The quadrate of oviraptorid dinosaurs

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The quadrate of oviraptorid dinosaurs is strongly pneumatized and differs from the quadrates of other non-avian theropods by: (1) two separate facets on the otic process for contacts with the squamosal and braincase; (2) the articular surface for the pterygoid extended to the articular surface of the medial mandibular condyle; (3) the mandibular process provided laterally with a quadratojugal process bearing the quadratojugal cotyla. In the above characters the oviraptorid quadrate resembles those in most ornithothoracine birds, but, contrary to the streptostylic quadrate of birds, the oviraptorid quadrate is monimostylic.

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Introduction

The theropod quadrate has so far received but little attention. While studying some skulls of the Late Cretaceous Oviraptoridae from Mongolia in the collection of the Institute of Paleobiology, Polish Academy of Sciences, Warsaw (abbreviated ZPAL), we noticed that the oviraptorid quadrates seem to deviate from those in other theropods, as well as in all other dinosaurs. One of the most striking features of the quadrates studied by us is the presence of a double instead of a single contact of the otic process with bones of the tympanic region. However, the exact structure of the otic process could not initially be ascertained due to the extensive development of the squamosals and the long, ventrally-directed paroccipital processes characteristic of Oviraptoridae, which hide the proximal ends of the quadrates in the skulls at our disposal, especially in those with an intact posterolateral region of the skull roof. In 1995, we were able to examine the oviraptorids in the Geological Institute of the Mongolian Academy of Sciences, Ulan Bator (abbreviated GIN), and our earlier observation was supported by a pair of isolated quadrates of an unknown oviraptorid, in which the otic processes were displayed.

Material

ZPAL MgD-I/95 – nearly complete skull with preserved right quadrate and partly exposed otic process, described as *Oviraptor* sp. by Osmólska (1976); GIN 100/30A – fragmentary skull with preserved right quadrate articulated with distal part of the quadratojugal; otic process partially exposed; GIN A (unnumbered specimen) – left and right quadrates; GIN B (unnumbered specimen) – distal half of right quadrate articulated with distal part of quadratojugal; ZPAL MgD-I/96 – fragmentary skull with left and right quadrates preserved (the left articulated with the distal part of the quadratojugal); otic processes partly exposed.

Specimens ZPAL MgD-I/95, GIN 100/30A, GIN A&B represent uncrested oviraptorids (probably *Ingenia yanshini* Barsbold, 1981 or *Conchoraptor gracilis* Barsbold, 1986) and come from the Upper Cretaceous red beds of Khermeen Tsav (?middle Campanian according to Gradziński *et al.* 1977, ?late Campanian according to Kielan-Jaworowska & Hurum 1997) at Khermeen Tsav, Omnogov aimak (southern Gobi province), Mongolia; specimen ZPAL MgD-I/96 represents an unidentified crested oviraptorid and comes from the Late Cretaceous Nemegt Formation (?early Maastrichtian according to Gradziński *et al.* 1977 and Kielan-Jaworowska & Hurum 1997) at Nemegt, Omnogov, Mongolia.

Description

The oviraptorid quadrate is a bone of massive appearence with a narrow otic process, lateromedially expanded mandibular process and wide, deep pterygoid ramus. The quadrate is extensively pneumatized in at least ZPAL MgD-I/96 and GIN A, if not all specimens. In GIN A, a large pneumatic foramen is placed anteromedially and somewhat below the mid-height (Fig. 1E). This foramen leads to an extensive sinus, which is subdivided by bony struts into numerous hollow compartments (Fig. 3D). The sinus extends into the shaft and mandibular process and into, at least, the basal part of the pterygoid ramus. Whether the sinus invades the otic process is uncertain.

