



Fig. 1. Juvenile megalosaurid *Sciurumimus albersdoerferi* (BMMS BK 11). (A) Overview of the limestone slab with the specimen as preserved. (B) Skull and hemimandibles under UV light in left lateral view. (C) Forelimbs under UV light. (D) Pelvic girdle under UV light. aof, antorbital fenestra; c, carpal; co, coracoid; f, femur; fu, furcula; h, humerus; hy, hyoid; il, ilium; is, ischium; mc, metacarpal; n, nares; o, orbit; pu, pubis; r, radius; s, sacral vertebra; u, ungual; ul, ulna. (Scale bars: 50 mm in A and 10 mm in B–D.)

coelurosaurs, in which it typically accounts for 40% or more of the antorbital fossa (11). The lacrimal has a long, thin anterior process, which laterally forms a large lacrimal antorbital fossa that is continuous between the dorsal and ventral part of the vertical strut, in contrast to most theropods but similar to *Torvosaurus* (12). The jugal seems to be excluded from the antorbital fenestra by the maxilla and lacrimal, which are in contact with each other. The postorbital is slender and T-shaped, with the ventral process ending above the ventral margin of the orbit. The infratemporal fenestra was obviously high and narrow, although its borders are only partially preserved. A triangular area along the frontoparietal suture has been reconstructed as bone; this structure occupies almost the same position and area as the open frontoparietal gap in the hatchling theropod *Scipionyx* (13). Although partially obscured by reconstruction, the borders of the bones around this gap do not show clear signs of breakage, making the interpretation of this area as a similar structure probable. However, a similar reconstructed area within the frontal probably represents a damaged area rather than an unossified one. The quadratojugal is considerably higher than long and has a broad dorsal contact with the broad ventral process of the squamosal. A large quadrate foramen is present in the quadratojugal–quadrate suture. A broad and deep longitudinal fossa is present on the posterior face of the basioccipital bone below the occipital condyle (Fig. 2B), as seen in other megalosaurids and spinosaurids (10).

The anterior end of the dentary is slightly raised dorsally over the first three tooth positions; the medial side of the dentary shows two Meckelian foramina anteriorly, as seen in other basal theropods (10). An anteroventrally opening mylohyoid foramen is present along the ventral margin of the splenial. A large mandibular fenestra is present, and the retroarticular process is short and stout. The premaxilla bears four unserrated teeth, and the 11 maxillary and 12–14 dentary teeth are strongly recurved and bear serrations on the distal but not on the mesial carina (Fig. 2A).

There are 10 cervical and 13 dorsal vertebrae. As in many basal theropods, the axis lacks pleurocoels, but single, large pneumatic foramina are present in the remaining cervicals (Fig. 2B). Anterior cervical vertebrae might be slightly opisthocoelous, but the posterior cervicals seem amphiplatycoelous. Cervical neural arches have pronounced prezygoepipophyseal laminae and large, elongate epipophyses, which considerably overhang the postzygapophyses posteriorly (Fig. 2B). Anterior dorsal vertebrae have a well-developed ventral keel and bear pleurocoels, whereas posterior dorsals are apneumatic. Posterior dorsal vertebrae seem to have rather poorly developed neural arch lamination and backswept transverse processes. The neural spines of the posterior dorsal vertebrae are unusual in being very low anteriorly, with a squared anterior end and a lobe-shaped posterodorsal expansion posteriorly (Fig. 2C and D). This expansion becomes more conspicuous in the posterior-most elements.

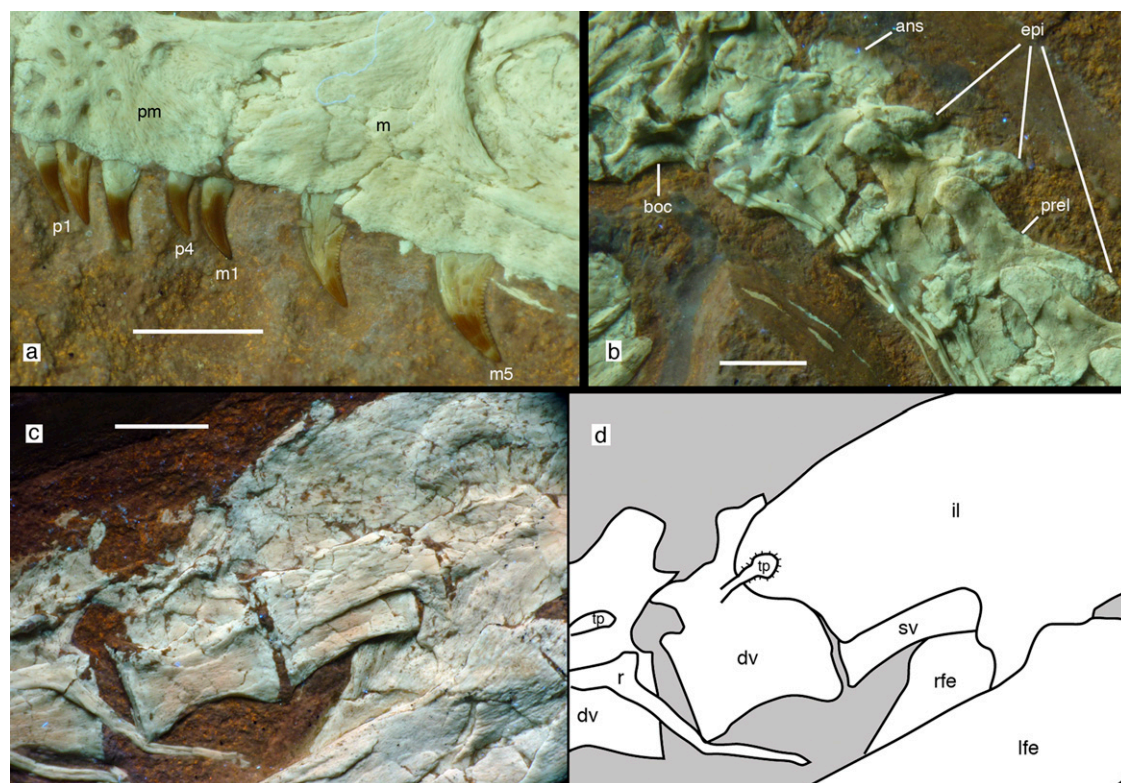


Fig. 2. Anatomical details of *Sciumimus albersdoerferi*. (A) Dentition of left premaxilla and anterior end of left maxilla. (B) Disarticulated occiput, atlas, axis, and anterior cervical vertebrae. (C and D) Posterior-most dorsal vertebrae and anterior part of ilium shown in a photograph (C) and in an interpretative drawing (D). All photographs were taken under UV light. ans, axial neural spine; boc, basioccipital; dv, dorsal vertebrae; epi, epiphyses; il, ilium; lfe, left femur; m, maxilla; m1 and m5, first and fifth maxillary tooth, respectively; p1 and p4, first and fourth premaxillary tooth, respectively; pm, premaxilla; prel, prezygoepiphysal lamina; r, rib; rfe, right femur; sv, sacral vertebra; tp, transverse process. (Scale bars: 5 mm in A and 10 mm in B–D.)

