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MODIFICATION IN THE SAURISCHIAN PELVIS AND THE PARALLEL DEVELOPMENT OF PREDATORY DINOSAURS*

Dolichoilia and brachyilia. Colbert (1964, 1970) isolated two pelvic structure types in predatory saurischians (Fig. 1): brachyilia in the prosauropods (a short anterior flange on the ischium, Fig. 1a) and dolichoilia in theropods (the anterior flange is long, Fig. 1b-j). Doing this, fundamentally, drew a possible line of demarcation between the most ancient groups of predatory prosauropod and theropod saurischians. The Triassic "carnosaurs", representatives of which have been assigned to prosauropods and theropods (Charig, et al., 1964), have a brachyiliac pelvis and are quite distinct from theropods, which is consistent with the specific nature of the mesotarsal joint structure in both groups. The brachyilia has made the commonality of prosauropods even more profound. In these prosauropods, however, differences in the methods of feeding and locomotion have already been noted in the infraorders Teratosauria and Plateosauria (Colbert, 1970). Teratosaurians were predators and had primitive bipedalism (which is not excluded from the vegetarian plateosaurians). This distinction may be completely justified, but the variety and insufficiency of material creates problems for formalizing, at least, the first of the taxa.

The distinction of the saurischian pelvic structure holds promise in two respects (Colbert, 1964). First, the presumed thecodont ancestors of the Saurischia had brachyilia; second, the dolichoilia presumably answered in greater degree the fundamental direction of evolution in the most ancient Saurischia that was preserved at an even later stage of their development—the perfection of bipedalism and predation. It is highly likely that in the early stage of saurischian development this was the main path for their most ancient branches (or one of the main paths if we assume that the sauropods might have originally developed as four-legged animals (see Charig, et al., 1965). For predatory Saurischia the extent of movement in the fundamental evolutionary direction is reflected in the brachyilia and dolichoilia. Brachyilia is associated with undeveloped bipedalism and less intense adaptation to predation. Dolichoilia most likely responded to the perfection of two-legged locomotion and accompanied the intensification of predatory features (teeth and the perfection of the "capturing" function of the wrist). The extinction of brachyiliac Saurischia (and thecodonts) at the end of the Triassic and during the transition from the Triassic to the Jurassic and the immense diversity of the latter in the late Mesozoic quite fundamentally show that dolichoilia was fundamental to the development of two-legged (and predatory) Saurischia (Barsbold, 1976).

Other modifications of the saurischian pelvis. Brachyilia and dolichoilia are, however, not the only features of the saurischian pelvis. Mongolian theropod material offered two new fundamental modifications in the saurischian pelvis that went beyond the changes that were normally seen in this extremely pliable, as it turned out, structure.

The first modification was confirmed in animals related to the family Dromaeosauridae (Fig. 1h) (Matthew et Brown, 1922). This modification is an inverted pubis rotated to the rear and

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downward instead of the usual forward and downward rotation (Barsbold, 1976). Consequently, the pubis is parallel to the axis of the ischium. Otherwise, the pelvis retains its theropod features—an undisputed dolichoilia, low ilium height characteristic of Cretaceous theropods, short ischium, a more distal displacement (to the center of the bone trunk) of the obturator process. In the future, for the sake of brevity, this modification could be called rotated dolichoiliac to distinguish it from the normal dolichoiliac found in true theropods. Along with this and the other features that distinguish the dromaeosaurid pelvis, the unusual enlargement of the edges of the posterior flange of the ischium calls attention to itself.

The second modification to the pelvis was found in a member of a new family of predatory saurischians from the Mongolian Late Cretaceous—the Segnosauridae Perle. The ilium in the *Segnosaurus* pelvis (Fig. 1j) had a very high and wide, laterally rotated anterior flange. The posterior flange, though, is short. In contrast to what is seen in true theropods, the ilia are quite far from the sacral spinous processes. A very distinct cubic projection developed in the dorsal region of the bone's posterior flange. This projection is presumably identifiable with the antitrochanter in ornithischians. The pubis has undergone an inversion that oriented it parallel to the ischium, just as in the dromaeosaurids. It also has a block-like distal enlargement. The ischium is approximately the same length as the pubis. The obturator process is displaced toward the distal end and connects with the pubis above this block-like enlargement (approaching it from the rear). The segnosaurid pelvis cannot be called dolichoiliac because the extreme shortness of the posterior flange removes it from any dolichoilia, including the rotated type. The segnosaurid pelvis is undoubtedly saurischian, having what looks like a reverse brachyilia in contrast to the normal brachyilia seen in prosauropods (palaeopods, according to Colbert, 1970), where the anterior flange of the ilium is short.

