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KINETICISM AND PECULIARITIES IN THE MAXILLARY STRUCTURE OF OVIRAPTORIDS (THEROPODA, SAURISCHIA)[*]

Until recently the oviraptorids—small predatory dinosaurs from the Late Cretaceous of Mongolia—were known only from the brief description of a single, and in many ways incomplete, skeleton (Osborn, 1924) from the Upper Cretaceous Bayn Dzak deposits (Shabarak Usu in the American publications) of southern Mongolia. Osborn assigned *Oviraptor* to the ornithomimids, which was subsequently accepted by other researchers (Romer, 1956; Maleyev, 1964; Kuhn, 1966).

A study of Mongolian ornithomimids and the revision of Canadian ornithomimids (Osmólska, et al., 1972; Russell, 1972) made it possible to firmly reject the assignment of oviraptorids to the ornithomimids. However, owing to the lack of data, no conclusions regarding the classification of oviraptorids could be drawn. American investigators, who at the time had been the only researchers into this interesting material, practically ignored oviraptorids after Osborn.

The grounds for a more thorough study of oviraptorids was established from work done in Mongolia by the Joint Soviet-Mongolian Palaeontological Expedition (JSMPE) and the Polish-Mongolian Palaeontological Expedition (PMPE) (Barsbold, et al., 1971; Kielan-Jaworowska & Barsbold, 1972; Kramarenko, 1974).

Elements of the JSMPE and PMPE discovered more than ten specimens, including a skull, mainly at the Khermin Tsav deposit in the southwest part of the country during the period 1971–1974. A study of some of the material (collected during the period 1971–1973) and familiarization with the holotype 6517 at the American Museum of Natural History (only the skull), brought to Warsaw from New York by Professor Z. Kielan-Jaworowska (Palaeontological Institute of the Polish Academy of Sciences) led to the segregation of oviraptorids into a unique family of theropods (Barsbold, 1976).

At present we can discuss three species of oviraptorids that developed successively during the second half of the Late Cretaceous:

1. *Oviraptor philoceratops* Osborn, 1924, Bayn Dzak, Djadokhta Formation (Bayandzag suite), presumably Lower Senonian (Kielan-Jaworowska, 1970, 1979; Barsbold, 1972).
2. Oviraptorids from Khermin Tsav, Barungoyot suite (lower stratum, presumably the lowermost Campanian strata.
3. Oviraptorids from Khermin Tsav and Bugin Tsav, Barungoyot suite (upper stratum), presumably the uppermost Campanian strata.

It is not our purpose here to present a classification study of oviraptorids (that work is in preparation). The various oviraptorids are distinguished mainly by the structure of their postcranial skeleton. The skulls of oviraptorids were not subject to any significant changes.

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The first investigator to study oviraptorids assumed that they fed on the eggs of reptiles, most likely those of the "horned" dinosaurs. According to the then widely held view of American investigators, the clutches of fossilized eggs in the bone-bearing strata of Bayn Dzak (Shabarak Usu) might have belonged to *Protoceratops*. This is reflected in the nomenclature of the first of the species to be discovered.

The entire structure of the oviraptorid skull testifies to the ability of the jaw to have developed powerful crushing forces, which suggests an adaptation to handling food that was much more solid than eggs. It then becomes possible to draw some conclusions about the ecology of this interesting group, which was markedly distinguished from other branches of theropods by its narrow specialization.

Because the oviraptorid skull has not been studied in sufficient detail, we will offer a brief characterization of its structure based on new data. The collection that was studied is preserved in the paleontology and stratigraphy laboratory of the Geological Institute of the Mongolian Academy of Science.

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SKULL STRUCTURE

The skull (Fig. 1) is tall, narrow in the rostral region, and broad in the postorbital regions. It has a very short facial region. The skull is "open": the orbit and lateral temporal fossae are very large, and the bones surrounding them are very narrow. The two small antorbital foramina are close to each other and the posterior foramen is much larger than the anterior. The large external narial fenestra is higher than the antorbitals. The adductor fossa (subtemporal fenestra) is quite long—two-thirds the length of the skull. The jaws are completely devoid of teeth.

The premaxilla forms a tall, massive foundation, presumably for the horny culmen. The two posterior processes on the bone bound the large region of the external narial fenestra, coming together at an immobile joint with the processes on the nasal to form the posterior edge of this fenestra. The ventral concave surface of the premaxilla forms the anterior region of the hard palate; at its posterior edge had developed a gradually deepening depression that was partially covered by the vomer in the ventral direction.

