Bull. Inst. r. Sci. nat. Belg.: Sciences de la Terre **56**, 281-372, 1986 Bull. K. Belg. Inst. Nat. Wet.: Aardwetenschappen

On the anatomy of *Iguanodon atherfieldensis* (Ornithischia: Ornithopoda)

by David B. NORMAN*

Abstract

The taxonomy of the species of the genus *Iguanodon* is reviewed. It is concluded that the small skeleton from Bernissart referred to as *I. mantelli* VON MEYER, 1832, is referable to the species *I. atherfieldensis* HOOLEY, 1925. *I. mantelli* is in turn an objective junior synonym of *I. anglicus* (HOLL, 1829) — the type species of the genus.

The osteology of *I. atherfieldensis* from Bernissart is completely reviewed and supplemented, where necessary, by information from the holotype. The osteology of *I. atherfieldensis* is compared to that of the closely related sympatric species *I. bernissartensis* and other well-described ornithopods: *Camptosaurus dispar, Ouranosaurus nigeriensis, Hypsilophodon foxii* and hadrosaurids. It is concluded that since sexually dimorphic attributes cannot be readily identified in *I. atherfieldensis* and *I. bernissartensis,* the size differential between these species may well reflect ecological partitioning as a result of competition between closely related species in the same environment; an analogous pattern is found in living vertebrate species. Comparisons with related genera of ornithopods permits a character analysis and systematic review of these advanced ornithopod dinosaurs; this has generated a cladogram in an attempt to resolve phylogenetic relationships.

The myology of the forelimb and hindlimb of *I. atherfieldensis* has been reconstructed as far as is presently possible and functional and evolutionary observations are made.

The excavations at Bernissart that took place between 1878 and 1881 were well documented and these records are preserved in the archives of the Royal Institute of Natural Sciences, Brussels.

Acknowledgements

This work would not have been possible but for the kindness and generosity of Dr. P. SARTENAER (Chef de Départment de Paléontologie) and Dr. P. BULTYNCK (Curator of fossil vertebrates) in allowing me to work on the collections at the Institut Royal des Sciences Naturelles, Brussels. This work was supported by the Royal Society and Science Research Council (B/RF/4940) and by a study visit grant from the Institut Royal des Sciences Naturelles de Belgique. I am also indebted to Dr. A.J. CHARIG and Dr. A.C. MILNER for access to the collections of the BMNH.

The manuscript of this paper has benefited from comments and criticisms from Dr. P. BULTYNCK (I.R.Sc.N.B.), Dr. T.S. KEMP (Oxford) and Dr. A.J. CHARIG (BMNH).

This work was undertaken at the Department of Zoology and University Museum, University of Oxford.

Introduction

The very rich fossil fauna and flora that was discovered in the Lower Cretaceous clays at Bernissart toward the end of the last century has attracted considerable palaeontological interest. The dominant members of the terrestrial fauna are the dinosaurs and particularly the abundant remains attributable to the genus *Iguanodon* (NORMAN, 1980). This second monograph is intended as the companion of the 1980 paper, and reviews the anatomy of the second species preserved at Bernissart: *Iguanodon atherfieldensis* HOOLEY 1925. In addition, some aspects of functional morphology in the species will be considered, as well as the history of the collections from Bernissart.

Until the early 1900's, the only reasonably well described representatives of the genus *Iguanodon* were (i) the so-called "Maidstone specimen" (a partial skeleton preserved in a block of Kentish Rag) which was described by MANTELL (1834, 1839, 1841) and also by OWEN (1851) and attributed to the species *I. mantelli* VON MEYER, 1832, and (ii) the Bernissart material attributed to either *I. mantelli* or *I. bernissartensis* (DOLLO, 1882). However in 1912, HOOLEY discovered the finely preserved partial skeleton of a small species of *Iguanodon* near Atherfield Point on the Isle of Wight. He produced several papers on this specimen attributing it to *I. mantelli* (HOOLEY, 1912), *I. bernissartensis* (HOOLEY, 1917) before finally describing it as a new species *I. atherfieldensis* HOOLEY, 1925.

The problem of the specific identity of the new specimen from Atherfield Point highlights a very significant point in relation to the taxonomic status of the genus as a whole. The published works on *Iguanodon* to that date were woefully inadequate, despite the relative abundance of comparative material, a point that was made quite forcibly by HOOLEY (1925: 51-60). The present work therefore is a comparative review presenting a thorough anatomical description of the small, articulated skeleton of the Bernissart iguanodontid referred to as

---

* Present address: Palaeontology Section, Earth Sciences Division, Nature Conservancy Council, Peterborough P.E1 1UA England.

I. mantelli (IRSNB 1551) with comparative information from the holotype of *I. atherfieldensis* (BMNH R5764), *I. bernissartensis* (NORMAN, 1980) and related iguanodontid dinosaurs where appropriate.

The small iguanodontid from Bernissart (IRSNB 1551) is represented by an almost complete skeleton which was found in virtually perfect articulation *in situ* at Bernissart (Fig. 1). The skeleton was cleared of matrix, as far as was possible at the time, before being studied by DOLLO (1882) and was subsequently mounted for display purposes in 1884 (Fig. 2). In addition to this material, there are also a few rather fragmentary remains of a rather smaller individual of the same species; these are presently in the Conservatoire of the Institut Royal des Sciences Naturelles, Brussels (IRSNB "2Fbis" - Appendix I) and have never previously been mentioned in any published or unpublished lists of the Bernissart fauna (CASIER, 1960, 1978; QUINET, 1972).

This present work was made possible because of the generosity of the Institut Royal des Sciences Naturelles who kindly allowed the specimens in their collections to be dismantled for further study. However, while it has proved possible to compile extensive information on the postcranial skeleton of the small species from Bernissart, the cranial anatomy was not so amenable. The reason for this is that the skull, as preseved, is laterally compressed. As a result it was presumably not thought prudent in the 1880's to try to clear all the matrix from the inner portions of the skull. In its present state, the surface of the skull is very well-preserved, although thickly coated with "gomme-lac" and cannot be readily examined internally. Indeed further preparation is potentially hazardous because it would involve removal of the "gomme-lac". From personal experience, the latter seems to provide considerable mechanical support in many of the Bernissart fossils and its removal tends to lead to a catastrophic disintegration of the extremely fraible fossil bone. Information on skull morphology has therefore been supplemented by details from the holotype and other fragmentary, but nevertheless well preserved, specimens available in the British Museum (Natural History).

REPOSITORY ABBREVIATIONS

BMNH	British Museum (Natural History);
IRSNB	Institut Royal des Sciences Naturelles de Belgique.

Taxonomy

Order ORNITHISCHIA SEELEY, 1888
Suborder ORNITHOPODA MARSH, 1881
Family IGUANODONTIDAE HUXLEY, 1870

Diagnosis

Medium to large-sized advanced ornithopods (5-10 metres long); antorbital fenestra reduced to a small aperture with no fossa anterior to its margin; dentary teeth are broadly and approximately diamond shaped in lingual view and asymmetrical, with primary and secondary ridges separated by a median groove, and distal denticulate margin rolled lingually to produce a slight cingulum; maxillary teeth narrow, lozenge-shaped asymmetrical in labial view with very prominent primary ridge which is displaced distally. Vertebral column comprises 11 cervicals, 16 or 17 dorsals, 5-7 sacrals and 40-50 caudals; pectoral girdle robust (scapular blade not strongly expanded distally, coracoids broad); humerus stout and relatively straight; carpus, massive and well-ossified, with metacarpal I incorporated into wrist; digit I of manus modified into conical ungual spine (first phalanx modified as a thin, flat plate); ilium deep posteriorly with a broad brevis shelf; ischium long, curved ventrally and "footed" distally; femur slightly longer than tibia, 4th trochanter crested and on the middle of the shaft, femoral shaft curved.

Genus *IGUANODON* MANTELL, 1825

1825 *Iguanodon* MANTELL: 179 (generic name only)
1828 *Iguanosaurus* RITGEN: 273 (objective junior synonym)
1841 *Streptospondylus* OWEN: 91 (subjective junior synonym)
1841 *Cetiosaurus* OWEN: 94 (subjective junior synonym)
1843 *Therosaurus* FITZINGER: (objective junior synonym)

TYPE SPECIES

Iguanodon anglicus (HOLL, 1829).

ADDITIONAL VALID SPECIES

Iguanodon hoggii OWEN, 1874; *I. dawsoni* LYDEKKER, 1888; *I. fittoni* LYDEKKER, 1889; *I. bernissartensis* BOULENGER, 1881*; *I. atherfieldensis* HOOLEY, 1925; and two dubious genera: *I. orientalis* ROZHDESTVENSKII, 1952 (as currently defined, this form is indistinguishable from *I. bernissartensis*) and *I. ottingeri* GALTON and JENSEN, 1979 (Based as it is on teeth, this taxon must be of dubious status until more associated material is discovered).

---

* I am indebted to Dr. Pierre Bultynck for pointing out that my attribution of the authorship of *I. bernissartensis* to VAN BENEDEN, 1881 (NORMAN, 1980) was incorrect.

Diagnosis

Iguanodontids of the Ryazinian to lower Aptian of Eurasia; skull long and tall in occipital view; supraoccipital exluded from the foramen magnum; premaxillae moderately expanded, dorsal median process of premaxillae extends backward between and below nasals; palpebrals, which articulate on prefrontal alone, loose, long and slender sometimes with a small accessory; predentary strongly denticulate anteromedially. Vertebral column comprises: 11 cervicals, 17 dorsals, 6-7 sacrals and 45+ caudals; neural spines of mid-dorsal series 2-3 times height of centrum and not expanded apically. Hatchet shaped sternal bones; tendency to ossify the cartilage of the median sternal plate; ossified ligaments in the carpus; (?) ungual of digit IV of manus lost, unguals of digits II and III flattened; metatarsal I splint-like; posterior ramus of pubis slender and shorter than ischium.

Iguanodon atherfieldensis HOOLEY, 1925

1925 *Iguanodon atherfieldensis* HOOLEY: 3.

Holotype:

BMNH R5764 a partial associated skeleton from the Wealden Shales near Atherfield Point, Isle of Wight, U.K.

Age:

Barremian - Lower Aptian.

Referred specimens:

IRSNB 1551 (an almost complete skeleton from the "Bernissartian" of Bernissart, Belgium). In addition to this fine specimen there are considerable collections of material referrable to this species at the British Museum (Nat. Hist.) both particularly from the Isle of Wight and Ockley in Surrey.

Diagnosis:

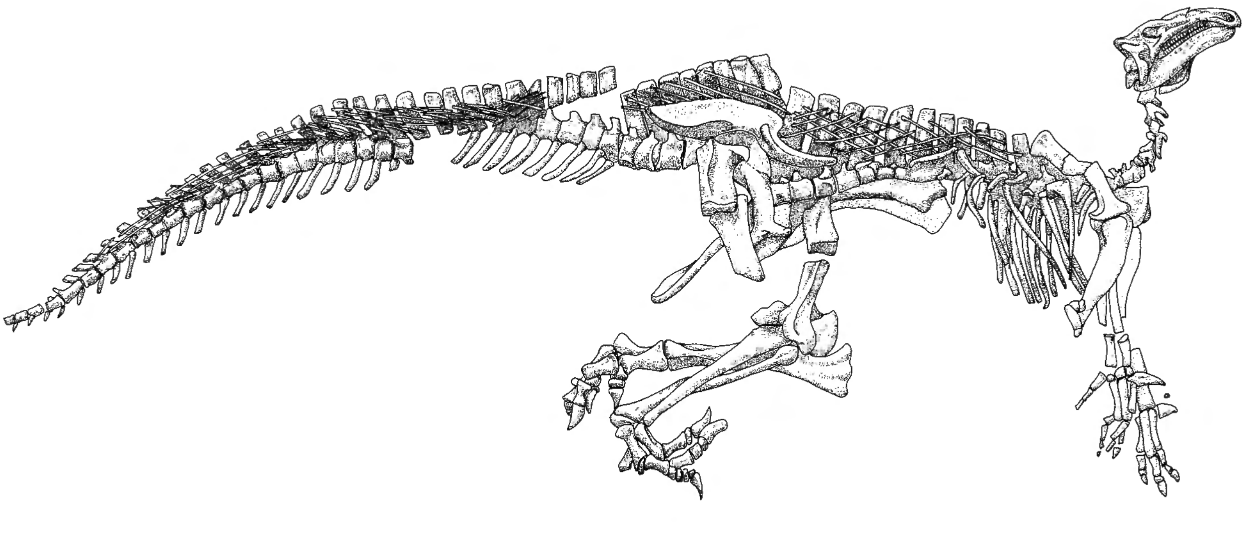
Small ('gracile') species of *Iguanodon* (6-7 metres in length). Skull long and low with slender lower jaw; palpebral long and slender (no accessory); no posterodorsal expansion of the supraoccipital plate (poorly ossified); maximum 23 vertical tooth positions in the maxilla — 20 in dentary. Posterior dorsal and anterior caudal vertebrae not strongly compressed, antero-posteriorly; dorsal and caudal neural spines tall and slender; sacrum composed of 6 true sacrals and 1 sacrodorsal. Scapula moderately expanded distally; coracoid foramen completely enclosed externally; phalangeal formula: 2, 3, 3, 3, 3. Brevis shelf of ilium not very well developed; anterior pubic ramus laterally compressed and very deep; metatarsal I narrow and spine-like. [Limb proportions differ markedly from its sympatric contemporary *I. bernissartensis* indicating a primarily though not exclusively bipedal mode of progression (Fig. 66).]

BRIEF DISCUSSION

A complete systematic review of the genus *Iguanodon* is beyond the scope of this paper. However a few comments are necessary in order to explain the foregoing taxonomic assignment.

The genus *Iguanodon* was founded by Gideon MANTELL in 1825 on the basis of seven teeth which had been collected from the Tilgate Forest area of the Wealden of Sussex; they were discovered in coarse conglomerate known as Tilgate Grit. Of these seven teeth, five have been re-located in the collections of the BMNH (NORMAN, 1977).

Fig. 1. – Iguanodon atherfieldensis. *IRSNB 1551 (T). The skeleton as originally preserved at Bernissart, from an original drawing by G. Lavalette (archives, IRSNB redrawn by D. Nicholls).*

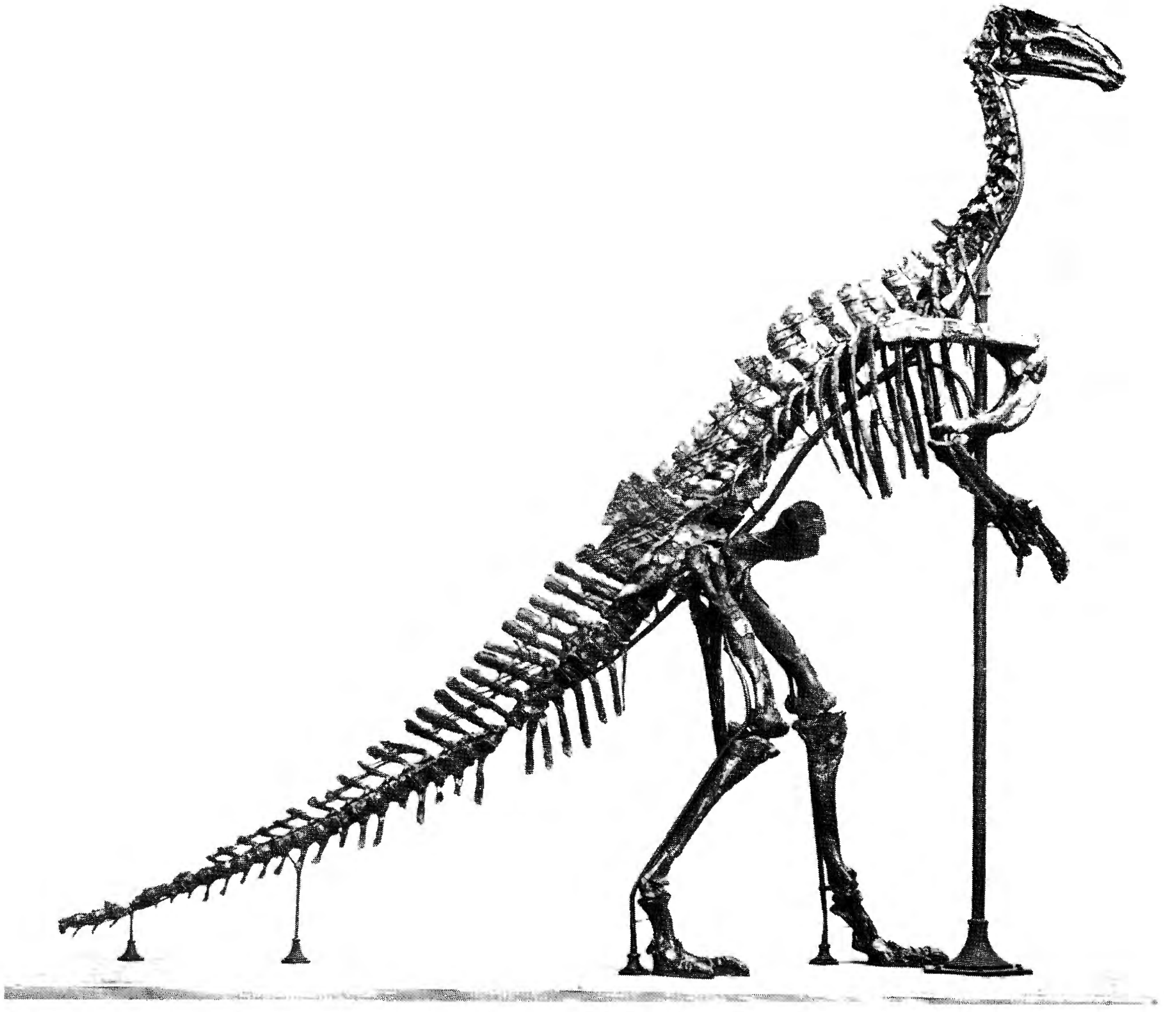


Because of the fluviatile nature of the deposits in which the teeth were found, there is no proven association (each may well have come from a different individual); these specimens therefore constitute a series of paratypes. From these, I have selected the best, and most frequently illustrated, example (BMNH R2392) as the lectotype (MANTELL, 1825: pl. XIV, figs. 1a, 1b).

Considerable taxonomic confusion surrounds the original material described by MANTELL because he failed to propose a specific name (notwithstanding the obvious problem created by erecting taxa on the basis of isolated teeth). HOLL (1829) was the first to propose a specific name for the teeth which MANTELL had described: *Iguanodon anglicum**. Unfortunately, HOLL published the first valid specific name for *Iguanodon* in an obscure publication which was either unknown to, or ignored by, most of the people working in this field. VON MEYER (1832) proposed the name *I. mantelli* for the material first described by MANTELL, and referred to it as well as some teeth described by CUVIER (1825) and some other fragments described by MURCHISON (1829) and MANTELL (1827). Following VON MEYER, most of the material subsequently discovered in southern England was referred by OWEN in his monographic review of British fossil reptiles (OWEN, 1841) to *I. mantelli* VON MEYER, 1832 [although OWEN incorrectly attributed the specific name to CUVIER].

Iguanodon mantelli VON MEYER, 1832, despite its prevalence in the literature on *Iguanodon* since the time of OWEN, is clearly an objective junior synonym of *I. anglicus* (HOLL, 1829). The name *Iguanodon mantelli* cannot therefore be maintained for material such as the renowned specimen (IRSNB

Fig. 2. – Iguanodon atherfieldensis. *IRSNB 1551 (T). The skeleton as mounted for display, circa 1884.*



---

* Incidentally *Iguanodon* transliterates as a masculine Greek noun, since the species name *anglicum* proposed by HOLL has the neuter gender ending, this is emended to the correct masculine form *anglicus*. Thus the type species of the genus becomes *Iguanodon anglicus* (HOLL, 1829).

1551) from Bernissart. It is also inadvisable to refer this skeleton to the type species *I. anglicus* for two reasons: (i) the type specimen is a tooth, and as such it is not sufficiently reliable for species-level identifications and (ii), the type tooth comes from the Tilgate Grit, which is currently dated as Hauterivian, while the material from Bernissart is more probably Barremian-Lower Aptian in age so that there would appear to be a significant time differential between type and referred material.

The taxonomic status of IRSNB 1551 ("*I. mantelli*") is therefore brought into question. Since 1841 several species of *Iguanodon* have been proposed. *I. hoggii* OWEN, 1874; *I. dawsoni* LYDEKKER, 1888; and *I. fittoni* LYDEKKER, 1889; these latter are all early Wealden Ryazinian-Hauterivian in age and are readily distinguished from the Bernissart species. Of the late Wealden forms that have been proposed, *Sphenospondylus* (= *Iguanodon*) *gracilis* (LYDEKKER, 1888) is an indeterminate series of dorsal vertebrae. By contrast, *I. bernissartensis* BOULENGER, 1881, is based on an excellent complete skeleton — IRSNB 1534 (NORMAN, 1980) [*I. seelyi* HULKE, 1822, is a subjective junior synonym of *I. bernissartensis*]. The remaining species: *I. atherfieldensis* HOOLEY, 1925, is represented by a well-preserved partial skeleton; comparison between these two specimens, the holotype of *I. atherfieldensis* (BMNH R5764) and the Bernissart skeleton (IRSNB 1551) reveals no significant difference in morphology, contrary to the statements of HOOLEY (1925). IRSNB 1551 is therefore referred hereafter to the species *I. atherfieldensis* HOOLEY, 1925.

Skull

GENERAL DESCRIPTION

The description of most of the superficial skull bones is based on IRSNB 1551. Additional information primarily concerning the anatomy of the endocranium, the dermal bones of the palate and the nasal and buccal cavities comes from the holotype (BMNH R5764) and other more fragmentary material in the collections of the British Museum (Nat. Hist.).

