may be estimated as 21.5 mm.

**ZPAL MgR-I/33** (p. 42; figs. 2 and 4).—The proximal articular ends of both radius and ulna were originally present. The radial capitulum still articulates with the humerus while the proximal end of the ulna is damaged. The distal epiphyses of both radius and ulna are missing.

### Carpals (ZPAL MgR-I/34)

The apparent fusion at the proximal end of the left metacarpals is possibly due to the coalescence of the distal carpals.

A robust, bipartite element, attached to the proximal end of right metacarpals III (fig. 1 D, E and 5 C), reveals a detailed similarity to the avian ulnare, including the flattened surface for the ulnar articulation. Yet it appears to be disproportionately large, having the following dimensions (in mm):

Maximal span between the "arms", including their thickness 1.9.  
Length from the apex of the bone to the end of either arm 2.1.

Table 4  
Dimensions of the forelimb skeleton (in mm)  
Paranthetic values are of fragments

	ZPAL MgR-I/33		ZPAL MgR-I/34		ZPAL MgR-I/91
	left	right	left	right	
Total length	44 est.		60 est.		—
Humerus:			18.7 est.		
length	14.0	(11.0+)	(11.5+)	(5.0+)	—
length of the pectoral crest	ca 4.5	—	ca 6.0	—	—
greatest proximal width (including the pectoral crest)	—	—	3.8	—	—
least diameter of the shaft	1.0	1.0	1.3	—	ca 1.2
Radius:					
length	15.9	—	(11.5+)	—	—
least diameter of the shaft	0.5	—	0.7	—	0.7
Ulna:			21.5 est.		
length	16.1	—	(13.5+)	—	—
least diameter of the shaft	1.0	—	1.4	—	1.3
Metacarpal II:					
length	(7.0+)	—	11.1	11.1	—
width of the shaft	0.7	—	1.2	1.2	0.9
Metacarpal III:					
length	7.5(?+)	—	11.8	(10.0+)	—
width of the shaft	0.7	—	1.25	1.25	0.75
Basal phalanx of the pollex:					
length	—	—	ca 2.6	ca 2.6	—
width at the mid-length	—	—	0.6	0.6	—
Terminal phalanx of the pollex					
length	—	—	ca 1.3	—	—
basal width	—	—	ca 0.8	—	—

### Metacarpals

There are clearly two well developed, nearly equally sized metacarpals. They are free (not fused) but remain in close contact. Certainly they represent metacarpals II and III of the avian hand. Both are flat-shaped, having the external surfaces flattened. Metacarpal II is oriented in the wing plane while metacarpal III is inclined so that the posterior margin is much more internal than the anterior margin.

**ZPAL MgR-I/34** (pls. 40–41 and 44; figs. 1 and 5).—The metacarpals adhere to one another over their entire length with no intermetacarpal space (fig. 1). Nothing can be determined about the morphology of the proximal articular end which are damaged on the right side. On the left side they are covered by a conglomerate of what appears to include some distal carpals elements, possibly not completely ossified at the time of death. The anterior margin of metacarpal II, both left and right, is proximally excavated, exactly where metacarpal I can be expected to have been present. In the distal part, the posterior margin of metacarpal II forms a flange overlapped by metacarpal III. Since this flange extends to the distal end of metacarpal II, the articular facet for digit II is triangular. The tuberosity of metacarpal II is marked by a smooth but distinct elevation.

Metacarpal III is perpendicular to metacarpal II. The posterior surface of metacarpal III is about twice the width of the external surface. The distal part tapers toward the facet for digit III.

**ZPAL MgR-I/33** (pls. 42–43; figs. 2 and 3).—The metacarpals are represented by bare shafts, with no traces of articular parts. Metacarpal II is straight, metacarpal III is gently arched (concave anteriorly). Thus the metacarpals contact each other only at their extremities and enclose the intermetacarpal space.

#### Digits (ZPAL MgR-I/34)

The pollex (pls. 40–41; figs. 1A, B and 5C) on both sides of the specimen is just anterior and adjacent to metacarpal II. The proximal extremity of the pollex is 1.6 mm distal to the proximal end of metacarpal II, leaving the space for metacarpal I. The two phalanges, basal and terminal, are preserved on the left side (indicated as one piece, *pb*, in fig. 1A).

### HINDLIMB

The length of epipodium (tibia or tibiotarsus) is approximately the same as the total length of autopodium because the distal phalanges (unguals) of the flexed foot remain at the level of the knee joint in specimen no. 33. The same can be inferred for specimen no. 88 where the distal phalanges, including the unguis, are situated in the same region of the nasal opening. It follows therefore that the metapodium metatarsus (or tarsometatarsus) is significantly (by the total length of the phalanges) shorter than the epipodium.

#### Femur and tibia (ZPAL MgR-I/33)

The leg bones are preserved only on the left side of the specimen no. 33 (pls. 42, 43; figs. 2 and 3).

The femur is represented by the major distal fragment which remains in the protracted position. The anterior profile of the bone is convex, the posterior concave; there is no trace of the rotular groove.

The tibia is represented by the proximal fragment which is but a little displaced relative to the femur and remains in the flexed position. The most proximal portion of the tibial shaft is convex anteriorly, slightly concave posteriorly and appears to be swollen. A small tuberosity is present in place of the outer cnemial crest. The fibular crest, beginning 1.2–1.3 mm below the proximal end of the tibia, is prominent and 2.5 mm long.

Dimensions of the leg bones (in mm):

Femur (distal fragment):	
length . . . . .	(6.5+)
greatest diameter . . . . .	1.5
least diameter . . . . .	1.0
Tibia (proximal fragment):	
length . . . . .	(5.0+)
greatest diameter . . . . .	1.4
least diameter . . . . .	0.8

#### Phalanges

The unguis, as preserved in specimens no. 33, no. 88 and no. 90, are moderately curved, and have shallow but distinct lateral sulci (pl. 45:2; fig. 4A); there are no flexor tubercles. In two specimens, no. 33 and no. 88, the unguis show the same embryonic position having the plantar side directed to the rostral end of the skull; i.e. to the caudal end of the embryo.

**ZPAL MgR-I/33** (pl. 43; fig. 3).—There are at least two obscure fragments of the phalanges. One is the unguis which constitutes the apparent bony bar between the nasal and the antorbital opening on the left side, the other phalanx entered the right nasal opening.

**ZPAL MgR-I/88** (pl. 41; fig. 4).—There are two phalanges remaining in articulation: the unguis and the penultimate phalanx, the former adhering by its dorsal side to the premaxilla.

Dimensions of the phalanges (in mm, based on specimens no. 88 and no. 90):

The penultimate phalanx: length . . . . .	3.6
width at the extremities . . . . .	1.0
least width at mid-length . . . . .	0.7
The unguis phalanx: length . . . . .	3.3
basal height . . . . .	1.3

## DISCUSSION

### PHYLOGENETIC POSITION

Both in the skull and the postcranial skeleton of the described specimens there are many avian features i.e. the characters shared with the Neornithes. These features are:

(1) High number of cervical vertebrae i.e. at least 13. In the theropods this number does not exceed 10 (OSTROM 1976*b*); in *Archaeopteryx* there are 9 cervicals (WELLNHOFER 1974).

(2) Scapula long, slender (Table 3) and tapering posteriorly. In specimen no. 33 the length/breadth ratio at the midlength of the bone is 18; in *Archaeopteryx* the scapula does not taper posteriorly and the ratio averages 12 (based on data from WELLNHOFER 1974); in the theropods the scapulae generally widen posteriorly and the ratio for *Deinonychus antirrhopus* is 9 (OSTROM 1969), for *Gallinimus bullatus* — 8.4 (OSMÓLSKA *et al.* 1972). The main function of the scapular blade is to provide insertion for the muscles holding the chest during flight (mm. serrati and mm. rhomboidei) and the scapulohumeralis posterior that may be important for the recovery stroke (SY 1936). The scapula is said to be longer in good fliers (STRESEMANN 1927–1934) e.g. in the swift (GADOW and SELENKA 1891) though the functional meaning of this correlation remains unclear.