The sacrum consists of five vertebrae; the posterior ones are considerably shorter than the anterior sacra. A total of 59 caudal vertebrae are preserved; a few elements probably are missing. Anterior caudal vertebrae lack ventral grooves or keels and have rather low, simple, posterodorsally directed neural spines. The exact position of the transition point cannot be established, but transverse processes are certainly absent posterior to caudal vertebra 20. Posterior caudals are elongate in shape and have short, bowed pre- and postzygapophyses, unlike the strongly elongate prezygapophyses in allosauroids and coelurosaurids. Chevrons are present in at least 36 vertebrae; they are simple rod-like structures in lateral view, without ventral anterior or posterior expansion. Slender gastralia are present, with the medial elements being longer and more robust than the lateral elements.

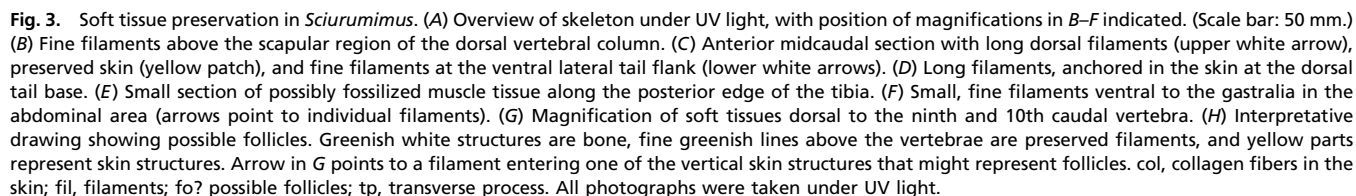
The scapula is more than 10 times longer than it is wide at its narrowest point, unlike the broader scapula in basal theropods, including megalosauroids but rather comparable to the scapulae in derived allosauroids and coelurosaurids (10, 11). It has a slight distal expansion that arises gradually from the shaft. The acromion process is expanded only moderately and gradually relative to the width of the shaft. The coracoid is oval, is shorter than it is high, and lacks a subglenoid process and a biceps tubercle, as seen in megalosauroids and spinosaurids. The left ramus of a small, slender furcula is exposed.

The forelimbs (Fig. 1C) are short and robust, as seen in some other megalosauroids (10), with a long manus accounting for ~45% of the length of the forelimb. The humerus is short and robust, with a triangular internal tuberosity and a well-developed deltopectoral crest. The radius and ulna are considerably shorter than the humerus, and the ulna is anteroposteriorly expanded proximally to form a concave facet for the humerus anteriorly

and a small but stout olecranon process posteriorly. The ulna is slightly more slender than the radius. A poorly ossified carpal is present and covers the proximal end of metacarpal I. The manus has three digits, with metacarpal I being less than half the length of metacarpal II and metacarpal III being shorter and considerably more slender than metacarpal II. There is no trace of a fourth metacarpal. Digit I is very robust, with phalanx I-1 exceeding the radius in width, as in compsognathids (14), and the ungual is more than half the length of the radius.

The ilium is elongate, with a gently curved dorsal margin and an undulate posterior end (Fig. 1D). There is no ventral hook anteriorly, but the anterior end has an unusual anterior “lip” dorsally (Fig. 2C and D). The medial brevis shelf is not exposed in lateral view. The pubic peduncle is anteroposteriorly longer than the ischial peduncle, as in other tetanurans (11). The pubis is slender, longer than the ischium, and the shaft is straight, with a moderately expanded distal boot. The ischium is slightly expanded anteriorly distally, and the large, hatchet-shaped obturator process is not offset from the pubic peduncle. The femur is stout and has a wing-like lesser trochanter that is approximately half the height of the slender greater trochanter (Figs. 1D and 2C and D). Tibia and fibula are slightly longer than the femur, and the fibula is distally expanded. The metatarsus is slender; metatarsals II and IV are of subequal length, and metatarsal V is transversely flat and anteriorly flexed. Metatarsal I is elongate and splint-like, rather than short and triangular as in most other tetanurans (11). In the foot, pedal ungual II is slightly larger than the other unguals.

Soft tissues are preserved in several areas of the skeleton (Fig. 3), and most seem to represent integumentary structures, with the possible exception of a short section of fossilized tissue



The protofeathers probably are monofilaments, because no branching patterns are visible in the well-preserved, long filaments above the tail; apparent branching patterns in a few places probably are the result of compaction of these structures (16). Because of the state of preservation, it cannot be established if these structures were hollow, like the filaments found in other dinosaurs (3, 14). The thickness of these filaments is ~0.2 mm in the long filaments in the dorsal tail region and less in the shorter filaments at the tail flank, back, and belly of the animal; the

filaments are comparable in size to the filamentous protofeathers found in *Sinosauropteryx* (14).

Discussion

To establish the phylogenetic position of *Sciurumimus*, we carried out several analyses using three large recently published matrices (*SI Text*). *Sciurumimus* consistently was found to be a basal tetanuran and recovered as a basal megalosaurid within Megalosauroidea in the most detailed analysis of basal tetanuran interrelationships yet published (Fig. 4) (17). Synapomorphies of megalosauroids and more restricted ingroups present in *Sciurumimus* include an elongate anterior process of the maxillary body, a medially closed maxillary fenestra, a very slender anterior process of the lacrimal, a lateral blade of the lacrimal that does not overhang antorbital fenestra, the presence of a deep fossa ventral to the basioccipital condyle, a splenial foramen that opens anteroventrally, a slightly dorsally expanded anterior end of the dentary, a pronounced ventral keel in the anterior dorsal vertebrae, the absence of a posteroventral process of the coracoid, and an enlarged manual ungual I.

Interestingly, the inclusion of *Sciurumimus*, without changes to any other codings, resulted in the recovery of a monophyletic Carnosauria that includes Megalosauroida and Allosauroida and represents the sister group to Coelurosauria. This result is in contrast to the vast majority of recent analyses, which depict the former two clades as successive sister taxa to coelurosaurs. Although this result certainly should be regarded with caution, given the early ontogenetic stage of *Sciurumimus*, this rather severe change to the phylogeny by the simple inclusion of an additional taxon highlights our still incomplete understanding of basal tetanuran evolution.

Sciurumimus represents the only complete megalosauroid known and helps clarify previously uncertain aspects of the anatomy of this group, such as the absence of a fourth digit in the manus. This absence highlights a surprisingly high level of homoplasy in this characteristic, given that the basal allosauroid *Sinraptor* (18), the neovenatorid *Megaraptor* (19), and the basal

tyrannosaur *Guanlong* (20) retain a rudimentary fourth metacarpal, whereas most derived allosauroids (21, 22) and also coelurosaurs (e.g., 14) have only three metacarpals. These variations suggest either that the fourth digit was reduced several times independently or that a reduction of this structure at the base of tetanurans was reversed in some taxa, possibly atavistically.

Several characters indicating that the *Sciurumimus albersdoerferi* type specimen represents a very young, probably early-posthatchling, individual include the body proportions, with a very large skull and rather short hindlimbs, lack of fusion in the skeleton (unfused neurocentral sutures in all of the vertebral column, unfused sacral vertebrae, lack of fusion between elements of the braincase) (23), a coarsely striated bone-surface texture in all skeletal elements (24), and a very regular pattern of tooth development in the maxilla, possibly indicating that no teeth had been replaced (25). This regular pattern differs from that in perinates of more derived coelurosaurs, where there is considerable heterogeneity in among the teeth (26).

