

THE PRESENCE OF A FURCULA IN TYRANNOSAURID THEROPODS, AND ITS
PHYLOGENETIC AND FUNCTIONAL IMPLICATIONSPETER J. MAKOVICKY^{1,*} and PHILIP J. CURRIE²¹Afdeling for Historisk Geologi og Palæontologi, Geologisk Institut, Øster Voldgade 10, DK-1350 København K. Denmark;²Royal Tyrrell Museum of Palaeontology P.O. Box 7500, Drumheller, Alberta, T0J 0Y0 Canada

ABSTRACT—The distribution of clavicles (or furculae) within the Dinosauria has been poorly understood, and until recently many workers argued that they were not even present. It is now known that allosaurids, oviraptorids, *Segisaurus*, and troodontids possessed clavicles. Fused clavicles (furculae) recovered with several recently discovered tyrannosaurid skeletons are described in this paper. A rerun of Bryant and Russell's (1993) congruence test was conducted against a new and larger tree reflecting new ideas about theropod phylogeny. The results more consistently show that clavicles are primitively present in theropods.

INTRODUCTION

The furcula, or fused clavicles, has been a “bone of contention” in the debate surrounding bird origins and theropod phylogeny. The first reference to clavicles in theropods was by Cope (1866), who mentioned the presence of possible, paired clavicles in *Dryptosaurus*. These elements are 45 cm long and were later reinterpreted as sections of pubic shafts (Cope, 1869). In his seminal work on bird origins, Heilmann (1926) stated that birds could not be directly descended from theropod dinosaurs, because the latter group had lost their clavicles. Evolutionary reacquisition of a lost trait would have been a serious breach of Dollo's (1893) law of irreversibility. The assumption that dinosaurs were characterized by loss of the clavicle was widespread. For example, in his description of the holotype of *Oviraptor* (AMNH 6517), the non-avian dinosaur with proportionally the largest and most robust furcula of all, Osborn (1924) identified the element as an interclavicle, thereby alluding to homology with crocodylians.

The first verifiable identification of a clavicular bone in a theropod was that of Camp (1936), who recognized the element in the ceratosaur *Segisaurus*, albeit as a diminutive unfused element. Its identity was proven by the unquestionable articulation with the acromion process of the scapula. More recently, Barsbold (1983) correctly identified the furcula in oviraptorosaurs, and this led to some speculation about the distribution of the bone among various theropod lineages. Thulborn (1984) suggested that furculae had been found in a number of theropod taxa, but had been misidentified as fused anterior gastralia. His list of taxa with purported furculae comprised *Allosaurus*, *Troodon*, and the tyrannosaurid *Albertosaurus*. Unfortunately, the element that Thulborn (1984) identified as a furcula in *Albertosaurus* has been lost since Lambe's (1917) original description (Bryant and Russell, 1993), and the presence of a rugose, asymmetrical suture on the curved element from *Troodon* (CMN 12340) proves that it is fused gastralia, as identified by Russell (1969). Gauthier (1986) did not find Thulborn's evidence for a furcula in *Allosaurus* convincing, and only found support for the distribution of this character within the clade Coelurosauria. Using the known distribution of clavicles within the Dinosauria and ambiguous evidence for endochondral formation of part of the furcula in recent birds, Bryant and Russell (1993) argue that the absence of this bone in most of the stem

groups leading to birds indicates that the avian furcula might be a neomorphic bone. However, an articulated allosaurid skeleton demonstrates that a furcula is in fact present in this group (Chure and Madsen, 1996). We present here the first concrete evidence for furculae in tyrannosaurids, and discuss its implications with regard to theropod phylogeny and functional anatomy.

Abbreviations—AMNH, American Museum of Natural History, New York; CMN, Canadian Museum of Nature, Ottawa; GI, Museum of the Geological Institute, Ulan Bator; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller.

DESCRIPTION

Three tyrannosaurid skeletons with furculae have been discovered in recent years. The first is that of a juvenile *Albertosaurus sarcophagus* (TMP 86.64.1) from the Horseshoe Canyon Formation (Campanian to lower Maastrichtian) in the Red Deer River Valley near Drumheller, Alberta. It includes the skull and most of the skeleton. The second is an almost complete, 5.1 m long skeleton of a juvenile *Gorgosaurus libratus* (TMP 91.36.500) from the Campanian Dinosaur Park Formation of Dinosaur Provincial Park, Alberta. Most recently, a furcula was recovered in an adult (body length approx. 10 m) *Gorgosaurus libratus* (TMP 94.12.602) from a Dinosaur Park Formation channel deposit. Our use of taxonomic nomenclature of North American tyrannosaurids follows Currie (in prep.).