The skull, which is 54 cms long, has the outward appearance of a tapering oblong, the highest portion of which is the skull table above and posterior to the orbital cavity (Figs. 3-7). From the skull table, the upper border curves downwards in a smooth curve to the edentulous premaxillary beak; the latter forms a step where it projects below the level of the maxillary tooth row. The ventral margin of the maxilla is slightly concave and the tooth row extends backward to lie beneath the orbit. The quadrate forms the posterior margin of the skull descending in a marked curve from the massive, overhanging, paroccipital process. The notch between the quadrate and the distal end of the paroccipital process presumably marked the position of the tympanic membrane (cf. OSTROM, 1961, in *Corythosaurus*). The extreme length of the quadrate results in the notable ventral displacement of the jaw articulation, a typical herbivore adaptation in reptiles. The triradiate jugal spans the gap between maxilla and the suspensorium (quadrate + pterygoid complex). The skull openings are particularly well

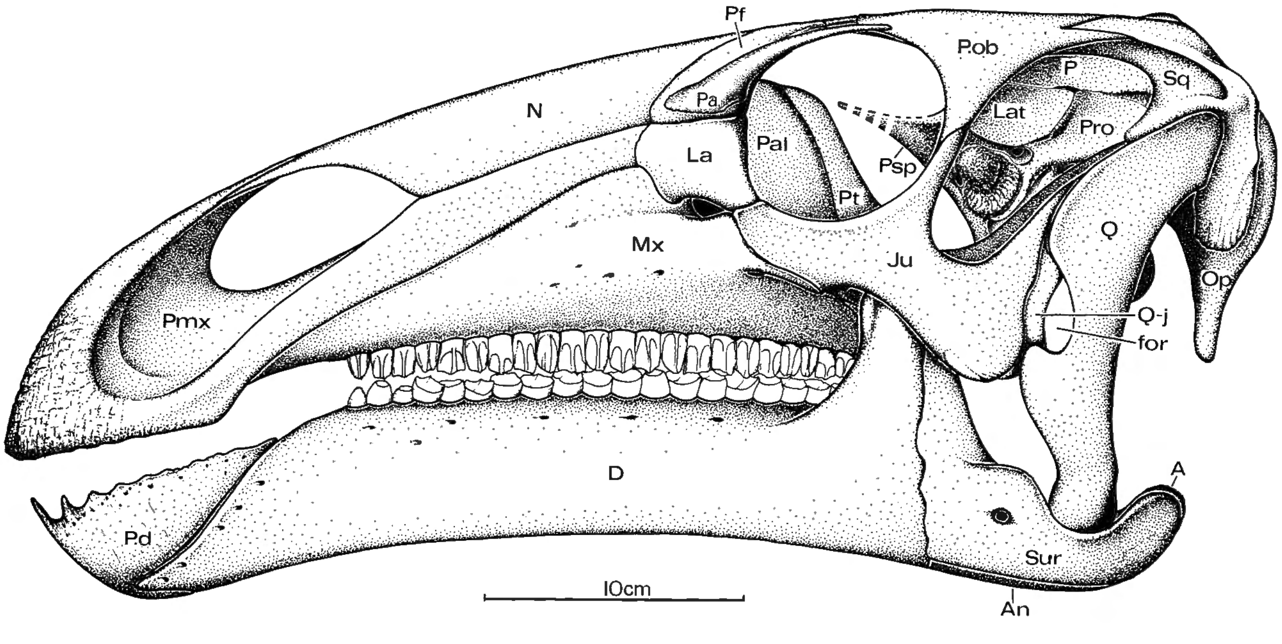


Fig. 3. – I. atherfieldensis. *Restoration of the skull and lower jaw in lateral view, based on IRSNB 1551 and BMNH R5764. (For abbreviations see pages 371-372).*

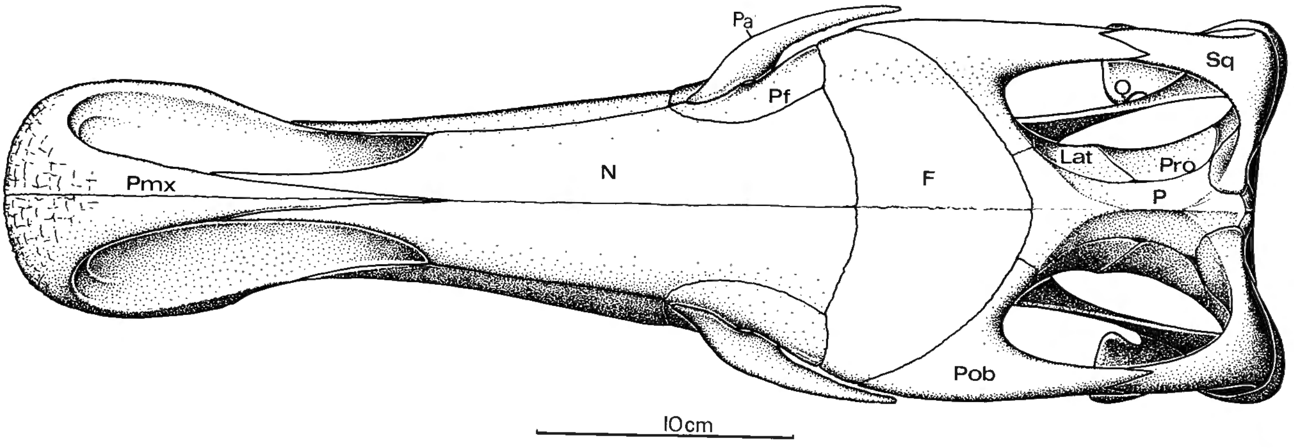
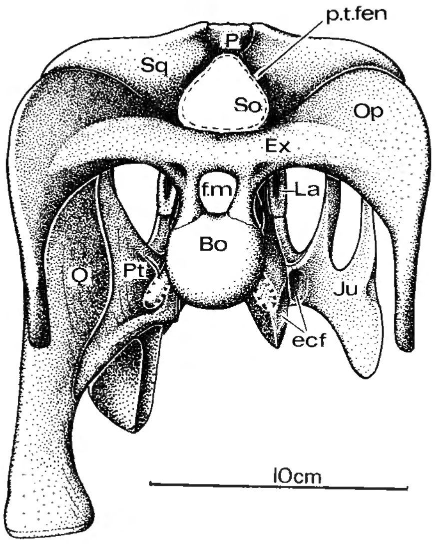


Fig. 4. – I. atherfieldensis. *Restoration of the skull in dorsal view, based on IRSNB 1551. (For abbreviations see pages 371-372).*

developed in *I. atherfieldensis,* especially that for the eye, a feature that is often attributed to the juvenile status of an individual. Unlike most other non-hadrosaur ornithopods, the palpebral (= supraorbital of others) bone follows the contour of the anterodorsal margin of the orbit, terminating as a sharp point above the posterodorsal orbital margin. The antorbital fenestra is reduced to a small aperture between the maxilla and lachrymal; there is no development of an antorbital fossa as is the case in *Hypsilophodon* GALTON, 1974) and related genera.

In dorsal view (Fig. 4) the extreme narrowness of the elongate snout region is immediately apparent, as is the lateral flaring of the premaxillae to form a spoon-like beak. The skull table is broadest across the orbits, the frontal plate is slightly concave and the supratemporal fenestrae are large elliptical slits separated by a small, median, sagittal crest.

Fig. 5. – I. atherfieldensis. *Restoration of the skull in occipital view, based on IRSNB 1551 and* I. bernissartensis *(NORMAN, 1980).*



Posteriorly (Fig. 5) the occiput is quite narrow and tall, flanked on either side by the large, wing-like paroccipital processes which extend obliquely outward and backward, and the pillar-like quadrates. Wedged between the paroccipital wings lies the small supraoccipital enclosed dorsally by the parietals and ventrally by the exoccipital bar. The exoccipitals form pillars on either side of the dorsoventral ellipse of the foramen magnum; the occipital condyle is roughly hemispherical, with a slight dorsal cleft where it forms the floor of the endocranial cavity.

Ventrally (Fig. 7) the extreme narrowness and great height of the naso-buccal cavity is striking. Anteriorly, the premaxillae form a low-vaulted roof to the anterior portion of the buccal cavity and a partial secondary hard palate. Lateral to the maxillary dentitions, the 'cheek' recesses are clearly shown. Posterior to the buccal cavity, the endocranium is partly shielded by the pterygoid elements of the palate; the sub-temporal fenestrae are large and each is subdivided by the oblique pterygoquadrate wing.

DERMAL BONES OF THE SKULL ROOF

The *premaxillae* (Figs. 3-8) are quite complex, forming the framework for the bones of the snout. Posterodorsally, they form a long curved and tapered, style-like process which lies beneath and partly within the midline, nasal suture. The lateral edges of this process are bevelled to receive the rostral process of each nasal. The premaxillae curve smoothly downward to the tip of the snout; this rostral area has a roughened and pitted external surface for the attachment and growth of a horny beak. On either side, the premaxillae are expanded laterally to produce a flared "beak", which is accentuated by the deep dorsolateral excavations for the external nares. Posterolaterally, each premaxilla develops an extremely long narrow process which

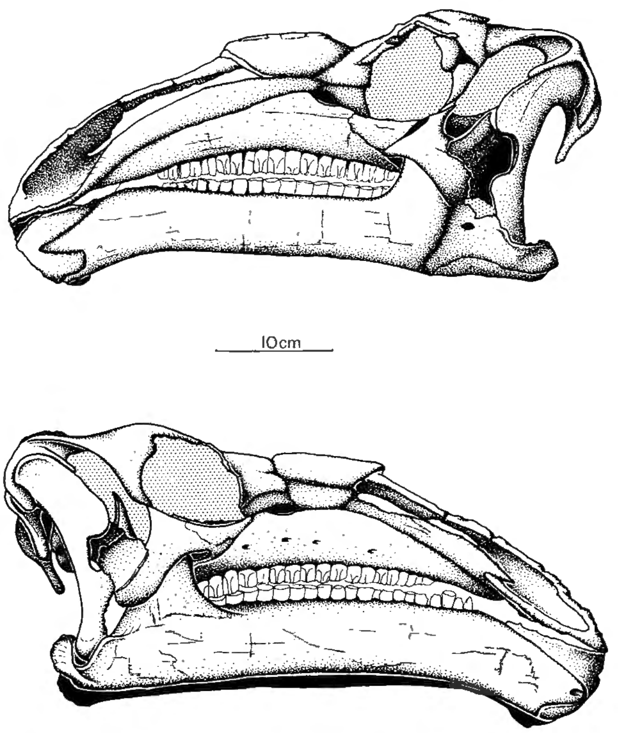


Fig. 6. – I. atherfieldensis. *IRSNB 1551. Lateral views of the skull as preserved.*

passes obliquely upward and backward toward the orbit, lying against the maxilla and terminating in an overlapping suture with the lachrymal. The nasals rest upon the posterodorsal portion of the premaxilla so that the large, trumpet-shaped external naris is entirely enclosed by nasal and premaxilla. Ventromedially, the premaxillae are moderately vaulted and extend backward to produce a small hard palate separating the anterior parts of the nasal and buccal cavities. The periphery of the premaxillary "beak" is somewhat thickened and irregular, with a series of pits arranged symmetrically on either side of the midline. These "pits" coincide with the position of bony spikes on the occlusal margin of the predentary and probably represent occlusal sockets. As in *I. bernissartensis* (NORMAN, 1980) there is a partial internarial septum.

The *maxilla* (Figs. 3, 6, 7, 9 and 10) is the stoutest bone in the skull and is approximately triangular in shape and is very similar in its general proportions to that of *I. bernissartensis*. The ventral margin describes a shallow concave curve terminating in a narrow spine-like anterior process which lies medial to the posterolateral margin of the premaxillary beak. The anterior 5 cms of the ventral margin of the maxilla is edentulous, but the remainder is devoted to accommodating an integrated battery of teeth in a continuous alveolar trough. The dentition is essentially straight for much of the length of the maxilla, but shows a distinct out-turning at its posterior end. Dorsal and lateral to its posterior end, the maxilla is overlapped by a thin, strap-like ectopterygoid which in turn curves outward to contact the jugal; the latter locks against a short, finger-like process developed from the lateral surface of the maxilla immediately beneath the orbit. Immediately anterior to the jugal, the maxilla is sutured to the lachrymal before separating from the latter to form a small antorbital fenestra. There is no fossa associated with the antorbital fenestra, as is found in hypsilophodontid ornithopods (GALTON, 1974) see Figure 67 E, but simply a small channel, lined by the lachrymal and maxilla, which is directed posteromedially toward the orbital cavity. Anterior to the antorbital fenestra, the maxilla contacts the premaxilla in a long oblique suture. Medially (BMNH R5764) the maxilla has a vertical inner surface. Above the alveolar margin there is a thin, textured alveolar parapet (Fig. 10), delimited dorsally by a shallow groove tracing the arcade of nutritive foramina which penetrate the maxilla at the base of each tooth family near the position of the presumed dental lamina (EDMUND, 1957).

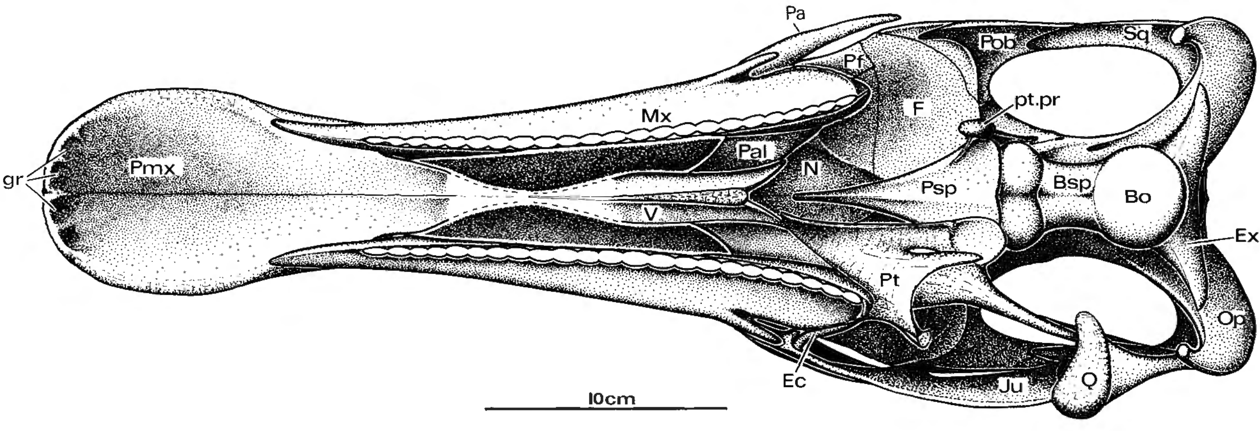


Fig. 7. – I. atherfieldensis. *Restoration of the skull in ventral view. Based on IRSNB 1551, BMNH R2501 and* I. bernissartensis *(NORMAN, 1980).*

Dorsally, the maxilla has a medial shelf which presumably formed the lateral part of the floor of the nasal cavity. Posteriorly the medial edge of the maxilla forms the attachment area for the pterygoid and palatine.

The external surface of the maxilla is quite prominently marked with foramina, both large and small which emerge obliquely on to the maxillary surface in the dorsal portion of the cheek recess. A similar arrangement is found in the dentary in the area of the cheek recess. The most reasonable interpretation of this phenomenon would appear to be that fleshy cheeks were present in this species and other ornithischians as proposed HOOLEY (1925), LULL and WRIGHT (1942) and GALTON (1973) and that the foramina represent a copious neural and vascular supply to this area.

The *nasals* (Figs. 3, 4, 7, 10 and 11) are thin, arched bones roofing the anterior portion of the snout posterior to the nostrils. In IRSNB 1551 (Fig. 6) they are laterally compressed and pushed backward. Sutured together for much of their length, they diverge anteriorly, where they become thin and style-like and lie in bevelled recesses along either side of the median dorsal process of the premaxillae. Posteriorly, the nasals meet and overlap the frontals in a transverse suture. Laterally the nasals form an oblique suture with the prefrontal, curving anteroventrally to meet the posterior end of the inferior premaxillary process. The ventral margin of each nasal is grooved (BMNH R5764) so that it locks on to the dorsal margin of the premaxilla. Anteriorly the nasals are smoothly emarginated to form the posterior margin of the external nares.

The *lachrymal* (Figs. 3, 7, 12) is approximately rectangular in external view; its posterior edge forming the anteroventral margin of the orbit. The ventral edge is arched dorsally above the antorbital fenestra and posteriorly contacts the dorsal part of the anterior tip of the jugal. Anterior to the antorbital fenestra, the lachrymal is overlapped by the dorsal edge of the maxilla and, as can be seen in BMNH R5764, is in fact wedged in position by a median peg-like projection from the maxilla (Fig. 9 lp) and the thin external wall. Anteriorly, the lachrymal is overlapped by the posterior extremity of the premaxilla and also dorsally by the prefrontal. The lateral surface of the lachrymal is slightly convex and has some low relief ornamentation. The orbital surface of the lachrymal is quite narrow and there is a large vertically elliptical lachrymal foramen which runs horizontally forward into the nasal cavity. The medial surface of the lachrymal is not visible in IRSNB 1551 but in BMNH R5764 the lachrymal is quite complex with several distinct depressions; ventrally these are for the lachrymal process of the maxilla and the lateral wall of the passage from the antorbital to the orbit. Dorsally, there are areas for the exit of the lachrymal duct and the lateral wall of the nasal cavity.

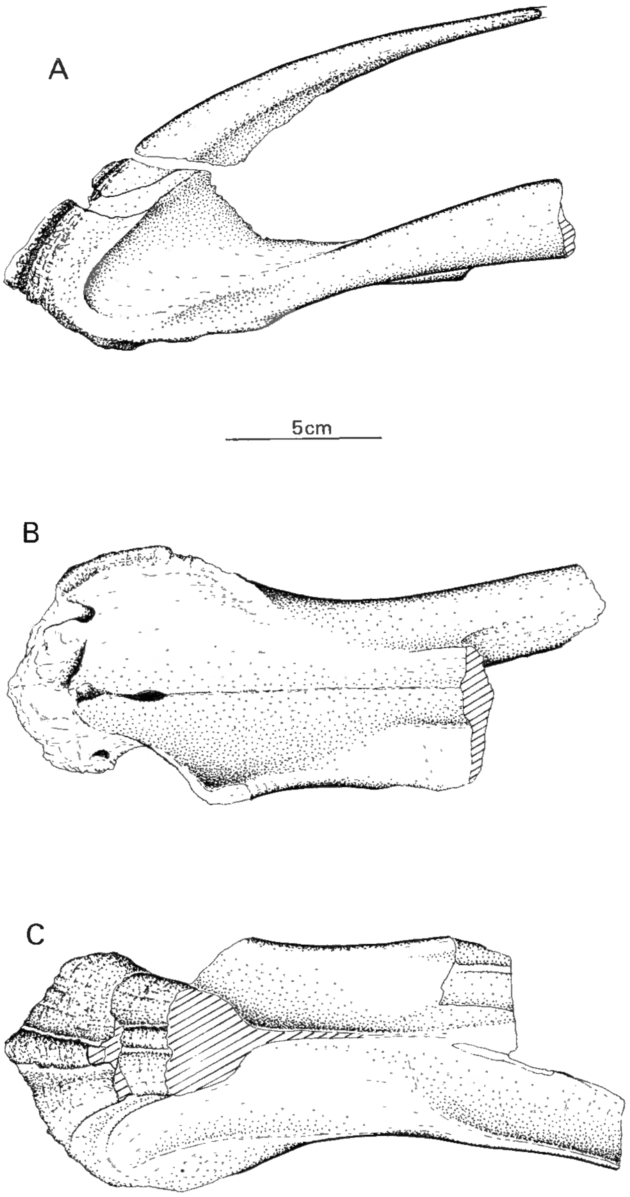


Fig. 8. – I. atherfieldensis. *BMNH R5764 (Holotype). Isolated premaxilla in lateral (A), ventral (B) and dorsal (C) views. Nasal extension removed in dorsal view.*

Dorsal to the lachrymal, the *prefrontal* (Figs. 3, 7, 10, 13) continues the margin of the orbit anterodorsally and is sutured to the nasal and frontal bones. In addition, the palpebral (= supraorbital) is attached albeit loosely to the slightly convex ventral part of its lateral surface. The suture with the nasal follows a curved path across the roof of the snout before meeting the frontal in a short transverse suture which ends on the orbital margin. The ventral portion of the orbital margin of the prefrontal is smoothly rounded, however as it sweeps posterodorsally, this develops into a slightly everted, rugose edge. The rugosity extends backward on to the frontal and postorbital where these lie adjacent to the palpebral and suggests that connective tissue tied the palpebral in position against these bones on the margin of the orbit. The prefrontal is quite thin and excavated internally (Fig. 13) where it encloses the nasal cavity.

The *frontals* (Fig. 4) form a very broad, flat plate between the orbits. Anteriorly the frontals are overlapped by the nasals in a transverse suture, which is continuous with the short frontal-prefrontal suture near the edge of the orbit. After a short orbital exposure, the frontals meet the postorbitals in a long curved suture which skirts the anterior margins of the supratemporal fenestra and terminates at a short junction, near the midline, with the parietals.

As in *I. bernissartensis,* the *parietals* (Fig. 4) are completely fused and form a roughly rectangular, saddle-shaped cap to the endocranium. The sagittal crest is well-developed and separates the large supratemporal fenestrae. Posteriorly the parietals are overlapped by tongue-like medial extensions of the squamosals, while anterior to the sagittal crest, the parietals diverge to meet the medial portion of the postorbitals.

The *postorbital* (Figs. 3, 4, 7) is a large, tri-radiate bone partially separating the orbital and temporal cavities. In lateral view the postorbital forms the posterodorsal portion of the orbit and produces a tapering, curved ventral (jugal) process which meets and overlaps the jugal thereby separating the orbit from the lateral temporal fenestra. Posteriorly the postorbital sends a curved and similarly tapering process to meet and overlap the squamosal separating the supratemporal from the lateral temporal fenestra; this posterior process is triangular in cross-section and distally it divides into two slender projections which lie in grooves on the dorsal and lateral surfaces of the squamosal.

The *squamosal* (Figs. 3, 4, 7, 14) forms the posterodorsal corner of the skull bounding the posterior part of the supratemporal fenestra and connects the braincase medially to the suspensorium ventrally and the postorbital region anteriorly. Medially the squamosal is firmly united to the anterior and lateral portions of the paroccipital process and the parietal. The posterior portion of the squamosal forms an oblique plate which lies against the paroccipital process; the anterior dorsal portion of this plate has a deep hemispherical depression which receives the head of the quadrate. Anterior to the socket for the quadrate, the squamosal develops an oblique ventral finger-like process which braces the quadrate against forward rotation. Above this latter process a stout process arches forward to meet and underlap the postorbital; this process is roughly triangular in cross-section, with a concave inner surface, facing the braincase and a slightly convex dorsal surface which is separated from the lateral surface by a distinct overhanging ledge.

The *jugal* (Figs. 3, 7, 15) spans the lower border of the orbit contacting the lachrymal anteriorly and curving upward and backward to meet the postorbital. Posterior to the postorbital-jugal bridge, the jugal also forms the lower half of the lateral temporal fenestra and contracts the anterior edge of the quadrato-jugal in a long overlapping suture. There is no dorsal contact between the jugal and the quadrate. The ventral border of the jugal is sinously curved. Anteriorly, the jugal rests against an oblique finger-like process developed on the lateral surface of the maxilla (BMNH R5764 - Fig. 9) and is also tied in position by the distal end of the strap-like ectopterygoid.

The *quadrato-jugal* (Figs. 3, 7) is a thin plate of bone which separates the jugal and the quadrate. Dorsally, the quadrato-jugal is spine-like and wrapped around the enterolateral margin of the quadrate and ventrally it spans the quadrate "notch" to enclose the quadrate foramen.

The *palpebral* (Figs. 3, 4, 16) found in all but the most advanced ornithischians (hadrosaurids) is a long slender element in this species. Its base is expanded and slightly concave, fitting against the convex lateral surface of the prefrontal. From this apparently articular area, the bone sweeps outward and upward following the dorsal margin of the orbit terminating as a sharp point lateral to the postorbital. The external surface is smooth and rounded, but the side adjacent to the orbit margin is very rugose presumably reflecting connective tissue attachment for this otherwise very loosely attached bone. There is no accessory palpebral as found in *I. bernissartensis* (NORMAN, 1980).