In the oviraptorid skulls studied here, the posterolateral regions of the skull roof are damaged and partly expose the proximal ends of the quadrates, revealing that the otic process is bent medially and posteriorly (Elżanowski in press). As the otic process is still articulated with the surrounding bones in these skulls, details of its articular region could not be determined. However, the proximal ends are displayed in quadrates of the specimen GIN A (Fig. 1). The better preserved left quadrate shows that, in addition to the contact surface for the squamosal, there is another well-defined, separate and posteromedially facing surface (Figs 1F, G; 3B), which contacts the braincase wall in the articulated skulls (Fig. 2C). The surface for the contact with the squamosal is the more extended one and consists of two parts: a squamosal capitulum proper, which is convex and placed at the apex of the otic process (Fig. 1B), and a flat, elongate surface that is the posteroventral continuation of the squamosal capitulum (Figs 1F, G; 3B). Thus the articular contact with the squamosal is very extensive. The contact surface for the braincase wall is placed ventral to the squamosal capitulum and medial to its posteroventral prolongation, oriented at an angle to the latter. It is suboval, flat, and

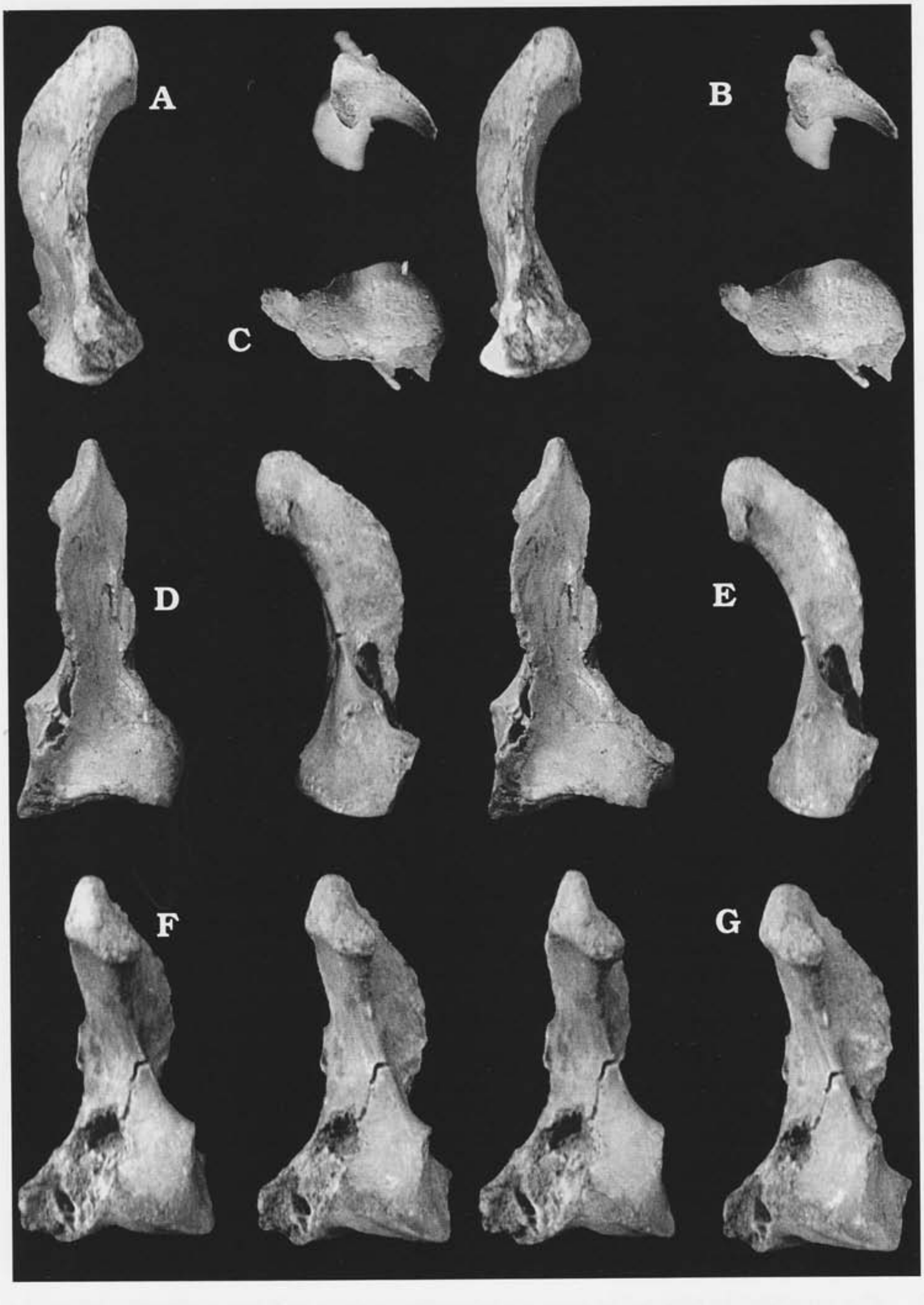

Fig. 1. **A–G**. Stereophotographs of the left quadrate of an undetermined oviraptorid (*Ingenia yanshini* or *Conchoraptor gracilis*), in lateral (**A**), proximal (**B**), distal (**C**), anterior (**D**), medial (**E**), posteromedial (**F**), and posterior (**G**) views; GIN A, × 1. Late Cretaceous, red beds of Khermeen Tsav, ?middle or ?late Campanian, Khermeen Tsav, Omnogov, Mongolia.

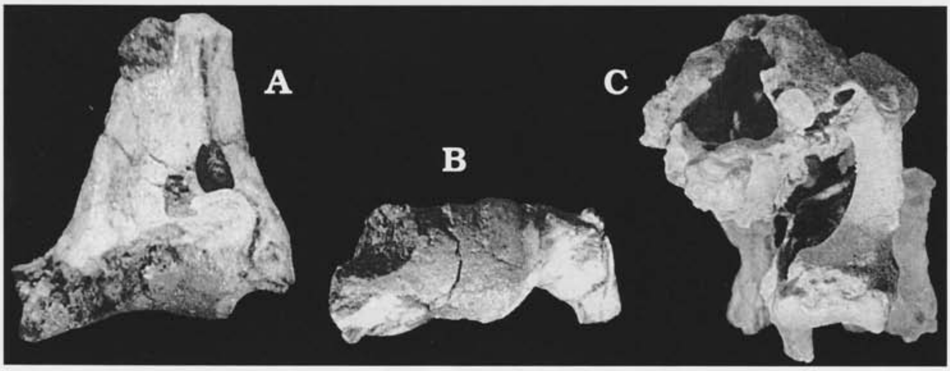