The dentition of *Sciurumimus* differs significantly from those of subadult or adult basal tetanurans in the slender and unserrated premaxillary teeth and strongly recurved maxillary teeth with only distal serrations. Given the rather uniform tooth morphology in most basal tetanurans (at least in respect to general morphology, such as tooth shape and presence and extent of serrations), the features seen here are regarded as juvenile characters. Thus, these differences support the assertion that juveniles of large theropod species fed on different prey items than adults (27). Conversely, this dentition is remarkably similar to that of basal coelurosaurs, which commonly have slender, more rounded premaxillary teeth that lack serrations (11, 28) and often have strongly recurved lateral teeth, frequently without mesial serrations in at least some teeth (14, 28, 29). This similarity might indicate that the dentition, as seen in compsognathids (14, 28, 30) and dromaeosaurids (29, 31), evolved by heterochronic processes or might reflect convergence resulting from similar prey preferences. This similarity also implies that the common practice of ascribing small, strongly recurved lateral teeth with reduced or no mesial serrations to dromaeosaurids or coelurosaurs in general (32–34) should be done with caution and that coelurosaur occurrences based on these tooth characters alone are of no use for inferring biogeographic or evolutionary patterns.

Sciurumimus is comparable in size to and basically is indistinguishable in proportions from the juvenile basal coelurosaur *Juravenator* (Table S1) (15, 35, 36). However, these taxa differ significantly in anatomical details (SI Text). Thus, if this observation is indicative of the condition in early-posthatchling theropods in general, these early-posthatchling theropods seem to have had remarkably similar proportions, and differences in allometric growth might account for the different body plans seen in adult theropods (37, 38). However, data on juvenile theropods are still very limited, and more information is needed to test this hypothesis.

The presence of type 1 feathers along the dorsal side of the tail, the ventral tail flank, and parts of the body in *Scieurumimus* show that the entire body of this animal was plumaged, as is the case in compsognathids (2). As a megalosaurid, *Scieurumimus* is the most basal theropod taxon yet reported with such integumentary structures and demonstrates that at least the juveniles of basal tetanurans had protofeathers. *Scieurumimus* thus helps bridge the considerable gap between basal ornithischians, for which monofilaments have been reported (4), and coelurosaurs, for which protofeathers [morphotype 1 (39)] or feathers generally seem to be present (2, 15, 40). As in tyrannosauroids (2), the preservation of scaly skin in adult basal tetanurans (41) therefore is no argument against the presence of feathers in this group in general, nor should the presence of scales in other dinosaur clades (2) be taken as such. Large adult dinosaurs might have lost feathers secondarily, just as today several groups of

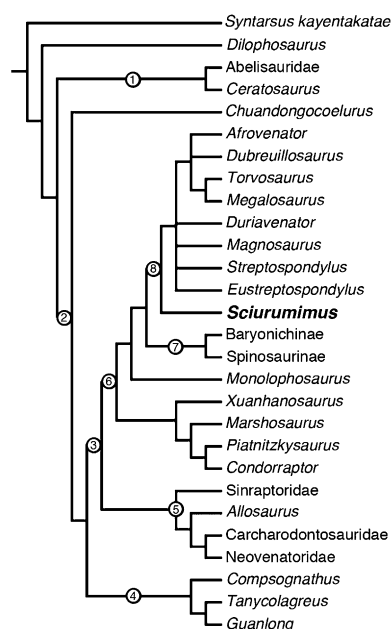


Fig. 4. Phylogenetic position of *Sciurumimus* in the analysis of Benson et al. (17). Clade names: 1, Ceratosauria; 2, Tetanurae; 3, Carnosauria; 4, Coelurosauria; 5, Allosauroidae; 6, Megalosauroidae; 7, Spinosauridae; 8, Megalosauridae. Numbers on the stem indicate stem-based taxa, numbers on the node indicate node-based taxa.

large mammals have lost hair. Furthermore, the joint presence of scales and filaments in some taxa (3, 15) indicates that the apparent lack of filaments in animals that preserve impressions of scaly skin in more coarse-grained sediments could be the result of taphonomic processes. Given that filaments in ornithischian dinosaurs (3, 4) are morphologically indistinguishable from protofeathers found in tetanurans and basal coelurosaurs, a filamentous body covering obviously represents the plesiomorphic state for dinosaurs in general, and, if one assumes that the hair-like structures of pterosaurs (5) are homologous structures, for ornithodiran archosaurs as well (42).

In the anterior midsection of the tail of *Sciurumimus*, the feathers seem to be anchored in the skin and are associated with dorsoventrally elongate skin structures (Fig. 3). Although collagen fibers in avian skin usually are oriented parallel to the body surface, these structures are perpendicular to the long axis of the body, and several show an elongated cup-shaped outline (Fig. 3). The only comparable structures in the avian skin are the follicles associated with the feathers (43), so we tentatively suggest that these structures might represent follicles. Thus, although several recent papers have argued that the origin of follicles was linked with the evolution of a rachis or barb ridges (2, 44, 45), *Sciurumimus* might

present evidence for the hypothesis that follicles were associated with the origin of feathers (39). Furthermore, there is a meshwork of thin, elongated soft tissue structures below this outer layer (Fig. 3). These structures most likely represent collagen fibers within the stratum compactum of the dermis, which is characterized by a high density of collagen bundles in birds (43). The fibers clearly are different from the filaments in their orientation and their luminescence under filtered UV light and thus provide evidence against the interpretation of similarly arranged and oriented filaments in Chinese theropods as decaying collagen fibers (46, 47).

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Supporting Information

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SI Methods: UV Photography

Most fossil skeletal remains and some mineralized soft parts from the Upper Jurassic plattenkalks of southern Germany and from the Middle to Late Mesozoic localities of Northeastern China are fluorescent under UV radiation. In most cases, this fluorescence allows a more precise investigation of morphological details of skeletal remains as well as soft parts. Delicate skeletal elements and remains of soft parts are poorly or not discernable in visible light but shine conspicuously under filtered UV. The technique can be used to differentiate bone sutures from cracks, to establish outlines of compressed skeletal elements more clearly, and to separate bones or soft parts from the underlying matrix and from each other.

During the past 10 y, H.T. has considerably improved techniques of UV investigation and UV-light photography of fossils from Solnhofen and Solnhofen-type Lagerstätten as well as from the Middle Jurassic to Early Cretaceous lacustrine deposits of the Jinlingsi and Jehol Group, Northeastern China, using powerful UV lamps and photographic documentation techniques (1–9). For our investigations we predominantly use UVA lamps with a wavelength of 365–366 nm.

Sometimes essential details of bones and soft parts are poorly or not visible to the naked eye or even under a microscope using UV light and can be demonstrated only by UV-light photography. The use of different filters allows selective visualization of peculiar fine structures. In most cases, a variety of different color-correction filters is necessary. Each limestone slab and bone or tissue reacts differently to different light wavelengths and is captured differently with varying exposures and filters. The right combination is needed to highlight the area of interest. The optimum filtering and exposure time must be tested in a series of experiments (1). The number and combination of filters varies greatly, and exposure times vary between 1 s and several minutes, depending on the nature of the fossil material and the magnification, intensity, and incident angle of the UV lamps. Filtering works optimally with analog photography using slide films, although digital cameras can be used also.

