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A review of coelophysoids (Dinosauria: Theropoda) from the Early Jurassic of Europe, with comments on the late history of the Coelophysoidea

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With 4 figures

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Abstract: We review the available materials of Early Jurassic European theropods and confirm several as belonging to the clade Coelophysoidea. These include the holotypic partial skeleton of *Liliensternus airelensis* (France), fragmentary remains referred to as *Sarcosaurus woodi* and *Sarcosaurus andrewsi* (England), and a distal tibia (Scotland). Although incomplete, these specimens indicate that a wide size range of coelophysoids existed in Europe throughout the Early Jurassic, much as in North America. The record of coelophysoids from other continents is also reviewed, with particular attention to the later history of the clade. Coelophysoids apparently remained common worldwide into the Early Jurassic. They appear to have gone extinct by the end of the Early Jurassic, although the poor Middle Jurassic record may yet reveal late survivors of the group.

Zusammenfassung: Das verfügbare Material europäischer unterjurassischer Theropoden wird untersucht und dabei mehrere als den Coelophysoidea zugehörig erkannt. Diese umfassen das Teilskelett von *Liliensternus airelensis* aus Frankreich, fragmentarische, zu *Sarcosaurus woodi* und *Sarcosaurus andrewsi* gestellte Reste aus England sowie eine distale Tibia aus Schottland. Obwohl unvollständig, zeigen die Stücke eine große Größenspanne der Coelophysoiden während des Unter-Jura, ebenso wie in Nordamerika. Die Belege dieser Gruppe von anderen Kontinenten werden ebenfalls betrachtet, mit besonderer Berücksichtigung ihrer späteren Entwicklung. Augenscheinlich blieben sie während des Unter-Jura weltweit häufig und scheinen am Ende des Unter-Jura ausgestorben zu sein, obwohl die spärliche Überlieferung im Mittel-Jura noch Überlebende der Gruppe liefern könnte.

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1. Introduction

Coelophysoids are a monophyletic group of primitive theropods, first diagnosed by Rowe (1989) as one clade within the larger group Ceratosauria (sensu Gauthier 1986). These predominately small-bodied carnivores were particularly diverse during the Late Triassic, when they were represented by *Coelophysis bauri* and *Gojirasaurus quayi* (North America), *Procompsognathus triassicus* and *Liliensternus liliensterni* (Europe), and several other poorly known and/or undescribed forms. These latter include materials referred to as *Eucoelophysis baldwini* (Sullivan & Lucas, 1999) and *Halticosaurus longotarsus* (= *Longosaurus longotarsus* Welles, 1984). *Zupaysaurus rougieri*, recently described as a basal tetanuran from the Late Triassic of Argentina (Arcucci & Coria 1997, 2003), may instead represent the first-known South American coelophysoid (Carrano & Sampson, in prep.). Overall, these taxa are often the most common Late Triassic carnivorous dinosaurs.

However, coelophysoid remains are also well known from the Early Jurassic, notable forms including *Dilophosaurus wetherilli, Segisaurus halli*, and *Syntarsus kayentakatae* (North America), as well as *Syntarsus rhodesiensis* (southern Africa). *Dilophosaurus sinensis* was recently described by Hu (1993) from the Early Jurassic lower Lufeng Formation of China, but its generic assignment has been questioned (Lamanna et al. 1998; Rauhut 2003). Ongoing systematic work by the current authors suggests that at least the skull described by Hu (1993) represents neither *Dilophosaurus* nor another coelophysoid, but instead is from a more derived theropod taxon. Nevertheless, a fused astragalocalcaneum from the same stratum (Welles & Long 1974) does apparently indicate the presence of a moderately sized coelophysoid. In addition, the (now destroyed) holotype of *Podokesaurus holyokensis* (Talbot, 1911) was almost certainly from a Early Jurassic coelophysoid similar to *Coelophysis* (Colbert, 1964). This small-bodied theropod from the Portland Arkose of Massachusetts exhibited several coelophysoid synapomorphies (including a long, ventrally curved pubis whose length exceeded that of the ischium, and an additional pubic foramen ventral to the obturator opening), but little more can now be said of its affinities.

In Europe, the partial skeleton of *Liliensternus airelensis* occurs in deposits that are either latest Triassic or Early Jurassic in age (Larsonneur & Lapparent 1966; Cuny et al. 1991; Cuny & Galton 1993). Among the only other coelophysoid remains noted from the European Early Jurassic are the vertebra, partially fused pelvis, and poorly preserved femur that constitute the holotype of *Sarcosaurus woodi* (Andrews, 1921), along with a more complete referred specimen (Huene 1932). Rowe (1989) and Rowe & Gauthier (1990) suggested that this taxon might represent a coelophysoid, noting similarities with the overlapping materials of *Liliensternus*. In addition, the holotype of *Sarcosaurus andrewsi* – a specimen with a truly confused and confusing taxonomic history (Huene 1926a, b, 1932, 1956) – may also belong to the Coelophysoidea. Finally, Benton et al. (1995) described a partial coelophysoid tibia from the Early Jurassic of the Isle of Skye, Scotland.

Together, these European materials are among the latest-known coelophysoids. Here we redeseribe them in the context of recent phylogenetic revisions, addressing their geographic and temporal (stratigraphic) significance.

Institutional abbreviations: See Appendix.

2. Systematic paleontology

Dinosauria	Owen, 1842
Saurischia	Seeley, 1888
Theropoda	Marsh, 1881
Coelophysoidea	(Nopcsa, 1928)

Liliensternus airelensis Cuny & Galton, 1993

Holotype: Caen Museum, unnumbered.

Locality: Airel Quarry, Normandy, France.

Horizon: Moon-Airel Formation; Rhaetian-Hettangian, Upper Triassic-Early Jurassic.

