

Bipedal browsing adaptations of the unusual Late Eocene–earliest Oligocene tylopod *Anoplotherium* (Artiodactyla, Mammalia)

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The first well-preserved, partial associated skeleton of *Anoplotherium latipes*, with critical details of tibia, femur, ulna and cervical vertebrae, is described from the UK earliest Oligocene. *Anoplotherium* and related genera are interpreted as facultatively bipedal, extended-limb, high browsers, based especially on the following: pelvis with flared ilia and long pubic symphysis; medially bowed tibiae shorter than femora; trunk vertebrae enlarging caudally; extensive attachment for supraspinous and deltoid muscles for raising the forelimbs; long muscular tail for balance; and large hind foot processes for attachment of suspensory ligaments. Although overall most like extinct ground sloths among bipedal browsers, *Anoplotherium* is unique in combining long muscular tail, hooves instead of claws and relatively short forelimbs. Primitive retention of the long tail facilitated an erect stance without need for the long, clawed forelimb support evolved by chalicotheres. Emphasis was instead on strengthening support by the hind-quarters. With only toe-number differences, *A. latipes* and *A. commune* may have been sexual dimorphs. The large *Anoplotherium* species would have been able to browse 2–3 m above the ground with no competition from other contemporaneous European terrestrial mammals. Bipedal browsing is an adaptation previously unrecognized in European Eocene communities. © 2007 Natural History Museum. Journal compilation © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, **151**, 609–659.

ADDITIONAL KEYWORDS: bipedality – Bouldnor Formation – Hampshire Basin – Hamstead Member – high-browser – Montmartre – palaeoecology – sexual dimorphism – UK.

INTRODUCTION

The genus *Anoplotherium* was named by Cuvier in 1804 (Cuvier, 1804b). It was only the fifth fossil mammal genus to be named, being preceded by *Palaeotherium* Cuvier, 1804a (earlier the same year), *Mammut* Blumenbach, 1799, *Megalonix* Jefferson, 1799 and *Megatherium* Cuvier, 1796. It was described from most of the skeleton by Cuvier (1804b, c, 1805, 1807a, b, c, d, 1808, 1812, 1822, 1825) through study of partially articulated remains and two incomplete skeletons, all from the latest Eocene Gypse (Première Masse) of Montmartre and other localities in the outskirts of Paris. Although relatively well known osteologically for 200 years, the possible lifestyles of *Anoplotherium* and of its close relative *Diplobune*

have been shown to be largely anecdotal or speculative (Dor, 1938). A more recent study of *Anoplotherium* (Abusch-Siewert, 1989) was largely limited to the question of presence or absence of manual digit II in the type species, *A. commune* Cuvier, 1804c, from Montmartre.

A feature of the material from Montmartre is that most of the bones are partially embedded in blocks of gypsum, which makes manipulation of bones in their original articulatory positions difficult or impossible. Many are also incomplete. Specimens were recovered subsequently at other sites, e.g. La Débruge (de Bonis, 1964) and Mormoiron (Roman, 1922) in southern France and Mähringen in southern Germany (Dietrich, 1936), although most consist of isolated bones, whilst compressional diagenesis of the La Débruge specimens is an additional problem (Gervais, 1859).

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Table 1. Measurements (mm) of teeth of the Ham 3 *Anoplotherium latipes*

Tooth	Length (mesiodistal)	Width (buccolingual)	
		Trigonid	Talonid
RI ¹	11.7	8.4	
RP ¹	18.0	10.5	
RP ²	19.3	13.5	
RP ³	20.7	16.6	
RM ¹	26.8	27.5	
LP ³	19.5	16.4	
LP ⁴	18.3	23.2	
RP ₂	22.0	11.3	
RP ₃	22.6	13.1	
RP ₄	22.6	16.6	
RM ₁	23.6	17.5	18.3
RM ₃	–	19.9	–

The relatively recent discovery by a succession of amateur palaeontologists of bones of *Anoplotherium latipes*, judged to belong to one individual, in an uncrushed state, largely free of adherent matrix, and representing much of the skeleton, in the earliest Oligocene log bed, lower Hamstead Member (mammal level Ham 3: Hooker, in press), Bouldnor Formation of the Isle of Wight (Figs 1A–D, 2–9, 11–13, 14K, 15–23, 27), provides an unrivalled opportunity to investigate functional anatomy in the genus and to test previous ideas of life style. It forms the mainstay of this study. The species identification is based on the presence of a second digit (Figs 1E–G, 15G, J, P, 21A, B, D, F) and large size judged especially from the teeth (Table 1, Fig. 2). The evidence that the bones belong to a single individual are as follows: there is no repetition of elements; left and right elements are near identical mirror-images of one another; and of those found, all anatomically adjacent bones articulate precisely. The bones reside mainly in the SMNS and the Dinosaur Isle Museum, Sandown, Isle of Wight, with an additional associated bone in the BMNH.

Four species names are currently applied within the genus *Anoplotherium*: *A. commune* Cuvier, 1804c, *A. latipes* (Gervais, 1852), *A. laurillardii* Pomel, 1851 and *A. pompeckji* Dietrich, 1922. *A. commune* and *A. latipes* are of identical size and differ from *A. laurillardii* and *A. pompeckji* by being larger. *A. commune* differs from *A. latipes* by lacking digit II on fore and hind feet, which is present also in both the other species. *A. pompeckji* differs from *A. laurillardii* only in different proportions, not in size, and this is the species least well characterized. All four species are clearly very closely related and it seems that even *A. latipes* and *A. commune* are morphologically and

dimensionally identical except for their feet. Questions of species distinctions are beyond the scope of this paper, although some issues of possible synonymy between *A. latipes* and *A. commune* are discussed below. Comparisons between the new *A. latipes* skeleton and the Montmartre *A. commune* material are in any case critical to understanding the functional anatomy of the genus. The resultant *A. latipes* reconstruction relies to an extent on bones known only in *A. commune*.

Anatomical abbreviations

acf, acetabular fossa; acn, acetabular notch; alar f, alar foramen; anp, anconal process; ap, acromion process; asp, anterior edge of neural spine; astf, astragalar facet; axis facet, facet for right main anterior facet of axis; bg, bicipital groove; bp, blunt process; bt, bicipital tuberosity; c, surface of centrum from which epiphysis has detached; cap, capitulum; capf, capitular facet; c art, central articulation; cb, coracoid border; ce, capitular eminence; cerv1, lateral exit of the first cervical nerve; cf, cuneiform facet; chf, facet for chevron bone; con, condyle; conf, condylar facet; cp, coracoid process; dc, deltoid crest; dens facet, facet for dens process of axis; ect, ectal facet; ectf, ectocuneiform facet; entf, entocuneiform facet; fa, fossa atlantis; ftl, fovea for teres ligament; gb, glenoid border; gt, greater tuberosity; gtr, greater trochanter; h, head; h  c, h  cker; ilc, iliac crest; isf, infraspinous fossa; latc, lateral condyle; lnf, lunar facet; lrf, lateral radial facet; lt, lesser tuberosity; ltr, lesser trochanter; map, metapophysis; m/cII, facets for metacarpal II; m/cIII, facets for metacarpal III; m/cIV, facets for metacarpal IV; m/tII, facets for metatarsal II; m/tIII, facets for metatarsal III; medc, medial condyle; mesf, mesocuneiform facet; mgf, magnum facet; mm, medial malleolus; mrf, medial radial facet; ob, margin of obturator foramen; oc facet, facet for right occipital condyle; of, olecranon fossa; patt, patellar trochlea; pcepi, posterior central epiphysis; ppc, posterior process of cuboid; ppm/tIII, posterior process of metatarsal III; ppm/tIV, posterior process of metatarsal IV; ppn, posterior process of navicular; pozyg, postzygapophysis; prezyg, prezygapophysis; profree, anterior part of cuneiform facet of unciform out of contact with cuneiform during pronation; pubs, pubic symphysis; raf, radial facet; rc, facet for rib capitulum; rdm, ridge demarcating m. subscapularis distally and m. levator scapulae and m. serratus ventralis proximally; rna, broken surface of right neural arch; rt, facet for rib tubercle; sac, attachment area for sacrum; scf, scaphoid facet; sgt, supraglenoid tubercle; sp, neural spine; spf, spinal fold; spp, spinous process; ssf, supraspinous fossa; ssp, scapular spine; stp, styloid process; supfree, posterior part of cuneiform facet of unciform out of contact with cuneiform during

supination; sus, sustentacular facet; tdrf, tubercle and depression for origin of m. rectus femoris; tibf, tibial facet; tp, transverse process; trf, trapezoid facet; trfo, trochanteric fossa; tro, trochlea; trof, trochlear facet; tub, tubercle; uf, ulnar facet; unf, unciform facet; vac, vertebrarterial canal.

Institutional abbreviations

BMNH, Natural History Museum, London; IWCMS, Isle of Wight County Museum Service (Dinosaur Isle Museum); MNHN, Muséum National d'Histoire Naturelle, Paris; SMNS, Staatliches Museum für Naturkunde, Stuttgart.

COLLECTION OF THE SPECIMEN AND ASPECTS OF TAPHONOMY

The Ham 3 skeleton has been collected over a remarkable timespan of about 35 years, as the cliff line at Bouldnor has receded. The first finds were made in 1967 and the last in 2002, nearly all by amateur palaeontologists. The earliest material was collected by Richard Ford and sold along with the rest of his pre 1985 collection to the SMNS. This included the left scapula, left humerus, proximal left ulna and a second phalanx, which were stated to have been 'lying together in an articulated position' (Ford, 1972). Their good preservation of delicate structures suggests that they were found in the foreshore exposures. Two years later, he found the posterior caudal vertebra on the beach nearby. In 1981, a left unciform was collected by David Ward and presented to the BMNH. Its association with the rest of the skeleton was uncertain until it was found to articulate perfectly with a proximal left M/T IV in the SMNS collections. Mike Smith visited the site regularly from 1993 until 1999, when his collection was sold to the IWCMS. He was able to collect at a time when the main bulk of the skeleton was eroding out and some bones were found in articulation or partial articulation *in situ*. The bones are relatively fragile and quickly become broken and eroded once they have found their way onto the flint shingle beach. Therefore, the quality of Mike Smith's collection, which forms the main bulk of the skeleton, is testimony to his dedication to the fieldwork. Despite this, some important elements have never turned up (e.g. the astragali) or are extremely fragmentary (e.g. the skull, which apart from a good selection of teeth consists only of small fragments of the frontal, palate, dentary and occiput). Mike Smith kept a record of where his *in situ* finds were made and drew sketch maps indicating cliff and foreshore occurrences. In 2000, Denver Fowler found the right M/T II on the beach. Near the end of the same year, John Quayle found both tibiae as they were emerging from the cliff.

He also saw the end of the right femur protruding from the cliff nearby and he and the author excavated it and recorded its orientation. The same day Victoria Quayle found fragments of both distal fibulae on the beach. Subsequently, John Quayle found part of the shaft of the left femur and in March 2002, the author found more of the same shaft. All this material is in the IWCMS.

From the author's experience of the femur in the cliff and on-site discussion with Mike Smith it is possible to estimate that the skeleton was scattered *in situ* over a distance of at least 10 m. It was largely disarticulated although not widely scattered. Some parts of the anatomy retained their articulation, whilst other parts, although separated, retained a position close to that of the original anatomy. Thus, the right metacarpals III and IV were found lying side by side with a first phalanx and the right ulna nearby. The two tibiae were lying nearly parallel, distal ends to the north (right) or north-west (left) (W. J. Quayle, pers. comm.); the right femur nearby was orientated with its proximal end pointing north-east. One of the proximal fibular epiphyses was found lying beneath the right femur, and the other lay nearby.

The log bed (= mammal level Ham 3) is a muddy sand up to c. 1 m thick, with drifts of plant debris, including seeds, and freshwater molluscs, often cemented with pyrite, plus scattered large logs up to 5 m long (Hooker, Collinson & Sille, 2004). It shows some cross-bedding and may have originally filled depressions in the underlying blue clays on which it has a sharp contact. Interpretation of its original sedimentary history, however, is complicated by post-depositional dewatering processes, which have caused ball and pillow structures, disrupting the bedding. The bed is truncated above by a disconformity at the base of the Nematura Bed, from the base of which descend burrow fills. In the foreshore, the strata are largely unweathered, but in the cliff, the log bed becomes weathered through leaching out of the clay component. Decomposition of pyrite has here resulted in dissolution of the molluscs and precipitation of gypsum crystals. Bone preservation in the unweathered foreshore exposures is therefore better than in the cliff.

The nature and degree of the disarticulation gives some clues to depositional rate in the log bed. The skeleton belongs to an immature animal as evidenced by loose or detached epiphyses, although M₃ and all permanent premolars are fully erupted (Fig. 2). Several bones have lost their epiphyses (distal left femur, proximal right ulna, several vertebrae) or exist as isolated epiphyses (distal right radius, proximal humerus, proximal fibulae, several vertebrae), whereas other bones still retain epiphyses, although still incompletely fused or unfused (proximal left ulna, distal right femur, proximal tibiae). The medial

condyle of the distal epiphysis of the right femur was displaced slightly, then cemented to the shaft probably at an early diagenetic stage. This evidence, together with the distribution of the bones, suggests that a partially decomposed carcass was transported by fluvial currents to the site of deposition. As decomposition continued, currents gently disarticulated the skeleton and some of the loose epiphyses. This process was aided by some scavenging (see below). Burial then

intervened to prevent complete disarticulation and therefore preceded total decomposition of the cartilaginous epiphyseal attachments.

Apart from the recent weathering effects on bones collected in the cliff, the bones are well preserved. There are nevertheless a few signs of scavenging. These take the form of circular puncture marks 6–7 mm in diameter and are attributable to tooth activity. One of the puncture marks is on the dorsal surface

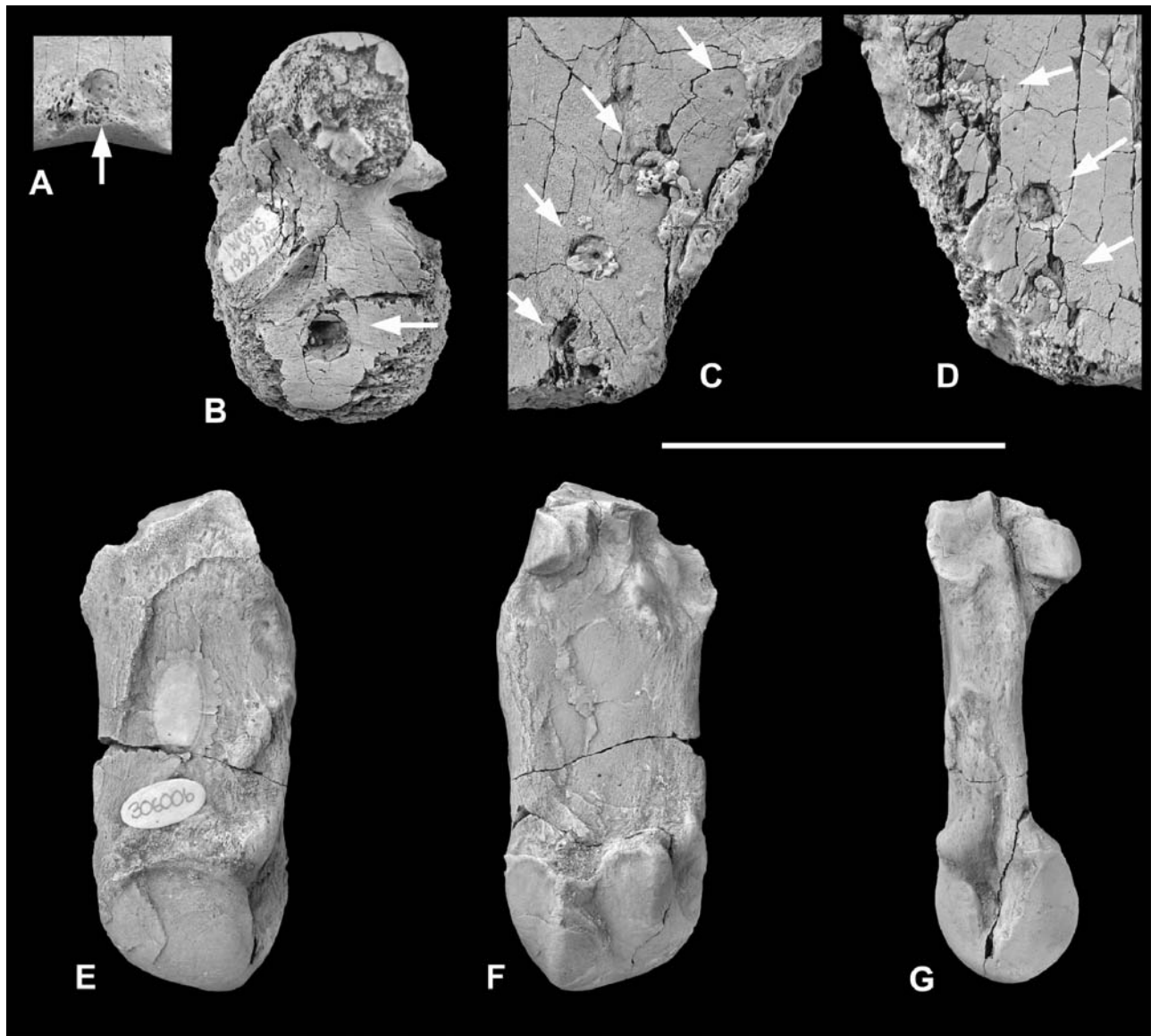


Figure 1. *Anoplotherium latipes*. A–D, Ham 3 skeleton, log bed, lower Hamstead Member, Bouldnor Formation, Bouldnor, Isle of Wight, UK (IWCMS. 1999.128). Bones showing tooth puncture marks, indicated by arrows. A, manual right first phalanx IV, distal end in dorsal view. B, anterior thoracic vertebra (?) in left lateral view. C and D, mediodistal portion of left ischium in dorsal (C) and ventral (D) views. E–G, lectotype left metatarsal II, Late Eocene lignites, La Débruge, Vaucluse, France (BMNH.30600b) in anterior (E), posterior (F) and lateral (G) views. Coated with ammonium chloride. Scale bar = 50 mm.

of the first manual phalanx IV near the distal end (Figs 1A, 15L). The absence of a similar mark on the ventral side of the bone (Fig. 15M) suggests that soft parts were still present, which would be much thicker ventrally than dorsally. A second is similar and is on the left side of the centrum of the ?3rd thoracic vertebra (Fig. 1B). It is not known if there had been a similar bite mark on the other side, as the surface is badly eroded, but, because of its location, the bite must have been made after soft-part decomposition was advanced. Also made at a late stage in decomposition is an arcuate series of circular puncture marks on either side of the ischial fragment near a medio-posterior break (Fig. 1C, D). Three on the dorsal side are followed by an incipient fourth, which consists of only a small dent, not puncturing the bone cortex. On the ventral side of the bone are three more punctures, which alternate with and lie just inside the arc of those on the dorsal side. The evenness of spacing, the circular shape, the constant size and the relative positions on each side are indicative of the snout end of the tooth row of a crocodilian. This evidence is further supported by the presence of teeth and scutes of crocodilians in the lower Hamstead Member. Comparison of the size, spacing and curvature of the series of puncture marks with skulls of the crocodilian *Diplocynodon* from the Late Eocene of Hordle, the genus commonly occurring in the Solent Group, suggests that the scavenger had a skull length of c. 400–500 mm. Little flesh can have remained on the ischium at the time of the bite and the scavenging must have been discontinued soon after. From the similarity in size and shape, it is probable that the two isolated puncture marks were made by crocodilians too. It seems likely overall therefore that decomposition took place in a subaqueous environment. Most bone breakage seems to have happened after modern erosion from the sediments.

Skeletonization of carcasses of animals the size of *Anoplotherium latipes* in water will take longer than in air as most insects will be denied access (Lyman, 1994). Nevertheless, it can take place as rapidly as 3 months (Weigelt, 1989: 8–9), varying with temperature (Lyman, 1994: 141). An average freshwater summer temperature for the lower Hamstead Member has been calculated to be 31 °C (Grimes *et al.*, 2005), much warmer than at the same latitude today. The cartilaginous joints holding together the epiphyses will take longer to decompose, although this is likely to be less than a year (P. Andrews, pers. comm., 2005). The presence of examples of nearly all the skeletal elements, which completely span all Voorhies's (1969) settling groups, indicates minimal transport after decomposition of the flesh. It is difficult to imagine the processes leading to minimal disarticulation of the Ham 3 skeleton taking more than 1 year, indicating rapid deposi-

tion of the log bed. This is an important conclusion as the log bed is terminated by a major sequence boundary, marking the sea-level fall at the onset of the Oi-1 glaciation (Hooker *et al.*, 2004). It is the only dominantly sandy bed in a mud sequence where the depositional rate was otherwise much lower (52 years cm⁻¹ for at least a part of the Bembridge Marls Member – Collinson, 1983; Hooker *et al.*, 2004).

SYSTEMATICS

ORDER ARTIODACTYLA OWEN, 1848

SUBORDER TYLOPODA ILLIGER, 1811

FAMILY ANOPLOTHERIIDAE BONAPARTE, 1850

GENUS ANOPLOTHERIUM CUVIER, 1804B

ANOPLOTHERIUM LATIPES (GERVAIS, 1852)

vp1972 *Ronzotherium*; Ford, pl. 2, fig. B–C, pls 3–4.

Types: Gervais (1852: plate explanation 36, pp. 1–2) quoted Gervais (1850) for the origin of the name *Eurytherium latipes* and this is the date usually quoted for the species. However, the name is not mentioned in this reference. The name must therefore date from Gervais (1852: plate explanation 36, pp. 1–2). This raises a problem of priority as Pomel (1851) named *Anoplotherium platypus* for what Gervais regarded as his *E. latipes*. However, Pomel's type description of *A. platypus* only stated that it was a three-toed species the same size as *A. commune*, but without figuring or mentioning any specimens. It could therefore be confused with *A. laurillardii*, which occurs at the same site and is only slightly smaller than *A. commune*. For this reason, *A. platypus* Pomel, 1851 is best regarded as a *nomen dubium* and should not take priority over *Eurytherium latipes* Gervais, 1852. Gervais (1852: plate explanation 36, pp. 1–3, unnumbered figure and pl. 15, fig. 10, pl. 36, fig. 1) characterized the species more clearly. In the BMNH, where much of Bravard's collection is located, the subject of Gervais (1852: pl. 15, fig. 10), a 'right' metatarsal II, can be tentatively identified as belonging to the left composite foot numbered BMNH.30600c, accepting reversal of the figure. Breakage and distortion of an individual nature are the basis for its recognition. Unfortunately, the distal half of this specimen has been restored in plaster. Another M/T II, the subject of Gervais's (1852) pl. 36, figs 2–4, has not been located in the Bravard Collection in the BMNH. Of Gervais's (1852, pl. expl. 36, p. 3) three figures of reconstructed feet, the left figure (see also Gervais, 1859: 168, fig. 17) is of a relatively small manus with slightly waisted metacarpals and has been identified as *Diplobune secundaria* by de Bonis (1964: 20–22). The specimen appears to be BMNH.30600d, although the figure would have to have been reversed and some phalanges added to the mount. The central figure of a larger

manus appears to represent *Anoplotherium* (see also Gervais, 1859: 168, fig. 18). The outlines of some of the bones resemble BMNH.30600a (M/C III is plaster), which according to size consists entirely of *A. laurillardii*. The right-hand figure (see also Gervais, 1859: 168, fig. 19) closely resembles a left composite pes (BMNH.30600b), which would have to have been reversed to a right in the illustration. de Bonis (1964: 19) suggested that most of the bones of this pes belong to *A. laurillardii*, except some of the tarsals, which he thought were closer to *A. latipes*. In fact, apart from the calcaneum and astragalus, all the bones match *A. latipes* for size, including the critical M/T II. M/T II and III are larger than these bones of *A. laurillardii* figured by de Bonis (1964: pl. 3, fig. 3). All these specimens constitute the syntypes. The syntype series must exclude the astragalus and calcaneum, the subjects of Gervais's (1852) pl. 36, figs 4–5, as doubt is expressed as to their identification in his text, although not in the identification on the plate itself. The type locality is La Débruge, Vaucluse, France, and the type horizon comprises unnamed lignites of middle Priabonian (Late Eocene) age (Mammalian Reference Level MP18). The fact that one of Gervais' figures represents a different genus (*Diplobune*), whilst others are composites of two different species of *Anoplotherium*, makes it important to select a lectotype. Accordingly, the left M/T II (BMNH.30600b), part of the composite foot figured by Gervais (1852: pl. expl. 36, p. 3, right figure) is selected here as lectotype of *Anoplotherium latipes* (Gervais, 1852) (Fig. 1E–G). The genus *Eurytherium* was synonymized with *Anoplotherium* by Schlosser (1883b: 153–154), an action followed by nearly all subsequent authors.

Material

Specimen 1: Incomplete skeleton of immature animal from the log bed, top of the lower Hamstead Member (earliest Oligocene), Bouldnor, Isle of Wight, UK (Hooker *et al.*, 2004). This bed is referred to mammal level Ham 3 by Hooker (in press). The skeleton comprises the following elements (museum repositories and numbers are appended, as is a published citation).