The maxilla is very small, especially lengthwise. Its functional edge is slightly convex and from the front connects very closely with the premaxilla. The posterior end of the functional edge is situated between the base of the lacrimal (medially) and the anterior end of the jugal (laterally). Closer to the posterior end the maxilla fuses with the vomer. The remaining joints with the adjacent bones are presumably immobile.

The nasal is extremely short and wide; its joint with the frontal is immobile. Three small depressions lie in a row on the medial edge; a fourth depression lies somewhat to the exterior of these. These are presumed to be associated with the development of the syndesmotic joint between the nasal and the culmen that is typical of many Anseriformes in the area of the mobile (flexible) zone of the culmen (Möller, 1969).

The lacrimal has a very compact process in the anteroposterior direction; its exterior edge forms a ridge-like projection. Its apical process is obliquely oriented, has a short anterior end that bounds the upper edge of the posterior antorbital foramen. The posterior end is very large and penetrates the angular space between the nasal and frontal. It is presumed that the joint between the lacrimal and the lower posterior process of the premaxilla was mobile. The process base has a notch from the outside in which the joint between the abutting ends of the jugal and maxilla is mobile.

With its upper and lower processes, the postorbital lies in groove-like depressions on the frontal and squamosal, respectively. The narrow lower process forms a mobile (sliding) joint with the jugal.

The jugal has narrow processes that connected movably with the adjacent bones.

The squamosal has a large process that participates in forming the infratemporal arch. The prequadrate process is quite long. The bone itself connects immovably with the parietal near the posterior outside segment of the infratemporal opening.

The quadrate has a long, anteriorly arched shaft and a wide medial lobe that joins with the pterygoid. The base of this shaft is wide and ventrally forms a saddle-like, concave surface for the maxillary joint. A depression on the lateral side of the base serves as the attachment point for the quadratojugal. The proximal head of the bone enters the joint socket at the boundary of the parietal, squamosal, and the lateral process of the opisthotic bones. A small groove on the outside edge of the quadrate shaft is covered laterally by an ascending process that is hypothetically identified with a passageway for the maxillary vein.

The quadratojugal has a thick body and narrow processes; the ascending process extends along the posterior edge of the prequadrate process to its base. The anterior and posterior processes on the bone are short. The bone itself is attached immovably to the base of the quadrate, entering the aforementioned depression on its lateral side.

The vomer (Fig. 2) is a two-part formation, each of which looks like a narrow wafer having two convex tori (lateral and medial). The anterior potion of the vomer covers a depression in the posterior edge of the ventral surface of the premaxilla. It is likely that the vomer did not have a mobile joint with the premaxilla here. The dorsal surface of the vomer fused with the maxilla by means of a short connector. The posterior end of the vomer joins with the pterygoid at a hinged joint.

The pterygoid has a narrow vomer process and a broad, thick body, the dorsal surface of which has a lengthwise groove. The lateral edge of the body projects downward at a right angle bounding the concavity on the its ventral surface from the outside. The anterior edge of the pterygoid is split, and its interface is a complex configuration that connects with the ectopterygoid and firmly enters this split. The transition to the posterior flange of the pterygoid, which has a rounded profile and is laterally connected with the quadrate flange, accomplished by means of a short, thick neck. The posterior flange of the pterygoid is firmly attached (fused) medially with the basisphenoid.

The vomerine process ends with a glenoid into which the posterior end of the vomer penetrates (Fig. 3). The spherical pterygoid-vomer joint made the vomer mobile. The interpterygoid fenestra was presumably very long and widened posteriorly.

The ectopterygoid has a massive base, as though expanding the anterior region of the pterygoid. A dorsal depression on the pterygoid extends to the base of the ectopterygoid and the lateral edge of the latter also project sharply ventrally. The ascending process of the ectopterygoid has a large, wide end that apparently joins movably with the jugal and maxilla.

The palatine is very small and connects like a narrow strip on the curve of the dorsal end of the ascending process of the ectopterygoid and by its anterior end lies on the posteroventral region of the maxilla. The narrow opening in this curve is presumably identified with the palatine. There is apparently no accessory palatal opening. The posterior end of the palatine probably extends to the anterior edge of the pterygoid. The space between the vomerine process of the latter and the palatine corresponds to the choana.

We will examine components of the neurocranium (Figs. 4, 5) in more detail.