Taxonomic history: The materials now described as *Liliensternus airelensis* were originally referred to the poorly known Late Triassic European theropod *Halticosaurus* (Larsonneur & Lapparent, 1966), along with *H. liliensterni* (Huene, 1934). *Halticosaurus* was traditionally allied with "podokesaurids" or "halticosaurids" (roughly equivalent to coelophysoids) as typified by taxa such as *Podokesaurus* and *Coelophysis.* The redescription of *H. liliensterni* made it the type species of the genus *Liliensternus* (Welles, 1984), and it was subsequently diagnosed as a ceratosaur (Gauthier 1986, Rowe 1989; Rowe & Gauthier 1990). However, these authors were unable to find synapomorphies that distinguished it from other ceratosaurs, and considered it a possible metataxon. Subsequently, both the genus *Liliensternus* and the species *L. airelensis* were given formal diagnoses by CUNY & GALTON (1993) and RAUHUT (2003).

Diagnosis: "Cervical vertebrae with dorsoventrally narrow, anteroposteriorly elongated posterior pleurocoel; deep infradiapophyseal fossa in anterior cervical vertebrae; horizontal ridge at the basis of the neural spine in cervical vertebrae; ilium with a triangular lateral bulge above the supra-acetabular crest." (RAUHUT 2003: 15).

Description: The morphology of this taxon has been thoroughly described by CUNY & GALTON (1993) and RAUHUT (2000), and we have little to add here.

We note that CUNY & GALTON (1993) described the sacrum as comprising four vertebrae, the two primordial sacrals plus one dorsosacral and one caudosacral. They likened this pattern to that seen in *L. liliensterni* and *D. wetherilli*, each of which apparently has four sacral vertebrae. We agree with the vertebral identifications presented by CUNY & GALTON (1993). However, most primitive neotheropods (including *Coelophysis* and *Syntarsus*) have sacra that consist of five vertebrae, with the fifth drawn from the posterior dorsal series. This additional dorsosacral can be difficult to identify if it is not well preserved, because it may bear only slight modifications of the transverse process for contact with the ilium. The posterior dorsal described by CUNY & GALTON (1993: 267, figs. 4C, 5) is missing its neural arch, and was found attached to dorsosacral 1. It may therefore represent dorsosacral 2, in which case *L. airelensis* had five sacral vertebrae.

Similar issues of preservation (and a miscounting of vertebrae by WELLES [1984]) obscure the true sacral counts of *D. wetherilli* and *L. liliensterni*. However, if better materials confirm the true presence of four sacrals in all three of these taxa, it might represent a synapomorphy of these otherwise similar forms.

Comments: There seems to be little question that this taxon is a coelophysoid, as it bears numerous relevant synapomorphies in the vertebrae and pelvis. These include a distinct posterior "pleurocoel" in the cervicals, anteroposteriorly long cervical centra, fusion of the sacral ribs to the transverse processes, and an anteriorly facing pubic peduncle on the ilium. The right pubis and ischium are articulated but a suture remains visible between them, so these elements may not be truly fused. (Additionally, the left pubis and ischium are disarticulated.) The presence of a pubic foramen (or pubic fenestra) below the obturator foramen cannot be determined. Other features, such as subequally sized iliac peduncles, a closed obturator foramen in the proximal pubis, and anteroposteriorly long dorsal centra, are characteristic of most primitive theropods and appear to be plesiomorphic (SERENO 1999; CARRANO et al. 2002; RAUHUT 2003).

RAUHUT (2003: 139) noted that a single synapomorphy (presence of a broad ridge extending from the posterior diapophyses to the ventral rim of the posterior centrum in the cervicals; character 98) supported a sister-taxon relationship between *L. airelensis* and *L. liliensterni*. We agree that these two taxa appear to be more similar to each other than to other coelophysoids. However, this ridge is occasionally faintly apparent in other coelophysoid cervicals, delineating the ventral edge of the postzygapophyseal fossa. It tends to be obscured in many specimens in which the cervicals are articulated (e.g., *Coelophysis bauri* and *Syntarsus rhodesiensis*), because the prezygapophysis of the succeeding vertebra usually lodges into this fossa. Therefore it may be that only the prominence of this structure characterizes *Liliensternus*.

Sarcosaurus woodi ANDREWS, 1921

Holotype: BMNH 4840/1, a vertebral centrum, partial pelvis and femur (Figs. 1-2.)

Referred specimen: Warwick Museum specimen, a partial postcranial skeleton.

Locality: Barrow-on-Soar, Leicestershire, England (holotype); Wilmcote, Warwickshire, England (referred specimen).

Horizon: *bucklandi* zone, Lower Lias; lower Sinemurian, Early Jurassic.

Taxonomic history: ANDREWS (1921) described *Sarcosaurus woodi* as an Early Liassic "megalosaurian", but even then, as now, that term had broad and somewhat vague connotations. Few workers have commented on *Sarcosaurus* since that time, but recently the taxon was diagnosed as a ceratosaur (ROWE 1989; ROWE & GAUTHIER 1990).

Comments on diagnosis: ROWE (1989) and ROWE & GAUTHIER (1990) were unable to find any autapomorphies in the holotype specimen of *Sarcosaurus woodi*. Our own examination yielded the same conclusion, and the materials on which ANDREWS (1921) founded this taxon would probably be insufficient to do so now. We are left in the unfortunate position of describing a taxon that is a *nomen dubium* based strictly on its preserved morphology, but one that is also probably distinct from other known taxa based on its provenance.

Description: ANDREWS (1921) provided a detailed, astute description of this taxon, so we recount only those features salient toward determining its phylogenetic relationships.

The single vertebral centrum is incomplete, lacking the left half of the neural arch and the posterior half of the centrum. It belongs to a posterior dorsal, as evidenced by the near absence of a distinct parapophyseal facet on the arch and the lack of a "pleurocoelous" fossa on the centrum (present in the anterior presacrals of nearly all neotheropods). The anterior face is weakly concave, and the neural canal is relatively small. The transverse process is inclined dorsally at an angle of 45°, and the prezygapophyses are positioned close to the midline, unlike the condition in neoceratosaurs.