(3) Coracoid long, slender and tapering in the midlength. In the theropods and *Archaeopteryx* the coracoids are plate-like (see OSTROM 1976*b*: fig. 14). The elongation of the coracoid can be possibly explained by the upward shift of the shoulder joint, above the center of gravity of the body, and the backward shift of the sternum with the associated bulk of pectoral muscles and internal organs.

(4) Forelimb skeleton very long, with (5) the forearm longer than the humerus and the metacarpus longer than half length of the humerus. The forelimb skeleton is more than twice as long as the thorax (glenoideum — acetabulum), the ratio based on the estimates for no. 33 being 2.2. This value falls well in the range of adult flying carinates and approaches that of *Archaeopteryx* (2.3 — see WELLNHOFER 1974). The forelimbs of the fossil embryos are then significantly longer than those of *Deinonychus antirrhopus* which has the longest forelimbs among the theropods yet the forelimb/thorax ratio amounts scarcely to 1.4 (based on BAKER'S skeletal reconstruction, in OSTROM 1969). The intramembral proportions found in the fossil embryos (Tables 5–6), are comparable with the modern advanced fliers (BÖKER 1927) and *Ichthyornis* (MARSH 1881) but do not occur in the theropods, including *Deinonychus*, nor in *Archaeopteryx* although in the latter the metacarpal II approaches the half of the humerus length (Table 5). Among modern vertebrates, flight is the only function known to require a comparable elongation of the forelimb mostly by means of increase of the length of distal parts.

In modern birds the relative length of the forelimb most often increases (KRAMER 1953) and the intramembral proportions commonly change postembryonally (MARPLES 1930). These changes are however not likely to have been significant in the further development of the described embryos since the forelimb was certainly working soon after hatching as implied by the strongly ossified skeleton. In the megapodes which are extremely precocial, both the relative

length of the wing skeleton and the intramembral proportions differ very little between hatching and adult stage (SUTTER and CORNAZ 1965, MASCHLANKA 1972), the postembryonal changes of the intramembral proportions being also minute in other galliform birds. Both in the malee fowl (*Leipoa ocellata*) and the chicken the relative lengths of humerus and ulna increase and, by the same, that of the manus decreases yet the changes do not exceed 4% of the total length of the wing skeleton (MASCHLANKA 1972).

(6) Internal tuberosity of the humerus prominent and roughly conical, with the apex pointing anconally and separated from the head by the capital groove; in theropods the internal tuberosity is elongated rather than conical; in *Archaeopteryx* there is no internal tuberosity. This structure gives the insertion site for the coracobrachialis and subcoracoscapularis muscles and may be related to the ability of folding the wing (OSTROM 1976a).

Table 5

Comparison of the length ratio  
humerus/ulna/metacarpal II

<i>Compsognathus longipes</i>	1 : 0.73 : 0.36	OSTROM 1978
<i>Deinonychus antirrhopus</i>	1 : 0.81 : 0.40	OSTROM 1969
<i>Gallinimus bullatus</i>	1 : 0.71 : 0.21	OSMÓLSKA <i>et al.</i> 1972
<i>Archaeopteryx lithographica</i>		WELLNHOFER 1974
Eichstätt specimen	1 : 0.88 : 0.43	
Berlin specimen	1 : 0.87 : 0.44	
London specimen	1 : 0.90 : 0.46	
ZPAL MgR-I/33	1 : 1.15 : 0.54	this paper
<i>Vanellus vanellus</i>	1 : 1.14 : 0.60	own data
<i>Leipoa ocellata</i> (chick 1 day old)	1 : 1.04 : 0.63	MASCHLANKA 1972

Table 6

Comparison of the length ratio arm/forearm in ZPAL MgR-I/33 and modern precocial carinates

Species or specimen	Stage	Humerus Ulna	Source
<i>Fulica atra</i>	at hatching	1.32	BÖKER 1927
	adult	1.20	
<i>Gallus domesticus</i>	at hatching	1.11	own data
	adult	1.06	
<i>Stercorarius skua</i>	at hatching	1.10	MAILLARD 1948
	adult	1.06	
<i>Anas platyrhynchos</i>	at hatching	1.07	BÖKER 1927
	adult	1.21	
<i>Uria troille</i>	at hatching	1.06	BÖKER 1927
	adult	1.30	
<i>Vanellus vanellus</i>	at hatching	0.97	GRAUL 1907
	adult	0.86	
<i>Leipoa ocellata</i>	at hatching	0.97	CLARK 1964
ZPAL MgR-I/33	advanced embryo	0.88	this paper

(7) Ulna twice as thick as the radius (Table 4). Both in the theropods and *Archaeopteryx* the ulna is thicker, but in neither of them the difference approaches half the breadth of the ulna. In modern birds this difference is obviously related to the function of support for the secondary flight feathers.

(8) Unpaired premaxilla having the maxillary processes possibly fused with the maxilla (suture is not marked). In *Archaeopteryx* the premaxilla appears to be paired and separated from the maxilla by a distinct suture (WELLNHOFER 1974).

(9) Large nasal opening that reduces the maxilla to the narrow bar. In *Archaeopteryx* the lateral surface of the maxilla is also narrow.

(10) Long nasal processes of the premaxilla overlapping the major part of the nasal which occurs on the surface only laterally. In *Archaeopteryx* the nasal processes of the premaxillae are very slender between the nasal openings but the nasals are exposed in the midline of the skull (see WELLNHOFER 1974: fig. 6).

(11) Toothless jaws, forming a robust beak. This character emphasizes the avian appearance of the skull, the lack of teeth representing an advanced character among birds, although the toothless beak also occurs among the cretaceous coelurosaurs.

Beside the avian characters, the described specimens show some features reminiscent of the theropods and *Archaeopteryx* rather than modern birds (*Neornithes*). These features which appear to be primitive are:

— The humeral head is truncate, not separated from the external tuberosity and convex-concave in the proximal view, the articular surface being bipartite with the external part extending onto the external tuberosity (fig. 6). Both the pneumatic (or anconal) fossa and the pneumatic foramen are missing and there is no lateral extension of the internal tuberosity (crus laterale tuberculi medialis, see FÜRBRINGER 1888). All these characters are perfectly consistent with the morphology of the humerus of *Gallinimus bullatus* (see OSMÓLSKA *et al* 1972).

— The glenoid surface is perpendicular to the external surface of the scapula.

— The quadrate is unusually large, its length equalling about one quarter of the skull length.

— The metacarpals are separated (possibly a juvenile character, see below).

The only closer relation, revealed by the embryos, is to *Wyleyia valdensis* described by HARRISON and WALKER (1973) on the basis of a single humerus from the Weald Clay (Lower Cretaceous, ?Barremian) of England. The positive characters, shared by the humeri of specimen no. 34 and *Wyleyia* (see fig. 6) are:

— The pectoral crest is long and equals about 1/3 of the total length of the humerus.

— The pectoral crest projects far laterally, being hardly deflected on the palmar surface which is only slightly concave.

— The pectoral crest has a small marginal ridge on the palmar surface at least distally.

— The pectoral crest has the distal profile curving rather abruptly to the shaft at an angle of about 45°.

— The humeral head is truncate and not separated from the external tuberosity.

— The humeral head is convex-concave in proximal view with the articular surface bipartite and clearly asymmetrical (see fig. 6).

— The internal profile of the proximal end of the bone is evenly concave without the projection of the bicipital crest.

There are also important differences between the embryonal humerus of the specimen no. 34 and that of *Wyleyia*. In contrast to *Wyleyia*, the anconal surface of the pectoral crest is flat (not concave) and the angle formed by the crest with the proximal margin of the head is lesser than that of *Wyleyia*. All these differences may be exaggerated since *Wyleyia* and specimen no. 34 in all probability represent different stages.

Two of the characters showed in common with *Wyleyia* are also shared with *Ichthyornis*. These are: the pectoral crest projecting laterally and the internal profile of the proximal end of humeral shaft evenly concave, without bicipital crest (MARSH 1880, HARRISON 1973, see also HARRISON and WALKER 1973). The lack of bicipital crest is certainly primitive but the lateral projection of the pectoral crest should be considered as an aberrant feature if *Archaeopteryx* is ancestral to birds. In modern birds these two characters never occur jointly. The least

palmar deflection of the pectoral crest occurs in the *Falconiformes* (see also FÜRBRINGER 1888) and the bicipital crest may be hardly marked or absent<sup>1</sup> in some other carinates (FÜRBRINGER 1888) including tinamous (fig. 6C).

