

# ORNITHODESMUS – A MANIRAPTORAN THEROPOD DINOSAUR FROM THE LOWER CRETACEOUS OF THE ISLE OF WIGHT, ENGLAND

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**ABSTRACT.** The holotype and only specimen of *Ornithodesmus chuniculus*, a sacrum from the late Wealden (= Barremian) of the Isle of Wight, is redescribed and is shown not to be pterodactyloid as previously described. Comparison with sacral vertebrae of pterodactyloids and of advanced theropod dinosaurs shows it to resemble most closely those of the small theropod *Saurornithoides*. Because *O. chuniculus* is the type species of *Ornithodesmus*, the genus is transferred to the Theropoda. It is assigned to the Troodontidae with uncertainty, because of the limited nature of the holotype. *Ornithodesmus chuniculus* cannot be diagnosed within the Troodontidae and is a *nomen vanum* within the family. If it is a troodontid, it represents the first record of a troodontid from the Wealden of Europe, and also the earliest record of this family. The undoubted pterodactyloid material from the Barremian of the Isle of Wight, '*Ornithodesmus*' *latidens*, requires a new generic name.

THE holotype of *Ornithodesmus chuniculus* from the Wealden of the Isle of Wight is a set of six co-ossified vertebrae (BMNH R187) described by Seeley (1887), who concluded that it was the sacrum of a bird. This identification was based on the presence of two features: (1) the co-ossification of successive neural spines resulting in a continuous neural blade; and (2) the presence of a 'neural platform' made up of horizontal laminar extensions of the bases of the neural arches. Three further characteristics which he noted to be shared with both birds and pterosaurs were: (1) fusion of sacral vertebrae through ankylosis; (2) the sacrum comprising at least five vertebrae; and (3) the presence of pneumatic foramina. However, as no pterosaurs were known to possess the neural blade or neural platform, Seeley argued that the specimen was an avian sacrum, even though it differed from those of modern birds in the small number (six) of vertebrae, the absence of recesses for the reception of mid-renal lobes, and the structure of the anterior articulation of the sacrum. Lydekker (1888, p. 42) catalogued the specimen as a reptile, indeterminate at ordinal level, noting that it could be dinosaurian or pterosaurian in origin.

Seeley (1901) attributed a greater part of a pterodactyloid skeleton (BMNH R176) from the Wealden of the Isle of Wight to *Ornithodesmus*, as the new species *O. latidens*. He associated the two specimens on the basis of supposed similarities in the sacrum, and hence *Ornithodesmus*, now comprising two species, was transferred to the Pterodactyloidea. Hooley (1913) described two more specimens of *O. latidens* (BMNH R3877 and R3878), also from the Wealden of the Isle of Wight, and was able to provide a detailed osteology of this species. However, he made no mention of the sacrum of *O. chuniculus* and very little reference to that of *O. latidens*. As a result of Seeley's (1901) and Hooley's (1913) descriptions, *O. latidens* has been treated as the effective type of the genus *Ornithodesmus* for the purposes of diagnosis (e.g. Wellnhofer 1978, p. 54), while Plieninger (1930) even reduced the senior *chuniculus* in synonymy with the junior *latidens*. Apart from a general assertion of similarity by Seeley (1901), no attempt has been made to compare the sacrum of *O. chuniculus* directly with those of pterosaurs, despite the differences noted by Seeley in his original (1887) description.

Independent reexamination of *O. chuniculus* by the senior author and by Christopher Bennett (University of Kansas) led both to the conclusion that it did not resemble the sacrum of

pterodactyloids as now known. The ensuing attempt to place this specimen systematically has resulted in this paper. The sacral vertebrae associated with the undoubted pterodactyloid '*Ornithodesmus*' *latidens* are quite distinct from those of *O. cluniculus* and are redescribed later in this work.

Interpretation of BMNH R187 necessitated comparative reference to two other specimens. One is the sacrum of *Saurornithoides junior* (Barsbold 1974, pl. 3, fig. 1; pl. 4, fig. 2) which comprises six ankylosed vertebrae and is about twice as long as that of BMNH R187, having a length of 199 mm. The other specimen is BMNH R4463, an undescribed small theropod sacrum (Pl. 1, figs 4–6; Text-fig. 2A–B) from the Late Cretaceous of Mexico Ranch, Red Deer River, Alberta, Canada. This specimen includes sacra 2–6 and is about one-and-a-half times as long as BMNH R187 (110 mm for sacra 2–6, as against 79 mm in BMNH R187). The anterior face of the centrum of sacral 2 appears to be clean and flat, implying that sacral 1 was not ankylosed to the rest of the sacrum. This specimen was catalogued as an ornithomimid, but bears a close resemblance to the sacrum of *Saurornithoides*. Although undetermined, it is sufficiently similar to BMNH R187 in size and configuration to be useful in interpreting damaged features on that specimen, and also for demonstrating the presence of a neural platform in the troodontid sacrum.

The following institutional abbreviations are used in this work: BMNH, Department of Palaeontology, The Natural History Museum, London, UK; GI, Geological Institute, Ulan Bator, Mongolia; TMP, Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA; Z.PAL, Institute of Palaeobiology, Warsaw, Poland.

#### SYSTEMATIC PALAEOLOGY

Subclass DIAPSIDA Osborn, 1903  
 Superorder ARCHOSAURIA Cope, 1891  
 Order SAURISCHIA Seeley, 1888  
 Suborder THEROPODA Marsh, 1881  
 ?Family TROODONTIDAE Gilmore, 1924

(= SAURORNITHOIDIDAE Barsbold, 1974; ? = ORNITHODESMIDAE Hooley, 1913)

*Diagnosis.* As given by Currie (1987, p. 73) with the following additional diagnostic characteristics of the sacrum: all six sacral vertebrae fully ankylosed; pneumatic foramina present on the first two sacra; ventral surface of sacra flattened with medial groove developing shallowly on sacral 2 and very pronounced on sacra 3–6; neural platform present.