The pelvis of *S. woodi* is incomplete but articulated, comprising two partial ilia and pubes but lacking nearly all of the ischia (Fig. 1). The pubes are fused to their respective ilia with little vestige of a suture. Although the ilia are incomplete, the preservation of the left and right elements is such that nearly the entire form of the bone is represented.

The ilium is similar to that of *Liliensternus liliensterni*, but even more closely resembles that of *Dilophosaurus wetherilli*. Both bear a rounded, lobate preacetabular blade and a squared-off postacetabular blade that is slightly shallower dorsoventrally than the main body of the ilium. As ANDREWS (1921: 571) noted, the ventral lobe of the preacetabulum descends close to the pubic peduncle, much more like the condition in (the relatively basal) *Ceratosaurus* than in (the more derived) *Megalosaurus*. A similar condition is observed in *Elaphrosaurus* and *Dilophosaurus*. The dorsal margin is gently convex (unlike the nearly straight margin in *L. liliensterni*), with a vertically striated longitudinal band along this edge that marks the origin of the Mm. iliotibiales. As is typical for neotheropods, both the pre- and postacetabular blades extend beyond their respective peduncles. The fossa for M. iliofemoralis internus is relatively small and does not extend onto the pubic peduncle. Further, both peduncles appear to be of similar size, and the supraacetabular shelf between them is pendant as in most primitive theropods. There is no prominent ridge between this crest and the lateral wall of the brevis fossa, as occurs in neoceratosaurs. A faint line appears to mark the contact with the pubis, indicating that the pubic peduncle faced somewhat anteriorly, as in coelophysoids. Medially, the ilia appear to have contacted five sacral vertebrae, the primitive condition for Neotheropoda (CARRANO et al. 2002). The brevis fossa is broad posteriorly, as in other coelophysoids and in most neoceratosaurs, with the lateral wall reaching farther ventrally than the medial wall.

Only the proximal one-third (approximately) of the pubes are preserved, and their ventral margins are incomplete. Nevertheless, they retain portions of the obturator passage, although it cannot be determined whether this was a notch or a foramen, nor whether a secondary pubic foramen was present as in *Syntarsus, Segisaurus*, and *Procompsognathus*. The proximal pubic shaft is straight. Near its contact with the ilium, the pubis forms a broad bulge that marks the origin of M. ambiens.

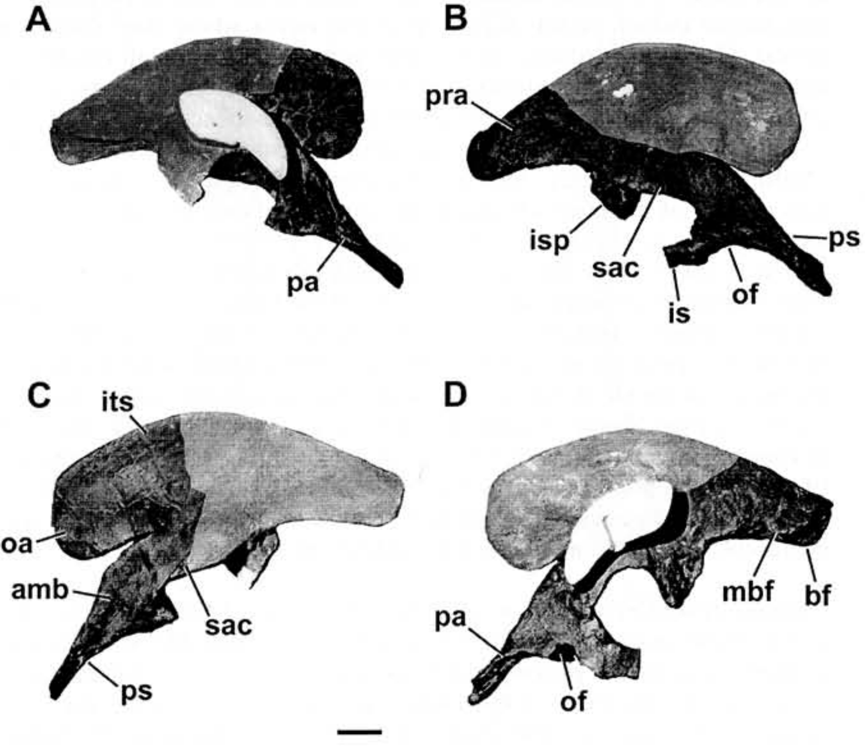

Fig. 1. Pelvis of *Sarcosaurus woodi*, BMNH 4840/1, holotype. Left pelvis in medial (A) and lateral (B) views; right pelvis in lateral (C) and medial (D) views. Lightened areas have been restored. The white object located centrally in A and D represents a mounting bracket formerly used to connect the left and right pelves. Abbreviations: amb, M. ambiens attachment sear; bf, brevis fossa; is, ischium; isp, ischiac peduncle of ilium; its, Mm. iliotibiales attachment scar; mbf, medial wall of brevis fossa; of, obturator foramen; pa, pubic apron; poa, postacetabular process; pra, preacetabular process; ps, pubic shaft; sac, supraacetabular crest. – Scale = 5 cm.

The ischia are almost entirely missing, but it appears that they may not have been fully fused to the ilia and pubes. This inference is supported by the presence of a visible ischial-pubic contact on the ventral portion of the acetabulum (which retains a portion of the ischia where they contact the pubes). The ischial peduncle of the ilium is broken. The overall condition of this pelvic "fusion" is reminiscent of *Carnotaurus sastrei* (Bonaparte et al. 1990), in which some, but not all, elements show evidence of coossification.

The femur of *Sarcosaurus* is rather poorly preserved, but nearly its entire length is present (Fig. 2). Although the proximal and distal ends are damaged, enough of the head remains to indicate that its orientation was anteromedial, as in most primitive theropods (Holtz 1998 [2000]; Carrano et al. 2002). A small, spike-like lesser trochanter is present, with a trochanteric shelf extending around to the lateral side of the bone. This condition particularly resembles that in *Liliensternus liliensterni*, as well as the "robust morph" of *Syntarsus rhodesiensis* (Raath, 1990). On the lateral surface of the proximal femur, a flat surface marks the greater trochanter, the likely insertion of the Mm. puboischiofemorales (Hutchinson 2001). The fourth trochanter is a relatively long but low ridge that sits adjacent to a weak fossa (the insertions for the Mm. caudofemorales). It is located approximately one-third of the way down the shaft. A shallow anterior intercondylar groove is present, but posteriorly the distal condyles are damaged.