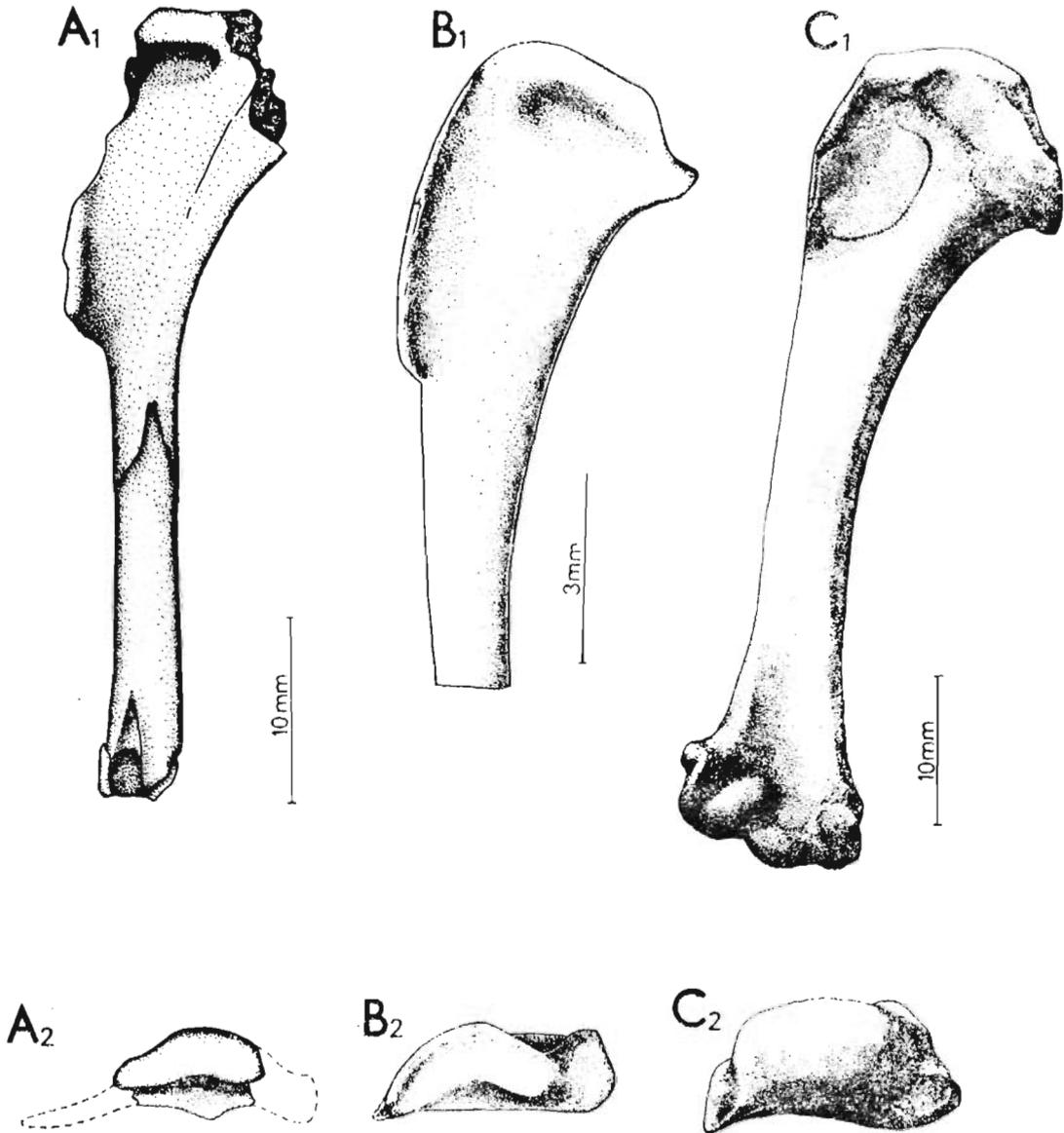


Fig. 6

Comparison of the right humeri in palmar (1) and proximal (2) view, A — *Wyleyia valdensis* from HARRISON and WALKER (1973), B — embryonic skeleton ZPAL MgR-1/34, C — *Crypturellus undulatus*. Not to scale.

The described embryos are in all probability closely related to birds. This conclusion appears to be well substantiated by the preserved avian features in both the postcranial skeleton and the skull. These two sets of characters seem to be largely independent of each other. This fact increases their value in phylogenetic argument. Similarity to *Wyleyia* gives an additional evidence of the avian affinities of the embryos.

<sup>1</sup> HARRISON (1973) stated that the bicipital crest is never wholly absent in modern birds. There is however some discrepancy as to what should be considered as a part of the internal tuberosity or the proximal part of the bicipital crest. The bicipital crest of *Ichthyornis* is said to be absent by HARRISON (1973) yet referred to as present by HARRISON and WALKER (1973).

In the framework of the present classification, the boundary between birds and their ancestors is determined by flight adaptations or anatomical features thought to represent them. This principle is implied in the allocation of *Archaeopteryx* which would never be recognized as bird without feather imprints. In the skeletal morphology the described embryos are certainly more avian than *Archaeopteryx* and, in any case, if their forelimb represents the wing, they should be assigned to birds.

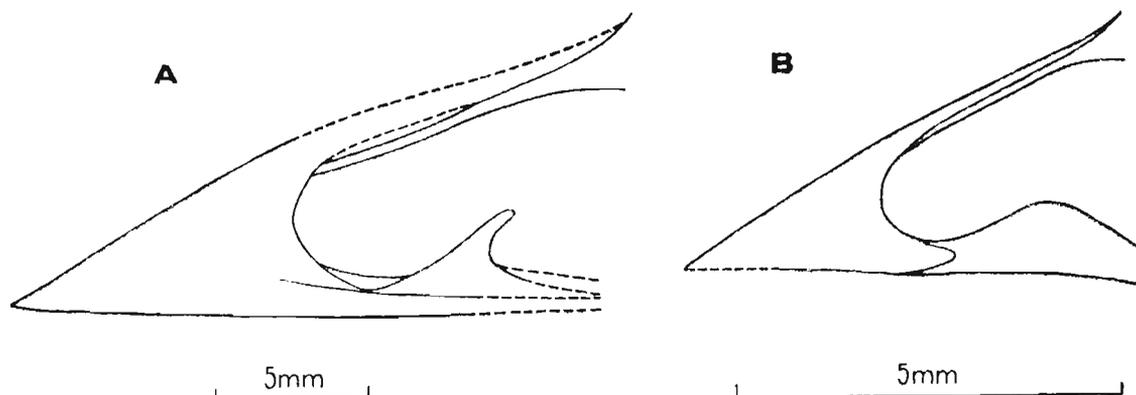


Fig. 7

Rostral parts of the skull, *A* — *Gobipteryx minuta*, adult, as previously restored by the author (ELŻANOWSKI 1076), *B* — outline restoration of the embryonic skull, based on two specimens: ZPAL MgR-1/88 and ZPAL MgR-1/33. Not to scale.

The embryonic skulls closely resemble the skull of *Gobipteryx* as restored previously by the author (ELŻANOWSKI 1976, 1977). The common features are:

- Straight culmen rises at the angle of  $30^\circ$  which brings about the similarity of general proportions.
- Anterior margin of the nasal opening is largely rounded.
- The beak is short and wide.
- The mandible has a distinct retroarticular process.
- Premaxilla overlaps the nasal throughout the length of the latter.
- The length of the quadrate equals about  $1/4$  of the skull length.

The latter three similarities are rather general yet constitute a peculiar combination of characters, which appears to be unknown in any other form. The only relevant difference is the lack of distinct ascending process of the maxilla in the embryonic skulls, although in specimen no. 88 (the better ossified one) the maxilla is arched dorsally and the remaining part of the process may have been unossified. The allocation of the embryos to *Gobipteryx* seems to be corroborated by size comparison. The skull of *Gobipteryx* is about twice as long as that of specimen no. 33. This is the ratio found in comparisons of adult skulls with those of hatching stages of the birds that have the beak growing isometrically relative to the braincase, as is the case with the short-billed species among shorebirds studied by SCHIESS (1963). This ratio also occurs in the chicken (pers. obs.). All in all it seems most probable that the described embryonic skeletons belong to *Gobipteryx minuta*, which originates from the same formation.