Fig. 2. Distal part of the right quadrate with articulated quadratojugal of an undetermined oviraptorid (*Ingenia yanshini* or *Conchoraptor gracilis*), in posterior (**A**) and distal (**B**) views; GIN B, × 1.5. Late Cretaceous, red beds of Khermeen Tsav, ?middle or ?late Campanian, Khermeen Tsav, Omnogov, Mongolia. **C**. Occipital view of the skull with right quadrate of an undetermined oviraptorid (*I. yanshini* or *C. gracilis*); note the exposed contact of the otic capitulum with the braincase wall; ZPAL MgD-II/95, × 1. Late Cretaceous, red beds of Khermeen Tsav, ?middle or ?late Campanian, Khermeen Tsav, Omnogov, Mongolia.

rough. This contact surface is referred to below as the otic capitulum, although it does not necessary imply homology with the otic capitulum of birds.

Although the cotylae for both capitula of the otic process are not displayed in the articulated skulls, some contact lines between the respective bones can be detected in ZPAL MgD-I/95 and in GIN 100/30A (Fig. 3F). They show that these contacts are extremely tight. The contact of the otic capitulum is with the opisthotic, at the base of the paroccipital process. The prootic-opisthotic suture is discernible in front of the contact. As visible in these specimens, the otic capitulum contacts the lateral wall of the braincase dorsal to the *fenestra ovalis* in ZPAL MgD-I/95 but posterodorsal in GIN 100/30A; this may reflect a taxonomic difference. It should be added here, that although the quadrate is unknown in *Chirostenotes* (Oviraptorosauria, Caenagnathidae), a concavity seems to be present at the base of the paroccipital process and might represent the otic cotyla (Sues in press).

The medial margin of the quadrate shaft is concave and rounded, while the lateral margin is thin and sharp for the most of its length. Below the mid-length of the shaft, the lateral margin is angularly incised (Figs 1F, G; 3A, B) and the margin there is thicker, rounded, and borders the quadrate foramen medially. The caudal surface of the quadrate is concave, mainly due to the backward curvature of the otic process (Fig. 1A, E).