DERMAL BONES OF THE PALATE

The *vomers* are not presently known in any specimen of *I. atherfieldensis.* In IRSNB 1551 lateral compression of the skull makes these elements totally inaccessible. An arrangement of the vomers similar to that seen in *I. bernissartensis* has been assumed (Fig. 10).

The *palatines* (Figs. 7, 10) are large curved plates of bone visible through the orbit. Attached to the posteromedial margin of the maxilla and backed by the anterior ramus of the pterygoid, they curve dorsally and medially forming the lateral wall to the posterior nasal cavity.

The *pterygoids* (Figs. 5, 7, 10) are complex, thin bones which connect the suspensorium to the braincase and anterior palatal elements. As was the case with the vomers these bones are largely unknown in the holotype of *I. atherfieldensis,* and are inaccessible in the referred specimen (IRSNB 1551). The posterior portion of the pterygoid overlaps the medial wing of the quadrate and a shallow groove for its reception can be seen on the quadrate of the holotype (BMNH R5764). The pterygoids are therefore reconstructed from *I. bernissartensis.*

The *ectopterygoid* (Fig. 7) is visible in IRSNB 1551 and is a thin strap-like bone which lies across the posterior end of the maxilla (Fig. 9) and curves sharply outward to contact the medial surface of the jugal. In the holotype the internal surface of the jugal (Fig. 15) shows a smooth, cup-shaped depression at the point of contact with the ectopterygoid.

As in most ornithopods, the ectopterygoid probably extends forward from the lateral surface of the maxilla across the maxilla to the jugal, effectively tying these bones together.

SUSPENSORIUM

No *epipterygoid* is preserved in *Iguanodon,* however the *quadrate* (Figs. 3, 5, 6, 7, 10, 17) is a very large element. Essentially pillar-like in occipital view (Fig. 5) its anterior surface is modified by the development of divergent wing-like plates: the jugal and pterygoid wings. The former is laterally positioned and contacts the quadrato-jugal; its anterior margin is notched in the middle for the quadrate foramen. The medial or pterygoid wing is very thin, deep and overlaps the pterygoid quite extensively. The head of the quadrate is small and convex and fits into a deep socket in the squamosal; behind this there is an oblique plate formed of the squamosal and in front a finger-like process is wrapped around the dorsal edge of the jugal wing (Fig. 14). The distal end of the quadrate is a somewhat obliquely expanded articular condyle.

The posterior edge of the quadrate is quite strongly curved, especially when compared to the much straighter form seen in *I. bernissartensis* (Fig. 67 B).

THE ENDOCRANIUM

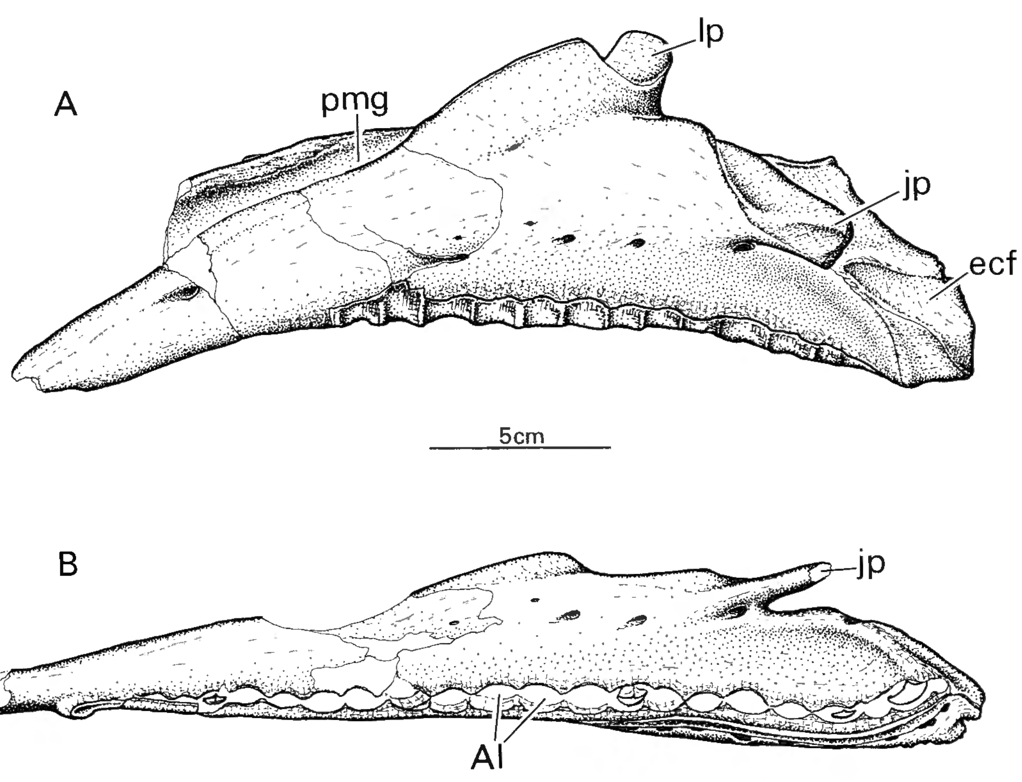
The endocranium is only partially visible in the referred specimen IRSNB 1551 and is totally absent from the holotype. The information comes from a particularly well preserved isolated endocranium (BMNH R2501 - Fig. 18) described in some detail by HULKE (1871) and ANDREWS (1897).

The *supraoccipital* (Figs. 5, 18) is not all well preserved either in IRSNB 1551 where it can be seen in occipital view or in BMNH R2501. It comprises a narrow, moderately thick plate of bone wedged into the centre of the occiput; it is enclosed ventrally by a horizontal bar formed by the exoccipitals, laterally by the base of the paroccipital processes and dorsally by the parietals (medially) and the squamosals (laterally).

In *I. bernissartensis* this bone is quite well defined (NORMAN, 1980) but in *I. atherfieldensis* this bone appears to be poorly ossified and rather indistinct.

The *exoccipitals* and *opisthotics* (Figs. 5, 18) appear to be indistinguishably fused in the specimens currently available; most probably these bones fused early in development (a common phenomenon).

Fig. 9. – I. atherfieldensis. *BMNH R5764 (Holotype). Isolated left premaxilla in lateral (A) and ventral (B) views. (Incomplete).*



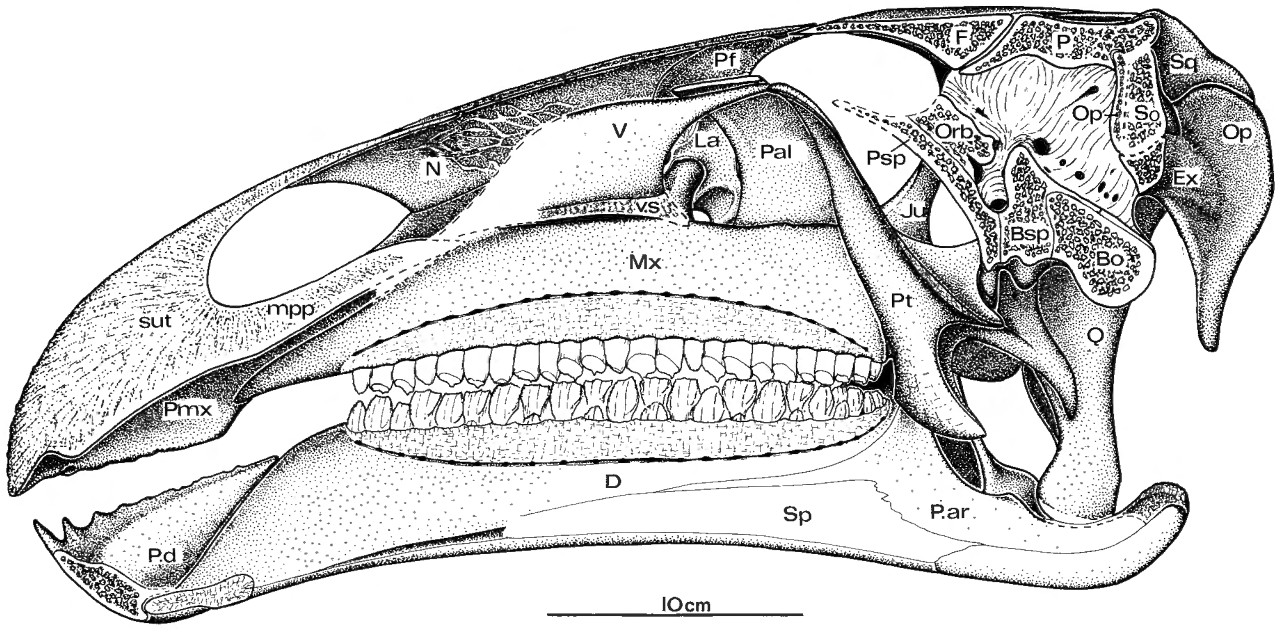


Fig. 10. – I. atherfieldensis. *Restoration of the skull and lower jaw in sagittal section. Based on IRSNB 1551, BMNH R5764, R2501 and* I. bernissartensis *(for profile of palate complex).*

The posterior "exoccipital" portion of the paroccipitals completely surround the foramen magnum excluding both the supraoccipital and the basioccipital. Laterally the paroccipitals sweep upwards and outwards to form large wing-like processes supporting the squamosal and quadrate. Distally the paroccipital processes curve sharply ventrally ending in hook-like projections behind the quadrate. The notch left between paroccipital wing and quadrate is assumed to have been an area for the tympanic membrane following COLBERT and OSTROM (1958) and OSTROM (1961) in hadrosaurids. However it should be noted that there is no obvious tympanic crest on the quadrate and, as WEVER (1978) has noted, many reptiles receive air-borne sounds through the skin covering the auditory meatus, an expanded depressor mandibulae, or through the quadrate. It is possible therefore that *Iguanodon* and ornithopods generally could have detected air-borne sounds without a definitive tympanum.

Anterior to the paroccipital wings, the lateral wall of the braincase is massive and thickened, here the opisthotic forms a small part of the otic capsule dorsally and ventrally it provides exits for various cranial nerves.

In typical reptiles the opisthotic forms the posterior part of the *fenestra ovalis* and extends backward to meet the exoccipital enclosing the exits for cranial nerves VIII-XI (see Fig. 18).

The *proötic* (Fig. 18) forms part of the concave inner wall of the temporal cavity; anteriorly, it is overlapped by the laterosphenoid, while ventrally it forms the posterior part of the Trigeminal fossa (for cranial nerve V), the channel for the Facialis (nerve VII) and the anterior margin of the fenestra ovalis. The proötic typically forms most, if not all of the osseus labyrinth. The internal surface of the cranial cavity bulges inward in the region of the inner ear constricting the cerebellar region of the brain cavity.

The *laterosphenoid* (= pleurosphenoid) (Fig. 18) forms the anterior part of the lateral wall of the braincase. Anteriorly the laterosphenoid sweeps outward to contact the postorbital creating a partial separation of the orbital and temporal cavities. The ventral edge of this bone is deeply recessed to carry the ophthalmic branch of cranial nerve V (Trigeminal) toward the posterior edge of the orbit.

The *orbitosphenoid* (Fig. 18) is well-ossified and forms the anteroventral floor of the endocranial cavity at the back of the orbital cavity. It is sutured to the laterosphenoid and (?) frontal laterally, the basisphenoid posteriorly, the parasphenoid ventrally and is pierced by several foramina.

In the dorsal midline the orbitosphenoid forms the floor to the passage for the olfactory nerves. Posteriorly there are exits for cranial nerves IV (Trochlear) and II (Optic) and a small foramen for the median palatine artery.

The sphenethmoid region of the skull was evidently cartilaginous and is not preserved in any of the fossils currently available.

The *parasphenoid* (Figs. 7, 18) of dermal origin forms the anteroventral surface of the braincase. In ventral view it is a triangular plate with a relatively short anterior cultriform process extending back as a flattened plate lying against the basisphenoidal tubera. The posterior corners of this plate form posterolaterally directed basipterygoid processes,

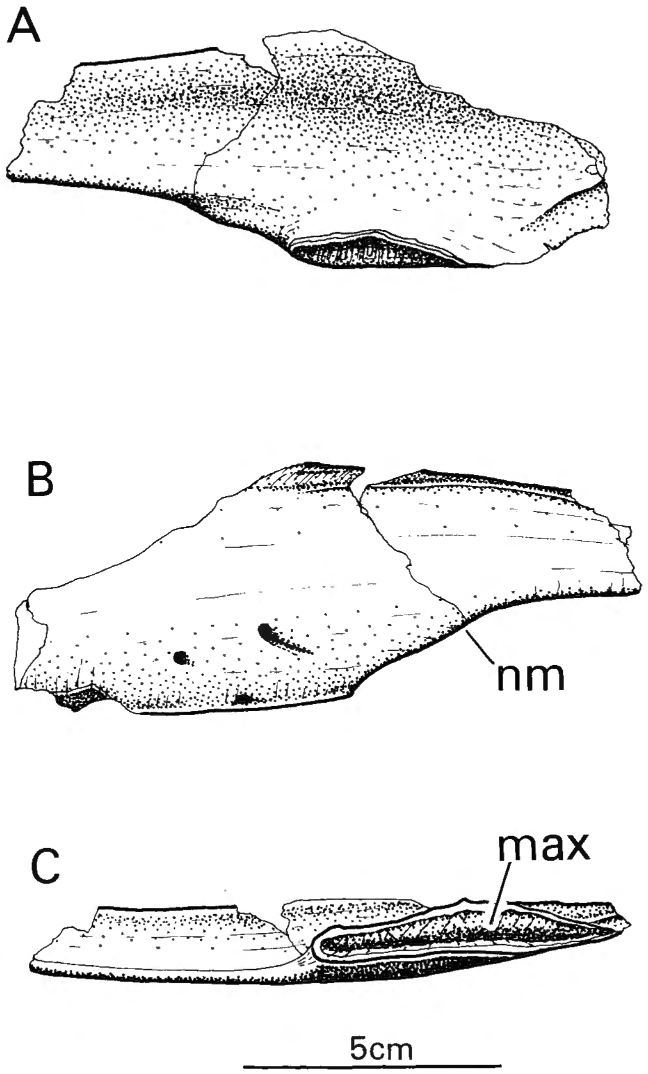
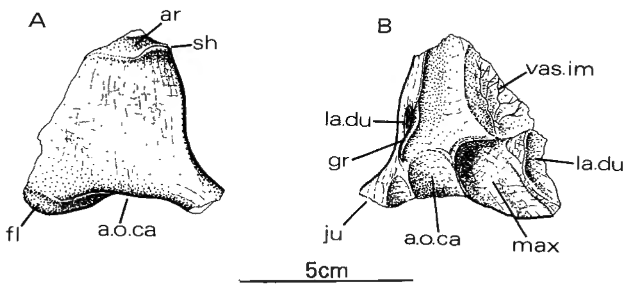


Fig. 11. – I. atherfieldensis. *BMNH R5764 (Holotype). Isolated right nasal in medial (A), lateral (B) and ventral (C) views.*

and it is not immediately obvious whether the parasphenoid or basisphenoid forms the entire basipterygoid process or whether the basisphenoid is covered superficially by parasphenoid.

Fig. 12. – I. atherfieldensis. *BMNH R5764 (Holotype). Isolated left lachrymal in lateral (A) and medial (B) views. (For abbreviations see pages 371-372.) (Incomplete).*



The *basisphenoid* (Figs. 6, 10, 18) forms the central portion of the floor of the braincase and is sutured to the parasphenoid anteriorly, the proötic and laterosphenoid dorsally and the basioccipital posteriorly. The posterior part of the basisphenoid is broad and developed into two large swellings, the basal tubera. The lateral surfaces of the basal tubera are convex but anteriorly, beneath the exit of the Facialis (nerve VII) there is an oblique groove running down to the aperture for the *Vidian canal* for the palatine branch of nerve VII. Anterodorsal to this groove there is a broad flange of bone beneath the trigeminal fossa with very prominent surface markings. Farther anteriorly the basisphenoid meets the orbitosphenoid along the plane of the pituitary fossa; cranial nerves III and VI emerge from the braincase along this suture.

The *basioccipital* (Figs. 6, 10, 18) forms the posterior foundation to the floor of the braincase and the occipital condyle. The latter is large, approximately hemispherical and posteroventrally directed. Anterior to the occipital condyle, the body of the basioccipital is sharply contracted and fused to the basisphenoid between the basal tubera.

Mandible

Each ramus of the lower jaw is very stoutly constructed (Figs. 3, 7, 10, 19) although the dentary symphysis is curiously small and weak. However, the symphysis is supported by the crescentic predentary. The main body of each jaw is twisted longitudinally, with medially positioned teeth and an elevated, laterally positioned coronoid process. Behind the latter, the jaw descends steeply to the jaw articulation. Behind the glenoid, there is a small, upturned retroarticular process. The mandibular (adductor) fossa is quite narrow and confined to the area between the coronoid process and the glenoid.

The lower jaw is remarkable for the proximity of each jaw ramus which leaves a very narrow parallel-sided buccal cavity.

The *predentary* is somewhat scoop-shaped and sits upon the spout-like anterior margins of the dentaries above the dentary symphysis. The predentary is anchored to the dentary margins by means of a bilobed ventral plate which locks against the dentaries on either side of the symphysis. The external surface of the predentary is slightly rough and irregular, particularly so near the upper occlusal margin where there are numerous small vascular foramina. In life the predentary was undoubtedly covered by a keratinous beak. The occlusal margins of the predentary are identical to *I. bernissartensis* (NORMAN, 1980) having a sharp, denticulate anterior median portion transforming gradually into a low lateral margin and inner occlusal shelf farther laterally and posteriorly.

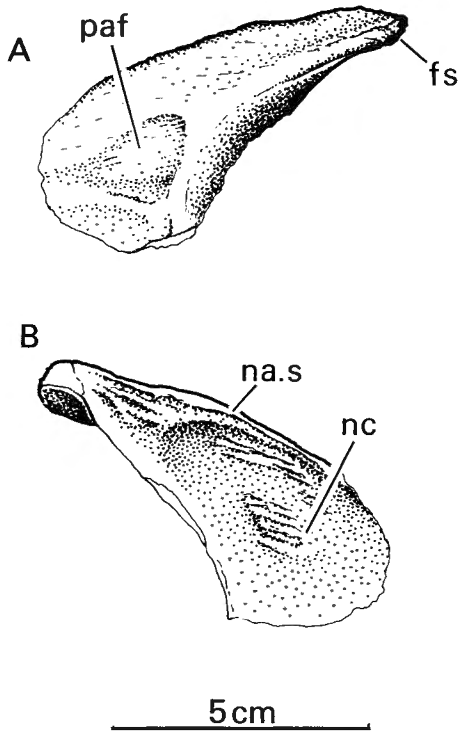


Fig. 13. – I. atherfieldensis. *BMNH R5764 (Holotype). Isolated left prefrontal in lateral (A) and medial (B) views. (Incomplete).*

The *dentary* tapers to a rounded point anteriorly and lateral to the small horizontal dentary symphysis. The dorsal border curves upward and backward marking the contact point with the predentary, there is then a short diastema before the development of the scalloped margin of the dental battery. The teeth are not anchored in separated sockets but rather in a continuous groove and are retained medially by an alveolar parapet (Fig. 19 al. p). Although there are no interdental plates, the internal alveolar walls of the dentary are moulded to the shape of the emergent roots and crowns of the teeth so that they are continuously supported. Beneath the alveolar parapet there is a shallow longitudinal groove with regularly spaced foramina which penetrate the base of the alveolar furrow and presumably supplying nutrients to the dental laminae. Lateral to the dentition, there is a broad shelf (cheek recess) at the posterior end of which arises the coronoid process.

Medially, below the alveolar parapet, the dentary is undercut by a long Meckelian groove which is shallow anteriorly but becomes very broad posteriorly and opens into the mandibular fossa. The postdentary bones key into the posterior and medial parts of the dentary.

The *coronoid* lies on the medial surface of the coronoid process of the dentary and is a small lozenge-shaped bone which can be just seen as a dorsal rim in lateral view.

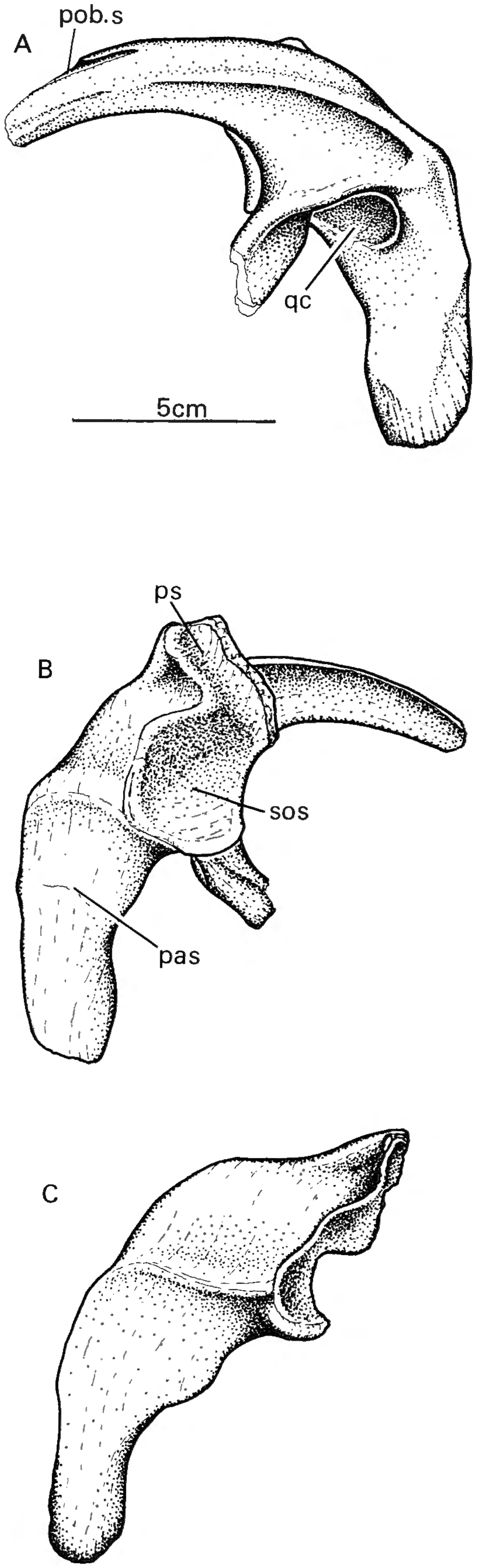


Fig. 14. – I. atherfieldensis. *BMNH R5764 (Holotype). Isolated left squamosal in lateral (A), medial (B) and occipital (C) views.*

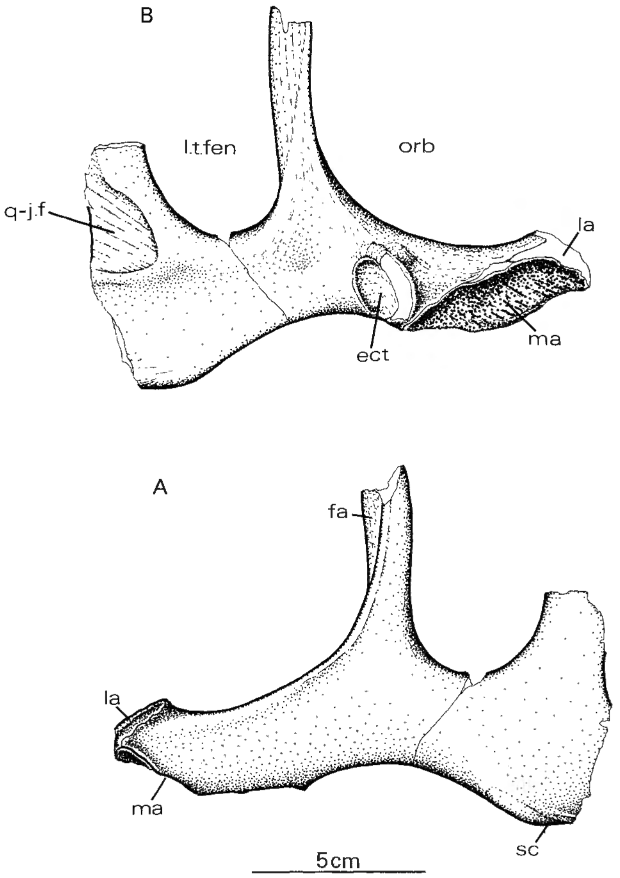


Fig. 15. – I. atherfieldensis. *BMNH R5764 (Holotype). Isolated left jugal in lateral (A) and medial (B) views.*

The *surangular* has a large lateral exposure, it slots into the posterior surface of the coronoid process and underlaps the dentary ventrolaterally. The dorsal border of the surangular descends steeply to the glenoid forming the lateral border of the mandibular fossa and contributing to more than half of the articular surface of the glenoid. A small surangular foramen runs into the mandibular fossa just anterior to the glenoid.

