"AVIAN" FEATURES IN THE MORPHOLOGY OF PREDATORY DINOSAURS[*]

The similarity between predatory dinosaurs and *Archaeopteryx* that in the past was known in only general features has recently been revealed (Ostrom, 1973, 1975a, b, 1976a). This similarity provides in no small measure a reason to think of theropods as the ancestors of birds, provoking thoughts of dinosaurs as possibly being warm-blooded animals having those inherent biological and ecological characteristics. New schemes for classifying sauropsids are being proposed that emphasize the close relationship between dinosaurs and birds (Bakker, 1971, 1975; Galton, 1970; Bakker, Galton, 1974; Thulborn, 1973, 1975; et al.). Similar opinions are disputed on the basis that, among other things, many researchers feel that dinosaurs were "cold-blooded" reptiles (Budylko, 1978; Bennet, Dalzell, 1973; Bennet, 1974; Feduccia, 1973, 1974; Hopson, 1976; et al.). Interest in the problem of the interrelationships between birds and dinosaurs has attracted the author's attention to primarily the "dinosaur" component, knowledge of which has recently been significantly expanded (Barsbold, 1982).

A comparative morphology of Mongolian predatory dinosaurs based on more complete material confirms the similarity between theropods and *Archaeopteryx* and reveals a number of new features (Barsbold, 1979, 1982). It is noteworthy that most of these features outwardly bear an "avian" character, whereas in the recently established similarity of theropods and *Archaeopteryx* (Ostrom, 1976a) the "dinosaur"—more precisely, the "theropod"—features dominate quite distinctively. The features examined below are confined only to those that were first encountered in the new Mongolian material. At the same time, these features are a fair illustration of the theropod origin of the "avian" features in the skeleton of *Archaeopteryx*.

Facial Crest. Oviraptorids have a high, unpaired lengthwise osseous outgrowth (Barsbold, 1979, 1982) that extends above the external nasal fenestrae from the dorsal region of the premaxilla to the anterior edge of the frontal bones inclusive (Fig. 1). The large posterior region of the crest was formed by the nasal bones. The lateral surface of the crest is openwork that consists of a network of thin osseous trabeculae. It is possible that the looser osseous tissue was not preserved in a fossilized state. The anterodorsal edge of the more solid edge of the crest had long narrow paired fenestrae (or pockets), the purpose of which is unclear, separated by a thin membrane. The depth of the fenestrae might have been limited by the height of the osseous edge (approximately 1 cm), or they were loosely associated with the narrow space between the crest walls. In all probability the crest was covered with a corneous helmet as is seen in cassowaries, the osseous base of which was fairly loose. In contrast with oviraptorids, the cassowary crest occupies the top of the skull right up to the occipital bones inclusive; i.e., the similar feature in birds becomes more specialized.

The function of the crest in oviraptorids and cassowaries is unclear. It may be an indicator of sex (maturity). There are indications that cassowaries use it to move thick brush, however this is hardly its main function. Because the skull was so poorly preserved, the first description of *Oviraptor* (Osborn, 1924) proposed the development of some sort of nasal horn that, in fact, proved to be the osseous base of the crest.

Middle ear cavity. The middle ear in dinosaurs is usually seen without osseous walls (more precisely, only with an internal osseous wall), which is comparable to modem reptiles. A middle ear cavity with osseous walls (Fig. 2) was first discovered in *Saurornithoides* and was called a "lateral depression" for descriptive purposes (Barsbold, 1979). This cavity was subsequently discovered in the segnosaurid *Erlikosaurus* (Barsbold, 1979; Perle, 1979). In these circumstances the bone-formed middle ear cavity resembles a capacious depression occupying the space bounded posteriorly by the paroccipital and anteriorly by the basipterygoid processes. In *Saurornithoides* the anterior region is made up of mainly the basisphenoid, the dorsal edge is the prootic bone, the posterior edge is the base of the paroccipital process, the ventral edge is the exoccipital and basioccipital bones, and the medial wall of the cavity is a pneumatic bone. Beneath the dorsal edge of the cavity is a long opening, presumably identified with the exit for nerve VII. Also, birds have an opening in a comparable location that attaches the middle ear cavity with the air sinuses inside the skull. On the outside and above the cavity edge is an opening for the trigeminal nerve. The posterior boundary of the cavity is occupied by a large opening that corresponds to the fenestra ovale, from which a shallow stapedial furrow extends along the anterior wall of the paroccipital process. Anteroventral to the fenestra ovale, close to the ventral edge of the cavity, are openings through which the sinuses open into the middle ear cavity. The cavity is covered on the outside by an area of the quadrate-pterygoid articulation that was well preserved in *Erlikosaurus*. This results in the cavity orifice being covered throughout most of its extent by a dual wall: the outer wall extends from the medial lobe of the quadrate bone and the inner wall extends from the pterygoid. The cavity is covered from behind the quadrate stem by a long, oval otic notch that bounds the outer ear. The avian middle ear cavity differs from that of the dinosaur in that only the periotic and exoccipital bones create it, whereas in dinosaurs the basisphenoid, which apparently is more primitive, is also a component.