The furcula of TMP 86.64.1 (Figs. 1A, 1B, 2A, 2B) measures 192 mm between the tips of the two articular facets (epicleidea). The anteroposterior length along the midline is 20.5 mm. The rami thin to 12.0 mm in length, then expand to 14.0 mm before tapering distally to a point. The furcula of TMP 91.36.500 (Figs. 1C, 1D, 2C, 2D) is damaged on the left side because it had slipped between two of the anterior dorsal vertebrae (fourteenth and fifteenth presacral segments) before burial. Although only the base of the left arm of the furcula was recovered, it can be restored because of the bone's symmetry. The rami are only about 10% shorter than those of TMP 86.64.1, and the estimated distance between the tips of the two articular facets is 172 mm. Nevertheless, it is more gracile than the furcula of TMP 86.64.1 and is 14.0 mm long on the midline, 7.5 mm at midpoint on the right arm, and 7.7 mm at the base of the distal articular facet. The furcula of the adult *Gorgosaurus*, TMP 94.12.602 (Fig. 3), is missing the tip of the right ramus. However, the preserved span is 201 mm, and with the tip restored

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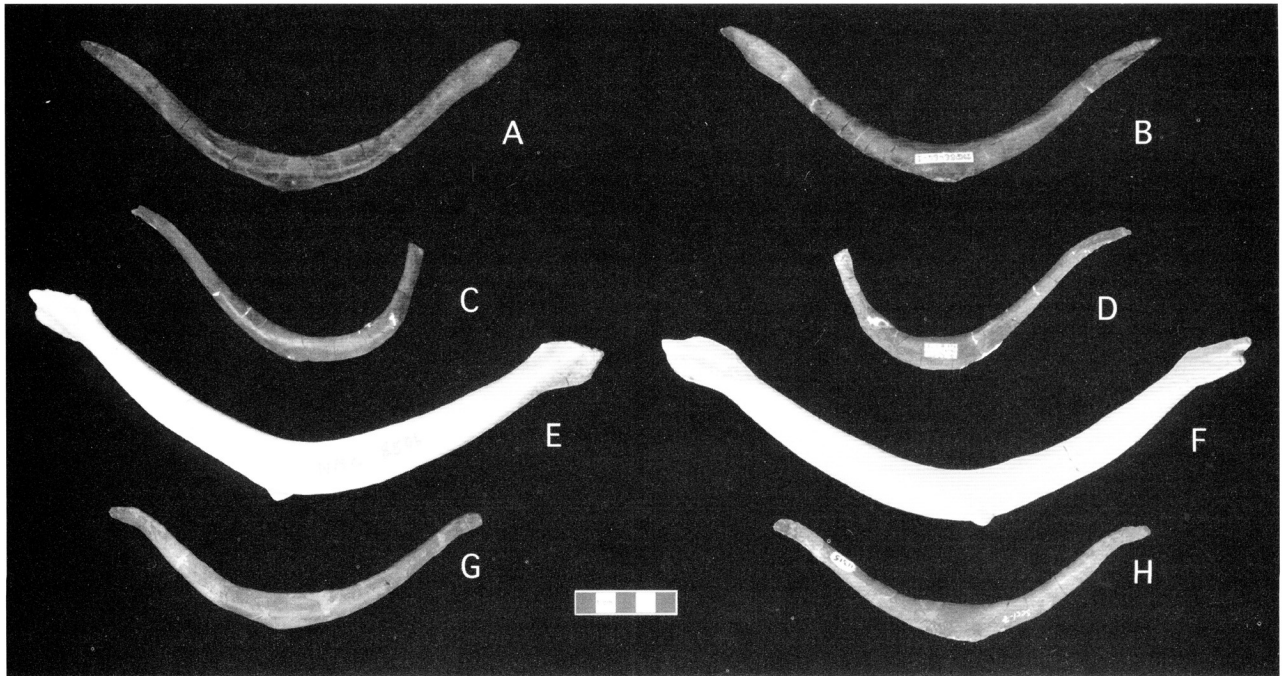


FIGURE 1. Anterior (left column) and posterior (right column) views of four tyrannosaurid furculae. The specimens are: **A, B**, TMP 86.64.1, *Albertosaurus sarcophagus*. **C, D**, TMP 91.36.500, *Gorgosaurus libratus*. **E, F**, CMN 8056, and **G, H**, CMN 11315, both *Daspletosaurus torosus*. Scale bar = 5 cm.

the estimated width is 225 mm. The maximum anteroposterior length (immediately to the right of the midline) is 30.5 mm. The rami thin to 14.5 mm in length, then the left one expands to 16 mm before tapering distally. The articular facet for the scapula is shallowly concave with low ridges that extend distally into three finger-like processes. A scar is present about halfway along each ramus (Fig. 3), and may mark the insertion of musculature or a sternoclavicular membrane.