The basisphenoid (a large area had been destroyed in the study sample) formed a convex platform at the base of the skull. This platform connected in the area of the sphenooccipital tubercles with the base of the occipital region and on the lateral wall with the opisthotic and prootic (the interfaces were only partial). The basipterygoid processes were not distinguishable (they are usually well-defined in theropods) and a similar joint was formed by the fusion of the medial surface of the posterior flange of the pterygoid with the ventrolateral region if the basisphenoid by means of a short broad strip.

The basioccipital (Fig. 6) makes up the posterior vertical wall of the occipital complex with the sphenooccipital tubercles at the lower corners. The occipital condyle is formed mainly by this bone, excluding its dorsolateral edges. Near the sphenooccipial tubercles the occipital is contiguous with the opisthotic anterodorsally.

The exoccipital is part of the dorsolateral edge of the occipital condyle. The lateral part of the bone (externally from the condyle) joins with the opisthotic anterodorsally and with the occipital ventrally.

The supraoccipital forms the dorsal edge and parts of the lateral edges of the large occipital foramen magnum. This bone is presumed to be very low; it immovably joined with the parietal behind an inflection of the latter from the roof onto the occipital surface.

The parietal forms the highest region of the cranial vault and is also part of the upper areas of the lateral wall and the occipital. The parietal immovably joins with the laterosphenoid on the lateral wall of, and with the frontal on the roof of the cerebral cranium.

The opisthotic occupies most of the posterior region of the lateral wall of the cerebral cranium. It is contiguous anteriorly with the prootic and ventrally with the basisphenoid. Its lateral process forms a joint with the squamosal anteriorly and with the lateral edge of the supraoccipital near the upper area of the occipital complex. The fenestra rotundum and fenestra ovalis are presumably identified with the openings in the upper region of the opisthotic.

The prootic is contiguous with part of the lateral cranial wall between the laterosphenoid (anteriorly) and the opisthotic. The extreme ventral region of the prootic presumably extended to the basisphenoid. The interface between the prootic and opisthotic was presumably a narrow ridge that extended from the area of the fenestra ovalis to the anterodorsal edge of the basisphenoid. The large opening in the ventral area of the bone at its interface with the laterosphenoid is identified with the exit for nerve V (Figs. 4, 5). A wide channel that is large at its origin extends from this opening. The channel was presumably a passageway for the ophthalmic nerve. A very short groove (purpose unknown) extends medially from this channel and drops into the previously described opening for the nerves III-IV.

The anterior segment of the channel runs along the ventral surface of the postorbital process on the frontal.

The long opening situated above and behind the exit for nerve V is identified with the exit for the facial nerve (VII).

The laterosphenoid forms the anterior region of the lateral cranial wall, connecting immovably anteriorly and dorsally with the frontal and dorsally with the parietal. At the inflection of the ventral and lateral surfaces of the laterosphenoid is an opening that presumably was associated with the anterior channel for the passage of the mid-cerebral vein

There is an unossified zone (Fig. 5) in the ventral surface of the anterior cranial region. This zone is bounded externally by the laterosphenoid, anteriorly by the orbitosphenoid, and posteriorly by the prootic. Apparently cranial nerves III and IV exited through the lateral edge of this zone, which was bounded by the medial edge of the ventral surface of the laterosphenoid.

The orbitosphenoid is contiguous with part of the bottom of the anterior region of the cerebral cranium in front of the unossified zone. The anterior boundary notch in this zone apparently corresponds to the exit for nerve II. In the anterior region of the orbitosphenoid, along the midline of the skull, is an opening into which enters a groove, extending from the exits for nerves III–IV. The possibility that a branch of the orbital or ophthalmic arteries ran through the opening from the exit for the lateral oculomotor nerve cannot be excluded. The ophthalmic artery of lizards passes through the exit for the optic nerve; in turtles this artery is associated with the opening for nerve III and is called orbital (Romer, 1956).

The paired presphenoids form the bottom of the olfactory tract, settling in front of the orbitosphenoid. The presphenoid is covered dorsally by the frontals.

The mandible of oviraptorids (Fig. 7) is characterized by its great height and openness in the anterior half and by the development of a large, dorsally located adductor process.

The dentary forms a massive base for the horny chin and two processes by means of which it joins movably with the posterior half of the mandible. The ascending process has a deep fissure at its end, into the groove of which enters the wedge-like, compact process of the surangular. The ventral process overlaps the anterior end of the angular externally and reaches the anteroventral edge of the surangular. The large mandibular fenestra is located between two processes on the dentary and the anterior edge of the surangular.