*Component genera.* *Troodon* (= *Stenonychosaurus*, *Pectinodon*), *Saurornithoides*, *Borogovia*, *Heptasteornis* and ?*Ornithodesmus*.

*Remarks.* In attributing *Ornithodesmus*, with caution, to the same family as *Saurornithoides* and *Troodon*, we must note that the senior family-level name derived from any of these genera is Ornithodesmidae Hooley, 1913, a name previously associated with the Pterodactyloidea. The very

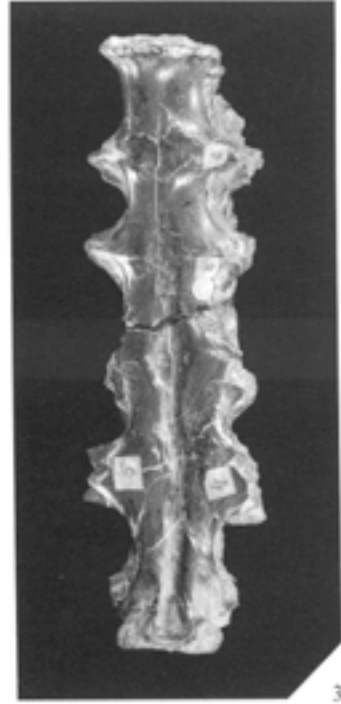
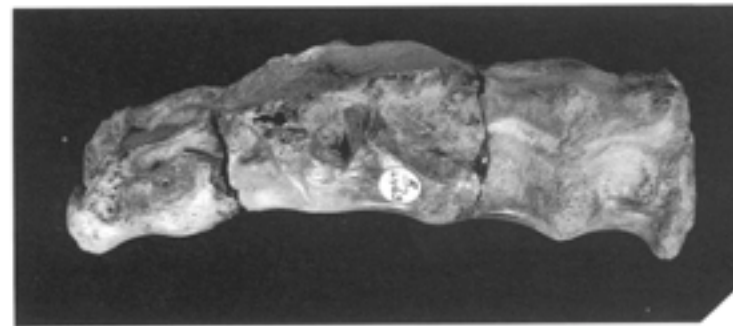
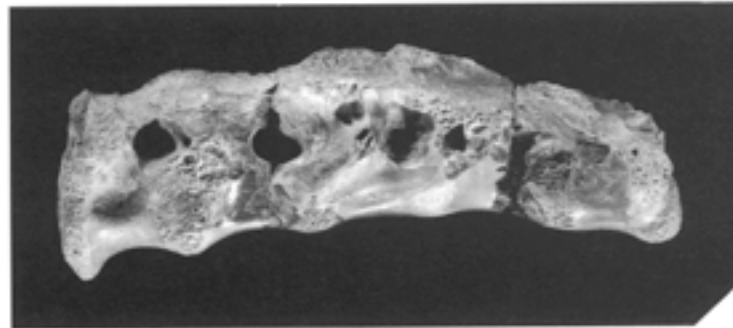
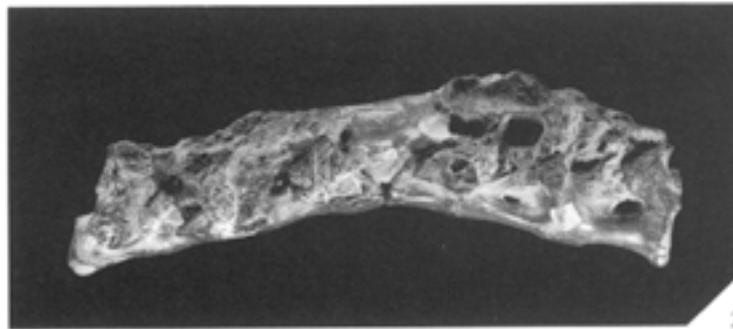
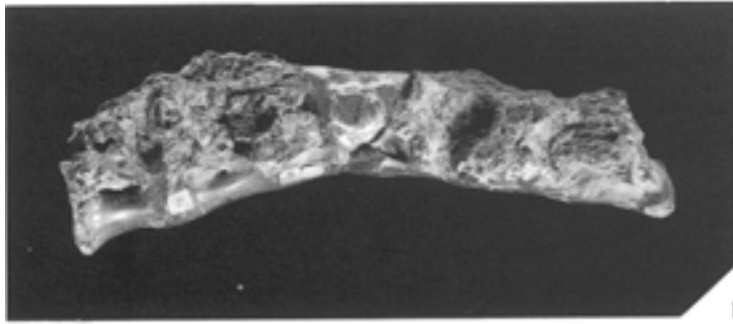
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#### EXPLANATION OF PLATE 1