The pterygoid ramus of the quadrate is anteromedially directed, deep, and wide. It is very thin distally and, for that reason, is incomplete in most specimens. The pterygoid ramus tightly overlaps the quadrate ramus of the pterygoid laterally, and continues ventrally to the medial condyle of the mandibular process in the form of a broad wing.

The mandibular process is very wide mediolaterally and has a sharply delimited articular mandibular surface. There are two rather flat mandibular condyles, which are separated by a wide, shallow, and somewhat obliquely, posterolaterally-anteromedially extending intercondylar depression (Figs 1C; 2B). The articular surfaces of both condyles are almost flat transversely, and their slope towards the intercondylar depress-

Table 1. Measurements of quadrates (in mm); e – estimated values.

	GIN			ZPAL MgD-I/	
	A	B	100/30/a	95	96
Total height	52	–	50	35e	55e
Shaft thickness in the middle (tr.)	10	–	–	7	14e
Dorsal width (tr., across otic capit.)	11	–	10e	7	–
Max.ventral width (tr.)	29e	24	26	18e	36e
Ant.-post. width of lateral condyle	–	12	17	8e	22e
Width (tr.) of articular surface	22	17	18	15	29e

ion is weak. The condylar surfaces are more convex anteroposteriorly than transversely, especially that of the medial condyle. The axis of the condyles is almost perpendicular to the sagittal plane of the skull. In the ventral view, the articular surface of the lateral condyle has a band-like shape, whereas that of the medial condyle is somewhat wider and roughly triangular. Lateral and somewhat dorsal to the articular surface of the lateral condyle, the quadrate sends a process for the contact with the quadratojugal (Figs 1C, D; 2A, B; 3A–C). This process bears a large concave surface that receives the large condyle on posteroventral extremity of the quadratojugal (Figs 2A; 3C). In the specimens GIN B and ZPAL MgD-I/96, the contact between the quadrate and quadratojugal is relatively loose, but, in most cases, this junction is very firm, often coalesced, and only a faint trace of the suture is visible between both bones.

Medially, the mandibular process bears an extensive, almost flat articular surface for contact with the pterygoid (Figs 1E–F; 3B). This surface extends to the medial margin of the trochlear surface of the medial condyle anteriorly, posteriorly its ventral limit is placed a short distance above this surface. The contact between the medial condyle of the quadrate and the posteroventral extremity of the pterygoid is continuous with the overlapping contact between the quadrate ramus of the pterygoid and the pterygoid ramus of the quadrate.

Although the above description is based on a small number of oviraptorid specimens, there is no doubt that the peculiar quadrate structure is characteristic of all representatives of the Oviraptoridae *sensu* Barsbold (1976), possibly with only some minor differences in proportions of the elements of the mandibular process.

Discussion

The dual contact of the oviraptorid quadrate with the tympanic region is the only known sure case among the non-avian theropods. Also in other respects the quadrate is very different from the quadrates of many remaining non-avian theropods, e.g., in having the transversely wide mandibular process, its width constituting 50–60% of the height of the quadrate; this ratio is usually about 40% in other maniraptorans. The massive mandibular process reflects a unique character of the oviraptorid mandibular articulation, and the presence of the quadratojugal process with the deeply concave cotyla for the latter bone. A pneumatic quadrate has been rarely reported in the

