Journal of Vertebrate Paleontology 22(3):728–733, September 2002

RAPID COMMUNICATION

A FURCULA IN THE COELOPHYSID THEROPOD *SYNTARSUS*

RONALD S. TYKOSKI[1], CATHERINE A. FORSTER[2], TIMOTHY ROWE[1], SCOTT D. SAMPSON[3], and
DARLINGTON MUNYIKWA[4]
[1]Jackson School of Geosciences, and the Vertebrate Paleontology Laboratory of the Texas Memorial Museum,
The University of Texas at Austin, Austin, Texas 78712-R7600, tykoski@mail.utexas.edu;
[2]Department of Anatomical Sciences, State University of New York at Stony Brook, Stony Brook, New York 11794;
[3]Utah Museum of Natural History and Department of Geology and Geophysics, University of Utah,
Salt Lake City, Utah, 84112-0050;
[4]National Museum of Natural History, Bulawayo, Zimbabwe

We report the occurrence of a furcula (fused clavicles) in both species of the Early Jurassic coelophysid theropod dinosaur *Syntarsus* (Coelophysidae sensu Holtz, 1994; =*Coelophysis* and *Syntarsus* and all descendants of their most recent common ancestor). The furcula is a median pectoral element formed by ontogenetic fusion of the left and right clavicles. It articulates laterally with a facet on the acromion process of the scapula, and medially with the sternum. Study of the holotype of *Syntarsus kayentakatae* (MNA V2623) uncovered a furcula in articulation with the left scapulocoracoid. Re-examination of elements previously identified as hyoids of *Syntarsus rhodesiensis* (QG 193) show these bones are actually furculae, nearly identical in morphology to that of *S. kayentakatae*. These specimens mark the earliest confirmed record of furculae to date, both temporally and phylogenetically. This suggests that the fusion of clavicles into furculae occurred much earlier in theropod evolution than previously believed.

Among extinct taxa, paired (i.e., unfused) clavicles have been reported in sauropodomorphs (Huene, 1926; Sereno, 1991) and in basal members of Ceratopsia (Osborn, 1924; Brown and Schlaikjer, 1940; Sternberg, 1951; Chinnery and Weishampel, 1998). Either paired clavicles or a furcula have been reported in various extinct non-avialian theropods, but our knowledge of their distribution throughout this clade is sporadic (Bryant and Russell, 1993; Makovicky and Currie, 1998). These elements are unreported in most extinct dinosaur species, and in the majority of cases it is unclear whether this reflects non-preservation, true absence, or non-recognition (Makovicky and Currie, 1998).

The ontogenetic fusion of the clavicles was long considered unique to birds, because furculae were discovered in *Archaeopteryx* and later in other Mesozoic birds (Dingus and Rowe, 1997). Identification of a furcula in the maniraptoran *Oviraptor philoceratops* (Barsbold, 1983) sparked recent critical reviews of the distribution of the furcula in non-avialian theropods (Thulborn, 1984; Bryant and Russell, 1993). More recently described oviraptorid specimens, including *Oviraptor* (Barsbold et al., 1990), *Ingenia* (Clark et al., 1999), and *Khaan* (Clark et al., 2001) are now known to possess robust U-shaped furculae. Similar discoveries led Bryant and Russell (1993) to suggest that the furcula was apomorphic of the theropod clade Maniraptora. Additional discoveries confirmed the presence of a furcula in the maniraptoran theropods *Velociraptor* (Norell et al., 1997; Norell and Makovicky, 1999), *Sinornithosaurus* (Xu et al., 1999b), and *Bambiraptor* (Burnham et al., 2000); the tyrannosaurids *Daspletosaurus*, *Gorgosaurus*, and *Albertosaurus* (Makovicky and Currie, 1998); the therizinosauroid *Beipiaosaurus* (Xu et al., 1999a); and in the more basal coelurosaur *Scipionyx* (Dal Sasso and Signore, 1998). The presence of a furcula in *Allosaurus*, a relatively basal tetanuran, was confirmed in collections from the Cleveland-Lloyd Quarry and in an articulated allosaurid from Dinosaur National Monument (Chure and Madsen, 1996).

Based upon this evidence, Makovicky and Currie (1998) suggested the furcula was apomorphic of Tetanurae (sensu Gauthier, 1986; =Neornithes and all theropods closer to Neornithes than to *Ceratosaurus nasicornis*). A similar view was echoed by Holtz (1998), although it was also suggested the element could be restricted to Avetheropoda (sensu Holtz, 1994; =the most recent common ancestor of Neornithes and *Allosaurus*, and all of that ancestor's descendants). Our evidence suggests an even more widespread and ancient origin for this element. The holotype of *Syntarsus kayentakatae* (Rowe, 1989) from the Kayenta Formation (Early Jurassic) of Arizona recently underwent additional preparation to facilitate its first detailed description (Tykoski, 1998). During the course of this work a furcula closely resembling that of *Allosaurus* (Chure and Madsen, 1996) was found articulated with the left scapulocoracoid. At the same time, furculae were recognized during a re-examination of the large collection of specimens of *Syntarsus rhodesiensis* (Raath, 1977) from the Early Jurassic Forest Sandstone of Zimbabwe (Olsen and Galton, 1984). Several disarticulated elements preserved in this collection that were previously interpreted as hyoids (Raath, 1977) are identical in form to the furcula in the holotype of *Syntarsus kayentakatae*. We describe the furculae in both species of *Syntarsus* below, and discuss their systematic implications.