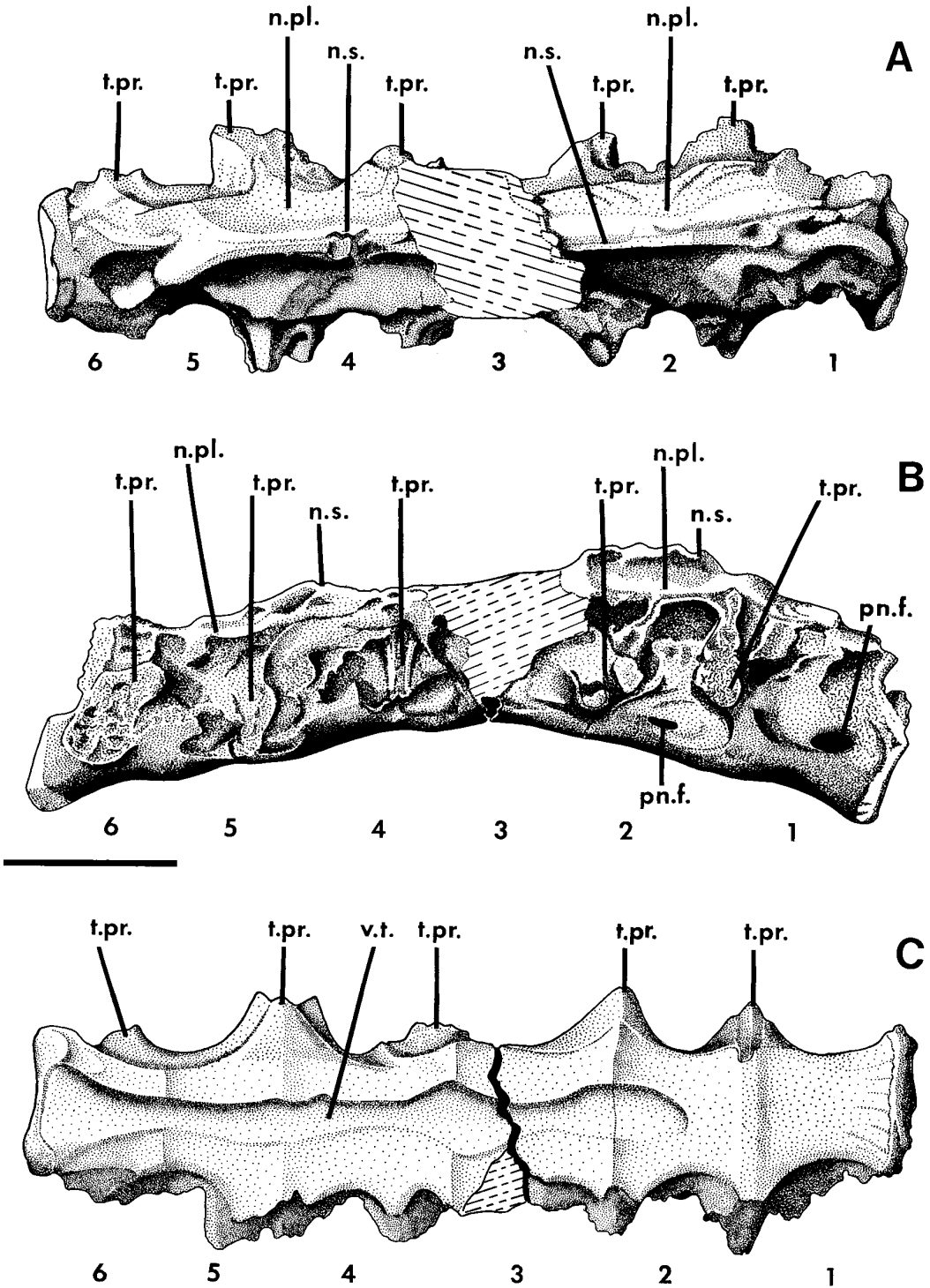
Figs 1–3. *Ornithodesmus cluniculus* Seeley, 1887. Holotype sacrum BMNH R187; Barremian; Isle of Wight, England; in 1, left lateral view; 2, right lateral view; 3, ventral view. All  $\times 0.7$ .

Figs 4–6. Troodontid sacrum BMNH R4463; Late Cretaceous, Red Deer River, Alberta, Canada; in 4, left lateral view; 5, right lateral view; 6, ventral view. All  $\times 0.63$ .

PLATE I



HOWSE and MILNER, *Ornithodesmus choniculus*



limited nature of the *Ornithodesmus* material means that it can only be attributed, with caution, to any family-level unit. For this reason, and in the interests of stability, the name Troodontidae Gilmore, 1924 is retained for the family.

Genus ORNITHODESMUS Seeley, 1887

*Type species.* *O. cluniculus* Seeley, 1887.

*Diagnosis.* As for the only species.

*Ornithodesmus cluniculus* Seeley, 1887

Plate 1, figs 1–3; Text-fig. 1A–C

- 1887 *Ornithodesmus cluniculus* Seeley, p. 206, pl. 12, figs 1–5.  
 1888 *Ornithodesmus cluniculus* Seeley; Lydekker, p. 42.  
 1901 *Ornithodesmus* Seeley, p. 174.  
 1930 *Ornithodesmus latidens* Seeley; Plieninger, p. 44 [*non* Seeley 1901].  
 1978 *Ornithodesmus cluniculus* Seeley; Wellnhofer, p. 54.

*Holotype and only specimen.* BMNH R187, a poorly preserved sacrum, 96 mm in length and comprising six ankylosed vertebrae.

*Locality and horizon.* Given as 'Brook' (probably Compton Bay), Isle of Wight, England; Wealden Marls = Wessex Formation (Daley and Stewart 1979), Barremian, Lower Cretaceous.

*Diagnosis.* All six sacral vertebrae fully ankylosed at a sacrum length of under 100 mm; sacral 6 shorter than sacral 5.