Fragmentary right dentary in two pieces, with P₂–M₁ and M₃ trigonid (IWCMS. 1999.128);
right I¹, P¹, P², P³, M¹, left P³, P⁴ (IWCMS. 1999.128);
fragments of palate (IWCMS. 1999.128);
fragment of frontal (IWCMS. 1999.128);
fragment of supraoccipital region (IWCMS. 1999.128);
fragment of atlas (IWCMS. 1999.128);
cervical vertebrae 4 and 7 (IWCMS. 1999.128);
thoracic vertebra 1, with separated posterior epiphysis, embedded in pyrite block (IWCMS. 1999.128);
thoracic vertebrae 3?, 4?, 6?, 7?, 11? and 12? (IWCMS. 1999.128);

lumbar vertebrae 2? and 4? (IWCMS. 1999.128);
lumbar vertebra 5? or 6?, neural spine with right postzygapophysis (IWCMS. 1999.128);
anterior caudal vertebra (IWCMS. 1999.128);
posterior caudal vertebra (SMNS.42098);
three complete vertebral epiphyses (2 anterior thoracics and one distal anterior caudal) and five fragments (IWCMS. 1999.128);
26 rib fragments, including proximal ends of left 4? and 5? and left and right 8? or 9? (IWCMS. 1999.128);
left scapula (SMNS.42098) (figured Ford, 1972);
right scapula in three pieces (IWCMS. 1999.128);
proximal epiphysis of right humerus (IWCMS. 1999.128);
left humerus lacking proximal end (SMNS.42098) (figured Ford, 1972);
proximal left ulna (SMNS.42098) (figured Ford, 1972);
right ulna lacking distal end (IWCMS. 1999.128);
proximal left radius (SMNS.41960a);
proximal right radius (IWCMS. 1999.128);
distal epiphysis of right radius (IWCMS. 1999.128);
left scaphoid (SMNS.41992);
left unciform (BMNH.M42661);
left metacarpal II (SMNS.42098);
distal left metacarpal III (SMNS.42098) (figured Ford, 1972);
distal left metacarpal IV (IWCMS. 1999.128);
proximal left metacarpal IV (SMNS.42066a);
right metacarpal III (IWCMS. 1999.128);
right metacarpal IV (IWCMS. 1999.128);
manual right first phalanx IV (IWCMS. 1999.128);
manual left or right second phalanx III or IV (SMNS.42098) (figured Ford, 1972);
manual? left or right second phalanx III or IV, parasagittal half (SMNS.42038a);
three fragments of left os innominatum of pelvis including acetabulum (IWCMS. 1999.128);
left femur lacking proximal end and distal epiphysis (IWCMS. 2002.41);
right femur (IWCMS. 1999.128Q);
left tibia (IWCMS. 1999.128Q);
right tibia (IWCMS. 1999.128Q);
proximal epiphysis of left fibula (IWCMS. 1999.128Q);
distal left fibula (IWCMS. 1999.128Q);
proximal epiphysis of right fibula (IWCMS. 1999.128Q);
distal right fibula and fragment of left or right fibular shaft (IWCMS. 1999.128Q);
left calcaneum (IWCMS. 1999.128);
left cuboid (IWCMS. 1999.128);
left ectocuneiform (IWCMS. 1999.128);
right mesocuneiform (IWCMS. 1999.128);
left metatarsal II (IWCMS. 1999.128);
left metatarsal III (IWCMS. 1999.128);
right metatarsal II (IWCMS. 2000.390);
pedal left first phalanx III (IWCMS. 1999.128);

Table 2. Measurements (mm) of vertebrae of the Ham 3 *Anoplotherium latipes*

Bone	Centrum					Zygapophyses			W Trans	Height	
	L	AW	AH	PW	PH	L	AW	PW	Proc	A	P
C4	59	33	23.5	47	34.3	71.5	(77)	91.5	–	69.5	86
C7	46	25.3	28.5	45.3	(26)	52.5	(88)	82.5	(118)	–	–
T1	41.3	–	–	32.5	30	50.4	86	(58.8)	(134)	–	–
T3?	35+	32	29+	–	–	–	(30.5)	–	(104)	–	–
T4?	33+	29	29.5	32	(31)	–	(36)	28	(95)	110+	110+
T6?	35+	(30.5)	(31.5)	–	–	–	(32)	(31.5)	–	–	–
T7?	33+	–	24+	–	–	–	–	–	–	–	–
T11?	46	28.5	–	41	31.5	–	–	–	–	–	–
T12?	46	(39)	(29)	40	31.5	–	(45)	44	–	–	–
L2?	57.5	35.5	36	46	38.3	–	(47)	–	–	91+	91+
L4?	54.5	35.6	36.7	37.4	36.8	–	(45)	–	–	–	–
ECau	50.2	29	30.6	34.7	31	56+	(51.5)	–	–	49.5+	49+
LCau	64	(26.5)	(26.5)	(27.7)	(25.5)	–	–	–	–	29+	26+

A = anterior; H = height; L = length; P = posterior; Trans Proc = transverse processes.

pedal right? first phalanx III? (IWCMS. 1999.128); sesamoid (IWCMS. 1999.128).

Specimen 2: Left humerus lacking distal end, Beckles Collection, Bouldnor Cliff, assumed lower Hamstead Member ('Hempstead') (BMNH.M4450) (Fig. 10).

Specimen 3: Distal right radius and ulna, apparently associated, Hastings Collection, 'N.W. Isle of Wight', probably also lower Hamstead Member, Bouldnor Cliff (BMNH.30029) (Fig. 14A–J).

DESCRIPTION

This description is based mainly on the Ham 3 skeleton, but supplementary specimens also from the Isle of Wight listed above, plus some from Montmartre are added for parts of the anatomy that were previously poorly known. Interpretation of structures has been aided by reference to Sisson & Grossman (1953) and Barone (1999). Bone measurements are given in Tables 2–4.

CERVICAL VERTEBRAE

The Ham 3 skeleton

Atlas: This is a right half fragment, thus much less complete than the two available atlases from Montmartre. However, the latter are both embedded in gypsum, one viewed dorsally (MNHN.GY213) the other ventrally (MNHN.GY214). In contrast, some details within the neural canal are visible on the Ham 3 specimen (Fig. 3A). Anteriorly on the dorsal surface of GY213 from Montmartre, is a pair of large openings, which can be identified as the alar foramina. Anterior breakage of the Ham 3 atlas means that only the pos-

terior edge of the alar foramen is preserved. Its position can be seen relative to the facets for the right occipital condyle, the right main facet for the axis and that for the dens of the axis. The canals are pyrite-filled, but a small foramen mid-way along the inside of the neural canal indicates the position of the lateral exit of the first cervical nerve. The nerve passed anterolaterally to the position of the alar foramen, then turned ventrally to emerge at the ventral alar foramen (Fig. 3B). The ventral opening in the vertebra (fossa atlantis) is large and oval in shape and is shared by the alar foramen and the vertebrarterial canal. The vertebrarterial canal exits posteriorly as illustrated by Cuvier. The pattern is very similar to that of the camelid *Lama*, again as Cuvier recognized.

C4: This vertebra is nearly complete, lacking only part of the left prezygapophysis, the extremities of the transverse processes and the central epiphyses (Fig. 3C–G). It has vertically oblique central articulations, the epiphyses of which were probably kidney-shaped (Fig. 3D–G). The anterior central articulation is particularly oblique, receding posteroventrally and making an angle of c. 50° to a horizontal plane passing through the zygapophyses. There is a prominent ventral keel (Fig. 3F). The lateral walls of the neural arch are perforated by substantial vertebrarterial canals. The length of the neural arch, measured from prezygapophysis to postzygapophysis, is greater than that of the centrum (Table 1). The neural spine is low, tilted posteriorly and bluntly bifurcating at the tip (Fig. 3D, E). In anterior and posterior views, the zygapophysial articulations are tilted laterally at a very low angle. In dorsal view, the width across the postzygapophyses is considerably greater than that across the prezygapo-

Table 3. Measurements (mm) of appendicular bones, except feet, of the Ham 3 *Anoplotherium latipes*

	Left	Right
Rib 3?		
Capitulum to tubercle	44.5	
Rib 4?		
Capitulum to tubercle	(47.6)	
Rib 8/9?		
Capitulum to tubercle	57	57
Scapula		
Length	310	–
Dorso-ventral at coracoid process	86	(81.5)
Mediolateral dimension of glenoid	54	55
Medial glenoid edge to acromion	98.5	–
Humerus		
Length	293+	
Shaft, maximum anteroposterior	85	
Width distal end	91+	
Width proximal edge, distal articulation	60	
Proximodistal diameter of trochlea	61	
Ulna		
Length of olecranon	57	–
Shaft minus epiphyses	–	332
Estimated total length with epiphyses	(355)	(355)
Anteromedial-posterolateral, distal end	–	43
Radius		
Mediolateral, proximal end	59+	60
Anteroposterior, proximal end	37.5+	36.7+
Mediolateral, distal epiphysis	–	70
Anteroposterior, distal epiphysis	–	50.5
Estimated total length with epiphyses	(268)	(268)
Innominate		
Width of ilium	206	
Acetabulum, dorsoventral diameter	62	
Acetabular fossa, dorsoventral diameter	37	
Femur		
Length		399
Proximal width		121+
Distal width		(99)
Lateral condyle, anteroposterior		86.5
Tibia		
Medial length to distal anterior process	305	311?
Anteroposterior, proximal end	86	84
Mediolateral, proximal end	103.5	96.5+
Anteroposterior, distal end, medial side	51.5	49.5
Anteroposterior, distal end, lateral side	42	41.5
Mediolateral, distal end	65	63.5
Fibula		
Anteroposterior, proximal end	35.5+	34.5+
Anteroposterior, distal end	37.5	37
Mediolateral, distal end	22.5	21.5

physes (Fig. 3C). Therefore in any circumaxial view, the vertebra is seen to expand posteriorly. Its identification as C4 is based partly on comparison with the cervical vertebrae from Montmartre and partly on its position in a sequence of posteriorly reducing length (cf. *Cainotherium* – Hürzeler, 1936; pl.3, figs 1, 2). Compared with the *Cainotherium* C4, the neural spine of the Ham 3 C4 is taller and angles posteriorly instead of anteriorly.

C7: This vertebra is also nearly complete, lacking only the distal part of the neural spine, small parts of the anterior and lateral edges of the prezygapophyses, the tip of the left transverse process and the posterior epiphysis (Fig. 3H–L). It is much shorter than the C4, the neural arch being about twice as wide as long in dorsal view (Fig. 3I). Anterior and posterior widths are approximately equal. The neural arch side walls are medio-laterally broad and not perforated by vertebral arterial canals (Fig. 3J, K). The transverse processes are long and slightly recurved, extending laterally without an inferior lamella. The neural arch, measured as in C4, is longer than the centrum (Table 1). The central articulations are slightly oblique (Fig. 3H). What remains of the neural spine is tilted slightly anteriorly and shows little narrowing in lateral view, implying that it was more than twice as long as the part now preserved. The anterior central articulation is rounded heart-shaped. The attachment for the posterior central epiphysis has the shape of a dorsoventrally compressed oval. The overall shape plus the absence of both vertebral arterial canals and of the inferior laminae of the transverse processes allow identification as C7.

Specimens from Montmartre

Cuvier omitted all except the atlas and a representation of the position of C7 in his skeletal reconstruction of *Anoplotherium* (Cuvier, 1825: pl. 62). This was probably partly because of the fragmentary nature of the Montmartre cervicals available to him and partly because he based his reconstruction largely on the skeleton from Antony, where the neck region is not preserved (Cuvier, 1807d). The Bouldnor and isolated Montmartre cervicals complement each other and together provide representatives, albeit fragmentary in the case of C5 and C6, of all seven cervical vertebrae. The Montmartre specimens are therefore described here.

Cuvier (1808: pl. 1) illustrated four cervical vertebrae. These included an atlas embedded ventrally in gypsum (MNHN.GY213 – figs 1–3), an anterior centrum fragment of an axis (MNHN.GY216 – figs 4, 5) and two more posterior cervicals (MNHN.GY221 – fig. 8 and GY194 – fig. 9). Also in the MNHN collections are an atlas embedded dorsally in gypsum (GY214) and an axis bearing most of the neural arch

Table 4. Measurements (mm) of foot bones of the Ham 3 *Anoplotherium latipes*

Bones	A-P proximal (dors-ventr)	Prox-distal length	M-L proximal	M-L distal
L scaphoid	39	26	22	17.7
L unciform	44.5	31	37.5	33.5
L M/C II	27	81.5	21.5	27
L M/C III	—	—	—	41
R M/C III	42	123.4	42.5	43.5
L M/C IV	34.5+	—	38.5	—
R M/C IV	37.2	113	38	42.5
Man phal1,IV	30	45.5	39	34.4
Man phal 2	26.4	39.2	32.5	31.3
Man? phal 2	—	35.3	—	—
L calcaneum	36.5 (tuber)	140	27.5 (tuber)	58.8 (sus)
L cuboid	51.4	33.5	31.6	35
L ectocun.	33.7	16.5	32.5	30.1
R mesocun.	25	14	13.9	13.3
L M/T II	31	80	15	30.5
R M/T II	30.5	80	14.5	31
L M/T III	26.5+	111	37	43
L Ped phal 1	29.6	48.3	38.3	34.5
R Ped phal 1	28+	47.3+	35.6+	31.4+
Sesamoid	17.5 (max.)	28	17.5 (max.)	

A-P = anteroposterior; dors-ventr = dorsoventral; M-L = mediolateral; Prox = proximal.

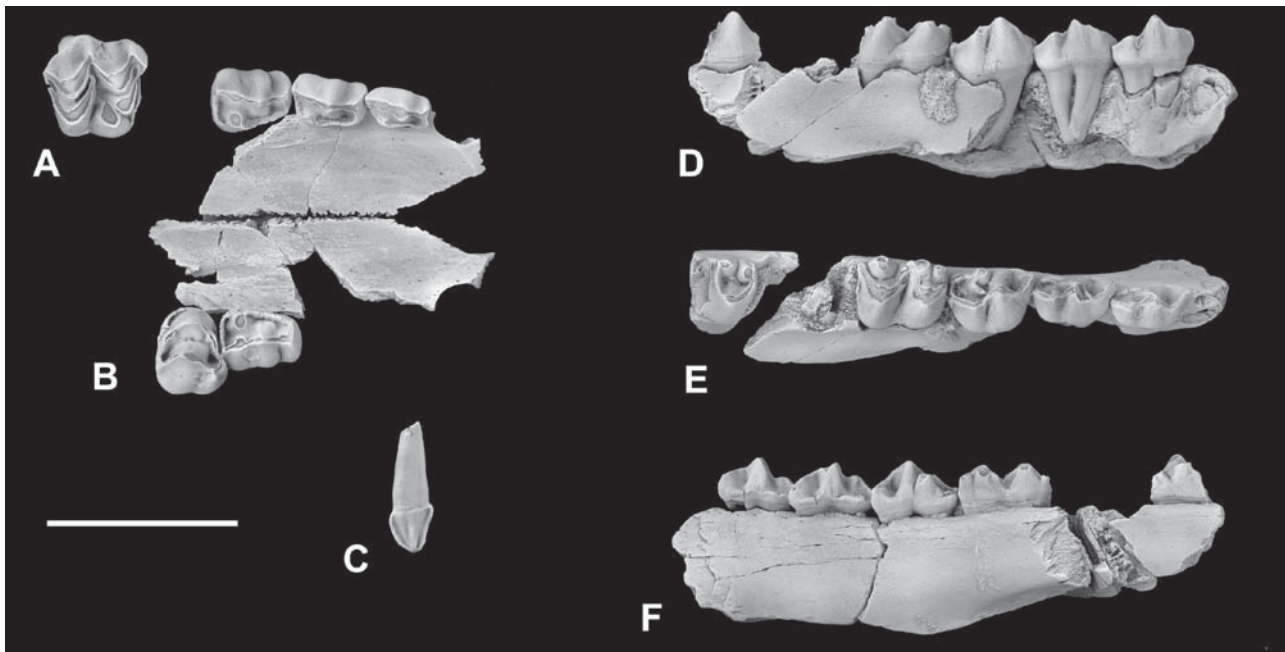


Figure 2. *Anoplotherium latipes*. Ham 3 skeleton, teeth and jaws (IWCMS. 1999.128). A, right M¹. B, anterior part of palate with alveoli for canines, crowns of left P³⁻⁴ and right P¹⁻³. C, right I¹. D–F, right dentary fragment in two parts with P₂₋₄, M₁ and trigonid of M₃. Views are crown (A, B, E), lingual (C, F) and buccal (D). Coated with ammonium chloride. Scale bar = 50 mm.

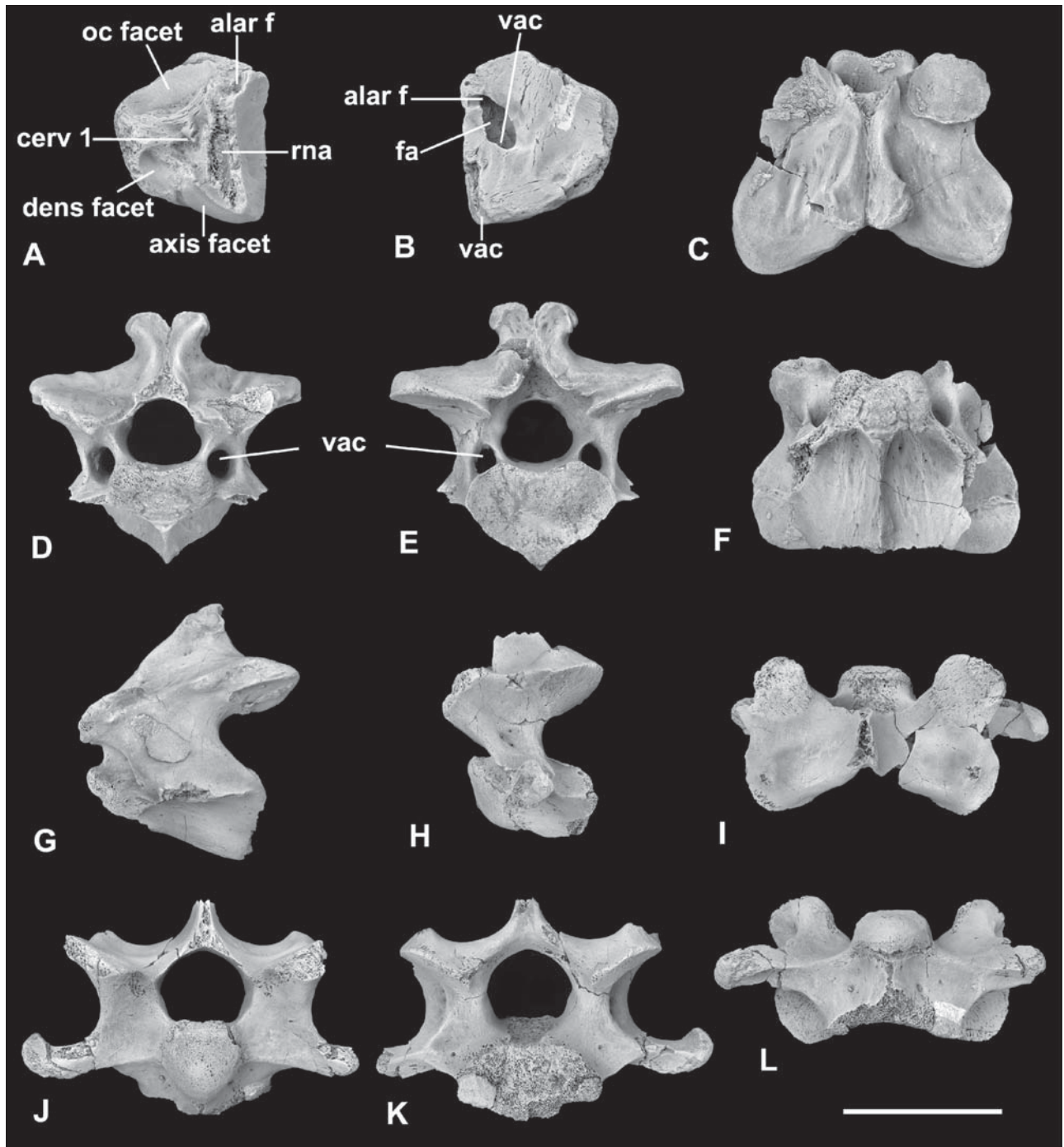


Figure 3. *Anoplotherium latipes*. Ham 3 skeleton, cervical vertebrae (IWCMS. 1999.128). A and B, right half fragment of atlas. C–G, C3. H–L, C7. Views are dorsal (A, C, I), ventral (B, F, L), anterior (D, J), posterior (E, K) and right lateral reversed (G, H). Coated with ammonium chloride. Scale bar = 50 mm.

and anterior centrum (GY215). The main features of the atlases are mentioned above in comparison with the Ham 3 atlas.

The axis GY215 (de Blainville, 1849: pl. 1) has the posterior half of the centrum broken away, but bears

most of the neural arch and spine with the left postzygapophysis and most of the anterior central articulation, including the odontoid process. The vertebra is elongate, being about twice as long as wide. The neural spine tapers anteriorly in lateral view. In

dorsal view the spine flares slightly, posteriorly, but extends no further than the postzygapophysis. It is considerably smaller than the fragmentary axis (GY216) figured by Cuvier (1808: pl. 1, figs 4, 5) and attributed by him to *A. commune*. GY216 consists only of the anterior part of the centrum, but is morphologically very similar to corresponding parts of GY215. The bone surface of GY215 is dense, not porous, so did not belong to a young animal. It is possible that GY215 belongs to the closely related but smaller anoplotheriid *Diplobune secundaria* (Cuvier, 1822), although its size integrates well with the rest of the cervical vertebrae of *Anoplotherium*. Its morphology contrasts with another primitive tylopod, *Cainotherium*, where the spine has a long posterior projection overhanging much of C3 (Hürzeler, 1936).

Cervical GY221 is damaged ventrally, missing the posterior half of the centrum and has its dorsal surface embedded in gypsum. It is crushed dorsoventrally, the centrum having been pushed into the neural canal. It has apparently suffered more damage since being figured by Cuvier. Nevertheless, it is similar in a number of respects to the Bouldnor C4. It differs in being longer, in having the width across the postzygapophyses less relative to that across the prezygapophyses and in having an evenly rounded anterior central articulation that does not recede posteroventrally. The vertebra is the longest in the C3–C7 range and so by analogy with *Cainotherium* (Hürzeler, 1936: pl. 3, fig. 1) is identified as a C3.

It is impossible to judge the length of GY194 as it is embedded anteriorly in gypsum. The position of a dorsal depression on the right side of the neural arch is

similar to that of the Bouldnor C7, suggesting approximately similar length and thus excluding identity with either C3 or C4. GY194 also cannot be C7 because of the much larger distal central articulation that is nearly circular instead of being a depressed oval, because of being narrower across the postzygapophyses, and because it is perforated by vertebrarterial foramina. The posterior part of the left lateral side of GY194 is well preserved, showing the ventral root of the neural arch. The entrance to the vertebrarterial canal is also exposed here and there is no sign of the origin of the large ventrally projecting inferior lamella of the transverse process that characterizes C6. GY194 is therefore identified as C5.

MNHN.GY217 from Montmartre was not figured by Cuvier. It consists only of the neural arch, is partially embedded anteriorly and dorsally in gypsum and the exposed parts have suffered breakage. Nevertheless, the ventral surface of the left side of the neural arch with pre- and postzygapophyses is visible, as are the dorsal surfaces of the left postzygapophysis and the right prezygapophysis. A short portion of neural spine is visible posteriorly. What can be seen of GY217 is quite similar to the Bouldnor C7 in overall length of the arch and angle of the postzygapophyses when viewed posteriorly. It differs in that the neural arch side walls are narrower mediolaterally. The degree of similarity to C7, the only difference being in width of the arch side walls, suggests that GY217 is a C6. The series of seven cervical vertebrae, combining information from the Ham 3 skeleton and specimens from Montmartre, is reconstructed in Figure 4.

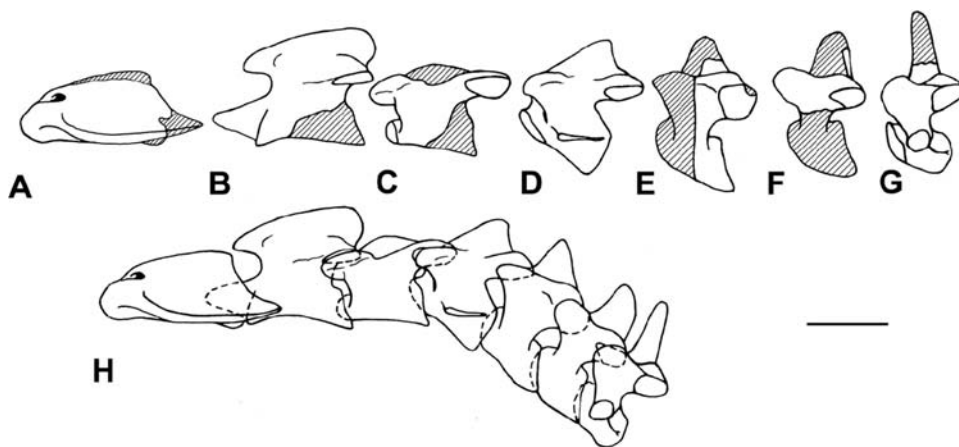


Figure 4. Reconstructed series of cervical vertebrae of *Anoplotherium*, based on Ham 3 *A. latipes* (D, G) and Montmartre *A. commune* (A–C, E, F), in left lateral view. A, Atlas (MNHN.GY213). B, Axis (MNHN.GY215). C, C3 (MNHN.GY221). D, C4 (IWCMS. 1999.128). E, C5 (MNHN.GY194). F, C6? (MNHN.GY217). G, C7 (IWCMS. 1999.128). H, full series of cervical vertebrae articulated in normal pose according to the individual reconstructions in A–G, where restored areas are shown hatched. Transverse processes in C–F have not been reconstructed, for lack of information. Scale bar = 50 mm.

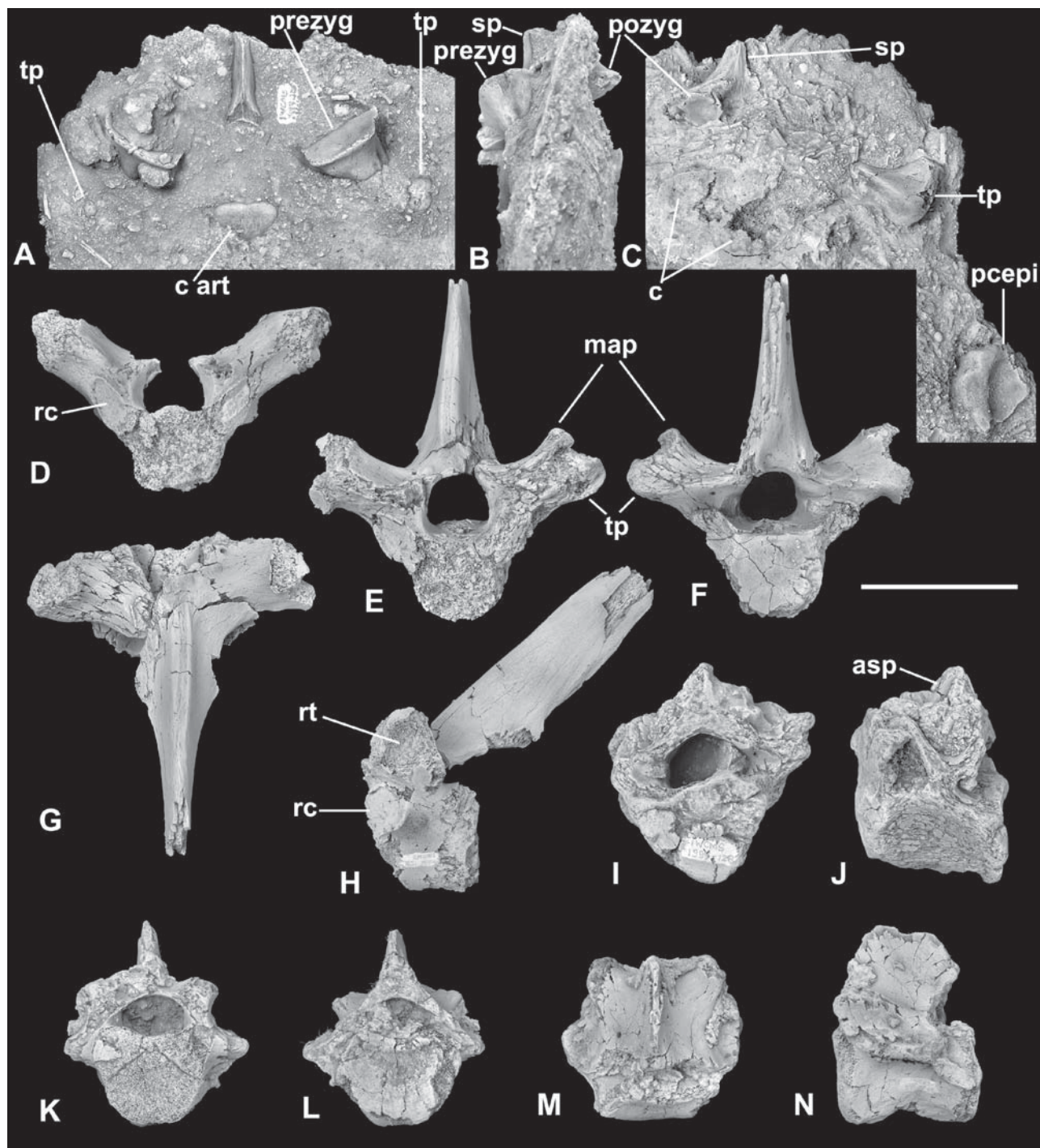


Figure 5. *Anoplotherium latipes*. Ham 3 skeleton, thoracic vertebrae (IWCMS. 1999.128). A–C, T1 embedded in pyrite slab. D, T3?. E–H, T4?. I–J, T11?. K–N, T12?. Views are anterior (A, D, E, K), left lateral (B, J, N), right lateral reversed (H), posterior (C, F, I, L) and dorsal (G, M). Coated with ammonium chloride. Scale bar = 50 mm.

