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A dromaeosaurid dinosaur with a filamentous integument from the Yixian Formation of China

Xing Xu*, **Xiao-Lin Wang***† & **Xiao-Chun Wu***‡

* *The Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, P.O. Box 643, Beijing 100044, People's Republic of China*
† *Natural History Museum, Changchun University of Science and Technology, 6 Ximingzhu Street, Changchun 130026, People's Republic of China*
‡ *Vertebrate Morphology Research Group, Department of Biological Sciences, The University of Calgary, 2500 University Drive NW, Calgary, AB T2N 1N4, Canada*

Dromaeosaurids, despite their notoriety, are poorly characterized meat-eating dinosaurs, and were previously known only from disarticulated or fragmentary specimens[1]. Many studies have denied their close relationship to birds[2,3]. Here we report the best represented and probably the earliest dromaeosaurid yet discovered, *Sinornithosaurus millenii* gen. et sp. nov., from Sihetun, the famous Mesozoic fish–dinosaur–bird locality in China[4,5]. *Sinornithosaurus* not only greatly increases our knowledge of Dromaeosauridae but also provides evidence for a filamentous integument in this group. It is remarkably similar to early birds postcranially. The shoulder girdle shows that terrestrial dromaeosaurids had attained the prerequisites for powered, flapping flight[6], supporting the idea that bird flight originated from the ground up[7,8]. The discovery of *Sinornithosaurus* widens the distribution of integumentary filaments among non-avian theropods[5,9,10]. Phylogenetic analysis indicates that, among known theropods with integumentary filaments or feathers[2,5], Dromaeosauridae is the most bird-like, and is more closely related to birds than is Troodontidae.

Theropoda Marsh 1881
Maniraptora Gauthier 1986
Dromaeosauridae Matthew & Brown 1922
Sinornithosaurus millenii gen. et sp. nov.

Etymology. '*Sinornithosaurus*' derived from Sino-Ornitho-Saurus, meaning a bird-like dinosaur from China; '*millenii*' derived from Millennium, Latin for one-thousand years, referring to its discovery near the end of the twentieth century.

Holotype. IVPP (Institute of Vertebrate Paleontology and Paleoanthropology) V12811 (Figs 1, 2).

Locality and horizon. Sihetun, western Liaoning, China. Layer 6, lower (Chaomidianzi[2]) Yixian Formation[4], Jehol Group; probably Early Cretaceous[11].

Diagnosis. Differing from other dromaeosaurids in the presence of ornament-like pits and ridges on the anterolateral surface of the antorbital fossa; the posterolateral process of the parietal turning sharply posteriorly; the dentary bifurcated posteriorly; unserrated premaxillary teeth; supracoracoid fenestra of coracoid; manual phalanx III-1 more than twice the length of phalanx III-2; pronounced tubercle near the midshaft of the pubis; posterodorsal process of the ischium; partially arctometatarsalian metatarsal III.

Description. *Sinornithosaurus* is a small dromaeosaurid, with a skull about 13 cm long (Figs 2, 3, Table 1). It has a relatively small antorbital fenestra and a large orbit, as in other dromaeosaurids. The antorbital fossa, anterior to the antorbital fenestra, is large and well-demarcated, although its posterodorsal margin is obscured by surface damage. The anterolateral surface of the antorbital fossa bears a number of pits and ridges. The latter are well-marked and show no trace of pathological origin. Two small maxillary fenestrae, normally seen in dromaeosaurids and some other theropods, lie in the antorbital fossa. The exposure of the frontal is extensive and is more than twice the length of the parietal. The prefrontal is sutured with the lacrimal as in *Deinonychus*[12]. The frontal process of the triradiate postorbital is not upturned, unlike those in other dromaeosaurids[13]. The parietals form a narrow sagittal crest, as in many non-avian theropods and birds. *Sinornithosaurus* is placed in Dromaeosauridae on the basis of the following shared derived features[13–15]: T-shaped lacrimal; large supratemporal fossa with a strongly sinusoidally curved anterior frontal margin; T-shaped quadratojugal (although the vertical bar is relatively shorter); widely open fenestra between the quadratojugal and quadrate; dentary with subparallel dorsal and ventral margins; ossified caudal rods increasing the lengths of prezygapophyses and chevrons (for more details, see Supplementary Information).

