The tenth skeletal specimen of *Archaeopteryx*

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We describe the tenth skeletal specimen of the Upper Jurassic Archaeopterygidae. The almost complete and well-preserved skeleton is assigned to *Archaeopteryx siemensii* Dames, 1897 and provides significant new information on the osteology of the Archaeopterygidae. As is evident from the new specimen, the palatine of *Archaeopteryx* was tetraradiate as in non-avian theropods, and not triradiate as in other avians. Also with respect to the position of the ectopterygoid, the data obtained from the new specimen lead to a revision of a previous reconstruction of the palate of *Archaeopteryx*. The morphology of the coracoid and that of the proximal tarsals is, for the first time, clearly visible in the new specimen. The new specimen demonstrates the presence of a hyperextendible second toe in *Archaeopteryx*. This feature is otherwise known only from the basal avian *Rahonavis* and deinonychosaurs (Dromaeosauridae and Troodontidae), and its presence in *Archaeopteryx* provides additional evidence for a close relationship between deinonychosaurs and avians. The new specimen also shows that the first toe of *Archaeopteryx* was not fully reversed but spread medially, supporting previous assumptions that *Archaeopteryx* was only facultatively arboreal. Finally, we comment on the taxonomic composition of the Archaeopterygidae and conclude that *Archaeopteryx bavarica* Wellnhofer, 1993 is likely to be a junior synonym of *A. siemensii*, and *Wellnhoferia grandis* Elżanowski, 2001 a junior synonym of *A. lithographica* von Meyer, 1861.   © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, **149**, 97–116.

INTRODUCTION

Until the recent discovery of a tenth skeleton (Mayr, Pohl & Peters, 2005), the Upper Jurassic Archaeopterygidae were known from a feather and nine skeletal specimens from the Solnhofen region in Germany. Eight skeletal remains have been described in detail (Elżanowski, 2002; Röper, 2004; Wellnhofer & Röper, 2005). Only a preliminary report exists of a recent find in private hands (Mäuser, 1997).

The last two and the fourth (Haarlem) specimen are very fragmentary, and only the Eichstätt specimen has a complete and well-preserved skull. Although archaeopterygids are no longer as rare as they were a few decades ago, important details of their anatomy remain controversial (e.g. Ostrom, 1991; Tarsitano, 1991; Elżanowski, 2002).

Here we describe the tenth skeleton, which is the most complete and best-preserved archaeopterygid

specimen to date. The almost complete skeleton is preserved on a single slab of pure limestone (Figs 1–3), and comes from an unknown locality and horizon of the Solnhofen area; its exact collection history is unknown to us. The existence of the specimen was first made aware to two of us (GM and DSP) at the very end of 2001, when it was offered for sale to Forschungsinstitut Senckenberg by a Swiss citizen. Unfortunately, Senckenberg could not raise the funds to acquire the specimen and it was then bought by a sponsor of the Wyoming Dinosaur Center; the Center ensures its permanent accessibility for scientific research. The specimen currently is on a 2-year loan term in Forschungsinstitut Senckenberg, where a cast will also be deposited.

Most bones exhibit little damage. Some presacral vertebrae, the tip of the tail, and the distal portion of the right foot are absent. The distal left humerus, distal right femur, and proximal right tibiotarsus were restored by the preparator (these parts of the skeleton show no reflection on the ultraviolet-induced fluorescence photograph, Fig. 2). The original slab is broken

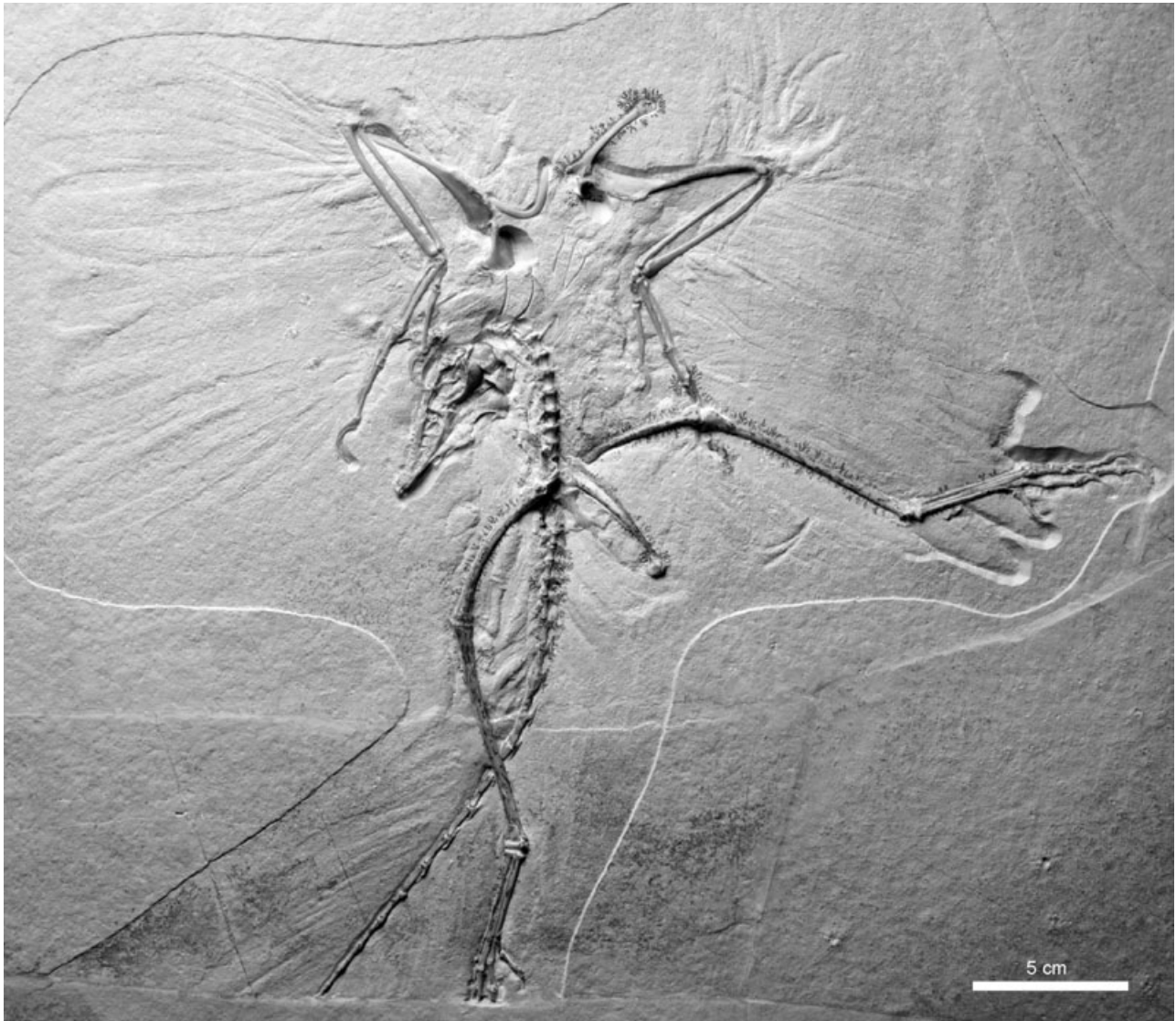*Corresponding author. E-mail: gerald.mayr@senckenberg.de

Figure 1. *Archaeopteryx siemensii* Dames, 1897, Thermopolis specimen (WDC-CSG-100).

into two pieces and was glued together; to make it rectangular, matrix not belonging to the original slab was added. The cranial section of the vertebral column and the pelvic girdle are dissociated, the skull and wings dislocated. The thoracic vertebrae are visible in ventral view, whereas the skull and forearms expose their dorsal surfaces. Compared with their original position, the wings are further turned at an angle of 180° against the postcranial half of the skeleton. If the slab represents the 'Hangendplatte' (upper slab), as is usual for the main slab of *Archaeopteryx* specimens (Elżanowski, 2002), the trunk of the animal was thus embedded in a dorsal side-up position, whereas the dorsal surfaces of the skull and the wings rested on the sediment.

In the most recent revision of the Archaeopterygidae, Elżanowski (2002) recognized four species: *Archaeopteryx lithographica* von Meyer, 1861 (the holotype of this species is controversial and either the isolated feather or the London specimen; see, for example, Bühler & Bock, 2002), *A. siemensii* Dames, 1897 (holotype is the Berlin specimen), *A. bavarica* Wellnhofer, 1993 (based on the Munich specimen), and *Wellnhoferia grandis* Elżanowski, 2001b (holotype is the Solnhofen specimen). In size and morphology, the new specimen corresponds best with the Munich specimen (Table 1), and we assign it to *A. siemensii* in the present study; as detailed in the discussion, we consider *A. bavarica* to be a junior synonym of this species.

Figure 2. *Archaeopteryx siemensii* Dames, 1897, Thermopolis specimen (WDC-CSG-100). Ultraviolet-induced fluorescence photograph showing the preserved bone substance.

The phylogenetic implications of the specimen have been discussed by Mayr *et al*. (2005) and are not repeated here.

MATERIAL AND METHODS

Measurements refer to the maximum length of a bone along its longitudinal axis.

According to their current or previous repositories, seven of the specimens are referred to as the London (Natural History Museum, London, UK, BMNH 37001), Berlin (Museum für Naturkunde, Berlin, Germany, HMN MB. 1880/81), Maxberg (formerly in the private collection Opitsch, now lost), Haarlem (Teyler Museum, Haarlem, Netherlands, TM 6428 and 6429), Eichstätt (Jura-Museum Eichstätt, Germany, JM SoS 2257), Solnhofen (Bürgermeister-Müller-Museum, Germany, uncatalogued), and Munich (Bayerische Staatssammlung für Paläontologie und Historische Geologie, München, Germany, BSP 1999 I 50) specimens. The new skeleton is designated the 'Thermopolis specimen'.