Institutional Abbreviations—**MNA**, Museum of Northern Arizona, Flagstaff; **QG**, originally catalogued at the Queen Victoria Museum, Department of Paleontology, Harare (formerly Salisbury), now curated at the National Museum of Natural History, Bulawayo.

DESCRIPTION

Syntarsus kayentakatae

The *Syntarsus kayentakatae* holotype (MNA V2623), described in detail by Rowe (1989) and Tykoski (1998), includes a small block containing the posterior cervical vertebrae and ribs, the anterior-most dorsal vertebrae and ribs, the left pectoral girdle, and left humerus (Fig. 1). The furcula lies just anterior to the left scapulocoracoid. Unlike the cervical and anterior

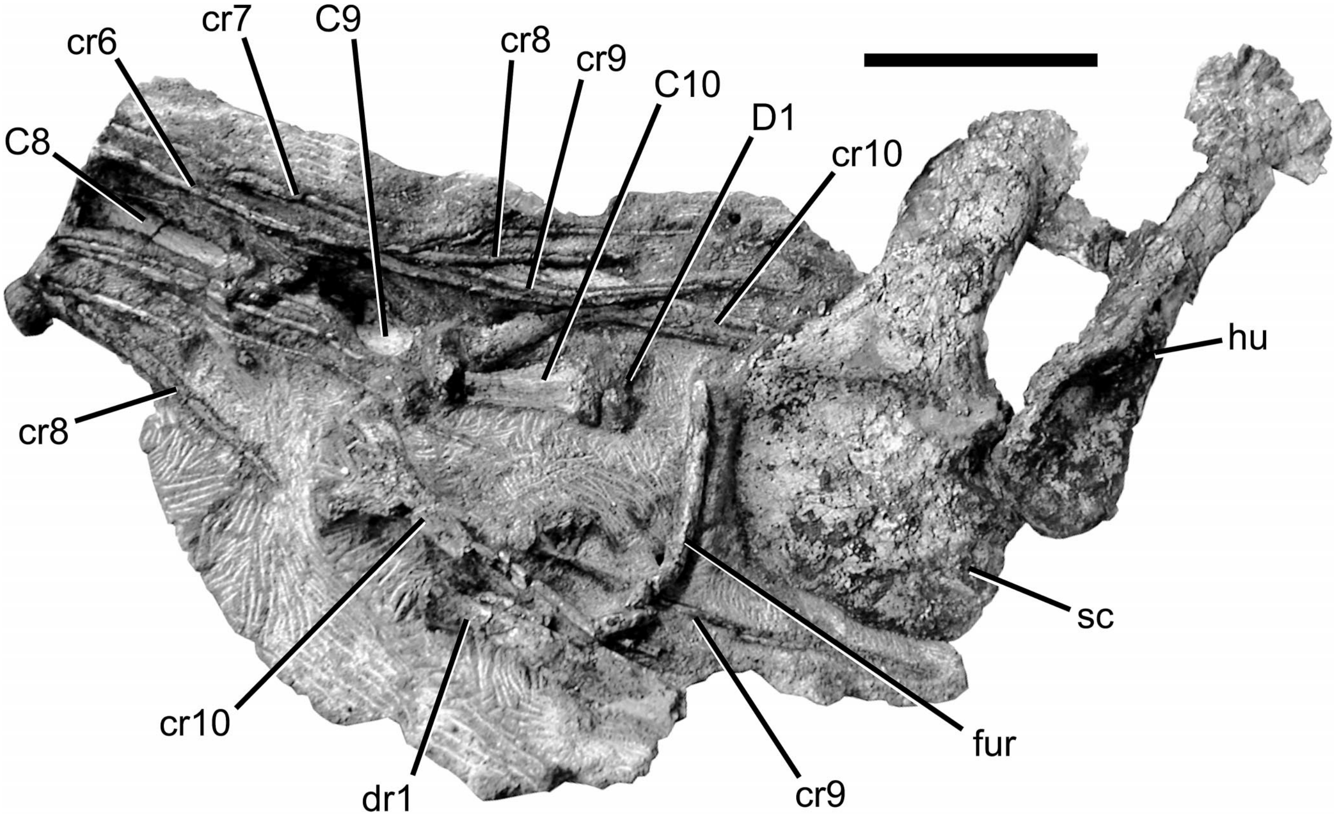

FIGURE 1. *Syntarsus kayentakatae* holotype (MNA V2623). Block containing posterior cervical vertebrae and ribs, first dorsal vertebra and ribs, furcula, left scapulocoracoid and humerus. **Abbreviations**: **C8**, eighth cervical vertebra; **C9**, ninth cervical vertebra; **C10**, tenth cervical vertebra; **cr6–10**, sixth through tenth cervical ribs; **D1**, first dorsal vertebra; **dr1**, first dorsal rib; **fur**, furcula; **hu**, humerus; **sc**, scapulocoracoid. Scale bar equals 5 cm.