Palatal complex (Fig. 3). A rather unusual palatal complex morphology is encountered in *Erlikosaurus* (Barsbold, 1979, 1982; Perle, 1979). The vomers have extremely long and wide plate-like projections that fuse ventrally to form a structure that is V-shaped in cross-section. The posterior wedge-shaped end of this structure extends almost to the basicranium, connects more dorsally with the pterygoids, slightly separates them more ventrally, and encloses the low edge that is compressed from the sides of the basisphenoid rostrum. The pterygoids are distinguished by their reduced size, their vomer processes are noticeably short and tightly abut the basicranium. More complete features with a similar morphology appear the palate of ostriches and especially in cassowaries, which have a palaeognathic palate. The palaeognathy in this segnosaurid, however, has a supposedly more primitive character. Features that are accepted as initially palaeognathic reduce to the following (Barsbold, 1979, 1982): very long vomers (in palaeognaths the anterior boundary of the basisphenoid rostrum lies between the diverging pterygoid processes of the vomers); reduction of the pterygoids, especially their vomer processes (this reduction in the processes is even more intense in the palaeognaths). Also, a number of typically palaeognathic features that may subsequently have been acquired are missing from the palate of *Erlikosaurus*—the juncture of the palatal bones with primarily the pterygoids and the divergence of the vomerine pterygoid processes.

Sternum. Data concerning the sternum in dinosaurs is almost nonexistent. This deficiency has now been eliminated due to several discoveries belonging to Mongolian dromaeosaurids and oviraptorids (Barsbold, 1979, 1982). The sternum (Fig. 4) is a lamellar, shield-like structure, convex anteriorly and concave posteriorly. Its configuration is fairly complex, the cranial edge is straighter as in *Velociraptor*, or forms wide, smooth notches on both sides of the central

prominence as in oviraptorids. This edge has narrow grooves into which the peripheral zone of the coracoids was inserted. The lateral edges of the sternum are very notched and thin, and apparently may have become the cartilaginous framework that attached the ribs.

Clavicles. Dinosaur clavicles are rarely found in a fossilized state, and when found they are poorly preserved. The remains of *Oviraptor* and *Segnosaurus* clavicles were initially described as interclavicles (Osborn, 1924; Camp, 1936). Recent *Oviraptor* discoveries have revealed a full representation of this structure in theropods (Barsbold, 1976a; Barsbold, 1979, 1981).

Oviraptorid clavicles (Fig. 5) in their general features resemble the wishbone of birds and are an arch-shaped structure with widely diverging rami that are convex anteriorly. The ends of these rami flatten into a wedge and dwindle to nothing. The area where the rami diverge has a wedge-shaped, caudally-oriented process. The clavicles are attached by their flattened ends with the scapular acromions. The forward edges of the scapulae are very thick and bend outward, forming fairly wide areas that are long and triangular and receive the flattened ends of the clavicular rami. The clavicles of *Archaeopteryx* are very similar to those of oviraptorids, but the means by which they attach to the scapula is not clear. However, from photographs of the pectoral girdle in the London specimen and from data obtained through a painstaking reconstruction by J. H. Ostrom (Ostrom, 1976a, Fig. 23; 1976b, Fig. 8), the anterior edges of the acromions in *Archaeopteryx* correspond precisely to those in oviraptorids and form the very same articular areas. With this in mind, we can say with almost complete certainty that the acromions in *Archaeopteryx* were specially adapted to attach to the ends of the diverging clavicular rami. Until now this fact has gone unnoticed because the exact location of the clavicles in the pectoral girdle was unknown. In birds the clavicles attach to the coracoids, which is probably associated with the evolution of their forelimbs into wings.