Comments: *Sarcosaurus woodi* resembles both *Liliensternus liliensterni* and *Dilophosaurus wetherilli*, but appears to be referable to neither. For example, whereas the proximal femur is strikingly similar to that of *L. liliensterni*, the morphology of the ilium more strongly resembles that of *D. wetherilli*. We were not able to identify autapomorphies on the fragmentary holotypic materials, and it has been suggested that *S. woodi* may represent a metataxon (Rowe & Gauthier 1990). However, given the extremely incomplete nature of the specimen, we suggest that *S. woodi* is probably a distinct taxon that is not currently diagnosable, rather than a fragmentary taxon that genuinely lacked autapomorphies in its complete fonn.

S. woodi appears to represent an animal about half the size of *D. wetherilli* and comparable in size to *L. liliensterni*, assuming that fusion of

Fig. 2. Femur of *Sarcosaurus woodi*, BMNH 4840/1, holotype. Left femur in posterior (A), anterior (B), medial (C), and lateral (D) views. Abbreviations: aig, anterior intercondylar groove; fn, femoral neck; gt, greater trochanter; ltr, lesser trochanter; trs, trochanteric shelf; 4tf, fourth trochanteric fossa; 4tr, fourth trochanter. – Scale = 5 cm.

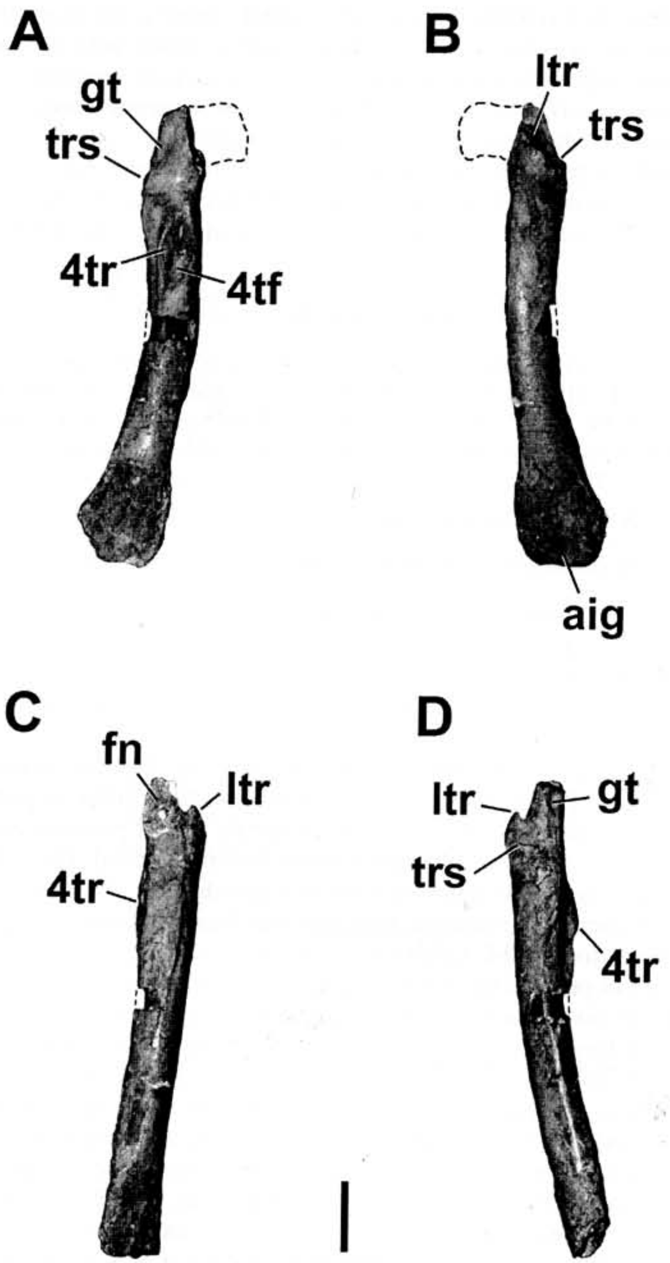

Fig. 2 (Legend see p. 544)

pelvic sutures is a reliable indicator of skeletal maturity. However, there are no compelling reasons to assume that growth ceased with the onset of such fusion, especially considering that (e.g.) fusion of separate astragalar ossification centers into a single "bone" early in ontogeny imparts no such constraints on later growth. Therefore *S. woodi* may well have reached considerably larger sizes than the holotypic specimen indicates.

Additional materials from the Liassic of Wilmcote have also been referred to *S. woodi* (HUENE, 1932). These are discussed in more detail below.

cf. *Sarcosaurus woodi* ANDREWS, 1921

Materials: Warwick Museum specimen, including two dorsal centra, partial right pubis, left and right femora, right and partial left tibiae, a distal fibula, distal left metatarsals II-IV, and a partial pedal phalanx (HUENE 1932: pl. II, figs. 4-17). A fragment of distal left pubis was found isolated and its association is dubious (HUENE 1932: 50).

Locality: Wilmcote, Warwickshire, England.

Horizon: *bucklandi* zone, Lower Lias; lower Sinemurian, Early Jurassic.

Description: These materials appear to represent the partial remains of a single individual, which come from a different locality but the same stratigraphic level as the holotype of *S. woodi*. They were described by HUENE (1932), who compared them extensively to *Elaphrosaurus* but felt they bore particular similarity to *S. woodi*.