These modifications testify to major changes in the saurischian pelvis. If we compare these with the normal dolichoiliac pelvis, the rotated dolichoiliac dromaeosaurid pelvis has, other than the pubis inversion that we have already mentioned, no significant differences. The reverse brachyiliac pelvis in the segnosaurids is, other than the inversion, characterized by features that were heretofore unknown in a saurischian pelvis—the presumed antitrochanter; the very curved, extremely wide anterior flanges, and; the shortness of the posterior flanges on the ilia.

Pelvic musculature. An examination of some of these fundamental muscle groups may shed light on the meaning of the various saurischian pelvis modifications, wherein a comparison with the muscles of the ornithischian pelvis is quite relevant. The number of reconstructed protractors and retractors has been held to a minimum and been limited to those groups than can justifiably be included. The topography and terminology of the muscles are taken from familiar references (Romer, 1923a, 1927; Galton, 1969, 1970).

If we adopt the muscle topography in the normal dolichoiliac pelvis (Fig. 2a) as our baseline then the ornithischian pelvis, in which the pubis is reoriented to the rear and down, hypothetically strengthens the retractor action of the ventral muscles (*mm. pubo-ischio-femoralis externus et internus*), which in turn is compensated by the differentiation of *m. pubo-tibialis* attached to the prepubis (Galton, 1969, 1970). From here it follows that the conclusion regarding the homologization of the pubis with the prepubis is correct (Beer, 1954, thought that it homologized with the postpubis) (Romer, 1923a, 1927, 1956; Galton, 1969, 1970). In this situation the prepubis is a new growth. Strengthening of the protractor component, however, is accomplished by not only these—*m. iliofemoralis,* which attaches to the antitrochanter, is differentiated and is particularly well-developed in hadrosaurs and ankylosaurs.

The retractor action of the ventral pelvic-femoral muscles was also strengthened in the rotated dolichoiliac pelvis of the dromaeosaurids (Fig. 2c) when the pubis inverted, just as in the ornithischians. Protraction was hypothetically strengthened due to the great differentiation of *m. ilio-tibialis,* which attached in the area of the anterior flange of the ilium. This flange was separated into two lobes. The intense enlargement of the bone's posterior flange edges is associated with strengthening either the pelvic-caudal muscles or the hind limb flexors *m. flexor tibialis externus* and *m. ilio-fibularis.*

The inversion of the pubis in the segnosaurid pelvis (Fig. 2d) strengthened retractor action in the ventral muscles *mm. pubo-ischio-femoralis externus et internus* in exactly the same way. However, the extreme width and height of the anterior flanges of the ilia and especially their great curvature confirm that protraction of the separately differentiated *ilio-tibialis* compensated retraction of the ventral muscles. Auxiliary protractor action was achieved by strengthening *m. iliofemoralis,* which was attached to the antitrochanter as in the ornithischians. However, it is possible that there is an alternative version: contraction of the ilium's posterior flange may have weakened retractor action in spite of the pubis inversion. The flexors *mm. flexor tibialis externus et ilio-fibularis* were attached to the antitrochanter (or to a formation that was not homologous to it, although this is more difficult to conceive). This scheme was presumed to be in the dromaeosaurs and to thereby compensate retractor weakening.

Thus, inversion of the pubis in the various saurischian pelvic modifications could have strengthened retractor action in the ventral pelvic-femoral muscles; this is compensated by differentiation of the protractors and the morphological manifestations of this phenomenon are commonplace. A new growth, the prepubis, thus appears in the ornithischian pelvis. There is a distinct cleavage in the anterior flange of the ilium into two lobes in the rotated dolichoiliac dromaeosaur pelvis that is associated with differentiation of the protractor attached here. The anterior flanges of the segnosaur ilia were very enlarged and turned radically outward. Further, the antitrochanter confirms the strengthening of protractors in the ornithischian pelvis and may have performed a similar function in the segnosaurs; however, the contraction of the ilium's posterior flange suggests that the hind limb flexors may have attached to the antitrochanter. The very same thing may be assumed on the basis of the great enlargement of the ilium's posterior flange and the rotated dolichoiliac dromaeosaur pelvis.