Opisthopubic pelvis. It has recently been shown that the pubic bone has been reoriented to lie parallel to the ischium in the saurischian pelvis of some theropods (Barsbold, 1976b, 1979, 1982; Perle, 1979; Barsbold, Perle, 1979; Barsbold, 1979; Barsbold, Perle, 1980). Rotation of the pubic bones has been established in Mongolian dromaeosaurids and segnosaurids, whose pelvic morphology in other respects is quite different (Fig. 6).

The dromaeosaurid pelvis, with the exception of the rotated pubic bones, is completely coelurosaurid in nature—the low ilia are dolichoiliac (Colbert, 1964) and the short ischia with large obturators clearly confirm this. The pubic bones, directed ventrally and posteriorly, are distinguished by their length and that their distal ends are laterally compressed. The segnosaurid pelvis deviates almost entirely from the theropod norm. Its ilia have an unusually wide anterior side that is arched sharply to the outside, and a reduced posterior side that dorsally bears a large cube-shaped outgrowth which was possibly used for attachment of the pelvic-femur and caudal muscles. In general, the configuration of the ilia are similar to the sauropod type (Perle, 1979). The pubic bones have large distal ends that are laterally compressed and directed ventrally and posteriorly. The ischia are slightly shorter than the pubic bones and their large obturators are displaced dorsally. Along the posterior side of the ischia, opposite the obturators, are smooth ridge-like convexities.

Evolution of Theropods and *Archaeopteryx*

The propubic pelvis is usually thought to be the predecessor of the ornithischian pelvis; however, there is no convincing proof of how such a metamorphosis might have occurred (Beer, 1954; Romer, 1927, 1956; Galton, 1970; Charig, 1972, et al.).

J. H. Ostrom (1976a), who has made the greatest contribution toward revealing the similarity between theropods and *Archaeopteryx*, had incomplete material with regard to the pelvis of the American dromaeosaurid *Deinonychus*, and for him an appearance of rotation in the pubic bones remained almost unknown. The rotation observed in the pelvis of the Berlin specimen was rejected by Ostrom, who explained it as being due to interment. At the same time, he apparently understood that the posterior rotation of the pubic bones in *Archaeopteryx* could not be explained merely by displacement after interment, which led him to the concept of a partial and incomplete reorientation in the pelvis of both animals. He thereby eliminated the most fundamental obstacle on his road to establishing similarity between Cretaceous theropods and *Archaeopteryx*, which in other respects has been shown very convincingly.

Another researcher (Walker, 1977), supporting quite another concept—kinship between crocodiles and birds—adapted the posterior rotation of the pubic bones in *Archaeopteryx* pelvis and therefore, apparently quite artificially, rotated posterior the pubic bones of a Jurassic crocodile (*Hallopus*)[1]. Walker emphasized that in order to recognize kinship between theropods (Saurischia) and birds it was necessary that the pubic bones in theropods should undergo a reorientation that, as he supposed, cannot be complete.

It is quite obvious that Ostrom and Walker, proponents of very different concepts, acted uniquely to overcome the same obstacle: they both tried to make the pelvis of each animal in their group similar in morphology to that of *Archaeopteryx*. In this regard it must be borne in mind that opisthopuby is still fairly unknown to researchers unfamiliar with the Mongolian material.

The opisthopubic saurischian pelvis may be interpreted as the "transition" from the original propubic pelvis to the derived ornithischian. The opisthopubic saurischian pelvis is encountered several times during the evolution of Saurischia, which is demonstrated by several groups of predatory dinosaurs—*Deinonychus* (dromaeosaurids), segnosaurids, and also with high probability *Archaeopteryx*. It is the ornithischian pelvis that is essentially opisthopubic, only more modified with the specific adaptations of herbivorous dinosaurs. The multiple, and apparently at different times, appearance of the opisthopubic pelvis reflects the parallel evolution of dinosaur lineages, so sharply revealed in predatory groups during the development of many skeletal morphologies (Barsbold, 1977, 1982; Barsbold, 1979).