#### EMBRYONIC CHARACTERS AND DEVELOPMENT

The animals represented by the described specimens certainly died before hatching. This is revealed by the adherence of bones to the inner side of the egg-shells (specimens no. 33, no. 34, no. 88 and no. 91) as well as the rolled-up position of skeletons no. 33 and no. 34. This position must have also occurred in no. 88, where the anterior part of the skull is associated with the pes, and in no. 91 where the posterior fragment of the skull adheres to the wing bones.

The specimens show a set of characters that result from the ossification pattern known in modern birds. These characters are:

(1) Basioccipital is separated from the exoccipital (no. 33). In the skua (*Stercorarius skua*) these bones remain separated until the 19th day after hatching (MAILLARD 1948).

(2) Otic process of the quadrate is well ossified while the orbital process appears to have been ossified only in the basal part (no. 33). In the studied modern birds, the orbital process ossifies postembryonally (SCHINZ and ZANGERL 1937, MAILLARD 1948).

(3) Neural arches are separated from the centra (no. 33 and no. 89) or neurocentral sutures are present (no. 34).

(4) Some epiphyses of the long bones are absent, especially the distal ones. Specimen no. 33 lacks the epiphyses on both extremities of the metacarpals and the distal epiphyses of the forearm bones, while in no. 34 only the metacarpal epiphyses appear to be incomplete.

(5) Metacarpal I is lacking while the metacarpals II and III as well as the pollex are present (no. 34). The small avian metacarpal I ossifies postembryonally while the well developed bony metacarpals II and III, and the ossification center of the pollex are present at hatching (SCHINZ and ZANGERL 1937, MAILLARD 1948).

(6) The mandibles are free (no. 88). In modern birds the time of symphysis formation is variable. In the chicken the anterior ossification centers of the dentary are partially fused across the midline almost from the moment of their first appearance (JOLLIE 1957). In the blackheaded gull (*Larus ridibundus*), incubating 22–24 days, the formation of symphysis begins on the 15th (SCHUMACHER and WOLF 1967) or 19th day (SCHUMACHER *et al.* 1972). In the duck, incubating 28 days, the mandibles fuse on the 22nd day (KOWALSKA 1973). In the nestling shoebill (*Balaeniceps rex*) the symphysis is still very weak (BÖHM 1930). In the lapwing (*Vanellus vanellus*) the dentary is said to become unpaired in the adult (GRAUL 1907).

Many other features of the described specimens may be or surely are embryonic or juvenile, yet this cannot be established with certainty since the adult structure must have been rather unique and remains unknown except for those parts of the skull which are described in *Gobipteryx*. The possibly embryonic features are:

(7) The coracoid has neither glenoid labrum nor distinct scapular articulation. The bone is similar to the coracoid of the one week-old chicken and appears to be unfinished. In the chicken, however, there is a distinct bony extension of the glenoid surface, in spite of the great contribution of cartilage.

(8) The metacarpals II and III are unfused. Other flight adaptations and close adherence with some overlapping suggest that subsequent fusion may have occurred soon after hatching.

(9) The sternum is lacking or represented by a small unidentifiable fragment. In modern birds the sternum ossifies mainly after hatching and the ossification proceeds slowly. In the chicken, the sternal centers of ossification appear in the 17th–19th day of incubation and the bone is finished 3 months after hatching (HAMILTON 1952). In the skua (MAILLARD 1948), crested grebe and pigeon (SCHINZ and ZANGERL 1937) ossification begins after hatching. In the 17 days king rail (*Rallus elegans*) the entire sternum is still cartilaginous and does not begin to ossify until 47 days posthatching (OLSON 1973). In the adult animals which developed from the described embryos, the sternum most probably had been extensively ossified to serve as the insertion structure for the muscles of a powerful forelimb.

(10) The proximal end of the tibia is swollen and clearly convex anteriorly. The shape is different from the adult condition and similar to that found in the one week chicken (pers. obs.) before the fusion of the bony epiphysis (see also HAINES 1942). A similar shape of the tibia was described by SHUFELDT (1886) in a young specimen of *Geococcyx californicus*.

The preservation of bones in skeletons no. 33 and no. 34 has been clearly selective (Table 1) which is the cause of the general similarity of the two specimens. Such differential preservation is easy to explain by the time and rate of ossification as well as the spacing of the bones. The most susceptible to destruction are those parts which are little ossified and most exposed exter-

nally. This applies to the skull which probably had been much delayed in ossification as compared with the shoulders, since skull ossification is largely independent of the mode of development (DANIEL 1957, ROGULSKA 1962) i.e. there is no correlation with the rate of development of the locomotory apparatus. Among the skull bones, most exposed are the soft laminae of the braincase roof (frontals and parietals) separated by large fontanellae; the jaws and the basicranial bones have a greater chance for preservation since the former are better ossified and the latter are anchored on the postcranial skeleton.

The major part of the cervical region (except for the posteriormost vertebrae) is devoided of any shelter and the cervical vertebrae, although well ossified at hatching, are extremely scattered (no. 33) or badly damaged (no. 34). Best sheltered is the shoulder region: the folded and well ossified parts of the forelimb support each other and cover the shoulder girdle, ribs and dorsal part of the vertebral column. The vertebral column ossifies anteroposteriorly at least in the precocial or semi-precocial birds studied by SCHINZ and ZANGERL (1937) and MAILLARD (1948). The sacral vertebrae, must have been less ossified than the cervicals and dorsals, still separated from the ilium and unable to give sufficient support for the pelvic girdle. Moreover, the pelvic bones fuse very late, well after hatching, and the acetabulum remains cartilaginous for a long time. The hindlimb is therefore held rather weakly. Being one of the most exposed parts of the embryo, the leg is gone along with the pelvis, except for the left side of no. 33 where fragments of the femur and tibia joined the skull.

Skeleton no. 34 is clearly better ossified and the embryo was certainly more advanced than no. 33. The diameters of long bones (Table 4) are significantly greater in the former. The same applies to the scapula that is twice as wide in no. 34 and the coracoid that is very stout in no. 34 and represented by a rather thin rod of bone in no. 33. The distal epiphyses of the forearm bones were completely ossified, and those of metacarpals at least partially in no. 34 while none of them is present in no. 33. The vertebral centra are present (perhaps with a few exceptions) throughout the preserved series in no. 34 while in no. 33 they seem to be absent in the thoracic vertebrae and scattered independently of the arches in the cervical region.

Comparison with the embryos of modern birds shows that the described fossils represent late stages of development and neither reveals any detail that would suggest death occurred significantly earlier than the hatching stage although this was probably the case with less advanced no. 33. To the contrary, the forelimb bones and the neural arches of the vertebrae in the shoulder region are much more developed than in known examples of the hatching stages in precocial birds such as the chicken (SCHINZ and ZANGERL 1937) or the skua (MAILLARD 1948). The one week chicken has all the epiphyses still cartilaginous, no trace of the external condyle of the ulna, the pectoral crest clearly incomplete and the internal tuberosity only slightly marked by a low ridge; the humeral head is mostly cartilaginous. In contrast, the less ossified skeleton no. 33 has the epiphyses of the humerus and at least the proximal epiphyses of the forearm bones well ossified. The forelimb skeleton of the more ossified skeleton (no. 34) must have differed little from the adult condition with the distal end of the ulna complete and the metacarpal epiphyses ossified at least partially; the humerus as preserved, appears to be finished.

The forelimbs of the described specimens are longer than in most modern carinates at hatching stage. The forelimb skeleton of the less advanced embryo (no. 33) estimated to be at least 44 mm long (Table 4) well compares to the 48.5 mm long wing skeleton of one day chick of the lapwing (*Vanellus vanellus*) (GRAUL 1907). The forelimb skeleton of the more advanced embryo no. 34 is evidently longer (Table 4) than that of the lapwing chick while the fossil embryo must have been significantly lighter. The combined length of the forearm and hand of no. 33 may be safely estimated as 30 mm while skull length (dorsosagittal) is estimated as 21 mm. Thus the distal parts of the forelimb skeleton are significantly longer than the head<sup>2</sup> (fig. 8).