THORACIC VERTEBRAE

There are seven vertebrae identified as thoracic. T1 is embedded in a slab of pyrite, but is partially visible

anteriorly and posteriorly (Fig. 5A–C). It is typical in having the transverse processes at the level of the centrum. This, together with widely separated prezygapophyses and posteriorly projecting postzygapophy-

ses, identifies it as T1. Anteriorly, it appears that it would have articulated well with C7 (Fig. 5A). The neural spine is broken off 3 cm above its base anteriorly, but what is left is orientated vertically. On the transverse process, what is left of the facet for the tubercle of the first rib appears deeply concave (Fig. 5C). The anterior epiphysis is in place; the posterior one has fallen away, but may be the one lying only 7 cm away on the same slab (Fig. 5C). In side view (Fig. 5B), it appears quite similar to the same bone in *Cainotherium*, but is proportionally shorter (Hürzeler, 1936: pl. 3, fig. 4).

Four more thoracics are more difficult to position in the column. They have centra that are no longer than high and bear long, dorsolaterally projecting transverse processes. They are relatively shorter than any of the thoracics in *Cainotherium*. The most complete has preserved most of its neural spine, which is angled posteriorly (Fig. 5E–H). Cuvier (1807d, pl. 23) showed a skeleton of *A. commune* from Antony with most of its thoracic vertebrae in articulation and visible in dorsal view in a matrix slab. The last (the 12th according to Cuvier's estimate by counting ribs on the Montmartre skeleton, MNHN.GY749) is badly abraded, but the seven more anterior ones all show long swept-back neural spines. It is possible, however, that the first two labelled lumbar by Cuvier are instead the 11th and 12th thoracics, but this cannot be confirmed as the specimen is missing. These four Bouldnor thoracics could then be attributed to the range 3–10. They can tentatively be placed in order according to the posterior trends of narrowing of the neural canal and reducing of the distance between the metapophysis and the midline, by comparison with *Cainotherium*. Two of these vertebrae have more or less complete neural arches, with nearly complete transverse processes, but only one has much of the neural spine preserved (Fig. 5E–H). An isolated fragment of neural spine may belong to the other vertebra (Figs 1B, 5D), but there is no actual fit. Its central articulations are abraded. The two vertebrae are very similar in shape, although the one lacking a spine has longer transverse processes and a slightly wider neural canal (Fig. 5D). Their similarity suggests that they may have been adjacent in the column, perhaps T3 and T4. The neural spine of the T4(?) makes an angle of about 45° to the posterior central articulation in lateral view (Fig. 5H). Its centrum is abraded anteriorly, but it retains the posterior epiphysis (Fig. 5E, F). The relatively anterior position of these vertebrae is also suggested by the large and deeply concave articulations for the rib tubercles.

The other two anterior thoracics also consist of centra with neural arches, but they are encrusted with pyrite and have suffered recent abrasion on the beach. The more complete of the two shows a left transverse process that, although abraded, appears to project less

far dorsally than that of the probable T4. What remains of its neural spine is angled posteriorly like T4(?). Its neural canal is also narrower than that of T4(?) and slightly more so than on the other poorly preserved anterior thoracic. These two vertebrae may therefore represent approximately T6 and T7.

There are two more thoracics, which are judged to be posterior by comparison with *Cainotherium*. The likely more anterior one of the two retains the neural arch and part of the spine, but this is broken posteriorly and there is much pyrite encrustation anteriorly, obscuring the anterior face of the centrum and arch (Fig. 5I, J). The posterior central articulation is better preserved and bears remains of the posterior epiphysis attached (Fig. 5I). The spine is narrow and is depressed with respect to the bases of the transverse processes. Its anterior edge slopes upwards posteriorly only about 20° from the plane of the posterior central articulation, thus steeply, but begins some distance posteriorly from the anterior edge of the arch (Fig. 5J). The right metapophysis is close to the midline. By comparison with modern artiodactyls and *Cainotherium*, this vertebra is probably T11.

The other posterior thoracic is better preserved, but is of a similar overall shape to T11(?) (Fig. 5K–N). The back of its neural arch, together with the postzygapophyses, is broken away, but anteriorly it is nearly complete, although with some pyrite encrustation. It retains its posterior epiphysis but has lost its anterior one. The neural spine differs from that of T11(?) in arising at the anterior edge of the arch and, although not well preserved above this, appears to have had a vertical or anteriorly tilted anterior edge (Fig. 5N). The spine is also extensive anteroposteriorly, reaching nearly the back edge of the arch as preserved. The bases of the transverse processes begin just below the floor level of the neural canal and appear to have had an essentially transverse orientation. The vertebra is probably T12, by comparison with *Cainotherium* (Hürzeler, 1936: pl. 3, fig. 10).

LUMBAR VERTEBRAE

There are three vertebrae identified as lumbar. Two are centra that retain their neural arches and parts of their processes (Fig. 6A–H). The third is a neural spine bearing the right postzygapophysis (Fig. 6J, L). The two more complete vertebrae are distinctly larger than the T11(?) and T12(?) and have relatively deeper centra. Their epiphyses have all become detached. The neural canals are similar one to the other and are larger than that of T12(?), but are in proportion to their overall size. As their central articulations are slightly higher than wide, they are probably anterior lumbar. Only one retains some of the neural spine (Fig. 6A–D) and both have lost the transverse

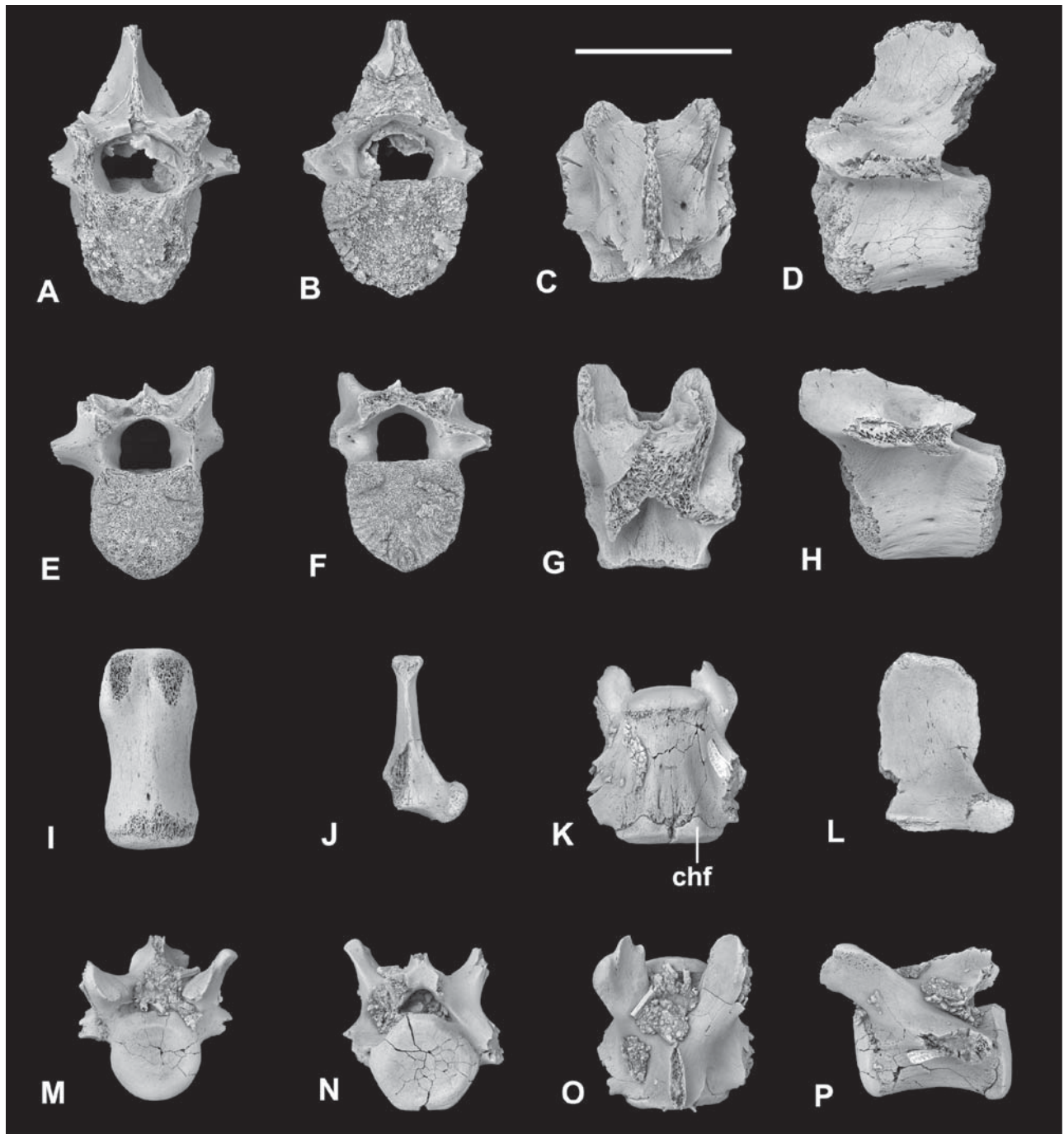


Figure 6. *Anoplotherium latipes*. Ham 3 skeleton, lumbar and caudal vertebrae (IWCMS. 1999.128). A–D, L2?. E–H, L4?. I, posterior caudal. J, L, posterior lumbar. K, M–P, anterior caudal. Views are anterior (A, E, M), posterior (B, F, J, N), dorsal (C, G, I, O), left lateral (D, H, P) and right lateral reversed (L.). Coated with ammonium chloride. Scale bar = 50 mm.

processes. The one without the neural spine has the neural arch broken posterodorsally, but its left prezygapophysis is nearly complete (Fig. 6E–H). This prezygapophysis has a stronger dorsal crest and appears to have been generally more expanded dorsally. The vertebra to which it belongs is probably the more poste-

rior of the two. A lumbar vertebra from Montmartre (MNHN.GY218) figured by Cuvier (1808: pl. 1, fig. 14) is probably the last or penultimate one (6th or 5th) as its right transverse process is angled anteriorly as on the last two lumbar in the Antony skeleton. It differs from both Bouldnor lumbar in having a centrum

wider than high and more enrolled prezygapophyses (now damaged). The more complete Ham 3 lumbar may perhaps be L2 and L4.

L2(?) is quite similar to that identified by Cuvier (1825: 238, pl. 53, fig. 3; incorrectly cited by him as being fig. 5), on the basis of the anterior facet for a rib, as L1 (MNHN.GY195). The L2(?) is nearly identical to another (MNHN.GY219), which lacks a rib articulation. The neural spine is slightly abraded anteriorly, although clearly nearly complete (Fig. 6D). Its anterior edge at first rises obliquely backwards, then turns vertically. The posterior edge is too damaged to interpret. The bases of the prezygapophyses survive and show that they were concave and could have partly embraced the postzygapophyses of the vertebra in front (Fig. 6A).

The lumbar vertebra that is represented solely by the neural spine and a postzygapophysis is complete dorsally, although a little abraded anteriorly and on the anterodorsal and posterodorsal corners (Fig. 6L). Its posterior edge is vertical as probably was its anterior edge. Its dorsal margin is slightly flared laterally, producing a flat dorsal edge (Fig. 6J). Even anterior breakage exposes an even thickness of spine throughout its length. Therefore, it probably did not flare anterodorsally. The postzygapophysis has a curvature whose radius reduces dorsally and spans about 180 degrees (Fig. 6J). It would therefore have articulated with a more enrolled prezygapophysis than those preserved on the two lumbar described above. In fact it would have resembled MNHN.GY218 (Cuvier, 1808: pl. 1, fig. 14). It is presumably therefore from a relatively posterior position in the lumbar series.

CAUDAL VERTEBRAE

An anterior and a posterior have been recovered. The anterior one (Fig. 6K, M–P) is nearly identical to the anterior of the two figured by Cuvier (1808: pl. 2, fig. 3) from the Montmartre skeleton (MNHN.GY749). Comparing this figure with Cuvier's (1807d: pl. 22, fig. 1), which shows the entire Montmartre skeleton, this vertebra is the 6th caudal illustrated. The junction between the caudal series and the sacrum is not preserved as there are no more anterior vertebrae in the skeleton. By comparison with another specimen from Montmartre (MNHN.GY750), which consists of a complete tail of 22 vertebrae plus damaged sacrum, the Ham 3 anterior caudal must be one of the first four. Both epiphyses are present on the Ham 3 caudal and show incomplete fusion (Fig. 6M, N, P). The distal epiphysis is flat and essentially pentagonal in outline (Fig. 6N). The ventral two points of the pentagon wrap slightly around the ventral surface of the centrum and were presumably the articulation points for the chevron bone (Fig. 6K). The prezygapophyses are large,

with a slightly concave facet (Fig. 6K, M–P). The transverse processes and the postzygapophyses are broken.

The Ham 3 posterior caudal (Fig. 6I) is a simple cylindrical centrum, with weak processes at either end. It resembles that figured by Cuvier (1825: pl. 38, fig. 4), although somewhat more elongate.

RIBS

These are mainly fragments of shaft, plus four proximal pieces with capitulum and tubercle. Of these four, two from the left side, by comparison of their articulations and the shortness of the blunt tuberosities distal of the tubercle with a modern ruminant, e.g. *Ovis*, may be the 4th and 5th ribs (Fig. 7A–F). They have a suboval cross-section and a deep fossa on the anterior surface between the capitulum and the tubercle (Fig. 7B, E). In both cases, the capitular epiphysis is missing. The other two are left and right and are mirror images of one another (Fig. 7H–I, J–K). They are likely therefore to have been in the same serial position. In terms of facet development, they fit best in the range of ribs 8–9. The right one has a distal break, which may be close to a fit with one of the shaft fragments (Fig. 7J–M). They are square in cross-section proximally where they bear shallow depressions anteriorly and posteriorly, but lack the fossa borne by the more anterior ribs (Fig. 7G, H). More distally, the rib cross-sections flatten and broaden (Fig. 7N) as Cuvier (1807d: pl. 22, fig. 1) noted for the Montmartre skeleton. The neck between the capitulum and tubercle is notably long. The capitulum is divided into two equal facets fitting equally to adjacent vertebrae (Fig. 7G). In *Ovis*, the anterior one is the more developed.

In contrast to *Ovis* and to *Cainotherium*, all these specimens have a much wider radius of curvature and the tubercles project dorsally much less. In this way they are like the ribs of *Chalicotherium* (Zapfe, 1979: 101–103, fig. 60).

FORELIMB

Scapula

The left scapula is complete in its length, but large parts of the glenoid and coracoid borders are broken away (Fig. 8A, B; Ford, 1972, pl. 3). It is nevertheless much more complete than that from Montmartre described by Cuvier (1807c: pl. 14, figs 7–9, reversed) from a distal fragment with glenoid and acromion process, also from the left side. The parts that overlap are very similar in size and morphology. Although much more fragmentary, the Ham 3 right scapula retains more of the coracoid border (Fig. 8C, D), so the two scapulae together give a good idea of the form of much

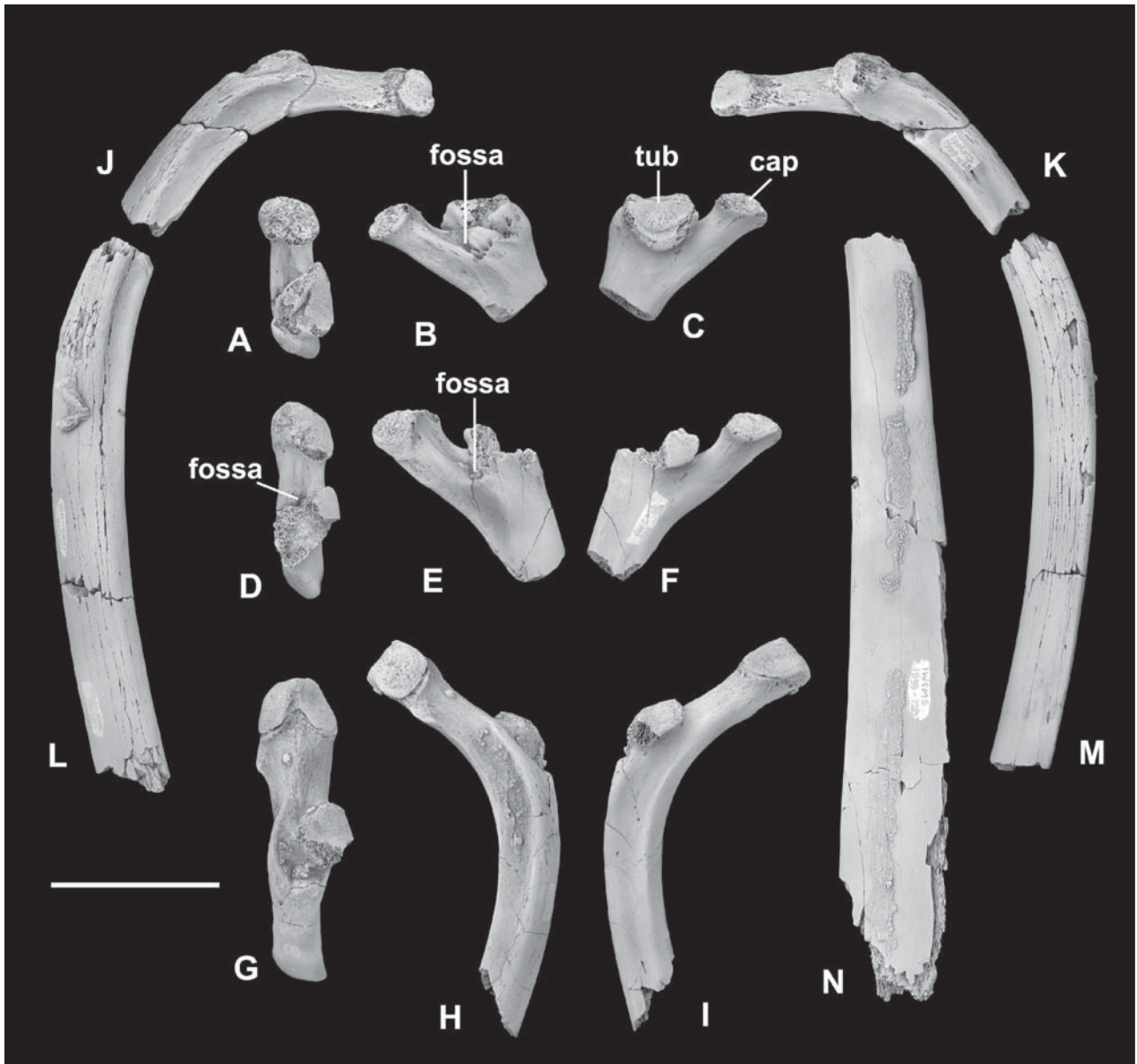
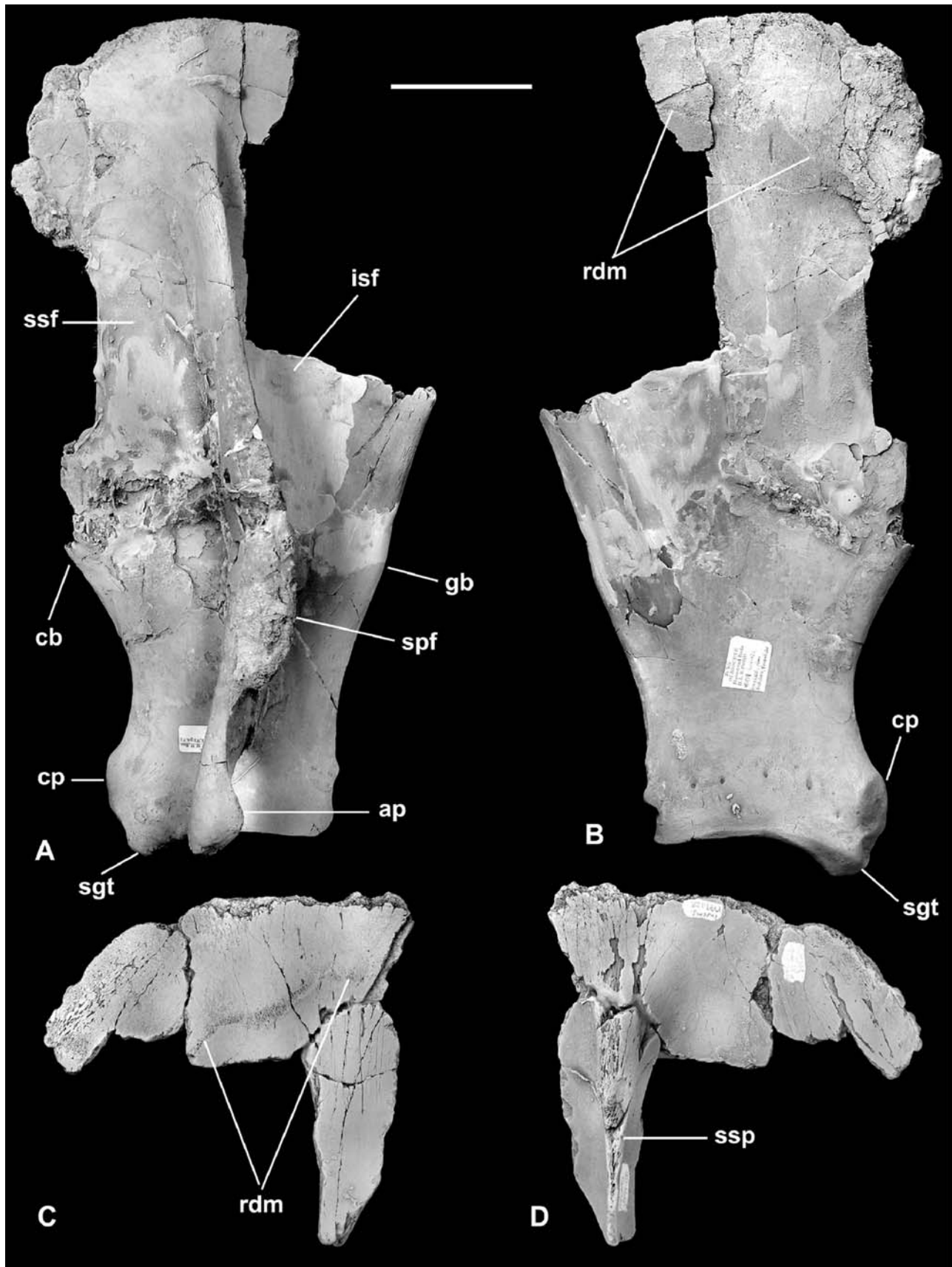


Figure 7. *Anoplotherium latipes*. Ham 3 skeleton, ribs (IWCMS. 1999.128). A–C, left 4th? head. D–F, left 5th? head. G–I, left 8th or 9th? head. J, K, right 8th or 9th? head. L, M, right shaft that may belong to right 8th or 9th? head. N, shaft of more posterior rib. Views are dorsal (A, D, G), anterior (B, E, H, J, L), posterior (C, F, I, K, M) and lateral (N). Coated with ammonium chloride. Scale bar = 50 mm.

of the bone. The coracoid border appears to have been convex, the glenoid border straight for at least the distal two-thirds of its length. Two scapulae of *Diplobune*, only lacking their proximal margins, are of similar shape (de Blainville, 1849, pl. 3). The supraspinous fossa is broader than the infraspinous fossa (Fig. 8A).

The overall shape is not unlike that of the modern tylopod *Camelus* (Walker, 1985), although in the latter the bone is narrower, particularly at the distal end of the supraspinous fossa, and the areas of the supraspinous and infraspinous fossae are less unequal. The spine is strong, its edge thickened and folded over

Figure 8. *Anoplotherium latipes*. Ham 3 skeleton, scapulae. A, B, left scapula (SMNS.42098). C, D, right scapula, proximal fragment (IWCMS. 1999.128). Views are lateral (A, D) and medial (B, C). Coated with ammonium chloride. Scale bar = 50 mm.