The surangular has a highly developed dorsal adductor process. Part of the anterior edge of the bone bounds the mandibular fenestra posteriorly and is divided into two unequal segments by a wedge-like process. Behind this fenestra, on the lateral surface of the bone, is a large elongated depression for attachment of the adductors of the mandible.

The articular has a broad, convex articulation surface and a flat retroarticular process.

The prearticular covers tile medial side of the articular and forms a long narrow process anteriorly that extends along the ventral edge of the mandible to the mandibular fenestra.

The angular extends from the base of the retroarticular process along the edge of the mandible. The anterior end of the bone is wedged between the splenial (medially) and the ventral process of the dentary.

The splenial has a very narrow posterior end located between the anterior process of the prearticular (dorsally) and the angular (ventrally). The anterior end of the splenial has a slight expansion that reaches the inner surface of the base for the dentary chin.

The basic adductors of the mandible (Fig. 8) in theropods form three groups—internal, external, and posterior (Luther, 1914; Lakjer, 1926). They were reconstructed by comparing the most thoroughly studied and in part the mandible of herbivorous dinosaurs that were similar to oviraptorids (Lull, 1933; Russell, 1935; Haas, 1956; Ostrom, 1961, 1964, 1966).

The highly developed adductor process on the mandible of oviraptorids performed the same role as the coronoid process in herbivorous dinosaurs and lizards. We may therefore consider the area of this process (the dorsomedial rugosity area) to be the attachment point for one of the fundamental internal mandibular adductors—m. pseudotemporalis, originating on the wall of the infratemporal foramen, presumably near parietal-basisphenoid joint.

The thick pterygoid significantly widens near its joint with the ectopterygoid and has prominent dorsal and ventral surfaces here. The pterygoid bears witness to developed muscles of the internal adductor group (m. pterygoideus). M. pterygoideus dorsalis is presumed to have its origin on the dorsal concave surface of the broad area of the pterygoid-ectopterygoid complex and the lateral flange of the pterygoid, whereas m. pterygoideus is on the ventral concave surface of this complex. On the mandible these muscles are attached to part of the ventral edge anterior to the base of the retroarticular process on both sides below the mandibular joint.

Among the external adductors the medial and superficial muscles (mm. adductores mandibulae externus medialis et superficialis) presumably attached at the wide lateral surface of the surangular posterior to the mandibular fenestra. It is possible that these muscles (or one of them, the medial) extended anteriorly, covering the fenestra, and attached to its anterior arc-like edge that was formed by the ascending and posterior processes of the dentary. In this case these muscles were more efficient when adducting the mandible because the forces they developed drew food into the mouth. It is presumed that the wide lateral depression on the narrow region of the surangular anterior to the mandibular joint was also a point of attachment for these muscles (or one surface muscle). Both muscles presumably originated on the medial side of the supratemporal arch, as occurs in lizards (Oerlich, 1956) and herbivorous dinosaurs (Ostrom, 1961, 1964).

The extended region on the posterior slope of the adductor process and its medial edge may have been an attachment point for the deep muscle in this group (m. adductor mandibulae profundus externus), whereas it originated on the wall of the infratemporal opening posterior to the pseudotemporalis muscle.

The muscle in the posterior group (m. adductor mandibulae posterior) attached near the deep, wide adductor fossa on the medial surface of the surangular posterior to the mandibular fenestra (this muscle may have extended anteriorly), attaching to the medial surface of the anterior edge of the fenestra which, just as with the adductors of the external group, could have increased its efficiency when adducting the mandible. The posterior muscle originated at the posterior edge of the lateral temporal fenestra, surrounding the long prequadrate process of the squamosal and the edge of the quadrate adjacent to it.

Kinetic Structure and Peculiarities in the Maxillary Apparatus Mechanism

The oviraptorid skull is morphologically quite theropod, despite a number of distinctive features. However, in a kinetic sense, it is extremely unique.

As we know, in the kinetic skull of several predatory reptiles there are two basic segments—the maxillary and cerebrocranial (the occipital, according to Versluys, 1910, 1912). It is quite possible to distinguish these segments in many theropods. A similar distinction in the skull of oviraptorids is meaningless in the kinetic sense because merging (rigid connection) of the basic elements of both segments into a kinetically uniform whole occurs. The maxillary segment breaks down into what is kinetically a completely independent subsection. The result is that the kinetic structure of the skull is quite different than that of other theropods.