The terms 'Aves' and 'avians' are used for the least inclusive clade including *Archaeopteryx* and modern birds (following Gauthier, 1986; this clade is termed Avialae by some authors; see also Gauthier & de Queiroz, 2001; Witmer, 2002).
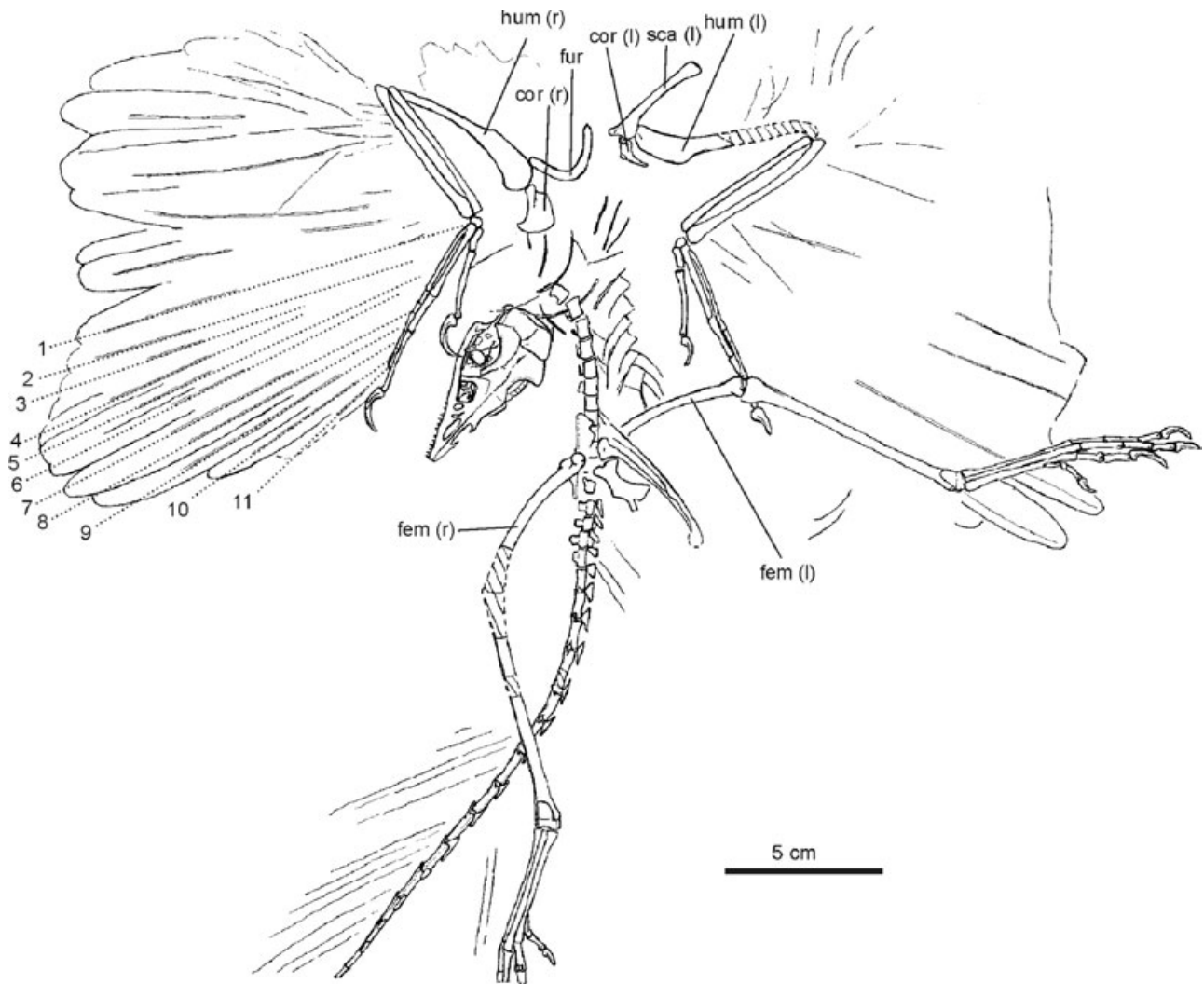
Figure 3. *Archaeopteryx siemensii* Dames, 1897, Thermopolis specimen (WDC-CSG-100). Interpretative drawing of the skeleton. The hatched elements were restored by the preparator. The primaries are numbered; their approximate course and area of insertion are indicated by the dotted line, which is orientated by the preserved impressions of parts of the rachises. cor, coracoid; fem, femur; fur, furcula; hum, humerus; sca, scapula. Left and right elements are indicated by (l) and (r), respectively.

SYSTEMATIC PALAEONTOLOGY

AVES LINNAEUS, 1758

ARCHAEOPTERYGIDAE HUXLEY, 1871

ARCHAEOPTERYX VON MEYER, 1861

ARCHAEOPTERYX SIEMENSII DAMES, 1897

Referred specimen
WDC-CSG-100, deposited in the Wyoming Dinosaur Center, Thermopolis, WY, USA.

Measurements
See Table 1.

Description and comparison
Skull: The skull (Fig. 4) is the only archaeopterygid skull exposed in dorsal view, allowing the recognition of some previously unknown osteological details. For example, contrary to all other avians, the premaxillary bones of *Archaeopteryx* are not co-ossified, not even in their most distal part, as in the enantiornithine *Gobipteryx* (Chiappe, Norell & Clark, 2001). In fact, in the new specimen, the distal ends of the premaxillae are not even in contact, so that there is a small notch at the tip of the snout. This may be an artefact of preservation, but it is notable that there is also a notch on the tip of the rostrum in the early

Table 1. Dimensions (in mm) of some major skeletal elements of the Thermopolis specimen in comparison with other Archaeopterygidae

	Thermopolis specimen	Munich specimen	Berlin specimen	Haarlem specimen	Maxberg specimen	London specimen	Solnhofen specimen	Eichstätt specimen
Skull	52.9	~45*	~52*	–	–	–	~65*	~39*
Humerus	56.9	~55.0†	63.0†	–	~72†	75.0†	83.0†	41.5†
Ulna	50.9	53.0†	56.2†	–	~62 (?)†	67.0†	~74.0†	36.5†
Metacarpal I	6.6	7.0†	~7.0†	10.0†	~10†	–	–	5.2†
Metacarpal II	23.5	25.0†	28.0†	–	~33†	34.4†	–	17.8†
Metacarpal III	22.0	23.0†	24.5–24.8†	29.4†	~30†	–	–	16.5†
Digit I/ph. 1	19.5	20.0†	21.5†	23.3	–	–	28.0†	15.4†
Digit II/ph. 1	12.8	12.5†	15.2–15.4†	–	~19†	–	19.0†	10.1†
Digit II/ph. 2	18.6	18.0†	~19.4†	–	~22†	–	27.0†	14.5†
Digit III/ph. 1	4.8	–	6.4†	–	–	–	7.9†	~4.8†
Digit III/ph. 2	4.2	–	4.0†	–	–	–	6.1†	~2.2†
Digit III/ph. 3	12.9	12.0†	12.3†	–	~16†	–	17.5†	9.5†
Femur	50.3	~46.5†	52.2†	–	~58†	~61.0†	~67.0†	37.0†
Tibia	74.6	~71.5†	71.0†	–	~79.5†	~82.0†	92.0†	~53.0†
Metatarsal II	35.1	–	~35.0†	–	~38†	~40.0†	45.0†	28.3†
Metatarsal III	39.6	40.5†	~37.0†	–	~42†	44.0†	~47.5†	30.2†
Metatarsal IV	36.3	37.0†	–	–	~39†	–	45.0†	27.3†
Digit I/ph. 1	6.1	7.1†	5.2–5.5†	–	–	8.8†	11.0†	5.5†
Digit II/ph. 1	10.6	~6.0†	8.2†	–	~9.5†	11.0†	12.0†	~7.1†
Digit II/ph. 2	8.8	–	7.0†	–	~10†	11.0†	12.5†	7.0†
Digit III/ph. 1	10.8	10.8†	9.6†	–	~11†	12.7†	13.7†	9.0†
Digit III/ph. 2	9.6	8.5†	9.0†	–	~10.5†	11.0†	11.8†	8.0†
Digit III/ph. 3	7.8	8.4†	8.2†	–	–	~9.5†	10.5†	7.0†
Digit IV/ph. 1	7.5	8.0†	7.0†	–	–	–	10.0†	6.1†
Digit IV/ph. 2	6.6	6.0†	6.4–6.6†	–	–	–	8.5†	5.0†
Digit IV/ph. 3	5.6	~5.5†	4.9†	–	–	–	NA	4.6–4.7†
Digit IV/ph. 4	5.6	–	5.6–5.8†	–	–	–	9.5†	4.9†

*After Wellnhofer (1993).
†After Elżanowski (2001b).

Cretaceous Confuciusornithidae (Chiappe *et al.*, 1999), whose premaxillae are fused, however. The virtually uncompressed snout forms a steep roof with a subtriangular cross-section; dorsally the premaxillary bones meet at an angle of about 85°. The nasal openings are elongate and measure nearly one-sixth of the length of the skull; there is a small foramen at their dorsodistal margin. The maxillare exhibits a nearly circular maxillary fenestra and a smaller, more distal, promaxillary fenestra (Figs 4, 5), most likely indicating pneumatization of the antorbital sinus (Witmer, 1990). These fenestrae occur in other theropods, but are much larger in *Archaeopteryx* than in, for example, dromaeosaurs (Norell & Makovicky, 2004: fig. 10.4).

Four premaxillary and eight maxillary teeth are visible; as indicated by a gap between the second and third preserved maxillary teeth, one maxillary tooth may be missing (Fig. 5). An isolated tooth of uncertain provenance lies close to the tip of the right premaxilla.

As in the other specimens of *Archaeopteryx*, the teeth show some variation in size and shape (Wellnhofer, 1992: fig. 19). The first and second premaxillary teeth are more peg-like, whereas most others have convex rostral and concave caudal margins, and a slightly caudally projecting tip. The fourth premaxillary tooth is the longest tooth, the eighth maxillary tooth the shortest. As in other archaeopterygid specimens, none of the teeth are serrated.