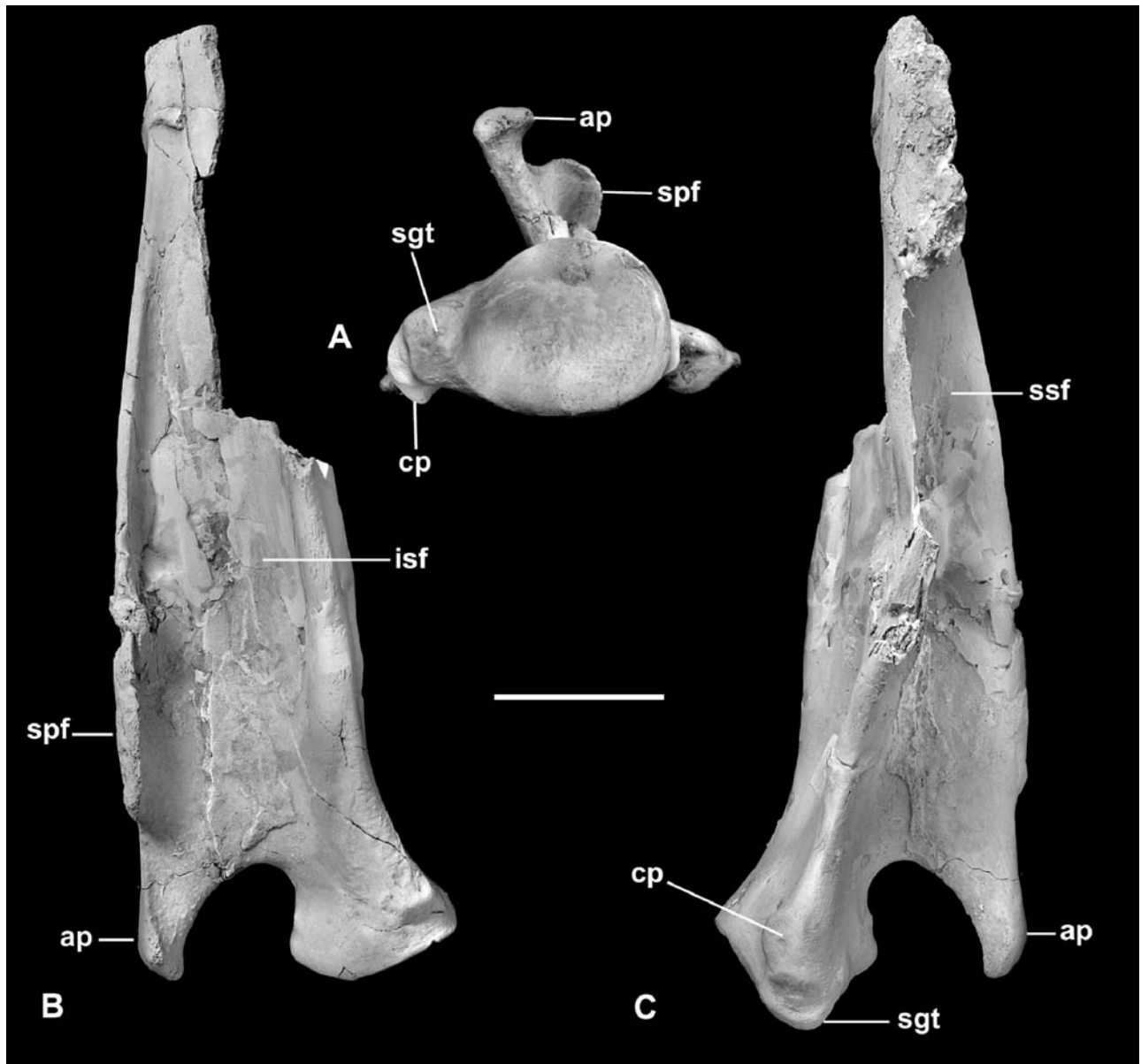


Figure 9. *Anoplotherium latipes*. Ham 3 skeleton, left scapula (SMNS.42098), in distal (A), ventral (B) and dorsal (C) views. Coated with ammonium chloride. Scale bar = 50 mm.

towards the glenoid border about a third of the distance from the glenoid cavity. The spine rises in height gradually distally, terminating in an acromion process that reaches the edge of the glenoid cavity (Figs 8A, 9B, C; Ford, 1972, pl. 3), unlike most modern artiodactyls, except camels. The coracoid process is reduced to a subterminal blunt knob that projects slightly dorso-medially (Figs 8B, 9A, C). The wide supraspinous fossa and apparently broadly curved coracoid edge are quite unlike those of the primitive tylopods *Cainotherium* (Hürzeler, 1936) and *Merycoidodon* (Scott, 1940), where the scapula is triangular with the supraspinous

fossa markedly narrower than the infraspinous fossa. The proportions are more like those of the chalicotheres *Moropus* (Holland & Peterson, 1914: fig. 76) although the latter differs in that the spinal fold is more proximal and there is no acromion. The concavity of the glenoid fossa is evenly curved dorsoventrally where it spans nearly 100° of arc. The curvature is less even and much shallower mediolaterally. There is a supraglenoid tubercle that projects distally from the edge of the glenoid fossa (Figs 8A, B, 9A, C). On the medial surface there is a faint wavy ridge subproximally (Fig. 8B, C) probably demarcating the m.

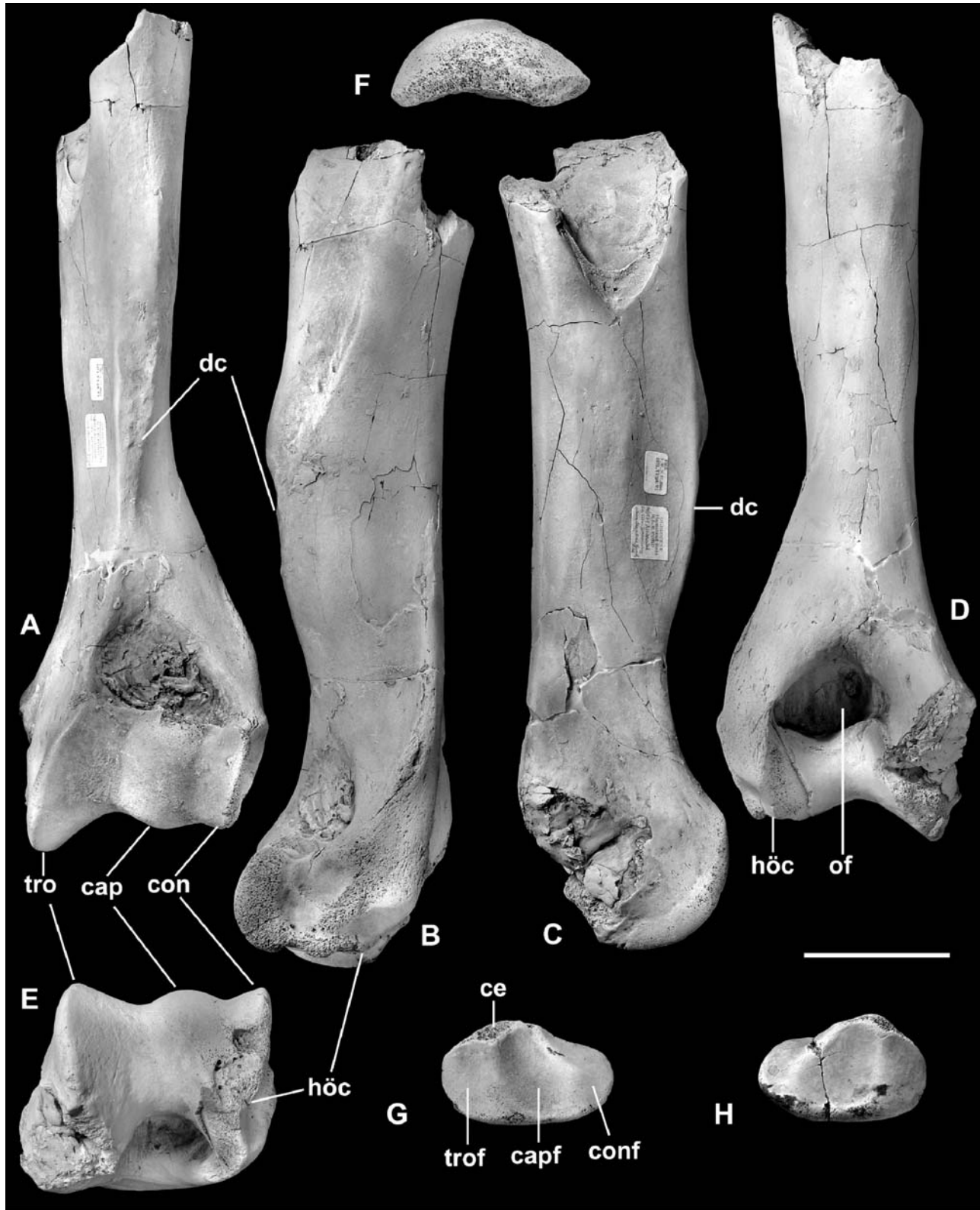


Figure 10. *Anoplotherium latipes*. Ham 3 skeleton, humeri and radii. A–E, left humerus lacking proximal end (SMNS.42098). F, right humerus, proximal epiphysis (IWCMS. 1999.128). G, right proximal radius (IWCMS. 1999.128). H, left proximal radius (SMNS.41960a). Views are anterior (A), lateral (B, F), medial (C), posterior (D), distal (E) and proximal (G, H). Coated with ammonium chloride. Scale bar = 50 mm.

subscapularis distally and the m. levator scapulae and m. serratus ventralis proximally.

Humerus

The left has the proximal end broken away prefossilization (Fig. 10A–E; Ford, 1972: pl. 4, fig. b), whereas the right is represented only by a detached proximal epiphysis (Fig. 10F). The characteristics of this bone are, on the distal articulation, a strong projecting and obliquely orientated trochlea and an evenly rounded capitulum with a distinct lateral flange (condyle) (Fig. 10A). Despite slight breakage on its edge distally and posteriorly, the capitulum and condyle continue round to the posterior side, where they merge (Fig. 10D, E; Cuvier, 1825: pl. 30, figs 2–4). At the point of merger is a small projection, referred to as a ‘höcker’ by Hürzeler (1936: 63, fig. 42) when describing it in *Cainotherium*. In *Cainotherium*, it is situated distally rather than posteriorly as in *Anoplotherium*. The structure appears to act as a stop for the radius at the point where the anconal process of the ulna reaches the bottom of the olecranon fossa of the humerus at maximum extension of the elbow (Fig. 10D). The difference in position between the two genera indicates greater extension capability for *Anoplotherium* than for *Cainotherium*.

On the shaft, a strong salient deltoid crest extends on the anterior surface for two-thirds of the length from the proximal end (Fig. 10A–C). The deltoid crest is less well developed in this individual than on a left humerus from Montmartre (Cuvier, 1825: pl. 59, figs 5–7) or on a left humerus lacking the distal end from Bouldnor Cliff (BMNH.M4450) (Fig. 11A–C). This is probably because the Ham 3 animal was immature. In medial view, the Montmartre specimen shows the shaft flaring proximally, the anterior margin leading to a prominent greater tuberosity, which, although truncated by breakage, still extends proximal of the head. The only largely undamaged part of the proximal end is the head articulation. M4450 is important in having a largely complete proximal end, although the greater tuberosity is abraded. Only about half of the anterior–posterior dimension is occupied by the head (Fig. 11A, E). In proximal view, the greater tuberosity makes an angle of c. 45 degrees to the sagittal plane. The lesser tuberosity projects medially and there is a distinct but broad bicipital groove, demarcated by anterior and posterior bicipital ridges (Fig. 11E). A ridge is also formed at the lateral end of the greater tuberosity (Fig. 11A). The lesser tuberosity

is positioned essentially as in *Sus*, but is orientated more anteroproximally and projects above the level of the head (Fig. 11B–D). It has a heavily rugose medial surface for insertion of the m. subscapularis.

Ulna

Both ulnae show the proximal articulation but the relatively short olecranon process is preserved only on the left (Fig. 12A, E, F, H). The right ulna has lost the unfused olecranon epiphysis (Fig. 13A, D, G, H). Nothing is preserved of the distal articulation of even the near complete right ulna. The shaft proximally is triangular in cross-section, but becomes subrectangular more distally. Its ‘antero-posterior’ axis is here obliquely orientated anteromedially–posterolaterally at c. 45° (Fig. 13A), much like modern *Sus*. Its posterior profile is gently concave and its anteroposterior depth is constant distal of the semilunar notch (Fig. 13D, G). The ulna of other primitive tylopods is quite different in shape. Thus, in *Cainotherium*, *Xiphodon* and *Merycoidodon*, it is more strongly concave posteriorly and in the first two the shaft is considerably reduced in its antero-posterior dimension.

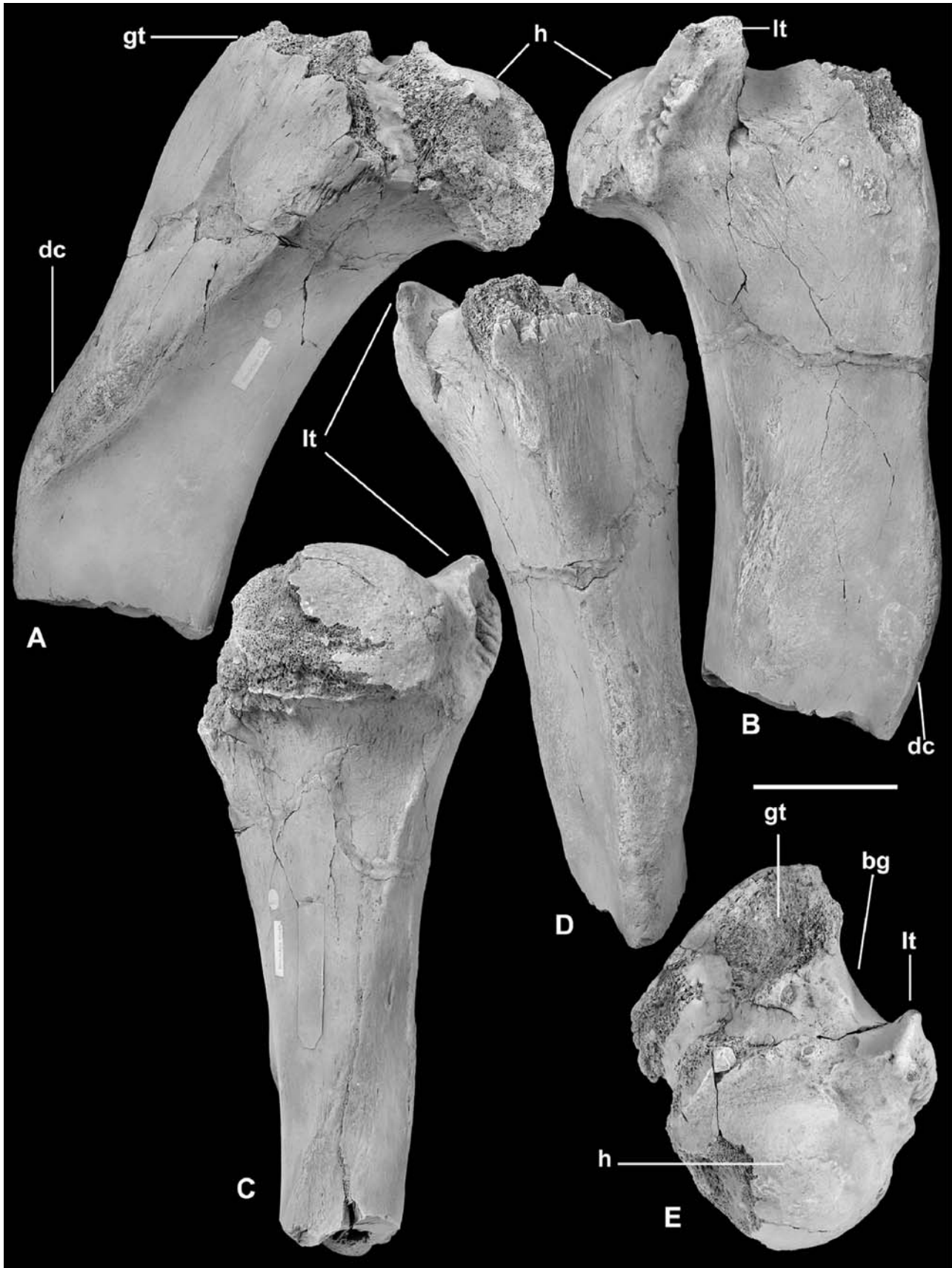
The semilunar notch has a long pointed anconal process, which fits into the deep olecranon fossa of the humerus. The semilunar notch owes its strongly sellar articulation to the deep medial facet that articulates with the extensive trochlea of the humerus. There are two separate facets for articulation with the head of the radius. They are angled obtusely towards one another. The lateral one is circular, whilst the medial one is more elongate proximolaterally–distomedially.

Despite slight distortion of the distal tip (from which probably only the distal epiphysis is missing), the right ulna shows near its preserved end a disto-posterior curvature of the anterior surface (Fig. 13A). This appears to match a similarly positioned curvature on a distal right ulna (BMNH.30029) from the Isle of Wight (Fig. 14B). The consequent match allows an estimated length for the complete ulna (Table 3). The distal end (styloid process) of the BMNH.30029 ulna bears a gently saddle-shaped facet for articulation with the proximal face of the cuneiform (Fig. 14B, F, I, J). This is the first ulna complete enough distally to have its articulation documented in detail.

Radius

This bone is represented by left and right proximal ends (Figs 10G, H, 12B–D, G, 13B, C, E, F) and a right

Figure 11. *Anoplotherium latipes*. Left humerus, lacking distal end (BMNH.M4450), from Bouldnor Cliff, in lateral (A), medial (B), posterior (C), anterior (D) and proximal (E) views. Coated with ammonium chloride. Scale bar = 50 mm.



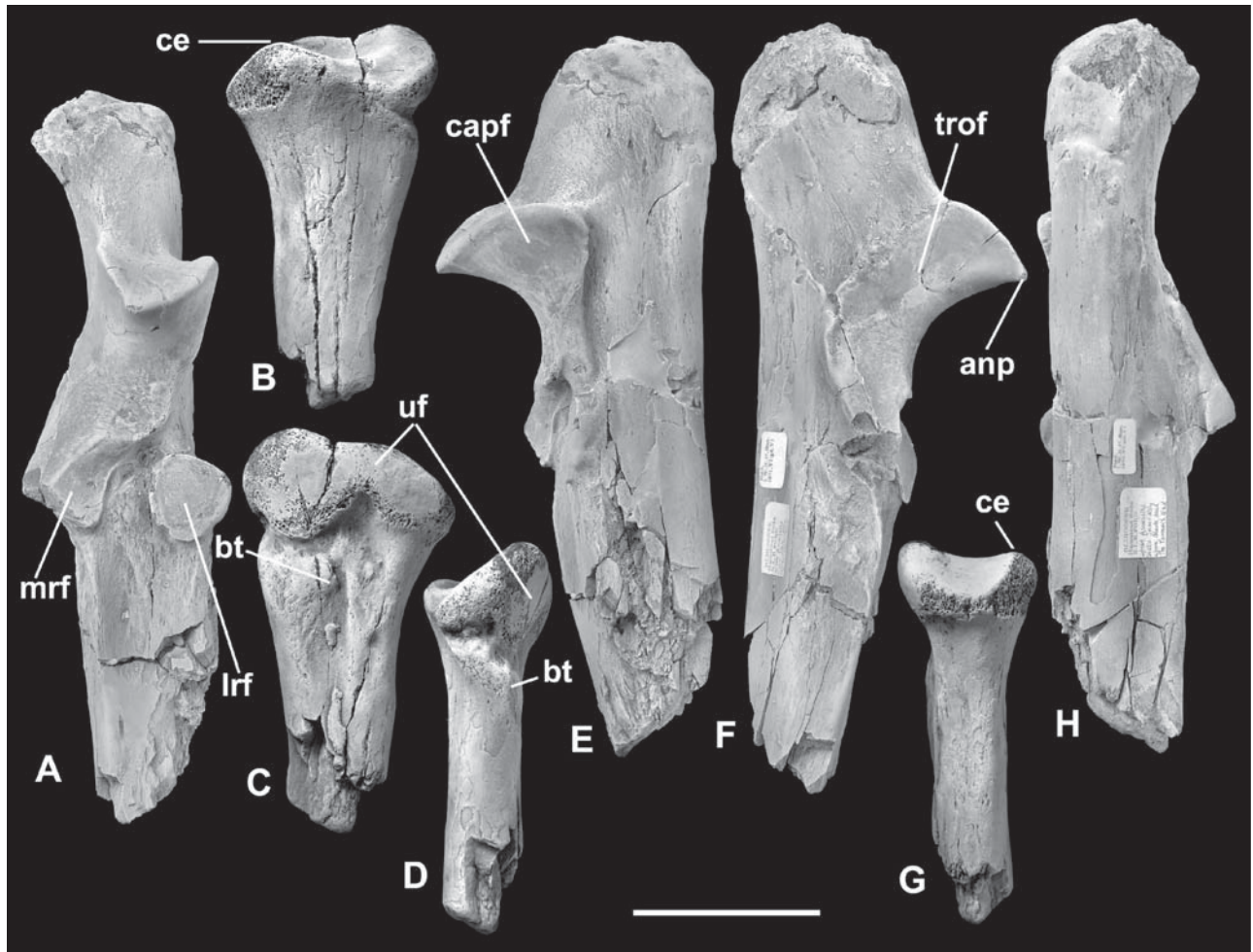


Figure 12. *Anoplotherium latipes*. Ham 3 skeleton, left proximal ulna (SMNS.42098) and left proximal radius (SMNS.41960a). Views are anterior (A, B), posterior (C, H), lateral (D, E) and medial (F, G). Coated with ammonium chloride. Scale bar = 50 mm.

distal epiphysis (Fig. 14K). The proximal articulation for the humerus is mediolaterally oval. Its anterior edge is sigmoidal, rising medially to form a broadly rounded capitular eminence (Figs 10G, H, 12B, G, 13C, F). The posterior edge has two very gentle proximal convexities (Figs 12C, 13B). The surface of the humeral articulation is divided into three facets by two ridges. Medially to laterally, these are for the trochlea, the capitulum and the condyle of the humerus (Fig. 10G, H). The ridge separating the trochlear and capitular facets arises at the capitular eminence and crosses the articulation approximately anteroposteriorly, but curving laterally as it reaches the posterior edge. The ridge separating the capitular and condylar facets arises anteriorly on the lateral side of the capitular eminence and crosses the articulation at first obliquely in a posterolateral direction, then curves posteriorly to meet the posterior edge. The trochlear facet is flat and slopes posteromedially. The capitular

facet forms a shallow hemispherical depression. The condylar facet is mostly nearly flat and it slopes anterodistally and slightly laterally. At its anterolateral end, however, it recurves towards the capitular eminence. The structure of the humeral articulation is nearly identical to that of the artiodactyls *Cainotherium* (Hürzeler, 1936: 64–65, fig. 43) and *Diacodexis* (Rose, 1990: 119, fig. 6) and of the mesonychid *Pachyaena* (O'Leary & Rose, 1995: fig. 9).

Posteriorly, at the proximal end is an irregularly kidney-shaped facet for articulation with the ulna. It is almost divided into two distally by a deep notch (Figs 12C, 13B). The lateral lobe is the larger of the two and nearly circular in shape. The medial lobe is oval, its long axis orientated proximolaterally-distomedially. The facet is gently convex posteriorly. The structure is similar to that described for *Cainotherium* (Hürzeler, 1936: 65, fig. 43C), but in this genus the facet is not emarginated distally. On the Ham 3



Figure 13. *Anoplotherium latipes*. Ham 3 skeleton, right ulna lacking epiphyses (reversed) (A, D, G, H) and right proximal radius (B, C, E, F) (IWCMS. 1999.128). Views are anterior (A, C), posterior (B, H), lateral (D, E) and medial (F, G). Coated with ammonium chloride. Scale bar = 50 mm.

proximal radii, the lateral and medial lobes clearly articulate with the lateral and medial radial facets, respectively, on the ulna. Although the homologous parts have similar outlines, those on the radius are distinctly larger, implying both proximodistal and mediolateral movements at this joint.

On the posterior surface immediately distal of the ulnar articulation, there is a narrow neck, deeply

grooved on the lateral half and with a v-shaped lateral notch. Immediately distal of the neck laterally is a weak bicipital tuberosity, which tapers and dies out distally (Figs 12C, D, G, 13B, E, F). Medial of the bicipital tuberosity is a narrow groove that widens and shallows distally.

The distal articular ends of the Ham 3 distal epiphysis and of BMNH.30029 show a large lunar facet

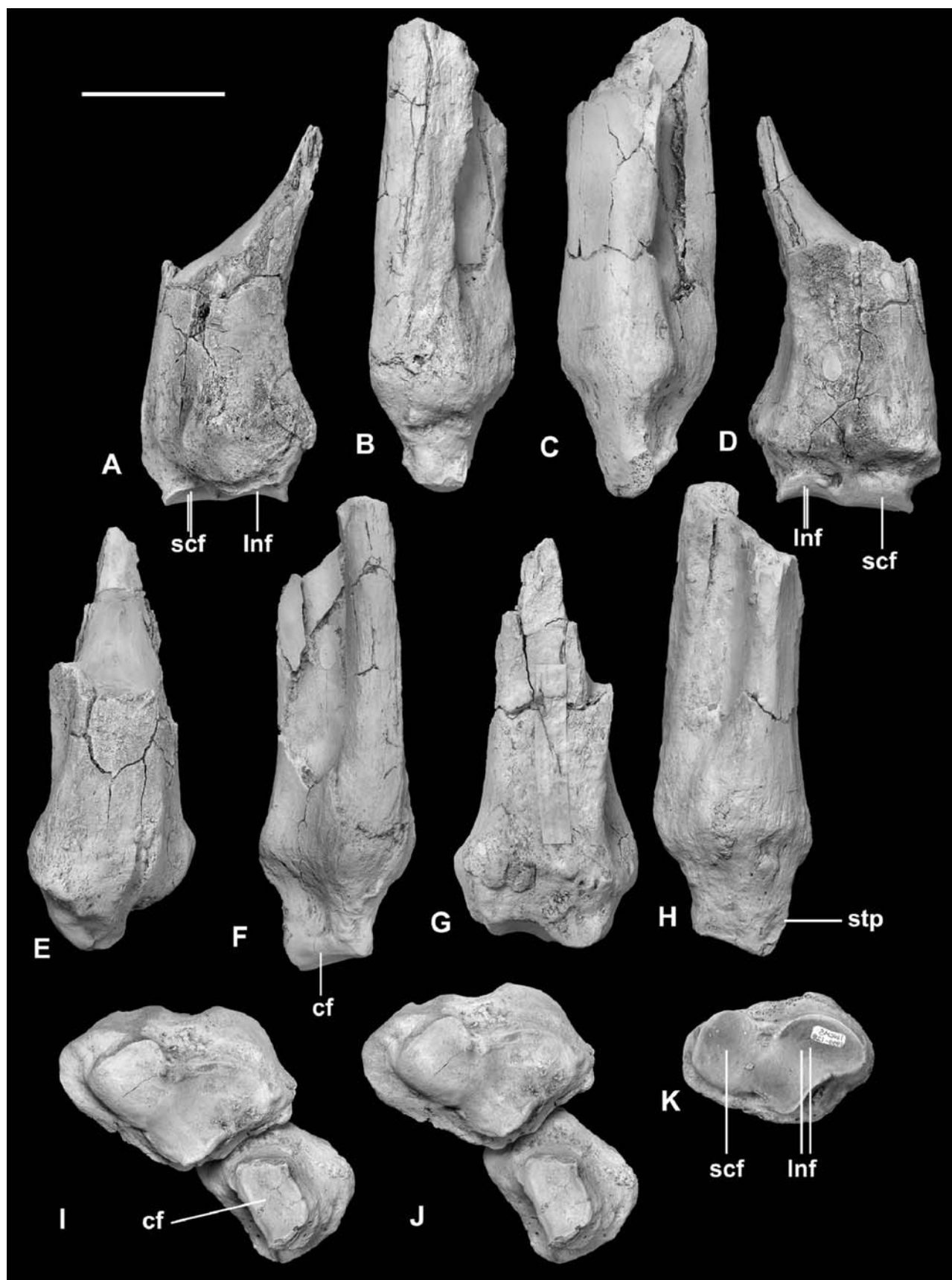


Figure 14. *Anoplotherium latipes*. A–J, associated right distal ulna (A, D, E, G) and radius (B, C, F, H) (reversed) (BMNH.30029) from N.W. Isle of Wight. K, Ham 3 skeleton, distal epiphysis of right radius (reversed) (IWCMS. 1999.128). Views are anterolateral (A), anterior (B), posterior (C), posteromedial (D), anteromedial (E), medial (F), posterolateral (G), lateral (H) and distal (I–K). The distal views of BMNH.30029 are shown articulated in the supinated (I) and pronated (J) positions. Coated with ammonium chloride. Scale bar = 50 mm.