dorsal ribs that roughly parallel the axial column, it lies perpendicular to the vertebral series and cervical ribs. In the course of post-mortem processes, the furcula was pivoted 180 degrees, so the anterior surface now faces posteriorly.

The tip of the left ramus of the furcula remains close to the acromion process of the scapula, but the rest of the bone is rotated counter-clockwise around this point. The distance from the tip of the left articulation (=epicleideal facet) to the most distant piece of the broken right ramus is 55.2 mm. Length from the midline to the tip of the intact left ramus is 33.2 mm. Given the symmetry of a complete furcula, total tip-to-tip breadth is estimated to be 65–68 mm. In anterior view, the furcula resembles a broad ''V'', with two relatively straight rami and an interclavicular angle of 140 degrees (Fig. 2A). In posterior and posterodorsal views a ventromedian swelling on the posterior surface, the apical ridge (=primitive or incipient hypocleideum), lends a more pointed profile to the ventral apex of the bone (Fig. 2B). The furcula bows anteriorly in dorsal view (Fig. 2C).

The right ramus of the furcula of MNA V2623 is broken and the right epicleideal facet is missing. The left ramus is intact, including the posterodorsally facing epicleidal facet for the acromion process of the scapula. It is not clear whether this is the natural orientation of the articular surface, or the result of postmortem distortion. The shaft narrows very slightly just medial to the articular surface, but there is no expansion of the epicleideal facet as in tyrannosaurids (Makovicky and Currie, 1988:figs. 1–3). The articular surface is flattened and rugose, bearing faint mediolaterally oriented grooves similar in texture to that described for the furcula of *Allosaurus* (Chure and Madsen, 1996:fig. 5).

Syntarsus rhodesiensis

At least five furculae are present in the collection of *Syntarsus rhodesiensis* in the National Museum of Natural History in Zimbabwe. These elements were originally described by Raath (1977:plate 10) in his very thorough treatment of this taxon. Most of the *S. rhodesiensis* furculae, as well as the other skeletal elements, were recovered from the Chitake and Maura River bone beds as disarticulated but well preserved pieces. QG 193 (CT6/E III; Fig. 3A) and QG 193 (CT6/E) were found associated with skull QG 193 (Raath, 1977:55). This association led Raath to speculate that this pair of elements belonged with the skull, and that they represented the second cornua of the hyoid apparatus.

Re-evaluation and examination of these elements in light of the recent discoveries in other theropods indicates that the elements in question are in fact furculae. Because the furculae are not directly associated with shoulder girdle elements, their size relative to the rest of the skeleton cannot be determined. Three furculae are complete, with spans of 51.4 mm (QG 193 (CT6/EIII)), 54 mm (QG 193 (CT6/E)), and 40.5 mm (QG 244 (CT6/F)) between distal tips of the rami. The furculae bow anteriorly, which would have allowed the rami to arch around the curved anterior border of the coracoid. This same general curvature is found in other theropod furculae, including those of avialians (Makovicky and Currie, 1998; Norell and Makovicky, 1999).

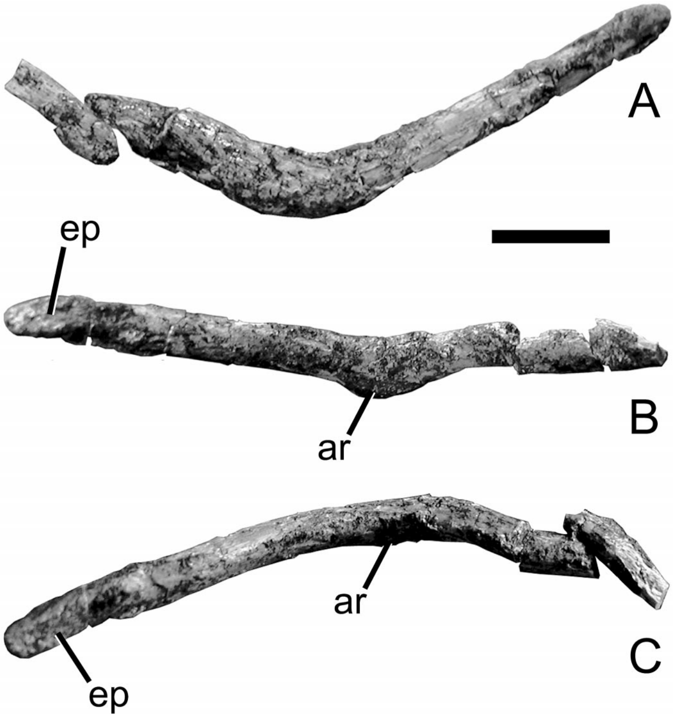

FIGURE 2. *Syntarsus kayentakatae* holotype (MNA V2623). Furcula in **A**, anterior; **B**, posterodorsal; and **C**, dorsal (anterior to top) views. **Abbreviations**: **ar**, apical ridge; **ep**, epicleidal facet. Scale bar equals 1 cm.