PARALLEL DIRECTIONS IN SAURISCHIAN DEVELOPMENT

Where do these pelvic modifications; topographic changes, and muscle differentiations lead? To answer that question, we must look at additional data.

In all likelihood the normal and rotated dolichoiliac pelves were accompanied by a very long and compact (pressed together) foot structure that must be thought of as an essential adaptation to fast running in "lightweight" forms (Gambaryan, 1972). In this case the limb is characterized by distal lengthening, thinning, and overall compactness. In bipedal ornithischians (ornithopods) and segnosaurs, as in palaeopods (prosauropods) the foot is distinctly different—the metatarsus is short, but more massive, the lateral digits are usually large (although they may completely disappear in a number of groups). These features bear witness to an adaptation to relatively slow running in "heavyweight" forms (Gambaryan, 1972).

Comparing these features in the foot with the pelvic modifications, we can say that only animals with the normal and rotated dolichoiliac pelves were adapted to running in the lightweight forms, and it must be acknowledged as a fundamental direction in the evolution of these groups. Running in the heavyweight forms was characteristic for saurischians with the normal and reverse brachyiliac pelves, i.e. for bipedal prosauropods and segnosaurs and for bipedal ornithischians (ornithopods). In the overall scheme of rapid locomotion these groups did not fully master bipedal locomotion. They evolved in other adaptive zones. In this regard we can see the "inadaptiveness" of the palaeopods that did not survive beyond the Triassic and Jurassic.

In saurischian development, pubis inversion might have been accomplished in many phases, which is confirmed in part by the incompleteness of this inversion in *Archaeopteryx* (Wellnhofer, 1974).

A multiphase inversion may very well have taken place. Morphologically, *Archaeopteryx* is very similar to dromaeosaurs (Ostrom, 1973, 1974a, b, 1975), and the establishment of pubis inversion in both groups (Barsbold, 1976) merely supports their kinship. The Late Jurassic *Archaeopteryx* is similar to late dromaeosaurs that appeared only in the Cretaceous. Ostrom (1975) opines that the transformation from dromaeosaurs to *Archaeopteryx* occurred in the second half of the Jurassic period.

It is not clear as to when the segnosaur ancestors began to branch. Segnosaurs are a parallel branch of true theropods that developed in an adaptive zone that did not require fast bipedal running. The delicate structure of the lower jaw and the weak teeth suggest that they fed on fish and possibly led an amphibian lifestyle. This was apparently true for oviraptorids as well (Barsbold, 1977).

Thus, a fundamental direction in the evolution of predatory saurischians was the mastery of bipedalism, which led to the adaptation of rapid running in lightweight forms that found expression among true theropods having a normal dolichoiliac pelvis and dromaeosaurs having a rotated dolichoiliac pelvis. These directions are beautifully illustrated by the wide adaptive variety of the normal dolichoiliac pelvis in true theropods of the Late Mesozoic. These adaptations proved to be much more various than was previously assumed (Barsbold, 1976). The possible descendance of *Archaeopteryx* from dromaeosaurs also holds great promise for a similar direction.

TOPICS IN THE TAXONOMY OF PREDATORY DINOSAURS

Establishing the taxonomic rank (above the family) of these branches is not a trivial problem. It is clear that predatory dinosaurs were more various and any basis for the level of kinship in the various branches must consider the fundamental direction in the evolution of predatory saurischians. In this plan true theropods, dromaeosaurs and segnosaurs must probably be segregated into taxa of the same rank.

In traditional classifications theropods are usually in the rank of a suborder. The theropod groups enumerated above may be placed an order lower, possibly at the infraorder level:

1) true theropods with a normal dolichoiliac pelvis;
2) dromaeosaurs with a rotated dolichoiliac pelvis; and
3) segnosaurs with a reverse brachyiliac pelvis.