In all three specimens, each clavicular ramus forms a sigmoid curve, with a concave dorsal bend near the tip (Figs. 1A, 1C, 2A, 2C, 3). Medially, each ramus bends ventrally, and meets its counterpart at the midline to form a large ventrally convex arc. Therefore, the furcula displays three curves in anterior view, a ventrally concave one on either side of the medial convex curve. The intraclavicular angle, measured between the tips of the furcula and the midpoint, is 112° in TMP 86.64.1, 107° in TMP 91.36.500, and 95° in TMP 94.12.602. The facet for articulation with the scapula is flattened and lightly striated (Figs. 1B, 2B, 3). Attachment between these two bones was apparently ligamentous. The epicleideal facets are asymmetrical in TMP 86.64.1, with the left one transversely broadened and spatulate, and the right one more tapered. Medial to the articular facets, the shaft becomes elliptical to subcircular in parasagittal section with the dorsal face forming a ridge. Toward the midline, the anteroposterior width of the furcula increases, and the transverse section is subtriangular adjacent to the midsection. At the midsection itself, a low ridge is present on the ventral face of the bone (Figs. 1A–D, 2A–D). The ridge is slightly offset from the anteroventral surface of the furcula. It is 29 mm long in TMP 86.64.1, but is less prominent and only about half that length in TMP 91.36.500. The right corner of the ridge is broken in the former to reveal dense bone structure. This ridge may be homologous to the hypocleideum seen on the furcula of some extant birds. The midsection of the bone has a smoothly finished surface, without any indication of the border be-

tween the two centers of ossification. Fractures in both TMP 91.36.500 and TMP 86.64.1 reveal a dense histology. Cross sections reveal that the bone is dense all the way through near the tip of each ramus, but closer to the midline a small medullary cavity is apparent. The bone is darker, denser, and not as smooth in texture as the respective gastralia of either of the two individuals.

Misidentified furculae were also recognized in two specimens of *Daspletosaurus* (Figs. 1E–H, 2E–H). The first of these is from the type specimen (CMN 8506) of *Daspletosaurus torosus*, a fully grown animal from the Dinosaur Park Formation (Russell, 1970). The second, more fragmentary specimen (NMC 11315) is from a smaller individual found near Scollard, Alberta, and was referred to *Daspletosaurus* sp., cf. *D. torosus* by Russell (1970). The furcula of CMN 8506 is the largest of the five furculae and has a span of approximately 250 mm and an interclavicular angle of 115° (Figs. 1E, 1F, 2E, 2F). This element is more anteroposteriorly flattened than any of the other furculae and has a deep oval cross section. Each ramus becomes constricted just medial to the epicleideal facet, and this constriction is more pronounced on the right ramus (Figs. 1E, 2E). The epicleideal facets are spatulate, expanded, and are more symmetrical than in the other known tyrannosaurid furculae. A pointed triangular process projects ventrally from near the apex of the furcula (Figs. 1E, 1F, 2E, 2F). It is displaced slightly posteriorly and to the right of the geometric apex of the furcula. The process is 15 mm wide at the base and has a height of 5 mm. The posterior surface is rugose and suggests that it served as a point for tendinous insertion. The smaller *Daspletosaurus* specimen (CMN 11315) is lacking the distal tips of both rami (Figs. 1G, 1H, 2G, 2H), but by comparison with the other specimens appears to be nearly complete. As preserved, it has a span of 163 mm and an interclavicular angle of 115° . In contrast to the larger *Daspletosaurus* (CMN 8605), the rami of the CMN 11315 furcula display proportionately greater anteroposterior