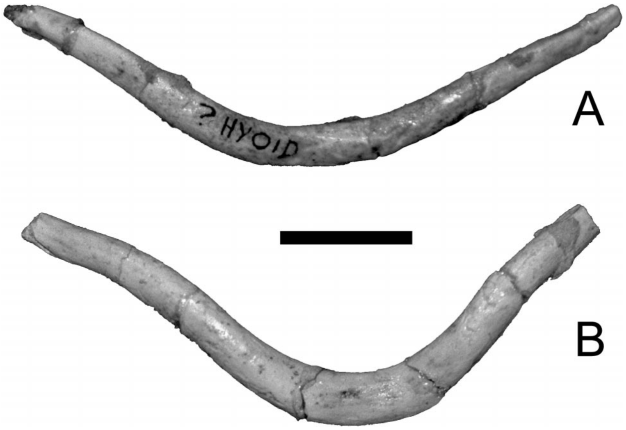

FIGURE 3. *Syntarsus rhodesiensis* furculae in anterior view: **A**, QG 193 (CT6/EIII); **B**, QG 244 (CT6/G), with distal end of left ramus broken and missing. Scale bar equals 1 cm.

While the furculae are fairly uniform in overall structure, the shapes of the rami are somewhat variable. The rami of four of the specimens are nearly straight in anterior view, resulting in a broad V-shape with interclavicular angles that vary from 130 to 140 degrees (Fig. 3A). However, one specimen (QG 244 (CT6/G)) has weakly sigmoidal rami, resulting in a narrower interclavicular angle of 115 degrees (Fig. 3B). The distal ends of the rami have small but well developed epicleideal facets on their posterior surfaces that taper distally and bear fine dorsolaterally directed striations. The margins of the epicleideal facets are slightly irregular. The rami taper only slightly distally, and do not appear to expand or thicken where they join on the midline as in some tyrannosaurids (Makovicky and Currie, 1998). There is no trace of a midline suture. The degree of development of the apical ridge is also variable. In the largest specimen (QG 193 (CT6/E)), a large anteroposteriorly compressed hypocleideum projects from the posteroventral edge of the furcula. In the smaller specimens, this process appears as only a small tubercle or ridge.

DISCUSSION

The *Syntarsus* furculae correspond to other known non-avialian furculae in all points of morphology including overall curvature, shape and proportions of the rami, possession of striated epicleideal facets, apical ridges (=hypocleidea), and, in the case of the articulated specimen of *S. kayentakatae*, its position relative to the scapula and coracoid. Much as in other nonavian theropods, this small sample exhibits minor variation in form, especially with regards to hypocleideum development and curvature of the rami. In the past, furculae have been mistaken for part of a rib, fused gastral arch segments, and hyoids in other theropods. For this reason, it is helpful to briefly compare these structures in *Syntarsus*.

The anterior cervical ribs of *Syntarsus* are extremely long, thin, and straight. Each is strongly bi-capitate, and a sharp process projects anteriorly beyond the heads. More posterior cervical ribs have larger heads that are widely spaced, with shorter anterior processes. Anterior dorsal ribs also bear large heads, curved shoulders, and a subcostal groove (Raath, 1977). The furculae lack both rib heads and an anterior process. Additionally, the rounded, smooth articular facets of all ribs are very different from the flattened, striated facets of the epicleidea of these furculae. The furculae show no signs of pathology or postmortem breakage on the midline, arguing against the possibility that they are damaged and subsequently healed rib shaft sections. The number of virtually identical elements identified as furculae also argues against a pathological interpretation.

Theropod furculae have been interpreted as fused anterior gastralia (Lambe, 1917; Russell, 1969; Madsen, 1976). A nearly complete abdominal basket was collected with the holotype of *S. kayentakatae* (Rowe, 1989; Tykoski, 1998). It consists of at least fifteen tightly packed gastral arch pairs. Two of the posterior median gastral arch elements appear fused along the midline, forming an acute U-shaped element that is vaguely furcula-like, but none of the anterior arch pairs exhibit midline fusion. Similar morphology can be seen the abdominal basket of *S. rhodesiensis* (holotype QG/1; Raath, 1969). In theropods, each medial gastral arch element bears a lateral groove for articulation with its complimentary lateral gastral arch element. No such groove is present on the furculae. Distally placed, striated facets do not occur on gastral elements, but are present as epicleideal facets on the furculae.