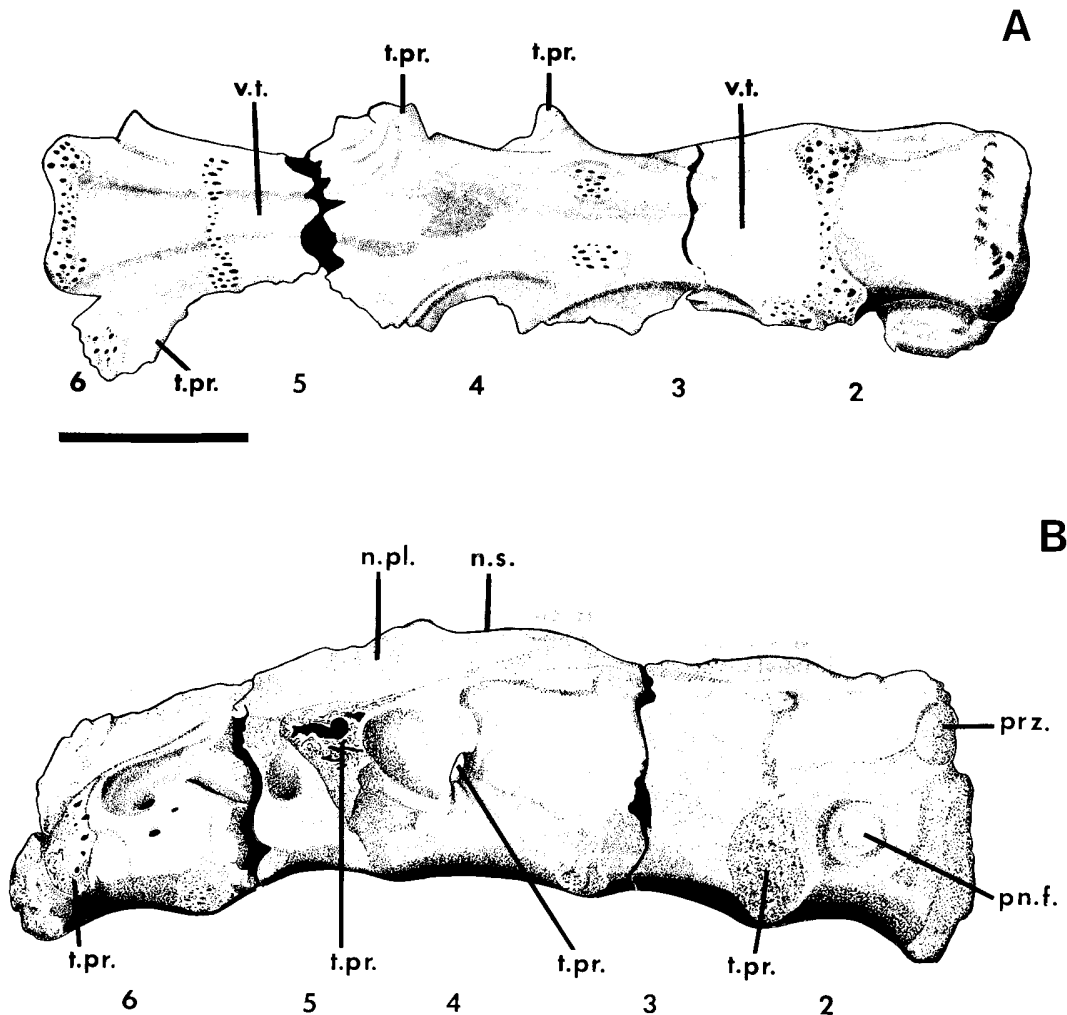
*Discussion.* The relative lengths of sacrals 5 and 6 serve to distinguish this sacrum from that of *Saurornithoides*, in which sacral 6 is the same length as sacral 5. It is impossible to diagnose *Ornithodesmus cluniculus* with respect to any other troodontids, as no other genera are represented by sacral material. *Ornithodesmus cluniculus* must be considered to be a *nomen vanum* (*sensu* Simpson 1945, p. 27; Simpson 1948, p. 31; Mones 1989) within the family Troodontidae, as the holotype and only specimen is insufficient for comprehensive comparative diagnosis.

*Description with comparisons.* The sacrum BMNH R187 (Pl. 1, figs 1–3; Text-fig. 1A–C) is 96 mm long and all six vertebrae are present. Most of the matrix has been removed and the ventral face of the specimen is well preserved, the dorsal and lateral surfaces being abraded to varying extents. It is slightly arched along its length (Text-fig. 1B) and is composed of six completely ankylosed vertebrae with strongly waisted centra. The first centrum is relatively deep, and succeeding centra are progressively shallower. The junctions between centrum 3 and adjacent centra are relatively conspicuous ridges, but the other junctions are poorly discriminated lines. In BMNH R4463 (Pl. 1, fig. 6), the corresponding ankylosed sutures are more clearly visible. The centra of BMNH R187 are roughly equal in length apart from the sixth centrum which is conspicuously shorter. The ventral midline lengths of the centra of BMNH R187 and other theropod sacra are presented in Table 1. BMNH R4463 resembles BMNH R187 closely in that the sixth sacral is shorter than the preceding vertebrae and also that sacrals 3 and 5 are slightly longer than 3 and 4. In the otherwise almost identical *Saurornithoides* sacrum, sacrals 5 and 6 are similar in length.