Additional Information on *Sciurumimus*

History of Find and Preparation of Specimen. The specimen was found during systematic excavations in the Rygol Quarry at Painten, Bavaria, Germany. First, the bony elements of the central area of the body appeared after cleaning on the floor of the excavation area, so the slab with the skeleton was excavated and brought into the laboratory for preparation. In the laboratory, the upper surface (the surface exposed in the quarry) was stabilized with ceramic glue (Knauf Uniflott) and was fixed to another slab. Then, the specimen was prepared mechanically from the underside. Damaged areas were reconstructed with Mapei Keraquick, which is clearly visible under UV light. Loose bones and sections were glued onto the specimen, but no arrangement or orientation of bones was changed. The specimen was studied by H.T. before preparation, so there can be no doubt about its authenticity.

Selected measurements for *Sciurumimus albersdoerferi*:

Total length of skeleton	719 mm
Skull length	79 mm
Posterior skull height	ca. 32 mm

Length of orbit	19.7 mm
Height of orbit	21.5 mm
Length of mandible	73.2 mm
Length of cervical series	69 mm
Length of dorsal series	102 mm
Length of sacrum	37.25 mm
Length of preserved caudal series	432 mm
Length of humerus	26.8 mm
Length of radius	17 mm
Length of metacarpal II	11 mm
Length of femur	50.6 mm
Length of tibiotarsus	54.2 mm
Length of metatarsal III	32.1 mm

Ontogenetic Stage of the Specimen. Although no histological sampling is possible in this unique specimen, several lines of evidence indicate that the holotype is an early juvenile, probably an early-posthatchling individual.

First, there is no fusion of any skeletal elements in the skeleton. In the vertebral column, the neurocentral sutures of the cervical, dorsal, and at least anterior caudal vertebrae are open, and the neural arches have disarticulated slightly from the centra in at least some elements. The sacral centra are preserved in articulation, but the posterior two sacra are displaced ventrally from the anterior end of the sacrum, demonstrating that the sacral vertebrae have not fused with each other, nor have the sacral ribs fused with the ilium. Although the pattern of neurocentral suture closure varies among dinosaurs (10), the lack of fusion in all vertebrae, with the possible exception of the distal-most caudals [which already are closed in hatchling crocodiles (11)], clearly indicates that the specimen of *Sciurumimus* is an immature individual. This identification is supported further by disarticulation in other elements that usually show very tight sutures or even fusion in theropods, such as the basioccipital and exoccipital or the distal ischium. Likewise, several skeletal elements, such as the carpal and distal tarsal bones, show poor ossification, and several joint surfaces, including the proximal articular end of the humerus, exhibit strongly porous surfaces, indicating poorly ossified articular ends.

Another indicator of the early juvenile stage of *Sciurumimus* is found in the surface structure of basically all bony elements. Both dermal and enchondral elements show a coarsely striated surface (Figs. S4 and S5). Such a surface structure corresponds to bone texture type I of Tumarkin-Deratzian et al. (12). According to these authors, in birds this texture occurs only in individuals of 50% or less skeletal maturity (i.e., hatching-year birds). Bone surface textures were found to be a useful ontogenetic indicator in a number of fossil amniotes (summarized in ref. 13), and thus this texture type represents an independent indication of an early ontogenetic stage for the specimen.

Finally, the maxillary dentition of *Sciurumimus* shows a conspicuous pattern of fully erupted teeth intercalated with empty tooth positions. A very similar pattern in *Scipionyx* was interpreted as an indication that no complete wave of tooth replacement had occurred (14), again indicating an early-posthatchling stage for the animal.

If the presence of a frontoparietal gap can be substantiated by future studies, that presence would represent a further ar-

gument for regarding the specimen as an early-posthatchling individual (15).

a subnarial foramen, the presence of at least weakly developed enamel wrinkles in the lateral teeth, opisthocoelous cervical vertebrae, a kinked anterior edge of the anterior caudal neural spines, the presence of an indentation between the acromion process of the scapula and the coracoid, a biceps tubercle that is developed as an obliquely oriented ridge, the presence of a broad ridge above the acetabulum on the ilium, and the presence of a well-developed extensor groove on the anterior side of the distal femur. However, making Neotetanurae monophyletic, excluding megalosauroids, requires only two additional steps. Thus, the interrelationships of basal tetanurans remain problematic and need additional investigation.

Codings for *Sciurumimus* in the matrix of Benson et al. (21) are as follows:

```
[0/1]?01?0?1001101?0?????0?0000-010210???010000??
000?0?00??11????00101??1????1?0?110000010020?00101?
00?111?0[1/2]?10[0/1]?11??0000000?001001?00200000?
1????0000[0/1]001011?-0001????[0/1]0?00?0?101001?1??
11???????01???????02???0010?010???00?00?0??
```

SI Discussion

The congruent results of the three phylogenetic analyses provide strong support for a basal tetanuran relationship of *Sciurumimus*, although some uncertainty about the exact phylogenetic position remains. As demonstrated by the analysis based on the matrix of Benson et al. (21), the combination of characters shown by *Sciurumimus* is most compatible with megalosauroid relationships. Although this outcome is supported by analyses in which all characters that we considered potentially ontogenetically variable were coded as “?” for *Sciurumimus*, the very early ontogenetic stage of the specimen leaves room for speculation about the possible effects of ontogenetic changes on the phylogenetic results, because little is known as yet about ontogenetic changes in nonavian theropod dinosaurs. On the other hand, the results show that even such very young individuals preserve enough phylogenetically relevant information to establish at least their approximate phylogenetic position.

Comparison with *Juravenator starki*. At first glance, the skeleton of *Sciurumimus* seems to be strikingly similar to that of *Juravenator starki* from the Kimmeridgian of Schamhaupten (25, 26). The two animals are contemporaneous up to the same horizon within the same ammonite subzone (27), come from the same geographical area (although from different subbasins within the Upper Jurassic limestone deposits of southern Germany), and are of closely matching size. Indeed, even in detailed comparison, the proportions of *Juravenator* and *Sciurumimus* are strikingly similar (Table S1).