<sup>2</sup> The head has been measured by SCHIESS (1963) together with the rhamphotheca. This influences the present comparisons very little since only greater differences in length are considered.

This is exceptional among birds and described only in two cases by SCHIESS (1963): in the megapodes and the little tern.

Contrary to all other birds the hatching megapodes have the wing at the same level of development as the leg i.e. the length of the wing skeleton as related to the adult length is the same as that of the leg (MASCHLANKA 1972). The advanced development of the wing enables the young megapodes to fly soon after hatching e.g. the chick of *Leipoa ocellata* is known to do so during 24 hours after emergence from the mound (FRITH 1962). The so called skeleton-sum of the hatching *Leipoa* chick amounts to 143% of that of the chicken of similar size at the same stage (MASCHLANKA 1972).

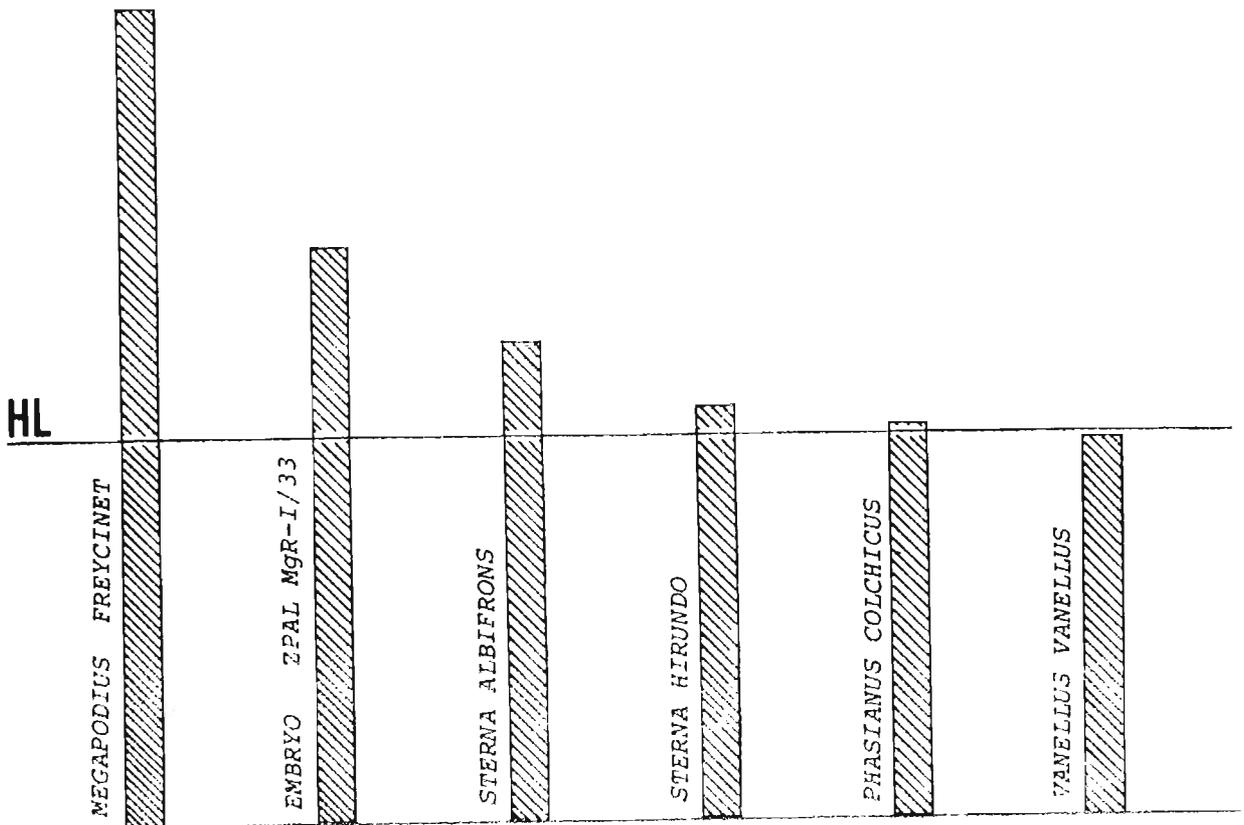


Fig. 8

Hatching lengths of the distal wing skeleton (forearm + hand) related to the length of head (HL). Data of recent species from SCHIESS (1963).

In the little tern (*Sterna albifrons*) the chicks leave the nest after one day and rise in the air after 15–17 days. The corresponding terms for a greater species, the common tern (*S. hirundo*) nesting in similar condition are 3 days and 4 weeks (MAKATSCH 1974).

Both functional and comparative premise strongly suggest that the exceptionally advanced ossification of the shoulder region and the wing skeleton are indicative of the early flight ability and extremely precocial development of the chicks which were emerged from the described embryos.

The neural arches of the cervicals and dorsals, like the forelimb skeleton, are exceptionally advanced in ossification. The zygapophyses are finished in skeleton no. 34 and nearly so in no. 33 while they are still largely cartilaginous in the hatching chicken (pers. obs.) or the hatching skua (MAILLARD 1948). A quite unusual phenomenon is the complete or nearly complete ossification of the high neural spines and fusion of two of them in no. 34. This peculiar development of the shoulder vertebrae presumably represents either flight or hatching adaptation.

In many adult carinates the dorsal vertebrae (most frequently 4-5) are fused and form a notarium which sometimes includes 1-3 posteriormost cervicals (STRESEMANN 1927-1934, RYDZEWSKI 1935). The nuchal blade of skeleton no. 34 may represent a part of the notarium and then other neural spines, that are still free, should be expected to fuse later on. There is however no trace of fusion between the transverse processes and the fusion involves only the two vertebrae which are classified as the posteriormost cervicals while the notarium is formed essentially of the dorsals, most frequently including 4-5 of them. The anterior location of the nuchal blade in the cervical region may reflect the anteroposterior sequence of ossification of the vertebral column although the more posterior segments appear to have been well ossified and finished, especially in no. 34, and yet do not show any trace of fusion. In the young pigeon the fusion of dorsal vertebrae is mentioned to begin from the centra, the neural spines fuse thereafter and the diapophyses at the end (MARTIN 1904). The dorsal centra may be initially fused in no. 34. The notarium is a prime example of flight adaptations (see e.g. TYNE and BERGER 1971) and the additional flight adaptations can be expected to develop as quickly as the wing skeleton.

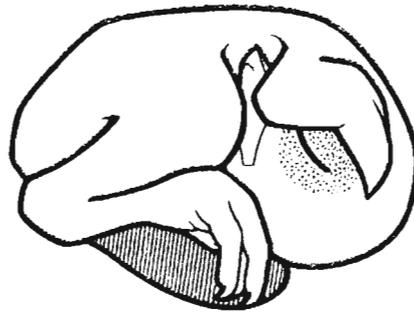


Fig. 9

Chicken's position in an advanced stage of tucking (about 19th day of incubation). The yolk sac is hatched.

The strongest and most protruding dorsally spines forming the nuchal blade of no. 34, are located at the boundary between the neck and the thorax i.e. the region which is braced against the shell at hatching birds (DRENT 1973, FREEMAN and VINCE 1974). This suggests the hatching function for the cervicodorsal spines. The way of hatching is largely determined by the prehatching posture which is very similar in the majority of birds (OPPENHEIM 1972, FREEMAN and VINCE 1974). At the earlier stages of development the embryo is simply rolled-up with the head in the ventral position. Several days before hatching (in the chicken from about the 17th day on) the head begins to rise from under the yolk sac and turns to one side of the embryo (most frequently to the right); thus the bill tip enters in between the body and the (right) wing, this process being referred to as tucking (fig. 9). Finally the prehatching position is achieved (in 19th day in the chicken) with the head tucked beneath the wing and the bill directed toward the air space. In this position the embryo makes the first pip-crack in the shell. Then the embryo rotates in a counter-clockwise direction from the site of the original pip-crack and the shell is progressively chipped around its circumference; in the result the blunt pole is cut in the form of a cap. Eventually, the cap is lifted off lid-like, by vigorous heaving movements of the shoulders coupled with extension of the legs (DRENT 1973, FREEMAN and VINCE 1974). In some birds there is little rotation before emergence and the line of pips is short (DRENT 1973). In the extreme case only one pip is made as described by WETHERBEE and BARTLETT (1962) for two species of the waders (*Scolopax minor* and *Catoptrophorus semipalmatus*), and the shell appears to be ripped by a ridge formed by the neural spines of the cervical and dorsal vertebrae. This provides the best example of the possible hatching function of the nuchal blade in the fossil embryos.