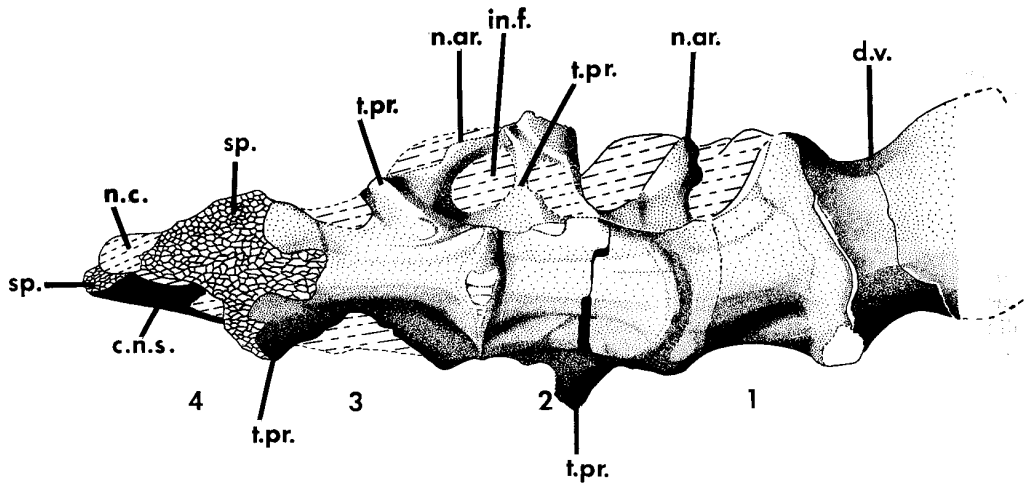
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TEXT-FIG. 1. *Ornithodesmus cluniculus* Seeley, 1887. Holotype sacrum BMNH R187; Barremian; Isle of Wight, England; A, dorsal, B, right lateral, and C, ventral views. Abbreviations for all text-figures: c.n.s., coossified neural spine; d.v., dorsal vertebra; in.f., intervertebral fenestra; n.ar., neural arch; n.c., neural canal; n.pl., neural platform; n.s., neural spine; pn.f., pneumatic foramen; prz., prezygapophysis; sp., spongiosa; t.pr., transverse process; v.t., ventral trough. Scale bar = 20 mm.

The ventral surface of the first sacral vertebra of BMNH R187 is transversely rounded and anteroposteriorly concave. Succeeding centra have flattened ventral faces and show neither transverse convexity nor anteroposterior concavity (Text-fig. 1C). A most conspicuous and characteristic feature of the ventral surface is a medial groove which arises shallowly in the mid-central region of the second sacral centrum, and runs posteromedially to terminate as an expansion at the ventral rim of the posterior edge of the sixth sacral centrum (Text-fig. 1C). The groove is a pronounced narrow trough with smooth rounded edges throughout. It widens over the line of ankylosis at the boundary between each pair of vertebrae. BMNH R4463 shows the same flattened underside to the centra and has an extremely similar but slightly less extensive ventral groove which appears to develop on the third sacral centrum, to be pronounced on sacrals 3–5 but to be weakly developed on sacral 6 (Text-fig. 2A). *Saurornithoides* also has very flattened undersides to the centra and has a pronounced ventral groove (described as a furrow by Barsbold 1974) on sacrals 3–5 but again weakly developed on sacral 6 (Barsbold 1974, pl. 3, fig. 1).



TEXT-FIG. 2. Troodontid sacrum BMNH R4463; Late Cretaceous, Red Deer River, Alberta, Canada: A, ventral, and B, right lateral views. For abbreviations see Text-figure 1. Scale bar = 20 mm.



TEXT-FIG. 3. '*Ornithodesmus*' *latidens* Seeley, 1901. Pterodactyloid sacrum BMNH R176; Barremian; Isle of Wight, England; in ventral aspect. For abbreviations see Text-figure 1. Scale bar = 20 mm.

The first and second sacral vertebrae of BMNH R187 each possess a pair of pneumatic foramina on the lateral walls of the centrum (pn. f. in Text-fig. 1B). Each foramen consists of a single perforation set in a deep excavation which accounts for much of the pronounced waisting of these two vertebrae. The sides of the posterior sacrals are too poorly preserved for the presence or absence of pneumatic foramina to be determined. In BMNH R4463, the second sacral has pneumatic foramina but none is visible on sacrals 3–6.

Transverse processes arise close to the junctions of adjacent vertebrae and have a characteristic configuration in BMNH R187, BMNH R4463 and *Saurornithoides*. The structure of the transverse processes in BMNH R187 (Text-fig. 1A–C) is as follows, with comparative comments on the other specimens where relevant.

Sacral 1 has only the stumps of transverse processes situated near the anterior end of the vertebra (sacral 1 absent or heavily damaged in the other specimens).

Sacral 2 has posterolaterally directed transverse processes situated very close to the anterior edge of the vertebra and with a slight contribution from the posterior end of sacral 1 (similar posterolaterally directed processes occur in BMNH R4463, close to the border with sacral 1 but apparently not so close as to have any structural contribution from that vertebra).

Sacral 3 has laterally directed transverse processes overlapping the junction with sacral 2 (in BMNH R4463, only stumps are present).

Sacral 4 has stumps of transverse processes just posterior to the junction with sacral 3 (in BMNH R4463, posterolaterally directed transverse processes are situated just behind the junction with sacral 3).

Sacral 5 has very wide, laterally directed, transverse processes overlapping the junction with sacral 4 (likewise in BMNH R4463).

Sacral 6 has posterolaterally directed transverse processes situated in the middle of the centrum (likewise in BMNH R4463).

Buttress-like diapophyses arise perpendicularly to the long axis of the sacrum above the transverse processes and fuse with horizontal laminae extending from the bases of the neural spines to give a neural platform, i.e. a continuous sheet of bone extended laterally on each side of the bases of the sacral neural spines (n. pl. in Text-fig. 1A–B). Where the diapophyses fuse with the neural platform, the latter is expanded in width and consequently bears an undulating margin with the expansions corresponding to the lines of fusion between the vertebrae. A similar neural platform is present in BMNH R4463 (Text-fig. 2B), but the *Saurornithoides* sacrum is too poorly preserved for the presence of a neural platform to be established.