The lacrimale is an 'L'-shaped bone with a pronounced nasal process; a prefrontal appears to be absent (the bone identified as a prefrontal in the Eichstätt specimen by Wellnhofer, 1974 has been considered as part of the lacrimale by subsequent workers, for example, Elżanowski & Wellnhofer, 1996; Paul, 2002). The orbital margin of the frontal forms a low rim. Owing to the fact that the brain cavity is collapsed, the frontal bones are not in medial contact. The caudal margins of the frontals are distorted
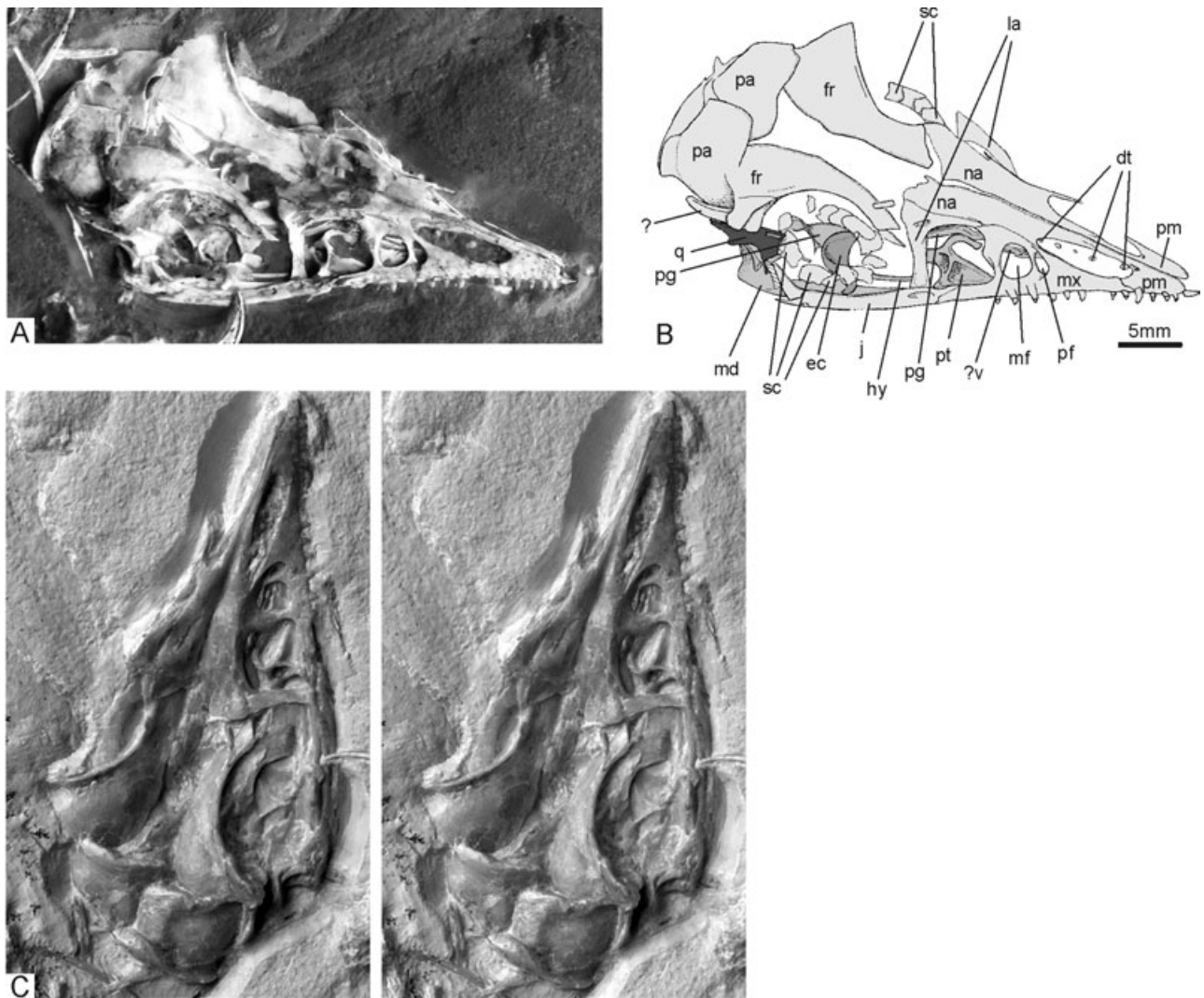
Figure 4. *Archaeopteryx siemensii* Dames, 1897, Thermopolis specimen (WDC-CSG-100). Skull. A, Ultraviolet-induced fluorescence photograph. B, Interpretative drawing. C, Stereo pair. dt, dentary teeth; ec, ectopterygoid; fr, frontal; hy, hyoid; j, jugal; la, lacrimal; md, mandible; mf, maxillary fenestra; mx, maxilla; na, nasal; pa, parietal; pf, promaxillary fenestra; pg, pterygoid; pm, premaxilla; pt, palatine; q, quadrate; sc, ossicles of sclerotic ring; v, vomer.

against the frontal margins of the parietals, resulting in the misleading impression of a 'temporal cavity' on the right side of the skull, caudal to the orbits. Five scleral ossicles are preserved in articulation in the left orbit, about 13 sclerotic plates (or fragments thereof) can be counted in the right orbit.

The palate of *Archaeopteryx* was poorly known until Wellnhofer (1993) and Elżanowski & Wellnhofer (1996) described the isolated palatal elements of the Munich specimen. The new skeleton provides further anatomical details of the shape and orientation of the archaeopterygid palatine, ectopterygoid, and pterygoid (Figs 4–6). The dorsal surface of the midsection of the right palatine is visible through the antorbital

fenestra, whereas most of the pterygoid wing and maxillary process are hidden by overlying sediment and bones. The bone is tetraradiate as in non-avian theropods, and the short jugal process, reported for the first time (Mayr *et al.*, 2005), contacts the jugal. The seemingly triradiate palatine of the Munich specimen exhibits a breakage line along its lateral margin (Elżanowski & Wellnhofer, 1996: fig. 4B), and a small associated fragment (Elżanowski & Wellnhofer, 1996: fig. 4E) may represent the broken jugal process. As in the Munich specimen, the dorsal surface of the palatine exhibits two marked depressions separated by a transverse crest. A small fracture in the bony wall of the deeper caudal depression indicates that it was
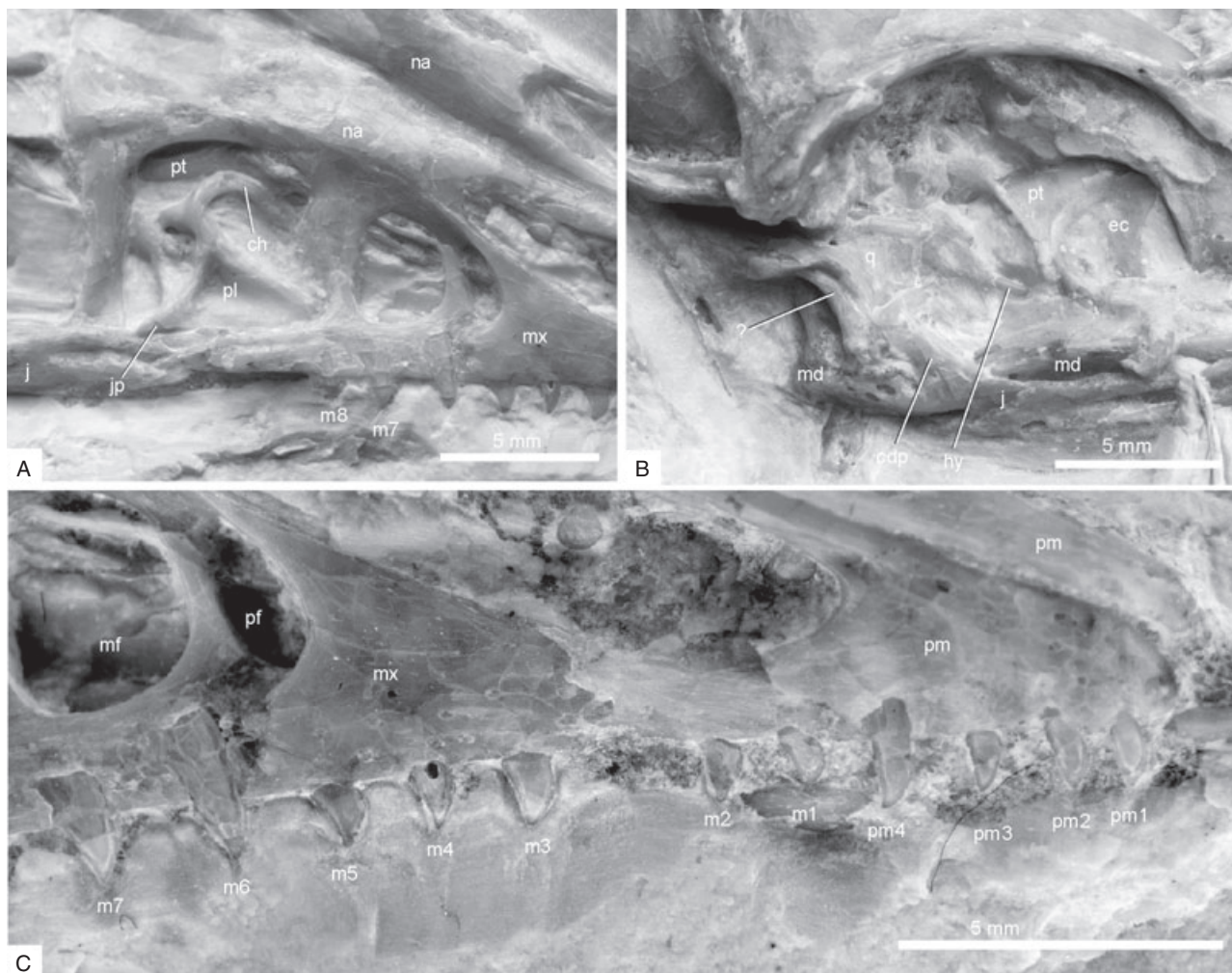
Figure 5. *Archaeopteryx siemensii* Dames, 1897, Thermopolis specimen (WDC-CSG-100). Skull. A, Detail of antorbital fenestra with palatine bone. B, Detail of right orbital region with pterygoid and ectopterygoid. C, Detail of dentition. cdp, caudodorsal process of jugal; ch, choanal process of palatine; ec, ectopterygoid; hy, hyoid; j, jugal; jp, jugal process of palatine; md, mandible; mf, maxillary fenestra; mx, maxilla; na, nasal; pf, promaxillary fenestra; pl, palatine; pm, premaxilla; pt, pterygoid; q, quadrate; ?, unidentified bone. The maxillary (m) and premaxillary (pm) teeth are numbered.

hollow and thus probably pneumatic. As assumed by Elżanowski (2001a), the hook-shaped choanal process touches the rostral portion of the pterygoid. Contrary to Elżanowski's (2001a) reconstruction (Fig. 6B), however, the lateral margin of the maxillary process contacts the jugal and maxillare. This difference from Elżanowski's (2001a) otherwise excellent reconstruction is a result of the fact that the palatine of *Archaeopteryx* has a jugal process and is thus wider than assumed by Elżanowski (2001a), and because the distal part of the skull appears to have been narrower than in Elżanowski's reconstruction (Fig. 6).

In the dorsal section of the maxillary fenestra, an elongated element can be discerned which we identify as part of the vomer (see Elżanowski & Wellnhofer,

1996; Elżanowski, 2001a). Also observable in the ventral portion of the maxillary fenestra is an osseous structure which may be part of the palatal shelf of the maxillare.