Unfortunately, there are few available overlapping elements between these two specimens. The dorsal vertebrae are probably from different parts of the column, but in any case the Wilmcote materials do not preserve enough of the neural arch to compare directly with the holotype dorsal. Their relatively long centra suggest coelophysoid affinities, and the lack of a distinct pleurocoelous foramen in the centrum indicates that these vertebrae were probably located posterior to D4. Otherwise, little more can be said of them. The proximal right pubis of the Wilmcote specimen preserves part of an obturator foramen but no features enabling a meaningful comparison with BMNH R.4840/1. A fragment of ilium is also present among the Wilmcote materials, but it was neither described nor illustrated by HUENE (1932).

Reasonably complete femora are known from both specimens. As in BMNH R.4840/1, the Wilmcote femora have an anteromedially directed head, a relatively long fourth trochanter, and some evidence of a trochanteric shelf. Unfortunately, these are all plesiomorphic features for theropods (e.g., HOLTZ 1998 [2000], CARRANO et al. 2002) and indicate neither conspecificity nor particular clade membership. However, it is equally important to note that they do not display any features inconsistent with the two specimens belonging to the same species.

The Wilmcote tibiae are the most important elements for determining the specimen's phylogenetic affinities. The right tibia is nearly complete, preserving most of the distal end intact. In distal view, this end shows the notched, circular profile that is characteristic of coelophysoid tibiae (CARRANO et al. 2002; see *S. andrewsi*, below). The proximal left tibia, although weathered, also has a profile similar to the tibia of coelophysoids such as *Liliensternus*. Both bones show a prominent fibular crest and a long, flat fibular contact facet, as are typical for neotheropods.

Finally, the Wilmcote specimen preserves a number of elements not present in the holotype of *S. woodi*. These include a distal fibula, parts of the three central left metatarsals, and a single pedal phalanx. None of these elements are particularly specialized above the basic neotheropod condition, and thus they do not show features that would allow more specific phylogenetic placement of the specimen.

Discussion: Although the Wilmcote specimen includes numerous skeletal elements, it is still very incomplete and presents little overlap with the holotype of *S. woodi*. Nevertheless, enough morphology is preserved to indicate that it is probably a coelophysoid, and one of approximately the same size as *S. woodi*. In the absence of apomorphic features on the holotype, it cannot be determined unequivocally whether these two specimens derive from the same taxon, because it is not possible to find a uniquely derived feature shared by both. However, their general morphological similarities, coupled with their identical stratigraphic provenance, make such a hypothesis tempting. Until better materials are found, we consider it prudent to refer to the Wilmcote materials as cf. *Sarcosaurus woodi*.

Sarcosaurus andrewsi HUENE, 1932

Holotype: BMNH R.3542, a right tibia.

Locality: Wilmcote, Warwickshire, England.

Horizon: Angulata Zone, Lower Lias; upper Hettangian, Early Jurassic.

Taxonomic history: This specimen has led a difficult taxonomic life. Originally described (with suitable generality) as a "megalosaurian" from the Lower Liassic (WOODWARD 1908), it was later referred to the genus *Megalosaurus* (HUENE 1926) and eventually formally named as a distinct taxon (HUENE 1932). Unfortunately, in doing so HUENE created considerable confusion regarding the affinities and identity of this specimen:

1) in the text of a single paper, Huene (1932) made this one element the type of two new taxa: *Sarcosaurus andrewsi* (p. 51) and *Magnosaurus woodwardi* (p. 219);

2) the first new species (*S. andrewsi*) was referred to a preexisting genus (type, *S. woodi*) despite the fact that the former only overlaps the referred specimen of *S. woodi* and is morphologically distinct from it (Huene 1932: 51);

3) the second new species (*M. woodwardi*) was also referred to a preexisting genus (type, *M. nethercombensis*), despite significant morphological differences and a temporal gap of at least twenty million years; and

4) Huene (1956) later referred to all three specimens (type and referred materials of *S. woodi* as well as BMNH R.3542) to two species of *Sarcosaurus* without mentioning *M. woodwardi*.

Waldman (1974) formally transferred this material to the genus *Megalosaurus,* but there is little evidence to support such an assignment. The specimen has been largely ignored since that time. We refer to this specimen as *Sarcosaurus andrewsi* following the most recent published opinion (Huene 1956).

Comments on diagnosis: BMNH R.3542 bears no discernible diagnostic features and we consider it a *nomen dubium*. Although it can only be distinguished from *S. woodi* by its larger size, it also cannot be specifically allied with that form beyond the fact that both probably reside within the clade Coelophysoidea, and both are from the same geographic area and similar (but not identical) temporal horizons. Synonymy of the two English Liassic coelophysoids remains a possibility, but will remain impossible to determine without more complete specimens.

Description: In spite of its problematic history, the specimen bears several striking resemblances to known coelophysoid tibiae (Fig. 3). Its size is closer to *Liliensternus, Gojirasaurus*, and *Dilophosaurus* than to *Coelophysis, Syntarsus*, or *Procompsognathus.* Nevertheless, its proportions are rather slender.

At the proximal end, the cnemial crest is distinct but small, and rounded at its end, lacking the dramatic expansion seen in neoceratosaurs and extending only slightly above the articular surface for the femur. This crest extends anteriorly but much less so than in tetanurans, and the lateral fibular fossa is shallow. The two proximal condyles are subequal in size, with the lateral condyle appearing much less marked and lobular than in most tetanurans. The fibular crest is distinct but low, forming a thin ridge that passes down the proximal onethird of the shaft. It is much less prominent than in *Ceratosaurus,* or tetanurans such as *Megalosaurus* and *Allosaurus*. Below, a small gap separates the crest from the long, thin fibular facet.