The neural arches are relatively rounded structures surrounding the neural canal. The leading edge of the neural arch of the first sacral extends forward as prezygapophyseal processes terminating in dorsomedially directed facets. The damaged neural spines are represented only by bases and broken stumps, but were clearly co-ossified to give a continuous blade-like structure (n.s. in Text-fig. 1A). The neural spines are thickened where they meet the laminae of the neural platform. In conclusion, not only are all six centra ankylosed in this sacrum but all the supra-central components (neural spines, neural arches, transverse processes) are co-ossified to give an entirely rigid structure.

The anterior articular surface of the centrum of the first sacral vertebra is very slightly concave and is a flattened oval shape. The posterior articular surface of the centrum of the sixth sacral vertebra is also slightly concave and is curved down at each side. This posterior articular surface is slightly upwardly directed in relation to the long axis of the sacrum. At each ventrolateral corner is a worn tubercle apparently bearing a ventrally directed oval facet (Text-fig. 1C), which presumably represents a secondary surface of articulation with the first caudal vertebra.

#### *Systematic position of Ornithodesmus cluniculus*

The only sacra that are significantly similar to that of *Ornithodesmus cluniculus* are those attributed to the theropod genera *Saurornithoides*, *Ornithomimus*, *Gallimimus* and *Chirostenotes*. The following material was used as the basis for systematic comparison.

*Saurornithoides*. Only one troodontid sacrum has been described and figured, namely that of *Saurornithoides junior* Barsbold, from the Upper Nemegt Beds of Mongolia (Barsbold 1974, pl. III, fig. 1; pl. IV, fig. 2). This comprises six ankylosed vertebrae and has a length of about 200 mm.

*Ornithomimus* and *Gallimimus*. Ornithomimids appear to have possessed five (Osmólska *et al.* 1972) or six (Russell 1972) sacral vertebrae. Where six are present they seem to be directly homologous to the six in BMNH R187. Where five are present as in *Gallimimus*, they are homologous to sacra 2–6 in BMNH R187 with dorsal 13 being homologous to sacral 1. Throughout this discussion, we have standardized on a homology based on six fused sacra and refer to dorsal 13 + sacra 1–5 of *Gallimimus* as sacra 1–6. The sacrum of *Ornithomimus* is represented by USNM 4736, the type specimen of *O. sedens* Marsh, 1892, from the Lance Formation of Niobrara County, Wyoming, USA, as figured by Gilmore (1920, fig. 67). This sacrum is almost five times as large in linear dimensions as BMNH R187 and includes only sacra 3–6 which are 305 mm long as against 62 mm for the equivalent vertebrae in R187. Gilmore described these as sacra 1–4, but it is now clear that one or two more vertebrae are incorporated into the anterior sacral series in ornithomimids, and that these were missing in Gilmore's specimen (Russell 1972, p. 377). The sacrum of the type specimen of *Gallimimus bullatus* Osmólska, Roniewicz and Barsbold, 1972 (pl. 45; fig. 9) was described as having five sacra but, as noted above, the last 'dorsal' appears to be homologous with the first sacral as identified by Russell (1972). This sacrum is eight times as long as BMNH R187 and sacra 3–6 (2–5 of Osmólska *et al.*) are 510 mm in length. The dimensions of the sacral vertebrae of a second smaller specimen of *Gallimimus* have also been taken from Osmólska *et al.* (1972) and are incorporated in Table 1.

*Chirostenotes*. The infraorder Oviraptorosauria comprises two families of small toothless theropods, the Caenagnathidae and the Oviraptoridae, all from the Late Cretaceous of North America and Mongolia. The Caenagnathidae is now believed to include the genus *Chirostenotes*, which possesses a sacrum comprising six ankylosed vertebrae (Currie and Russell 1988, fig. 1). The Oviraptoridae



are reported to possess six (*Oviraptor*) or seven (*Ingenia*) presacral vertebrae (Barsbold 1983), but these have not been figured, and the sacrum of *Chirostenotes* of necessity is taken as representative of the oviraptorosaurs.

When *Ornithodesmus cluniculus* was first described as a primitive bird (Seeley 1887), troodontid, ornithomimid and oviraptorosaur dinosaurs had not been recognized as such, although a few ornithomimid fragments had been named. Shortly after the description of recognizable ornithomimids by Marsh (1890), *Ornithodesmus* was erroneously associated with pterodactyloid material, without precise comparisons with bird-like dinosaurs ever being made.

The above redescription has shown that *Ornithodesmus cluniculus* may be placed systematically by means of the following morphological features.

1. Pneumatic foramina present in the first two sacral vertebrae. The first sacral is a modified dorsal implying the presence of such foramina and pleurocoels in the posterior dorsal series. This is a characteristic of the Theropoda *sensu* Gauthier (1986, p. 19) although Upper Cretaceous Troodontidae lack pleurocoels in the posterior dorsals (Currie 1987). The *Saurornithoides* sacrum is too poorly preserved for such foramina to be visible, but they are present in sacrals 1–4 in *Gallimimus* (dorsal 13 and sacrals 1–3 of Osmólska *et al.* 1972). In *Chirostenotes*, sacrals 1–6 all bear pleurocoels, but they are very small in 4–6 and might well be missed in a poorly preserved specimen.

2. Sacrum comprising at least four ankylosed vertebrae. The presence of at least four sacrals is a characteristic of the Theropoda (Currie and Russell 1988, p. 974). Most theropods have at least five presacrals, but *Dilophosaurus* and *Compsognathus* retain four.