Hyoid elements, identified as the ceratohyals, have been recovered and identified for a number of theropod taxa, including *Coelophysis*, *S. kayentakatae*, and *Scipionyx* (Colbert, 1989; Rowe, 1989; Tykoski, 1998; Dal Sasso and Signore, 1998). Ceratohyals taper distally, and they gently curve or slightly bend near midshaft. However, theropod ceratohyals are never angled to the degree seen in the furcula, nor are they symmetrical. Ceratohyals also lack striated facets at their distal ends, as well as tubercles or ridges at mid-shaft. The presence of in-place hyoids in the holotype of *S. kayentakatae* eliminates the possibility that the bone we identify as the furcula may be a misidentified ceratohyal.

It is difficult to say unequivocally whether the furcula arose many times independently or was lost more than once, and for which taxon or taxa its presence is diagnostic. This is because our current knowledge of the distribution of clavicular elements among non-avian theropods is incomplete, and because there is

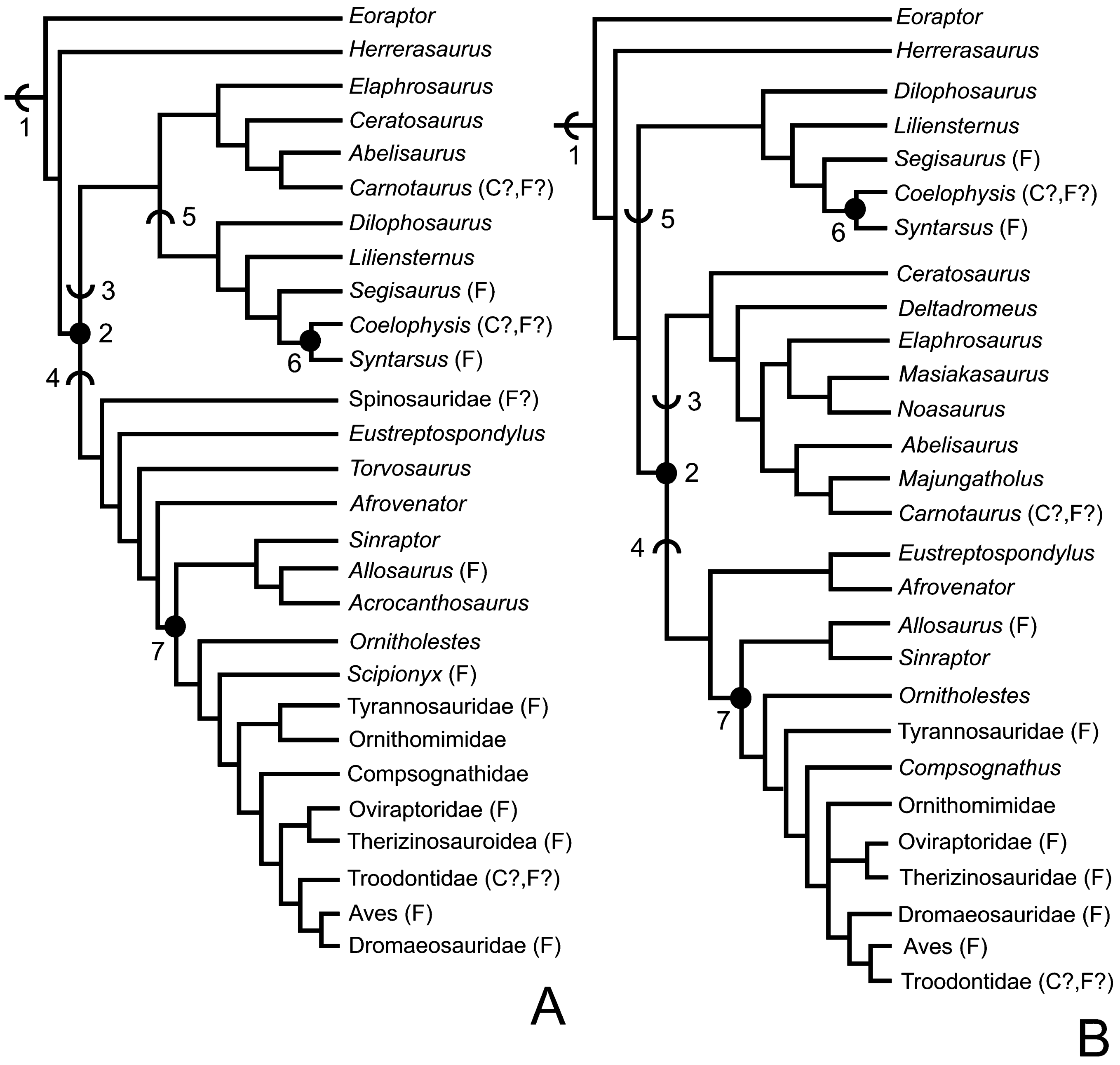

FIGURE 4. Reported distribution of furculae and clavicles within Theropoda. **A**, hypothesis of theropod phylogeny adapted mainly from Holtz (1998). Coelophysoidea is within Ceratosauria, similar to findings of Rowe (1989), Rowe and Gauthier (1990), Holtz (1994), Rowe et al. (1997), and Sereno (1999). Use of *Eoraptor* and *Herrerasaurus* as basal theropods, and coelophysoid ingroup relationships from Sereno (1999). **B**, combined hypotheses of theropod phylogeny adapted from Forster et al. (1998), and Carrano et al. (2002). Coelophysoidea is sister taxon to unnamed stem clade containing Neotheropoda, similar to findings of Forster (1999), and Sampson et al. (2001). Coelophysoid ingroup relationships from Sereno (1999). Taxa in which clavicles are preserved and fused to form furcula are followed by (F). Taxa in which clavicles preserved but identification as either paired clavicles or a furcula is uncertain are followed by (C?, F?). Taxa in which furcula is reported but unconfirmed, or is incomplete and may potentially be paired elements are followed by (F?). Solid circles denote node-defined clades. Arcs indicate stem-defined clades. **1**, Theropoda; **2**, Neotheropoda; **3**, Ceratosauria; **4**, Tetanurae; **5**, Coelophysoidea; **6**, Coelophysidae; **7**, Avetheropoda.

no clear consensus with regards to hypotheses of theropod phylogeny (Fig. 4A, B). There is growing evidence that fusion of the clavicles to form a furcula occurred repeatedly within Coelophysoidea (Holtz, 1994; =*Coelophysis* and all theropods more closely related to it than to *Ceratosaurus*). An individual clavicle was described in the type and only known specimen of the coelophysoid *Segisaurus halli* (Camp, 1936), the implication at the time being that paired clavicles were present. However, new preparation of this specimen also reveals that the element in question is a furcula (Senter and Hutchinson, 2001). *Segisaurus* is known from slightly younger sediments than *Syntarsus*, and its phylogenetic position within Coelophysoidea is uncertain at this time. Paired, unfused clavicles were reported and figured in the Late Triassic coelophysid taxon *Coelophysis bauri* (Padian, 1997:fig. 3g). Conflicting with this description, elements that may prove to be furculae were more recently reported in other specimens of *Coelophysis* (Downs, 2000:fig. 2E). If the latter is confirmed, it will constitute the earliest temporal occurrence of the furcula.