However, despite these similarities in general morphometrics, the two taxa show numerous differences in anatomical details (based on ref. 26 and on observations on the type of *Juravenator* by O.W.M.R. and C.F.), even though comparison sometimes is hampered by the different preservation (*Sciurumimus* is exposed in lateral view, but *Juravenator* is exposed in dorsolateral view for most elements; see ref. 26). Thus, in the skull of *Juravenator*, the anterior margin of the antorbital fossa is rectangular, rather than gently rounded, the maxillary fenestra is relatively smaller, the antorbital fossa is smaller, the ventral process of the postorbital is more massive and notably curved, the ventral (quadratojugal) process of the squamosal tapers to a point, and the posterior premaxillary teeth bear serrations, whereas they are more slender and devoid of serrations in *Sciurumimus*. In the vertebral column, *Juravenator* differs from *Sciurumimus* in the following characteristics (in the following all characters listed refer to the situation in *Juravenator*): cervical epipophyses are small, barely (if at all) overhanging the postzygapophyses; prezygoepipophyseal laminae

in the cervical vertebrae are absent; a posterior pleurocoel is present in a midcervical centrum; anterior-most dorsal vertebrae are distinctly elongate; neural spines in the anterior caudal vertebrae are triangular and strongly posteriorly inclined; the posterior caudal vertebrae are relatively more elongate; posterior caudal prezygapophyses are more elongate and are directed anteriorly rather than anterodorsally; distal chevrons are skid-like. In the pectoral girdle and forelimb, the following differences can be established: The scapula is less slender and has a distinctly curved blade; the supraglenoid fossa is triangular, with an acutely angled posterior rim; the internal tuberosity of the humerus is confluent with the proximal humeral articular surface, forming a rectangular edge on the medial side of the proximal humerus; the ulna lacks a proximal expansion and olecranon process; and the shaft of the ulna is more massive than the shaft of radius. In the pelvis and hindlimb, *Juravenator* differs from *Sciurumimus* in the lack of an anterior dorsal lip of the ilium (the presence of which represents an autapomorphy of *Sciurumimus*); the relatively smaller pubic peduncle of the ilium; a more reduced supraacetabular crest, which is confluent posteriorly with the lateral brevis shelf; a pronounced antitrochanteric lip on the ischial peduncle of the ilium; a rectangular rather than undulate posterior end of the postacetabular blade of the ilium; an obturator process on the ischium [erroneously identified as pubis by Chiappe and Göhlich (26)] that is offset from the pubic peduncle; the lack of a distal expansion of the ischial shaft; the short and triangular metatarsal I; a metatarsal IV that is distinctly longer than metatarsal II; and the shorter and more robust metatarsal V. These numerous differences strongly indicate that the two animals cannot be referred to the same taxon, despite their similar size and proportions.

Looking at the phylogenetic position of *Juravenator* led to some interesting results. To test the position of this taxon, we also coded it in the matrices of Smith et al. (19) and Choiniere et al. (20) and analyzed the matrices under the parameters outlined above. When analyzed together with *Sciurumimus*, *Juravenator* was found to be the sister taxon to this genus in both analyses, with otherwise no changes in the phylogenetic position of *Sciurumimus* (i.e., both taxa were found to be basal, non-neotetanuran tetanurans). However, when *Sciurumimus* was removed from the analyses, *Juravenator* was found to be a basal coelurosaur in both cases (Figs. S9 and S10).

As is the case with *Sciurumimus*, the type of *Juravenator* most probably is an early-posthatchling individual, because it lacks any fusion of skeletal elements, lacks ossified carpal and distal tarsal elements altogether, and shows a coarsely striated surface texture in all skeletal elements (see ref. 26). Several of the characters shared by *Sciurumimus* and *Juravenator* and interpreted as synapomorphies of these taxa in the analyses probably are ontogenetically variable, e.g., the round orbit, anterodorsally sloping ventral strut of the lacrimal (related to the size and shape of the orbit), absence of a posteroventral process in the coracoid, absence of a ventral hook on the preacetabular blade of the ilium, and poorly developed attachment of the iliofibularis muscle on the fibula (in all three muscle-attachment areas). Thus, analysis of these two early juveniles together with otherwise subadult and adult theropods might give erroneous results, and we consider the phylogenetic position of *Juravenator* to be uncertain. *Juravenator* shows a highly unusual combination of characters (26), and further analysis of its affinities is necessary to establish its phylogenetic position firmly. However, such a detailed reappraisal of *Juravenator* is beyond the scope of this paper.

These phylogenetic results further suggest that the frequent referral of early juvenile theropods such as *Juravenator* (25) and *Scipionyx* (15) to the Compsognathidae simply might reflect the similarities between these taxa and the (also juvenile) type specimen of *Compsognathus longipes*, and thus the phylogenetic status and content of the Compsognathidae should be reevaluated.

Codings for *Juravenator*. The matrix of Smith et al. (19) for *Juravenator* is as follows:

Sciurumimus specimen helps bridge the considerable gap between both filamentous integument structures. Thus, protofeathers probably represent the plesiomorphic state for dinosaurs (46, 47). However, scaly skin impressions are known in many dinosaur groups (e.g., Ceratopsia, Stegosauria, Hadrosauridae, Sauropodomorpha, Ceratosauria, basal Tetanurae, and basal coelurosaurs) (25, 41, 48–53). These scales usually are nonoverlapping and polygonal in shape (41).

However, we do not regard the presence of both scales and protofeathers in early dinosaurs as problematic. Most fossil skin impressions are incomplete and are preserved only as small, regionally distributed patches; from these impressions one can conclude only that a particular body region was covered with scaly skin. The examples of *Psittacosaurus* and *Juravenator* in which both scales and protofeathers are present show that different integument structures can be present in the same animal. Furthermore, recent studies in evolutionary developmental biology indicate that scale and feather development are regulated by the same set of signal molecules. Thus, only small changes within the pathways can lead to different integument structures (54–57), and it seems likely that feathers could be lost secondarily in several lines independently. Finally, although scaly skin impressions might be preserved in various sediments, including even coarse sandstones, the preservation of fine filaments, such as those found in *Sciurumimus*, requires very special conditions, so taphonomic processes also play a major role in our understanding of the distribution of integumentary structures in theropod dinosaurs. This last conclusion is supported by the recent find of the large tyrannosauroid theropod *Yutyrannus*, which was preserved in a suitable environment and has filamentous feathers preserved (58).

Interestingly, the bodies of pterosaurs also were covered with monofilaments (59, 60), recently named “pynofibers” (7). If filamentous protofeathers are primitive for dinosaurs, it seems very likely that these pynofibers are homologous to the protofeathers of dinosaurs (61), and thus the origin of feathers leads back to ornithodiran origins.

The preserved integument structures of *Sciurumimus* provide additional information on the morphology of protofeathers and

the origin of feathers. In one area, on the dorsal side of the tail, protofeathers and skin are preserved in direct association. The structures can be differentiated by their different luminescence under UV light. The protofeathers seem to be anchored in the skin, indicating that these integument structures might have grown from follicles. Indeed, conspicuous, dorsoventrally elongated skin structures are preserved where the filaments reach the skin; these structures might represent direct evidence for these follicles. This possibility is interesting, because it has been suggested that follicle formation was a late event in feather evolution and took place with the evolution of vaned feathers (62–64). This scenario was based on the feather embryogenesis of some recent bird species, in which barb ridge formation occurs before follicle formation. The hypothesis that unbranched protofeathers apparently grow from a follicle supports the idea that feather evolution is highly correlated with follicle formation (65, 66). Further support for this idea comes from *Psittacosaurus*, in which the bristles extend under the skin layer (44), lending additional support for the homology of ornithischian filaments with theropod protofeathers and bird feathers.