The shoulder girdle and forelimb of *Sinornithosaurus* closely resemble those of early birds (Fig. 4a–d). As in *Archaeopteryx*[16,17], the articulated left scapula and left coracoid form an angle of less than 90°, and the scapula is shorter than the humerus (0.63) and ulna (0.77), and forms most of the laterally facing glenoid. The anterolateral part of the right coracoid of *Sinornithosaurus* is distorted by lateromedial folding (Fig. 4c), and was broader in life and differed little from those of other dromaeosaurids, such as *Deinonychus*[18] and an undescribed specimen of *Saurornitholestes* (TMP (Royal Tyrrell Museum of Palaeontology) 88.121.39), except for the presence of a supracoracoid fenestra. The coracoid bears a pronounced biceps tubercle and its lateral profile is almost identical to that of *Archaeopteryx*[19]. The furcula, half of which is extensively

Table 1 Lengths of selected elements of *Sinornithosaurus millenii* (IVPP V12811)

Skull	130*
Mandible	125
Left scapula	85
Right coracoid	44
Right sternum	84*
Posterior two dorsal vertebrae	26
Five sacral vertebrae	65
Right humerus	134
Right ulna	110
Metacarpal II	63
Three phalanges of manual digit II	89
Left ilium	85
Left pubis	116
Left ischium (along posterior edge)	52
Left femur	148*
Right tibia (preserved length)	125
Metatarsal III (longest)	93
Four phalanges of foot digit III	73

* Estimation. Length measurements are given in millimetres.
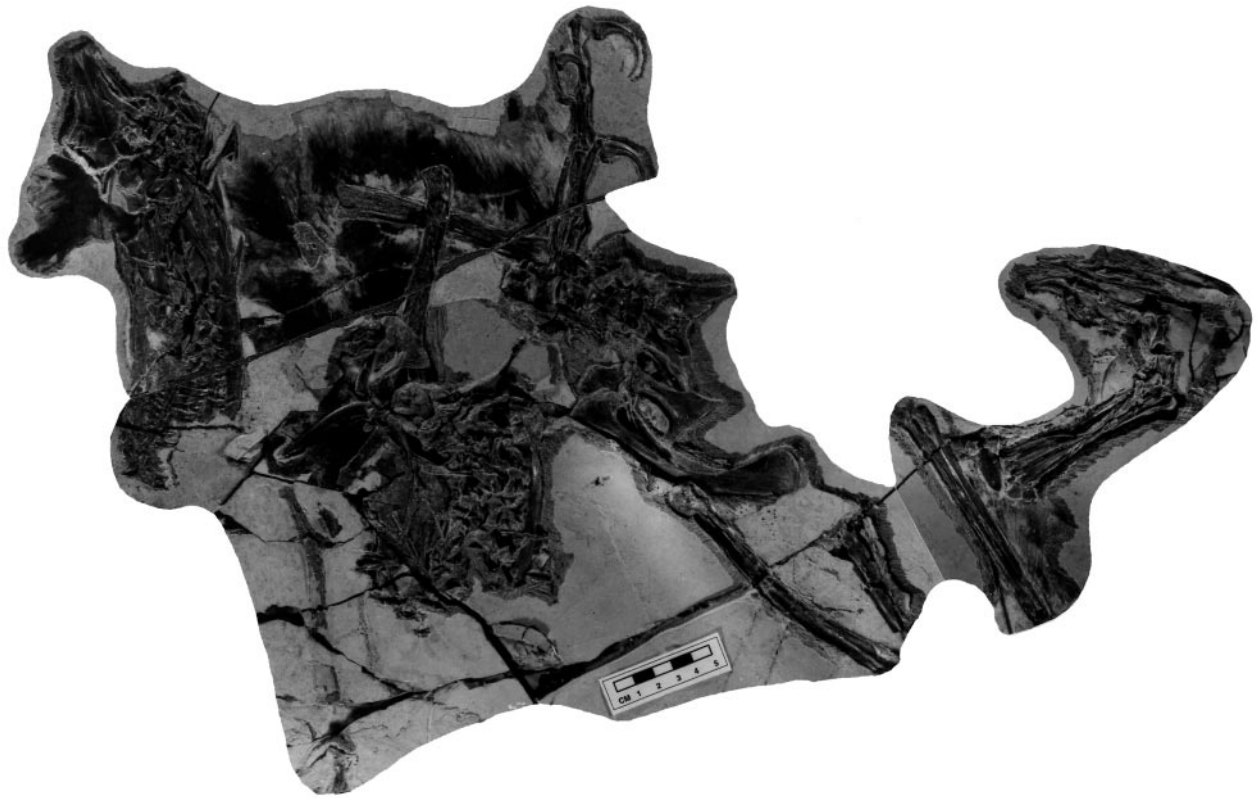
Figure 1 *S. millenii*, Holotype, IVPP V12811. The posterior part of the skull is disarticulated from the snout and lower jaws and turned 180° in the opposite direction. The postcranial skeleton is also not articulated, but the bones retain a close association. Integumentary filaments have been displaced, lacking their direct relationships to bony elements.