Whether the clavicles were paired, fused, or absent is uncertain for most other basal theropods, ceratosaurs, and basal tetanurans. A right clavicle was reported in the abelisaurid *Carnotaurus sastrei* (Bonaparte et al., 1990). However, Bonaparte et al. (1990:24) considered this interpretation tentative, adding ''. . . some portion of it may be missing.'' Recent internet-based news stories and images suggest that a spinosaurid specimen with an associated furcula has been found, but we consider these reports unconfirmed until the evidence has been published in a more permanent and technical format. Among more derived non-avian theropods, Russell and Dong (1993) reported a paired clavicle in the troodontid *Sinornithoides youngi*. However, the medial margin of this element appears broken and its identification as an unfused clavicle cannot be confirmed (P. Makovicky, pers. comm.). We are unaware of any verified reports of paired clavicles in any non-avialian theropod.

CONCLUSION

The presence of a furcula in *Syntarsus* is currently the earliest confirmed temporal record (Early Jurassic) of this element, and with some other coelophysoids it is potentially the most phylogenetically basal record of this element within Theropoda. The furcula was once considered an ossification unique to birds. Overwhelming evidence that birds are theropods has brought the realization that many non-avialian theropods possess features long thought exclusive to birds. It should be no surprise to find the furcula in such basal taxa, given the increasing amount of attention given theropod furculae (Gauthier, 1986; Bryant and Russell, 1993; Holtz, 1994, 1998; Chure and Madsen, 1996; Dingus and Rowe, 1997; Makovicky and Currie, 1998; Sereno, 1999). Whereas previous work was able to establish the presence of the furcula in many tetanurans (Chure and Madsen, 1996; Makovicky and Currie, 1998; Holtz, 1998), the confirmation of this element in both *Syntarsus* and *Segisaurus*, and its possible presence in *Coelophysis*, implies a wider distribution in Theropoda. At present, a strict parsimony interpretation of distribution of the furcula would conclude it arose independently in some coelophysoids and among tetanurans. However, phylogenetic hypotheses supporting the position of coelophysoids within Ceratosauria (sensu Rowe, 1989; =*Ceratosaurus* and all theropods more closely related to it than to Neornithes) (Gauthier, 1986; Rowe, 1989; Rowe and Gauthier, 1990; Holtz, 1994, 2000; Rowe et al., 1997; Sereno, 1999) suggest the furcula may be diagnostic of Neotheropoda (sensu Holtz, 1994; =Ceratosauria and Tetanurae, and all descendants of their most recent common ancestor) (Fig. 4A). Other phylogenetic hypotheses remove Coelophysoidea from Ceratosauria and place the clade as sister taxon to an unnamed stem-clade encompassing Neotheropoda (Forster, 1999; Sampson et al., 2001; Carrano et al., 2002) (Fig. 4B). The latter hypotheses give reason to suspect the furcula may diagnose a clade more inclusive than Neotheropoda. Given the abundant missing data with respect to basal theropods, the furcula may yet prove apomorphic for Theropoda.