The *angular* lies along the posterior ventral end of the jaw and has a small lateral exposure on the mandible; it also has an overlapping suture with the dentary and sits in a groove along the ventral surface of the surangular.

The *splenial* is a thin elongate plate of bone which lies across the Meckelian groove from a position close to the symphysis and terminates medial to the glenoid fossa between the prearticular dorsally and the angular ventrally.

The *articular* is a small lozenge-shaped bone lying between the surangular and preaticular forming the medial part of the articular surface of the glenoid and the medial part of the retroarticular process.

The *prearticular* lies dorsal to the spenial and against the medial surface of the dentary. Posteriorly it forms the medial margin of the mandibular fossa, skirting the medial edge of the glenoid and terminating along the side of the articular.

Hyoid elements

The hyoid apparatus (Fig. 20) is represented by slender, curved bones which have been found in association with the mandible in several specimens. These elements have been homologized with the 1st ceratobranchials of living reptiles (NORMAN, 1980). In *I. atherfieldensis* these bones are particularly long and slender, quite broad and abruptly truncated anteriorly with a very "unfinished" anterior surface suggestive of a cartilaginous capping; they taper posteriorly and are quite strongly curved (convex ventrally).

Dentition

The teeth of *I. atherfieldensis* are virtually indistinguishable from those of *I. bernissartensis* (NORMAN, 1980) to such an extent that the description applied to the latter could equally well apply to *I. atherfieldensis*. The main differences are simply those of size. The number of vertical tooth positions

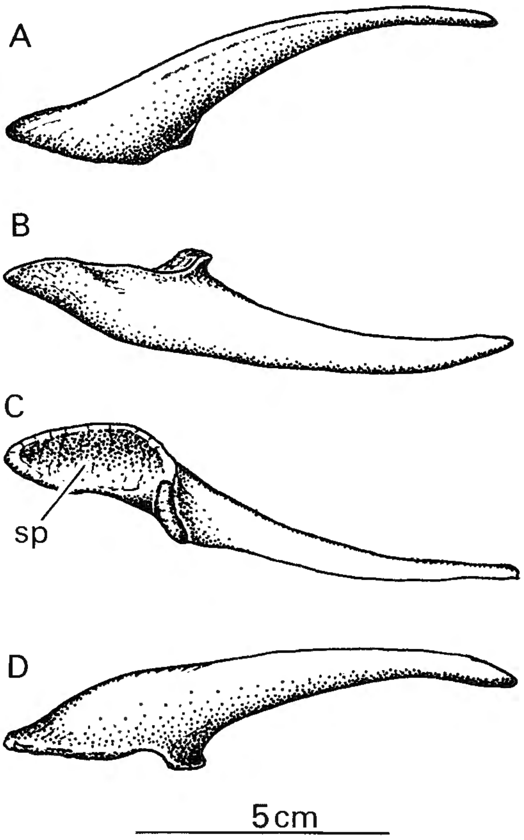


Fig. 16. – I. atherfieldensis. *IRSNB 1551. Palpebral (left) in lateral (A), dorsal (B), medial (C) and ventral (D) views.*

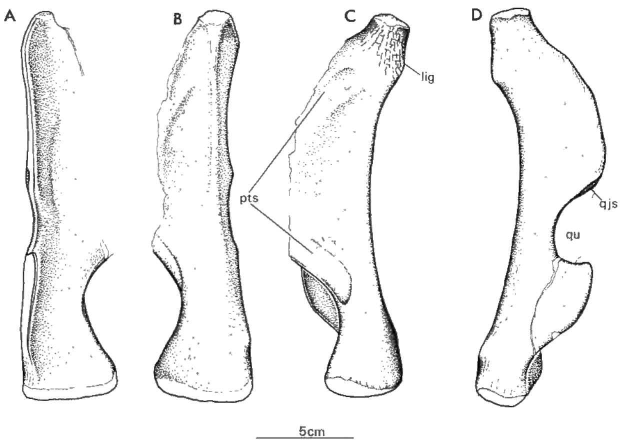


Fig. 17. – I. atherfieldensis. *BMNH R5764 (Holotype). Quadrate (right) in anterior (A), posterior (B), medial (C) and lateral (D) views.*

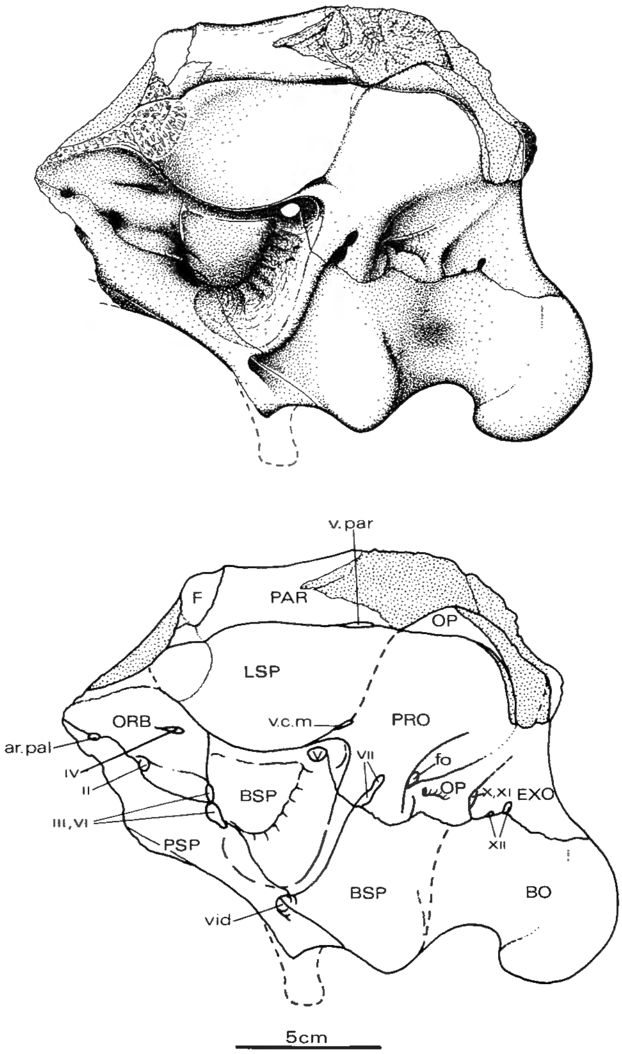


Fig. 18. – I. atherfieldensis. *BMNH R2501. Isolated partially eroded endocranium. (For abbreviations see pages 371-372.)*

(families) in the jaws differs: *I. atherfieldensis* possesses approximately 23 maxillary tooth families compared to 29 in full-sized *I. bernissartensis;* similarly in the mandible there are 21 tooth families in *I. atherfieldensis* compared to 25 in *I. bernissartensis.*

Maxillary and dentary teeth are illustrated in figures 21 and 22 for a direct comparison of teeth in the two species.

The principal characteristics of the teeth are as follows. *Dentary teeth* (Fig. 21) have long tapering roots which have shallow vertical grooves down anterior and posterior edges to accomodate the closely packed crowns of adjacent successional teeth. The crown of the tooth is laterally compressed and somewhat leaf-shaped in medial aspect with a denticulate margin. The medial face of the crown is thickly enamelled and traversed by a series of ridges; the largest or most clearly defined is posterior to the middle of the crown and extends to the posterior corner of the truncated tip of the crown. Another, less clearly defined ridge extends up the face of the crown anterior to the first but tends to merge with the surface of the crown before reaching the crown tip. Between these two ridges there is a shallow vertical depression. In addition to these two main ridges, there may be a variable number of subsidiary ridges which are extensions of the bases of the marginal denticles. Just below the widest part of the crown, the posterior denticulate margin of the crown curls inwards to produce an obliquely inclined cingulum.

Dentary teeth also tend to vary in shape depending on their position within the dentition: those found most anteriorly tend to be rather more lanceolate, while those farther posteriorly tend to be somewhat broader.

The *maxillary teeth* (Fig. 22) differ quite markedly from those of the dentary. The roots are again long and tapering in mature teeth and have similar longitudinal grooves in them for successional crowns. However the crowns are very different. By comparison to the dentary crowns, those of the maxilla are very narrow. The thickly enamelled surface of the crown is lateral rather than medial and has a strongly denticulate margin. The lateral surface is dominated by a very large ridge arising from the base of the crown and extending to the apex posterior to the midline. The remainder of the crown surface is relatively smooth apart from a few subsidiary ridges of variable extent.

Axial skeleton

The vertebral column of *I. atherfieldensis* is known almost completely as a result of the information furnished by the holotype (BMNH R5764) which lacks most of the tail, and the referred skeleton

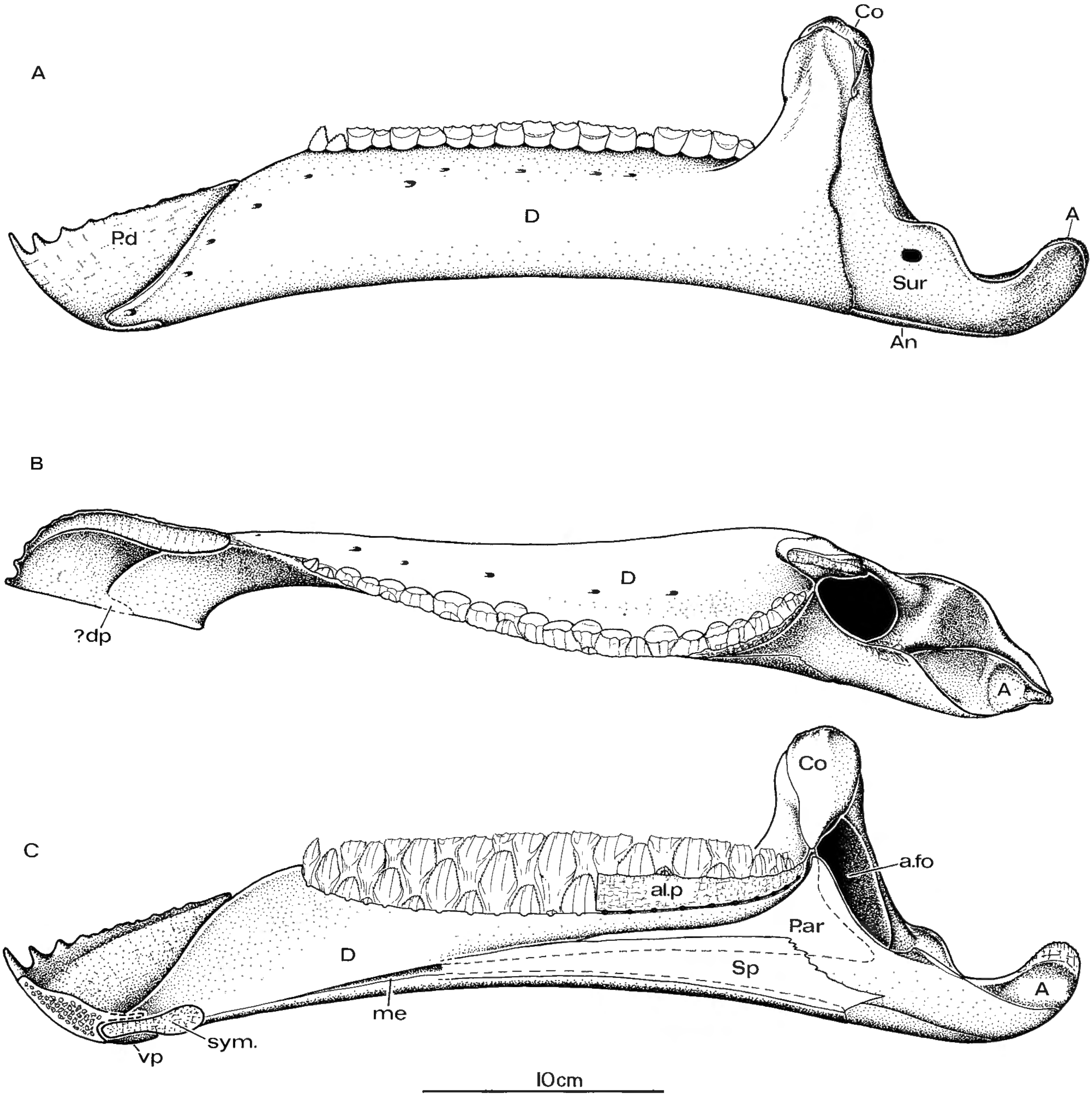


Fig. 19. – I. atherfieldensis. *Restoration of the lower jaw based on IRSNB 1551 and BMNH R5764. A, lateral view, B, dorsal medial view, C, medial view.*

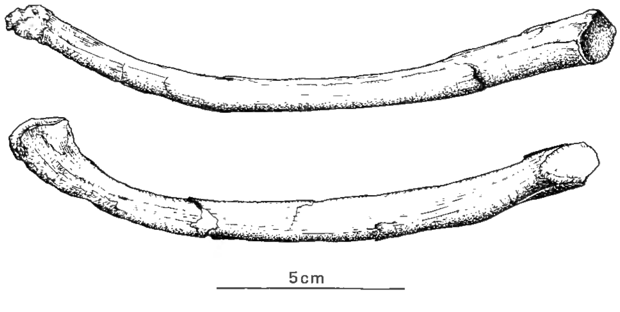


Fig. 20. – I. atherfieldensis. *IRSNB 1551. Left and right hyoid bones in lateral and medial views respectively.*

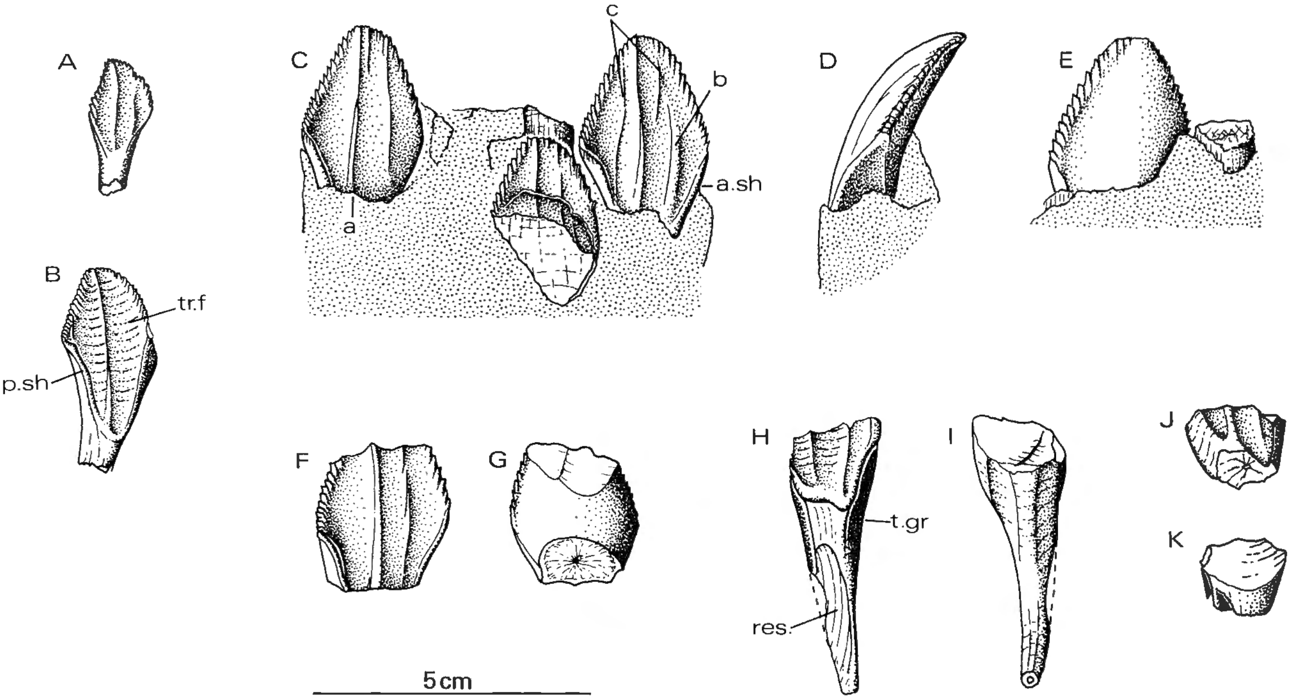
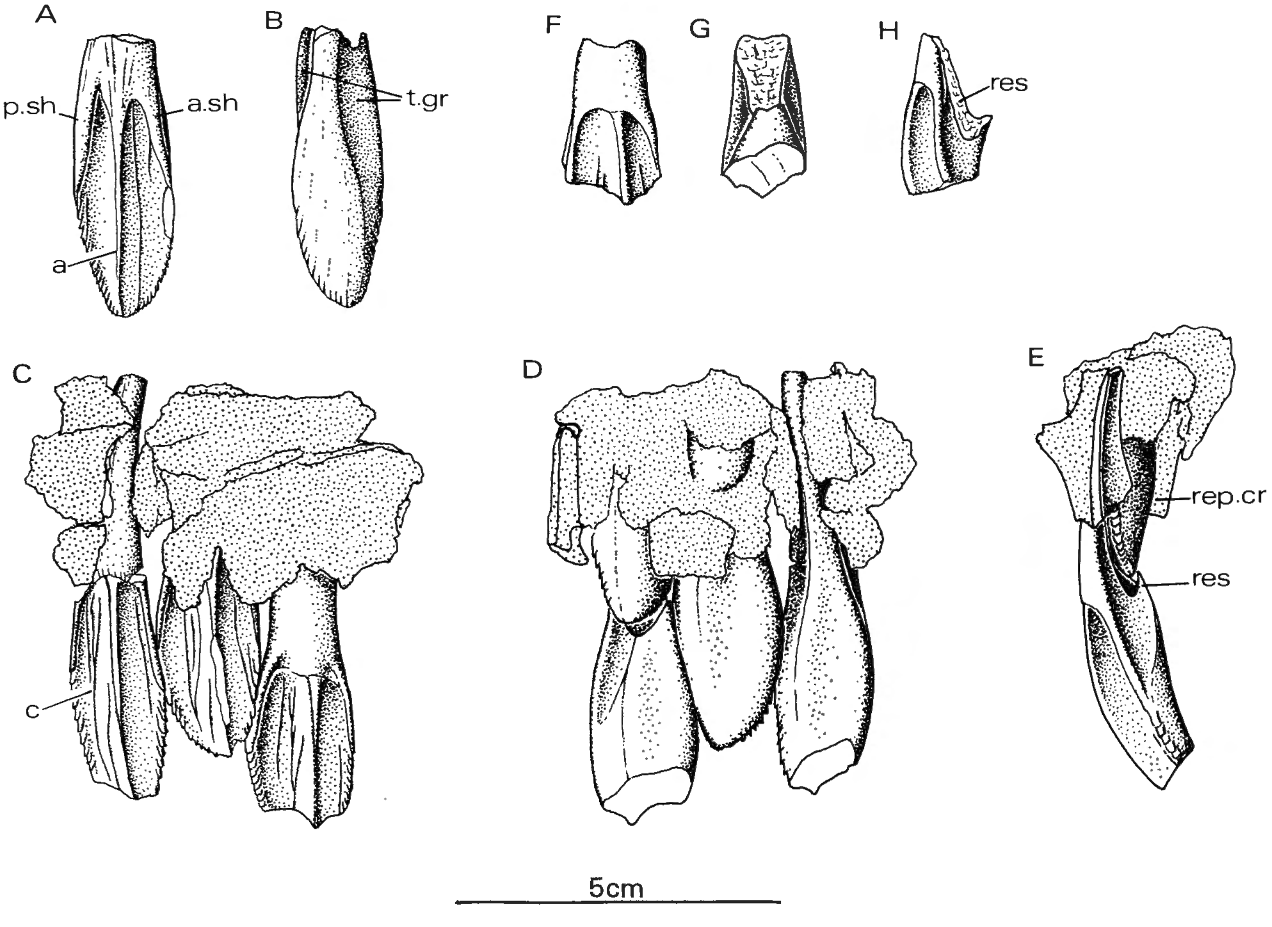


Fig. 21. – I. cf. atherfieldensis. *Illustrations of various dentary teeth. A, lingual view (BMNH 40100); B, lingual view (R134); C, lingual view BMNH 40100, also D, mesial view, and E, labial view; F, G, lingial and labial views of isolated crown (BMNH 40100); H, I, isolated worn tooth, with resorption facet on root in lingual and labial views; J, K, lingual and labial views of terminally resorbed shed tooth. (For abbreviations see pages 371-372.)*

Fig. 22. – I. cf. atherfieldensis. *Maxillary teeth. A, B, lateral and lingual views of unworn crown (BMNH R134); C, D, E, labial, lingual and distal views of tooth bearing maxilla (BMNH 40100); F, G, H, heavily worn maxillary tooth with completely resorbed root (BMNH 40100). (For abbreviations see pages 371-372.)*



(IRSNB 1551) which is more complete but not so well preserved.

CERVICAL VERTEBRAE

The Proatlas

HOOLEY (1925) briefly described and figured the proatlas of *I. atherfieldensis* (BMNH R5764). Unfortunately, this specimen is now missing from the collections of the British Museum (Nat. Hist.). The only remaining proatlases are the associated left and right proatlas, preserved, in position, on a single specimen of *I. atherfieldensis* (IRSNB 1551) which was commented upon but not described at all by DOLLO. These have been restudied in an attempt to understand better the structure and probable function of these enigmatic bones.