We will examine the kinetic structure of the oviraptorid skull (Fig. 9). The skull of these dinosaurs has three subdivisions, two of which are mobile. The first mobile subdivision is the rostral unit comprising the premaxilla, which serves as the base for the horny culmen. The second subdivision comprises specifically the maxillary unit, including the premaxilla and vomer, which have fused to form a unit. The third, immobile, subdivision is a large part of the skull comprising the immovably fused (other than the jugal) posterior elements of the maxillary and the entire cerebrocranial (in a metakinetic sense) segments of other reptiles.

The first two sectors of the oviraptorid skull are mobile relative to each other and to the third, immobile, sector. Thus, the rostral sector has a mobile (presumably sliding) joint with the nasal and lacrimal, which belong to the cerebrocranial segment, and with the premaxillary sector as a whole. The latter is movably joined in a similar manner with the lacrimal and jugal and forms an articulation with the pterygoid (the cerebrocranial segment). The jugal occupies a special location in the cerebrocranial segment. It was probably weakly secured at its contact with the lacrimal by the postorbital and quadratojugal. In principle, the jugal could be distinguished as an independent segment; however, it joins with the immobile parts of the unified cerebrocranial segment and could hardly have played any significant role in kinesis.

We will examine the nature of the mobility in the rostral and premaxillary sectors. The axis of rotation in the rostral unit is situated near the upper arch of the external narial fenestra and perpendicular to the plane of the mobile anterior upper-premaxillary and anterior medial processes of the nasal. Due to the fact that at other points the premaxilla connected with the adjacent bones by a more or less loose abutment, when rotating about this axis—called the rhynchokinetic (by analogy with rhynchokinesis in birds)—the premaxilla slides along its respective contacts.

We must return to one curious feature. As we mentioned, there are four small foramina near the medial edge of the nasal, three of which lie in a row; the fourth lies somewhat to the outside of the first (Figs. 1, 8). These foramina presumably indicate a syndesmotic relationship between the nasal and horny culmen that covers the premaxilla. A similar relationship in the Anseriformes (Möller, 1969) reinforces the flexible zone of the culmen which was prone to movement when the rostrum opened and closed. The presumably syndesmotic relationship between the culmen (rostral sector) and nasal (cerebrocranial sector) in oviraptorids may have performed a similar function.

The axis of rotation for the maxillary unit is in an unexpected location—in the joint formed by the posterior end of the vomer and the vomerine process of the pterygoid (Fig. 3). The development of this joint, unknown in other reptiles, is a fundamental confirmation of the kinetic independence of the maxillary sector. The axis of rotation of this sector, distinguished here under the term infrakinetic, is perpendicular to the plane of symmetry of the skull. The maxillary sector, like the rostral sector, has adjoining contacts with the adjacent elements and during rotation slides along the contacts.

The oviraptorid mandible, as in other predatory dinosaurs, comprises two fundamental subdivisions—the anterior, formed by the dentary (serving as the base for the horny culmen) and the posterior, which includes all the remaining components of the mandibular ramus (Fig. 9). The mobility of the connection in both subdivisions is noteworthy: the ascending process of the dentary (the anterior subdivision) has an expansion at its end, into which the abutting process of the surangular (the posterior subdivision) is deeply wedged. The contact on the ventral process of the dentary is adjoining, which allows it to slide along the adjacent edge of the surangular (the posterior subdivision). The anterior subdivision of the jaw might have rotated about the axis perpendicular to the plane of the groove connection on the ascending process of the dentary with the surangular. In this case the posterior end of the ventral process of the dentary slid for a limited distance along the ventral edge of the mandible.

The rostral and maxillary sectors and the anterior subdivision of the mandible all participated in crushing food. The kinetic subdivisions of the skull and the mandible had to go into motion when the jaws were crushing food because counterpoint forces arose. Two basic positions for food in the mouth can be identified (Fig. 10).

1. Food in the anterior region of the jaw, between the rostral sector and the anterior subdivision of the mandible. The counter-force sets both kinetic subdivisions, the rostral and anterior mandible, into motion.

2. Food more deeply in the mouth, involving the maxillary sector; the rostral sector remains conditionally motionless and the anterior subdivision of the mandible acts as in the situation above. Any interceding position relies on including one of the kinetic units. When food is at the interface between both units, they might have moved in unison.