3. Extensions of the sacral diapophyses form a neural platform. Similar neural platforms are present in BMNH R4463 (Text-fig. 2B), *Ornithomimus* and *Chirostenotes*, but not in *Gallimimus* where the diapophyses remain unconnected. The *Saurornithoides* sacrum is too poorly preserved for the presence of a neural platform to be established.

4. Sacrals 2, 4 and 6 have posterolaterally directed transverse processes, while sacrals 3 and 5 have laterally directed transverse processes. This also characterizes troodontids, ornithomimids (if the posterior dorsal is homologized with the first sacral in R187) and *Chirostenotes*.

5. Sacrum comprising six ankylosed vertebrae. The presence of six sacrals appears to be restricted to the Troodontidae (Barsbold 1974), the Oviraptorosauria (Barsbold 1983; Currie and Russell 1988) and some Ornithomimidae (Russell 1972), although most of the latter have only five co-ossified sacrals (Osmólska *et al.* 1972). In *Saurornithoides*, such preserved fragments of neural spine that are present show evidence of co-ossification of the spines. However, in *Gallimimus* the spines are closely appressed but not co-ossified.

6. Sacral centra 2–5 have broad flattened undersides with a medial groove present throughout their length. *Saurornithoides* also has very flattened undersides to the centra and has a pronounced ventral groove on sacrals 3–5 (Barsbold 1974, pl. 3, fig. 1). Gilmore (1920) described the corresponding groove in *Ornithomimus* (USNM 4736) as prominent on sacrals 3–5 (his 1–3). Osmólska *et al.* (1972, p. 119) referred to a medial depression on sacrals 2–5 (their 1–4) in *Gallimimus*. This feature characterizes the *Saurornithoides* and the Ornithomimidae, but not *Chirostenotes*.

7. The ventral surface of the centrum of sacral 6 is broadly flattened with a medial groove. This occurs in *Saurornithoides* and BMNH R4463, but not in ornithomimids (*Ornithomimus*) or *Chirostenotes*. In both of the latter, sacral 6 is narrower with a convexly curved underside which is not flattened and has only a slight groove.

8. All six sacrals co-ossified, indicating maturity, in a sacrum slightly less than 100 mm long. Scaled against small theropods, this suggests a total length of no more than one-and-a-half metres for an adult animal, considerably less than known ornithomimids, which had adult sizes of 3 metres or more, but of similar size to troodontids.

9. Sixth sacral centrum shorter than fifth sacral centrum. This is also the condition in BMNH R4463. In *Saurornithoides*, the two centra are approximately the same length. In *Ornithomimus* and *Gallimimus*, the sixth sacral is longer (Table 1).

Characters 1 and 2 serve to identify this specimen as a theropod sacrum. Characters 3 to 5 identify

TABLE 1. Ventral midline lengths (mm) of centra of sacral vertebrae. \* = approximation. Information from Gilmore 1920, p. 133 (*Ornithomimus*); Osmólska *et al.* 1972, p. 120 (*Gallimimus*); Barsbold 1974, p. 15 (*Saurornithoides*).

Sacral vertebra	1	2	3	4	5	6
<b>Troodontidae</b>						
<i>Ornithodesmus</i> (BMNH R187)	17	16	18	15	16	13
Indeterminate troodontid (BMNH R4463)	—	21.4	23.5	22.3	25.6	17.6
<i>Saurornithoides</i> (GI no. SPS 100/1)	34*	31*	31.0	31.0	36.0	36.2
<b>Ornithomimidae</b>						
<i>Ornithomimus</i> (USNM 4736)	—	—	71	71	79	84
<i>Gallimimus</i> (GI no. DPS 100/11)	98	95	92	85	115	118
Z.Pal Mg.D-I/94	41	40	40	39	41	44

it as a sacrum of a maniraptoran theropod and a member of either the Troodontidae, the Ornithomimidae or the Oviraptorosauria. Character 6 identifies it as either a troodontid or an ornithomimid. Characters 7 and 8 identify it as a troodontid. The significance of this identification will be considered in the discussion below. As noted in the discussion following the diagnosis, there is little basis for comparative diagnosis of *Ornithodesmus* within the Troodontidae, because only *Saurornithoides* has an associated sacrum. Character 9 is a notional distinguishing character, but *Ornithodesmus cluniculus* is, to all intents and purposes, a *nomen vanum* within the Troodontidae.

#### THE SACRUM OF '*ORNITHODESMUS*' *LATIDENS*

The holotype of '*Ornithodesmus*' *latidens*, (BMNH R176) is a set of associated pterodactyloid elements. The sacrum associated with this material is certainly pterodactyloid as it forms part of an articulated vertebral column, the anterior region of which is a notarium of pterodactyloid type. This needs to be emphasized, because one major non-pterodactyloid fragment was originally incorporated in BMNH R176, namely a skull-table of the crocodile *Theriosuchus* (Buffetaut 1983). Seeley (1901) regarded the holotype of *O. cluniculus* and the sacrum of BMNH R176 as sufficiently morphologically similar to be considered congeneric, although he did not specify the similarities. Hooley (1913) made only brief mention of the sacrum of BMNH R176, noting that it was impossible to determine its overall form because of its fragmentary condition. However, there is sufficient structure preserved to demonstrate that the sacrum of the pterosaur '*O*'. *latidens* is a typical pterodactyloid sacrum and hence distinct from that of *O. cluniculus*. This sacrum will be described and illustrated more fully by the senior author as part of a complete redescription of '*O*' *latidens*. The following short description is provided simply to demonstrate the distinct nature of these two sacra.