The ectopterygoid, which appears to be homologous to the avian uncinatum (Elżanowski, 1999), is preserved in its original position, with the convex margin directed caudally. Its shape corresponds to the ectopterygoid of the Munich specimen (Elżanowski & Wellnhofer, 1996: fig. 4F). Its position in the new specimen agrees with that reconstructed by Elżanowski (2001a), except that the caudomedial margin tightly joins, and slightly overlaps, the rostral end of the prequadrate wing (Elżanowski, 2002; triangular wing of Elżanowski & Wellnhofer, 1996) of the right ptery-
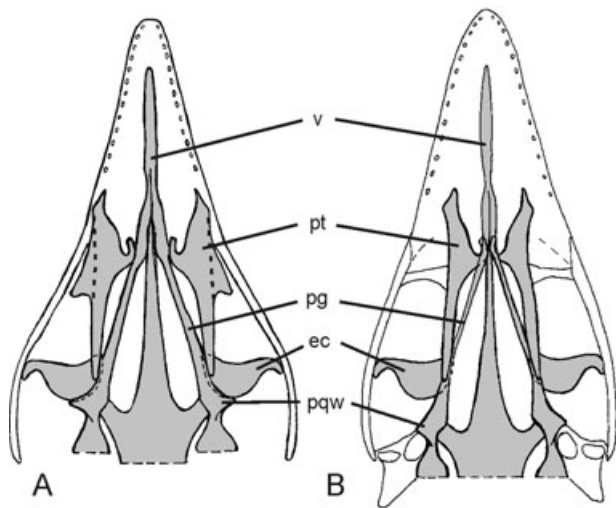
Figure 6. A, Reconstruction of the palate of *Archaeopteryx siemensii* Dames, 1897, according to information on the shape of the palatine and the position of the ectopterygoid from the new specimen. B, Reconstruction of Elżanowski (2001a). In A, the lateral margin of the broken palate of the Munich specimen is indicated by a broken line. ec, ectopterygoid; pg, pterygoid; pqw, prequadrate wing; pt, palatine; v, vomer.

goid, whereas it contacts the rostral blade of the pterygoid alone in Elżanowski's (2001a) reconstruction (Fig. 6). The hook-shaped jugal process meets the jugal.

The pterygoid also resembles the corresponding element of the Munich *Archaeopteryx* and confirms the hypothesized orientation of this element by Elżanowski & Wellnhofer (1996) and Elżanowski (2001a). In WDC-CSG-100, the caudal part and the rostral blade, which contacts the choanal process of the palatine (Elżanowski, 2001a), are visible, whereas the intervening section is hidden under overlying bones. The portion caudal to the prequadrate wing is markedly twisted. The new specimen confirms the interpretation by Elżanowski & Wellnhofer (1996) that the prequadrate wing is directed laterally, but its caudal margin, which was identified as the articulation facet for the quadrate by Elżanowski & Wellnhofer (1996), does not contact the quadrate in the new specimen. We thus conclude that the prequadrate wing of the pterygoid of *Archaeopteryx* braced the ectopterygoid and did not contact the quadrate (Fig. 6), as in other non-avian theropods.

The temporal region of WDC-CSG-100 (Fig. 5) is difficult to interpret and is apparently not completely preserved in the specimen, as neither a squamosal nor a postorbital can be discerned. These bones are shown to be present in the Munich specimen, in which a squamosal with a process for articulation with the postorbital can be identified (Elżanowski & Wellnhofer, 1996: fig. 6B). We assume that these bones were lost when the slab was split. A structure that, at first glance, resembles the dorsal temporal bar (Fig. 4), whose presence in *Archaeopteryx* has been controversial (Elżanowski, 2001a; Paul, 2002), is either a rib, as other ribs are preserved in close proximity, or the dorsal margin of the right prootic (unfortunately, the depth of this structure cannot be discerned). There is a well-developed occipital crest caudally adjacent to the parietal bones.

The caudal end of the jugal bifurcates into a slender quadratojugal and a marked caudodorsal process, as reconstructed by Elżanowski (2001a). We could not, however, identify the quadratojugal itself, which, in *Archaeopteryx*, is a small, 'L'-shaped bone (Elżanowski & Wellnhofer, 1996).

A substantial portion of the right quadrate seems to be preserved, although this bone appears to be damaged, making the identification of osteological details impossible. An osseous bar just caudal to the presumed caudal margin of the quadrate has so far defied identification.

Most of the mandible is hidden under the skull. Only the caudal part of the right ramus is visible caudal to the jugal and continues above the jugal. The tips of five dentary teeth, presumably from the left mandibular ramus, can be seen through the right nasal opening.

There is a thin osseous bar in the right orbit, above the right mandibular ramus, which we consider to be part of the hyoid (Figs 4, 5). The caudal part of this bar is covered by plates of the sclerotic ring, but apparently continues lateral of the prequadrate wing of the pterygoid and terminates on the right quadrate.

Vertebrae: The morphology of the vertebral column of *Archaeopteryx* is still rather poorly known. In the new specimen, three incompletely prepared cervical vertebrae in articulation are situated underneath the right manus; three caudally adjacent ones, also in articulation, are still hidden in the sediment and only visible on the X-ray photograph (Fig. 7). These six cervical vertebrae are not in articulation with either the thoracic vertebrae or the skull, and only few osteological details can be discerned on the X-ray photograph. They are visible in ventral view and increase in length with increasing distance from the dorsal vertebrae. The vertebra closest to the dorsal series is only slightly longer than wide, whereas the most cranial one is nearly twice as long as wide. The cranial ends bear well-developed transverse processes.

The centra of the seven most caudal dorsal vertebrae, from the thoracosacral series, are well preserved (Fig. 8). These are exposed in ventrolateral view and
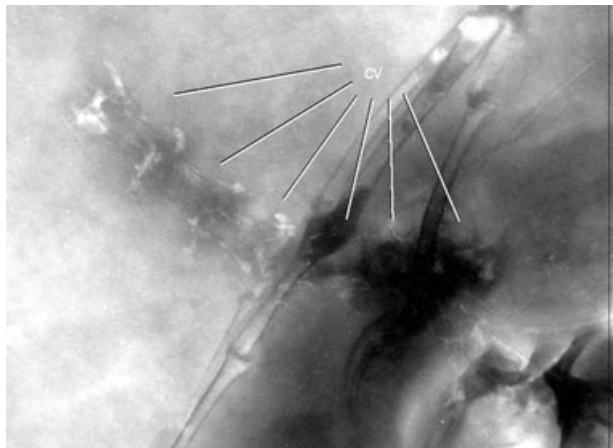
Figure 7. *Archaeopteryx siemensii* Dames, 1897, Thermopolis specimen (WDC-CSG-100). X-Ray photograph showing cervical vertebrae and part of right manus. cv, cervical vertebrae.

have convex lateral and ventral surfaces. Contrary to other Mesozoic non-neornithine birds, e.g. Confuciusornithidae and Ichthyornithidae (Peters, 1996; Chiappe *et al*., 1999; Clarke, 2004), they do not bear marked lateral excavations ('pleurocoels'), but only shallow, elongate depressions. As in the basal dromaeosaur *Microraptor* (Hwang, Norell & Gao, 2002), the preserved dorsal vertebrae do not exhibit pneumatic foramina, whose presence has been observed for some cervical and cervicothoracic vertebrae of *Archaeopteryx* (Britt *et al*., 1998), and also appear solid on the X-ray photograph. The second and third dorsal vertebrae exhibit small concave parapophyses at the cranial end of the centrum, which are slightly elevated, but not set on small stalks as appears to be the case in *Microraptor* (Hwang *et al*., 2002) and *Confuciusornis* (Chiappe *et al*., 1999). Transverse processes cannot be discerned. As in the basal avian *Rahonavis* (Forster *et al*., 1998), there is, however, a marked laterally directing infradiapophyseal fossa at the base of the neural arches (partly filled with sediment in the specimen). Other details of the neural arches are not visible.

Given the presumed number of 23 presacral vertebrae in *Archaeopteryx* (Elżanowski, 2002), ten presacral vertebrae are missing or at least not visible in the new specimen (there appear to be additional vertebrae beneath the cranium, but this cannot be clearly discerned on the X-ray photograph).

We assume that five vertebrae are fused into a synsacrum (Fig. 8) as in other specimens of the Archaeopterygidae (Elżanowski, 2002), although the transition between the dorsal and sacral vertebrae is difficult to ascertain (the vertebra which is here identified as the caudalmost dorsal vertebra, 'd14', in Fig. 8 also appears to be tightly sutured to the caudally adjacent one, here identified as the cranialmost synsacral vertebra; in this case, six vertebrae would be fused into the synsacrum, as in *Rahonavis*, Forster *et al*., 1998). The boundaries between the centra can still be discerned.

Twenty tail vertebrae are preserved (the distal half of the 20th is missing) and, given the number of 21–22 tail vertebrae in other Archaeopterygidae (Wellnhofer, 1974; Elżanowski, 2002), the distalmost one or two vertebrae seem to be missing (Fig. 8). The second to fourth tail vertebrae bear well-developed transverse processes, the fifth a small one. These vertebrae also bear large, plate-like chevrons, which become much lower and more elongated towards the distal tail vertebrae. The chevrons at the tip of the tail are very small. The tail is twisted along its longitudinal axis, i.e. the proximal third is seen in ventrolateral view, the midsection in lateral view, whereas the distal section, beginning with the 16th caudal vertebra, exposes its ventral surface. Thus, it can be discerned that the 17th–19th tail vertebrae are strongly mediolaterally compressed, with very narrow centra (the width of the 17th centrum is only 0.7 mm). The lengths of the centra of the tail vertebrae are (in mm): 3.8 (second), 4.2 (third), 4.2 (fourth), 5.4 (fifth), 6.5 (sixth), 7.9 (seventh), 9.5 (eighth), ~10.0 (?) (tenth), 11.1 (11th), 10.9 (12th), 10.9 (13th), 10.6 (14th), 10.6 (15th), 10.1 (16th), 9.1 (17th), 9.1 (18th).

Ribs and gastralia: Only a few ribs are preserved in the specimen, owing to the fact that the thoracic vertebrae proper are lacking. Some ribs are damaged, so that it can be discerned that they were hollow. For the first time, the gastralia are seen in ventral view (Fig. 8). Their arrangement is not symmetrical, because the elements form a zigzag pattern as in the Confuciusornithidae (Chiappe *et al*., 1999: fig. 33). Of the seven caudal rows, elements from both sides are preserved and each row apparently consists of four elements; on each side, two of these overlap for nearly half of their length; of the four cranialmost rows, only the right elements are visible.