covered by other elements, gently curves in a 'boomerang'-shaped configuration (Fig. 2), differing from that of *Velociraptor*[20] but resembling that of *Archaeopteryx*[16]. Its shaft is compressed and tapers distally. A pair of ossified sterna appear similar to those of other dromaeosaurids[21], including *Saurornitholestes* (TMP 92.36.333). The length of each sternum is slightly more than twice its width, and its constricted anterolateral side bears a series of possibly five rib attachments (Fig. 2). These coastal facets on the sternum imply the presence of hinged sternocostal joints in dromaeosaurids, which is not concordant with recent arguments about the ribcage–pectoral girdle complex and the respiratory pattern of theropods[22]. As in other dromaeosaurids and birds[1,21], the coracoid facet of the sternum faces much more anteriorly than laterally. The forelimb has the greatest relative length of those known among non-avian theropods, and it is estimated to be about 80% of the length of the hindlimb. This is also indicated by the ratios of the ulna to the scapula (1.29) and the ulna to metatarsal III (1.18). These ratios are less than 1.0 in most other non-avian theropods. Metacarpal III is bowed laterally, as in other dromaeosaurids and birds[3].

Sinornithosaurus is also more bird-like than other non-avian theropods in the following derived features of the pelvic girdle and hindlimb (Fig. 4e, f): pubic peduncle of ilium broader than acetabulum[3]; open acetabulum tending to close off medially[8,23]; posteroventrally directed pubis bearing a short symphysis (less than half the length of the bone), and its distal end cup-like[1]; short ischium plate-like and less than half the length of the pubis, indicating, as in *Velociraptor*[1], *Unenlagia*[8] and birds[3], the absence of ischial symphysis; thin fibular shaft about 1/7 of the diameter of the tibia[3].

It has been stated that the forelimbs of dromaeosaurids could not move like those of *Archaeopteryx* because of the posteroventrally facing glenoids[8,24]. This assumption is based on *Deinonychus*[18], the scapula and coracoid of which are actually incomplete. We believe that the glenoid was formed primarily by the scapula in *Deinonychus*, judging from the glenoid part of the coracoid, and may have faced laterally as in *Sinornithosaurus*, *Velociraptor*[1] and *Saurornitholestes* (TMP 88.121.39). That the coracoid and scapula form a sharp angle, as in *Sinornithosaurus*, may also be true for other dromaeosaurids. The shoulder girdle, as exemplified in *Sinornithosaurus*, is similar to that of *Archaeopteryx*[19]. A laterally facing glenoid is consistent with an avian mode of movement (elevation and relevant rotation and abduction) of the forelimb[8,24]. The modifications of the scapulocoracoid and coracosternal articulations in Dromaeosauridae altered the orientation of the shoulder girdle, perhaps enabling a wider, more avian range of motion at the glenohumeral joint. Because *Sinornithosaurus* and other dromaeosaurids were bipedal, cursorial terrestrial dinosaurs and are closely related to birds (see below), the anatomical modification of their shoulder girdles supports a cursorial origin for avian flight[6,7].