ACKNOWLEDGMENTS

Thanks go to Chris Bell, Matt Carrano, Dave Dufeau, Jon Franzosa, Ted Macrini, Lyn Murray, Pamela Owen, Dennis Ruez, and Chris Schneider for their constructive criticisms of early drafts of this manuscript. Discussion with Peter Makovicky proved very helpful early in this work. Thanks also go to Thomas Holtz and Peter Makovicky for their very constructive reviews of this manuscript. John Hutchinson provided useful information concerning *Segisaurus halli*. We also thank Kristina Curry Rogers for providing photographs of the *Syntarsus rhodesiensis* specimens, and Luci Betti-Nash for preparing the *S. rhodesiensis* figures. Bruce Rubidge and Mike Raath kindly provided access to some of the *S. rhodesiensis* specimens. This work was made possible, in part, by a grant from the Dinosaur Society.

LITERATURE CITED

Barsbold, R. 1983. [Carnivorous dinosaurs from the Cretaceous of Mongolia. Transactions of the Joint Soviet-Mongolian Paleontological Expedition] 19:5–120. [Russian]

Barsbold, R., T. Maryanska, and H. Osmólska. 1990. Oviraptorisauria; pp. 249–258 *in* D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria. University of California Press, Berkeley.

Bonaparte, J. F., F. E. Novas, and R. A. Coria. 1990. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. Natural History Museum of Los Angeles County, Contributions in Science 416:1–41.

Brown, B., and E. M. Schlaikjer. 1940. The structure and relationships of *Protoceratops*. Annals of the New York Academy of Sciences 40:133–266.

Bryant, H. N., and A. P. Russell. 1993. The occurrence of clavicles within Dinosauria: implications for the homology of the avian furcula and the utility of negative evidence. Journal of Vertebrate Paleontology 13:171–184.

Burnham, D. A., K. L. Derstler, P. J. Currie, R. T. Bakker, Z. Zhonghe, and J. H. Ostrom. 2000. Remarkable new birdlike dinosaur (Theropoda: Maniraptora) from the Upper Cretaceous of Montana. University of Kansas Paleontological Contributions, New Series 12–13:1–14.

Camp, C. L. 1936. A new type of small bipedal dinosaur from the Navajo Sandstone of Arizona. University of California Publications, Bulletin of the Department of Geological Sciences 24:39–56.

Carrano, M. T., S. D. Sampson, and C. A. Forster. 2002. The osteology of *Masiakasaurus knopfleri*, a small abelisauroid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 22:510–534.

Chinnery, B. J., and D. B. Weishampel. 1998. *Montanoceratops cerorhynchus* (Dinosauria: Ceratopsia) and relationships among basal Ceratopsians. Journal of Vertebrate Paleontology 18:569–585.

Chure, D. J., and J. H. Madsen Jr. 1996. On the presence of furculae in some non-maniraptoran theropods. Journal of Vertebrate Paleontology 16:573–577.

Clark, J. M., M. A. Norell, and L. M. Chiappe. 1999. An oviraptorid skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avian-like brooding position over an oviraptorid nest. American Museum Novitates 3265:1–36.

———, M. A. Norell, and R. Barsbold. 2001. Two new oviraptorids (Theropoda: Oviraptorosauria), Upper Cretaceous Djadokhta Formation, Ukhaa Tolgod, Mongolia. Journal of Vertebrate Paleontology 21:209–213.

Colbert, E. H. 1989. The Triassic Dinosaur *Coelophysis*. Bulletin of the Museum of Northern Arizona, 57, 160 pp.

Dal Sasso, C., and M. Signore. 1998. Exceptional soft tissue preservation in a theropod dinosaur from Italy. Nature 392:383–387.

Dingus, L., and T. Rowe. 1997. The Mistaken Extinction—Dinosaur Evolution and the Origin of Birds. New York, W. H. Freeman, 322 pp.

Downs, A. 2000. *Coelophysis bauri* and *Syntarsus rhodesiensis* compared, with comments on the preparation and preservation of the fossils from the Ghost Ranch *Coelophysis* Quarry. New Mexico Museum of Natural History and Science Bulletin 17:33–38.

Forster, C. A. 1999. Gondwanan dinosaur evolution and biogeographic analysis. Journal of African Earth Sciences 28:169–185.

———, S. D. Sampson, L. M. Chiappe, and D. W. Krause. 1998. The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. Science 279:1915–1919.

Gauthier, J. A. 1986. Saurischian monophyly and the origin of birds. Memoirs of the California Academy of Science 8:1–55.