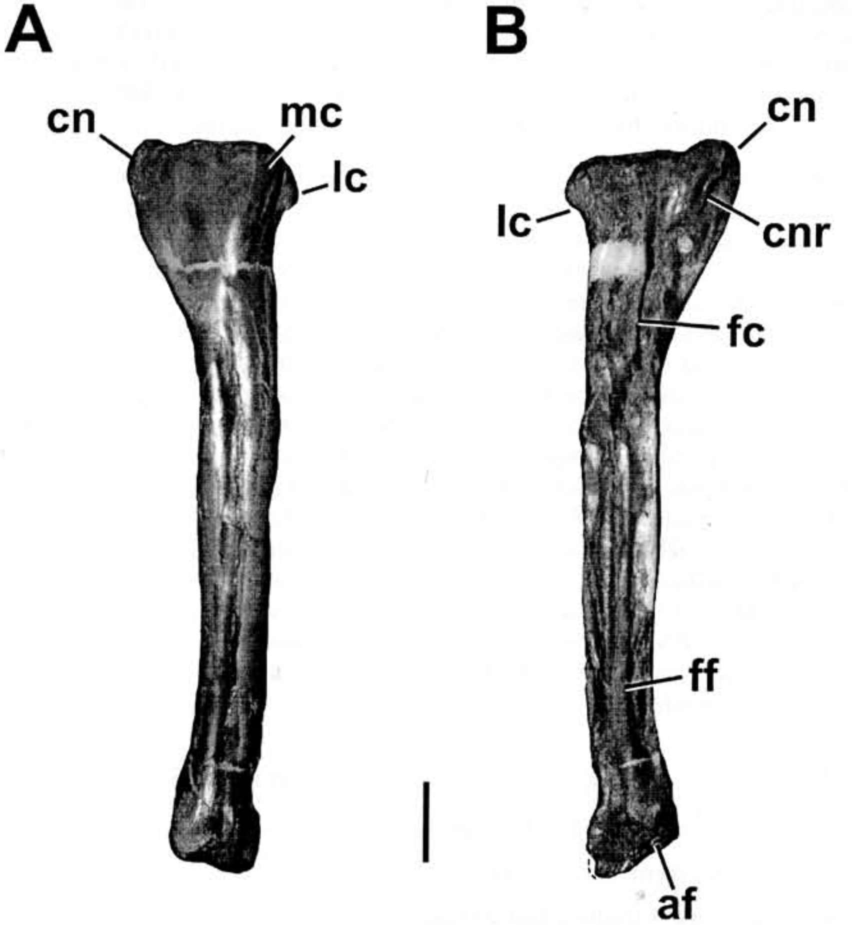

Fig. 3. Tibia of *Sarcosaurus andrewsi* (= *Magnosaurus woodwardi*), BMNH R.3542, holotype. Right tibia in medial (A) and lateral (B) views. Abbreviations: af, astragalar facet; cn, cnemial crest; cnr, cnemial crest ridge; fc, fibular crest; ff, fibular facet; lc, lateral proximal condyle; mc, medial proximal condyle. – Scale = 5 cm.

The distal end has a rounded outline in distal view, as in most coelophysoids (Woodward 1908: fig. 1); it is not elongate mediolaterally as in tetanurans and neoceratosaurs (CARRANO et al. 2002). The facet for the ascending process of the astragalus is low and forms a notch in the anterolateral edge of the distal tibia, suggesting that the corresponding astragalar ascending process was also low and rather blocky (instead of laminar). The distal tibia did not back the fibula to any significant degree.

Comments: BMNH R.3542 clearly represents a neotheropod tibia, as evidenced from the prominent fibular facet and fibular crest. It also appears to be a coelophysoid, based on the characteristic rounded profile of the distal end and the condition of the astragalar notch, both of which are intermediate between the conditions in *Herrerasaurus* and tetanurans.

HUENE (1932) obviously felt (at least until page 219) that this specimen could be allied with *Sarcosaurus woodi*, a claim he later reiterated (HUENE 1956). At the time, he provided little direct data to support such an inference, but the presence of two moderately sized coelophysoids in the same restricted temporal and geographic interval is intriguing. The tibia of BMNH R.3542 is from a distinctly larger animal than the type of *S. woodi*, and closer in size to *D. wetherilli*. If *S. woodi* indeed represents an adult, then perhaps two coelophysoids are indeed present in the English Lias. However, as we have noted above, fusion may be an unreliable indicator of maximum individual (and therefore maximum taxon) size, so the possibility that *S. woodi* and BMNH R.3542 represent the same taxon must remain a possibility. Until more materials are discovered, it is best to refer to this specimen to Coelophysoidea indet.

Coelophysoidea indet. (BENTON et al. 1995)

Specimen: NMS.G 1994.10.1, a distal left tibia.

Locality: Southern Strath, Isle of Skye, Scotland.

Horizon: Upper Broadford Beds Formation; Sinemurian, Early Jurassic.

Description: BENTON et al. (1995) originally described NMS.G 1994.10.1 as the proximal right tibia of a ceratosaur, but in fact the specimen represents the distal end of a left tibia. In all respects this element conforms to the distal tibiae of coelophysoid taxa such as *Coelophysis, Syntarsus*, and *Liliensternus*. It has a nearly circular outline in distal view (BENTON et al. 1995: fig. 2e), with a lateral notch that marks the articulation of the low, blocky astragalar ascending process. This outline is more elliptical than that of *Herrerasaurus,* but much less so than those of tetanurans (e.g., *Majungatholus, Allosaurus*). The tibia clearly did not extend laterally behind the fibula, as it does in more derived theropods, but was positioned nearly entirely medial to it. Along the lateral side of the shaft, a flat facet marks the contact with the fibular shaft, as is typical of neotheropods (BENTON et al. 1995: fig. 2a-c). Although its size is more characteristic of coelophysids, at this point NMS.G 1994.10.1 cannot be identified more specifically than Coelophysoidea indet.

3. Discussion

The Early Jurassic record of European coelophysoids is poorly documented. Nonetheless, the above-mentioned specimens record the presence of several coelophysoid taxa in the Early Jurassic of Europe. Although three of the forms described herein are too fragmentary to diagnose formally, all can be placed within the clade Coelophysoidea. As such, they provide a significant temporal extension for this group within Europe, whose longevity there is now comparable that in Africa and North America. Both large- and small-bodied forms are present, ranging from tens to hundred of kilograms (based on the equations of ANDERSON et al. 1985). This represents an overall size range similar to that seen in the Late Triassic and Early Jurassic of North America, as well as the Late Triassic of Europe.