The only birds hatching from a different stance are the megapodes (FRITH 1962, BALTIN 1969). The prehatching position of the megapodes does not differ from the head-between-legs stance characteristic of the earlier stages. Thus the shell can not be pipped in the usual site and egg-tooth disappears long before hatching. The shell is broken by "wriggling the shoulders" (FRITH 1962) or bracing the back against the shell (BALTIN 1969); the force is provided by the extension of the legs. In the same way the chick makes room in the upward movement in the mound.

The prehatching position with the head between the legs appear to be primitive since a comparable posture occurs in the crocodiles (NEILL 1971). Although the development of the megapodes is recently thought to be secondary (BALTIN 1969) their method of hatching resembles that of turtles and snakes (OPPENHEIM 1972).

In the skeleton no. 33 the skull is preserved in ventral position; this may be also inferred for no. 88, where the phalanges of one toe adhere to the rostral part of the skull. The skeleton no. 34, however, appears to show the head-under-the-wing position, since the rostral fragment of the beak (premaxilla — not mentioned in the above description and not denoted in fig. 1B), pointing anteriorly, lies between the right coracoid and metacarpals, and the three anterior cervicals are deviated to the right side (fig. 1D).

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## EXPLANATION OF PLATES 40-45

### PLATE 40

#### Embryonic skeleton ZPAL MgR-I/34

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav I, Gobi Desert, Mongolia

- 1a. Dorsal view; see also fig. 1C.
- 1b. Left lateral view; see also fig. 1A.
- 1c. Right dorsolateral view.
- 1d. Right lateral view; see also fig. 1B.
- 1e. Ventral view; see also fig. 1D.
- 1f. Anterior view; see also fig. 1E.

Stereophotographs, all  $\times 2.5$

*Photo: B. Drozd*

### PLATE 41

#### Fragment of the embryonic skeleton ZPAL MgR-I/88

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav I, Gobi Desert, Mongolia

- 1a. Right lateral (and somewhat ventral) view of the mandible, with the egg-shell fragment best exposed.
- 1b. Right ventrolateral view of mandible.
- 1c. Right lateral view of the skull.

#### Embryonic skeleton ZPAL MgR-I/34

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav I, Gobi Desert, Mongolia

- 2a. Right anterolateral view.
- 2b. Left anterolateral view.
- 2c. Left dorsolateral view.
- 2d. Right ventrolateral view.

Stereophotographs all  $\times 2.5$

*Photo: B. Drozd*

## PLATE 42

## Embryonic skeleton ZPAL MgR-I/33

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav I, Gobi Desert, Mongolia

- 1a. Left lateral view of the partially developed specimen; egg-shell fragments on the left, other egg-shell piece projects above the vertebral column, on the right;  $\times 2.5$ .
- 1b. Dorsal view of the partially developed specimen; egg-shell fragments on the right;  $\times 2.5$ .
- 1c. Stereo-photograph of the ventral aspect with the skull fragment seen in dorsal view;  $\times 2.5$ .
- 1d. Stereo-photograph of the left lateral aspect;  $\times 2.5$ .
- 1e. Stereo-photograph of the left dorsolateral aspect;  $\times 2.5$ .
- 1f. Stereo-photograph of the dorsal aspect;  $\times 2.5$ .
- 1g. Dorsal (19th) vertebra (neural spine is broken), left lateral view;  $\times 15$ .
- 1h. Section of the egg-shell of the same specimen;  $\times 300$ .

*Photo: E. Wyrzykowska 1e-1j  
L. Łuszczewska 1g  
G. Mierzejewska 1a*

## PLATE 43

## Embryonic skeleton ZPAL MgR-I/33

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav I, Gobi Desert, Mongolia

- 1a. Left lateral view of the posterior part of the skull fragment, covered by the forearm bones and metacarpals;  $\times 8$ ; see also fig. 2A.
- 1b. Left lateral view of the anterior part of the skull fragment, with the bones below the nasal opening;  $\times 8$ ; see also fig. 2A.

## Embryonic skeleton ZPAL MgR-I/34

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav I, Gobi Desert, Mongolia

- 2a. Skull fragments with the ?basitemporal (bt) in the middle;  $\times 10$ .
- 2b. Anterior cervical vertebrae;  $\times 10$ ; see also fig. 5J.
- 2c. Dorsal view of the shoulder region with the left scapula (rotated) in medial view;  $\times 8$ ; see also fig. 5G.
- 2d. Right lateral view of the shoulder girdle after the separation of the humerus fragment;  $\times 8$ .

*Photo: B. Drozd 1a-b, 2c-d  
L. Łuszczewska 2a-b*

## PLATE 44

## Fragments of the embryonic skeleton ZPAL MgR-I/92

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav I, Gobi Desert, Mongolia

- 1a. Fragment with the coracoid (c);  $\times 6$ .
- 1b. Fragment with the phalanges (ph) of the foot;  $\times 6$ .

## Fragments of the embryonic skeleton ZPAL MgR-I/91

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav I, Gobi Desert, Mongolia

- 2a. Forearm bones (r radius, u ulna and metacarpals II and III) associated with the skull fragment(s);  $\times 6$ .
- 2b. Humerus (h) appressed on the forearm bones (r radius, u ulna),  $\times 6$ .

## Embryonic skeleton ZPAL MgR-I/34

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav I, Gobi Desert, Mongolia

- 3a. Nuchal blade in left lateral view;  $\times 10$ ; see also fig. 5A.
- 3b. Nuchal blade in right lateral view;  $\times 10$ ; see also fig. 5B.
- 3c. Scapular head in right lateral view;  $\times 10$ .
- 3d. Anterior part of the right scapula in dorsal view;  $\times 10$ ; see also fig. 5H.
- 3e. Distal extremity of the ulna articulated with the metacarpals;  $\times 10$ ; see also fig. 5E.
- 3f. Distal part of the right metacarpus in lateral view;  $\times 10$ ; see also fig. 5C.
- 3g. Shoulder region in right lateral view;  $\times 8$ . see also fig. 5D.