Coracoid: The morphology of the coracoid of *Archaeopteryx* has been controversial, owing to the fact that none of the hitherto known specimens shows a complete view of this bone (compare the reconstructions in, for example, de Beer, 1954; Ostrom, 1976; Martin, 1991; Wellnhofer & Tischlinger, 2004). In the new specimen, nearly the entire right coracoid is exposed in cranial view and, in addition, the lateral surface of the left one can be seen (Fig. 9). The body of the bone is of subrectangular shape, with a concave lateral margin and a well-developed lateral process. Except for the more pronounced lateral process, it agrees well
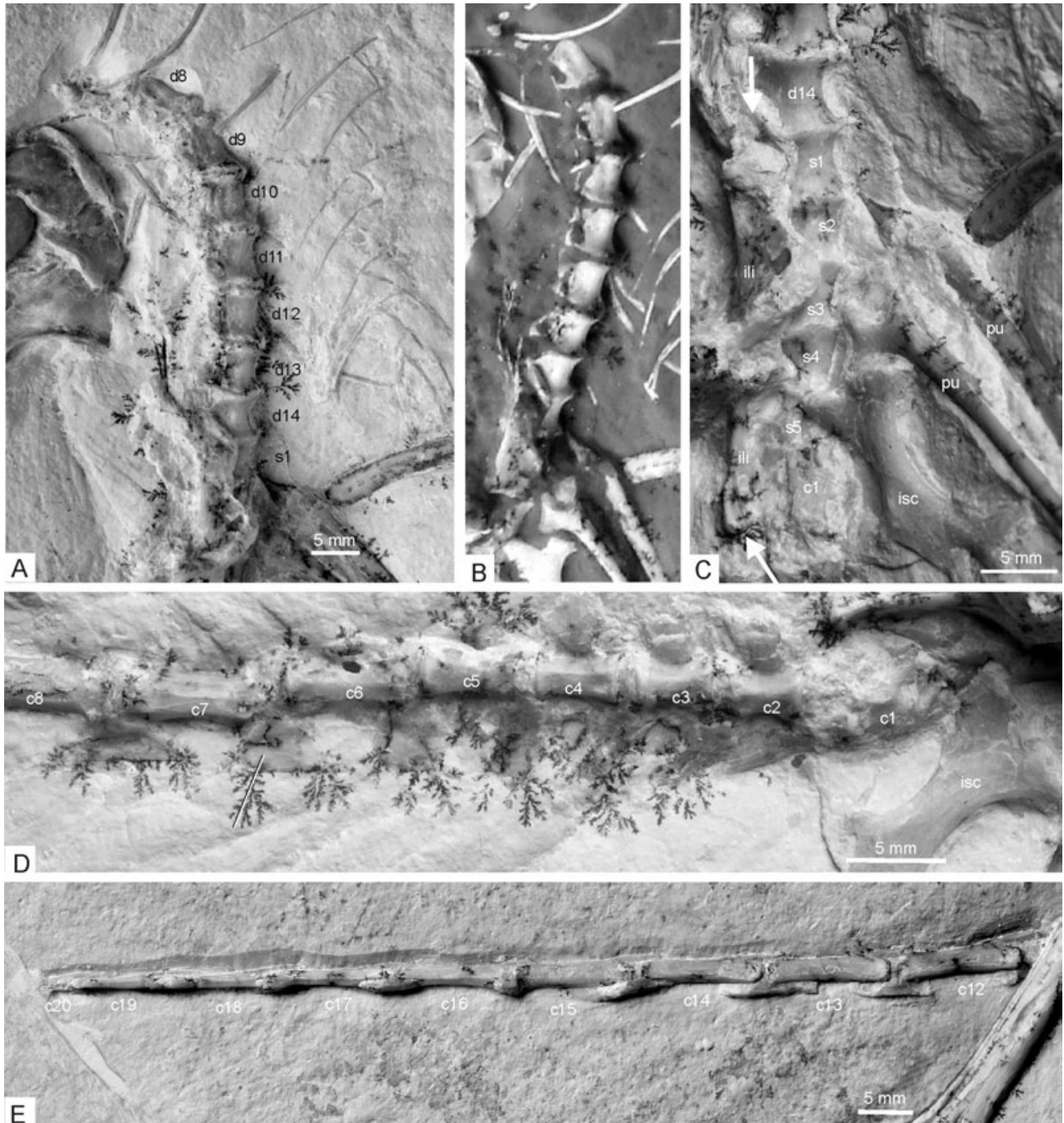
Figure 8. *Archaeopteryx siemensii* Dames, 1897, Thermopolis specimen (WDC-CSG-100). Vertebral column. A, Dorsal vertebrae in ventrolateral view. B, Ultraviolet-induced fluorescence photograph of dorsal vertebrae. C, Sacrum in ventral view. D, Proximal section of caudal vertebrae in ventrolateral view. E, Distal section of caudal vertebrae in lateral and ventral view. ili, ilium; isc, ischium; pu, pubis. The dorsal (d), sacral (s), and caudal (c) vertebrae are numbered. The arrows indicate the cranial and caudal ends of the ilium.

in its shape with the coracoid of the basal avian *Sapeornis* as reconstructed by Zhou & Zhang (2003a: fig. 6f), whereas the coracoid of other basal avians, such as *Jeholornis* and *Confuciusornis* (Chiappe *et al.*,

1999; Zhou & Zhang, 2003b), is narrower and more elongated. The distal (sternal) margin is slightly convex. As already noted by de Beer (1954), the bone is bent craniocaudally along a line running obliquely
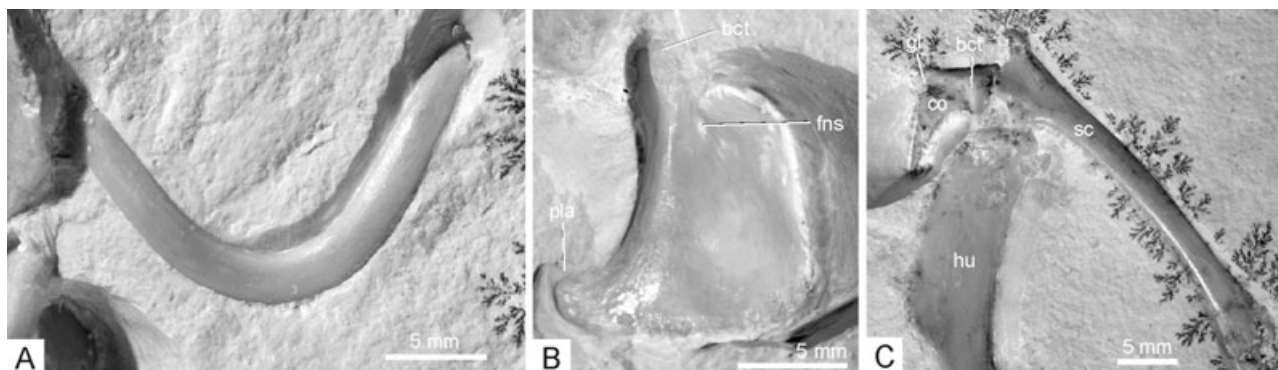
Figure 9. Elements of the pectoral girdle of *Archaeopteryx siemensii* Dames, 1897, Thermopolis specimen (WDC-CSG-100). A, Furcula. B, Right coracoid. C, Left coracoid, scapula, and humerus. bct, biceps tubercle; co, coracoid; fns, foramen nervi supracoracoidei; gl, glenoid process of coracoid; hu, humerus; pla, lateral process of coracoid; sc, scapula.

from the biceps tubercle to the edge corresponding to the angulus medialis (Baumel & Witmer, 1993) of the coracoid of extant birds. The biceps tubercle (preglenoid process of Elżanowski, 2002) is elongated. In lateral view, the bone resembles the coracoid of the basal dromaeosaur *Sinornithosaurus* (Xu, Wang & Wu, 1999). It widens towards the glenoid extremity, the sternal extremity is narrow; the area between the biceps tubercle and the glenoid is concave. There appears to be a small foramen for the supracoracoideus nerve (Fig. 9). However, although this foramen is preserved in the expected position and appears to be real, there are similar foramina near the medial margin of the bone which seem to be preparation artefacts. The medial margin does not exhibit any incisions, which were assumed by de Beer (1954: fig. 4) for the London specimen.

Scapula: The left scapula is exposed in lateral aspect (Fig. 9); the right scapula is still hidden in the matrix, but visible on the X-ray photograph (Fig. 10). The bone is much shorter than the humerus, the left scapula measures 35.0 mm. The acromion is narrow, the surface between it and the glenoid fossa concave. The corpus of the scapula widens slightly toward its truncate caudal end (contra Martin, 1985: fig. 3). Apart from the narrower acromion, the scapula of *Archaeopteryx* is similar in morphology to that of *Sinornithosaurus* (Xu *et al.*, 1999). The left coracoid and scapula join at an angle of about 90°, but, as in all other Archaeopterygidae with the possible exception of the London specimen (de Beer, 1954), are not fused.

Furcula: The boomerang-shaped furcula (Fig. 9) has its cranial surface exposed, and is similar in shape to that of the London specimen. The bone is curved craniocaudally, with the midsection of the scapi clavicularum protruding most strongly cranially. As in the Confuciusornithidae (Peters, 1996; Chiappe *et al.*,

1999), the extremitas omalis is simple and rounded. An acromial process is not developed. The furcula appears to have been only loosely connected to the other pectoral bones, which may explain its absence in the Eichstätt and Berlin specimens.

Sternum: In concordance with other specimens of the Archaeopterygidae, there are no ossified sternal plates. The alleged presence of an ossified sternum in the Munich specimen has recently been disproved (Wellnhofer & Tischlinger, 2004).