Indeed, the Late Triassic record of European coelophysoids is quite diverse, albeit rather fragmentary (RAUHUT & HUNGERBÜHLER 1998 [2000]) (Fig. 4). They are represented by *Halticosaurus longotarsus* and *Procompsognathus triassicus* (middle Norian, Germany), *Pterospondylus trielbae* (late Norian-Rhaetian, Germany), *Liliensternus liliensterni* (late Norian, Germany; HUENE 1934), *Dolichosuchus cristatus* (lower or middle Norian, Germany), and material referred to ?*Syntarsus* sp. (Norian?, Wales) Both *D. cristatus* and *L. liliensterni* are moderately large taxa, equivalent in size to *Gojirasaurus* and *Dilophosaurus,* whereas most of the remaining forms are *Syntarsus*-sized or smaller.

Other Early Jurassic European theropods are either indeterminate or belong to distinct clades. Indeterminate forms include "*Megalosaurus*" *lydekkeri* (BMNH 41352, a single tooth from the Liassic of Lyme Regis, England) and "*Megalosaurus*" *terquemi* (teeth from the Hettangian of Lorraine, France; HUENE 1926). The Liassic theropod knee joint formerly included in the holotype of *Scelidosaurus harrisonii* (NEWMAN, 1968) probably belongs to a basal tetanuran. It cannot be diagnosed more specifically, but nonetheless represents one of the earliest known tetanurans.

No definitive Middle Jurassic coelophysoids are known, but specimens from northern Mexico (MUNTER & CLARK, in press) indicate that this clade survived until at least the latest Early Jurassic. BENTON et al. (1995) noted that "a small undescribed ceratosaurian caudal vertebra" was discovered in the Bathonian sediments of the Isle of Skye. However, without additional information it cannot be said whether "ceratosaurian" in this context means "coelophysoid", "ceratosaur" (*sensu stricto*), or neither (i.e., an indeterminate theropod more primitive than typical tetanurans).

Thus coelophysoids were not only present in the Early Jurassic of Europe, but were at least as common there as other forms of theropods. In contrast, nearly all known Early Jurassic theropods from North America are coelophysoids, as was the case for the Late Triassic of both continents. The existing Middle Jurassic records from Europe, South America, and China indicate that coelophysoids were absent from these faunas. Still, the poor terrestrial Middle Jurassic record on most continents suggests that we should view the purported absence of coelophysoids from these regions and strata with caution. Regardless, the clade certainly appears to have gone extinct by the Late Jurassic, unless (as suggested by NOVAS, 1992) *Elaphrosaurus bambergi* is indeed a coelophysoid. If so, it represents the last surviving member of this clade. Recent studies, however, suggest that *Elaphrosaurus* is actually a primitive neoceratosaur (e.g., HOLTZ 1998 [2000]; CARRANO et al. 2002; RAUHUT 2003), and thereby one of the earliest known members of that clade.

Finally, several recent studies (CARRANO et al. 2002; RAUHUT 2003) have suggested that the clade Coelophysoidea may be paraphyletic. In particular, the taxon *Dilophosaurus wetherilli* was found to lie outside other coelophysoids, forming a clade with more derived theropods. Although ongoing work (CARRANO & SAMPSON, in prep.) now seems to support the original placement of *Dilophosaurus* within the traditional Coelophysoidea, the implications of a paraphyletic Coelophysoidea should be considered. In the case of the European materials discussed here, the most significant implication is that certain forms might be more closely related to *Dilophosaurus* than to coelophysoids *sensu stricto*.

In such a case, the European diversity of true coelophysoids would be reduced if some taxa indeed fell outside this clade. However, at least one of the forms discussed here – *Liliensternus airelensis* – can be allied with Coelophysoidea sensu stricto. Thus the group certainly appears to have survived into the Early Jurassic of Europe. It cannot be determined whether any of the remaining specimens are more closely related to *Dilophosaurus* or Coelophysoidea.

4. Conclusions

This paper addresses the phylogenetic affinities of five theropod dinosaur specimens from the Early Jurassic of Europe. The coelophysoid identification of one (*Liliensternus airelensis*) is strongly supported. The remaining four specimens – representing *Sarcosaurus woodi, Sarcosaurus andrewsi*, and a smaller taxon from the Isle of Skye – are redescribed and reinterpreted