The body of *Sinornithosaurus* was apparently covered by a layer of integumentary filaments (Figs 1, 2). These filaments are not in their original positions, owing to posthumous displacement, but are distributed as patches underneath or close to most bony elements, including the skull. They have been exposed by preparation only in a small part of the specimen and have sometimes been cut off near the edges of elements that needed to be exposed (see Fig. 1). The anatomical structure of these filaments is not discernible, but in appearance they differ little from the external filaments of other theropod dinosaurs[2,5,10] or even the plumulaceous feathers of *Confuciusornis* (IVPP V11307) from the same locality. The filaments generally reach 40 mm in length. Those near the postcranial elements seem longer than those around the skull. The filaments around the tibia are relatively sparse. It is uncertain whether *Sinornithosaurus* had, in life, rectrix-like structures, as seen in both *Caudipteryx* and *Protarchaeopteryx*, or remix-like
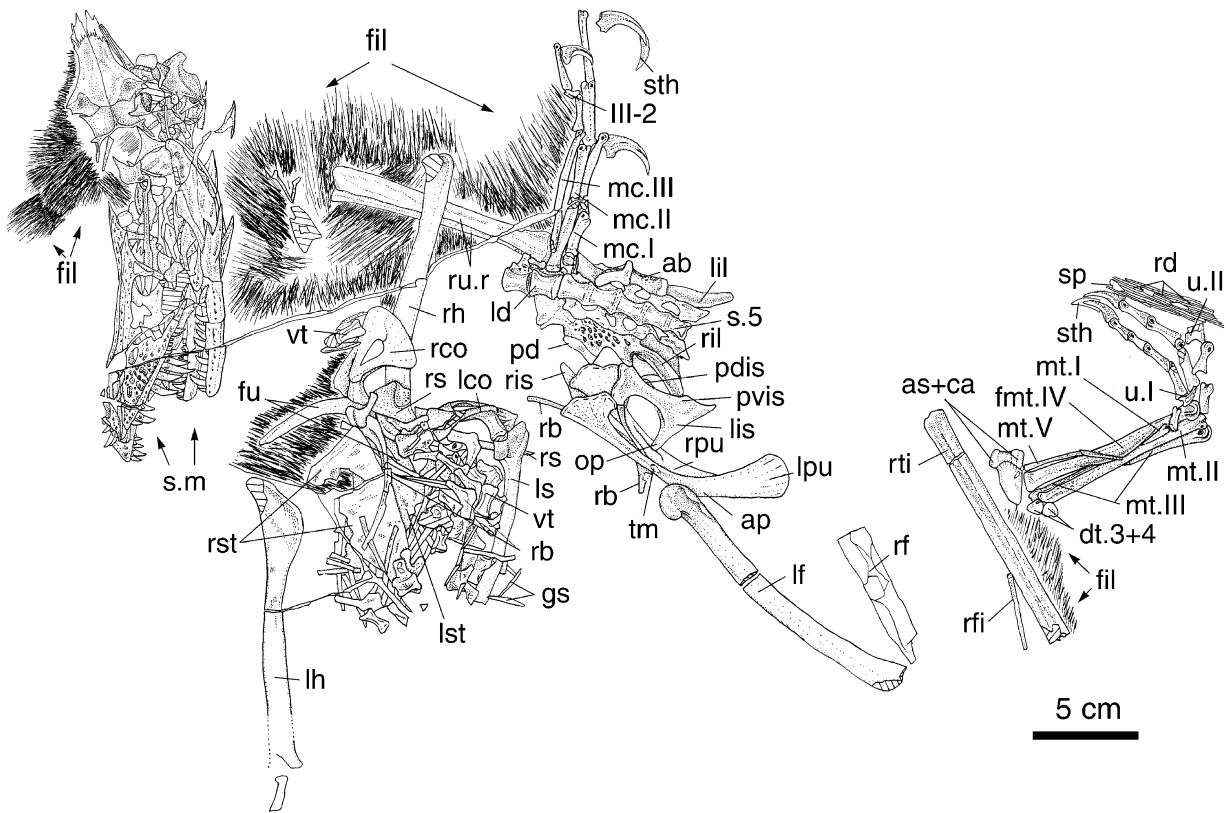
Figure 2 *S. millenii*. Drawing of the specimen shown in Fig. 1; the specimen represents an adult individual, as indicated by the five co-ossified sacral vertebrae and the partially fused astragalus and calcaneum. Abbreviations: ab, acetabulum of ilium; ap, apron of pubis; as + ca, astragalus and calcaneum; dt.3 + 4. distal tarsals 3 + 4; fil, integumentary filaments; fmt.IV, enlarged ventral flange of metatarsal IV; fu, furcula; gs, gastralia; lco, left coracoid; ld, last dorsal vertebra; lf, left femur; h, left humerus in anteromedial view; lil, left ilium; lpu, left pubis; lis, left ischium; ls, left scapula; lst, left sternum; mc.I–III, metacarpals I–III; mt.I–V, metatarsals I–V; op, obturator process; pd, pubic peduncle of ilium; pdis, posterodorsal process of ischium; pvis, posteroventral process of ischium; rb, rib; rco, right coracoid; rd, elongated prezygapophyses and chevrons of mid- and posterior caudal vertebrae; rf, right femur; rfi, right fibula; rh, right humerus; ril, right ilium; ris, right ischium; rpu, right pubis; rs, right scapula; rst, right sternum in ventral view; rti, right tibia; ru.r, right ulna and radius; s.m, skull and mandible; sp, spine of caudal vertebra; sth, horny sheath; s.5, sacral vertebra 5 (the last); tm, tubercle for muscle attachment; u.I, ungual of digit I of pes; u.II, enlarged, slashing ungual of digit II of pes; vt, vertebra; III-2, phalanx 2 of digit III of manus.