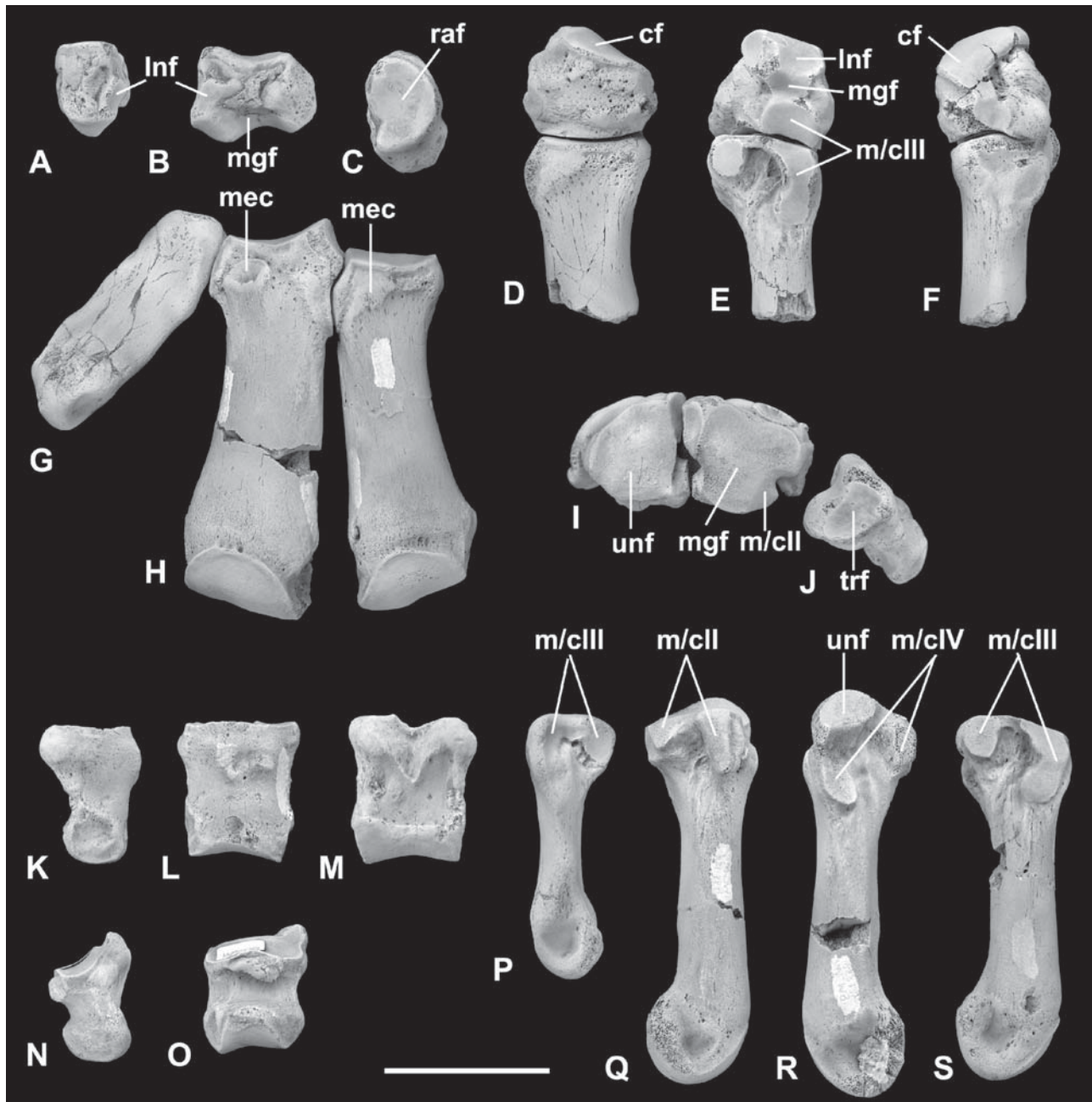


Figure 15. *Anoplotherium latipes*. Ham 3 skeleton, manus. A–C, left scaphoid (SMNS.41992). D–F, left unciform (BMNH.M42661) and proximal metacarpal IV (SMNS.42066a) articulated. G, J, P, left metacarpal II. H, I, right metacarpals III and IV, reversed (IWCMS. 1999.128), to show articulation (G) and juxtaposition (J) with left M/C II. K–M, manual right first phalanx IV, reversed (IWCMS. 1999.128). N, O, manual left or right second phalanx III or IV (SMNS.42098). Q, R, right M/C III, reversed. S, right M/C IV reversed. Views are anterior (A, D, G, H), lateral (B, F, P, R), proximal (C, I, J), medial (E, K, Q, S), dorsal (L, O), ventral (M) and medial or lateral (N). Coated with ammonium chloride. Scale bar = 50 mm.

and a smaller scaphoid facet separated by an obtuse ridge (Fig. 14I–K). The posterolateral edge of the articulation is very slightly concave and oblique, where it meets the distal end of the ulna. Although the non-articular bone surface is not well preserved, the distal radius of BMNH.30029 shows a concavity subterminally on the posterolateral side, which fits into a convexity subterminally on the anteromedial side of the associated ulna (Fig. 14A–D). The nature of this orientation and articulation is discussed under the functional interpretation below.

Carpals

These have been extensively described by Cuvier (1805: pl. 51) and Abusch-Siewert (1989). Only the left scaphoid and left unciform of the Ham3 skeleton have been recovered (Fig. 15A–F) and it is necessary to consider material from Montmartre in order to establish the nature and function of the articulations (see below under interpretation).

Metacarpals

M/CII, III and IV are present (Fig. 15D–J, P–S). M/CII is 65% of the length of M/CIII and proportionally smaller (Fig. 15G, J). M/CIII and IV each bears a small blunt tubercle on the anterior surface, respectively near and at the proximal end, for insertion of the m. extensor carpi radialis (Fig. 15H). The nature of the metacarpal articulations is discussed in the functional interpretation section below.

Manual phalanges

Based on *A. commune* specimens from Montmartre, manual first phalanges (Fig. 15K–M) can be distinguished from their pedal equivalents (Fig. 21H–J) by the nearly dorso-ventrally transverse orientation of their proximal articulations. In the pedal phalanges, these articulations are proximo-ventrally sloping (Cuvier, 1825: pl. 42, fig. 3 – manual: pl. 47, fig. 2 – pedal). The individual digits to which they belong can be ascertained by manual articulation. The single manual first phalanx of digit IV has a pair of small foramina piercing the plantar surface (Fig. 15M). Proximally on the dorsal surface there is a low tuberosity of uncertain function (Fig. 15L).

The proximal articulations of both the manual and the pedal second phalanges slope proximo-ventrally, so are less easy to distinguish. However, the pedal ones are relatively shorter. The complete one belonging to the Ham 3 skeleton closely matches in proportions that of an articulated series of manual phalanges of one digit III or IV from Montmartre (BMNH.46731) and is so identified (Fig. 15N, O). The parasagittal half second phalanx is also similar as far as can be judged.

HIND LIMB

Pelvis

The left os innominatum (Figs 16, 17) comprises three separate pieces: a nearly complete ilium, a middle portion with the acetabulum (and a possible tenuous fit with the ilium) and a lateral fragment of the ischium with part of the margin of the obturator foramen. The ilium is very broad with a strongly rounded iliac crest and a concave ventrolateral edge, the two meeting at a sharp angle. From study of two innominates (MNHN.GY189 and GY749) and a sacrum (MNHN.GY196) from Montmartre and the apparent fit of the Ham 3 acetabulum-bearing piece with the ilium, it can be calculated that the lateral part of the ilium was orientated at a very shallow angle to the horizontal, flaring laterally from its approximately 45° dorsal attachment to the sacrum. The axis of orientation of the acetabulum is parallel with the plane of the ilium and is therefore shallowly ventrolateral (Fig. 16). From these incomplete specimens, a complete pelvis from Mormoiron, France, can be reidentified as a large species of *Anoplotherium*. It has been figured by Roman (1922: pl. 3, fig. 2) incorrectly as *Palaeotherium magnum* Cuvier, 1804b. The specimen appears somewhat crushed, which probably accentuates diagenetically the low angle orientation of the ilia. It is nevertheless the most completely known pelvis of *Anoplotherium*. It differs from the pelvis of *Palaeotherium magnum* in having a shorter iliac body and a relatively longer ischium, so that the acetabulum lies approximately midway between the anterior and posterior pelvic extremities instead of further posteriorly (Roman, 1922: pl. 3, fig. 2). The posterior margin of the pelvis is also straight, not emarginated as in *P. magnum* (Roman, 1922: pl. 1) and, partly as a consequence, the pubic symphysis is very long (Fig. 26). The acetabulum faces slightly posteriorly as shown by Roman's illustration. On its anterior rim is a tubercle and depression for origin of m. rectus femoris (Figs 16A, 17A, C). The bony structure is not well marked in other ungulates, but a similar arrangement of tubercle and depression is found in *Chalicotherium* (Zapfe, 1979: figs 63–65). The Ham 3 innominate shows a large acetabular fossa, with the acetabular notch situated posteriorly (Fig. 16). In most mammals, this notch is posteroventral (e.g. Walker, 1985). *Chalicotherium*, however, is an exception and resembles *Anoplotherium* (Zapfe, 1979: 109, fig. 65).

Femur

The right femur (Figs 18, 19) is essentially complete, although there has been some post-mortem, prefossilization abrasion to the femoral head and to the medial condyle and weathering appears to have been respon-

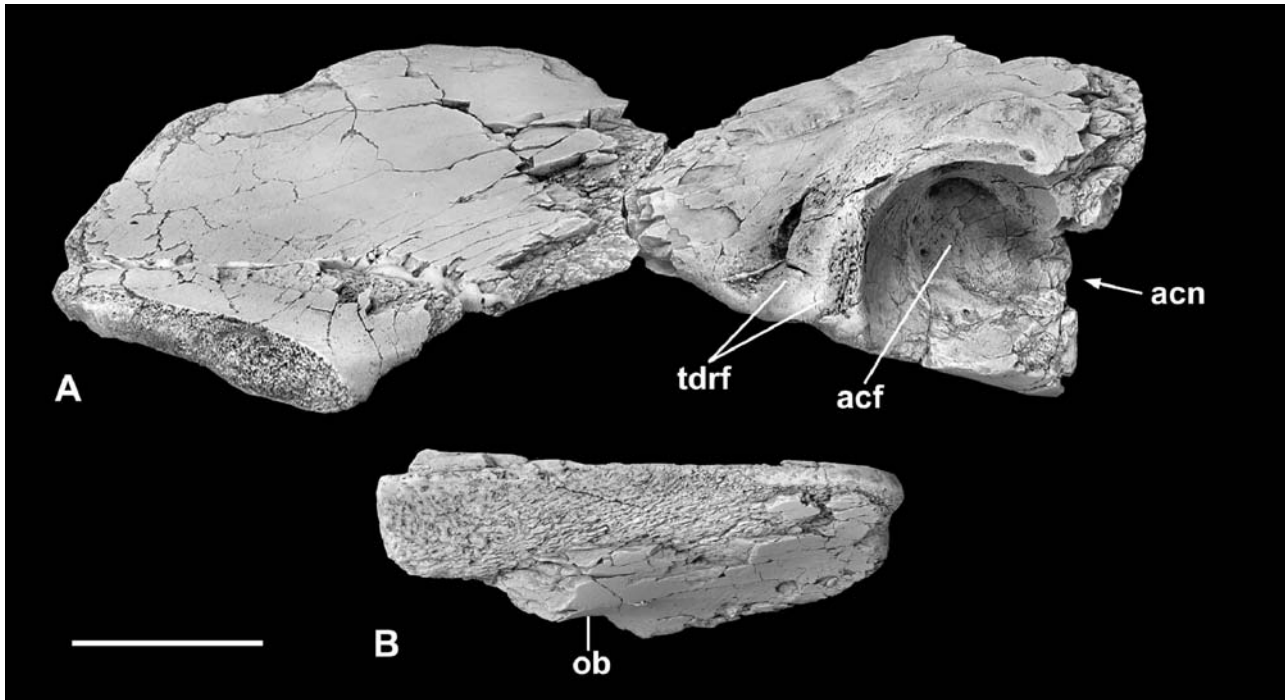
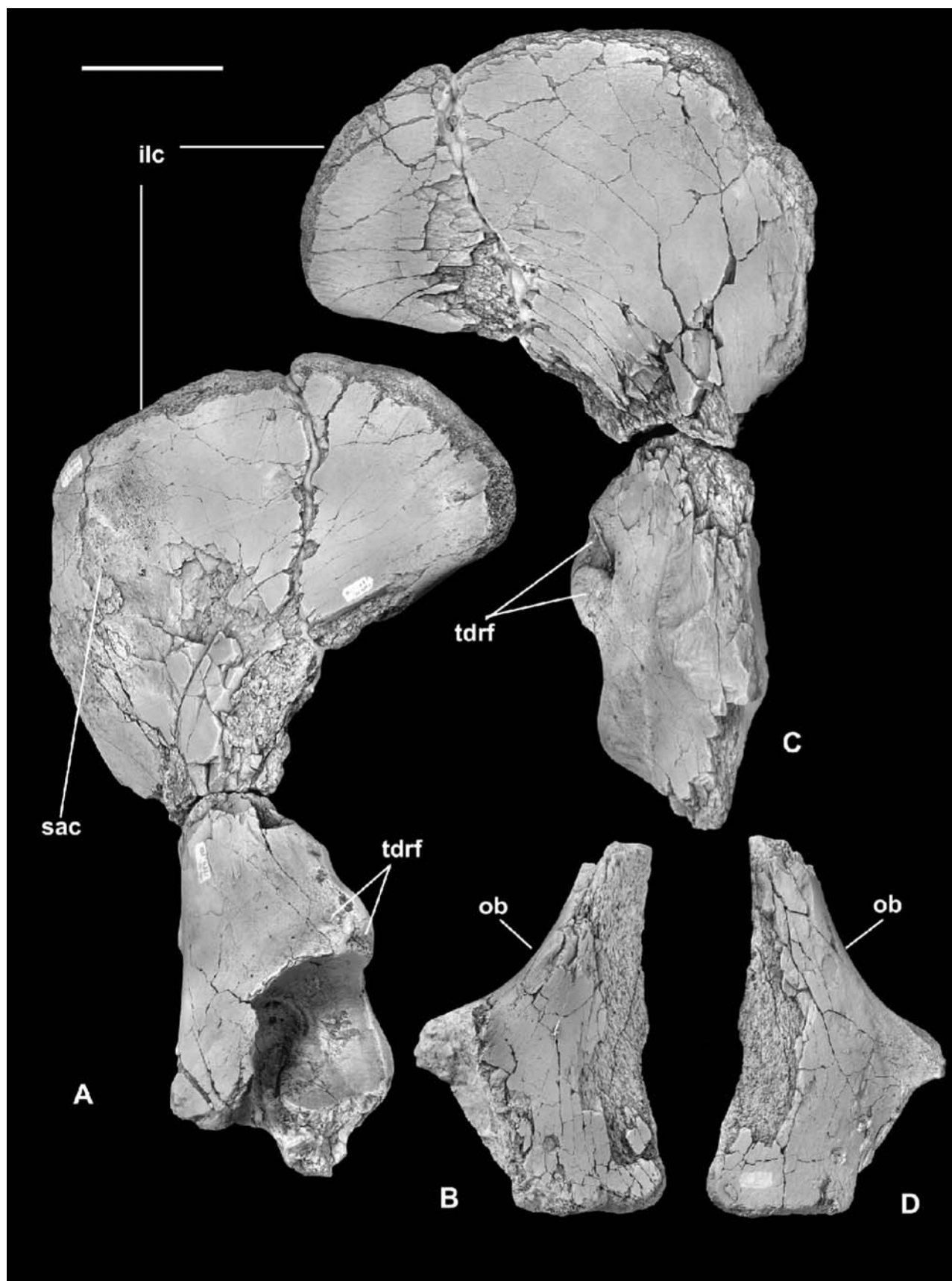


Figure 16. *Anoplotherium latipes*. Ham 3 skeleton, left os innominatum (IWCMS. 1999.128) in lateral view. A, ilium fragments with acetabulum. B, ischium fragment. Coated with ammonium chloride. Scale bar = 50 mm.

sible for loss of surface detail. It is nevertheless more complete and better preserved than previously described specimens of this bone, e.g. from Montmartre (Cuvier, 1825: pl. 25, figs 7–10, pl. 29, fig. 1). The shaft is nearly straight, but the proximal quarter of the bone is angled slightly anteriorly (Fig. 19C, D). The lesser trochanter marks the change in orientation. It forms a broad posterior swelling that is also slightly salient on the medial wall (Figs 18, 19A, D). The head appears to have been hemispherical, although its surface has suffered some breakage and abrasion; it is of limited distal extent scarcely extending onto the proximal side of the neck (Fig. 19A). The fovea for the teres ligament is 16 mm in diameter and posteromedially situated. Its large size parallels that of the acetabular fossa. The abrasion raises some doubts over the reliability of its size and position. However, they are confirmed by a femur of *Diplobune secundaria* from Montmartre (MNH.N.GY234: Cuvier, 1807a: pl. 4, fig. 9, as *A. commune*, here re-identified as *Diplobune* on the basis of size and the shape of the associated astragalus) and an isolated head from Montmartre (BMNH.OC7) the correct size for *A. commune*. On the Ham 3 femur, the bridge between the head and greater trochanter is narrow. The greater trochanter as preserved extends scarcely proximal of the head, but the extremity shows breakage, and so would almost certainly originally have extended a lit-

tle further proximally. Of living artiodactyls, this is most like pigs and camels, other members of the order, including other European tylopods like *Cainotherium* and *Xiphodon* having a distinctly more proximally extended greater trochanter. Compared with other artiodactyls, the neck is long, extended proximomedially rather like some bears. The trochanteric fossa is wide and shallow medially, deepening laterally to undercut the lateral wall (Figs 18B, 19A). Like all other artiodactyls except the primitive *Diacodexis*, *Messelobunodon* and *Gujaratia*, there is no third trochanter (Franzen, 1983; Rose, 1985; Bajpai *et al.*, 2005).

In anterior view (Fig. 18A), the distal articulation appears angled slightly laterally with respect to the long axis of the bone, although this is an artefact caused by post-mortem breakage and displacement on the medial side of the unfused condylar epiphysis. In distal view, the distal end is slightly wider mediolaterally than 'high' anteroposteriorly (Fig. 19B). The patellar trochlea is distinctly grooved, with the medial ridge slightly higher than the lateral ridge. The medial condyle appears narrower than the lateral condyle, although this difference results from erosion of the inner parts of both condyles, affecting the medial one more than the lateral one. Three distal femora from Montmartre show the medial condyle to be slightly wider and more broadly rounded than the



lateral one [MNHN.GY97 (Cuvier, 1807a: pl. 1, fig. 8 reversed), GY98 (Cuvier, 1807a: pl. 1, fig. 10 reversed), GY100].

Tibia: The tibia is shorter than the femur and is a robust bone with prominent crests and processes for muscle attachment (Fig. 20A–F). It is much more complete than any described from Montmartre (Cuvier, 1825: pl. 25, fig. 11, pl. 27, fig. 13, pl. 29, figs 5, 6), none of which preserves the medial malleolus. In anterior or posterior view, it is bowed medially and the shaft flares proximally (Fig. 20A, C). Its proximal articular surface is extensive and wider mediolaterally than anteroposteriorly (Fig. 20F). In anterior or posterior view, it is tilted slightly laterally with respect to the long axis of the bone. The facets for articulation with the femoral condyles are gently concave, the medial one narrower than the lateral one. Their planes dip slightly medially and laterally from the spinous process.

The distal extremity is wider mediolaterally than anteroposteriorly (Fig. 20E). The medial malleolus is large and long, curving laterally at its distal end (Fig. 20A–D) to insert into a deep cotylar fossa in the middle of the medial wall of the astragalar body (astragalus missing from the Ham 3 skeleton, but the cotylar fossa is characteristic of this bone in all three-toed *Anoplotherium* examined). This peg and socket structure appears to act somewhat like an axle, guiding and strengthening rotation of the astragalar trochlea at the crural joint. The deep grooves and the sharp tibial crest of the distal articulation of the tibia are slightly oblique to the anteroposterior axis of the bone. There is no torsion between proximal and distal ends.

Fibula: This is represented by both distal and proximal ends, although enough of the narrow shaft is present, especially on the left side, to demonstrate the former presence of a complete bone (Fig. 20G–L), as is recorded for *A. commune* from Montmartre (Cuvier, 1807a: pl. 4, fig. 3, pl. 5, fig. 1). The distal end is about twice as long (antero-posteriorly) as wide and sub-rectangular to oval in outline. Cuvier (1807a: pl. 3, figs 15, 16) illustrated a similar distal fragment of *A. commune* from Montmartre. In medial or lateral view, it has a concave distal facet (Fig. 20H, I), which articulates with the ectal facet of the calcaneum. The anterior extremity extends distally further than the posterior extremity of this articulation. Medially, there is a vertical facet for articulation with the lateral

trochlear wall of the astragalus (Fig. 20H). This medial facet of the fibula is restricted to the anterior two-thirds of the medial wall and is obliquely elongate, extending proximo-posteriorly from the antero-distal extremity. Posterodistal of the facet is a small fossa presumably for ligamental attachment to the lateral wall of the astragalar body. A roughened surface proximal of the astragalar facet suggests a distal attachment to the tibia bound by ligaments or cartilage. Thus together, the distal end of the fibula and the medial malleolus of the tibia enclose the proximal half of the astragalus and prevent its lateral movement (see also distal articulated fragment from Montmartre – de Blainville, 1849: pl. 4).

Of the two proximal fibular epiphyses (Fig. 20J–L), the left is the better preserved. Both are acutely wedge-shaped in cross-section, tapering proximally so that the articulation slopes roughly distomedially (Fig. 20K). The articular surface would fit underneath the posterior side of the lateral condyle of the tibia (Fig. 20D), although the Ham 3 tibiae are too encrusted with matrix and an extraneous bone fragment for much of the proximal fibular facet to be observed. However, manipulation provides an approximate fit, with the long axis of the fibular head having an oblique anterolateral–posteromedial orientation. The posteromedial extremity appears to have overhung slightly the posterior margin of the tibia. Anteriorly on the lateral surface, there is a slightly raised area perhaps for origin of the m. peroneus longus. The closest comparison among modern artiodactyls is with the Suidae (e.g. *Hylochoerus*), where in its immature unfused state the shape of the tibial facet and the presence of a blunt process marking its posterior limit (Fig. 20J, L) are quite similar. In contrast, however, the articular surface is vertical instead of sloping.

Tarsals: The calcaneum is short and robust compared with that of typical *A. commune* (Cuvier, 1804c: pl. 38, fig. 12; 1825, pl. 13, fig. 12). However, the sustentacular facet is angled more proximally than in typical *A. latipes* (Fig. 21B), so that overall it articulates better with *A. commune* astragali from Montmartre (BMNH.OC186, OC187, 29506) than with an *A. latipes* astragalus from Quercy (BMNH.M1844). As noted above, the extended and incurved medial malleolus of the tibia needs a relatively deep cotylar fossa in the astragalus with which to insert and articulate, such as is found better developed in *A. latipes* than in *A. commune*. Thus the structure of the Ham 3 calcaneum is somewhat intermediate between the two

Figure 17. *Anoplotherium latipes*. Ham 3 skeleton, left os innominatum (IWCMS. 1999.128). A, C, ilium fragments with acetabulum. B, D, ischium fragment. Views are dorsal (A, B) and ventral (C, D). Coated with ammonium chloride. Scale bar = 50 mm.



species. The calcaneum articulates convincingly with the left cuboid, indicating that both belong to the same individual (Fig. 21B, C). The left ectocuneiform articulates perfectly with left metatarsal III, also indicative of belonging to the same individual (Fig. 21B, E). There is a facet on the lateral side of the former for articulation with the mesocuneiform, which in this skeleton is only represented on the right side. Moreover, the lateral surface of this mesocuneiform is damaged so that its facets are not preserved. Medially, it bears a small entocuneiform facet (Fig. 21A). It is like the same bone in specimens of *A. latipes* from La Débruge in having a gently concave distal facet and a strongly concave proximal facet, both curved in the parasagittal plane (Fig. 21A, B, G).

Metatarsals

M/TII and III are present (Fig. 21A, B, D–F). M/T II is 72% of the length of M/T III and proportionally smaller. Medially, it bears a facet for the entocuneiform (Fig. 21A, F). The nature of their articulations is discussed in the functional interpretation section below.

Pedal phalanges

There are two pedal first phalanges, which appear mirror images of one another. They each are pierced on their plantar surface by a single small foramen (Fig. 21I). The better preserved of the two (Fig. 21H–J) articulates well with left M/TIII, suggesting that the other is its homologue on the right side.

FUNCTIONAL INTERPRETATION OF ANOPLOTHERIUM OSTEOLOGY

Cuvier (1805, 1808) noticed a number of unusual features of the postcranial skeleton of *Anoplotherium commune*. Firstly, although it had cloven hooves like a pig or a camel, i.e. its foot was paraxonic, there was evidence from medial facets at the proximal end of metacarpal III of the presence of a sizeable metacarpal II, but according to lateral facets at the proximal end of metacarpal IV, evidence of only a vestigial metacarpal V. The greater than vestigial nature of M/C II was indicated by a single isolated example of this bone, which was, however, much shorter than M/C III or IV and asymmetric in shape. It was, nevertheless, sufficiently well developed to have a distal articulation for a phalanx (Cuvier, 1805: 276–277, pl. 3, figs 8–11).