Although both the specimens are imperfect, nevertheless most of their structure can be deduced. In dorsal view (Fig. 23, 24) they are more or less triangular, the apex of which is posterior; the lateral edge is concave lengthways, rounded vertically and ends abruptly at a sharp edge. Medial to this lateral edge, the dorsal surface becomes flatter to meet the sharp medial and anterior borders. The anterior surface consists of an elongate undulating concave facet, bounded by a raised edge; this facet is obliquely orientated, the long axis being inclined ventromedially. The medial edge is acute and possesses a broad, more or less triangular facet, which is slightly concave, and ventro-medially directed.

Articular relationships.

The large ventromedially directed concave facet is effectively the postzygapophysis of the proatlas, and sits on the smooth convex anterior extremity of each neural arch of the atlas (Fig. 23, 24); this area is not clearly demarcated as a zygapophysis on the atlas. The remaining obliquely inclined anterior facets are puzzling, but were evidently shaped so that they could articulate against the occiput of the skull. To determine the relationships of these bones with the occiput, they were correctly articulated on the neural arches of the atlas and then with the occiput of the skull in the specimen in question (IRSNB 1551). It was found that the concave facet on each proatlas fitted comfortably against the posteroventral edge of the adjacent exoccipital.

Function.

Each proatlas probably formed a stiff linkage between atlas and skull, above the occipital condyle; if this was so, it would have helped to assist the enormous tensile stresses exerted by the occipital musculature to keep the long skull in a horizontal position and helped to prevent dislocation of the neck at the occipital condyle. It would seem probable, therefore, that dorsoventral flexure of the head (nodding movements) were achieved by flexure between the cervical vertebrae rather than exclusively at the occipital condyle, since this joint was greatly stiffened by the proatlases.

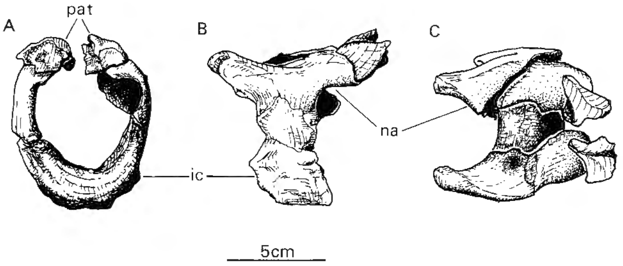


Fig. 23. – I. atherfieldensis. *IRSNB 1551. Proatlas/Atlas complex. A, B, C - anterior, lateral and dorsal views, as preserved.*

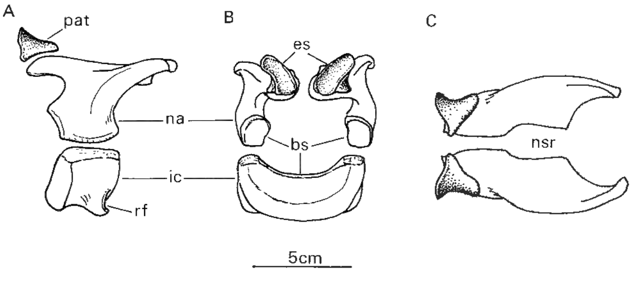
Atlas

The atlas consists of an intercentrum, an odontoid and two neural arches (Fig. 23, 24). The *intercentrum* is a subcrescentic bone which anteriorly has a shallow, anterodorsally directed, concave depression for the occipital condyle; its ventral margin is everted and rounded. Above and behind this depression there is a smooth depression to receive the ventral surface of the odontoid; on each side of this depression there are slightly rounded, rugose shoulders for attachment of the neural arches. Posteriorly, the surface is convex vertically and articulated against the axis and the axis intercentrum; the ventrolateral corners of this surface possess prominent concave depressions for articulation of the atlantal rib.

The *odontoid* is not preserved in either BMNH R5764 or IRSNB 1551, although it is preserved in several specimens of *I. bernissartensis* (IRSNB 1535, 1536 - NORMAN, 1980). Typically it has the form of a slightly dorsally flattened cylinder. The posterior end is broadest and flattened where it abuts against the axis; the sides taper slightly anteriorly to an obliquely truncated anterior end, the anterior surface of which articulated against the posterodorsal surface of the occipital condyle and ventrally with the atlas intercentrum.

The *neural arches* are fused neither to each other

Fig. 24. – *Reconstruction of proatlas/atlas complex cf.* I. atherfieldensis.



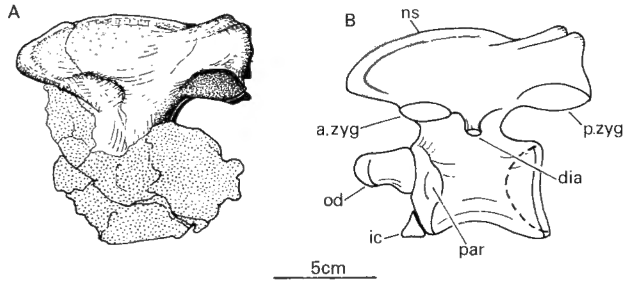


Fig. 25. – I. atherfieldensis. *IRSNB 1551. Axis. A. Lateral view as preserved, the centrum is badly crushed. B. Restoration.*

nor to the intercentrum. Ventrally, the pedicles of each neural arch are expanded and rugose where they articulate against the intercentrum; the anterior end of this articular surface faces obliquely forward and is concave and served as an additional area of articulation with the occipital condyle (Fig. 24). Above their bases, the neural arches contract and curve upwards and inwards, enclosing the neural canal. Anteriorly, they develop into flattened, rounded processes (prezygapophyses) which support each proatlas; posteriorly, the dorsal surface of each arch is flat and overhangs the neural canal, from the posterolateral corner of each there is developed an elongate, tapering transverse process, and medial to this there is a distinct elongate notch in the medial surface of each neural arch. This notch served to accommodate the large anterior expansion of the neural spine of the axis; on the ventral surface of each neural arch, just lateral to this notch, there is a large postzygapophyseal facet.

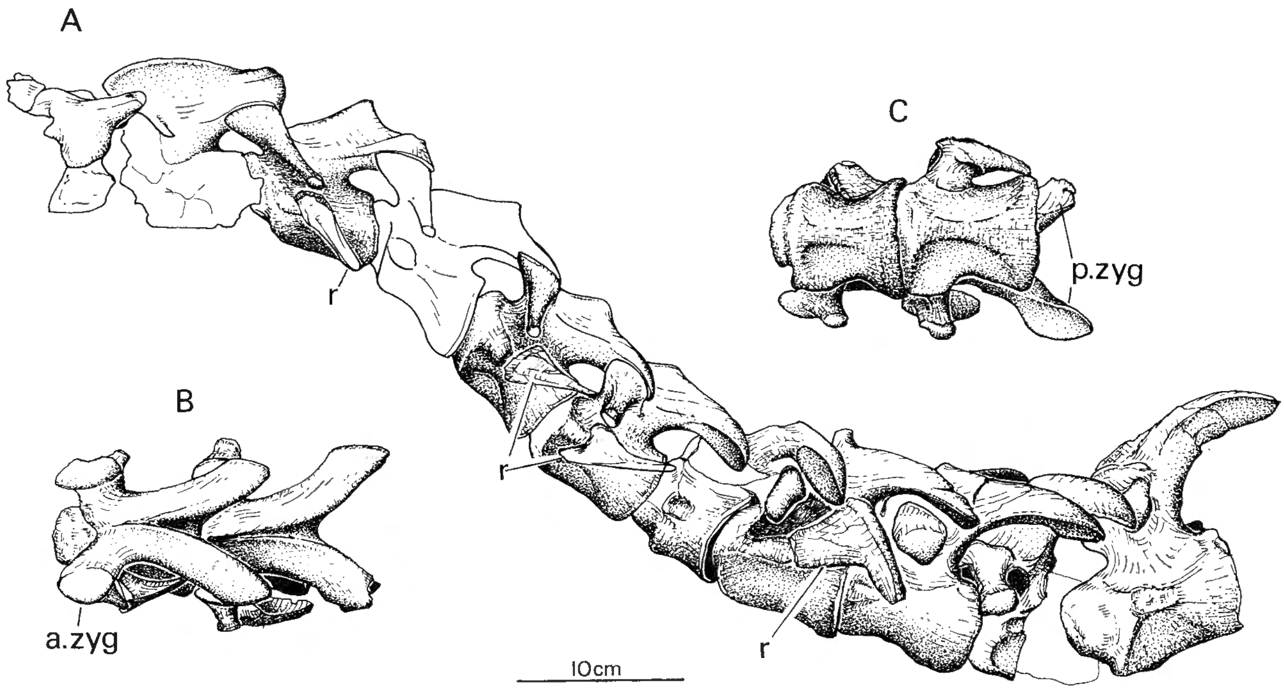
Axis

Is missing in BMNH R5764 and the centrum is badly crushed in IRSNB 1551 (Fig. 25). The centrum is elongate and strongly opisthocoelous; its anterior surface was undoubtedly similar to that in *I. bernissartensis* (NORMAN, 1980) - essentially flat with a shallow crescent-shaped axis intercentrum along its ventral edge. The centrum of the axis is expanded at both ends and contracted about the middle; its ventral surface is rounded and not keeled as in succeeding cervicals. The neural arch is very well developed and dominated by a huge expansion of the neural spine. The transverse process is reduced and arises from quite low down on the side of the neural arch, between pre- and postzygapophyses, extending obliquely backwards to form a small diapophysis. Anteriorly, the zygapophyses project forward, on either side of the huge hook-like anterior extension of the neural spine. These zygapophyseal facets are unusual in that they face obliquely anterolaterally instead of anterodorsally, as in the remaining cervicals. The neural spine curves upwards and backwards from its anterior end. At its highest point, just posterior to the transverse process, it is abruptly notched and then divides into two ventrolaterally directed postzygapophyses which overhang the posterior end of the centrum quite considerably.

Cervical vertebrae 3 - 11 (Fig. 26)

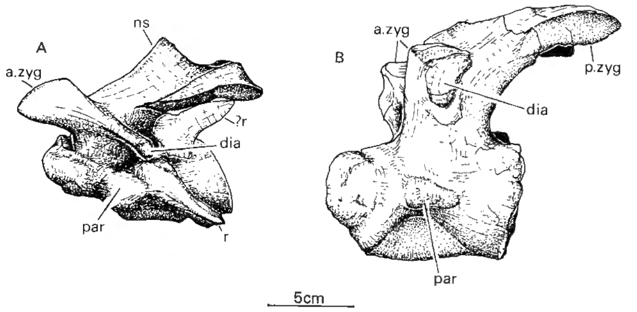
The centra of this entire series are strongly opistho-

Fig. 26. – I. atherfieldensis. *IRSNB 1551. A. Articulated cervical vertebral series as preserved in lateral view. B. Dorsal view of cervicals 5 and 6. C. Ventral view of cervicals 5 and 6.*



coelous and possess large, hemispherical anterior articular surfaces. The latter are not entirely convex, having a slightly flattened centre which bears a small concave pit. In lateral view, these anterior hemispherical surfaces can also be seen to be distinctly upwardly directed; this is especially so in the more posterior members of the series. Ventrally, the centra are transversely compressed with a thick, rounded, rugose-surfaced keel; this is narrowest anteriorly, just behind the margin of the anterior articular ball, and widens posteriorly as it gradually merges with the posterior margin of the centrum. Above the keel, the lateral walls of the centrum are concave and rise upwards to the middle of the centrum, where they meet a horizontal ridge, which, anteriorly, forms the parapophysis. Dorsal to this ridge, the sides of the centrum are again contracted before sweeping upwards into the base of the neural arch. The neural arch is quite complex in the cervical series. It forms a large smooth arch over the neural canal and is anchored to the centrum by robust neurapophyses. From the outer surface of the arch, there are developed two paired processes: the lower, more anteriorly placed transverse processes, which support the large prezygapophyses on their anterodorsal surfaces and also, at their distal ends, provide the diapophyses for the articulation of the cervical rib heads. The large, curved postzygapophyses arise from the midline above and between the transverse processes and diverge so they curve upwards and backwards to their distal articular ends, where they are flattened ventrally to form the zygapophyseal articular facets. The parapophyses of the cervical series are quite small horizontally elongate depressions, situated immediately behind the articular margin of the anterior surface of the centrum, and about mid-way up the side of the centrum. The neurocentral suture lies above the parapophysis in all the cervicals except for the 11th, in which it skirts the dorsal border of the parapophysis. The parapophysis of this latter cervical is also larger and more rounded than the preceding; this is probably an adaptation to bear the thrust from a larger rib.

Fig. 27. – I. atherfieldensis. *IRSNB 1551. A. Cervical 3 in lateral view - rib crushed against centrum. B. Cervical 11 in lateral view.*



In the anterior region of the cervical series, the centra are quite low, slightly dorsoventrally compressed, cylinders (Fig. 26, 27); however, progressing along the series they gradually become broader, and especially deeper, so that they become, by stages, transformed into the deeper, laterally compressed form of the succeeding dorsal series (Fig. 29). Concomitant with these changes, there are several others which herald transformation from cervical to dorsal vertebra. The neural spine, so prominent in the dorsal series (Fig. 29), is virtually absent in the anterior cervicals (3 - 7), being represented by a small ridge at the median junction between the postzygapophyses (Fig. 27). In the remaining members of the series (8 - 11), the neural spine undergoes some development: at first it is merely a slightly raised crest on the neural arch, but by the last cervical it has become a prominent hook-shaped structure, very similar and only slightly smaller than that of the first dorsal vertebrae. The neural spines of several cervicals in IRSNB 1551 have been erroneously restored. In similar fashion, the prezygapophyses undergo gradual changes through the series. At first (cervicals 2, 3) they form large forwardly directed processes, comprising almost the entire transverse process, overhanging the convex anterior articular surface of the centrum (Fig. 27 A). In more posterior members of the series, the prezygapophyses become less prominent and cease to overhang the centrum anteriorly, retreating backwards on to the dorsal surface of the now laterally directed transverse processes, and lie vertically above the parapophyseal facets (Fig. 27 B). The transverse processes become increasingly large posteriorly. In the second and third cervicals, they are principally forwardly directed oblique processes supporting the prezygapophyses, with small postero-ventrally directed oblique diapophyseal processes. Subsequently, as the ribs become larger and the prezypapophyses retreat, the transverse processes become considerably larger and laterally directed, the diapophyses becoming both larger and higher to support the larger posterior cervical ribs.

When naturally articulated (Fig. 26), the cervical series describes a smooth sigmoid curve, as a result of the shape of the articular surfaces of the centra, and modifications to the neural arches. The anterior portion of the series (esp. 3-5) is convex dorsally. This is achieved in three ways: the centra are slightly shorter along their ventral edges than along the dorsal; the large size and downward inclination of the anterior articular hemispheres of these centra; and by the anteroposterior elongation of the neural arches, the pre- and postzygapophyses of which overhang the centra considerably. Toward the posterior end of the series, the curvature is reversed (i.e. concave dorsally) and this is achieved by the reverse of the above modifications: the anterodorsally directed anterior articular hemispheres, the much shorter anteroposterior length of the neural arch and the posterior migration of the prezygapophyses.

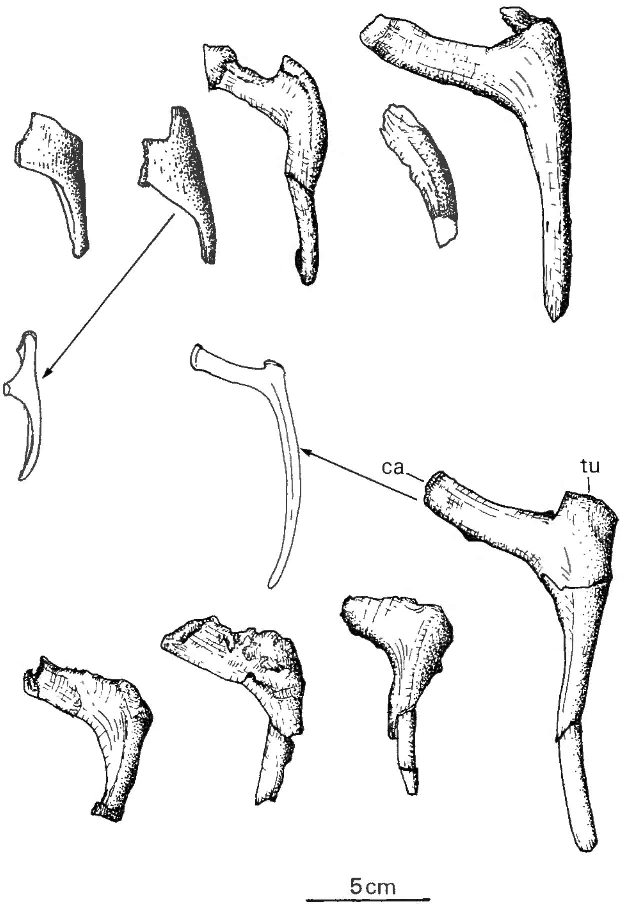
CERVICAL RIBS

Atlantal rib
This was figured by HOOLEY (1925: 5, II) from BMNH R5764 although it was not described and has since been lost; that of IRSNB 1551 is also missing.

Typically, the atlantal rib is a single-headed elongate, laterally compressed rod the head of which is slightly expanded and fits against a cup-shaped depression on the ventrolateral corner of the atlas intercentrum (NORMAN, 1980, for *I. bernissartensis*).

Cervical ribs 2 - 11
Only a few fragmentary remains of the cervical ribs are preserved in both specimens of *I. atherfieldensis* (Fig. 28). These few remnants display the same general characters seen in *I. bernissartensis*. The anterior ribs are short bodied with widely divergent rib heads, while more posterior ones develop a longer, ventrally curved shaft and large, but less divergent rib heads.

Fig. 28. – I. atherfieldensis. *IRSNB 1551. Fragmentary remains of cervical ribs, as preserved.*



DORSAL VERTEBRAE

There are seventeen dorsal vertebrae. Sixteen of these are freely articulating; the last however is functionally a part of the sacrum, even though it possesses a normal dorsal rib, it is therefore described with the sacrum.

The first two dorsal vertebrae are transitional in that they demonstrate a gradual loss of the cervical vertebral characters. The *first dorsal* is recognized as the first pre-sacral vertebra to bear a parapophyses above the neurocentral suture (Figs. 29, 30). The centrum is quite strongly opisthocoelous, although this is not as marked as in the cervical series; the anterior articular surface of the centrum is also moderately convex. The ventral half of the centrum is quite strongly compressed, producing a moderately large rounded ventral keel above which the lateral surface is depressed. The parapophysis is a quite large and circular depression at the base of the neural arch. The neurapophyses are quite short anteroposteriorly and rather broad transversely, due to the buttressing for the parapophysis and transverse process. The transverse process is large and arches upward and outward, ending abruptly at the blunt, rounded diapophysis; the prezygapophyses are borne far out on the dorsal surface of each transverse process at some distance from the midline. The neural spine arises from the anteromedian roof of the neural arch, between the bases of the transverse processes, and arches upward and backward ending in a slightly hooked apex; it descends in a concave curve from the summit and divides near its base to follow the dorsal margin of the large, divergent postzygapophyses.

The centrum of the *second dorsal* vertebra is only slight opisthocoelous and anteriorly has a very feebly convex articular surface. Its ventral surface is less strongly compressed laterally than that of the first dorsal, and there is merely a slight median rounded ridge; the sides of the centrum are less depressed; the parapophysis is larger and forms an elliptical depression (Fig. 29). The neural arch is more or less similar to that of the first, but the neural spine is larger and less hook-shaped, the prezygapophyses are almost adjacent and the postzygapophyses are similarly smaller and closer together.

By the *third* or *fourth* dorsal, the transition from typical cervical to dorsal vertebral form is complete. The centrum is now amphipatyan with a slight median ventral ridge joining the anterior and posterior articular margins; these latter form a slightly everted, rugose rim (Figs. 29, 30). The lateral surface of the centrum is concave longitudinally, convex vertically and merges above with the robust

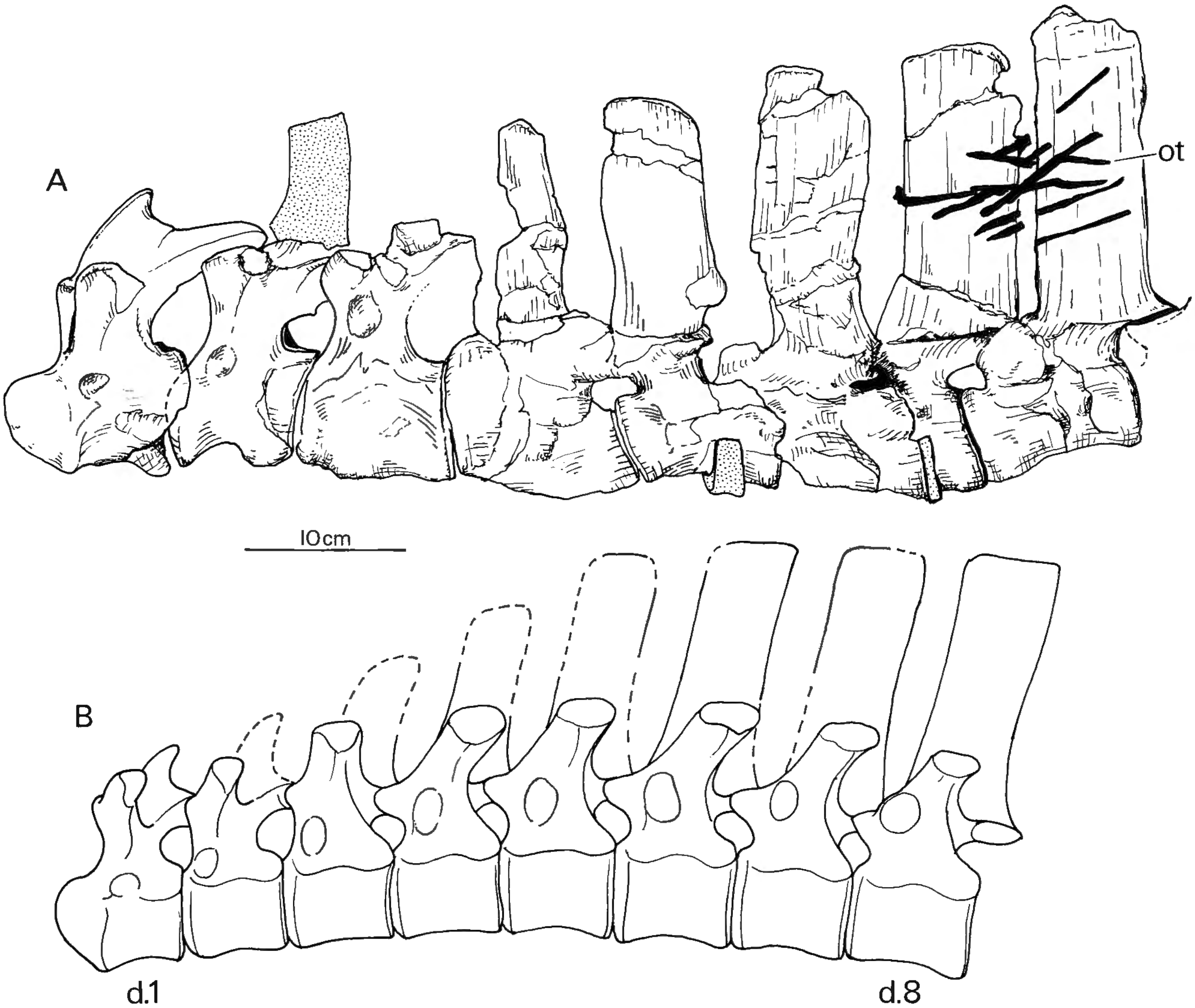
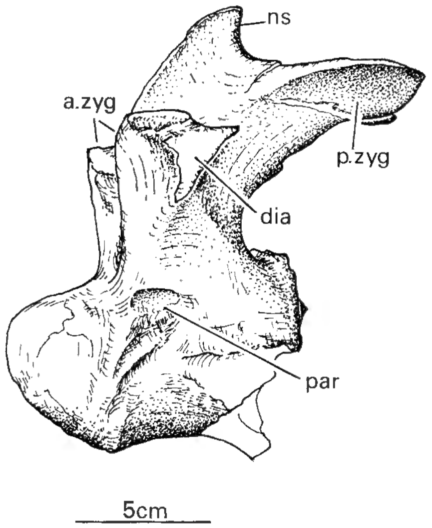