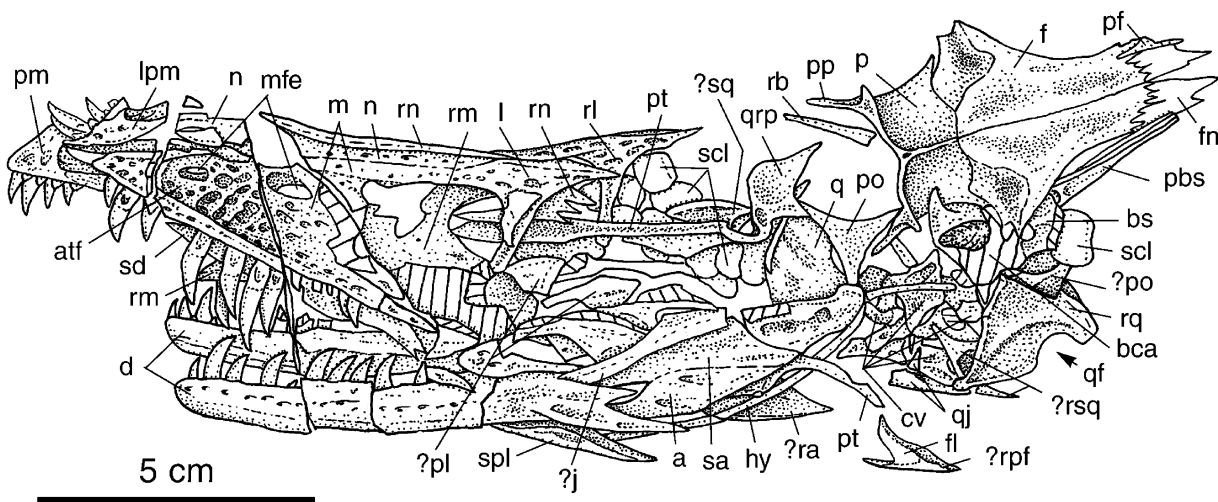
Figure 3 *S. millenii*, skull with lower jaws. Abbreviations: a, angular; atf, antorbital fossa; bca, braincase; bs, basisphenoid; cv, elements of the disarticulated first and second cervical vertebrae; d, dentary; f, frontal; fl, facet for lacrimal; fn, facet for nasal; hy, hyoid; l, lacrimal; lpm, left premaxilla in medial view; m, maxilla; mfe, maxillary fenestrae; n, nasal; p, parietal; pbs, parabasisphenoid process; pf, left prefrontal (the anterolateral part overlapped by the lacrimal was not preserved); pm, right premaxilla in medial view; po, left postorbital; pp, posterolateral process of the parietal; pt, pterygoid; q, quadrate; qf, fenestra between quadratojugal and quadrate; qj, quadratojugal; qrp, quadrate ramus of pterygoid; rb, rib; rl, right lacrimal in medial view; rm, right maxilla in medial view; rn, right nasal; rq, right quadrate in anteromedial view; sa, surangular; scl, sclerotic bones; sd, supradentary bone; spl, splenial; ?j, ?left jugal; ?pl, ?palatine; ?po, ?right postorbital; ?rpf, ?right prefrontal; ?rsq, ?right squamosal in ventral view; ?sq, ?left squamosal; ?ra, ?right angular. Most elements of the palate and braincase are obscured by cracks and dislocation.
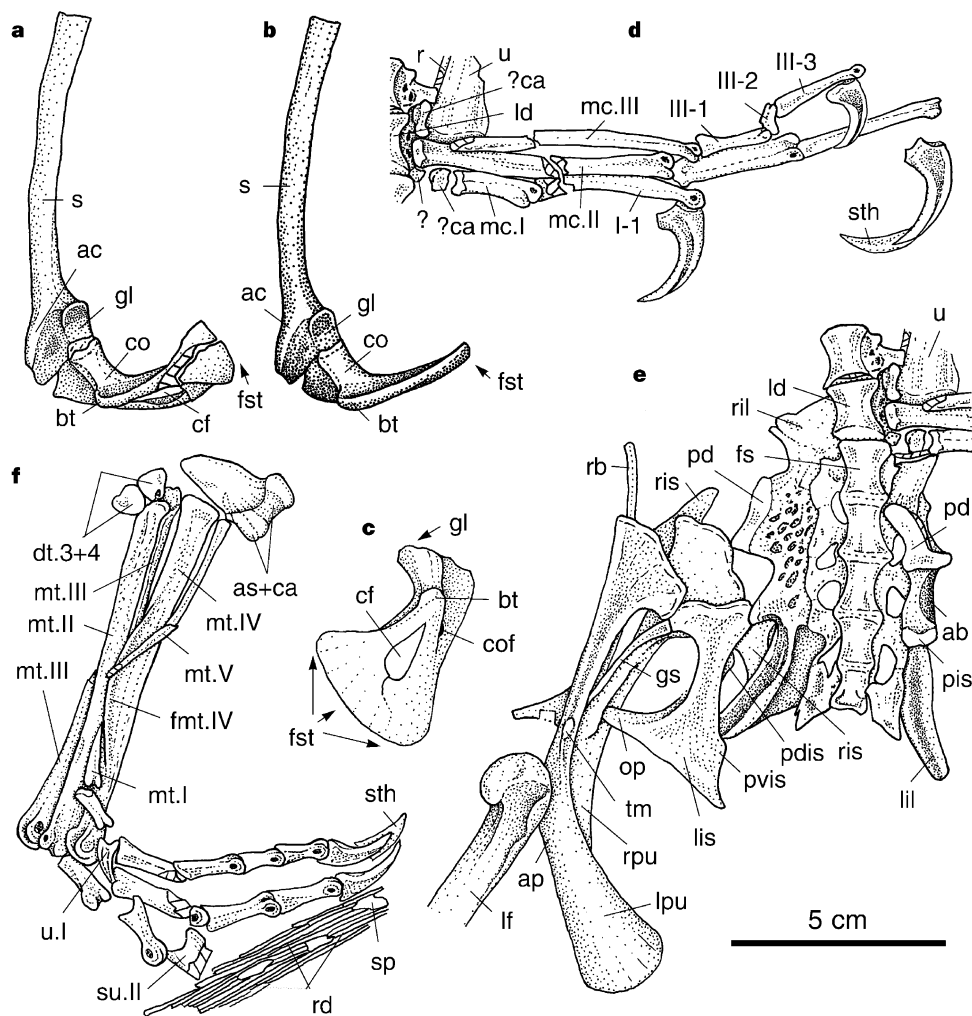
Figure 4 *S. millenii*, selected elements of the postcranial skeleton. **a**, **b**, Left scapula and coracoid in lateral view (original, **a**; reconstructed, **b**). **c**, Right coracoid in ventral view, with its anteromedial portion slightly folded. **d**, Right manus mainly in posteroventral view. **e**, Sacrum (in ventral view) and pelvic girdles. **f**, Tarsals, right pes (mainly in posteroventral view) and partial tail. Abbreviations: ac, acromion; bt, biceps tubercle; cf, supracoracoid fenestra; co, coracoid; cof, coracoid foramen; ?ca, ?carpal; fst, facet for sternum; fs, first sacral vertebrae; gl, glenoid of shoulder girdle; pis, ischial peduncle of ilium; r, radius; s, scapula; su.II, slashing ungual of digit II of pes; u, ulna; I-1, phalanx 1 of digit I of manus; III-1, III-2, III-3, phalanges 1–3 of digit III of manus; u, ulna ; ?, possibly a carpal. For other abbreviations see Fig. 2.
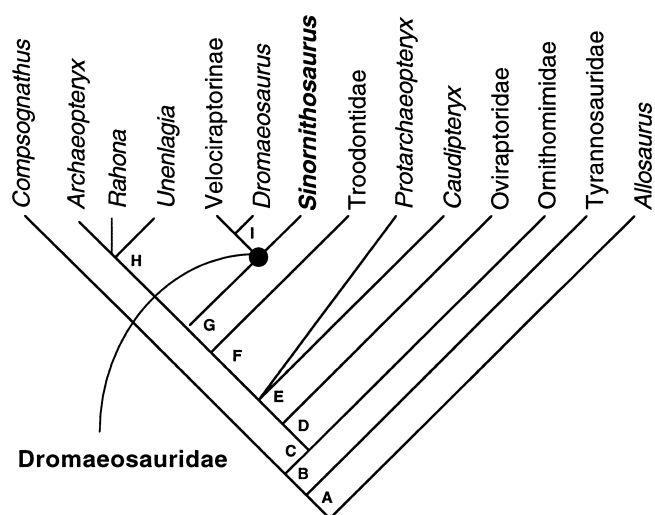
Dromaeosauridae