Theropod subdivisions, recently suggested by Barsbold (1976), in the rank of infraorders must then be lowered to the rank of superfamilies. When this is done, the family Saurornithoididae (Barsbold, 1974) must be excluded from the deinonychosaurs and assigned to theropods having the normal dolichoiliac pelvis.

LITERATURE CITED

R. Barsbold, “The evolution and systematics of predatory dinosaurs” in: *Paleontology and Biostratigraphy of Mongolia* (in Russian), Nauka, Moscow (1976), pp. 68-75.

R. Barsbold, “The evolution of predatory dinosaurs” in: *Fauna, Flora and Biostratigraphy of the Mongolian Mesozoic and Cenozoic*. *Works of the Joint Soviet-Mongolian Paleontological Expedition*, Vol. 1 (in Russian), Nauka, Moscow (1977), pp. 48-56.

P. P. Gambaryan, *Running in Mammals* (in Russian), Nauka, Leningrad (1972), pp. 3-334.

A. Perle, “Segnosauridae—a new family of theropods from the Mongolian Late Cretaceous”, this publication, pg. 45.

A. J. Charig, J. Attridge, and A. W. Crompton, “On the origin of the sauropods and the classification of the Saurischia” in: *Proc. Linnean Soc. London. Zool*., 176, pp. 197-221, 1965.

E. H. Colbert, “Relationships of the saurischian dinosaurs”, *Amer. Mus. Novit*., No. 1281, 24 pp. (1964).

E. H. Colbert, “Saurischian dinosaurs from the Triassic of Brazil”, *ibid*, No. 2405, 39 pp. (1970).

P. M. Galton, “The pelvic musculature of the dinosaur *Hypsilophodon* (Reptilia: Ornithischia)”, *Postilla Peabody Mus*., Yale Univ., No. 131, pp. 4-64 (1969).

P. M. Galton, “Ornithischian dinosaurs and the origin of birds”, *Evolution*, 2, No. 24, pp. 448-462 (1970).

J. H. Ostrom, “The ancestry of birds”, *Nature*, 242, pg. 136 (1973).

J. H. Ostrom, “Archaeopteryx and the origin of flight”, *Q. Rev. Biol.*, 49, pp. 27-47 (1974a).

J. H. Ostrom, “The pectoral girdle and forelimb function of *Deinonychus*”, *Yale Peabody Mus. Nat. Hist. Postilla*, 165, pp. 1-11 (1974b).

J. H. Ostrom, “The origin of birds”, *Ann. Rev. Earth Planet. Sci*., 3, pp. 55-57 (1975). 14. A. S. Romer, "Crocodilian pelvic muscles and their homologues”, *Bull. Amer. Nat. Hist*., 48, pg. 553 (1923a).

A. S. Romer, “The pelvic musculature of saurischian dinosaurs”, *Bull. Amer. Nat. Hist*., 48, pp. 605-617 (1923b).

A. S. Romer, “The pelvic musculature of the ornithischian dinosaurs”, *Acta Zool*., Stockholm, 8, pp. 225-275 (1927).

A. S. Romer, *Osteology of the Reptiles*, Chicago University Press, Chicago (1956), 772 pp.

P. Wellnhofer, “Das fünfte skelletexamplar von *Archaeopteryx*”, *Palaeontographica (Abt. A)*, No. 147, pp. 169-216 (1974).

Figure Captions

Figure 1. Pelvic structure in various saurischians. a) brachyiliac in prosauropods; b-g) normal dolichoiliac in various theropods; h) rotated dolichoiliac in dromaeosaurids; j) reverse brachyiliac in segnosaurids.

Figure 2. Reconstruction of the pelvic musculature in normal dolichoilia of a) Saurischia; b) Ornithischia; c) dromaeosaurs; and d) segnosaurs.
a – m. ambiens; if (a, p) – m. ilio-fibularis (a – anterior, p – posterior regions); cfb – m. caudi-femoralis brevis; ilt – m. ilio-tibialis (T – two subdivisions); ifb – m. fibularis; flte – m. flexor tibialis externus; pt – m. pubo-tibialis; pif (e, l) – m. pubo-ischio-femoralis (externus, internus).