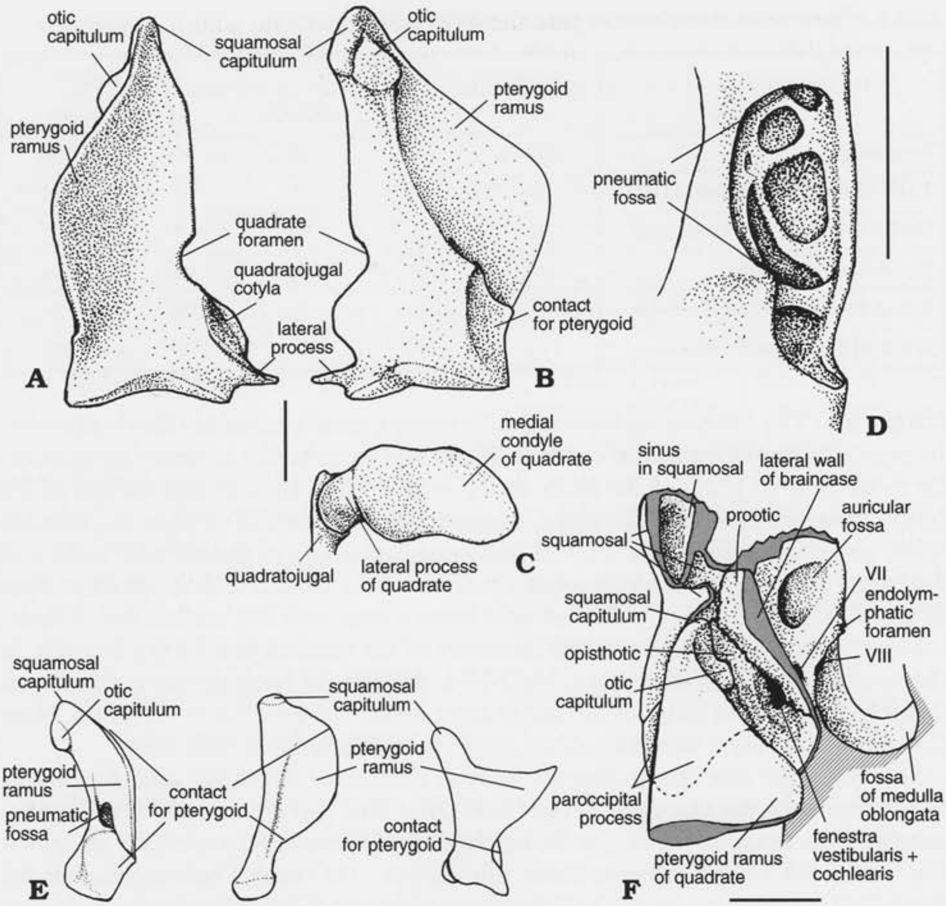

Fig. 3. Reconstruction of the left oviraptorid quadrate, in anterior (**A**) and posterior (**B**) views; based on specimens: GIN A, B, ZPAL MgD-II/95, 96. **C**. Distal view of the right quadrate and quadratojugal (GIN B, reversed). **D**. Details of the pneumatic fossa on the medial side of the left quadrate (GIN A); visible subdivision of the pneumatic space. **E**. Comparison of quadrate in oviraptorids, *Allosaurus* and birds, lateral views; not to scale. **F**. Schemmatic drawing of contacts of the otic process in the oviraptorid skull, anteroventral view. Scale bars – 1 cm.

theropods, being known only in the tyrannosaurids (Witmer 1990; Molnar 1991) and troodontids (Barsbold *et al.* 1987; Currie & Zhao 1994). In the oviraptorid quadrate, the pneumatic foramen is more ventrally placed than in the troodontids, and it is more like that in the tyrannosaurids and birds.

In some non-dinosaurian archosaurs, proximal end of the quadrate may bear more than one separate facets for contact with the adjoining skull bones: in the majority of neognathous birds the quadrate is double-headed, and two or three proximal articular processes occur in crocodylomorphs. There is but little resemblance between the oviraptorid quadrate and quadrates of primitive crocodylomorphs, e.g. *Sphenosuchus* Haughton, 1915 (Walker 1990) and *Dibothrosuchus* Simmons, 1965 (Wu & Chatterjee 1993), and for that reason they will not be considered here.

It is more reasonable to compare the oviraptorid quadrate with the quadrates of birds, especially given that the Huxley-Ostrom hypothesis of birds as the theropod dinosaurs (Gauthier 1986) is favoured by the majority of researchers at present.