Repository of the Specimen. The holotype specimen of *Sciurumimus* belongs to the private Painten collection of the Albersdörfer family, where it bears the collection number 1687. However, the scientific availability of the specimen is guaranteed by its inclusion in the register of cultural objects of national importance of Germany (Verzeichnis national wertvollen Kulturgutes). Under the Act to Prevent the Exodus of German Cultural Property (KultSchG; Bundesgesetzblatt I: 1754; 1999), the inclusion of the specimen in this list prevents its being sold outside Germany and guarantees that its repository is always known and that changes of repository must be announced. Furthermore, the type specimen of *Sciurumimus albersdoerferi* is deposited as a permanent loan at the municipal Bürgermeister Müller Museum in Solnhofen, Bavaria, where it also is available for additional scientific study and bears the specimen number BMMS BK 11.

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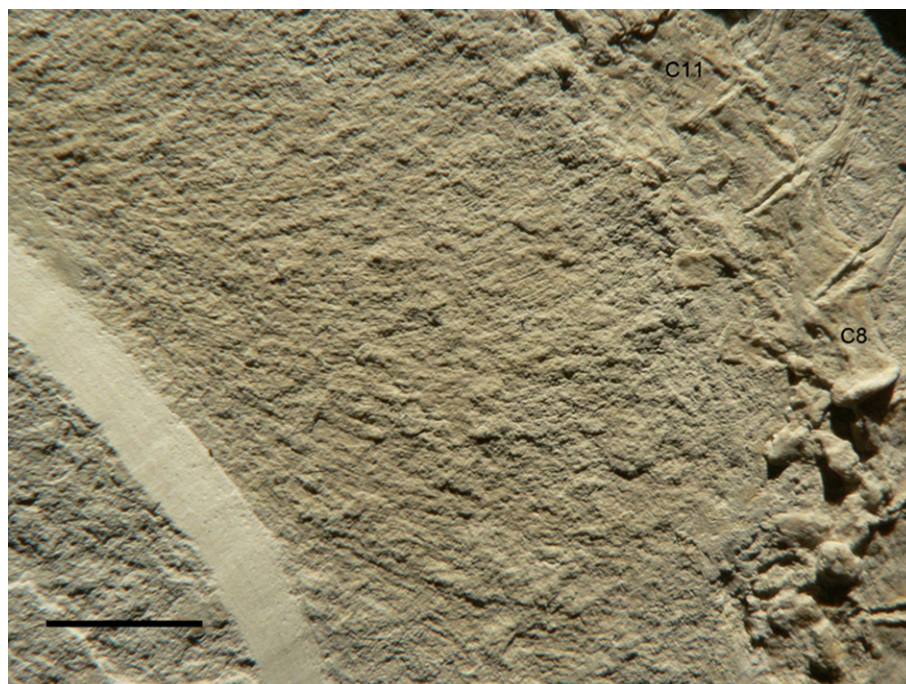


Fig. S1. Impressions of filaments dorsal to anterior caudal vertebrae under normal light. C, caudal vertebra. (Scale bar: 10 mm.)

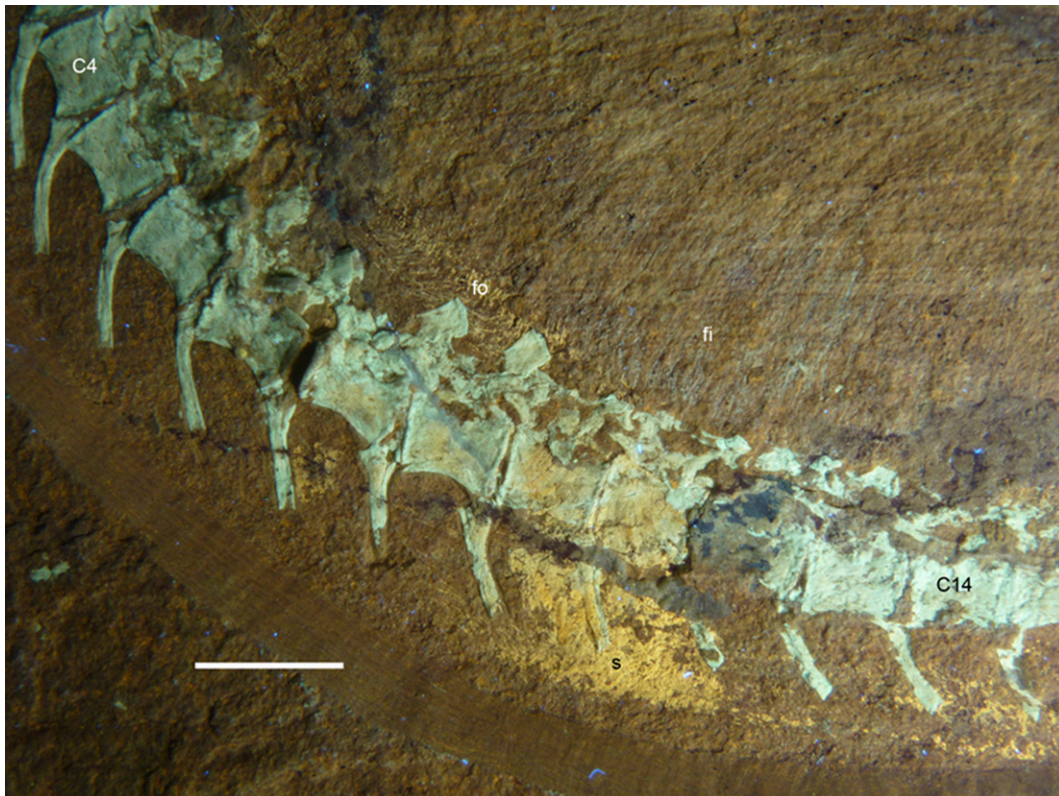


Fig. S2. Soft tissue preservation in the anterior caudal region of *Sciurumimus* under UV light. C, caudal vertebra; fi, filaments; fo, possible follicles at the base of filaments; s, skin. (Scale bar: 10 mm.)

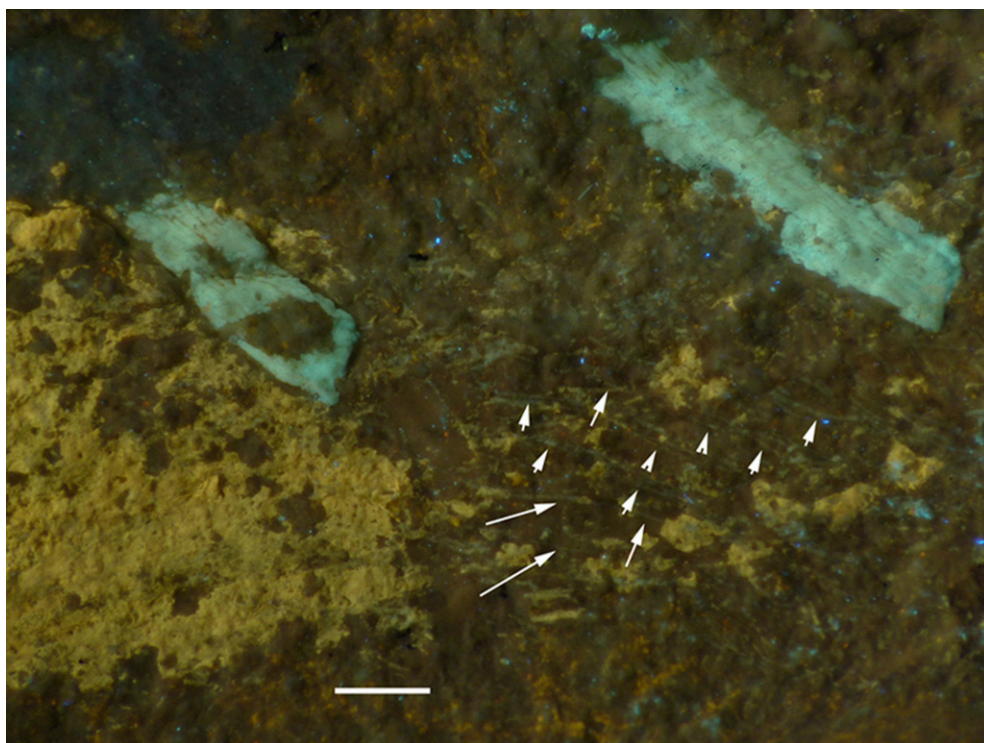


Fig. S3. Short filaments on the ventral tail flank below the 12th and 13th caudal vertebra. Arrows and arrowheads point to single filaments.