Fig. 29. – I. atherfieldensis. *IRSNB 1551. Dorsal vertebral series 1-8, as preserved. Reconstruction of articulated series based on above and BMNH R5764.*

neurapophyses. The parapophyses are large subcircular depressions on the anterolateral surface of the neurapophyses. Immediately anterior and medial to these are the forwardly projecting prezygapophyses, which overhang the anterior margin of the centrum. Between the adjacent dorsomedially facing prezygapophyses there is a narrow cleft ending posteriorly as the roof of the neural canal, which immediately gives rise to the leading edge of the neural spine. The spine rises steeply and has a sharp anterior edge, ending in a thickened, blunt, dorsal edge; the posterior edge is thicker than the anterior and, as it descends, it divides to buttress the postzygapophyses, between which is a concave recess. The neural spine is typically slightly inclined posteriorly, roughly rectangular and between three and four times the height of the vertebral centrum. The moderately small postzygapophyses face ventrolaterally and also overhang the posterior margin of the centrum. From the anterolateral edge of the postzygapophysis there is a thin shelf of bone which

Fig. 30. – I. atherfieldensis. *IRSNB 1551. 1st Dorsal vertebra in lateral view.*

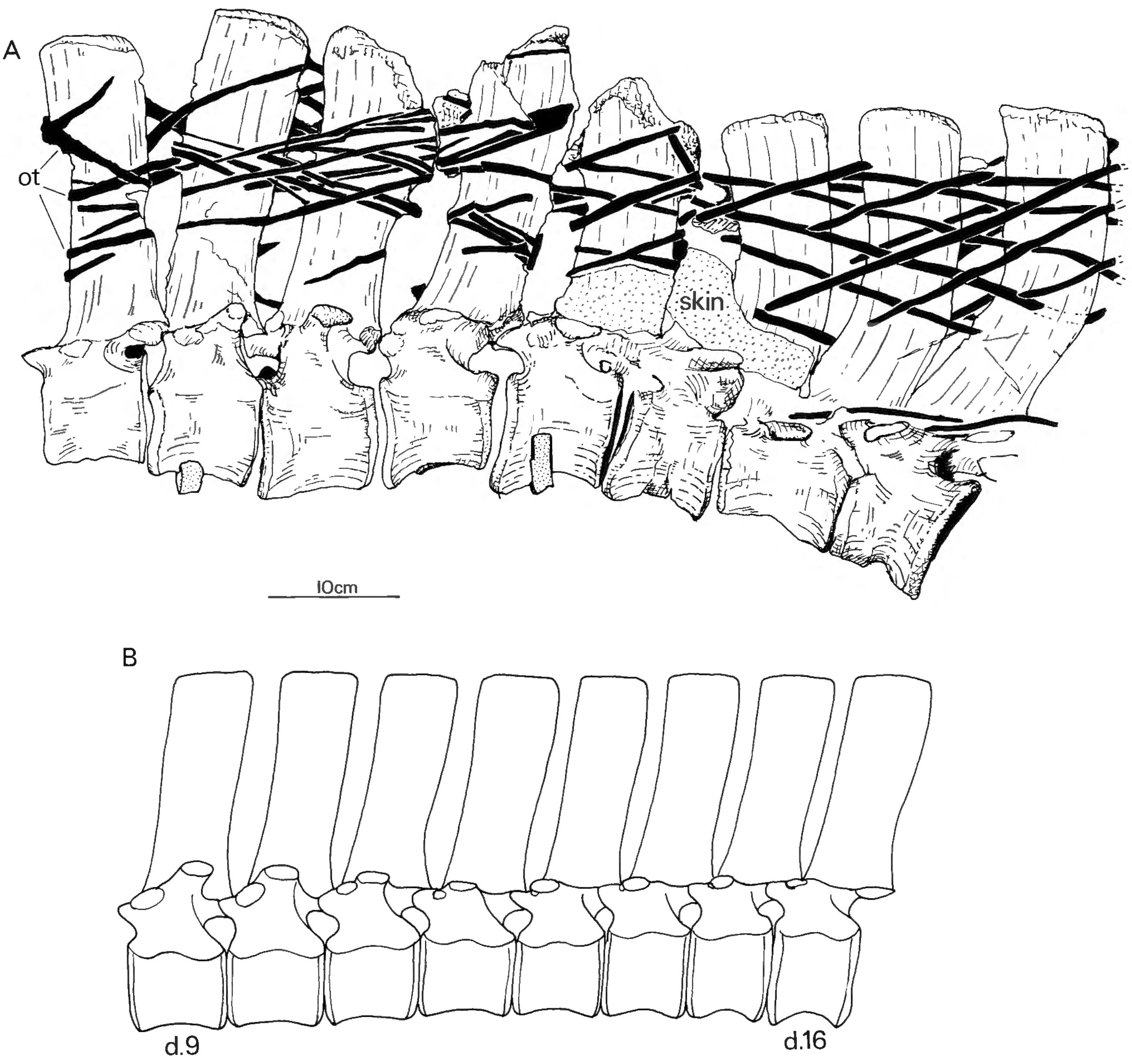


curves forward and outward to the distal end of the transverse process. The latter is elongate rising obliquely from the side of the neural arch; in cross-section it is more or less triangular, with a flat or slightly convex dorsal surface, and a medial ventral buttressing ridge developed from the ventral posterior margin of the neurapophysis; this separates two slightly concave recesses. The anteroventrally directed recess on the transverse process usually bears some evidence of ligaments scars where additional support was given to the neck of the rib. The neural canal is small and circular and entirely enclosed by the neurapophyses, which are fused medially, above the neurocentral suture.

This description applies to the majority of the dorsal series (3 - 11). The more posterior members (12 - 16) are however sufficiently different to merit a short description.

The posterior dorsals (Figs. 31, 32) are more anteroposteriorly compressed than are the more anterior dorsals, and they possess more strongly everted articular margins. The centra are slightly opisthocoelous, while the anterior surfaces of the centra are roughly flat with convex edges. Ventrally, the walls of the centra are laterally compressed forming a sharp ridge and, above this, the lateral walls are very strongly expanded; this can be more readily appreciated by comparing ventral views of middle and posterior dorsal centra (Fig. 31). Whereas the articular surfaces of the middle dorsals are laterally compressed and subovate, those of the posterior dorsals are very broad, subcircular and slightly

Fig. 31. – I. atherfieldensis. *IRSNB 1551. Posterior dorsal vertebrae 9-16, as preserved. Reconstruction of articulated series of dorsals based on above and BMNH R5764.*



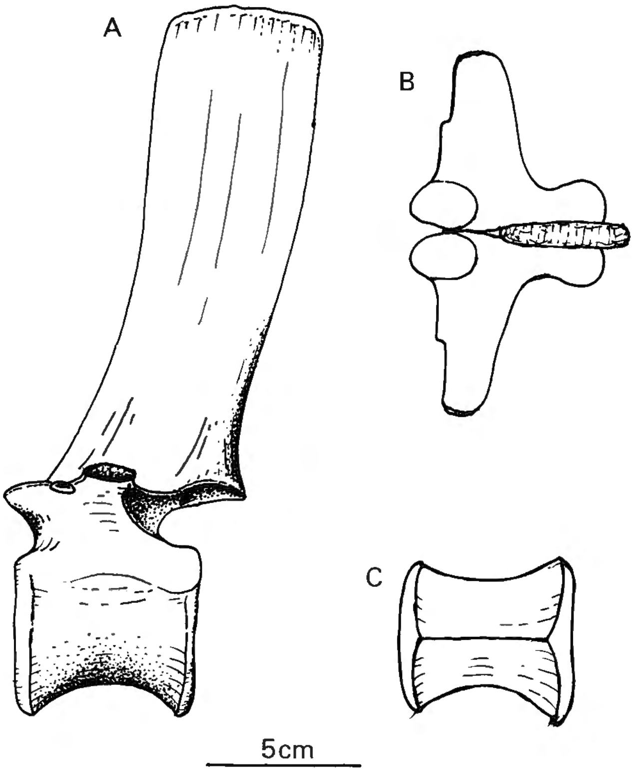
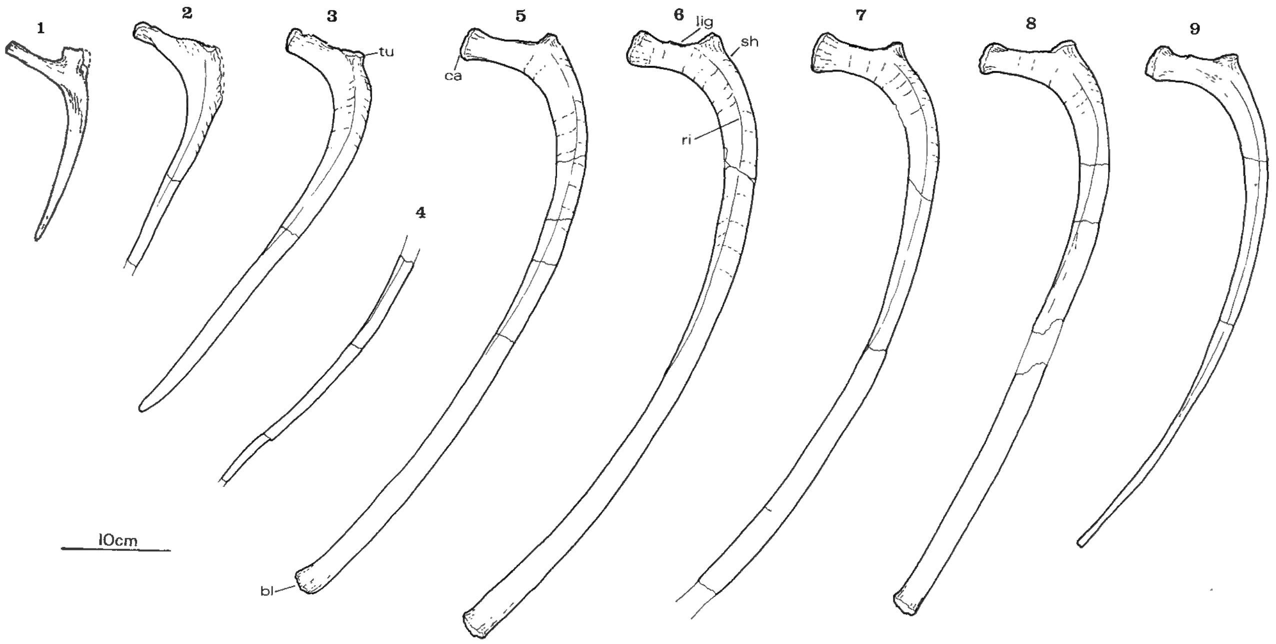


Fig. 32. – I. atherfieldensis. *IRSNB 1551. Isolated posterior dorsal vertebra, partly restored.*

dorsoventrally compressed. In lateral view, they also show tne unusual feature of being slightly posteriorly inclined so that, when naturally articulated, they slope upwards and backwards to the sacrum. The neural arches of the posterior dorsals are low and very robust, and the transverse processes curve outward horizontally and forwards; the zygapophyses are large and horizontal. It should be noted that the pronounced forward curvature of the neural arches of the posterior dorsals of *I. atherfieldensis* (BMNH R5764) is in no way the distinctive character which HOOLEY (1925) supposed it to be: it is found in all individuals of this species and *I. bernisartensis*. There are several characters, apart from those already mentioned, which show progressive change throughout the dorsal series. The parapophysis is moderately large, subcircular and situated on the anteroventral margin of the neurapophysis in the first dorsal; in succeeding dorsals the parapophysis becomes larger, vertically ovoid and rises up the side of the neurapophysis, coming to lie directly behind the anterior zygapophysis and beneath the leading edge at the base of the transverse process in dorsal 7. Subsequently, the facet becomes rounded and decreases in size, becoming horizontally oval and migrates downwards along the transverse process toward the diapophysis. In the last free dorsal (16), the parapophysis forms a step on the anterior edge of the transverse process, separated by a short distance from the diapophysis. In dorsal vertebra 17, the last functionally incorporated in the sacrum, but which still possesses a free dorsal rib, the parapophysis and diapophysis are united as a single facet (Figs. 33, 34). The diapophyses of the dorsal series are high anteriorly, being supported on the oblique transverse processes which are steeply angled (50° to the vertical), long and robust. Progressing backward along the series, the transverse processes become lower and become directed obliquely posteriorly. At about the position of the 9th dorsal, the transverse process becomes more slender, is almost horizontal

Fig. 33. – I. atherfieldensis. *BMNH R5764 (Holotype). Anterior dorsal rib series.*



and perpendicular to the long axis of the vertebral column. The diapophysis therefore gradually descends along the dorsal series to lie at the same level as the parapophysis. Toward the hind end of the series, the transverse processes lie horizontally, are slightly anteriorly recurved and are relatively thin, dorsoventrally compressed structures. The diapophysis becomes a rather poorly defined area on the distal end of each, which is overlapped by the flap-like tuberculum of each rib (Fig. 34).

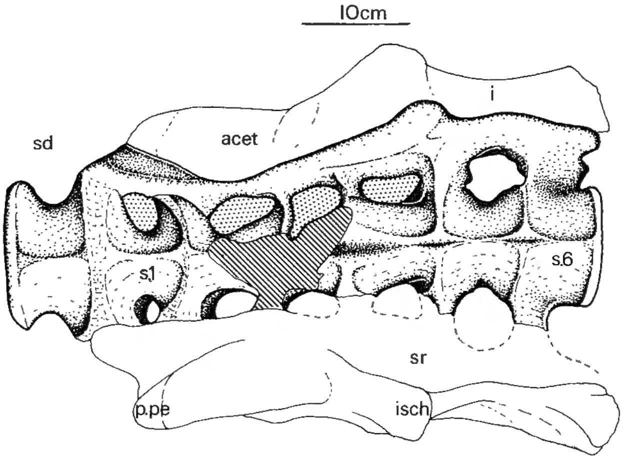


Fig. 35. – I. atherfieldensis. *BMNH R5764 (Holotype). Sacrum, as preserved, in ventral view. Stipple = matrix, crosshatching = broken surface.*

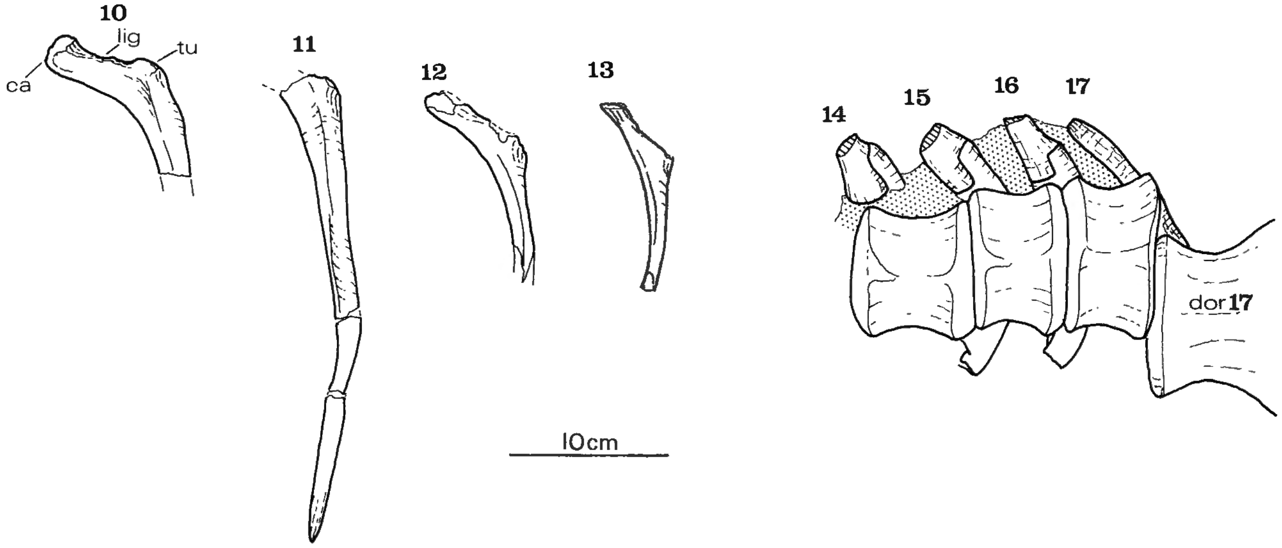
DORSAL RIBS

There are seventeen dorsal ribs, of which sixteen are two-headed, only the last being single-headed (Figs. 33, 34). The *first* dorsal rib is similar to those of the last cervicals. Its capitulum is small, rounded and convex and is supported on a long slender, curved capitular process; the tuberculum is quite large, concave and is supported on a short process on the dorsal surface on the capitular process, which merges with the latter to form the shaft of the rib. The shaft is moderately long and curved. In cross-section it is convex externally and concave internally; the distal end is rounded and compressed. The *second* rib is larger than the first; the capitular condyle is large, vertically oval and is supported by a thick laterally compressed process. Along the dorsal edge of this process, the tuberculum is perched on a short process and has a dorsomedially directed concave facet. Beyond this region, the shaft curves sharply downward so that the area around the tuberculum forms a distinct shoulder. From the anterodorsal edge of the tuberculum there is developed a prominent rounded ridge which curves down the anterior edge of the rib shaft and forms the rounded leading edge father distally, a permanent feature in the anterior and middle dorsal series of ribs. The distal end of the shaft tapers to a flattened rounded point.

In the succeeding series of ribs (3 - 10) the essential characters are very similar to those of the second (Fig. 33). The main trends through this series are: an increase in the length of the rib shaft, reaching a maximum at position 6 or 7 and gradually declining posteriorly and the development of a blunt distal end to these ribs where they presumably articulated against the cartilaginous sternal ribs. Between the two rib heads the posterodorsal edge of the capitular process is heavily scarred by ligaments which helped to bind the ribs firmly against the transverse processes.

In the more posterior members of the dorsal rib series, the rib shaft becomes progressively shorter and more slender and the distinctive shoulder is lost (Figs. 33, 34). The capitulum becomes progressively smaller and the tuberculum becomes flap-like

Fig. 34. – I. atherfieldensis. *BMNH R5764 (Holotype). Posterior dorsal rib series. Stipple = matrix.*



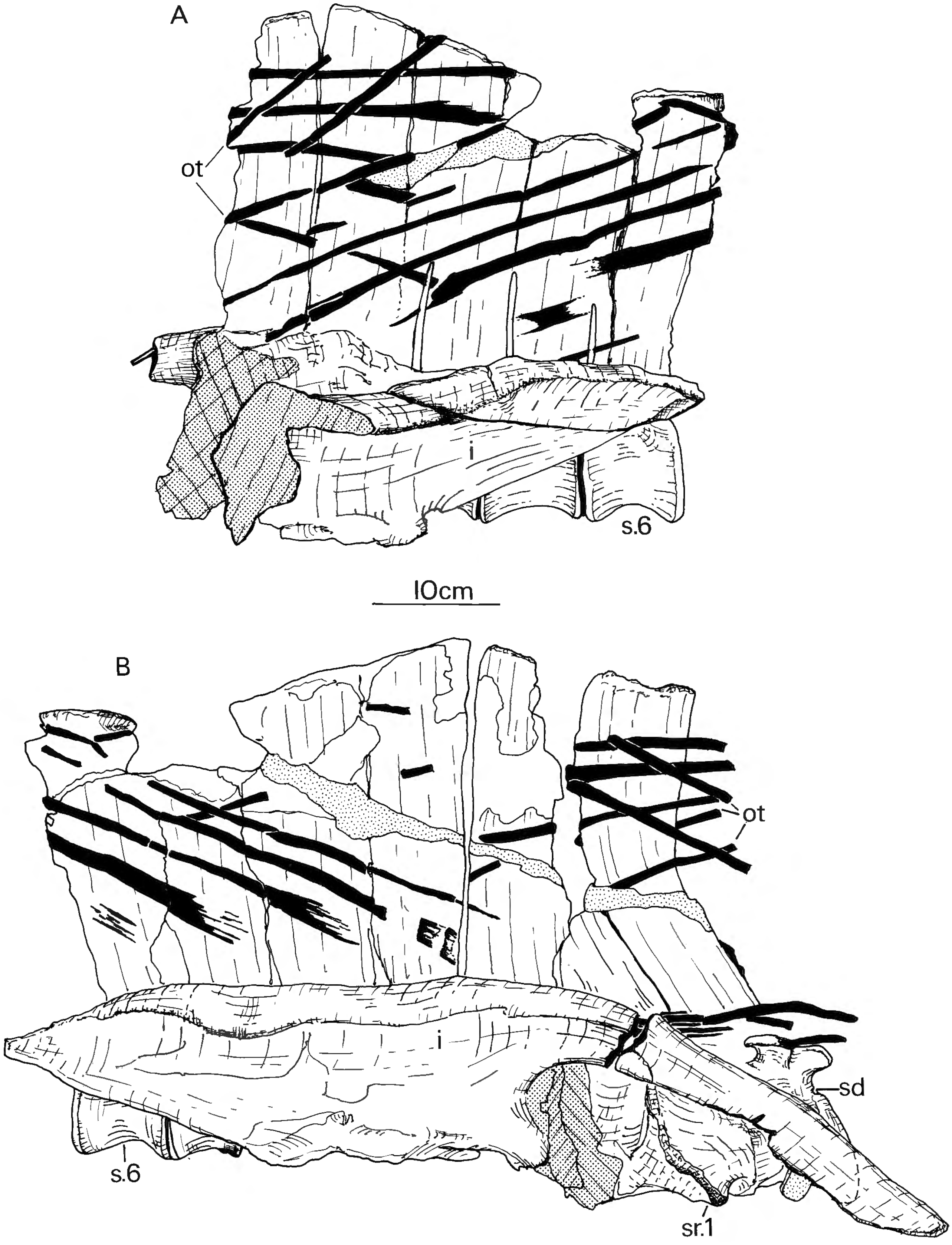


Fig. 36. – I. atherfieldensis. *IRSNB 1551. Lateral views of sacrum and pelvis, as preserved.*

and overlaps the distal end of the transverse processes. In the most posterior members, the proximal heads of these ribs are 'stepped' as the tubercular and capitular facets are separated by only a short interval. This 'step' gradually diminishes until the last dorsal rib, which has a bluntly truncated proximal end, where both rib heads are confluent.