Figure 5 Cladogram showing phylogenetic relationships of Dromaeosauridae (including *Sinornithosaurus*) within the derived theropods. This is a strict consensus tree of our four most parsimonious trees based on 106 characters and 14 taxa (tree length = 183; consistency index = 0.639; retention index = 0.697). Multistate characters are unordered; tree produced using the branch-and-bound option of PAUP[30]. Synapomorphies for each node were determined by acceleration transformation (ACCTRAN). *Sinornithosaurus* is the basal member of Dromaeosauridae, which can be defined mainly by the following six unambiguous synapomorphies: characters 86 (lacrimal T-shaped); 88 (supratemporal fossa covering most of frontal process of postorbital and extending anteriorly on dorsal surface of frontal to at least level of posterior orbital margin); 90 (quadratojugal Y- or T-shaped); 91 (quadratojugal fenestra widely open); 96 (in lateral view upper and ventral margins of dentary subparallel); and 100 (ossified caudal rods extending lengths of prezygapophyses and chevrons). The close relationship of Dromaeosauridae to birds is primarily based on 10 unambiguous synapomorphies (node G): characters 39 (body of coracoid forming sharp angle with body of scapula); 46 (metacarpal III bowed laterally); 59 (pubic shaft projecting posteroventrally relative to long axis of sacral vertebrate); 65 (shape of ischial shaft mediolaterally compressed and plate-like along entire length); 104 (ulna longer than metatarsal III); 105 (glenoid of pectoral girdle facing laterally); 106 (articular facet of coracoid on sternum almost anterior); and the other three (characters 15, 92 and 93) of the 10 synapomorphies are unknown in *Sinornithosaurus*. For the list of the synapomorphies of the other clades see Supplementary Information.