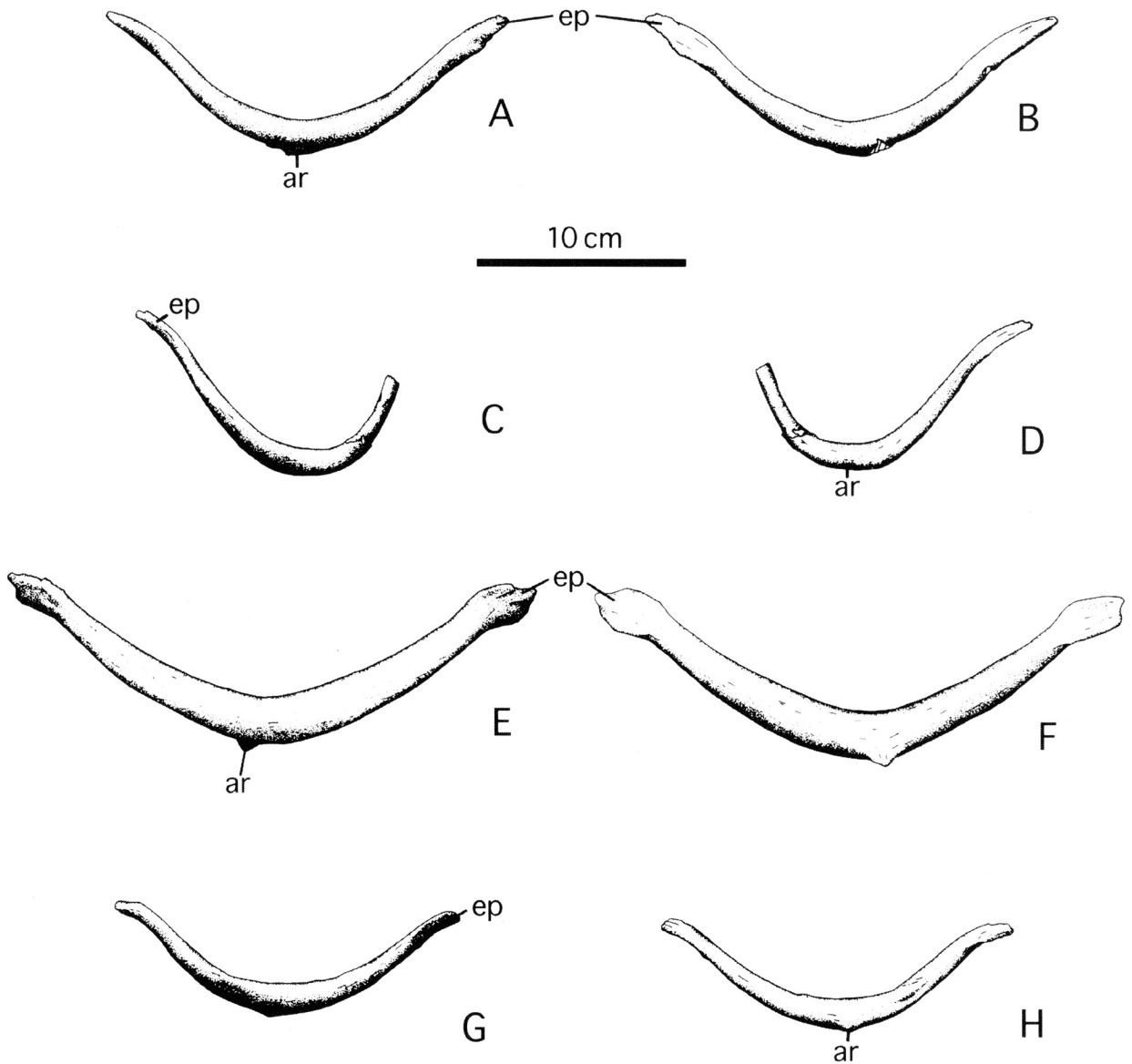


FIGURE 2. Illustrations of the four furculae corresponding to photographs in Figure 1. **Abbreviations:** ar, apical ridge (hypocleideum); ep, epicleideal facet.



FIGURE 3. Posterior view of the furcula of TMP 94.12.602, *Gorgosaurus libratus*. **Abbreviations:** ep, epicleideal facet; s, scar.

curvature (Fig. 1G). As in TMP 86.64.1, the dorsal edge is attenuated in the area of the midline. Ventrally, the furcula bears a robust ridge, which extends for 32 mm and forms the apex of the bone.

The two *Daspletosaurus torosus* furculae can be distinguished from those of *Gorgosaurus libratus* by their less pronounced curvature and wider interclavicular angle. TMP 94.12.602 was only slightly smaller than CMN 8506 (*Daspletosaurus torosus*), which has a furcula that is about 10% wider. In contrast to the *Daspletosaurus* furcula, the furcula of the larger *Gorgosaurus* is much broader on the midline with a wide U-shaped curve, the interclavicular angle is sharper although the rami are of nearly the same length, the sigmoid curvature of each ramus is more pronounced, and the epicleideum is less expanded (Fig. 3). Similar but less pronounced differences exist between the smaller individuals of each taxon. The differences