Fig. S4. Lateral side of the left dentary of *Sciurumimus* showing striated texture of bone surface.

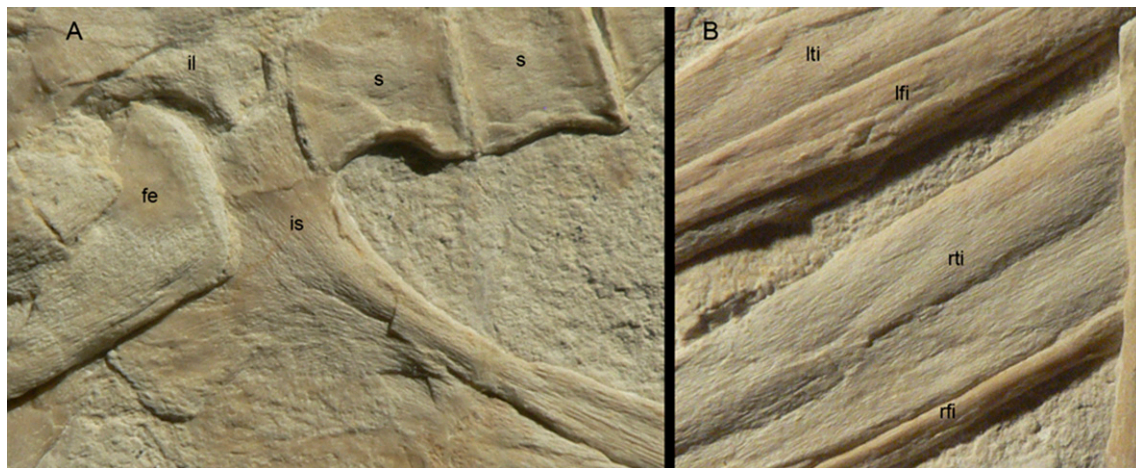


Fig. S5. Striated texture of bone surface in sacral vertebrae and pelvic and limb elements of *Sciurumimus*. (A) Ischial peduncle of the left ilium, posterior sacral vertebrae, and proximal end of femur and ischium. (B) Tibiae and fibulae. fe, femur; il, ilium; is, ischium; lfi, left fibula; lti, left tibia; rfi, right fibula; rti, right tibia; s, sacral vertebra.

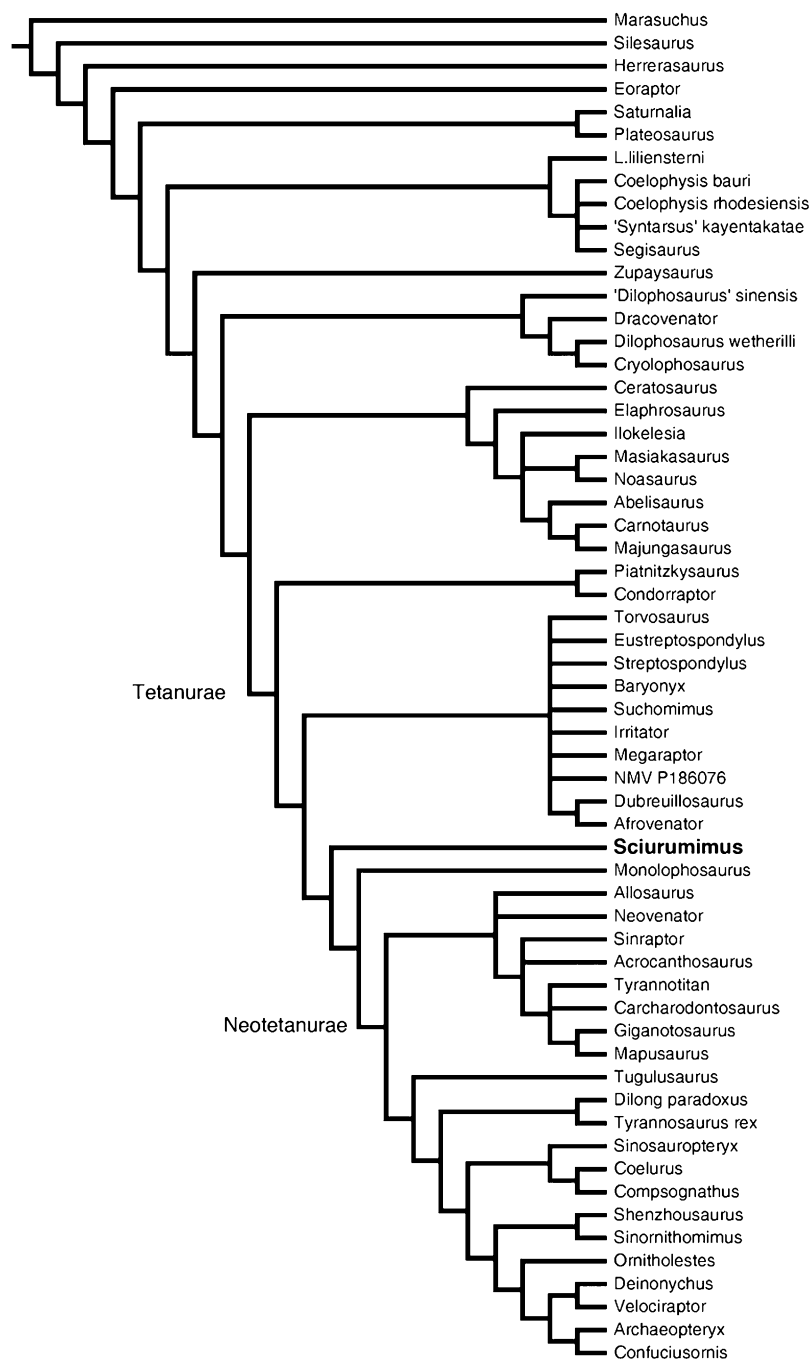
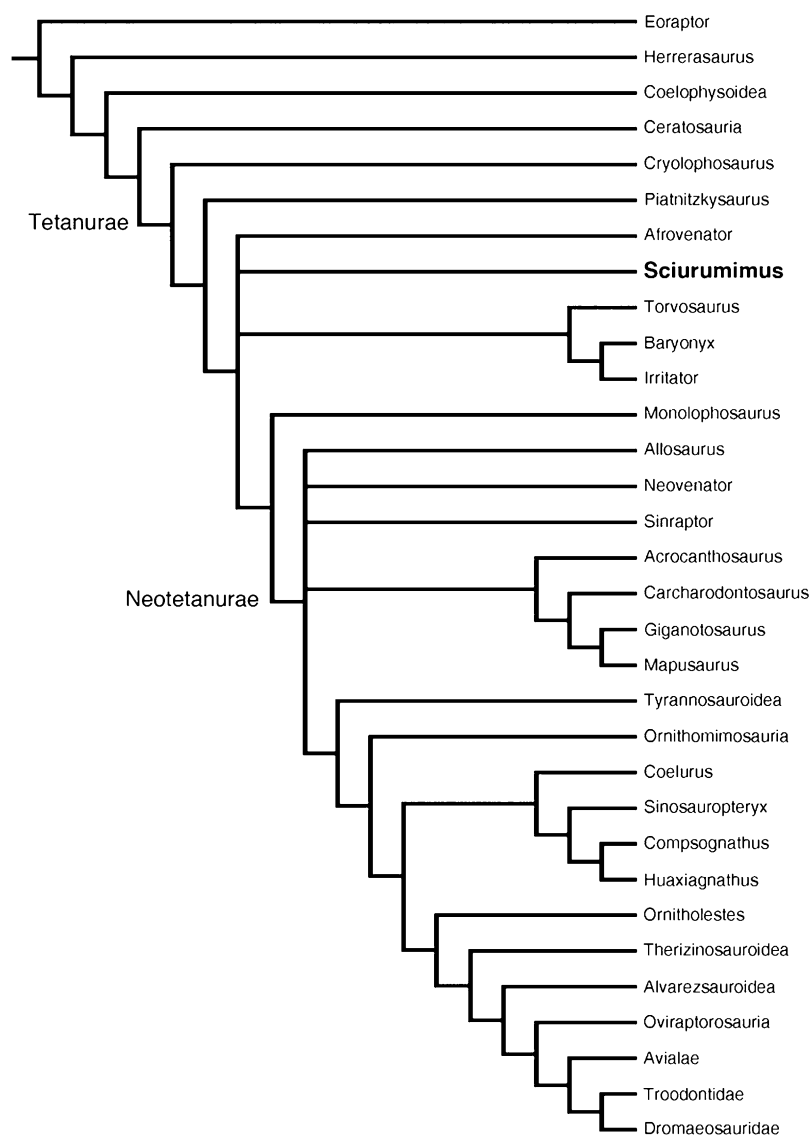