structures, as seen attached to the arm of *Caudipteryx*, because evidence of the direct relationship of the preserved filaments to the relevant bones is obscured by preservation. The broad distribution of the filaments across the body of *Sinornithosaurus* further demonstrates that the clusters of fine filaments in *Sinosauropteryx*[5] do not represent internal collagenous fibres for skin support in semi-aquatic animals[25], but integumentary derivations of terrestrial animals. *Sinornithosaurus* is the fifth kind of theropod known to possess integumentary filaments. It is possible that these filaments indicate an insulatory layer that served to maintain body heat[2].

It has been proposed that birds are descendants of derived theropods[6,16,26], but there has been no consensus as to which theropod group is most closely related to birds. Dromaeosauridae[27,28], Troodontidae[3,29] and *Caudipteryx*[2] have all recently been suggested to be closely related to birds, but previous studies have not considered all of these taxa simultaneously, making their results arguable. We investigated the phylogenetic position of *Sinornithosaurus* using a data matrix of 106 characters and 14 taxa[3,13] (see Supplementary Information). We included all of the theropod taxa that have been proposed to be closely related to birds[2,3,8]. As with a previous study[2], we did not include characters relative to integumentary filaments and feathers because we cannot determine whether their absence in most other derived theropods is real or merely an artefact of preservation. Our analysis indicates that *Sinornithosaurus* is a basal dromaeosaurid and strongly supports the view that Dromaeosauridae and birds (where Aves is Avialae[26]) are more closely related to each other than either is to Troodontidae (Fig. 5, node G). Our analysis also indicates that *Protarchaeopteryx* and *Caudipteryx* are more remote from birds than is Troodontidae. We re-analysed the data matrix by sequentially adding steps to test the robustness of the relationships between the taxa. The close relationship between Dromaeosauridae and birds is the most robust and did not collapse until five more steps had been added. The currently established phylogenetic relationships among derived theropods seem to support the presence of true feathers in Dromaeosauridae, but the validity of this interpretation cannot be confirmed until more direct evidence is available. □