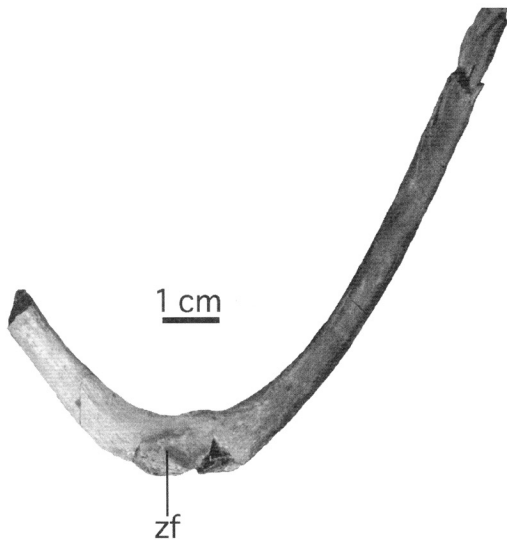


FIGURE 4. Fused gastralia of a tyrannosaurid. Note that there is no sigmoid curvature in the shafts as opposed to the furculae. **Abbreviation:** zf, zone of fusion.

in furcular morphology between the larger and the smaller animals suggest that they are phylogenetic rather than allometric. If the furcula is taxonomically distinctive between *Daspletosaurus* and *Gorgosaurus*, it would mean that the latter taxon had a deeper, narrower chest than the former. The single *Albertosaurus* furcula is qualitatively intermediate in form between the *Daspletosaurus* and *Gorgosaurus* morphologies. In his diagnosis of *Daspletosaurus*, Russell (1970) remarked that the forelimb of this genus was larger and more powerful than that of "*Albertosaurus*" (*Albertosaurus* + *Gorgosaurus* of our usage). Of the five furculae currently known, CMN 11315 is similar in size to TMP 91.36.500 and CMN 8506 is similar to TMP 94.12.602. In both size classes, the *Daspletosaurus* furcula appears more robust than in *Gorgosaurus*, confirming Russell's diagnosis. The small sample size for each taxon does not allow an assessment of individual variation, however, and greater confidence in these characters must await further finds.

DISCUSSION

Historically, clavicles in theropods have often been identified as gastralia, or vice versa (Lambe, 1917; Madsen, 1976; Thulborn, 1984). Indeed, much of the criticism of purported theropod furculae is based on the argument that the bones in question are gastralia (Bryant and Russell, 1993). In theropods, a single gastral arch is composed of two segments on either side of the midline. The proximal end of each medial gastral rod tapers gradually to a point, and bears a lateral groove for the more slender proximal gastral element. Toward the ventral midline, the shaft of each medial element becomes thicker in diameter, and a cross section of the shaft is elliptical. At the midline, the ends of the opposing, medial elements of each gastral arch overlap. The overlapping ends are broadened, rugose, and have complicated articular facets that contact each other and adjacent gastral arches. The anteriormost and caudalmost gastral arches may fuse on the midline, but the former zone of contact remains visible (Fig. 4). In transverse section, the center of the bone contains a medullary channel, and the bone is not as dense as that of the furcula.

TMP 86.64.1 and TMP 91.36.500 have both the clavicles and gastralia preserved, thus allowing for direct comparison of these

elements. The furcula of TMP 86.64.1 differs from the gastralia of the same specimen in many ways, including its sigmoid curvature, distinct and slightly spatulate epicleidea, and more compact histology. These characters and the presence of a ventral ridge indicate a different function from that of the gastralia. Furthermore, the complete coossification of the two rami, and the different histology and preservation as revealed by bone color, suggest that the furcula underwent a different ontogenetic process than most gastralia. It is more difficult to distinguish a tyrannosaurid furcula from the anteriormost gastral segment. However, the first gastral segment is more massive, has more gradually tapering, straighter arms, and does not have distal articular facets. TMP 86.64.1 only includes a partial set of articulating gastralia, and it cannot be determined whether or not the most anterior gastralia constitute the first arch because the medial segments are unfused. Although the first preserved segment is incomplete, it was more than 400 mm across. If there was another segment anterior to this one, it would have been even larger and more massive. Because the furcula is less than half the size, there is no chance of misidentifying it as the first, fused gastral segment. For all of these reasons, it is evident that the furcula and gastralia of TMP 86.64.1 are not homologous.