Humerus: The cranial surface of the right humerus is exposed (Fig. 10), whereas the left one is seen from its caudodorsal side (the distal half of this bone has been restored by the preparator). In contrast with modern birds but as in the ninth specimen and non-avian theropods (Wellnhofer & Röper, 2005), the main plane of the distal end is twisted at an angle of about 45° against that of the proximal end. The proximal end of the humerus lacks any of the fossae and sulci characteristic of extant birds, and the caput humeri is directed more ventrally than in extant birds. The crista deltopectoralis measures slightly more than one-third of the entire length of the bone. In concordance with other Mesozoic avians (e.g. Confuciusornithidae, *Jeholornis*), it projects laterally without any cranial deflection known in extant birds. The caudal surface of the humerus is flat, the cranial surface medial of the crista deltopectoralis slightly convex. There is a small crista bicipitalis. The distal end of the right humerus remains embedded in the sediment, but is discernible on the X-ray photograph (Fig. 10). Its shape appears similar to the distal humerus of the basal avian *Sapeornis* (Zhou & Zhang, 2003a: fig. 7), with the condylus ventralis protruding furthest distally and the condylus dorsalis being orientated more obliquely to the longitudinal axis of the humerus than in neornithine birds.
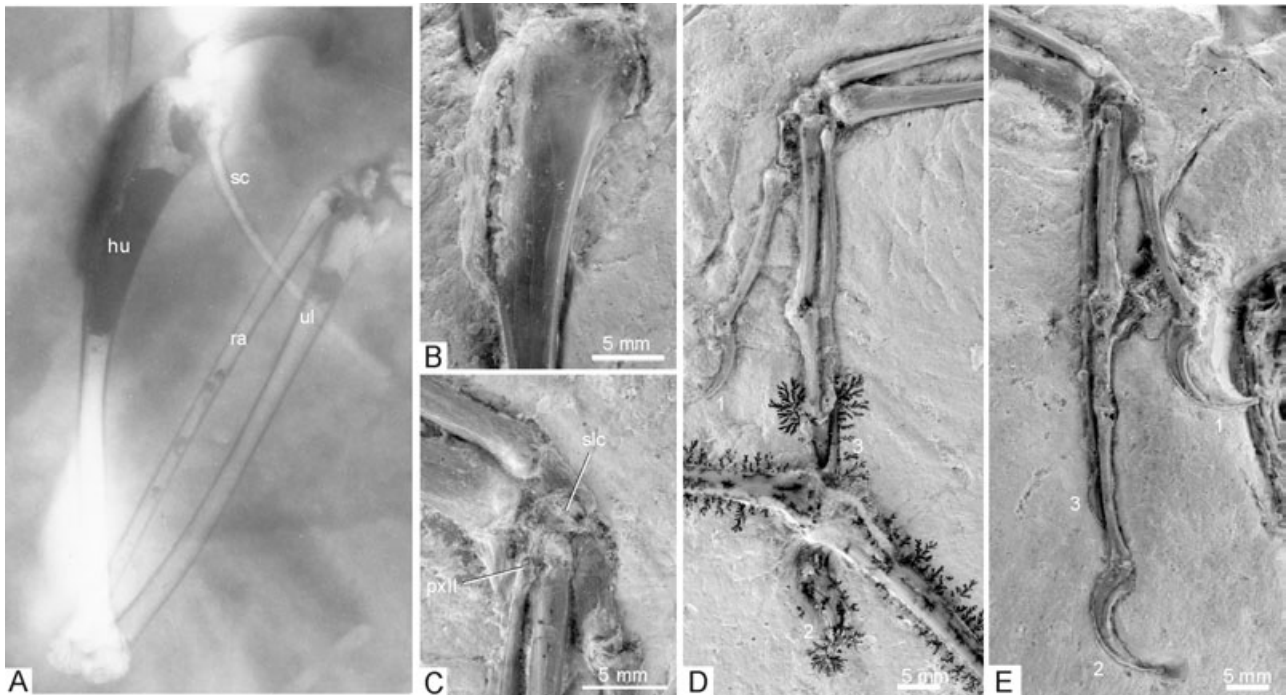
Figure 10. *Archaeopteryx siemensii* Dames, 1897, Thermopolis specimen (WDC-CSG-100). Wing bones. A, X-Ray photograph showing right scapula, humerus, ulna, and radius. B, Cranial aspect of proximal end of right humerus. C, Detail of right wrist. D, Left manus. E, Right manus. hu, humerus; pxII, proximal end of second metacarpal; ra, radius; sc, scapula; slc, semilunate carpal; ul, ulna. The fingers are numbered.

Ulna and radius: Both ulnae have their dorsal surfaces exposed and are preserved complete and uncrushed. The shaft is very slender in its midsection, but widens towards the distal end; it is only slightly wider than the shaft of the radius, whereas the ulna is much wider than the radius in *Microraptor* (Hwang *et al.*, 2002; Xu *et al.*, 2003). An olecranon is virtually absent, as is a well-developed processus cotylaris dorsalis. In contrast with the basal avian *Rahonavis* (Forster *et al.*, 1998), even faint papillae remigales cannot be discerned.

The distal end of the radius exhibits a pointed tuberculum aponeurosis ventralis (Baumel & Witmer, 1993). Details of the proximal ends of both radii cannot be observed.

Carpalia and metacarpals: Only the semilunate carpal bone is visible in the specimen (Fig. 10; three other carpal bones may be visible on the ultraviolet-induced fluorescence photograph of the left wing, but their identification is uncertain). It mainly caps the second metacarpal and only the cranial edge contacts the first metacarpal, whereas 'it caps all of metacarpal I and part of metacarpal II' in *Microraptor* (Hwang *et al.*, 2002: 19). The metacarpals are seen from their dorsal side. As in the Eichstätt specimen, the proximal end of the third metacarpal lies above (dorsal to) the proxi-

mal end of the second metacarpal; it is situated further distally than the proximal end of the second metacarpal (pro Elżanowski, 2002; contra Gishlick, 2001). The second and third fingers are tightly joined, but in contrast with the Berlin, Eichstätt, and Solnhofen specimens, as well as the ninth one, they do not cross (Fig. 10). Also in contrast with these specimens, the second phalanx of the third finger is only slightly shorter than the first (Table 1). The third phalanx of the third finger is very thin, much thinner than the second phalanx, indicating a considerable degree of reduction of this finger.

The keratinous sheaths of the ungual phalanges are well preserved on the first and second right manual digits. As in the other specimens, they show no sign of wear (Peters & Görgner, 1992). Also as in most other specimens, their concave surface is directed cranially.

Pelvis: The elements of the pelvis are disarticulated and have moved from their original position (Fig. 11). Few details of the poorly preserved right ilium can be discerned; the preacetabular part has a concave lateral surface, the tapering postacetabular part is seen in ventral view and is mediolaterally wide. The right ischium is visible in lateral view and exhibits the characteristic derived archaeopterygid shape. The proximal end bifurcates into two processes for articu-
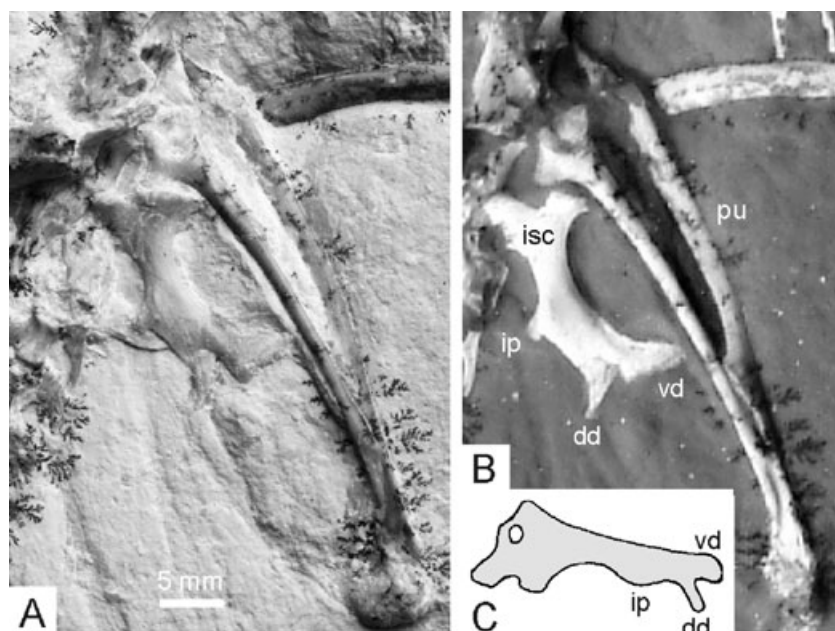
Figure 11. *Archaeopteryx siemensii* Dames, 1897, Thermopolis specimen (WDC-CSG-100). Pelvic girdle (A, B) and ischium (C) of the London specimen. A, Elements as preserved. B, Ultraviolet-induced fluorescence photograph. C, After Elżanowski (2002), not to scale. dd, dorsodistal process; ip, intermediate process; isc, ischium; pu, pubis; vd, ventrodistal process. The arrows indicate the cranial and caudal ends of the ilium.

lation with the ilium and pubis, respectively. The ventral margin is concave, the dorsal margin bears a process in its midsection (intermediate process of Elżanowski, 2002; posterior process of Hwang *et al*., 2002). The distal end bifurcates into two processes that were termed dorsodistal and ventrodistal processes by Elżanowski (2002) (the latter corresponds to the obturator process of non-avian theropods). The narrow dorsodistal process is separated from the wider ventrodistal one by a deep incision. In its shape, the ischium corresponds to that of the Eichstätt and Munich specimens as reconstructed by Wellnhofer (1974, 1993). It is dorsoventrally wider than the ischium of *A. lithographica* as reconstructed by Elżanowski (2002: fig. 6.4), and there are no proximodorsal process and foramen obturatum. The ischium of *Archaeopteryx* resembles the corresponding bone of *Microraptor* (Hwang *et al*., 2002) and, to a lesser degree, the basal troodontid *Sinovenator* (Xu *et al*., 2002), in which the distal end is not bifurcated by a notch between the two processes.

There is a marked pit on the lateral surface of the expanded proximal end of the right pubis. As in the London and Eichstätt specimens (Elżanowski, 2002), the pubic boot is partially replaced by a calcite mass, possibly indicating the former presence of cartilage. Proximal to the pubic boot, the pubic apron extends over almost half of the length of the pubis.

Femur: The right femur is seen in medial view (its distal portion has been restored by the preparator), the left one from its craniomedial side. The shaft of the bone is craniocaudally curved. The femoral head is orientated nearly perpendicular to the longitudinal axis of the bone. On the cranial surface of the proximal end, there is a depression between the lesser trochanter and the femoral head. As in other basal avians (e.g. Confuciusornithidae, Chiappe *et al*., 1999) and in *Microraptor* (Hwang *et al*., 2002), but contrary to modern birds, the cranial surface of the distal end lacks a patellar sulcus (Fig. 11).

Tibia and tarsal bones: The right tibia is seen in cranial view, the left in craniomedial view (Fig. 12); the proximal part of the right tibia has been restored by the preparator. The proximal end of the tibia is similar to that of *Microraptor* (Hwang *et al*., 2002), with a well-developed cnemial crest that slants laterally. The cranial surface of the tibia is slightly convex over most of its length, whereas it is essentially flat in its distalmost section. For the first time, the proximal tarsals are clearly visible in the new specimen (Mayr *et al*., 2005). The condylar portion of the astragalus and the calcaneus are proximodistally low, only about half the size of the proximal tarsals of the dromaeosaurs *Microraptor* (Hwang *et al*., 2002: fig. 28) and *Sinornithosaurus* (Xu *et al*., 1999: fig. 4). The calcaneus is
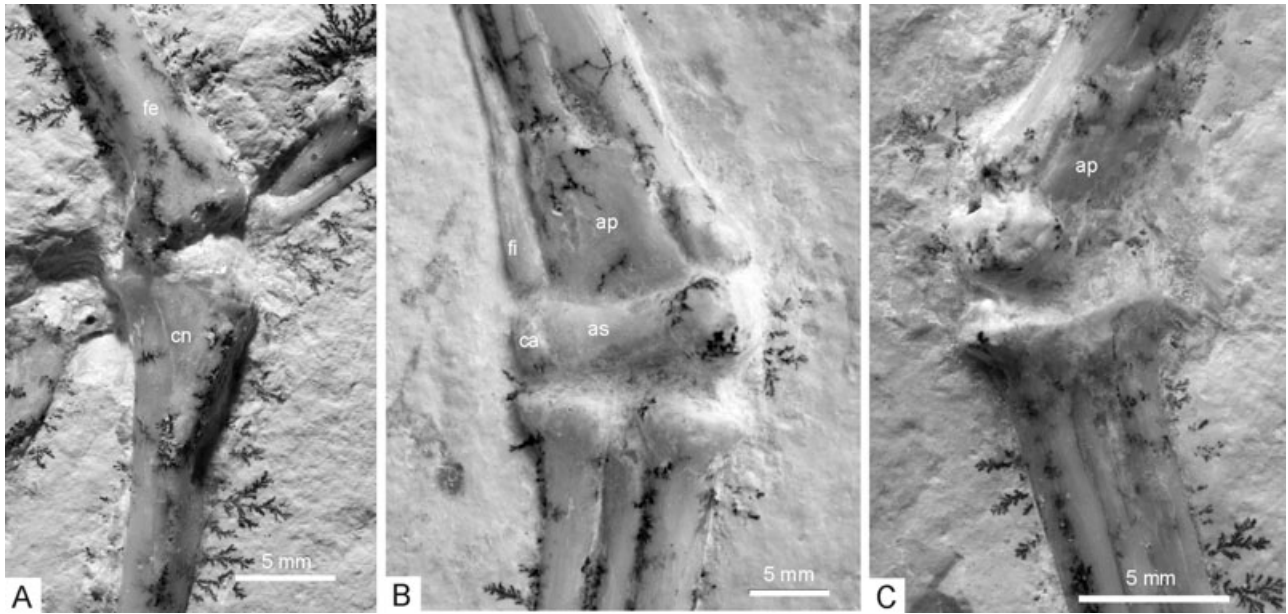
Figure 12. *Archaeopteryx siemensii* Dames, 1897, Thermopolis specimen (WDC-CSG-100). Hindlimb elements. A, Distal end of left femur and proximal end of left tibia. B, Right tarsus in cranial view. C, Left tarsus in craniomedial view. ap, ascending process of astragalus; as, astragalus; ca, calcaneus; cn, cnemial crest of left tibia; fe, distal end of left femur; fi, fibula.