Secondly, the species had a long tail consisting of 22 vertebrae, which was far longer and thicker than that of any modern ruminant (the group in which he placed camels, whose relationships seemed closest to *Anoplotherium*). The more proximal of these caudal vertebrae also bore prominent processes and many except for the most distal ones had chevron bones associated with them (Cuvier, 1808: 277, pl. 2, figs 1–4). Cuvier made a comparison between the tail of *Anoplotherium* and that of a kangaroo or an otter. This led him later (Cuvier, 1825: 247–248) to conclude an amphibious otter-like lifestyle for *Anoplotherium*. This idea was expanded upon by Gervais (1859), who described the species *Anoplotherium latipes* from the southern French site of La Débruge, which bore a second digit on both fore and hind feet. Gervais postulated that the three-toed feet of this species were webbed, giving further support to Cuvier's idea. He was followed by Schlosser (1883a).

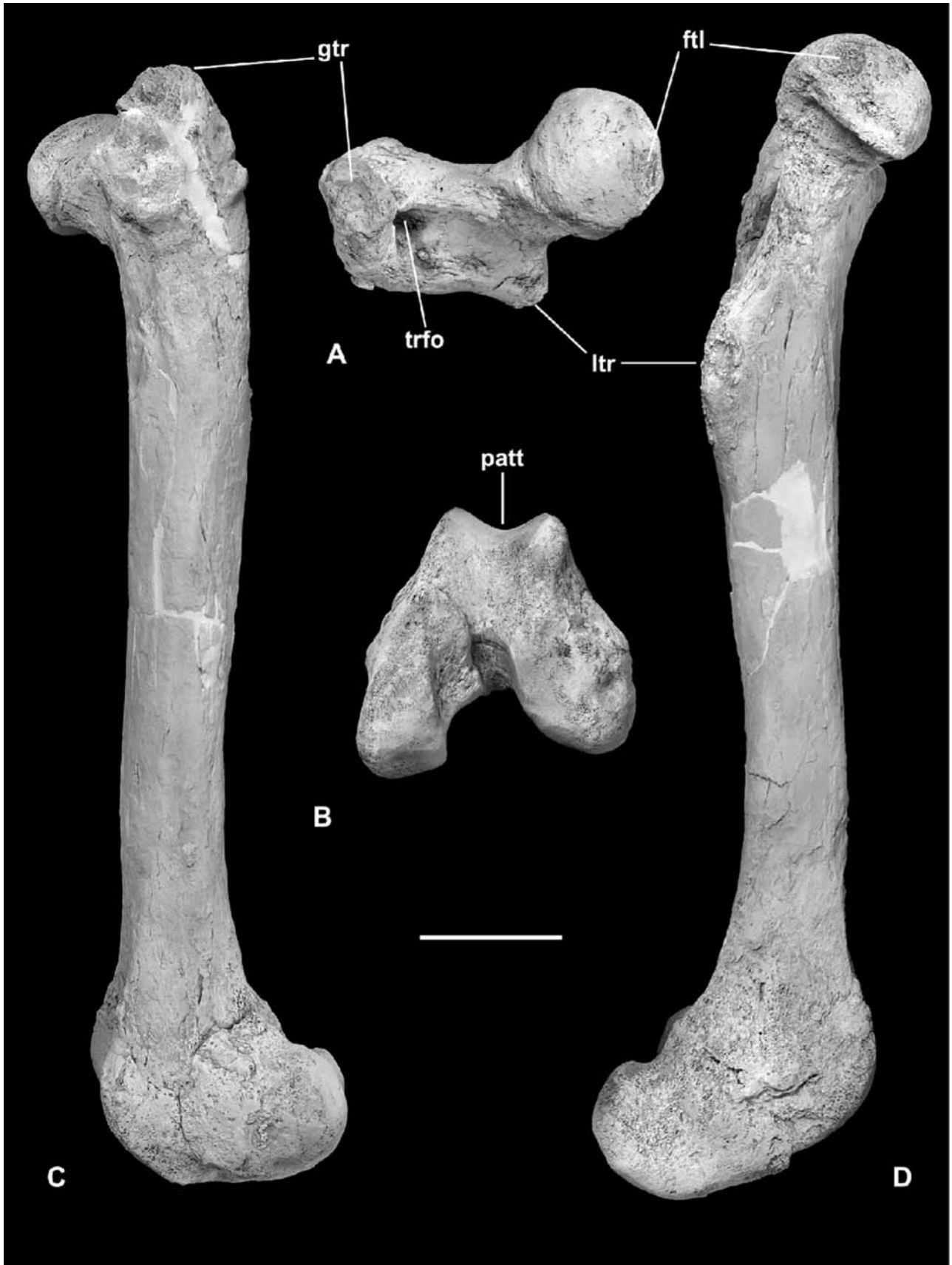
These ideas were later countered by Dor (1938). Dor showed that in structure the caudal vertebrae of otters are quite different from those of *Anoplotherium*. Moreover, the trunk vertebrae of *Anoplotherium* had the rigidity of a typical ungulate, which would not allow the lumbar movement that accompanies tail undulation in otters. Dor also could not envisage a hoofed unguligrade mammal with webbed feet being able to walk on land.

More recently, Abusch-Siewert (1989) interpreted *Anoplotherium commune* as having normally only a vestigial M/C II, Cuvier's example of this bone (Cuvier, 1805: pl. 52[3], figs 8–11), lost for at least 157 years (de Blainville, 1849: 28), simply representing a rare occurrence of a better developed second digit, that was in the process of evolutionary loss. She envisaged *Anoplotherium commune* as a slow unguligrade runner. Function is considered in more detail here with particular reference to the material from the Hampshire Basin.

NECK

Cervicals 4–7 are characterized in lateral view by an obliquity of their centra (Fig. 3G, H). Thus, when articulated with their adjoining anterior and posterior surfaces orientated vertically, the neck would normally have had an anterior upward slope (Fig. 4). The extreme obliquity of the anterior central articulation of C4 and posterior flaring indicate a change in orientation of the neck vertebrae, as C4 is unlike C3 or C7 (the best known) in these respects. Vertebral orientation depends on the nature of the articulation of both

Figure 18. *Anoplotherium latipes*. Ham 3 skeleton, right femur, reversed (IWCMS. 1999.128), in anterior (A) and posterior (B) views. Coated with ammonium chloride. Scale bar = 50 mm.



centra and zygapophyses of two adjacent vertebrae. Unfortunately, the posterior central articulation of the Montmartre C3 is unknown, but all the zygapophyses are preserved. Aligning its postzygapophyses with the prezygapophyses of C4 makes the ventral surface of C4 dip posteroventrally. The anterior half of C5 is unknown so cannot be articulated with C4. Nevertheless, its posterior half is quite similar to that of the Ham 3 C7. Positioning C7 in approximate articulation with C4 suggests that C5 articulated slightly posteroventrally to C4. A tentative reconstruction of the neck vertebrae of *Anoplotherium* suggests a ventral bend between C3 and C4 (Fig. 4B). Some bears (Ursidae) show slight ventral curvature of the neck through a morphology similar to that of *Anoplotherium* (pers. obs.), and all do erect bipedally to a greater or lesser extent. The change in angle is between C3 and C4 (*Thalarcos*, *Selenarcos*) or between C3, C4 and C5 (*Tremarcos*, *Ailuropoda*). The more marked bend in *Anoplotherium* could be necessary because of a lack of dorsoventral movement at the atlas-axis joint, which is mobile in this sense in bears.

The neural arches of these vertebrae in *Anoplotherium* are well developed and appear large compared with the centra. Such disproportionately large cervical arches and obliquely articulating centra are similar to those of the chalicotheres *Moropus* (Holland & Peterson, 1914: 262–269) and *Chalicotherium* (Zapfe, 1979: 77–84), although the obliquity is less extreme and the prezygapophyses do not project as far anteriorly in *Anoplotherium*. Such morphology is indicative of the neck musculature being better developed dorsally than ventrally, suggesting that the posterior part of the neck was habitually held in an obliquely upward sloping posture (Coombs, 1983: 11, 37, 39). Other primitive tylopods like *Cainotherium* (Hürzeler, 1936) or merycoidodonts (Scott, 1940: pl. 71, fig. 7) have dorsal and ventral parts more equally developed and less obliquity of the central articulations.

TRUNK

Articulating the proximal rib fragments of the Ham 3 skeleton with approximately appropriate thoracic vertebrae shows that when complete a torso much broader than that of a modern ruminant (e.g. *Ovis*) would have been delimited (Fig. 22). This fits with Ellenberger's (1980) conclusion from trackways that *Anoplotherium* had a barrel-shaped trunk. The lateral projection of the ribs is due partly to the rib curvature (Fig. 7) and tubercle position and partly to the dorso-

laterally projecting transverse processes on the thoracic vertebrae (Fig. 5D–F). In isolation, the function of a trunk of this shape is uncertain, but, of more interest is that it is associated with an anterior to posterior increase in size of the centra of trunk vertebrae, a feature found typically in bipedal types because of the need to support the body in an upright stance. Moreover, the Montmartre first lumbar vertebra (MNHN.GY195: Cuvier, 1825: pl. 53, fig. 3) has a complete neural spine that shows no distal anterior or posterior flaring. The neural spines of adjacent vertebrae would have been separated by spaces (e.g. also Fig. 6L), thereby allowing a degree of lordosis in bipedal stance, as in the gerenuk, *Litocranius* (Richter, 1970), a facultative biped.

TAIL

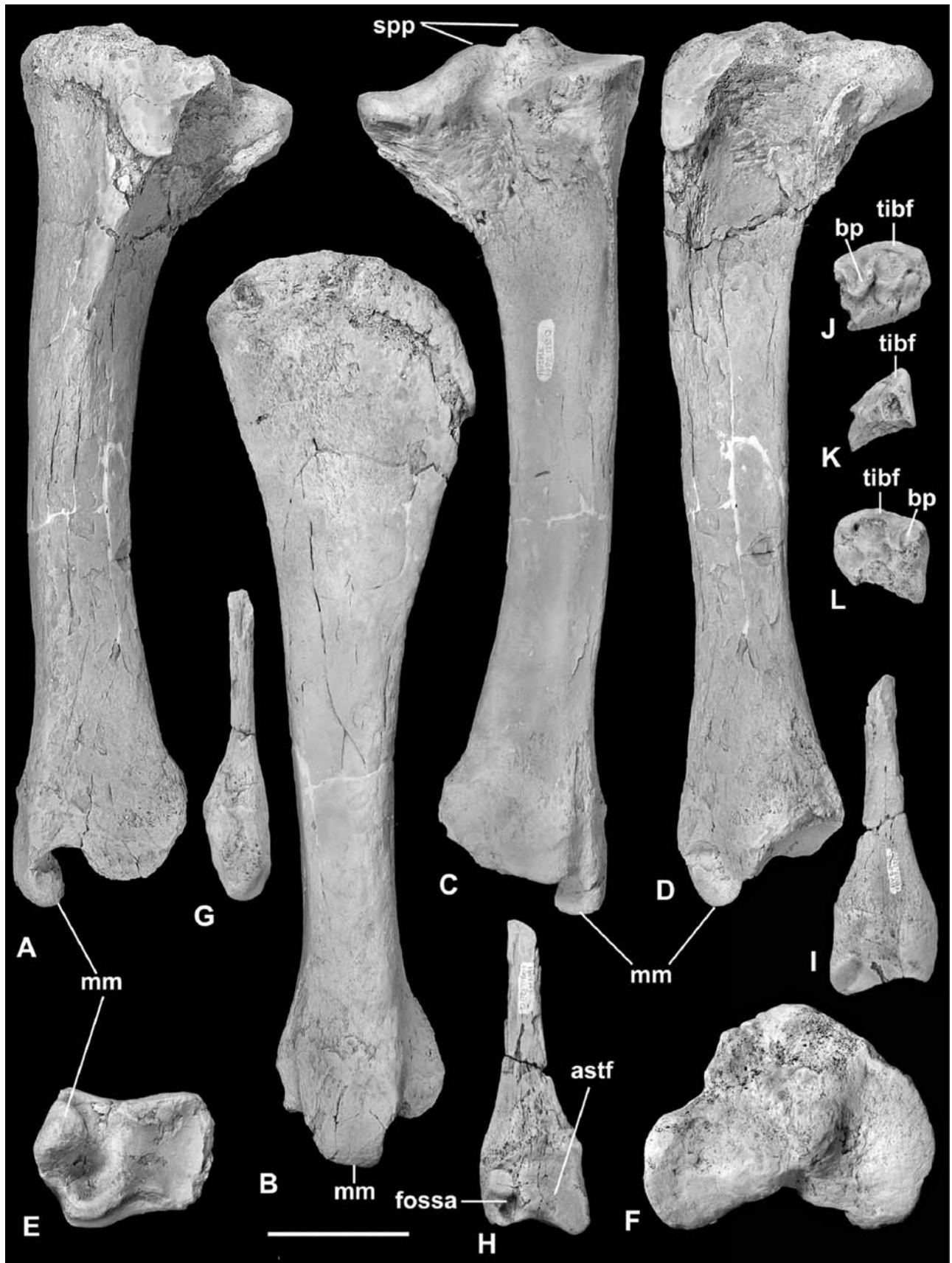
Dor (1938) has shown that the tail vertebrae of *Anoplotherium* are not morphologically close to those of either an otter or a kangaroo, contra Cuvier. Nevertheless, Dor's claim of similarity between distal caudals of *Anoplotherium* and those of typical modern ungulates is not convincing (Dor, 1938: figs 3, 4). It is true that the distal caudals of *Anoplotherium* (Fig. 6I) have less prominent processes than does the kangaroo (*Macropus*), but the pattern is more similar to this animal than to, for example, *Bos* or *Equus*. In *Anoplotherium*, the anterior processes are better developed than the posterior ones, whereas in *Bos* the transverse processes are restricted to the posterior end and in *Equus* they are restricted to the middle. The existence of small chevron bones on many of the caudals, not just the most anterior, cannot be ignored. Also, although *Anoplotherium* has no more caudals than the maximum recorded for *Bos* and *Equus* (Barone, 1999), they are much larger. The result is therefore a much longer and thicker tail. Greater similarity in the morphology of individual vertebrae and in general proportions of tail to body exists with terrestrial carnivorans like cats and dogs, which suggests that the tail of *Anoplotherium* performed a balancing function.

FORELIMB

Shoulder and upper arm

The size of the supraspinous fossa of the scapula, which is slightly larger than the infraspinous fossa, is indicative of the origin of a large m. supraspinatus. This matches the prominent greater tuberosity of the humeral head where this muscle inserts. The projecting acromion and the midway thickening of the

Figure 19. *Anoplotherium latipes*. Ham 3 skeleton, right femur, reversed (IWCMS. 1999.128), in proximal (A), distal (B), lateral (C) and medial (D) views. Coated with ammonium chloride. Scale bar = 50 mm.



scapular spine are interpreted to have provided attachment for the origins of the m. deltoideus, whose large size is indicated by the anterior prominence and distal extent of the deltopectoral crest of the humerus, where it inserts. These two muscles complement each other in raising the forelimb in a parasagittal or near-parasagittal plane. It is interesting that their humeral insertions are considerably more major than in the chalicotheres *Moropus* and *Chalicotherium* (Holland & Peterson, 1914; Zapfe, 1979). The large projecting lesser tuberosity of the proximal humerus suggests powerful adduction of the upper arm by the m. subscapularis.

Elbow

The structure of the distal humeral and proximal radial and ulnar articulations provides evidence of a degree of pronation–supination capability, something that was recognized a century and a half ago by Pomel (1851). Manipulation of the proximal radial fragments on the ulnae of the Ham 3 individual demonstrated the maximum degree of pronation–supination of the radius. It was measured by comparing photographs of proximal views in extreme positions. The result was a rotation of about 13°. From manipulation and from the pattern of the opposing facets of radius and ulna proximally, there appears to have been slight rotation in a transverse plane at the same time as medial shift. Thus, with supination the radial head slides distomedially down the long axis of the medial facet of the ulna and shifts proximo-medially on the lateral facet (Fig. 23).

With the elbow fully extended, the long axis of the ulna makes an angle of about 135° to that of the humerus. This is a greater degree of extension than is possible in *Cainotherium*, where the 'höcker', which acts as a stop to the radius, is more anteriorly situated (Hürzeler, 1936).

Wrist

The articulation between the ulna and radius distally is best seen in two associated distal right portions from the Isle of Wight (BMNH.30029). In the absence of a complete radius from Bouldnor and of a complete uncrushed ulna of *Anoplotherium* from any site, the orientation of the distal end of the radius with respect to that of the ulna must be judged indirectly. It is done here by both aligning the near complete Ham 3 right ulna with the BMNH.30029 ulna distal end and by

comparison of proximal and distal radius ends from Bouldnor with a complete left radius from Montmartre (MNHN.GY123, figured by Cuvier, 1825: pl. 51, figs 16–18, reversed). The subterminal convexity on the anteromedial side of the ulna, which fits into the subterminal concavity on the posterolateral side of the radius, allows a degree of pronation–supination as demonstrated proximally at the elbow (Fig. 14A–D). Using the proximo-distal plane based on an imaginary line drawn between the medial and lateral edges of the proximal radial articulation of the ulna as a reference, the long axis of the distal articulation of the radius in distal view can be estimated to approximate this plane when pronated (Fig. 14J). When supinated, it is a line drawn across the two anterior ridges of the radius that coincides with this plane (Fig. 14I).

The two facets on the distal end of the radius for the scaphoid and lunar (Fig. 14A, D, I–K) indicate that little movement other than palmarflexion appears to have been possible here. The distal end of the ulna (Fig. 14B, F, I, J) and proximal face of the cuneiform (the latter from study of Montmartre specimens) share a gently saddle-shaped facet, which allows slight medio-lateral movement and some palmarflexion. In the absence of relevant bones of a single individual, it is difficult to judge the amount of palmarflexion, but would have been restricted by the pisiform, which articulated postero-proximally with the cuneiform and postero-distally with the ulna. There is a distinct pisiform facet on the cuneiform, but on the ulna it is represented by a palmar continuation of the cuneiform facet (de Blainville, 1849: pl. 3).

The axis of the convex component of the sellar cuneiform facet of the ulna has an anteromedial–posterolateral orientation as in *Sus* (Walker, 1985). It is different, however, in other primitive tylopod groups. Thus, this axis is anteroposterior in *Cainotherium* and mediolateral in *Merycoidodon*. When pronated, the ridge separating the lunar and scaphoid facets of the radius is oblique to the anteroposterior plane of the bone (Fig. 14J, K) as in *Sus*, *Hippopotamus* and *Cainotherium* (Hürzeler, 1936; Walker, 1985: fig. 44). In modern families of tylopods and ruminants and in the extinct tylopods *Merycoidodon* and *Xiphodon*, it is more or less parallel with this plane. In *Sus* the radial facet of the lunar is correspondingly oblique and is similar to that of *Anoplotherium* as noted by Cuvier (1805: 268, pl. 51 [2], fig. 1, no. 1). In *Sus*, the oblique orientation of the distal facets of the radius and ulna result in a splayed foot posture during walking. This is evident from their tracks (Bang & Dahlstrom, 1974:

Figure 20. *Anoplotherium latipes*. Ham 3 skeleton (IWCMS. 1999.128). A–F, left tibia. G–I, left distal fibula. J, K, proximal left fibular epiphysis. L, proximal right fibular epiphysis. Views are anterior (A, G), medial (B, H), posterior (C), lateral (D, I), distal (E), proximal (F), posteromedial (J, L) and anterolateral (K). Coated with ammonium chloride. Scale bar = 50 mm.

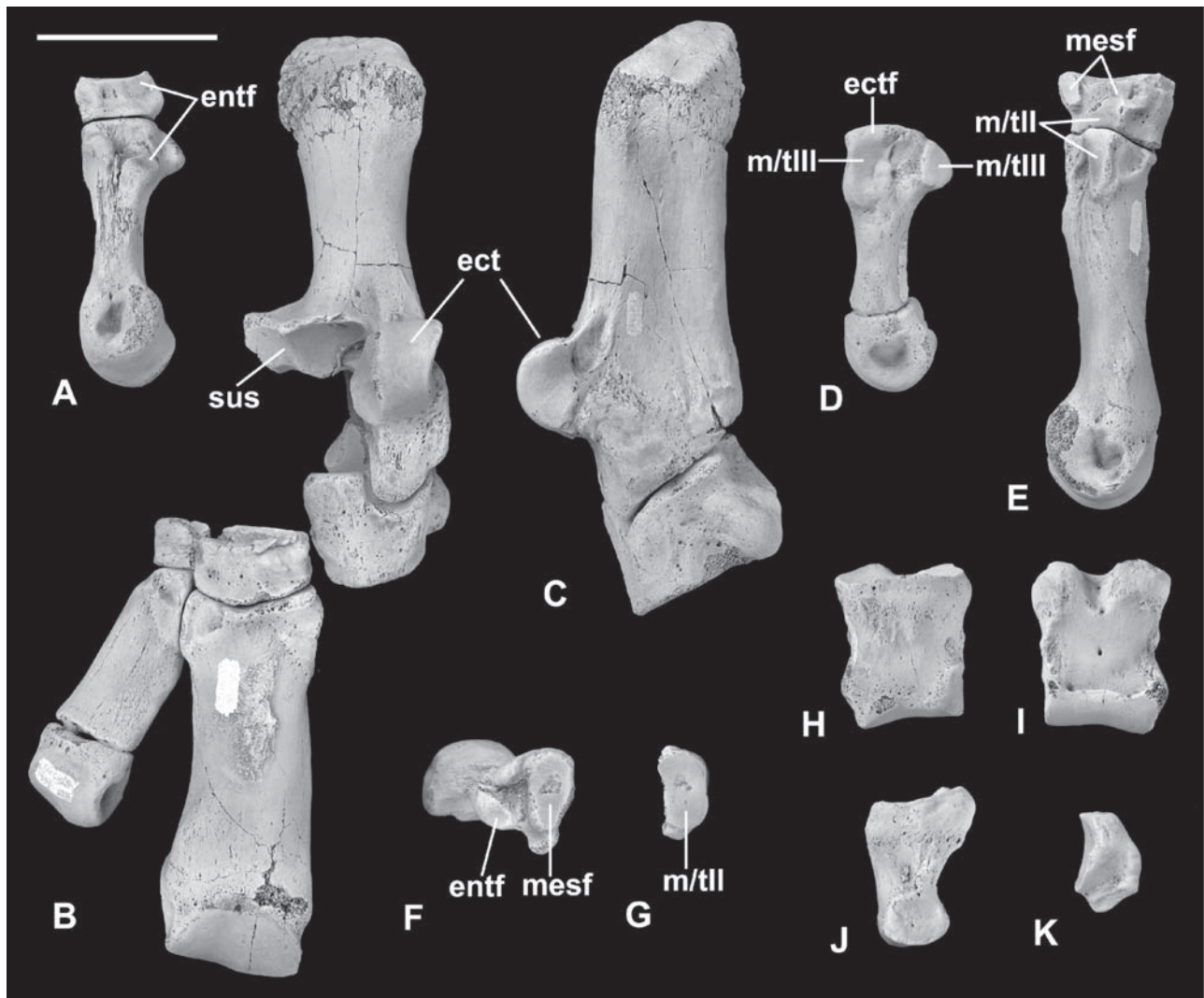


Figure 21. *Anoplotherium latipes*. Ham 3 skeleton. A, right metatarsal II and right mesocuneiform articulated (IWCMS. 1999.128). B, partial pes articulated shown as left, comprising left calcaneum, left cuboid, right mesocuneiform (reversed), left ectocuneiform, left metatarsal III (IWCMS. 1999.128) and left metatarsal II (IWCMS. 2000.390). C, left calcaneum. D, left M/T II. E, left ectocuneiform and M/T III articulated. F, right M/T II. G, right mesocuneiform. H–J, pedal left first phalanx III (IWCMS. 1999.128). K, sesamoid (IWCMS. 1999.128). Views are medial (A, E), anterior (B), lateral (C, D, J), proximal (F), distal (G), dorsal (H), ventral (I) and medial or lateral (K). Coated with ammonium chloride. Scale bar = 50 mm.

65). Consistent with the morphology, a splayed foot orientation of *c.* 16°, when pronated, is also indicated for *Anoplotherium* during walking by trackways attributed to this genus (Ellenberger, 1980). When supinated, the carpus and the rest of the manus of *Anoplotherium* would have been held at an even more oblique angle to the parasagittal plane.

It is noteworthy that the distal facets of neither the radius nor the ulna allow any rotational movement with the first carpal row about the proximo-distal axis. Therefore, the distal pronation–supination motion of the radius against the ulna must be accommodated in

the wrist between the carpal bones themselves. The only carpal that has facets of a shape and size that could allow such movement against adjacent carpals is the cuneiform. An associated partial right manus of *A. commune* from Montmartre (BMNH.M2212), consisting of proximal M/CIII–IV, cuneiform and unciform, is informative in this respect (Figs 24A, B, 25). The unciform facet on the cuneiform is smaller in area than the cuneiform facet on the unciform (Fig. 24A, B). Unlike the former, the latter facet curves disto-palmarly. When the anterior faces of cuneiform and unciform are aligned, this disto-palmar extension of the

cuneiform facet on the unciform makes no contact with the cuneiform (Fig. 25A). This is its position when the radius and ulna are supinated. In order to make contact with the disto-palmar part of the cuneiform facet on the unciform, the cuneiform has to rotate slightly posterolaterally and slide disto-palmarly, losing contact with the unciform more anteriorly (Fig. 25B). This is its position when the radius and ulna are pronated.

Articulation between the cuneiform and the only other adjacent carpal, the lunar, appears to have been complex. An isolated right lunar from another individual from Montmartre (BMNH.29468) suggests how it might have taken place. The cuneiform facet on the lunar is gently concave, but angled, the anterior half vertically orientated, the posterior half tilted slightly distally. The lunar facet on the cuneiform is convex

and more strongly angled than the cuneiform facet on the lunar, but the anterior and posterior halves have similar relationships, one with the other, in the vertical plane to those of the lunar bone. The stronger curvature on the facet of the cuneiform, however, indicates two articulatory positions for the cuneiform on the lunar, which would apparently allow for its movement on the unciform described above.