SACRUM

There are two complete and moderately well preserved sacra BMNH R5764 (Fig. 35) and IRSNB 1551 (Fig. 36), and some rather better preserved but unfortunately fragmentary specimens: BMNH R6620, "11f", R6498 (Fig. 37). The sacrum consists of seven co-ossified vertebrae (Fig. 35). However, the ribs of the first vertebra are thin and style-like and do not contact the ilium (Fig. 34); the remaining six pairs of sacral ribs belong to vertebrae 2 - 7. The first sacral is therefore technically a dorsal vertebra although it is functionally a part of the sacrum, since it is sutured against the first true sacral and supports the base of the first sacral rib.

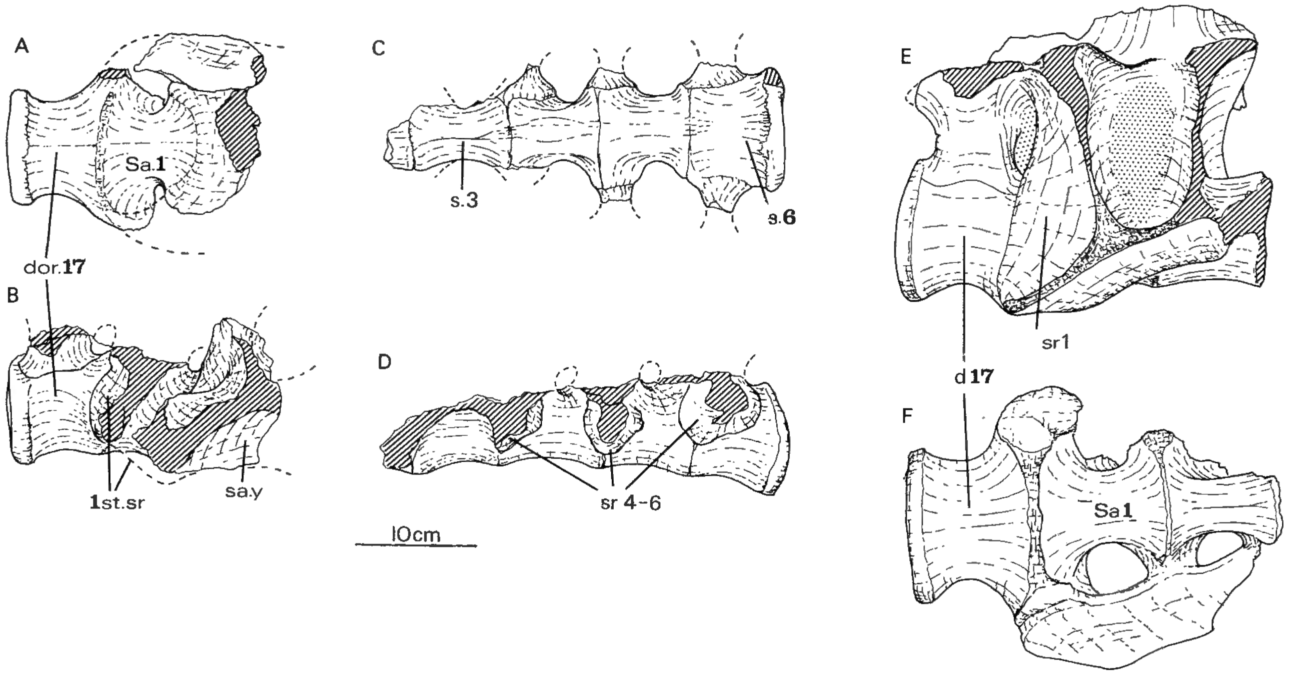
The sacrodorsal has a broad, subcircular, slightly convex anterior face, slightly indented dorsally for the neural canal. The articular margins are, as with the preceding posterior dorsals, everted and rugose. Behind the articular face, the centrum is strongly contracted before becoming once more broadly expanded posteriorly, where it is sutured to the first, true sacral vertebrae; this posterior surface is subquadrangular owing to a ventrolateral expansion of the sides where they support the anterior margin of the first sacral rib. Dorsally, the neural arch, which is supported upon short and robust neurapophyses, is curved forwards away from the sacrum, as are the transverse processes and the large prezygapophyses. The postzygapophyses appear to be fused to the succeeding prezygapophyses.

The centrum of the first true sacral is very broadly expanded anteriorly and posteriorly and strongly contracted between, with a slight median ventral keel (Figs. 35, 37). The lateral walls, which are vertical, are deeply concave anteroposteriorly between the first and second sacral ribs (Fig. 37). The neural arch has shifted forward so that it lies across the hind end of the first sacral, thereby strengthening the suture between these two vertebrae. This repositioning of the neural arch occurs throughout the remaining sacrals and forces the lateral spinal nerves to exit across the dorsal surfaces of the centra between successive neural arches, rather than via the usual intervertebral spaces, as is usual for the presacral and caudal vertebra. Laterally, the neural arch is completely co-ossified to its sacral rib.

In succeeding sacral vertebrae, the centra become at first slender and keeled, but subsequently (4 - 6) become again broader and develop a flattened or slichtly depressed haemal surface (Fig. 35). The last sacral is the largest of the posterior members and has a very strongly everted, rugose articular margin; the articular face of the centrum is planar but tends to become slightly concave in its dorsal half. In lateral view, the sacral series describe a smooth scalloped arch; the neural spines are tall and co-ossified (fig. 36).

Each sacral rib is borne at the junction between

Fig. 37. – I. cf. atherfieldensis. *BMNH R6620, (A) ventral, (B) left lateral; R6498 (C) ventral, (B) left lateral; "11f" (E) lateral, (F) ventral. Incomplete sacral series ("11f" in Hooley catalogue BMNH).*

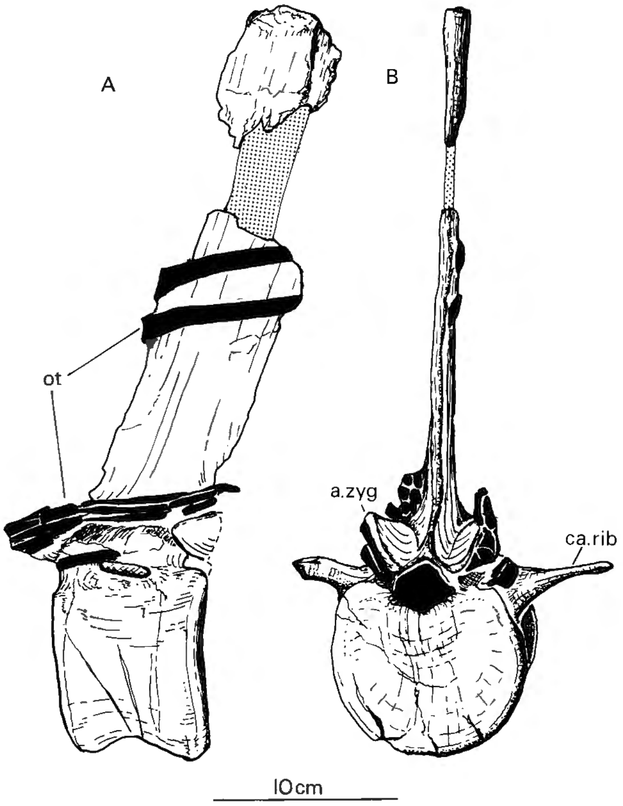


two sacral centra. The base of each rib is firmly sutured to the ventral surface of the transverse process and to the lateral surface of the neural arch. The transverse processes of the first four sacral vertebrae are large and possess robust, rounded distal ends which articulate against small apophyses on the medial surface of the ilium (Fig. 54). Immediately beneath these, the lateral edges of the sacral ribs are thin, but expand rapidly ventrally so that the ventral edge of succeeding ribs meet and fuse together to form a massive horizontal bar; this is firmly attached to the ventromedial surface of each ilium (Fig. 54). The last two sacral vertebrae (5 and 6) are slightly different from their predecessors in that their transverse processes and sacral ribs are compressed together, forming a narrow posterior end to the sacral rib bar. This is reflected on the internal surface of the ilium, where the last two sacral rib facets are confluent and indistinct (Fig. 54). It should also be mentioned that the very large ventral expansion of the first sacral rib not only supports the pubic peduncle of the ilium medially, but also provides an area for attachment of the pubis.

CAUDAL VERTEBRAE

The caudal vertebrae are very incomplete in the holotype. However, the referred specimen (IRSNB 1551) has an almost complete tail (33 vertebrae preserved) which shows the main features of this series (Fig. 42). The first caudal vertebra (Fig. 38) is typically large, subquadrangular and rather obliquely inclined forwards. The articular surfaces of the centrum are broad and approximately amphiplatyan, although the anterior surface bears a slight bulge in its dorsal half, which articulates against an adjacent recess in the corresponding posterior surface of the last sacral vertebra. The ventral surface of his vertebra is flattened or slightly rounded, and the sides are vertical, sweeping outwards dorsally into the base of the fused caudal rib. The caudal rib curves outwards horizontally from the dorsolateral surface of the centrum as a dorsoventrally flattened process, with a bluntly rounded distal end. Above the caudal rib, the neural arch is low and robust; the prezygapophyses project obliquely forwards and upwards, and between them, the large, narrow, neural spine rises upwards and backwards, to a blunt thickened dorsal edge. Curving downward and forward from the dorsal edge, the posterior edge of the neural spine bears, near its base, the postzygapophyses which face obliquely ventrolaterally. The posteroventral margin of the articular surface of this vertebra does not bear a chevron (haemal arch) and consequently does not bear an everted haemapophysis.

Fig. 38. – I. atherfieldensis. *IRSNB 1551. First caudal vertebra in lateral (A) and anterior (B) views.*



The *second caudal* vertebra (Fig. 39) is slightly less broad than its predecessor, its articular surface having a slightly more rectangular appearance in anterior view. Its ventral surface is slightly narrower, and is more convex transversely. In lateral view, the centrum is forwardly inclined, as in the first of this series. This trend continues over the next few anterior caudals and produces a distinct slope to the base of the tail, as it drops away from the sacrum — a similar slope was also noted in the most posterior members of the dorsal series. The lateral sides of the centrum are flat or slightly convex vertically, and slightly concave anteroposteriorly, between the everted anterior and posterior articular margins. The remaining characters of the caudal rib, neural arch and neural spine are essentially similar to the first caudal. The posteroventral margin of this centrum bears the first haemapophysis for the anterior half of the head of the chevron bone (haemal arch). This facet has the form of a moderately deep excavation in the ventral margin of the centrum around which there is a thickened everted lip of bone.

In the succeeding anterior caudal vertebrae (3 - 15), the vertebrae are more or less similar (Fig. 40). They are quite strongly laterally compressed, with flattened sides and strongly convex ventral surfaces. The articular surfaces are amphiplatyan, and roughly rectangular in end view. On the ventral margins of both the articular surfaces there are large concave haemapophyses; the posterior of these is always larger with slightly more promi-

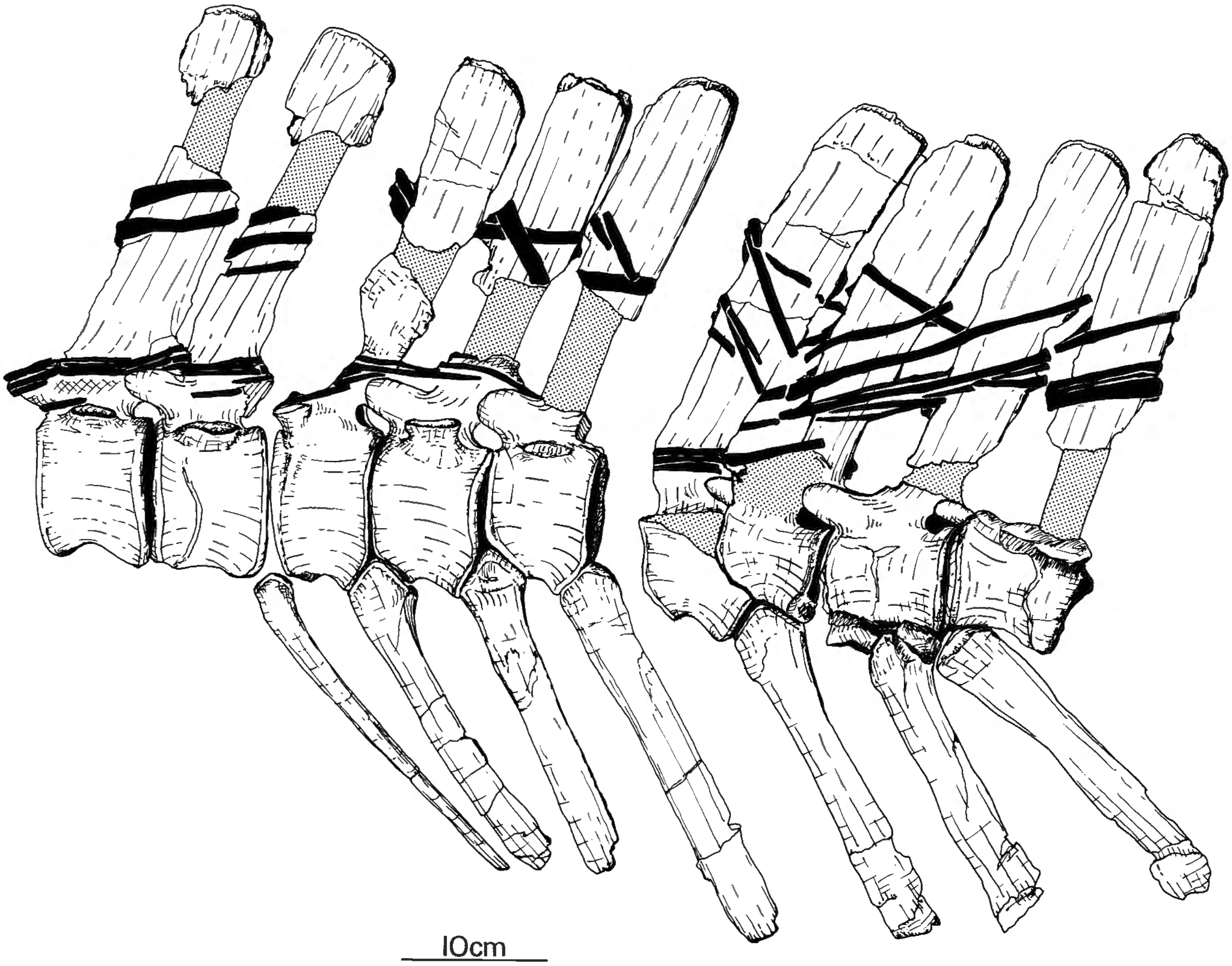
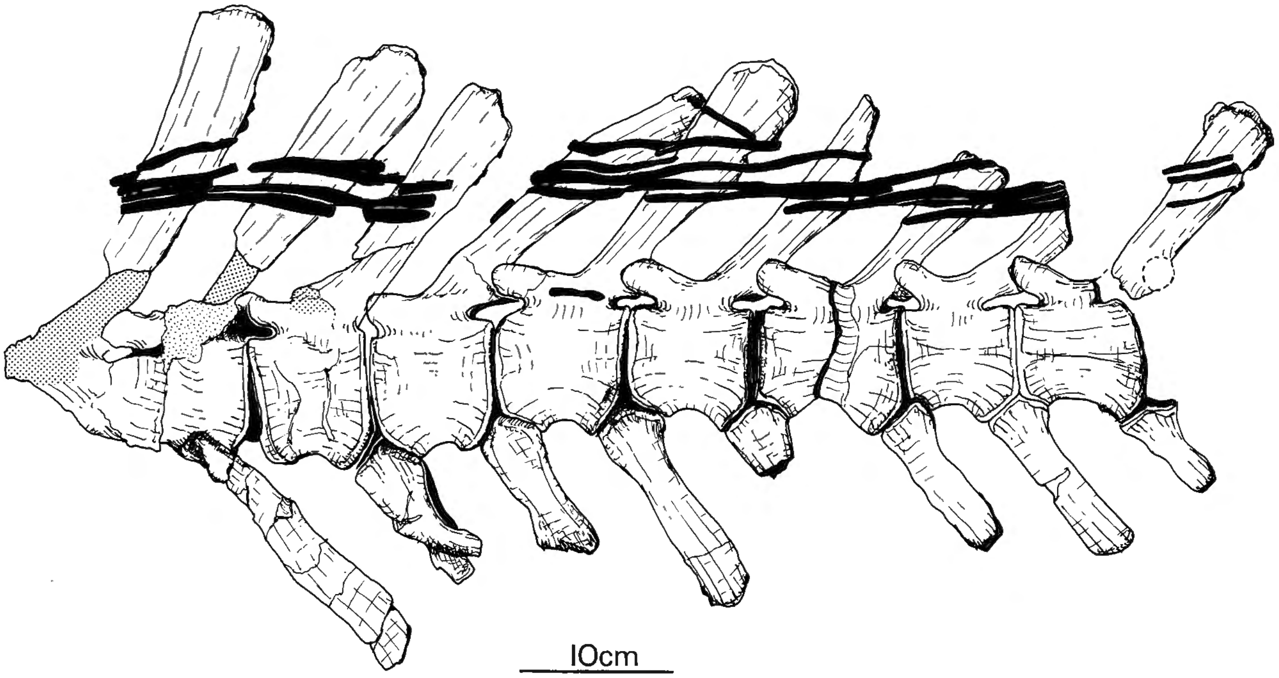


Fig. 39. – I. atherfieldensis. *IRSNB 1551. Series of anterior caudal vertebrae.*

Fig. 40. – I. atherfieldensis. *IRSNB 1551. Series of middle caudal vertebrae.*



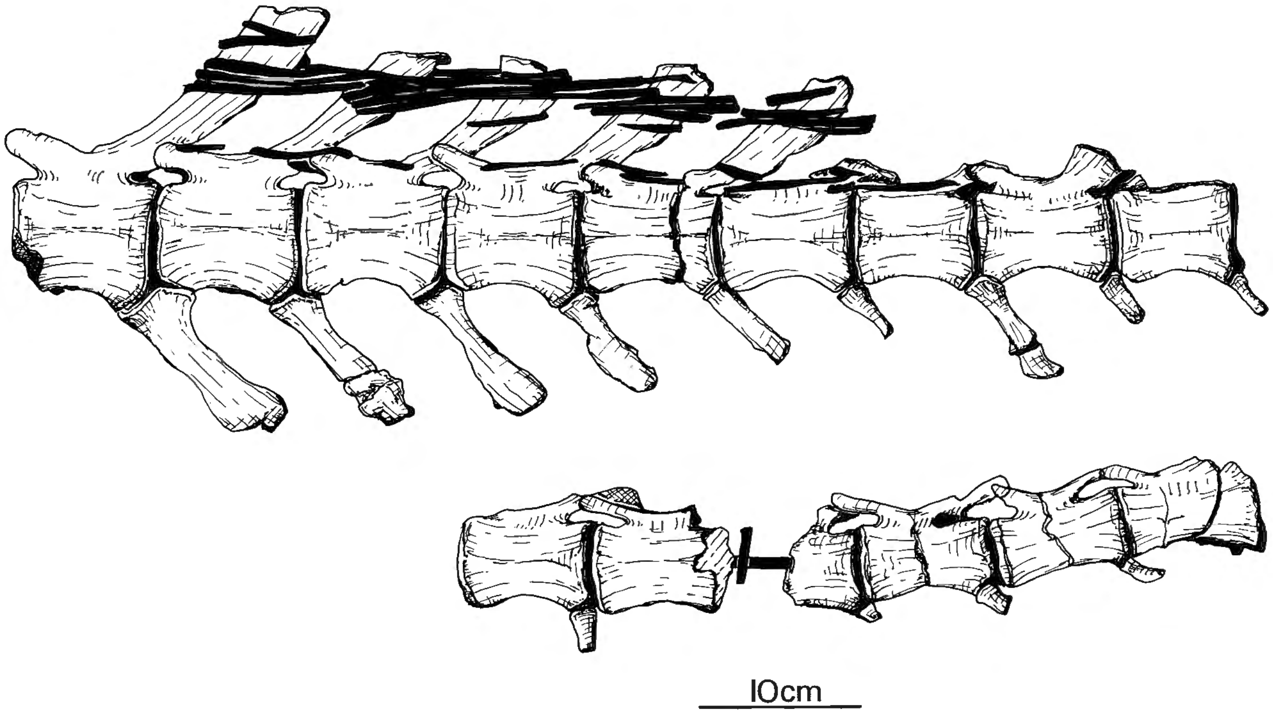
nently everted edges (Fig. 39). The caudal ribs are prominent dorsoventrally flattened processes; they are largest at the anterior end of the series and become progressively shorter distally. The surfaces of these ribs are quite noticeably striated in all individuals and these markings probably represent the areas for origin of parts of the caudi-femoral musculature. Toward the end of this series, the vertebrae become smaller in all their dimensions. The most noticeable changes in structure are a decrease in size of the caudal ribs and the decrease in height of the neural spines. Between the 15th and 16th caudal vertebrae, the caudal rib declines from a short process, to a rudimentary nubbin and is eventually lost altogether. This transition (Fig. 40) marks the change from the anterior caudal to the middle caudal series.

The *middle caudal* series of vertebrae are a long series which gradually diminish in size toward the distal end of the tail and extend from caudal 16 into the late thirties, (by comparison with *I. bernissartensis*) the last of this series being the last vertebra to bear a chevron bone. In the anterior part of this series, the centra are moderately tall, hexagonal cylinders (Fig. 40) with ampliplatyan faces. In place of the caudal ribs of the anterior series, there remains a horizontal ridge across the middle of the centrum; this produces a very angular appearance to the centrum which becomes more pronounced posteriorly along the series. Between the haemapophyses, the ventral surface is flat. The neural arch is low and narrow and carries the tall backwardly inclined neural spine; the prezygapophyses are prominent and oblique and clamp around the postzygapophyses which are perched against the posterolateral sides of the neural spine. Progressing along the neural spines become smaller and more steeply inclined, and the chevrons become smaller while their proximal ends tend to become divided into separate heads. Toward the end of the series the neural spine reduces to a short, backwardly directed spine supporting the postzygapophyses. The remainder of the tail (34 - ?45) is not preserved in any specimen.

CHEVRON BONES (haemal arches)

The first chevron is found to articulate between caudals 2 and 3, and is well preserved in IRSNB 1551 (Fig. 38). Its proximal end is expanded and bears a median transverse ridge, which separates the oblique anterior and posterior facets which articulate against the caudal haemapophyses. Below the proximal head, there is a large haemal canal, bounded on either side by the haemal arches. Ventrally, the haemal arches coalesce to form a transversely compressed haemal spine, which tapers to a point and is slightly curved backwards. The following six or seven chevrons are the largest in the tail and differ only slightly from the first; proximally they have the same form, but the distal haemal spine is larger and less style-like having a more blade-like form. Progressing farther back along the caudal series, the chevrons steadily become smaller, forming a mirror image of the neural spines.