One significant peculiarity in the jaw structure of oviraptorids is profound—the development of powerful crushing forces. This is seen in the short working surfaces of the jaws along with the reduced length of the mandibular lever arm, all of which increase the force applied by the muscles. The development of the adductor process on the mandible elevated—relative to the axis of the lever arm—the point at which force was applied (Ostrom, 1964) and was governed by the same objective—to increase strength and thereby produce greater crushing forces. Also, in the comparatively small skull the adductor fossa is disproportionately large, confirming the development of massive adductor muscles. Noteworthy is the rostrum. It was laterally compressed, which increased the pressure that the jaws could have applied per unit area of food. It was previously mentioned that the paired vomer is equipped with a lengthwise edge knob, which suggests it participated in creating pressure on food from the crushing forces of the jaws. The connecting line on the "buccal" region of their working surfaces is not horizontal as in other theropods, including the edentate ornithomimids, but sloped due to the convexity of the anterior mandibular arch.

If the angle of the connecting line of the jaws and the force (F) applied to food is shown graphically (Fig. 11) then the component vector (F_1) is directed along the connecting line of the jaw. In this case the food must counteract the applied force.

From what has been said, we may conclude that the edentate jaws of oviraptorids were adapted to crushing food that was harder and more solid. What might oviraptorids have eaten? We think they may have eaten mollusks. In crushing mollusk shells, the danger to oviraptorid jaws might have been mechanical damage. The mobility of the kinetic subdivisions of the skull ensures amortization of the subcritical loads on the jaws. Connection of the jaws along the sloped line when chewing especially hard food eases its rapid withdrawal from the action of crushing jaws.

We must pause briefly to discuss monimostyly in oviraptorids caused by morphological features in their skull structure.

The uniqueness of the oviraptorid skull is also seen in the monimostyly (immobility of the quadrate). We said earlier that their pterygoid is fused with both the base of the basisphenoid and with the quadrate. In the metakinetic skull of predatory reptiles, the pterygoid and quadrate belong to the maxillary sector (Frazzetta, 1962; Russell, 1964, 1967). However, in the oviraptorid skull they belong to the cerebrocranial segment. The fusion of these three elements produces a rigid structure that prevented any mobility in the quadrate. The fixing of this structure as the support for the mandible is useful when heavier loads are applied to the latter. Consequently, the oviraptorid skull was at the same time both monimostylic and kinesis.

There are examples where a specific streptostyly is seen in the akinetic skull of some hadrosaurs (Ostrom, 1961). The streptostyly in toothed theropods may be fairly developed, which is associated with a type of kinesis other than is found in theropods. In ornithomimids, the second group of edentate theropods, monimostyly in a metakinetic skull is presumed (Osmólska, et al., 1972).

OVIRAPTORID ECOLOGY

At present we can say that there were bodies of fresh water in Mongolia and other expansive regions of Central Asia during the Late Cretaceous in which mollusks occupied a primary position. These belonged mainly to the families Trigonioididea (bivalves) and Ampularridae (Gastropoda), representatives of which were distinguished by their thick, strong shells (Martinson, 1961; Barsbold, 1972). Massive accumulations of these are found quite often and in the bone-bearing layers of many ancient reptile graveyards, such as the Nemegt, Bugin Tsav, Khermin Tsav groups, and others so that the oviraptorid food supply must have been ensured. Naturally, it is difficult to confirm that the oviraptorid diet was more diversified. It may have included reptile eggs, entire nests of which were entombed in these same bone-bearing layers. The specialization of the oviraptorid jaw apparatus argues that their food was more solid than eggs.

Oviraptorids must have developed a number of specific adaptations from feeding on mollusks that might have given them the ability to swim. The high location of the external narial fenestrae may be one indicator of such a lifestyle. In the postcranial skeleton, an examination of which is beyond the scope of this article, are a number of features that draw our attention to this possibility. Thus, the neural and haemal processes of the caudal vertebrae are very long, which is typical of the tail found on reptiles capable of swimming. Even more significant, it seems that in the tridactyl manus of oviraptorids the second and third digits are very small and thin, but did not lose their full complement of phalanges. Typically the ungual phalanges on these digits are narrow and very small, whereas on the first digit this phalanx is distinctive because of its large size, mass. and curvature. This is an important argument that swim membranes may have developed on the digits of the manus. In feeding on mollusks the oviraptorids were most likely capable of swimming and diving to capture food with their massive rostrum and, probably, membranous manus with sharp claws that did not lose the typically theropod “grasping” features.