However, study of more carpals shows that there is individual variation in the development of facets between the cuneiform and lunar. Thus, the cuneiform facet of another lunar (MNHN.GY150) is less obtusely concave than on BMNH.29468. Therefore, the nature of the movement between the cuneiform and lunar of different individuals postulated above may not be reliable. Two articulated mani from Montmartre with all the carpals except the pisiform represented appear to show the relevant articulations. However, one of these (MNHN.GY137: de Blainville, 1849: pl. 3, top left) has the lunar restored posteriorly, whilst the other (MNHN.GY138) has the cuneiform broken away laterally, thus not showing the full extent of its unciform facet. Nevertheless, the facetting between the lunar and cuneiform in GY138 is complete. Here, the angles of the facets essentially match, not allowing a shift of the cuneiform from articulation with the anterior facet on the lunar to articulation with the posterior facet as suggested above. However, manipulation of the lunar, cuneiform and unciform in this specimen does allow the rotation of the cuneiform on the unciform as postulated and contact is thereby retained by the cuneiform with the lunar posteriorly. Anteriorly, the lunar facet of the cuneiform has a rounded distal edge, which merges with the unciform facet, and more of

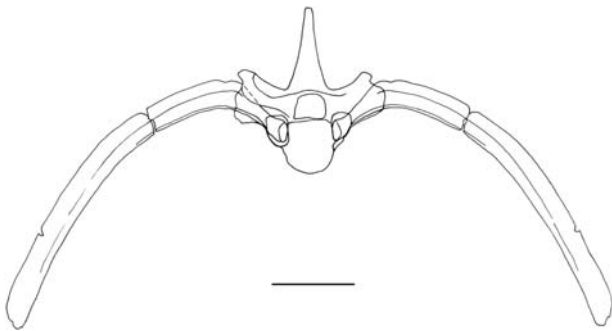


Figure 22. *Anoplotherium latipes*. Ham 3 skeleton. Reconstruction of dorsal part of rib cage in anterior view by articulating thoracic vertebra 4? and 8th or 9th ribs (see Fig. 7). Scale bar = 50 mm.

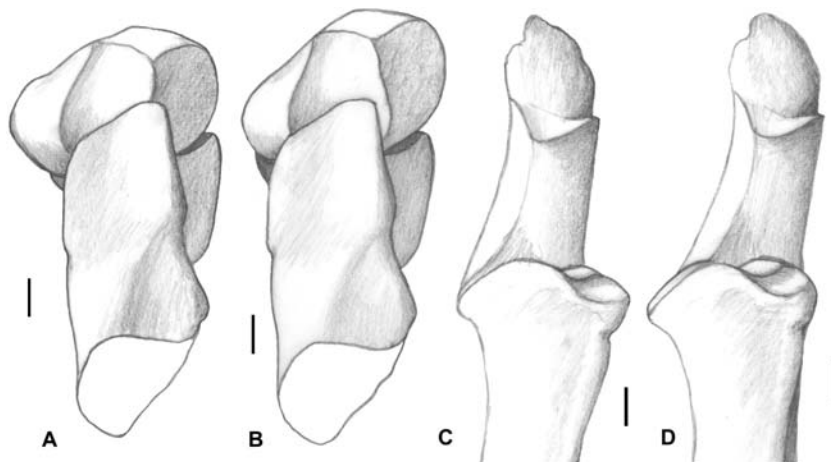


Figure 23. *Anoplotherium latipes*. Ham 3 skeleton. Reconstruction of pronation and supination articulatory positions of proximal left ulna and radius. A, C, pronated. B, D, supinated. Views are anteroproximal (A, B) and anterior (C, D). Scale bars = 10 mm.

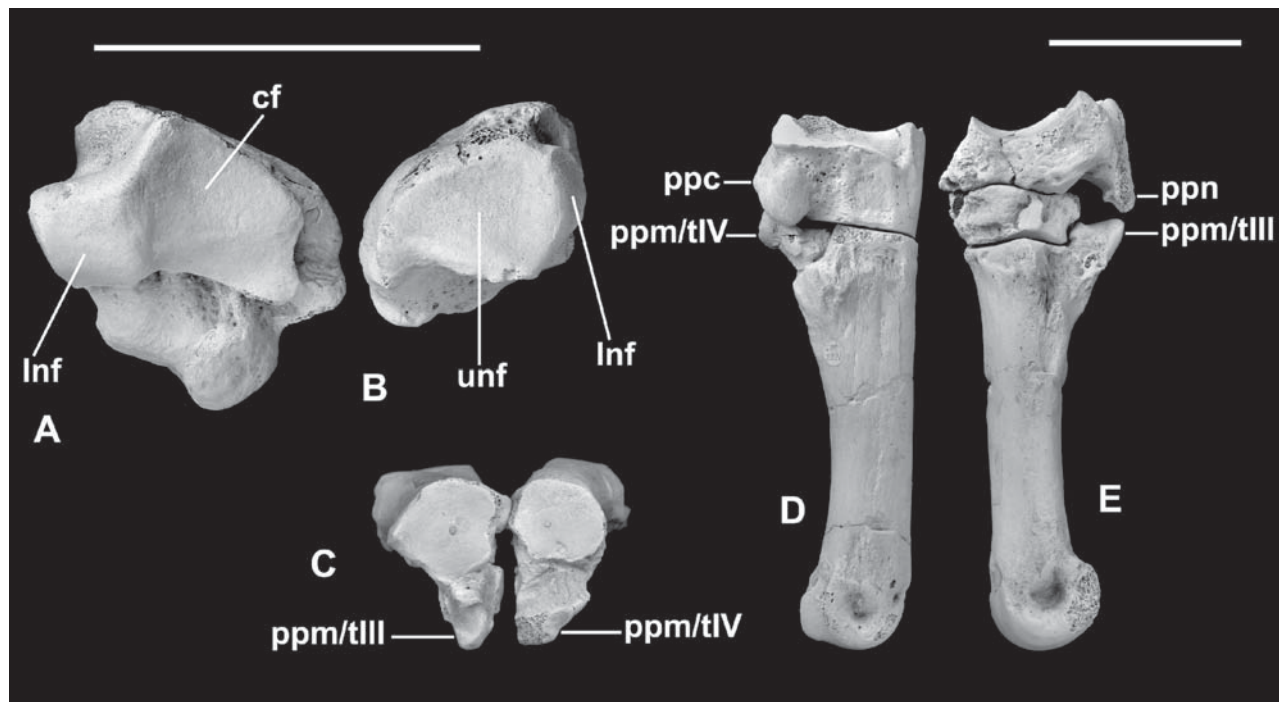


Figure 24. *Anoplotherium commune*, Gypse, Montmartre. A, B, right associated unciform (A) and cuneiform (B) (BMNH.M2212). C–E, right associated cuboid (D), navicular and ectocuneiform (E), metatarsal III (C, E) and metatarsal IV (C, D) (BMNH.M2221). Views are proximal (A, C), distal (B), lateral (D) and medial (E). Coated with ammonium chloride. Scale bars = 50 mm, the larger for A–B, the smaller for C–E.

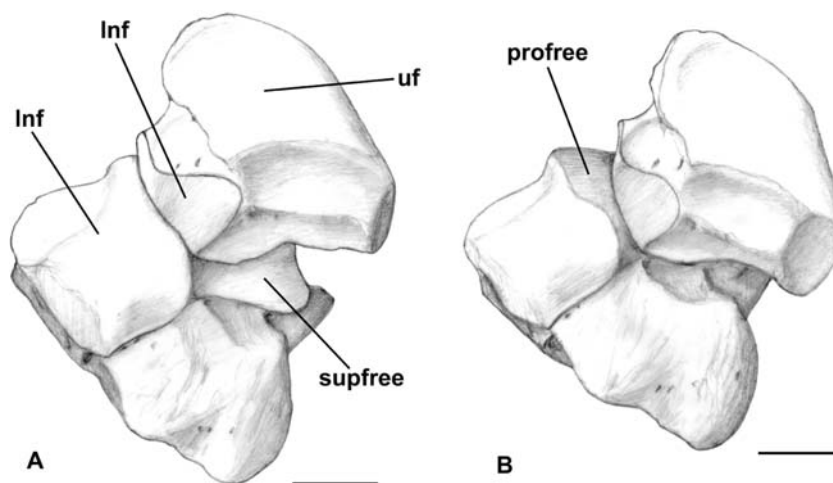


Figure 25. *Anoplotherium commune*, Gypse, Montmartre. Right cuneiform and unciform (BMNH.M2212) in proximo-postero-medial view, shown articulated during supination (A) and pronation (B). Scale bar = 10 mm.

this distal part contacts the lunar as the cuneiform slides on the unciform. Contact is then lost between the cuneiform and lunar proximally. Based on observation of both GY137 and GY138, the proximal facets of the unciform and magnum in contrast fit well for size and angle with the opposing distal facets of the

lunar and scaphoid, indicating that no palmarflexion was possible at this part of the mid-carpal joint.

Although unknown for any artiodactyl today, limited pronation–supination was also possible in the related extinct tylopods *Cainotherium* (Hürzeler, 1936) and *Merycoidodon* (pers. observ.), but how this

was accommodated in the wrist has not been documented. In contrast, in another extinct tylopod *Xiphodon*, the two bones are immovable at an irregular articulation (Pomel, 1851).

The limited involvement of the wrist of *Anoplotherium* in pronation–supination contrasts with many primates, where much more of the mid-carpal joint is mobile (e.g. Beard & Godinot, 1988; Godinot & Beard, 1991). Some taxa (e.g. hominids and the ground sloth *Megatherium*) have resolved the problem by removing the ulna from contact with the carpals (Coombs, 1983; Gray, Pick & Howden, 1901). Others (e.g. felid carnivorans) have a proximo-distally orientated articulation between the ulna and cuneiform, allowing rotation (pers. observ.). The relatively limited degree of pronation–supination and of carpal accommodation in *Anoplotherium* suggests that the adaptation is not primary, but that forelimb mobility has re-evolved from a primitive ungulate parasagittal gait associated with acquiring hooves and full terrestriality.

Hand

The alignment of the anterior surface of the cuneiform with those of the other carpal bones occurred with supination, not pronation, so supination appears to have been the more natural hand position. Given this pronation–supination ability of *Anoplotherium*, one might expect the enigmatic second manual digit (when present) to have performed some prehensile function in connection with food procurement like the thumb of primates or the enlarged radial sesamoid of the giant panda (*Ailuropoda*). However, through manipulation of apparently composite three-digit hands of *Anoplotherium* from La Débruge, no rotation or even abduction–adduction of digit II with respect to the other digits was possible. The possibility of some movement in the parasagittal plane has been investigated by examination of the relevant facets in the Ham 3 specimen. Although the opposing proximal facets have concave (M/C II) and convex (M/C III) elements, their sizes match and appear to have allowed no movement (Fig. 15P, Q). Nevertheless, the articulation between these two metacarpals does not follow an anteroposterior plane. In fact digit II was immovably abducted in a mediopalmar direction (Fig. 15G–J), which, together with the adduction performed by the m. subscapularis, could have helped with support amongst branches when standing bipedally.

Manipulation of the metacarpals and phalanges indicates their range of movement in a parasagittal plane. That between right M/C III and right first phalanx III (Fig. 15H, K, L, P), when a sesamoid (e.g. Fig 21K) is inserted, allows no palmarflexion beyond the longitudinal axis. That between left first phalanx III and a manual second phalanx allows only a little palmarflexion because of the proximo-ventral projec-

tion of the proximal articulation (Fig. 15K, N). No unguals belonging to the Ham 3 skeleton have been found, but manually articulating a range of isolated *Anoplotherium* unguals from Montmartre, Quercy and the Isle of Wight produces palmarflexion beyond the longitudinal axis of up to about 30°.

The presence of an m. extensor carpi radialis inserted proximally on M/CIII and IV (Fig. 15H) suggests extension and slight abduction capabilities of the hand as indicated for humans (Gray *et al.*, 1901: 396, 400) and the leptictid *Palaeictops* (Rose, 1999), for example.

HINDLIMB

Hip

The greatly flared ilia indicate significant development on their dorsal surfaces of the gluteal musculature associated with extension of the femur thereby raising the trunk to an erect stance, as in humans and as interpreted to be the case in the ground sloth *Megatherium*. Consistent with the ilial structure are the relatively long ischia and a pubic symphysis that is 43% of the length of the entire pelvis (Fig. 26; Roman, 1922: pl. 3, fig. 2), thus well developed for withstanding exorotational forces such as experienced in an erect stance (Coombs, 1983). The chalicotheres *Moropus* and *Chalicotherium* have ilia slightly less flared than in *Anoplotherium* and a much shorter pubic symphysis (Holland & Peterson, 1914: pls 59, 61; Zapfe, 1979: 107–110). The prominent attachment for origin of m. rectus femoris suggests a strong muscle, one of whose actions is extension of the knee joint. The posterior positioning of the acetabular notch, being like *Chalicotherium*, indicates a re-orientation of the teres

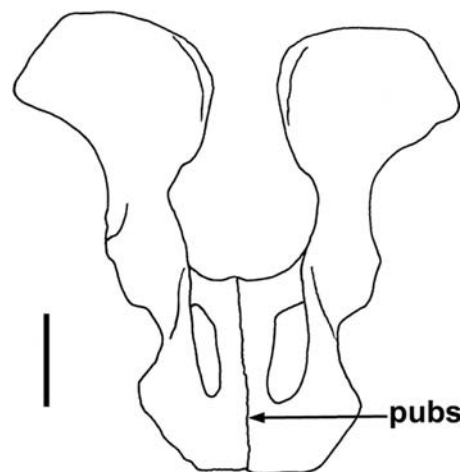


Figure 26. *Anoplotherium latipes*, Mormoiron. Pelvis in dorsal view, redrawn from Roman (1922: pl. 3, fig. 2). Scale bar = 100 mm.

ligament, which might be associated with a femur habitually more posteriorly rotated with respect to the pelvis than is normal in quadrupedal mammals.

Leg

The laterally bowed tibia (Fig. 20A, C) shows that when articulated with the femur, the hind leg would have been bent medially at the knee (knock-kneed). If the femora were held vertical in the parasagittal plane, the tibiae would have splayed distally (Fig. 27). Alternatively, the femora could have converged distally as in *Homo*, giving the tibiae a vertical orientation.

Foot

The pes is robust, with the metatarsals slightly shorter than the metacarpals. According to material from Montmartre it was unguligrade (Abusch-Siewert, 1989). The gently convex proximal articulation of M/T II is matched by the gently concave distal facet of the mesocuneiform. That of the metatarsal is slightly longer than that of the mesocuneiform but is

unlikely to have allowed any plantarflexion of the second pedal digit at the upper metatarsal joint (Fig. 21A, F, G). The proximal facets situated anteriorly between M/T II and M/T III (Fig. 21D, E) have essentially the same shape as those between M/C II and M/C III, but the long plantar processes of the metatarsals also bear opposing facets more posteriorly. These are flatter and in the Ham 3 individual are only visible on M/T II (Fig. 21D), that area of M/T III being broken. However, they can be observed on La Débruge specimens, where they vary somewhat intraspecifically in size and shape. As with the metacarpals, no movement appears to have been possible between M/T II and M/T III, but digit II was also abducted in a medioplantar direction (Fig. 21B).

The large proximal posterior processes of M/T III and IV in Montmartre specimens (e.g. BMNH.M2221) are projected slightly proximally (Fig. 24C–E). They are matched in size in the tarsal region by posterior processes on the cuboid and navicular which have a distal projection so that they nearly meet those of the metatarsals. These structures suggest the attachment of powerful suspensory ligaments to prevent excess dorsiflexion under load.

In the absence of an astragalus belonging to the Ham 3 individual, it is difficult to reconstruct the orientation of the ankle to the tibia. However, a left *A. latipes* astragalus from Quercy (BMNH.M1844), despite breakage to the proximal end of the lateral trochlear ridge, fits adequately with the left calcaneum and well with the left tibia of the Ham 3 individual. By articulating the bones manually, it can be seen that the long axis of the foot (i.e. parallel with the tuber of the calcaneum) is oblique to the tibia, which must therefore have splayed laterally at an angle of *c.* 10° to the parasagittal plane, in order to have ensured a vertical foot (Fig. 27).

Trackways attributed to *Anoplotherium* and *Diplobune* (the latter genus always three-toed) show no ground impression of either M/C II or M/T II (Ellenberger, 1980). This would accord with the medially angled orientation of the second digit compared with the third and fourth when walking, thus preventing the shorter digit II from touching the ground. Because of the symmetry of the two main digits, the footprints also imply that the foot was held vertical in its antero-posterior plane. Therefore, during walking, the tibiae must have been splayed as calculated above. However, it is possible that M/T II could have been used as a prop during vertical erection of the trunk. For M/T II to make contact with the ground, the feet themselves would have to have maintained a digitigrade stance and shown lateral splaying vertically from the parasagittal plane at an angle of *c.* 30°, the tibiae therefore in excess of 40°. It would be necessary to find footprints showing an impression of the 2nd digit

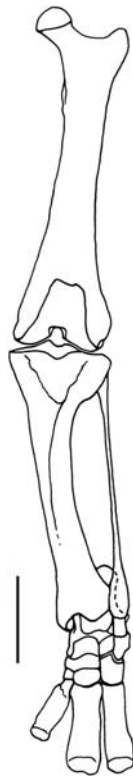


Figure 27. *Anoplotherium latipes*. Ham 3 skeleton. Reconstruction of left leg in anterior view, with knee bent in probable normal standing position, showing distally splayed tibia. Scale bar = 100 mm.

to test this hypothesis. Lateral spacing of the large *Anoplotherium* footprints (*Anoplotheriipes lavocati* Ellenberger, 1980) provide independent evidence of quadrupedal stance while walking. The footprints are 37–40 cm apart, measuring between their outer edges (Ellenberger, 1980: 53). Using the Mormoiron pelvis (Roman, 1922, where the reduction must be to a quarter, not to a third as stated) and the Ham 3 right femur, it is estimated that the lateral distance between the greater trochanters of the femora would have been c. 31 cm. Given the 10° splaying of the tibiae calculated above, and their correct articulations with the femur, the femora must have converged slightly distally (at an angle of c. 4° vertically to the parasagittal plane), giving the animal a 'knock-kneed' stance. The spacing of the feet of the Ham 3 skeleton on this basis (from the lateral edges of digit IV) is estimated at c. 34 cm. This is reasonably consistent with Ellenberger's footprint measurements, given that the Ham 3 animal was immature. The individual *Anoplotherium* footprints also show slight lateral splaying horizontally from the parasagittal plane by about 16° (Ellenberger, 1980: 52, fig. 15, pl. 1). As there is no torsion between the proximal and distal ends of the tibiae, the femora would have been rotated slightly postero-laterally, their necks being orientated antero-medially partly for this reason and partly because of their independent anterior deflection. The postero-lateral rotation of the femur would also be consistent with the postero-lateral orientation of the acetabulum (Figs 16, 17). Moreover, the postero-medially positioned teres fovea (Fig. 19D) would then be opposite the acetabular fossa.

ADAPTATIONS FOR BIPEDAL BROWSING

COMPARISONS WITH OTHER BIPEDAL BROWSERS

Many of the morphological features and functional attributes of *Anoplotherium* described above are indicative of habitual extended limb bipedality for foraging (Slijper, 1946; Coombs, 1983), although not for the purposes of normal walking or running. Notable are: the flared ilia for muscle attachment to raise the trunk vertically; long pubic symphysis to withstand the axial stresses under an erect stance; posterolaterally directed acetabula and slightly postero-laterally rotated hind limbs; short (compared with the femora) medially bowed tibiae, providing support in a splayed stance; trunk vertebrae enlarging in a posterior direction along the column to bear the increased weight of a vertical trunk region; lumbar vertebral spines allowing a degree of lordosis; extensive attachment areas on scapula and humerus for supraspinous and deltoid muscles for raising the forelimbs; oblique central articulations and strongly developed neural arches on

cervical vertebrae 4–7 to maintain the neck obliquely upright; long muscular tail for balance; first phalangeal articulations differently orientated on fore versus hind feet; probable powerful suspensory ligaments to prevent excess dorsiflexion under load; and possibly broad rib cage functioning to bring the centre of gravity nearer the vertebral column. These features can be found to a greater or lesser degree in modern and fossil bipedal browsers, namely the living gerenuk [*Litocranius walleri* (Brooke, 1878), see Richter, 1970], gorilla [*Gorilla gorilla* (Savage & Wyman, 1847), see Gregory, 1950], giant panda [*Ailuropoda melanoleuca* (David, 1869), see Davis, 1964] and the extinct genera *Megatherium*, *Moropus*, *Chalicotherium* and *Homalodotherium* (see Coombs, 1983). In particular, the moments of resistance calculated for the vertebral centra of *Anoplotherium* (Fig. 28) are very similar in pattern to those of *Moropus*, *Litocranius* and a pathologically forelimbless goat (*Capra hircus* Linnaeus, 1758) (Slijper, 1946; Richter, 1970; Coombs, 1983). Limb bone proportion indices are also important, although less diagnostic in isolation. For *Anoplotherium*: the brachial index (radial length as percentage of humeral length) is 81.2, closest to the chalicotheres *Ancylotherium* and *Chalicotherium*, the primitive tylopod *Agriochœrus*, the ground sloth *Megalocnus*, the anteater *Tamandua*, the marsupial *Vombatus*, the giant panda *Ailuropoda* and the proboscidean *Elephas*; the crural index (tibial length as a percentage of femoral length) is 76.4, closest to the chalicotheres *Tylocephalonyx* and the ground sloths *Megatherium* and *Acratocnus*, the bears *Ursus* and *Ailuropoda*, *Gorilla* and *Vombatus*; the intermembral index (length of humerus plus radius as a percentage of length of femur plus tibia) is 84.9, closest to *Agriochœrus*, the ground sloth *Hapalops*, the anteater *Myrmecophaga*, the monotreme *Tachyglossus*, and the bovids *Litocranius* and *Capra*; the olecranon index (olecranon length as a percentage of ulna length) is 16.1, closest to *Elephas* and the ground sloth *Megalo-*

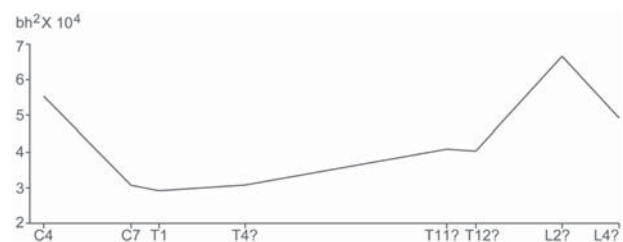


Figure 28. Graph of moments of resistance (bh^2) of vertebral centra of the Ham 3 skeleton, calculated after Slijper (1946), i.e. maximum breadth \times height² in millimetres of posterior articular surface.

nyx (Coombs, 1983: tables 3, 5). Of these, *Tachyglossus*, *Vombatus*, *Tamandua*, *Myrmecophaga*, *Elephas*, *Capra* and *Agriochoerus* clearly have adaptations very different from those of *Anoplotherium* and are not consistently close across the different indices. The most consistently similar taxa are the ground sloths and the chalicotheres, which have been interpreted to be extended-limb bipedal browsers (Coombs, 1983: 25–44, 57–62).

Two indices are distinctive of *Anoplotherium* and relate to development of the deltoid muscle for raising the forelimb. They are: width of the supraspinous fossa relative to that of the infraspinous fossa of the scapula; and distal extent of the deltopectoral crest of the humerus. Table 5 shows these indices for a range of living and extinct mammals. Most have the supraspinous fossa narrower than the infraspinous fossa and the deltopectoral crest extending distally for less than 60% of the length of the humerus. Notable exceptions with wider supraspinous fossae and longer deltopectoral crests are the anoplotheres *Anoplotherium* and *Diplobune*, and various ground sloths (*Megatherium*, *Megalonyx*, *Nothrotheriops*) interpreted to have been bipedal browsers (Coombs, 1983). Other bipedal taxa like the chalicothere *Moropus* have a wide supraspinous fossa, but short deltopectoral crest (NB: the scapula of *Chalicotherium* is incompletely known, Zapfe, 1979); or, like gorilla and bears, have fairly long

deltopectoral crests, but narrow supraspinous fossae; whereas the garenuk has very low values for both indices, like typical quadrupedal bovids. The foraging adaptations associated with bipedality of these other taxa largely involve different aspects of their anatomy.

Despite the similarities between *Anoplotherium* and known modern or postulated extinct bipedal browsers, there are some interesting differences. For instance, all have a shorter pubic symphysis than *Anoplotherium*, only the ground sloths share with it a long muscular tail (albeit much more strongly developed), the latter and the chalicotheres have clawed unguals, and *Ailuropoda* and *Gorilla* have prehensile thumbs or thumb analogues (Gregory, 1950; Davis, 1964). In the case of *Chalicotherium* and *Gorilla*, the difference might be related to the fact that these genera have a semi-erect stance with the elongated forelimbs helping to support the body on the ground. The bipedal stance of *Anoplotherium* would have involved the forelimbs being free of the ground and therefore a greater need for appropriate support structures in the pelvis, hind limbs and the muscular tail. On the other hand, *Moropus* is not quadrupedally erect, yet it is no more like *Anoplotherium* than is *Chalicotherium*. There is a mosaic of adaptations to bipedal browsing and the only traits common to all are the caudally enlarging trunk vertebrae and the separated neural spines allowing lordosis (Fig. 29).

TRAIT	<i>Anoplotherium</i>	<i>Moropus</i>	<i>Chalicotherium</i>	<i>Megatherium</i>	<i>Megalonyx</i>	<i>Nothrotheriops</i>	<i>Litocranius</i>	<i>Ailuropoda</i>	<i>Gorilla</i>	<i>Homalodotherium</i>
High brachial index	X		X	X	X	X	X			X
High intermembral index		X	X	X	X	X			X	X
Low crural index	X		X	X	X	X		X	X	X
Long neck		X					X			
Cranially directed glenoid on scapula		X	X							
Prominent long deltopectoral crest (humerus)	X			X				X		X
Wide entepicondyle (humerus)		X	X	X	X	X		X		X
Large long supinator crest (humerus)		X	X	X	X	X		X		X
Side-to-side deviation in wrist (with or without rotation)	X	X	X	X	X	X		X	X	X
Hook-like manus		X	X	X	X	X				X
Long metacarpals		X	X				X			X
Long sacrum, well fused to pelvis				X	X	X				?
Flared ilium	X		X	X	X	X		X	X	X
Large tail	X			X	X	X				
Weight-bearing pes different from manus	X	X	X	X	X	X			X	X
Long pubic symphysis	X						X			
Trunk vertebrae enlarging caudally	X	X	X	X	X	X	X	X	X	X
Supraspinous fossa larger than infraspinous fossa (scapula)	X	X		X	X	X				?
Prehensile manus								X	X	
Posteriorly tilted acetabulum	X	X	X	X	?	X			X	
Broad rib cage	X		X	X	?	X		X		?
Medially bowed tibia	X		X	X	X	X		X		X
Trunk vertebral spines separated by gap (lordosis)	X	X	X	X	?	X	X	X	X	X

Figure 29. Bipedal browsing adaptations in living and extinct mammal genera, expanded from Coombs (1983: fig. 4).