Holtz, T. R., Jr. 1994. The phylogenetic position of the Tyrannosauridae: implications for theropod systematics. Journal of Paleontology 68: 1100–1117.

——— 1998. A new phylogeny of the carnivorous dinosaurs. Gaia 15: 5–61.

Huene, F. von. 1926. Vollständige Osteologie eines Plateosauriden aus der Schwäbischen Trias. Geologische und palaeontologische Abhandlungun 15:129–179.

Lambe, L. M. 1917. The Cretaceous theropodous dinosaur *Gorgosaurus*. Geological Survey of Canada Memoir 100:1–84.

Madsen, J. H., Jr. 1976. *Allosaurus fragilis*: a revised osteology. Utah Geological and Mineral Survey Bulletin 109:1–163.

Makovicky, P., and P. J. Currie. 1998. The presence of a furcula in tyrannosaurid theropods, and its phylogenetic and functional implications. Journal of Vertebrate Paleontology 18:143–149.

Norell, M. A., P. Makovicky, and J. M. Clark. 1997. A *Velociraptor* wishbone. Nature 389:447.

———, and P. J. Makovicky. 1999. Important features of the dromaeosaurid skeleton II: information from newly collected specimens of *Velociraptor mongoliensis*. American Museum Novitates 3282:1–45.

Olsen, P. E., and P. M. Galton. 1984. A review of the reptile and amphibian assemblages from the Stormberg of southern Africa, with special emphasis on the footprints and the age of the Stormberg. Palaeontologia Africana 25:87–110.

Osborn, H. F. 1924. *Psittacosaurus* and *Protiguanodon*: two lower Cretaceous iguanodonts from Mongolia. American Museum Novitates 127:1–16.

Padian, K. 1997. Pectoral Girdle; pp. 530–536 *in* P. J. Currie and K. Padian (eds.), Encyclopedia of Dinosaurs. Academic Press, San Diego.

Raath, M. A. 1969. A new coelurosaurian dinosaur from the Forest Sandstone of Rhodesia. Arnoldia 28:1–25.

——— 1977. The anatomy of the Triassic theropod *Syntarsus rhodesiensis* (Saurischia: Podokesauridae) and a consideration of its biology. Ph.D. dissertation, Rhodes University, Salisbury, 233 pp.

Rowe, T. 1989. A new species of the theropod *Syntarsus* from the Early Jurassic Kayenta Formation of Arizona. Journal of Vertebrate Paleontology 9:125–136.

———, and J. Gauthier. 1990. Ceratosauria; pp. 158–168 *in* D. B. Weishampel, P. Dodson, and H. Osmolska (eds.), The Dinosauria. University of California Press, Berkeley.

———, R. S. Tykoski, and J. Hutchinson. 1997. Ceratosauria; pp. 106–110 *in* P. J. Currie and K. Padian (eds.), Encyclopedia of Dinosaurs. Academic Press, San Diego.

Russell, D. A. 1969. A new specimen of *Stenonychosaurus* from the Oldman Formation (Cretaceous) of Alberta. Canadian Journal of Earth Sciences 6:595–612.

———, and Z.-M. Dong. 1993. A nearly complete skeleton of a new troodontid dinosaur from the Early Cretaceous of the Ordos Basin, Inner Mongolia, People's Republic of China. Canadian Journal of Earth Sciences 30:2163–2173.

Sampson, S. D., M. T. Carrano, and C. A. Forster. 2001. A bizarre new predatory dinosaur from Madagascar. Nature 409:504–506.

Senter, P., and J. R. Hutchinson. 2001. New information on the skeleton of the theropod *Segisaurus halli*. Journal of Vertebrate Paleontology 21(3, Suppl.):100A.

Sereno, P. C. 1991. Basal archosaurs: phylogenetic relationships and functional implications. Society of Vertebrate Paleontology Memoir 2:1–53.

——— 1999. The evolution of dinosaurs. Science 284:2137–2147.

Sternberg, C. M. 1951. Complete skeleton of *Leptoceratops gracilis* Brown from the Upper Edmonton member on Red Deer River, Alberta. Bulletin of the National Museum of Canada 123:225–255.

Thulborn, R. A. 1984. The avian relationships of *Archaeopteryx*, and the origin of birds. Zoological Journal of the Linnean Society 82: 119–158.

Tykoski, R. S. 1998. The osteology of *Syntarsus kayentakatae* and its implications for ceratosaurid phylogeny. M.S. thesis, The University of Texas at Austin, Texas, 217 pp.

Xu, X., Z.-L. Tang, and X.-l. Wang. 1999a. A therizinosauroid dinosaur with integumentary structures from China. Nature 399:350–354.

———, X.-L. Wang, and X.-C. Wu. 1999b. A dromaeosaurid dinosaur with a filamentous integument from the Yixian Formation of China. Nature 401:262–266.

Received 13 March 2001; accepted 18 January 2002..