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Methane formation from long-chain alkanes by anaerobic microorganisms

Karsten Zengler*, **Hans H. Richnow**†, **Ramon Rosselló-Mora***, **Walter Michaelis**† & **Friedrich Widdel***

* *Max Planck Institute for Marine Microbiology, Celsiusstrasse 1, D-28359 Bremen, Germany*
† *Institute for Biogeochemistry and Marine Chemistry, University of Hamburg, Bundesstrasse 55, D-20146 Hamburg, Germany*

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Biological formation of methane is the terminal process of biomass degradation in aquatic habitats where oxygen, nitrate, ferric iron and sulphate have been depleted as electron acceptors. The pathway leading from dead biomass to methane through the metabolism of anaerobic bacteria and archaea is well understood for easily degradable biomolecules such as carbohydrates, proteins and lipids[1,2]. However, little is known about the organic compounds that lead to methane in old anoxic sediments where easily degradable biomolecules are no longer available. One class of naturally formed long-lived compounds in such sediments is the saturated hydrocarbons (alkanes)[3–5]. Alkanes are usually considered to be inert in the absence of oxygen, nitrate or sulphate[6], and the analysis of alkane patterns is often used for biogeochemical characterization of sediments[7,8]. However, alkanes might be consumed in anoxic sediments below the zone of sulphate reduction[9,10], but the underlying process has not been elucidated. Here we used enrichment cultures to show that the biological conversion of long-chain alkanes to the simplest hydrocarbon, methane, is possible under strictly anoxic conditions.

To study methane formation (methanogenesis) from long-chain alkanes, hexadecane (n-$C_{16}H_{34}$), a representative of this class of