*Photo: B. Drozd 1a-b, 2a-b, 3g  
L. Łuszczewska 3a-j.*

## PLATE 45

## Fragment of the embryonic skeleton ZPAL MgR-I/89

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav I, Gobi Desert, Mongolia

1. Fragments of the forelimb bones and three arches of dorsal vertebra (dv);  $\times 6$ .

## Fragment of the embryonic skeleton ZPAL MgR-I/90

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav I, Gobi Desert, Mongolia

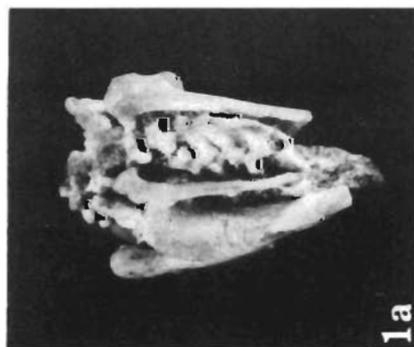
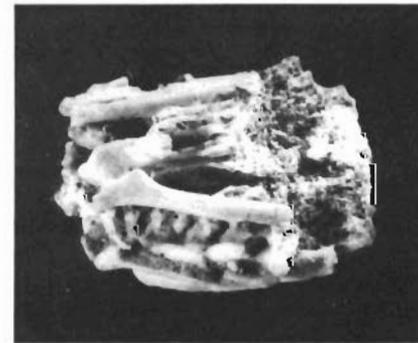
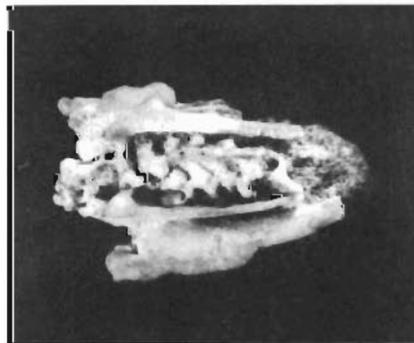
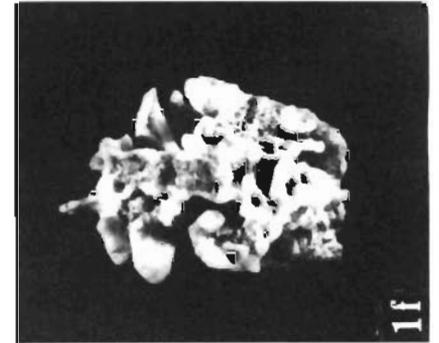
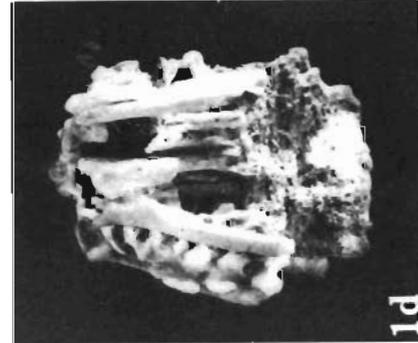
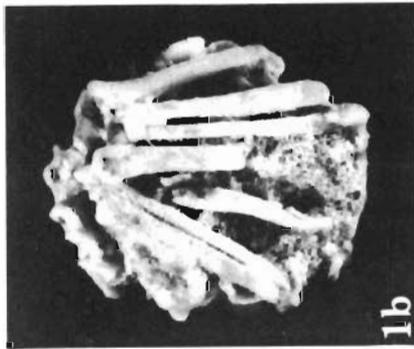
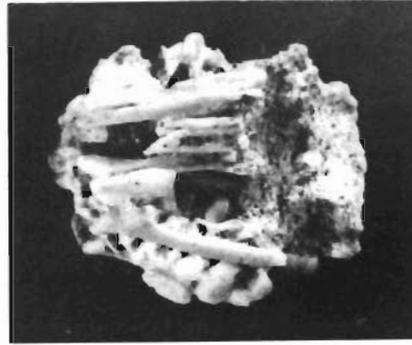
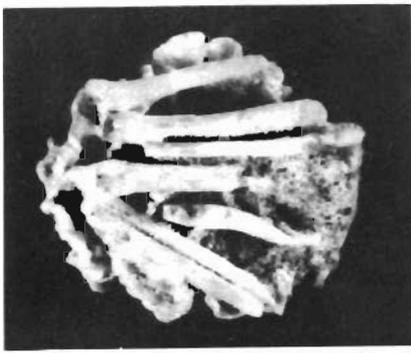
2. Ungual in lateral view;  $\times 33$

## Embryonic skeleton ZPAL MgR-I/34

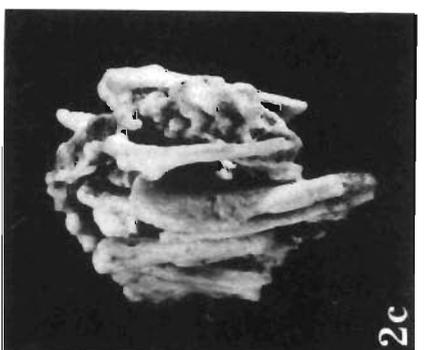
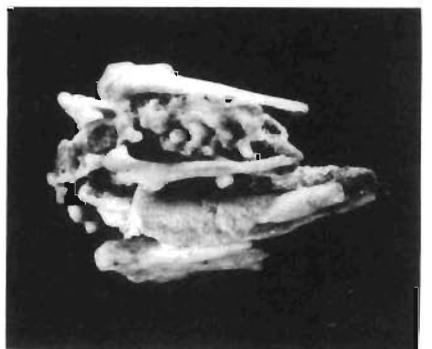
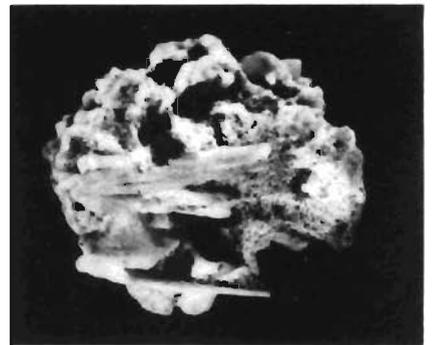
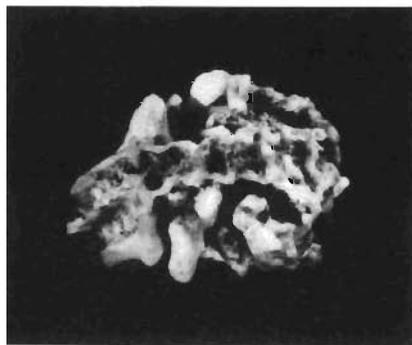
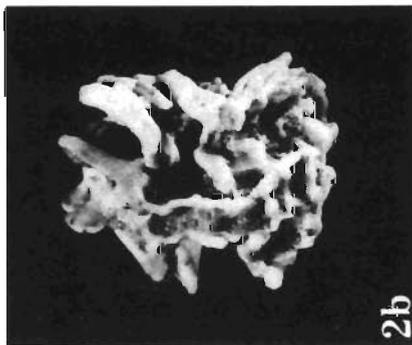
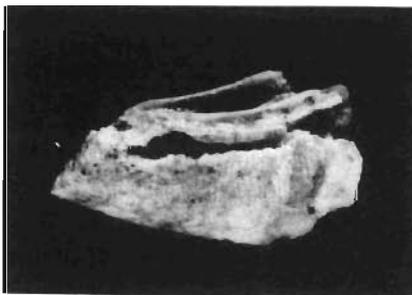
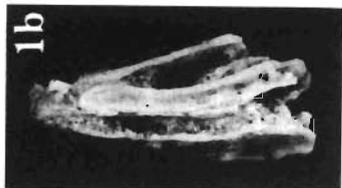
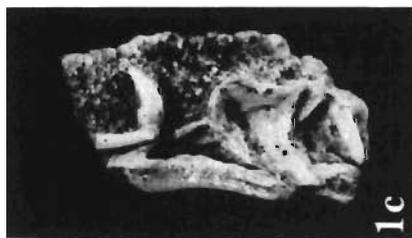
Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav I, Gobi Desert, Mongolia