very narrow, reaching only the width of the distal end of the fibula; the astragalus and calcaneus are separated by a narrow furrow, but may have been at least partly fused. As in other theropods, the astragalus forms a broad, 5.6-mm-long ascending process, which covers most of the cranial surface of the distal tibia. The ascending process is separated from the condylar portion of the astragalus by a transverse groove. The condyles of the astragalus are separated by a broad and shallow concavity, the medial condyle is more pronounced than the lateral one. On the medial side, there is a marked furrow between the distal part of the medial margin of the ascending process of the astragalus and the tibia. The distal end of the tibia further protrudes medially beyond the astragalus as in ornithomimosaurs (Barsbold & Osmólska, 1990) and the basal avian *Jeholornis* (Zhou & Zhang, 2002: fig. 3). Except for the latter feature, which appears to have not been recognized by previous authors, the tarsus of *Archaeopteryx* agrees well with the restoration of Paul (2002: fig. 10.14), but is very different from that of, for example, Martin (1991: fig. 43). The thin fibula widens distally just before it contacts the calcaneus. Distal tarsals cannot be discerned (Fig. 12).

Metatarsals: The three-dimensionally preserved metatarsals are seen in dorsal view and appear to be unfused over their entire lengths (Fig. 13). In their morphology and arrangement, the metatarsals compare well with those of *Microraptor* (Hwang *et al*., 2002). The third metatarsal is the longest and lies slightly dorsal to the second and fourth in the distal half of the metatarsus, but slightly ventral to them in the proximal half. The proximal ends of the second and fourth metatarsals are mediolaterally and dorsally expanded, whereas the third metatarsal becomes narrower in its proximal half and is proximally pinched by the second and fourth metatarsals. The foot of *Archaeopteryx* thus approaches the arctometatarsalian condition (Holtz, 1995), although, in the typical arctometatarsalian foot, the proximal end of the third metatarsal is much more compressed. The distal section of the third metatarsal is slightly widened, but subapically exhibits a shallow concavity on its medial side, on the level of the distal end of the second metatarsal. The distal end of the second metatarsal is displaced further plantar than that of the third and fourth metatarsals. Mediolaterally, the second metatarsal is approximately twice as wide as the fourth and extends slightly less far distally; the proximal section of the shaft has a subrectangular cross-section. The fourth metatarsal is very narrow mediolaterally, but its distal end may have been expanded dorsoventrally. The distal articular surfaces of the metatarsals are smooth and lack the ginglymoid condition (according to Hwang *et al*., 2002; the articular surface of the second metatarsal is ginglymoid in *Microraptor*). The distal ends of the second and third metatarsals have
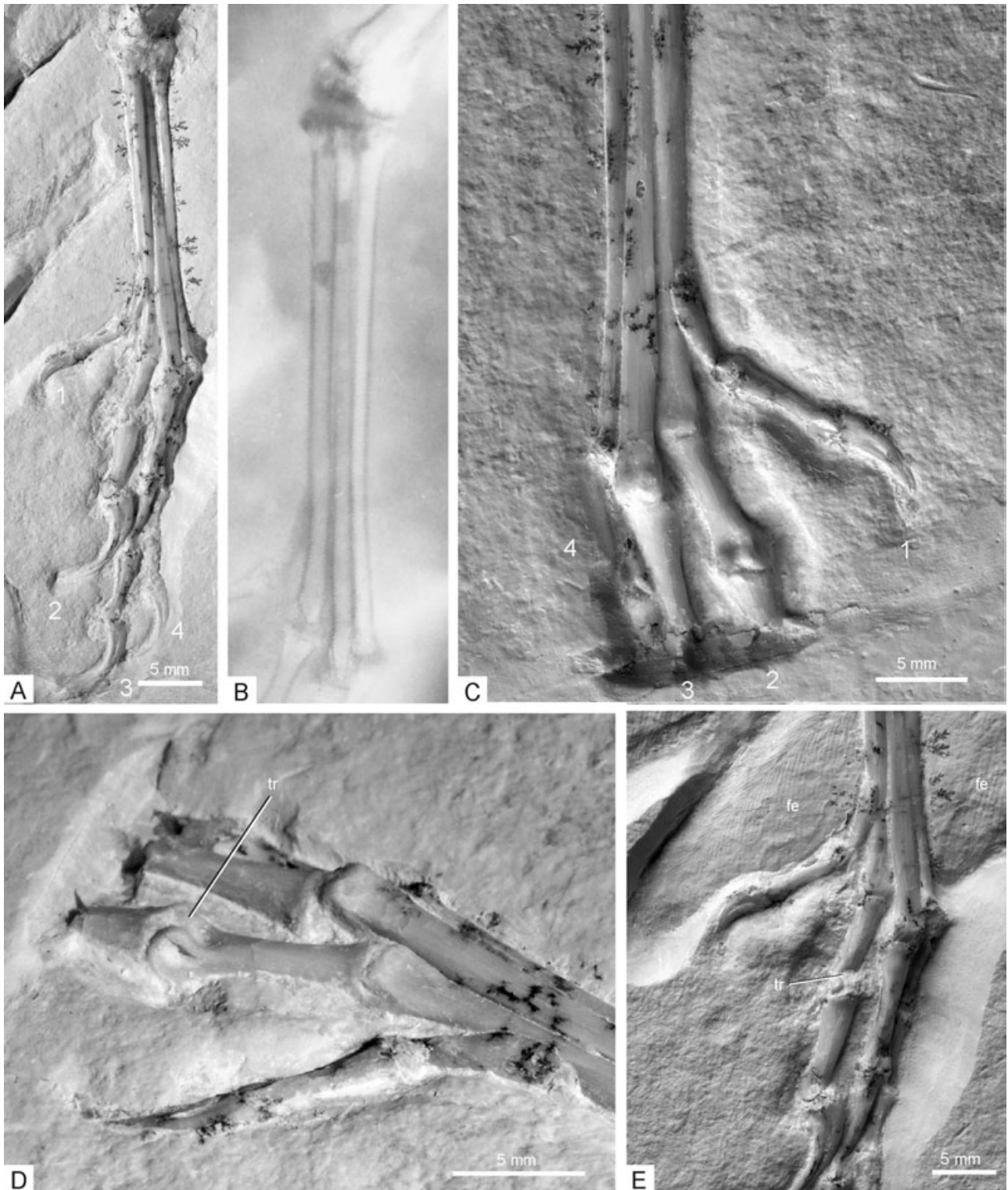
Figure 13. *Archaeopteryx siemensii* Dames, 1897, Thermopolis specimen (WDC-CSG-100). Feet. A, Left foot. B, X-Ray photograph of left foot. C, D, Distal end of right foot in dorsal (C) and dorsomedial (D) view. E, Distal end of left foot. fe, feather impressions; tr, proximodorsally expanded articular trochlea of first phalanx of second toe. The pedal digits are numbered.

an essentially flat dorsal surface, whereas that of the fourth metatarsal is raised to a small point. A fifth metatarsal is not visible, but is expected on the plantar surface of the metatarsals (Wellnhofer, 1992). In its proportions, the metatarsus of WDC-CSG-100 corresponds to that of the Berlin and Munich specimens. It is more slender than that of *A. lithographica* as exemplified by the London, Solnhofen, and Maxberg specimens. The ratio of maximum length to minimum width at midsection is 9.1 for the metatarsus of the new specimen and 6.2 for that of the Solnhofen specimen (after Wellnhofer, 1992: fig. 16).

Toes: As detailed by Mayr *et al*. (2005), and also assumed by Middleton (2002), the first toe of *Archaeopteryx* was not fully reversed as in modern birds (contra, for example, Wellnhofer, 1993). In the new specimen, it is spread medially on both feet (Fig. 13). Metatarsal I attaches to the medial (not medioplantar, contra Elżanowski, 2002) side of the second metatarsal, in approximately its distal quarter, whereas it attaches to the plantar surface of the tarsometatarsus in modern birds with a fully reversed hallux (Middleton, 2001); its proximal section even protrudes slightly further dorsad than the second metatarsal (Fig. 13). Moreover, the shaft does not exhibit the torsion characteristic for birds with a fully reversed hallux (Middleton, 2001). As in *Confuciusornis* (Peters, 1996; Chiappe *et al*., 1999), the articulation of the first toe is ball-like and medially protruding. Mayr *et al*. (2005) detailed that the hallux is also medially directed in the Solnhofen and Berlin specimens, in which the first toe is preserved/visible on one foot only. In the Solnhofen specimen, the metatarsals are seen from their plantar side and the proximal phalanx of the first toe from its medioplantar side; in the Berlin specimen, much of the dorsal aspect of the first toe is visible, whereas the metatarsus is seen from its medial side. In both cases, the respective aspect of the first toe would not be visible if it was fully reversed. The feet of the London and Eichstätt specimens are preserved in lateral or medial view, and the impression of a reversed first toe in these specimens may thus be an artefact of preservation, with the medially spread toe being brought level with the sedimentation layer via compaction (Mayr *et al*., 2005).