*Description.* The sacrum of BMNH R176 (Text-fig. 3) is incomplete and comprises the first three sacral vertebrae, visible in ventral and lateral aspect, together with the anterior region of the fourth sacral. Most of the dorsal and dorsolateral regions of the sacrum are obscured by matrix and by overlying metacarpal elements which have distorted the neural spines of the third and fourth sacra. For each of the first three sacral centra, the length (measured along the ventral midline) and width (across the mid-ventral surface) are as follows: (1) 15 mm, 11.25 mm; (2) 13 mm, 11.50 mm; (3) 12 mm, 9.25 mm. Thus there is a gradual decrease both in length and width along the anterior sacral series. The centra are waisted and become shallower posteriorly.

The sacral vertebrae are fully ankylosed as a synsacrum. The zones of fusion between the centra are thickened ventrally as smooth ridges which disappear ventrolaterally (Text-fig. 3). The ventral

surfaces of the centra are not flattened and there is no medial trough. Instead, the ventral surface of each centrum is concave anteroposteriorly and smoothly convex transversely. The transverse processes (t. pr. in Text-fig. 3) are represented by abraded bases. They originate immediately behind the anterior margins of the vertebrae at progressively lower levels from the first to the third sacral, with that of the fourth originating at the same level as the third. The transverse processes of the first sacral originate high on the laminae of the neural arches and immediately behind the vertical plane of the anterior margin of the centrum. On the right side, the broken transverse process is represented by a horizontally elongate triangular cross-section. The transverse processes of the second, third and fourth sacra are stouter, broad-based structures originating on the centra. The bases of these processes are angled obliquely backwards at about 50° to the axis of the sacrum. From each transverse process base, an anterodorsal and posterodorsal ridge extend up to become confluent with the neural arch.

The laminae of the neural arches of adjacent sacra are fused, obliterating the zygapophyses. Between the neural arches of the third and fourth sacra, the zone of fusion can be seen as a thin line with thickening of the bone on either side of it. The laminae rise and curve steeply towards the apex of the neural arch. On the left side, the neural arches are sufficiently exposed that it is clear that no neural platform is present.

The neural spines of sacra 1–3 are fragmentary but can be seen to be discrete structures ankylosed at their dorsal extremities to form a continuous dorsal bar of bone. At the level of the fourth sacral vertebra, this bar is subrectangular in cross-section and is 5 mm deep, 3.5 mm wide across its upper margin and 2 mm wide across its ventral margin. A similar bar was described in *Pteranodon* by Eaton (1910). The neural spine of the fourth sacral (c.n.s. in Text-fig. 3) is relatively intact and is thickened anteriorly, narrowing to a slender blade posteriorly.

*Systematic position.* BMNH R176 is a pterodactyloid sacrum, characterized by the presence of progressive narrowing of centra posteriorly, transverse processes orientated obliquely backwards, and neural spines united by a bar of bone along their dorsal edges, combined with the absence of ventral flattening of the centra, absence of ventral groove and absence of neural platform. In all these features it differs from the troodontid sacrum BMNH R187 described above. It is similar in size to BMNH R187 and both comprise at least four ankylosed vertebrae with some fusion of the neural spines, but these are the only significant resemblances.

#### DISCUSSION

The Troodontidae were small maniraptoran theropod dinosaurs growing to 2 m in total length. They had relatively large brains, widely spaced eyes, slender jaws with coarsely serrated teeth, long arms and retractable second digits on the feet. All previously described troodontid genera, namely *Troodon* (= *Stenonychosaurus*, *Pectinodon*), *Saurornithoides*, *Borogovia* and *Heptasteornis*, derive from the Campanian to Maastrichtian of North America and Eurasia. A literal interpretation of this chronological range might suggest that the troodontids were a late-appearing group of theropods. However Currie (1987) has argued that the troodontids are the closest relatives of birds. If the Troodontidae were the sister-group of the Avialae of Gauthier (1986) (i.e. the avian clade from *Archaeopteryx* upwards), then troodontids could be expected to be present from at least the Tithonian onwards when their sister-taxon first appears in the record. Milner and Evans (1991) redescribed *Lisboasaurus estesi* from the Oxfordian of Guimarota, Portugal, as fragments of a small maniraptoran theropod which could be either a troodontid or an avialan. The presence of Lower Cretaceous troodontids might therefore be predicted on cladistic grounds. There are sufficiently few rich Lower Cretaceous microvertebrate assemblages that the previous absence of early Cretaceous troodontids can be argued to be based on negative evidence.

Although its limited nature and stratigraphical separation from other troodontids necessitates caution in attribution, the sacrum of *Ornithodesmus cluniculus* does appear to represent the first record of a troodontid dinosaur from the Wealden of Europe and the earliest record of a

troodontid. In view of the apparent closeness of troodontids to birds, it is ironical to note that *Ornithodesmus cluniculus* was originally identified as the sacrum of a primitive bird by Seeley (1887), before being reassigned to the pterosaurs.

With the transfer of *Ornithodesmus cluniculus* to the Theropoda, a change in the nomenclature of the Isle of Wight Wealden pterosaur material is necessary. Seeley's species *latidens*, with the holotype BMNH R176, continues to be the valid name for the remaining described Isle of Wight pterosaur material. The unity of this material is clear and will be established by the senior author when work in progress is completed. This material now lacks a valid generic name and, as no similar form has been described from elsewhere, a new generic name is required. Pending the redescription and renaming of this material by the senior author, we suggest that it be referred to as '*Ornithodesmus*' *latidens*.

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