The new preparation of the skull of the London specimen (Whetstone 1983) and discoveries of the fifth (Eichstätt) and seventh skeletons of *Archaeopteryx*, both with sufficiently well preserved and articulated quadrates, have initiated the discussion concerning the structure of the quadrate in this ancient bird, and its proximal contacts, either with the prootic (Wellnhofer 1974; Elżanowski & Galton 1991), or opisthotic (otoccipital: Whetstone 1983), or squamosal (Walker 1985; Raath 1985; Chatterjee 1991; Elżanowski & Wellnhofer 1996). All these authors have agreed that the quadrate was single-headed in *Archaeopteryx*, in spite of the results obtained by the computed tomography of the Eichstätt skull (Haubitz *et al.* 1988), which suggested that there were two heads on the otic process. The double-headedness of the quadrate in *Archaeopteryx* was also considered unlikely by Elżanowski & Wellnhofer (1996). We had no opportunity to study the quadrate of the London *Archaeopteryx* skull, considered by Whetstone (1983) as the 'unidentified skull bone', by Walker (1985) as the right, and by Chatterjee (1991) as the left quadrate. However, if the bone indeed represents the quadrate, which seems convincing, its single articular surface (the squamosal capitulum) on the otic process is elongated in the ventromedial direction (Chatterjee 1991: fig. 30a, b) and slightly resembles the otic process in the oviraptorids with its extended articular surface for the contact with the squamosal. It should be mentioned here that the Early Cretaceous hesperornithid *Enaliornis* Seeley, 1870, was the stratigraphically oldest bird with a double-headed quadrate (Witmer 1990).

Although the otic and squamosal capitula are separate in the oviraptorids, the otic process is not bifurcated (contrary to that in most birds), leaving no space for the dorsal tympanic diverticulum. Also, different from most birds, the otic capitulum has the flat and rough surface in the oviraptorids, indicating an immovable contact with the braincase wall. In addition to this evidently rigid contact, the very extensive and mostly tight contact of the otic process with the squamosal, and some other features of the skull construction, indicate that the oviraptorid quadrate was monimostylic (see also Barsbold 1983). Contrary to that, the double-headed quadrate is associated with the streptostylic quadrate in birds, thus the functional meaning of the dual contact of the quadrate was entirely different in both groups. It should be also mentioned that in the oviraptorids it is the opisthotic, not the prootic (as typically in birds), which receives the otic capitulum.

The contact of the single-headed otic process is variable in the non-avian theropods, either exclusively with the squamosal, e.g., in the dromaeosaurids (Currie 1995; Osmólska, personal observation) and *Tyrannosaurus rex* (Molnar 1991). However, as the dorsal contact(s) is (are) rarely displayed in the described non-avian theropods, its nature remains mostly unknown. In two theropods which expose a number of bird-like characters, *Avimimus* Kurzanov, 1981 and *Mononykus* Perle *et al.*, 1993, the quadrate is not sufficiently well known to allow detailed comparisons. However, according to Perle *et al.* (1994), the otic process has only a single contact with the skull in *Mononykus*, and the respective cotyla is formed of the prootic and squamosal. No information is available on the otic process in *Avimimus*. Based on Kurzanov's (1987) paper, the mandibular process extends ventrally well below the pterygoid contact in *Avimimus*, and, at least in this respect, its quadrate is different from that in the oviraptorids.

The pterygoid ramus slightly and gradually narrowing towards the medial condyle of the quadrate is a distinctive feature of the oviraptorids. In other non-avian theropods, the pterygoid ramus is abruptly narrowed some distance above the condyle (Fig. 3E). In most birds the pterygoid ramus (= orbital process) is also wide close to the distal end of the quadrate, but its narrow shape is quite diffrent from that in the oviraptorids. In *Archaeopteryx*, the shape of the pterygoid ramus (Elżanowski & Wellnhofer 1996: fig. 7b) resembles rather that in the non-avian theropods than in ornithurine birds (Chiappe *et al.* 1996). Compared with the pterygoid ramus of the *Archaeopteryx* and the non-avian theropods, this in the oviraptorids extends further anteromedially. A similar development of the pterygoid ramus has been reported in *Erlikosaurus andrewsi* Perle, 1981 (Clark *et al.* 1994).