The trochlea of the proximal phalanx of the second toe is proximodorsally expanded (Fig. 13), indicating that the toe was hyperextendible, as in dromaeosaurs, troodontids, and the basal avian *Rahonavis* (Mayr *et al*., 2005). According to current phylogenies (e.g. Gauthier, 1986; Sereno, 1999; Hwang *et al*., 2002; Xu *et al*., 2002; Benton, 2004), this feature must be regarded as a synapomorphy of Paraves, i.e. a clade (Troodontidae + Dromaeosauridae + Aves) that is lost in birds more derived than *Archaeopteryx* and *Raho-*

navis. Just proximal to the expanded trochlea there is a marked depression on the dorsal surface of the proximal phalanx of the second toe. Such a depression is also present on the distal end of the proximal phalanx of the third toe which lacks, however, a dorsally protruding articulation. The depressions of the insertion area of the collateral ligaments are marked. The flexor tubercles of the ungual pedal phalanges are weak. The fourth toe consists of five phalanges, but there are only four in the Solnhofen specimen. The keratinous sheaths of the ungual phalanges of the second and fourth digits of the left foot are well preserved.

Feathers: The specimen exhibits well-preserved wing and tail feather impressions. Impressions of the barbs are best visible in the distal portion of the primaries; barbules cannot be discerned. On the right wing, the rachises of 11 primaries can be counted (Fig. 3). The most distal (11th) primary is the shortest, the fourth the longest. The approximate lengths of the primaries are as follows (in mm; the minimum lengths of some primaries of the Berlin specimen, from Rietschel, 1985, are given in parentheses): 118 (first; 130), 123 (second), 125 (third; 135), 133 (fourth), 129 (fifth; 145), 125 (sixth), 120 (seventh; 140), 117 (eighth), 106 (ninth; 125), and 87 (tenth; 95). The length of the 11th primary cannot be measured, but appears to have been at least 47 mm (some barbs are preserved in that area). Three primaries insert on the second phalanx of the second digit, two on the first, and the remaining six on the metacarpal (Fig. 3). The same insertion pattern was inferred by Rietschel (1985) for the Berlin specimen. The distalmost primary apparently inserts in the midsection of the second phalanx, which indicates that the ungual phalanx of the second digit was not covered by feathers and was therefore functional. At least the eighth to tenth primaries have an asymmetric vane.

In the Berlin and London specimens, the odd-numbered rachises are only preserved as 'shaft shadows' without impressions of the vanes (Rietschel, 1985; Elżanowski, 2002). This led some previous workers to assume that the primaries of *Archaeopteryx* were arranged in two different levels (Elżanowski, 2002). However, in the new specimen, a distinction between shafts and shadow shafts cannot be made, and at least the four most distal primaries (eighth to 11th) exhibit true shaft impressions.

The exact number of secondaries cannot be counted, but may have been about 12–15 as assumed for the Berlin specimen (Stephan, 1987).

Many rachises exhibit a furrow along their midline which, by comparison with modern birds, indicates that, as in the Berlin specimen (Heinroth, 1923), their ventral surfaces are exposed, whereas, as noted above, the forearm skeleton is seen from its dorsal side (see

Helms, 1982 for an explanation of this kind of preservation). Curiously, however, in the distal part of the right wing, the outer vanes overlap the inner ones of the distally adjacent feathers, as is characteristic of the dorsal aspect of a modern birds' wing. Especially in the proximal area of the secondaries of the left wing, marked furrows can be discerned, which measure up to 50 mm and run obliquely to the longitudinal axis of the secondaries, at an angle of about 30°. We assume that these are impressions of the coverts, by comparison with modern birds probably the lower ones which run more obliquely than the dorsal coverts. It thus appears likely that impressions of the ventral surfaces of the wings are preserved.

Although the impressions of the primaries are rather faint, there are marked, fuzzy furrows at the 'elbow joint' which may stem from the tertiaries. Similar furrows of uncertain identity can also be found next to the proximal end of the right humerus and below the left tibia.

The number of preserved tail feathers cannot be counted, as both the rachises and the feather margins left an impression in the sediment. Again, impressions of barbs are visible, although they are fainter than those in the wings. All tail feathers meet the vertebrae at the same angle of about 30°. The length of those inserting on the 11th and 12th caudal vertebrae is about 65 mm, whereas the feather attaching to the 14th vertebra measures about 75 mm. The impressions of the feathers attached to the proximal seven tail vertebrae are more irregular than the feathers attached to more distal vertebrae.

Impressions of hindlimb feathers cannot be discerned (see Christiansen & Bonde, 2004 for their presumed presence in the Berlin specimen).

DISCUSSION

TAXONOMIC ASSIGNMENT OF THE NEW SPECIMEN

In size and morphology, the new specimen most closely resembles the Munich and Berlin specimens (see Table 1). However, the taxonomy of the Archaeopterygidae is still very controversial, which makes it difficult to assign the new specimen to a particular species without a taxonomic revision of the known specimens, which is beyond the scope of this study.

As noted in the 'Introduction' section, Elżanowski (2002) recognized four species and two genera within the Archaeopterygidae. Other authors, however, considered only a single species, *A. lithographica*, to be valid, with the differences in size and morphology between specimens due to differences in age and/or sex (e.g. de Beer, 1954; Wellnhofer, 1974, 1992; Ostrom, 1976; Houck, Gauthier & Strauss, 1990). Wellnhofer (1993) and Wellnhofer & Röper (2005)

assumed that there are two species, *A. lithographica* and *A. bavarica*.

Based on the amended data of Houck *et al*. (1990), Senter & Robins (2003) performed 'major-axis regressions' to evaluate the taxonomic status of known archaeopterygid specimens. Because of morphological differences, the latter authors accepted the validity of *Wellnhoferia grandis*, which they excluded from their analysis. They concluded that all other archaeopterygid specimens belong to a single species, *A. lithographica*. Their approach is, however, countered by the fact that Houck *et al*. (1990) assigned *W. grandis* to *A. lithographica* using the same method ('major-axis regressions'). If one accepts the validity of *W. grandis*, as assumed by Senter & Robins (2003), one must conclude that similar proportions do not disprove the taxonomic distinctness of archaeopterygid specimens.

The Berlin specimen (the type of *A. siemensii*) is distinctly smaller than the London specimen (the type of *A. lithographica*) (Table 1). Although Senter & Robins (2003) dismissed morphological differences as not present, we concur with Elżanowski (2002) that the flexor tubercles of the pedal ungual phalanges are much less developed than those of the London specimen.

The Munich specimen closely resembles the Berlin specimen in size and morphology, and we consider it likely that both specimens are conspecific. The main reason for erection of the species *A. bavarica* for this specimen was the presence of an ossified sternum (Wellnhofer, 1993). However, Wellnhofer & Tischlinger (2004) recently showed that the alleged sternum of the Munich specimen is part of the coracoid. In limb proportions, which were listed as further evidence distinguishing *A. bavarica* from *A. siemensii* (Wellnhofer, 1993), the Thermopolis specimen is intermediate between *A. bavarica* and *A. siemensii* (the humerus/ ulna ratio of the new specimen is 1.12 as in *A. siemensii* vs. 1.04 in *A. bavarica*; the femur/tibia ratio, however, is 0.67 vs. 0.74 in *A. siemensii* and 0.65 in *A. bavarica*).

We agree with Elżanowski (2001b) that the Solnhofen specimen, the holotype of *W. grandis* Elżanowski, 2001b, represents a different species from the Munich and Berlin specimens. The question is whether it is also different from the London specimen, the holotype (or proposed neotype, see Bühler & Bock, 2002) of *A. lithographica*. The main diagnostic characters of *Wellnhoferia*, given by Elżanowski (2001b, 2002), are as follows: fourth pedal digit with only four phalanges and with the ungual being the longest phalanx; first manual digit with ungual approximately one-third the length of the basal phalanx; first and second phalanges of the third manual digit fused (only listed by Elżanowski, 2002); second

metatarsal tapered proximally (only listed by Elżanowski, 2002); pedal claws with well-developed flexor tubercles; and the tail being shorter than other specimens (not listed by Elżanowski, 2002). The number of phalanges in the fourth toe is unknown for the London specimen and the similar-sized Haarlem and Maxberg specimens, although de Beer (1954) assumed that there were only four phalanges in the London specimen. This hypothesis was considered as speculative by Wellnhofer (1992) and Elżanowski (2001b), but the same must apply for the opposite assumption that there are five phalanges. Also, the relative proportions of the phalangeal length of the first manual digit cannot be compared with the London specimen, in which the first digit of the manus is not preserved (de Beer, 1954). The same applies to the proportions of the third manual digit. The number of tail vertebrae of the Solnhofen specimen can only be estimated, as the tip of its tail is not preserved (Wellnhofer, 1992; Elżanowski, 2001b). The Solnhofen and London specimens not only agree in size (Table 1) and limb proportions (Houck *et al*., 1990), they also share a constriction in the middle of the crown of the premaxillary teeth (Wellnhofer, 1992), the presence of well-developed flexor tubercles on the pedal ungual phalanges (poorly developed in the Berlin and Munich specimens), and have a proportionally stouter metatarsus (see above). We thus conclude that it has not been convincingly shown that the Solnhofen and London specimens are not conspecific.

We thus consider at least two species of the Archaeopterygidae to be valid, *A. lithographica* and *A. siemensii*, and assign the Thermopolis specimen to the latter. The new specimen provides additional evidence for the distinctness of *A. siemensii*, in that the shape of its ischium (this bone is less well preserved in the Berlin specimen) is very different from that of *A. lithographica* (Fig. 11).

PALAEOBIOLOGICAL IMPLICATIONS

The tooth morphology of *Archaeopteryx* is consistent with it primarily having fed on insects and other invertebrates (Elżanowski, 2002), and the taxon thus had a different diet than similar sized deinonychosaurs, which have much larger, serrated teeth and probably preyed mainly on small vertebrates (Makovicky & Norell, 2004; Norell & Makovicky, 2004). The hyperextendible second toe of at least the large dromaeosaurs is generally considered to be a killing device (Norell & Makovicky, 2004). However, as its ungual phalanx is not hypertrophied in *Archaeopteryx*, and because of the presumed insectivorous diet of this taxon, it appears unlikely that the second toe could be hyperextended for the same purpose in the 'urvogel'.

We concur with Elżanowski (2002) that *Archaeopteryx* spent most of its time on the ground. Our observation that the first toe was not fully reversed but medially spread (Mayr *et al*., 2005) indicates that the 'urvogel' did not have a perching foot and was not adapted to an arboreal way of living as many modern birds. The fact that the first toe of *Archaeopteryx* was spread medially, and not directing forwards as the other three toes, by itself indicates that the foot already had some grasping function, either to assist perching or to manipulate food.

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