The relatively short spans of the furculae in TMP 86.64.1, TMP 91.36.500, and other theropods, impose restrictions on the widths of the rib cages. A number of articulated theropod specimens, including *Segisaurus* (Camp, 1936), oviraptorids (AMNH 6517, GI 100/30, GI 100/42), *Sinornithoides* (IVPP V9612), and an allosaurid (Chure and Madsen, 1996), show that the furcula or clavicles of nonavian theropods articulated with the anterior edge of the acromion process of the scapula, without contacting the coracoid. In life, the furcula would have been a ventrally directed V, and together with the scapulocoracoids, it would have braced the anterior end of the thoracic rib cage. The anteroposterior curvature of the furcula would project the apex of the bone above and in front of the coracoids. Correct articulation of the furcula suggests a tall narrow rib cage with the opposing coracoids abutting on the ventral midline (Fig. 5), as suggested by Paul (1988), and seen in *Sinornithoides* (Russell and Dong, 1993) and mounted specimens of *Ingenia* (GI 100/30), *Oviraptor* (GI 100/42), and *Tyrannosaurus* (AMNH 5027).

The sternum in tyrannosaurids (Lambe, 1917) would have been posterior to and between the coracoids as in oviraptorids and *Carnotaurus* (Bonaparte et al., 1990). The tyrannosaurid sternum is composed of two sternal plates, each with a deep groove-like articulation along the anterior edge for the reception of the coracoid. Lateral to each articular groove is a small process (Lambe, 1917), which would have locked the posteroventral corner of the coracoid. A similar coracoid-sternal articulation was proposed for megalosaurs by Bakker et al. (1992). The mobility of the two scapulocoracoids would have been restricted by the furcula in front and the sternum behind (Fig. 5). The shafts of the clavicular rami are rigid, and there appears to have been little possibility for large excursions of one scapulocoracoid relative to the other, because this would have required torsion or flexion of the furcula and torsion of the sternum. In *Oviraptor* (AMNH 6517, GI 100/42), *Ingenia* (GI 100/30), and dromaeosaurids (GI 100/25, TMP 92.36.333), the sternal plates are relatively larger than in tyrannosaurids. Furthermore, oviraptorids bear a large posteriorly directed spike at the midpoint of the furcula in a position corresponding to the hypocleideum of extant birds. In the holotype of *Oviraptor philoceratops* (AMNH 6517), this spike is triangular in section, with distinctly concave ventroposterior faces.

Barsbold (1983) presented a schematic reconstruction of the pectoral girdle of oviraptorosaurs, where the furcular spike contacts the anterior edge of the fused sternal plates. Such an arrangement would have displaced the coracoids far from the

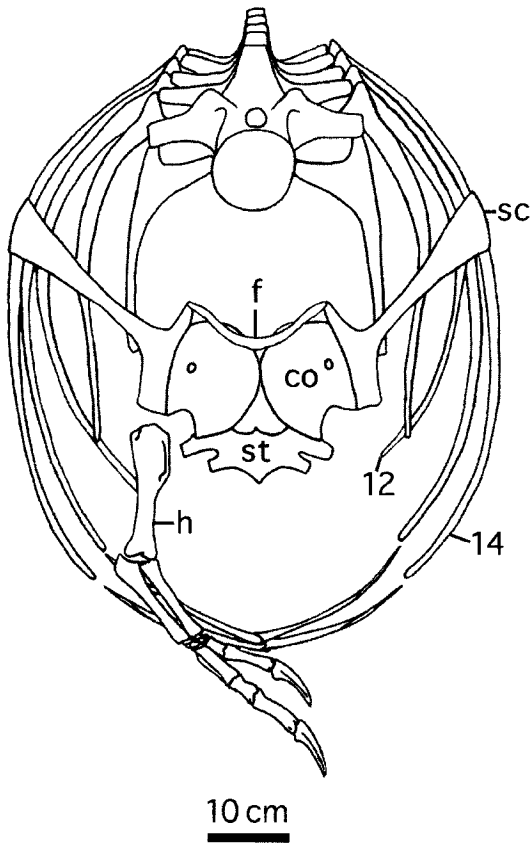


FIGURE 5. Schematic reconstruction of a tyrannosaurid rib cage and shoulder girdle in anterior view. The reconstruction is based mainly on measurements from TMP 91.36. 500 although a sternum was added, scaled down from Lambe (1917). Costal cartilage attachments between ribs and sternum are not reconstructed. **Abbreviations:** co, coracoid; f, furcula; h, humerus; sc, scapula; st, sternum. Numbers designate position of ribs.

midline in order to allow the ventral end of the furcula to approach the sternum. Also, the scapula would need to be positioned nearly vertically in order to direct the apex of the furcula posteriorly. The narrow width of the furcula and its articulation with the acromion would permit neither such a lateral position of the coracoids nor a vertical, diverging orientation of the scapulae. Therefore, it is doubtful that there was contact between the furcula and sternum.