Archaeopteryx, extremely similar to late predatory dinosaurs, could hardly begin its ascent directly from the Pseudosuchia branch without passing through the "dinosaur", or more precisely the "theropod", stage that is part of the early period of their evolution. It is namely here that the explanation for their very close similarity with late predatory dinosaurs can be found. Since an independent *Archaeopteryx* lineage supposedly was formed sometime during the transition between the Triassic and Jurassic among a large number of parallel lines of late theropods, departing from these kindred groups by an increasing evolutionary shift leading that led them to develop in a specific adaptation zone that was not innate to theropods.

An entire set of "avian" features was widely disseminated in parallel lineages of Late Triassic predatory dinosaurs. In not one of these late theropod lineages in which these features had been more distinctly formed is a complete set of similar features. In other words, the dissemination of these features as a whole is considerable. All the same, two categories of these features are distinguishable: the first category contains those features that are almost universal among predatory

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[1] That *Hallopus* is a crocodile which ordinarily belongs to the theropods is as yet unproven.

dinosaurs—the "avian" feet, the morphology of the forelimbs, etc. which are characteristic for late lineages (Barsbold, 1977). The second category contains features that are more specific: an "avian" middle ear that has disappeared in saurornithoidids and Segnosauria, the arch-shaped clavicles in oviraptorids (and *Archaeopteryx*), etc. It may be assumed that in the lineage similar to that of *Archaeopteryx* the most prominent avian features were combined together (Simpson, 1946). This means that in the dinosaur, more precisely the theropod, lineages "ornithization" took place fairly early. During this process, which was in its initial stages during the Late Triassic development of theropods, lineages were formed that led to birds. It is easily assumed that *Archaeopteryx* is merely one of those lineages (even if a dead end), but regardless of the extent to which "real" birds deviate from it, the similarity to its theropod ancestor is visible. Along with this, the ratite sternum and supposedly original palaeognathic palate in some predatory dinosaurs probably bear witness that the evolution to birds was accomplished through more than one parallel lineage that gave rise to theropods which lived during the time of the Triassic-to-Jurassic transition. Ratite and non-ratite birds may belong to different but kindred lineages that branched off very early from common ancestors that were directly associated with late theropods. Ratites developed a number of features in parallel with non-ratites, although in a different adaptation zone.

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FIGURE CAPTIONS

Fig. 1. Skull and lower jaw of *Oviraptor philoceratops* (SPS specimen 100/42), from the right; the large crest has paired fenestrae indicated by the arrow. Dots are used to indicate the lateral surface of the crest that has been destroyed.

Bo) Basioccipital; F) Frontal; Il) Ilium; Is) Ischium; L) Lachrymal; Ls) Laterosphenoid; Mx) Maxilla; N) Nasal; Or) Orbit; Pl) Palate; Pm) Premaxilla; Pr) Prootic; Qu) Quadrate; Sc) Scapula; as) acromion; bsc) basisphenoid capsule; bpt) basipterygoid; cam) middle ear cavity; cpb) parabasal duct opening; cr) crest; cor) coracoid; f) clavicles; fcor) coracoid fenestra; Op) Opisthotic.

Fig. 2. Middle ear cavity of *Saurornithoides junior* (SPS specimen 100/1), from the left; inside the cavity traversing the crest of its medial wall with air sinuses and openings (for the egress of the cranial nerves and fenestra ovalis).

Fig. 3. Palatal complex of *Segnosaurus galbinensis* (SPS specimen 100/111), in plan view from below; the separating posterior end of the vomers encloses the boundary of the basisphenoid rostrum.

Fig. 4. Sternum of oviraptorid and dromaeosaurid from the front. a) *Ingenia yanshini* (SPS specimen 100/42); b) *Velociraptor mongoliensis* (SPS specimen 100/25).

Fig. 5. Clavicles and their attachment to the acromions in *Oviraptor philoceratops* (SPS specimen 100/42): a) clavicles, from the front; b) attachment of the clavicles to the acromions, from the right.

Fig. 6. Opisthopubic pelvis from the left (no scale): a) segnosaurid (*Segnosaurus galbinensis*, SPS specimen 100/111); b) dromaeosaurid (*Adasaurus mongoliensis* SPS specimen 100/20).