We may assume that oviraptorids were amphibiotic. The flooding of land masses and the widespread development of hydrographic networks during the Late Cretaceous promoted the development of ecological niches favorable to oviraptorids and freed them from competition with other predatory dinosaurs. The ecological uniqueness of oviraptorids is yet one more piece of evidence for the wide radiation of dinosaurs prior to their extension at the end of the Mesozoic.

LITERATURE CITED

(Not included.)

FIGURE CAPTIONS

Fig. 1. Oviraptorid skull, Khermin Tsav, lateral view (reconstruction).

ant_1 – antorbital foramen; ant_2 – accessory antorbital foramen; co – occipital condyle; f – frontal; j – jugal; l – lacrimal; lf – lateral temporal fenestra; mx – maxilla; n – nasal; nr – external narial fenestra; or – orbit; pa – parietal; pmx – premaxilla; po – postorbital; pq – pterygoid flange of the quadrate; q – quadratojugal; so – sphenooccipital tubercle.

Fig. 2. Oviraptorid skull, Khermin Tsav, ventral view (reconstruction).

bs – basisphenoid; ect – ectopterygoid; if – infratemporal fenestra; in – internal narial fenestra; pt – pterygoid; q – quadrate; v – vomer; vpt – vomerine process of the pterygoid.

All other nomenclature is the same as in Fig. 1.

Fig. 3. Vomer-pterygoid joint (reconstruction, lateral view).
All nomenclature is the same as in Figs. 1, 2.

Fig. 4. Braincase of the Khermin Tsav oviraptorid, lateral view (reconstruction). The bones in the orbital and temporal (from the suspensorium) regions were displaced.

fo – foramen ovalis; fs – fenestra associated with the sinus system; lt – laterosphenoid; op – opisthotic; orb – orbitosphenoid; pre – presphenoid; pro – prootic; vm – opening for the mid-cerebral vein; n.z. – unossified zone; V, VlI – exits for the respective cranial nerves.

Fig. 5. Braincase of the Khermin Tsav oviraptorid, ventral view (reconstruction). The bones in the orbital and temporal (from the suspensorium) regions were displaced.

oa – canal for the orbital artery; olt – passageway for the olfactory nerve.

All other nomenclature is the same as in Figs. 1 and 4.

Fig. 6. Skull of the Khermin Tsav oviraptorid, posterior view (reconstruction).

bo – basioccipital; bpt – basipterygoid process; ex – exoccipital; fm – occipital foramen; fv – foramen for the premaxillary vein; soc – supraoccipital.

All other nomenclature is the same as in Figs. 1, 2, and 4.

Fig. 7. Mandible of the Khermin Tsav oviraptorid, lateral view (reconstruction).

ad – adductor process; emf – external mandibular fossa; d – dentary; rt – retroarticular process; sa – surangular.

Fig. 8. Basic adductors that closed the mandible in oviraptorids (reconstruction).

1 – m. pseudotemporalis; *2* – m. pterygoideus (dorsalis, ventralis); *3* – mm. adductores mandibulae externus medialis, superficialis; *4* – m. adductor mandibulae externus profundus; *5* – m. adductor mandibulae posterior.

The location at which the syndesmotic connection between the horny culmen and nasal developed is shown by an arrow and a heavy dotted line.

Fig. 9. Kinetic subdivisions of the oviraptorid skull and mandible (schematic).

cr – cerebrocranial segment; mx – maxillary sector; r – rostral sector; *1* – anterior subdivision of the mandible; *2* – posterior subdivision of the mandible.

Fig. 10. Two positions for food in the mouth of an oviraptorid (schematic).

1 – in the rostral sector and the anterior subdivision of the mandible; *2* – in the premaxillary sector and posterior subdivision of the mandible; ic – infrakinetic axis; ms – mesokinetic axis; A – axis of rotation for the posterior subdivision of the mandible. Fine lines indicate the location of the kinetic subdivisions during rotation about the respective axes as a function of where the food was positioned in the mouth. Arrows indicate the directions of rotation for these subdivisions. Thick lines show the attachment of the basic adductors in the mandible.

Fig. 11. Vectors of the force applied to food. The force arose during compression by the jaw (schematic). F_1 enables the food to be extracted from under the influence of the applied force.