In modern birds, the posterior (ventral) edge of the furcula serves as an attachment for the sternobranchialis head of the *M. pectoralis* (Dial et al., 1987). The pectoralis provides the main contribution to the downstroke of the avian wing during flight, and the sternobranchialis depresses and protracts the humerus (Dial et al., 1987). In nonavian theropods, the glenoid was oriented posteroventrally rather than laterally as in birds (Jenkins, 1993). Therefore, contraction of the pectoralis would serve to adduct the humerus and extend the front limb in front of the trunk. Extensive musculature was evidently present in many maniraptoriforms (Holtz, 1996) as evidenced by the large furcula and deltopectoral crest. It would have provided a powerful adduction of the humerus during raptorial forelimb extension. A robust furcula may have acted as a spacer (Ostrom, 1976) or brace between the scapulocoracoids of either side and resisted forces that would have displaced the pectoral girdle during prey

handling. In tyrannosaurids, the forelimb was reduced, and the proportionally diminutive size of the furcula is probably related to this reduction. Olson and Feduccia (1979) suggested that the proportionally large furcula of *Archaeopteryx* served as an anchor for an enlarged *M. pectoralis* that would have provided this taxon with flight capabilities. The presence of a furcula in at least some tetanurine theropods suggests that this feature is an exaptation in the evolution of avian flight. The energy storing, spring-like properties of the furcula of some birds (Jenkins et al., 1988) apparently evolved within the Ornithomorphes, and were not present in nonavian theropods.

In spite of the small sample size ($n = 5$), the span of the furcula appears to correlate very well with estimated body length (coefficient = 0.97) in North American tyrannosaurids. Such a result is to be expected, because the span of the furcula bears directly on the position of the shoulder girdle and the width of the anterior part of the rib cage. The height of the furcula at the thinnest point on the rami has a high correlation with the overall body length ($c = 0.94$), but the height of the epicleidal facets shows a lower correlation (0.90). Midline height and interclavicular angle show no strong correlation with body size, and appear to be more variable dimensions of the furcula. The correlation coefficients between most parameters of the furcula against body length, as well as the observed slight asymmetries of all specimens, suggests that tyrannosaur furcula display a large degree of morphological variation. This is consistent with the dermal nature of clavicles.

The occurrence of fused clavicles in tyrannosaurids affects the distribution of this character in phylogenetic studies of the Theropoda. According to Gauthier's (1986) hypothesis, the presence of furculae in tyrannosaurids and allosaurids (Chure and Madsen, 1996) suggests that the element may be a tetanurine, rather than a coelurosaurian synapomorphy. More recent phylogenetic theories presented by Holtz (1994) and Sereno (1995) suggest that tyrannosaurids are in fact coelurosaurids. In none of these phylogenies are tyrannosaurids placed as a sister group to a subclade where all terminal taxa possess furculae. Rather, the known patchy distribution of the furcula within theropods is most parsimoniously interpreted either as a number of independent evolutions of clavicular fusion (Holtz, 1994), or as a large number of independent losses of a plesiomorphic feature. Because clavicles are of dermal origin, the absence of a furcula may reflect an unossified, and perhaps juvenile stage, or simply be due to non-recovery or misidentification.

Bryant and Russell (1993) argue that the absence of clavicles in basal theropods and most other dinosaurs might indicate that these secondary shoulder girdle elements in maniraptorans are neomorphic structures. They propose a test of congruence that requires the absence of clavicles in at least 1, 4, 10, 20, 25 specimens of a taxon and an infinite number of specimens, in order to accept the de facto absence of clavicles in the fossils (negative evidence) as a true indication of absence in the taxa. In order to assess the significance of furculae in tyrannosaurids and allosaurids, Bryant and Russell's (1993) test was conducted against a new and larger tree reflecting recent ideas about saurischian phylogeny presented by Holtz (1994) and Sereno et al. (1994) for theropods, and Upchurch (1994) and Gauffre (1995) for sauropods and prosauropods, respectively (Fig. 6). The results (Table 1) show that presence of clavicles in theropods is either ambiguous ($n \leq 4$) or certain in all categories save that of $n = 1$. Within all categories more stringent than $n = 1$, presence of clavicles in neotheropods was unambiguously present. Because of the absence of clavicles in pterosaurs, *Marasuchus* and most ornithischians, the test suggests that clavicles are neomorphs in Saurischia. Nevertheless, in view of evidence for dermal clavicular origins in galliforms (Russell and Joffe, 1985), presence of clavicles in some ceratopsian ornithischians (Brown and Schlaikjer, 1942), and the reduced state of clavicles