The presence of the lateral process on the mandibular condyle, with the deep cotyla for the quadratojugal, is another feature of the oviraptorid quadrate exceptional for the non-avian theropods. The quadratojugal cotyla on the lateral face of the mandibular process and the quadrate pneumaticity were considered by Chiappe (1995) and Chiappe *et al.* (1996) as synapomorphies of the unnamed group of birds, including the Ornithurae and *Patagopteryx* Alvarenga & Bonaparte, 1992. In many birds, the quadratojugal cotyla is placed on the lateral surface of the lateral mandibular condyle, but in some (e.g., in *Ciconia)* this cotyla is placed on the short process, resembling that in the oviraptorid quadrate.

Conclusions

The afore mentioned resemblances between the quadrates in birds and oviraptorids concern: (1) the similar nature of pneumaticity, (2) the far posteroventral descent of the pterygoid ramus, (3) the presence of the otic process which has the dual contact with the adjoining bones of the tympanic region, and (4) the presence of the quadratojugal cotyla. These far-reaching similarities seem to add some arguments to the hypothesis by Elżanowski (1995 and in press), which assumes a close relationship between Oviraptorosauria and birds. However, pneumaticity of the quadrate is a feature also present in the Tyrannosauridae, which seem rather distant relatives of birds (Russell & Dong 1993; Holtz 1994). Also the contact of the otic capitulum with the braincase is more anterior in birds (on the prootic) while it is far more posterior (on the opisthotic at the paroccipital process root) in the oviraptorids. Unlike in birds, the quadrate was immovable and the contact of the otic capitulum with the braincase wall (as well as that of the squamosal capitulum with the squamosal) was tight and rigid in the oviraptorids. Taking into account the fusion that occurred between the quadrate and quadratojugal in the posteroventral region of their contact in most known oviraptorid specimens, as well as the significant depth of the quadratojugal cotyla on the quadrate and the large size of the quadrate condyle on the quadratojugal, this structure served for strengthening the quadrate-quadratojugal junction. Even in the specimens in which it was not fused, it appears immovable.

The anatomy of the Oviraptoridae is still incompletely known. Therefore establishing whether the bird-like characters of the oviraptorid quadrate are homologous with those of the birds seems premature. Our osteological study of the Mongolian Oviraptoridae is in progress, and for this reason we restrain in the present paper from any phylogenetic conclusions until more anatomical data are available.

Acknowledgements

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Kość czworoboczna dinozaurów z rodziny Oviraptoridae

TERESA MARYAŃSKA i HALSZKA OSMÓLSKA

Streszczenie

W czasie badań czaszek dinozaurów z rodziny Oviraptoridae z osadów późnej kredy Mongolii, znajdujących się w zbiorach Instytutu Paleobiologii Polskiej Akademii Nauk w Warszawie (ZPAL) i w Instytucie Geologii Mongolskiej Akademii Nauk w Ułan Bator (GIN) zaobserwowano, że ich kość czworoboczna (*quadratum*) różni się od kości czworobocznej innych teropodów, a także innych dinozaurów, następującymi cechami: (1) obecnością dwugłówkowego wyrostka skroniowego (*processus oticus*), kontaktującego zarówno z kością łuskową jak i z boczną ścianą puszki mózgowej; (2) wyrostkiem oczodołowym (*processus orbitalis*), dochodzącym w swej cześci tylnej do powierzchni stawowej medialnego kłykcia wyrostka żuchwowego (*processus*

mandibularis); (3) obecnością na wyrostku żuchwowym bocznego wyrostka zaopatrzonego w dołek stawowy dla kości czworoboczno-jarzmowej; (4) rozległą pneumatyzacją. Cechy te występują także u większości ptaków z grupy Ornithothoraces, obejmującej wszystkie współczesne i kopalne ptaki z wyjątkiem praptaka (*Archaeopteryx*) i przedstawicieli późnokredowej rodziny Alvarezauridae, i mogą świadczyć o bliskim związku filogenetycznym owiraptoridów i ptaków. Jednak wniosek o homologii cech kości czworobocznej w obu grupach wymaga dodatkowych badan czaszki i szkieletu pozaczaszkowego. Kość czworoboczna owiraptoridów jest nieruchomo zestawiona z resztą czaszki (monimostylia), czym różni się od kości czworobocznej ptaków, która wykazuje znaczną ruchomość w stosunku do czaszki (streptostylia).