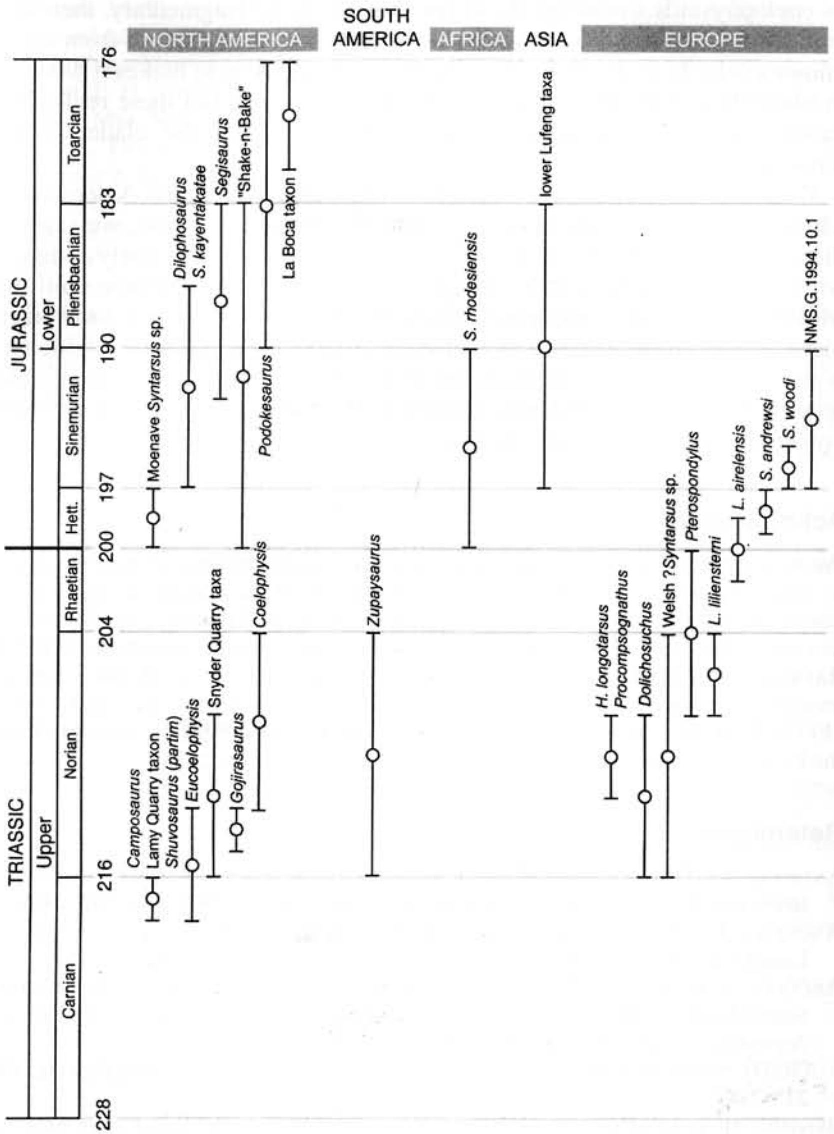

Fig. 4. Geographic and temporal distributions of coelophysoid taxa. Temporal data are illustrated as ranges to reflect the uncertainty surrounding many of the age assignments of these taxa; they should not be interpreted as indications of actual taxon longevity. Boundary dates based on GRADSTEIN et al. (1995).

as coelophysoids. Although the latter specimens are fragmentary, their age and provenance suggest that they likely represent taxa distinct from other known coelophysoids. Unfortunately, their incompleteness makes it difficult to place them with any greater phylogenetic precision, but these reidentifications extend the European range and diversity of the clade Coelophysoidea.

Coelophysoid remains have also been identified from South America and China, the latter also from Early Jurassic deposits. As a result, we suggest that a high diversity of coelophysoids persisted well into the Early Jurassic, with more derived theropods remaining comparatively uncommon until the Middle Jurassic. The replacement of the latter by the former may have taken place later in North America than elsewhere, but the record is far too incomplete for this pattern to be analyzed in detail. Regardless, no coelophysoid remains have been confidently identified anywhere on Earth from deposits younger than the latest Early Jurassic.

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Appendix

Comparative theropod materials used in this study are presented below in a phylogenetic hierarchy. All specimens were examined firsthand or as casts, except those indicated by an asterisk (of which only published materials and photographs were studied). Institutional abbreviations: **AMNH**, American Museum of Natural History, New York; **BMNH**, The Natural History Museum, London; **CM**, Carnegie Museum of Natural History, Pittsburgh; **HMN**, Humboldt Museum für Naturkunde, Berlin; **KMV**, Kunming Museum, China; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, MA; **MNA**, Museum of Northern Arizona, Flagstaff; **MOR**, Museum of the Rockies, Bozeman, MT; **MWC**, Museum of Western Colorado, Fruita, CO; **NMS.G**, National Museum of Scotland, Geology, Glasgow; **OUM**, Oxford University Museum, Oxford, England; **PVSJ**, Museo Provincial de San Juan, Argentina; **QG**, Queen Victoria Museum, Harare, Zimbabwe; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart; **UCM**, University of Colorado Museum, Boulder; **UCMP**, University of California Museum of Paleontology, Berkeley; **UMNH**, Utah Museum of Natural History, Salt Lake City; **UPLR**, Universidad Provincial de La Rioja, Argentina; **USNM**, United States National Museum, Washington, DC.

- THEROPODA
  - *Herrerasaurus ischigualastensis* (MCZ 7063, 7064; PVSJ 53, 373, 407))
  - NEOTHEROPODA
    - COELOPHYSOIDEA
      - Coelophysoidea indet. (NMS.G 1991.10.1)
      - *Dilophosaurus sinensis* (KMV 8701*)
      - *Dilophosaurus wetherilli* (UCMP 37302, 37303, 77270)
      - *Gojirasaurus quayi* (UCM 47221)
      - *Liliensternus airelensis* (Musée de Caen*)
      - *Liliensternus liliensterni* (HMN MB.R.2175)
      - *Sarcosaurus andrewsi* (BMNH R.3542)
      - *Sarcosaurus woodi* (BMNH 4840/1; Warwick Museum*)
      - *Zupaysaurus rougieri* (UPLR 076)
      - COELOPHYSIDAE
        - *Coelophysis bauri* (AMNH 2701-8, 2715-53, 7243, 7246; MCZ 4326, 4331-32)
        - *Podokesaurus holyokensis* (YPM 314, cast of holotype)
        - *Procompsognathus triassicus* (SMNS 19591)
        - *Segisaurus halli* (UCMP 32101)
        - *Syntarsus kayentakatae* (MNA V.2623)
        - *Syntarsus rhodesiensis* (QG 1, 203, 208, 302, 691)
    - CERATOSAURIA + TETANURAE
      - CERATOSAURIA
        - *Ceratosaurus nasicornis* (MWC 1.1; UMNH VP 5728; USNM 4713)
        - ABELISAUROIDEA
          - *Elaphrosaurus bambergi* (HMN MB R.38-44)

TETANURAE
  SPINOSAUROIDEA
    Eustreptospondylus oxoniensis (OUM J.13558)
    Megalosaurus bucklandi (OUM J.13560, 29881-5, BMNH R.1100-1)
  NEOTETANURAE
    ALLOSAUROIDEA
      Allosaurus fragilis (CM 11844; MCZ 3897; MOR 693; USNM 4734; UMNH VP 6000)