Table 5. Width of supraspinous fossa of scapula as percentage of infraspinous fossa – $[(W.Sf.) \times 100/W.Lf.]$ – and length of deltopectoral crest of humerus from proximal end as percentage of humeral length – $[(L.Dp.) \times 100/L.H.]$ – in a range of living and extinct mammals

Name	$(W.Sf.) \times 100/W.Lf.$	$[(L.Dp.) \times 100/L.H.]$	Source
<i>Hapalops</i> sp.*	142	63	Scott (1903); specimen
<i>Megalonyx jeffersoni</i> *	(133)	67	Leidy (1855); specimen
<i>Megatherium americanum</i> *	121	65	
<i>Anoplotherium commune/latipes</i> *	118	67	specimen; Cuvier (1825)
<i>Moropus elatus</i> *	116	48	Holland & Peterson (1914)
<i>Camelus dromedarius</i>	113	41	Walker (1985)
<i>Enhydra lutris</i>	113	51	
<i>Diplobune secundaria</i> *	110	68	de Blainville (1849)
<i>Hystrix</i> sp.	110	56	
<i>Nothrotheriops shastense</i> *	108	61	Stock (1925)
<i>Bradypus</i> sp.	99	48	
<i>Aonyx capensis</i>	97	43	Walker (1985)
<i>Panthera tigris</i>	91	48	
<i>Meles meles</i>	91	59	
<i>Mellivora capensis</i>	83	52	Walker (1985)
<i>Vombatus ursinus</i>	83	53	
<i>Homalodotherium cunninghami</i> *	(82)	68	Scott (1930); Lydekker (1893)
<i>Gorilla gorilla</i>	80	62	Gregory (1950)
<i>Orycteropus afer</i>	75	63	Walker (1985)
<i>Diceros bicornis</i>	73	44	Walker (1985)
<i>Melursus ursinus</i>	71	63	
<i>Ailuropoda melanoleuca</i>	68	58	Davis (1964)
<i>Myrmecophaga tridactyla</i>	67	51	
<i>Chalicotherium grande</i> *	(62)	36	Zapfe (1979)
<i>Agriochoerus latifrons</i> *	62	47	Scott (1940)
<i>Crocota crocuta</i>	61	49	
<i>Trogosus</i> spp.*	60	59	Gazin (1953)
<i>Merycoidodon gracilis</i> *	60	50	Scott (1940); specimen
<i>Giraffa camelopardalis</i>	59	39	Walker (1985)
<i>Vulpes vulpes</i>	59	44	
<i>Equus</i> sp.	58	41	Walker (1985)
<i>Diprotodon optatus</i> *	58	58	
<i>Stylinodon mirus</i> *	56	48	Schoch (1986)
<i>Procavia capensis</i>	50	45	
<i>Dendrohyrax dorsalis</i>	50	48	
<i>Sus scrofa</i>	48	40	
<i>Loxodonta africana</i>	44	44	Walker (1985)
<i>Hippopotamus amphibius</i>	44	53	Walker (1985)
<i>Oryctolagus cuniculus</i>	44	41	
<i>Uintatherium anceps</i> *	40	61	Marsh (1886)
<i>Cainotherium</i> sp.*	40	48	Hürzeler (1936)
<i>Homo sapiens</i>	39	53	Gray <i>et al.</i> (1901)
<i>Dasyurus novemcinctus</i>	39	50	
<i>Gazella soemmerringi</i>	34	42	
<i>Litocranius walleri</i>	30	38	

*Denotes extinct taxon.

They are arranged in descending order of percentage width of the supraspinous fossa. Percentage values of the supraspinous fossa greater than 100 and of the deltopectoral crest greater than 60 are shown in bold type. Values in parentheses are estimates based on reconstructions by their authors. A blank source box indicates measurements taken direct from specimens.

The very long tail with small chevron bones, yet relatively weak processes, has no close analogue among other mammals. The only extended-limb bipedal browsers with similar but more extreme adaptations in this respect are the ground sloths *Megatherium*, *Megalonyx* and *Nothrotheriops* (Fig. 29; Coombs, 1983), which have tails shorter than that of *Anoplotherium*, but much stouter and with more robust chevron bones as well as stronger vertebral processes. In the ground sloths, the tail is thought to have been used as a prop during bipedal browsing, with a wrist structure adapted for reaching and pulling (cuneiform not contacting the ulna) (Mendel, 1979; Coombs, 1983). *Megatherium* also has greatly flared ilia and a long sacrum well fused to the pelvis (Coombs, 1983) unlike some bipedal browsers (e.g. *Litocranius*, *Ailuropoda*, *Chalicotherium* and *Moropus*), all of which have short to very short tails. Moreover, *Megatherium*, as a member of the order Xenarthra, primitively has a strong tail, unlike pecoran artiodactyls, perissodactyls and ursid carnivorans, where it has been substantially reduced in the course of evolution. Early primitive artiodactyls, in contrast, had long tails (e.g. *Amphirhagatherium*, *Messelobunodon*, *Diacodexis* – Franzen, 1981; Rose, 1985; Erfurt & Altner, 2003). *Litocranius*, *Ailuropoda* and chalicotheres were probably preadapted through tail reduction to develop bipedality differently from xenarthrans. In *Anoplotherium*, the already longish tail was further lengthened and endowed secondarily with chevron bones as a muscular structure, which combined with a long pubic symphysis, long ischium and flared ilia to facilitate bipedality. The extreme difference in length of fore and hind limbs in *Gorilla* and *Chalicotherium* means a semi-erect stance while retaining all four feet on the ground. The clawed or prehensile grasping manus perhaps provided more body support in the absence of a functional tail, when standing on the hind legs than was necessary in *Anoplotherium*. The clawed unguals would also have given similar support to short-tailed *Moropus* when standing on its hind legs. It remains difficult to understand, however, how *Litocranius* can function as a bipedal browser with such minimal adaptations as slightly longer ischium and pubic symphysis, posteriorly enlarging trunk vertebrae, spaces between lumbar neural spines (to allow lordosis) and slightly different development of some of the hind limb muscles (Richter, 1970). However, relatively small body size may be a facilitating factor.

THE POSSIBILITY OF SEXUAL DIMORPHISM

Why does *Anoplotherium* have no claws or prehensile 'thumb'? In fact, not all bipedal browsers do. *Litocranius* lacks any forelimb grasping ability. *Anoplotherium* does, nevertheless, show limited pronation–

supination of the hand, a divergent second digit in the three-toed species, and limited palmarflexion in the wrist and between the second and third phalanges, which combined may have provided a small degree of grasping. On the other hand, the two-toed species had only the pronation–supination and limited plantarflexion capability. An alternative hypothesis that the divergent digit II was used for intraspecific fighting, *A. latipes* being the male and *A. commune* the female of a single species, is investigated below.

Problems of differentiating *A. latipes* from *A. commune* are longstanding. Stehlin (1910: 944) was unable to find a reliable dental character that separated them. He felt that any small differences could be accounted for by individual variation, something supported by the author's personal observations. In the absence of characters, Stehlin was left to conclude that most large *Anoplotherium* jaws from La Débruge and Quercy must belong to *A. latipes* because of the rarity of bones belonging to two-toed feet at these sites. de Bonis (1964) also was unable to separate *A. latipes* from *A. commune* on anything other than foot structure. Table 6 gives statistics of measurements of lower molars of *A. commune* and *A. latipes* (undifferentiated) from a variety of sites spanning almost their entire known temporal range, which totals at least 2 Myr. Sites include the type localities of both species, namely Montmartre and La Débruge, respectively. Table 6 also gives similar data for the smaller species *A. laurillardii* from its type locality La Débruge and for all three species combined. Coefficients of variation for lengths of M_1 , M_2 and M_3 of *A. commune* and *A. latipes* (undifferentiated) are low, indicative of a single species (Gingerich, 1974). Widths of these teeth show higher coefficients of variation than do the lengths. However, when the measurements of the *A. laurillardii* teeth are added, all the coefficients of variation increase greatly, indicating more than one species. At a single site, it could be argued that two recently formed sister species might retain teeth morphologically and dimensionally identical, but with differently adapted feet. However, reproductive isolation over 2 Myr would surely result in some degree of dental if not other anatomical differentiation, at least in size. This long-term homogeneity is here proposed as strong evidence for considering *A. commune* and *A. latipes* to represent a single species, *A. commune* Cuvier, 1804c being the senior synonym.

If *A. commune* and *A. latipes* are conspecific, they must be dimorphic for digit number. Figure 30 shows length–width proportions of astragali of *Anoplotherium* from a variety of sites. The cluster of small values from La Débruge is judged to represent *A. laurillardii*, the remainder *A. commune* plus *A. latipes*. Those from Montmartre (*A. commune* type assemblage) form an extended plot, overlapping for

Table 6. Statistics of length and width measurements of lower molars of *Anoplotherium* from various sites

Name	Tooth	Dimension	N	OR	Mean	S	V
<i>A. commune/latipes</i>	M ₁	Length	12	20.6–23.6	22.1	0.84257	3.81
<i>A. laurillardi</i>	M ₁	Length	5	17.8–19.2	18.6	0.50299	2.70
All three species	M ₁	Length	17	17.8–23.6	21.1	1.82447	8.65
<i>A. commune/latipes</i>	M ₁	Width	8	14.0–18.3	15.2	1.33838	8.81
<i>A. laurillardi</i>	M ₁	Width	5	10.9–12.4	11.8	0.73007	6.19
All three species	M ₁	Width	13	10.9–18.3	13.9	2.04507	14.91
<i>A. commune/latipes</i>	M ₂	Length	21	24.0–28.5	25.9	1.16896	4.51
<i>A. laurillardi</i>	M ₂	Length	4	20.9–21.7	21.3	0.36969	1.74
All three species	M ₂	Length	25	20.9–28.5	25.1	2.03312	8.10
<i>A. commune/latipes</i>	M ₂	Width	17	14.0–19.0	16.6	1.17892	7.10
<i>A. laurillardi</i>	M ₂	Width	3	12.5–12.8	12.6	0.17321	1.38
All three species	M ₂	Width	20	12.5–19.0	16.0	1.82581	11.41
<i>A. commune/latipes</i>	M ₃	Length	11	37.6–42.8	40.8	1.54278	3.78
<i>A. laurillardi</i>	M ₃	Length	3	33.0–35.7	34.4	1.35278	3.93
All three species	M ₃	Length	14	33.9–42.8	39.4	3.07833	7.81
<i>A. commune/latipes</i>	M ₃	Width	12	16.3–19.9	17.6	1.05784	6.01
<i>A. laurillardi</i>	M ₃	Width	3	14.2–14.8	14.5	0.30000	2.07
All three species	M ₃	Width	15	14.2–19.9	17.0	1.59081	9.36

A. laurillardi from La Débruge; *A. commune* and *A. latipes* (undifferentiated) from La Débruge, Montmartre, Entreroches and sites in the Isle of Wight in the Bembridge Limestone Formation and in the Bembridge Marls and lower Hamstead members of the Bouldnor Formation.

N = number of specimens; OR = observed range; S = standard deviation; V = coefficient of variation.

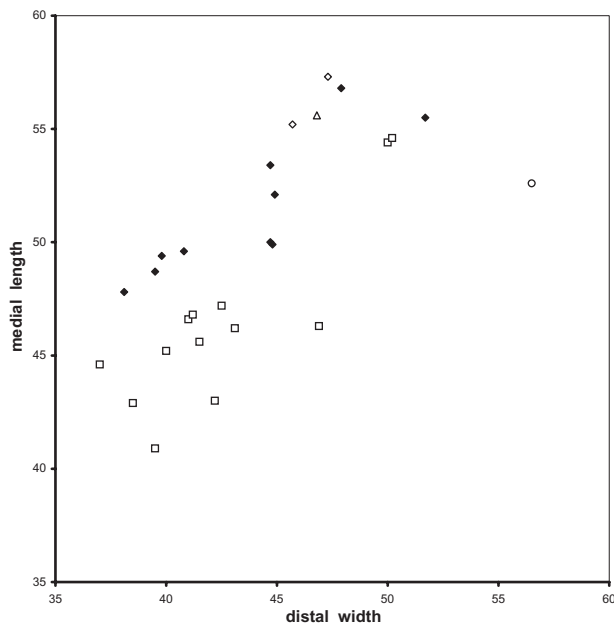


Figure 30. Scatter diagram of medial length versus distal width in millimetres of astragali of *Anoplotherium laurillardi* from La Débruge and of *A. commune* and *A. latipes* (undifferentiated) from La Débruge (□), Montmartre (◆), Quercy (○) and sites in the Isle of Wight in the Osborne (◆) and lower Hamstead (△) members.

width, but not length, with *A. laurillardi*. The four smallest values from Montmartre appear to belong to young animals according to the rather porous bone observed in some. These form a narrow trace, enlarging essentially equidimensionally, in contrast to the older animals, which have a wider scatter. Here there is overlap with two specimens from La Débruge, which on Stehlin's criterion of relative abundance should belong to *A. latipes*. It is pertinent also that the widest astragalus from Montmartre fits well with the calcaneum, but not with the tibia, of the Ham 3 skeleton. In contrast, a wider astragalus from Quercy (BMNH.M1844) fits well with the tibia (although less so with the calcaneum), partly because of the articulation of its recessed cotylar fossa with the laterally curved medial malleolus. This suggests considerable variation in the proportions of different parts of the pes, further supporting conspecificity of *A. commune* and *A. latipes*. The shape of the Montmartre plot shows width variation increasing with size. This could be construed as an ontogenetic trend, with width increasing disproportionately in a sexual dimorph (likely to be male) that bears an extra toe. This should not cause problems with support of an extra digit in a young animal for two reasons: firstly, it seems likely that pedal digit II did not contact the ground, at least during normal gait; secondly, although the navicular

of '*A. latipes*' is distinct distally from '*A. commune*' because of articulation with a sizeable mesocuneiform (de Bonis, 1964: pl. 2, figs 7, 9), mesially it is quite variable in width, overlapping with '*A. commune*', a variability that could also be ontogenetically controlled.

It is unclear whether the hind digit II would provide extra balance, while standing bipedally, given that it may not have reached the ground. There may have been genetic linkage, through serial homology between fore and hind feet as in the giant panda (*Ailuropoda*) or talpids (Davis, 1964: 324; Sanchez-Villagra & Menke, 2005). Nevertheless, a structure that allowed a male to stand as tall as possible, demonstrating aptitude for high browsing, might have been a criterion for female *Anoplotherium* choice. The divergent manual digit II might have allowed interlocking of hands of sparring partners like antler tines do in deer. The activity may also have been enhanced by the adduction of the forelimbs by means of the strong subscapularis muscles.

The idea of *A. latipes* being the male and *A. commune* being the female of a single species has other problematic implications. It would at first sight suggest that the female was less well adapted to high browsing than the male, as other species of *Anoplotherium* and all species of the closely related genus *Diplobune* are entirely three-toed. This scenario might imply different feeding habits for the two sexes. However, this seems unlikely as there are no differences in their dentitions. Alternatively, it might point to a difference in habits between *A. commune/latipes* on the one hand and *A. laurillardi* and species of *Diplobune* on the other, both sexes in the last two examples participating in intraspecific sparring. On commonality grounds in the subfamily Anoplotheriinae, the absence of digit II in *A. commune* or female *A. commune/latipes* should represent a reversal from the three-toed state. These behavioural scenarios, although unsupported by direct evidence, are logical possibilities, whilst sexual dimorphism for toe number in a single species is supported by evidence of minimal variation in any other parameter, and an ontogenetic trend in astragalar proportions. Moreover, both dimorphs occur at the principal known sites: Bouldnor (Hooker *et al.*, 2004), Montmartre (Abusch-Siewert, 1989) and La Débruge (de Bonis, 1964). Although the three-toed dimorph is more common at La Débruge and rarer at Montmartre, this could result from behavioural and/or taphonomic factors, rather than from the different original distributions of distinct species.

CONCLUSIONS

It is concluded therefore that *Anoplotherium* with a primitively long tail was able to adapt to bipedal

browsing by making relatively more extreme adaptations to its tail, pelvis and hind limbs without the need to adopt an upright quadrupedal stance or evolve prehensile supporting structures on its manus. The strength of pelvis and balancing tail, the large lumbar vertebrae and splayed hind legs thus were apparently sufficient to support a vertical posture for an otherwise not highly modified trunk. Thus, the strongly posteriorly angled neural spines of its thoracic vertebrae are typical of a quadrupedal ungulate like a goat (*Capra*), not nearly vertical as in chalicotheres and Slijper's 'bipedal' goat (Slijper, 1946; Coombs, 1983).

The short, stout proportions and the oblique orientation of the long axis of the *Anoplotherium* astragalus are found not only in the anoplotheriine *Diplobune*, but also in members of the subfamily Dacytheriinae, namely *Dacrytherium elegans* (Pictet & Humbert, 1869: pl. 28, fig. 11) and *D. ovinum* (Depéret, 1917: pl. 17, figs 2, 3 as '*Choeropotamus*' – see Hooker & Weidmann, 2000: 94). The astragalus is unknown in the only other remaining dacytheriine genus *Catodontherium*, after removal of *Leptotheridium* to the Xiphodontidae (Hooker & Weidmann, 2000) and of *Tapirulus* to the Choeropotamidae (Hooker & Thomas, 2001). This implies that splayed tibiae were at least widespread if not consistently present in the family Anoplotheriidae, suggesting that all were probably adapted to bipedal browsing. Alternatively, Sudre (1983) has suggested that the small late (Oligocene) species of *Diplobune* [*D. minor* (Filhol, 1877)] may have climbed trees, although this hypothesis has not yet been supported by more evidence than mobility of the radius.

RECONSTRUCTION AND PALAEOECOLOGY

On the basis of the above description and interpretation, a reconstruction is made of the Ham 3 skeleton in both quadrupedal (Fig. 31) and bipedal (Fig. 32) stance. This shows a general body form more like a canid carnivoran than an artiodactyl. The animal may have been slightly taller at the shoulder than at the hips, although this depends on whether the scapula is correctly positioned on the trunk. The limbs are robust and include large scapulae and pelvis. The long axis of the tibiae and the anterior–posterior axis of the feet splay slightly laterally from the sagittal plane. The tail is long and robust and the feet are unguligrade as recognized by previous authors. The neck is convex dorsally, the apparently normal position showing a bend between C3 and C4 in bipedal stance, allowing the skull to maintain a horizontal orientation. The forearm is shown pronated in quadrupedal stance and supinated in bipedal stance. When standing bipedally the forelimbs could extend horizontally beyond the snout, but not when reaching upward for maximum

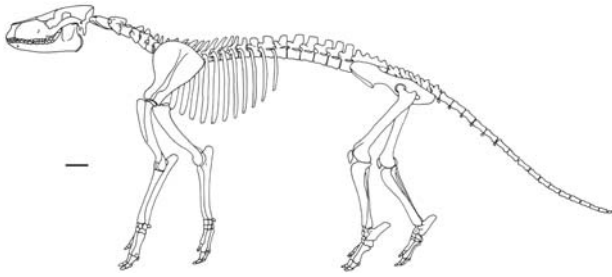


Figure 31. Reconstruction of the Ham 3 *A. latipes* skeleton in quadrupedal stance, supplemented by some elements from *A. commune* specimens from the Gypse of Montmartre and Antony (especially parts of the vertebral column – see text) and from scaled up *A. laurillardi* specimens from the Quercy Phosphorites (cranium, MNHN.Qu399) and La Débruge (dentary, BMNH.30622). Left lower forelimb and pes shown at maximum extension relative to humerus and tibia + fibula, respectively. Forelimbs pronated. Scale bar = 100 mm.

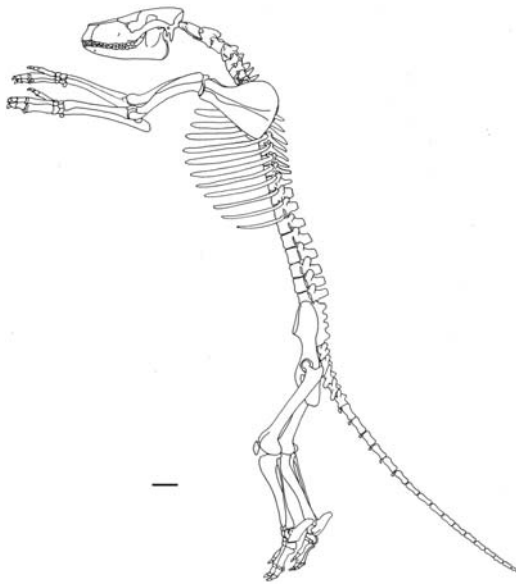


Figure 32. Reconstruction of the Ham 3 *A. latipes* skeleton in bipedal stance, supplemented as in Figure 30. Forelimb supinated. Neck at normal articulatory position. Scale bar = 100 mm.

browsing height. Bipedal stance is shown with the back at an angle of *c.* 15°. A steep angle more like that of a gerenuk is considered more likely than the *c.* 45° angle suggested for *Chalicotherium* (Zapfe, 1979), because of the evidence for free-standing in *Anoplotherium*. Compared with Cuvier's and subsequent authors' reconstructions, the new one shows a proportionally longer trunk, larger scapula, pelvis with more laterally angled ilia and more neck details. It reflects

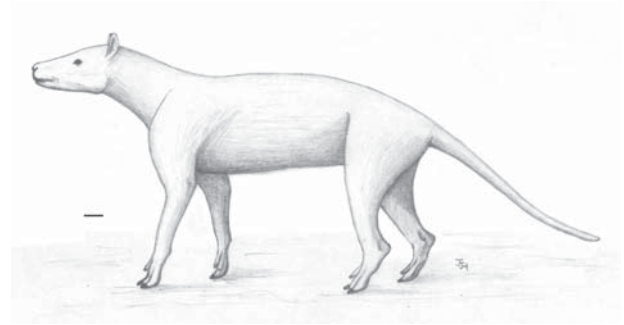


Figure 33. Flesh reconstruction of the Ham 3 *Anoplotherium latipes* specimen in quadrupedal stance, based on the skeletal reconstruction in Figure 30. Scale bar = 100 mm.



Figure 34. Flesh reconstruction of the Ham 3 *Anoplotherium latipes* specimen in bipedal stance, based on the skeletal reconstruction in Figure 31. Scale bar = 100 mm.

the improved knowledge of the skeleton from the Ham 3 specimen. Figures 33 and 34 show flesh reconstructions of the Ham 3 animal in both quadrupedal and bipedal stance.

Reconstruction of the Ham 3 *Anoplotherium latipes* skeleton gives a head and body length of about 2 m. Height at the shoulder in quadrupedal stance would have been a little over 1 m (Fig. 31). The Ham 3 animal was immature; its humerus is estimated to have been 330 mm long by comparison for proportions with the complete Montmartre humerus (MNHN.GY86: Cuvier, 1825: pl. 59, figs 5–7). The large adult proximal humerus (BMNH.M4450) is on the same basis estimated to have been 410 mm long. This gives a

head and body length of 2.5 m and a shoulder height of 1.25 m for adult *A. latipes*. Standing bipedally with back, neck and head at an angle of say 15° from the vertical the Ham 3 animal could have reached a height for browsing of 2.5 m (Fig. 32). BMNH.M4450 could have reached just over 3 m.

At full stretch, the forelimb could not have reached higher than the tip of the snout. This contrasts with *Chalicotherium*, which could have reached considerably higher (Zapfe, 1979: 270, fig. 155). This suggests that the forelimb was not used for pulling and tearing, only for support. This is consistent with the absence of claws or a prehensile organ on the manus.

Palaeotherium magnum magnum Cuvier, 1804b is the only contemporary of *Anoplotherium latipes/commune* in its geographical range that matches it for size. The Mormoiron *P. magnum magnum* skeleton (Roman, 1922; Abel, 1924) can be compared with *A. latipes/commune* for potential browse height. Its head plus neck measures 1040 mm; its forelimb from humerus to hooves also measures 1040 mm (measured from cast). Thus, browse height in quadrupedal stance would be just over 2 m. Its trunk measures 1350 mm and its hind leg 1090 mm. If back, neck and head were held at 30° from the vertical in bipedal stance, *P. magnum magnum* could have reached just over 3 m, but nearer 3.5 m if the stance was more vertical. This would equal or exceed the height reached by *A. latipes/commune*. However, there is no evidence that *P. magnum magnum* was adapted for bipedality. Although the long neck suggests high browsing, it may alternatively be an adaptation for reaching down to drink. It seems unlikely that *P. magnum magnum* or indeed any other terrestrial member of the latest Eocene–earliest Oligocene pre-Grande Coupure European mammal fauna could have competed effectively with *Anoplotherium latipes/commune* for browsing in the 2–3 m height range. Modern high browsers can reach heights of 5.8 m in the case of the quadrupedal giraffe (MacDonald, 1984) and more than 2 m for the bipedal gerenuk (Kingdon, 1997).

Today, bipedal browsers inhabit a variety of environments: gerenuk in dry savannah with scattered trees, gorilla in rainforest, giant panda in montane bamboo woodland. Ecological diversity analysis (Collinson & Hooker, 1987; Hooker, 1992) indicates a gradual opening up of the forested environments in the course of the Late Eocene and earliest Oligocene, with progressive (although fluctuating) reduction in the percentage of arboreal and scansorial species and increase in percentage of large species (over 45 kg). This was more marked earlier in southern French faunas than in southern English ones (Hooker, 1992). The delay of *Anoplotherium* in reaching southern England could thus reflect the temporal offset in the opening up of the environment between northern and southern

Europe. The habitat change between the faunas of the Lacey's Farm Member and of the Osborne Member (the first appearance datum of *Anoplotherium* in the UK) are not easy to establish as the Lacey's Farm Member fauna is relatively poorly known. Differences between the better known and little older Hatherwood Limestone Member fauna and that of the Osborne and Seagrove Bay members are therefore more reliable. The differences are minor, but do reflect a reduction in the arboreal component, namely loss of the two species of the adapid primate genus *Leptadapis* (*L. magnus* and *L. assolicus*), at least one of which also occurs in the Lacey's Farm Member. A slight increase in the greater than 45 kg size class and terrestrial locomotor class results from the addition of *Anoplotherium* itself to the Osborne fauna.

As the habitat changes seem to have been gradual, it is possible that it was a threshold effect that allowed *Anoplotherium* to invade southern England, as there was probably no marine barrier between Britain and continental Europe at the time (Pomerol, 1973). Oxygen isotopic analysis suggests a small drop in temperature between the Lacey's Farm and Osborne members (Grimes *et al.*, 2005), but renewed warming during deposition of the succeeding Bembridge Limestone Formation apparently did not result in a less open habitat and *Anoplotherium* remained in southern England until the Grande Coupure. A change to drier conditions may have been a factor in producing more open habitats. Such drier conditions are suggested by colour mottling in the Osborne Member and calcretes and silcretes in the Bembridge Limestone Formation (Daley, 1989; Daley, Edwards & Armenteros, 2000). However, it is not clear how widespread such conditions were and similar sediments also occur slightly lower in the Headon Hill Formation sequence in the Cliff End and Lacey's Farm members. A detailed dental study to ascertain the diet of *Anoplotherium* could shed light on the problem.

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