Fig. S6. Strict consensus cladogram of the analysis based on Smith et al. (19).



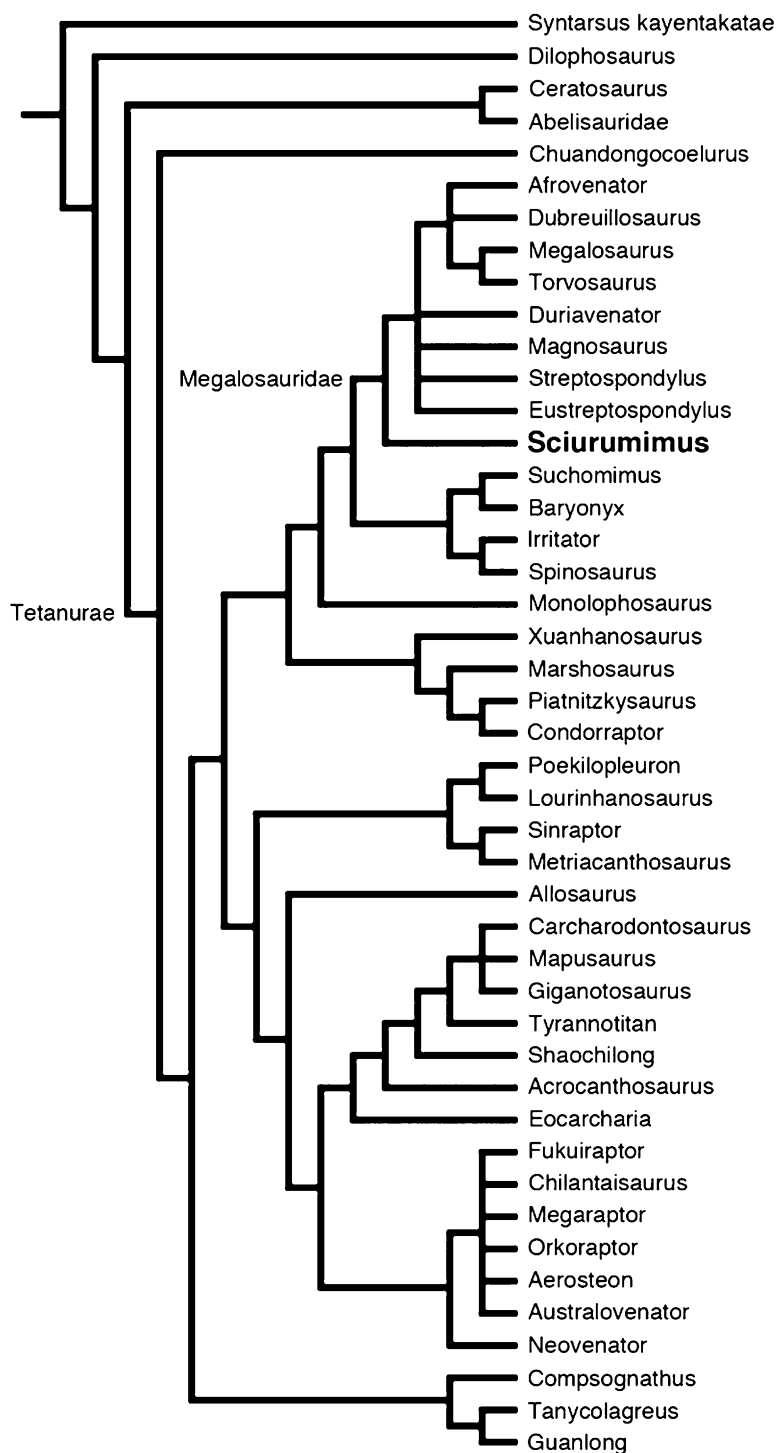
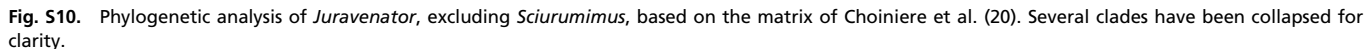


Fig. 58. Reduced consensus tree of the analysis based on the matrix of Benson et al. (21).

Fig. S9. Phylogenetic analysis of *Juravenator*, excluding *Sciurumimus* based on the matrix of Smith et al. (19).



Measurement	<i>Juravenator</i> (in mm)	<i>Sciurumimus</i> (in mm)
Skull length	82	79
Scapula length	42	42
Humerus length	27	26.8
Radius length	ca. 19	17
Mc II length	9	8.8
Femur length	52	50.6
Tibiotarsus length	58.1	54.2
Mt III length	34	32.1

Rauhut et al. www.pnas.org/cgi/content/short/1203238109