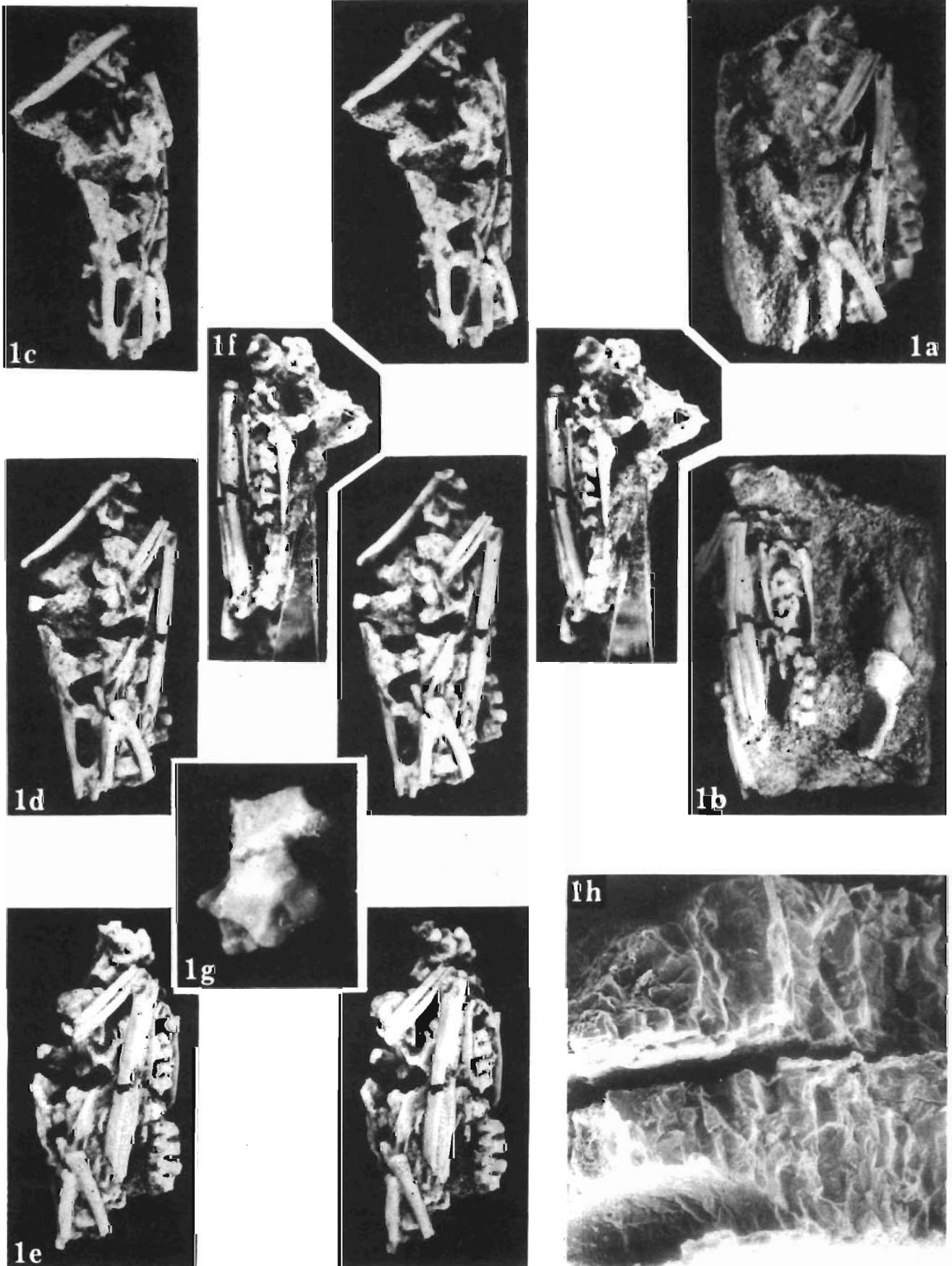
3. Proximal part of the left humerus in anconal view;  $\times 10$ .
- 4a. Head of the right humerus in anconal view;  $\times 35$ .
- 4b. The same in medial view;  $\times 26$ .
- 4c. The same in palmar view;  $\times 26$ .
- 4d. The same in oblique (mediopalmar) view;  $\times 26$ .

*Photo: B. Drozd 1  
W. Skarżyński 2, 4a  
L. Łuszczewska 3  
J. Macewicz 4b-d.*

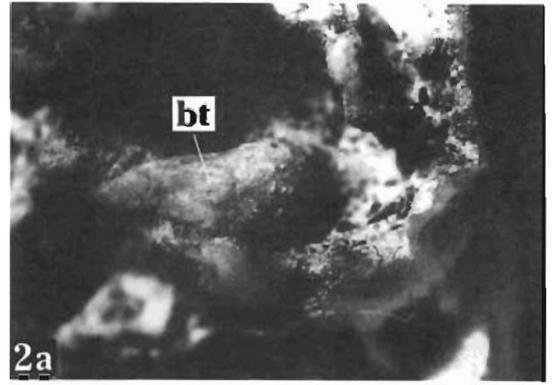
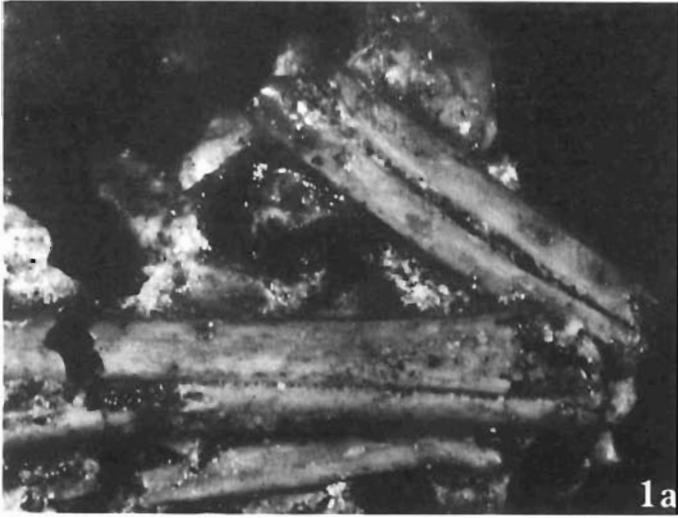


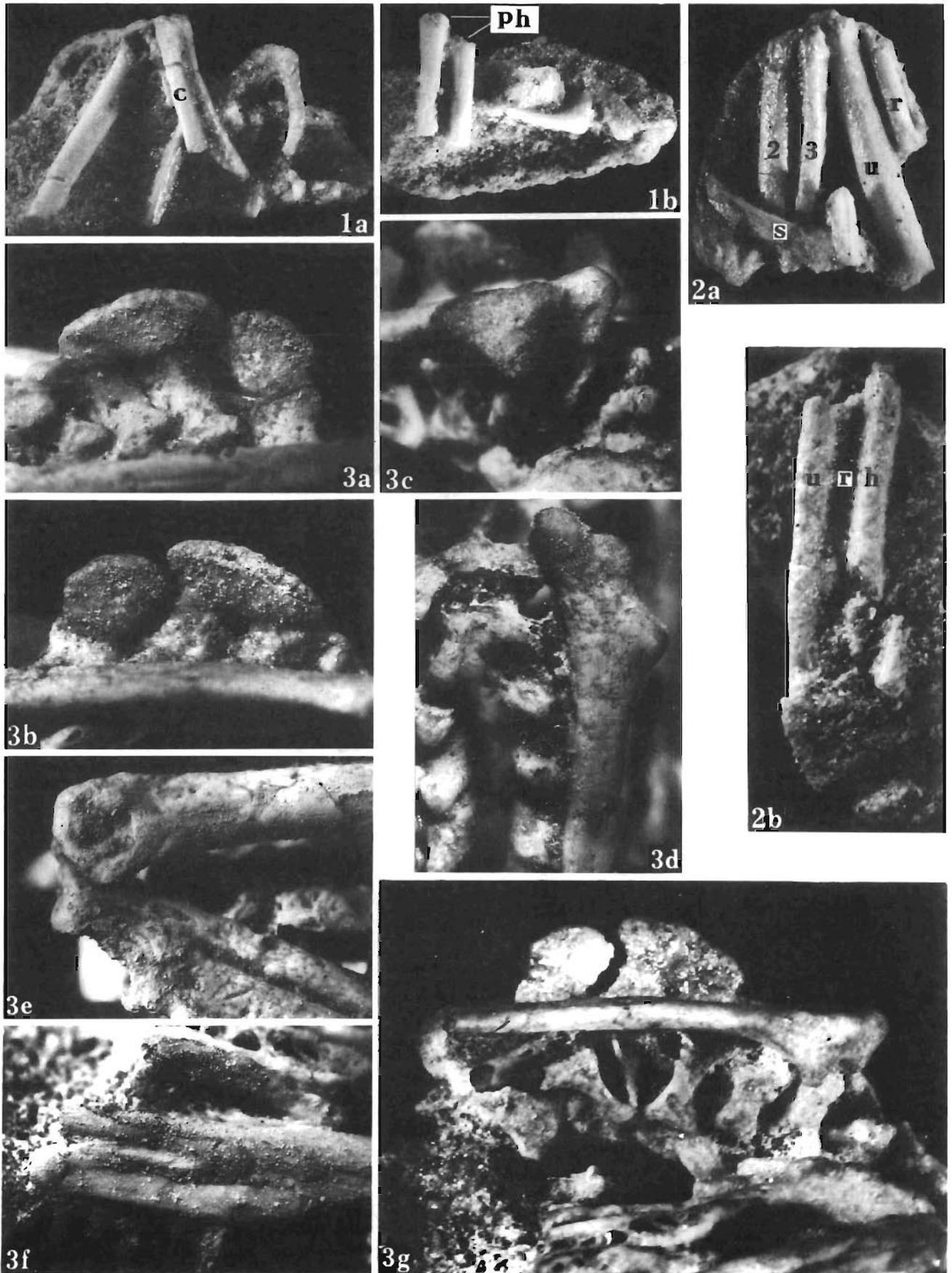
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