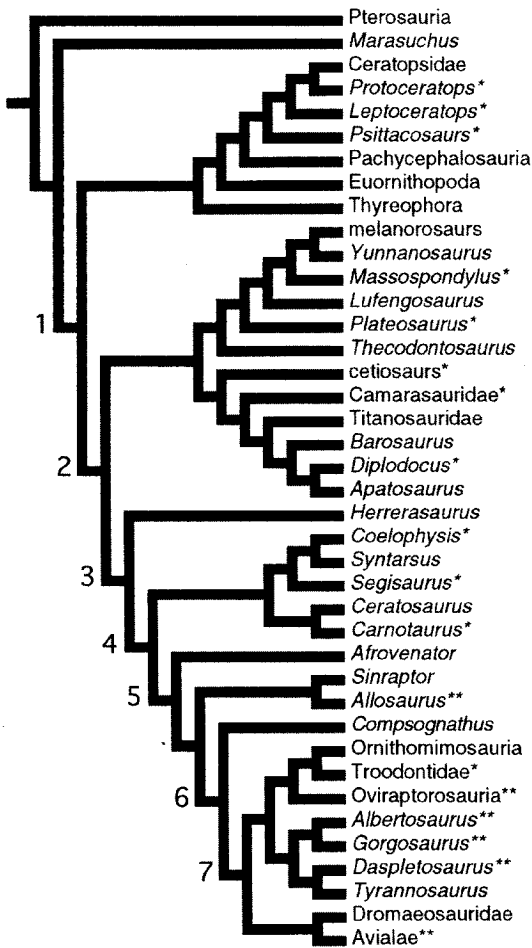


FIGURE 6. Tree depicting ornithodiran phylogeny. The homology test conducted to see whether the avian furcula corresponds to the primitive tetrapod clavicle was run on this tree, which is a composite of phylogenetic schemes presented by Gauthier (1986), Sereno (1986), Holtz (1994), Sereno et al. (1994), Upchurch (1994) and Gauffre (1995). Taxa known to possess clavicles are marked with an asterisk. Two asterisks indicate that the clavicles are fused to form a furcula. Numerals indicate the following clades listed in Table 1: 1 = Dinosauria; 2 = Saurischia; 3 = Theropoda; 4 = Neotheropoda; 5 = Tetanurae; 6 = Coelurosauria; 7 = Maniraptoriformes.

in most sauropodomorphs and basal theropods, it is quite probable that this result may be caused by lack of ossification and independent reduction or loss of clavicles in various lineages. Thus, clavicles are either neomorphic for saurischians or primitively present in all dinosaurs and the avian furcula is not a

TABLE 1. The table summarizes the results of our rerun of Bryant and Russell's (1993) congruence test. Presence or absence of clavicles for internal nodes on the cladogram shown in Figure 6 was tested for five different levels of acceptance of negative evidence. n indicates the minimum number of specimens required to accept the absence of clavicles (negative evidence) in a taxon as indicative of true phylogenetic loss.

Clade	n = 1	n ≥ 4	n ≥ 10	n ≥ 20	n ≥ 25
Dinosauria	absent	absent	absent	absent	absent
Saurischia	absent	equivocal	present	present	present
Theropoda	absent	equivocal	present	present	present
Neotheropoda	absent	present	present	present	present
Tetanurae	absent	present	present	present	present
Coelurosauria	absent	present	present	present	present
Maniraptoriformes	absent	present	present	present	present

maniraptoran (maniraptoriform in our topology) neomorph structure as suggested by Bryant and Russell (1993). Judging from the ease with which other tetrapod groups have lost the clavicles, we feel that the latter conclusion is correct, in spite of requiring an additional evolutionary step relative to the former.

It must be borne in mind that the "test of congruence" is based on a number of arbitrarily chosen criteria, as admitted by Bryant and Russell (1993). First, the results are highly dependent on the number of taxa included, and by the number and quality of specimens representing each taxon. Ideally, all dinosaurian taxa where the pectoral girdle is preserved should be included for a complete test, although this still would be affected by highly variable preservational biases. For example, the ceratosaur *Segisaurus* is known only from one partial skeleton, but has a well-preserved pectoral girdle with an articulated clavicle. In contrast, many good and nearly complete specimens of tyrannosaurids are known, but only the five specimens described here have preserved furculae. Likewise, *Coelophysis* is known from hundreds of articulated specimens, but clavicles have only been tentatively identified in one individual (K. Padian, pers. comm.). This bias suggests that the ligamentous bond between the furcula and acromia often decayed posthumously, and that the furcula was consequently easily lost during preburial transport. The lack of furculae in some specimens may also testify to a wide scope of individual and ontogenetic variation, although this is improbable considering the high level of ossification of most juvenile theropods and indeed dinosaurs in general (Currie and Peng, 1993; Geist and Jones, 1996).

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