Fig. 41. – I. atherfieldensis. *IRSNB 1551. Middle and posterior caudal vertebrae.*



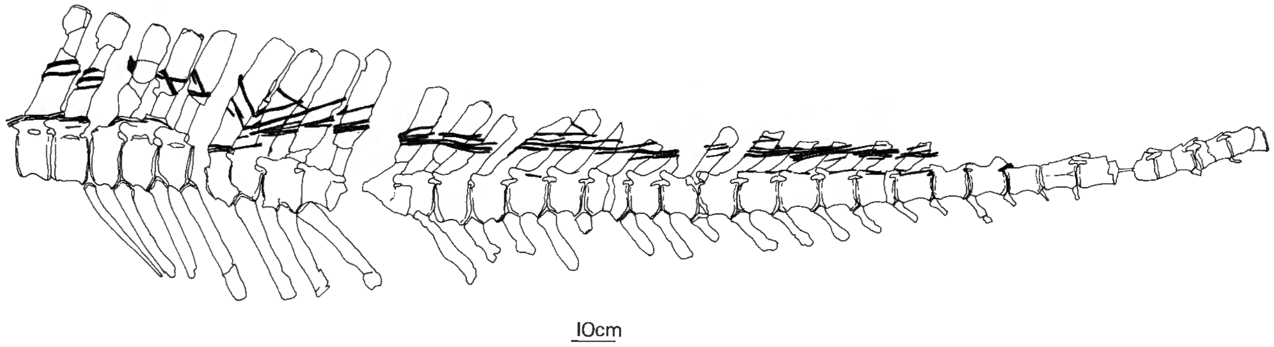


Fig. 42. – I. atherfieldensis. *IRSNB 1551. Complete candal series and ossified tendons, as preserved.*

OSSIFIED TENDONS

These are quite well preserved in BMNH R5764, but they are rather scattered, as preserved, and do not show their original distribution. However, the Bernissart specimen possesses rather less disturbed lattices of ossified tendons (IRSNB 1551) (Figs. 29, 31, 36, 39-42).

Ossified tendons are to be found throughout most of the length of the vertebral column, from about cervical 10 to about caudal 20. They are scattered more or less regularly on either side of the neural spines, and the transverse processes of dorsals, sacral ribs as described in *I. bernissartensis* (NORMAN, 1980).

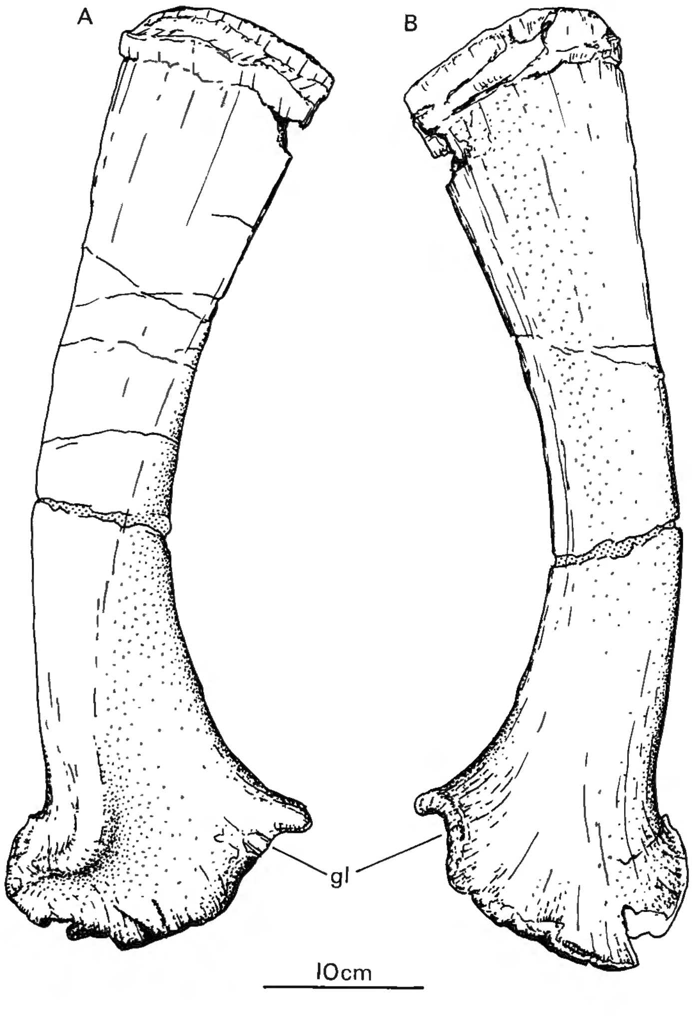
One peculiarity of *I. atherfieldensis* is that the ossified tendons are fused to the sacral neural spines (Fig. 36). I am not aware of this phenomenon in other ornithopods disnosaurs.

Appendicular skeleton

PECTORAL GIRDLE

In *I. atherfieldensis* the *scapula* is moderately slender and bowed, so that it follows the contour of the rib cage (Fig. 43). The proximal end of the blade is thick and expanded. The anterior edge of this end curves forwards to produce a rugose triangular boss, which has been termed the "clavicle facet" in other ornithischians. A thick buttressing ridge curves backwards across the lateral surface from this facet, before curving upwards (distally) along the external surface of the blade, with which it rapidly merges. Beneath the "clavicle facet" the anterior edge of the scapula is thin and slightly curved, but soon meets the broad, thickened rugose sutural surface for the coracoid. On the medial edge of this suture there is a shallow channel which forms a portion of the internal passage for the coracoid foramen (Fig. 43). Posteriorly, this suture ends abruptly at a transverse ridge beyond which there is a smooth concave embayment, the glenoid. On the external surface, adjacent to the glenoid, there is a shallow depression, and above and behind this a prominent buttress develops which supports the posterodorsal margin of the genoid. In posterior view the glenoid is a crescent-shaped depression, rather than a cup-shaped socket. Above the glenoid, the thick buttress contracts rapidly into the shaft, the posterior edge of which is thick proximally, becoming thinner and sharper towards the distal end, which is transversely flattened and anteroposteriorly expanded. This distal portion of the

Fig. 43. – I. atherfieldensis. *IRSNB 1551. Scapula in lateral (A) and medial (B) views.*

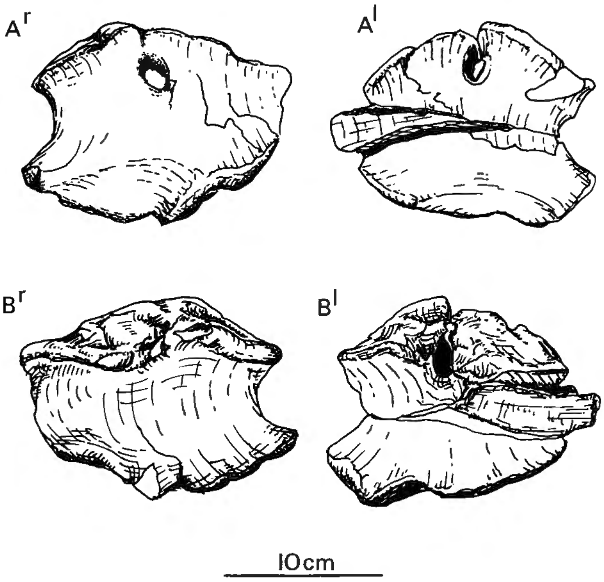


shaft is slightly convex in external view and its dorsal edge is heavily scarred as if for attachment of a short cartilaginous suprascapula. The anterior edge is sharp near the distal end, but becomes thicker and rounded as it approaches the proximal end. The narrowest part of the blade of the scapula, just above the proximal end, is roughly elliptical in cross-section, the external surface being more convex than the internal; the section becomes gradually more compressed and convexoconcave distally.

The *coracoid* is sutured to the scapula along its thick dorsal edge (Fig. 44). Posteriorly, the scapular suture abruptly ends and is replaced by a smooth, broad, concave depression which, with the adjacent depression on the scapula, forms the entire humeral glenoid. Beneath the thickened margin of the glenoid, the posterior edge of the coracoid is excavated to produce a hook-shaped structure. Medial and anterior to the rounded posterior end there is a rugose rounded slightly convex edge which formed an area of attachment to the sternal cartilage. The external surface of the coracoid is roughly convex and bears a moderately well developed diagonal ridge; it is also pierced by the coracoid foramen just below the junction between scapular suture and glenoid, which passes obliquely upward to emerge on the medial surface between the scapula and coracoid. Internally, the coracoid in concave.

There is a pair of *sternal bones* (Fig. 45). Each sternal is a moderately broad hatched-shaped bone. The external surface of the "blade" is flat and its medial edge is thin, straight and rugose. Anteriorly, this edge becomes thicker and rather bluntly rounded. The lateral edge describes a shallow concave curve and is thick and rounded; it produces

Fig. 44. – I. atherfieldensis. *IRSNB 1551. Coracoid in lateral (A) and medial (B) views. (Superscripts indicate left or right).*



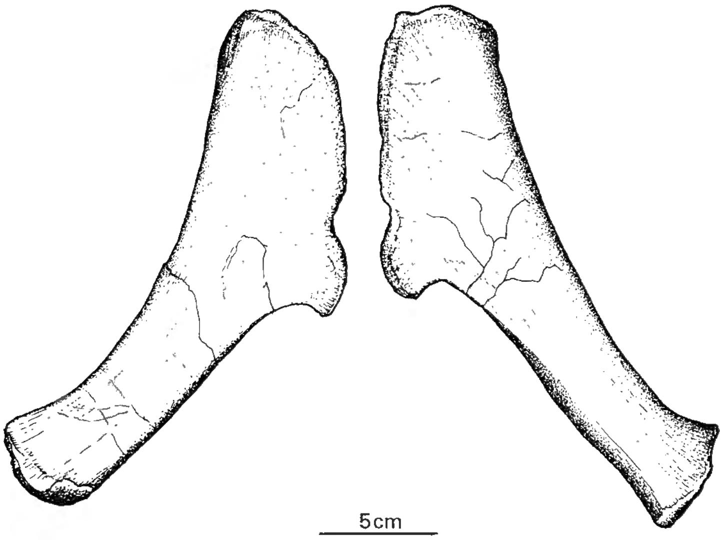
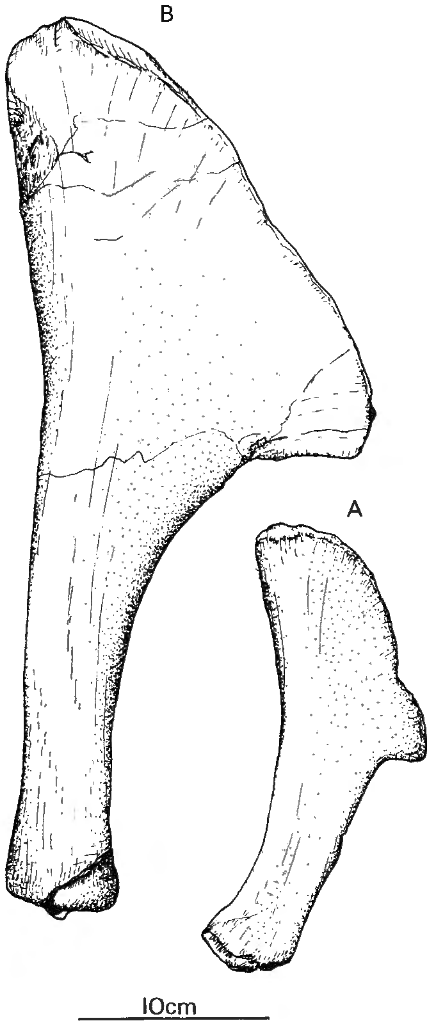


Fig. 45. – I. atherfieldensis. *IRSNB 1551. Sternal bones, left and right in ventral view.*

Fig. 46. – I. atherfieldensis. *IRSNB 1551. Right sternal bone in ventral view (A) compared with the right sternal bone of* I. bernissartensis *IRSNB 1536 (B).*



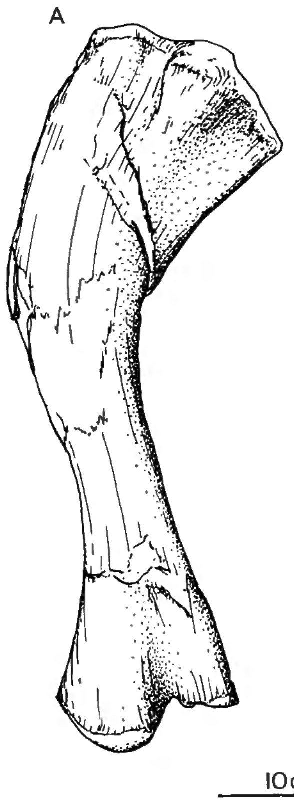


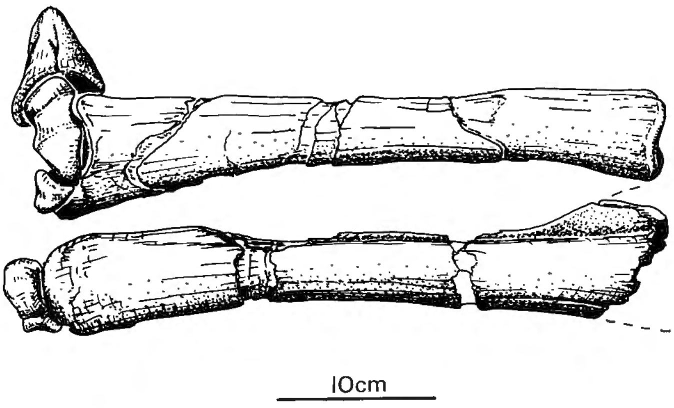
Fig. 47. – I. atherfieldensis. *IRSNB 1551. Humerus in posterior (A) and anterior (B) views.*

a postero-laterally directed rod with rounded and slightly angular sides. The distal end of this rod is slightly expanded and rugose and may have formed the area of attachment for some of the presumably cartilaginous sternal ribs. The internal surface of the sternal bone is very slightly concave.

The sternal bones are slightly separated along the midline by a strip of sternal cartilage which probably broadens anteriorly to link with the coracoids.

The sternal bone of *I. bernissartensis* is very similar although considerably larger than that of the former species (Fig. 46). They have been preserved *in situ* in several Bernissart specimens which accounts for our knowledge of the position of these bones (NORMAN, 1980). No intersternal ossification is known in *I. atherfieldensis.*

Fig. 48. – I. atherfieldensis. *IRSNB 1551. Radius and ulna (left) in lateral view. Capsals preserved partially.*



FORELIMB

The *humerus* in *I. atherfieldensis* (Fig. 47) is not twisted axially but there is a strong sigmoid curvature to the shaft. The proximal end is broad and anteroposteriorly flattened, producing a shallow concave anterior surface and convex posterior surface. In the centre of the proximal end is an expanded articular condyle, the head of the humerus, which is supported by a buttress on the posterior (dorsal) surface and by two narrower shoulders on either side. From the medial shoulder, the shaft curves concavely outward and downward to the distal ulnar condyle. From the lateral shoulder, the shaft drops almost vertically for a short distance before swelling outwards and developing a thickened rugose edge, the deltopectoral crest. Just above the middle of the shaft, this edge contracts and the shaft tapers slightly before expanding into the distal, radial condyle. The radial and ulnar condyles are separated by a shallow intercondylar groove, which is moderately deep posteriorly, but smaller and shallower anteriorly. The radial condyle is rather shallow and poorly developed anteriorly in comparison to the ulnar condyle (cf. BMNH R5764) which bulges outwards. Immediately above the radial condyle, the surface of the shaft is shallow and depressed and receives the proximal head of the radius, when the forearm is fully adducted.

The *ulna* (Figs. 48, 49) is poorly preserved in IRSNB 1551. It possesses a large and prominent olecranon process, which is blunt and rounded posteriorly. Ventrally, the surface is transversely rounded and this edge describes a slight sigmoid curvature longitudinally toward the expanded distal end. Dorsally, the surface is more complex (Fig. 49). The mediodorsal edge is developed into a prominent triangular crest, the medial surface of which is vertical and slightly concave. Laterally, this crest bears a broad transverse shelf formed by the main body of the ulna and this bears a shallow concave depression with low striations. This facet receives the proximal head of the humerus, and the surface striations probably reflect the presence of a ligamentous attachment between these two bones. Farther anteriorly, the crest gradually merges with the shaft producing a very slight but discernible, ridge which runs obliquely across the dorsal surface of the shaft to the distal end, and there forms the *medial* edge of the distal radial facet (Fig. 49). Anterior to the proximal radial facet, the dorsal shelf at first quite broad, gradually diminishes as the shaft tapers towards the distal end.

The distal end of the ulna is laterally compressed

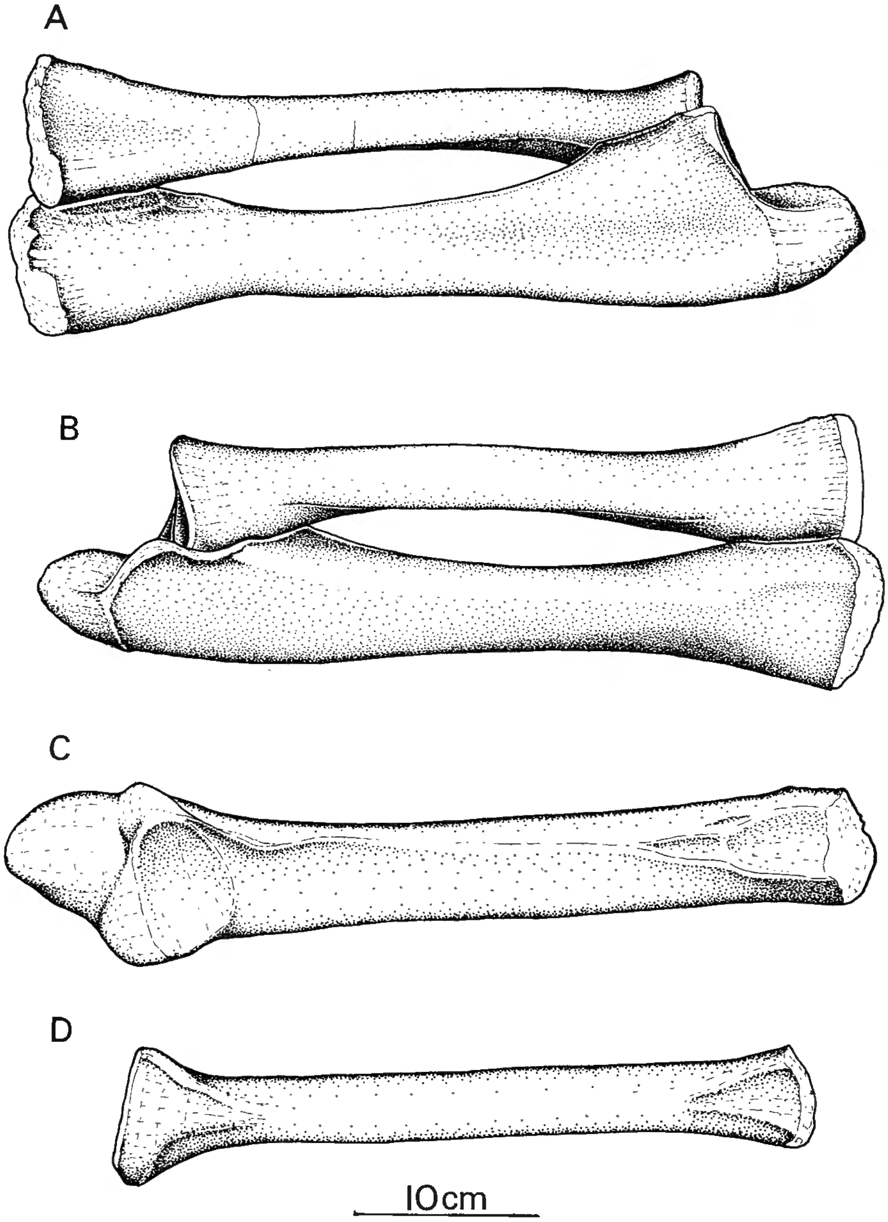


Fig. 49.
I. atherfieldensis. *BMNH R5764 (Holotype). Right radius and ulna. (A) medial view, (B) lateral view, (C) ulna in dorsal view, (D) radius in ventral aspect.*

and moderately deep. The lateral surface is slightly convex, while the medial surface is slightly concave. On the dorsal margin of the medial surface there is a shallow longitudinal depression which receives the distal end of the radius. The distal surface articulates with the carpus and is moderately smooth and convex; on the ventro-medial surface there is a small convex facet (Fig. 49) which is overlapped by a posterior flange of distal carpal V.

The *radius* is a long, slender cylindrical bone expanded at both ends (Figs. 48, 49). The articular surface of the proximal end is very slightly concave, oval in outline and set at a slight angle to the shaft (Fig. 49). Its ventral surface is rounded transversely and adapted to articulate against the corresponding surface on the ulna. From the proximal end, the shaft tapers slightly and in cross-section is subcircular, with a flat ventral surface. The radius is slightly bowed dorsally along its length, and becomes transversely compressed toward the distal end. The distal articular surface is rough but moderately convex. The ventrolateral surface of this end bears a shallow flattened area which articulated against the ulna.

The *carpals* were first described by HOOLEY (1925) using both of the well preserved carpalia of the holotype. In *I. atherfieldensis* the carpalia appear to have been partly co-ossified as they are in *I. bernissartensis,* but there is no evidence of the strap-like ossified ligaments seen in the latter species.

The carpus of *I. atherfieldensis* is very similar to that described in *I. bernissartensis* (NORMAN, 1980) in all of its characteristics. As a consequence only a very general description is given here.

The proximal carpals (*radiale, intermedium* and *ulnare*) can be identified in *I. atherfieldensis* (Fig. 50). The *radiale* is a large, block-like element on the dorsal half of the carpus, forming much of the facet for the radius and is fused to metacarpal I. There appears to be the outline of a small perforating foramen between the radiale and metacarpal I in proximal view. The distal surface of the radiale is excavated to receive the 2nd metacarpal. The *intermedium* is a large irregular bone on the lateral surface of the carpus, projecting proximal to wedge between the radius and ulna. Laterally this bone is sutured to carpal III and forms part of the articulating surface for metacarpal III. The *ulnare* appears to be a small flattened element sutured to carpals IV and V and forming part of the facet for the ulna.

The distal carpals are less clear in this species than in *I. bernissartensis*. Carpal I is not visible and has probably fused to metacarpal I. Carpal II is similarly not visible and was probably cartilaginous perhaps forming the margins of the socket for metacarpal II by analogy with *I. bernissartensis*. Carpal III seems to lie medial to the intermedium on the distal surface of the wrist. Carpal IV probably forms the medial part of the articular facet for metacarpal IV, and carpal V is a round nubbin of bone forming an oblique articular surface on the distal and lateral edge of the carpus.

Metacarpal I is a very short, broad, block-like bone which has become functionally incorporated into the carpus and is probably fused with carpal I and sutured firmly against the radiale (Fig. 50). For descriptive purposes the manus will be described as though held horizontally, with the palm facing downward.

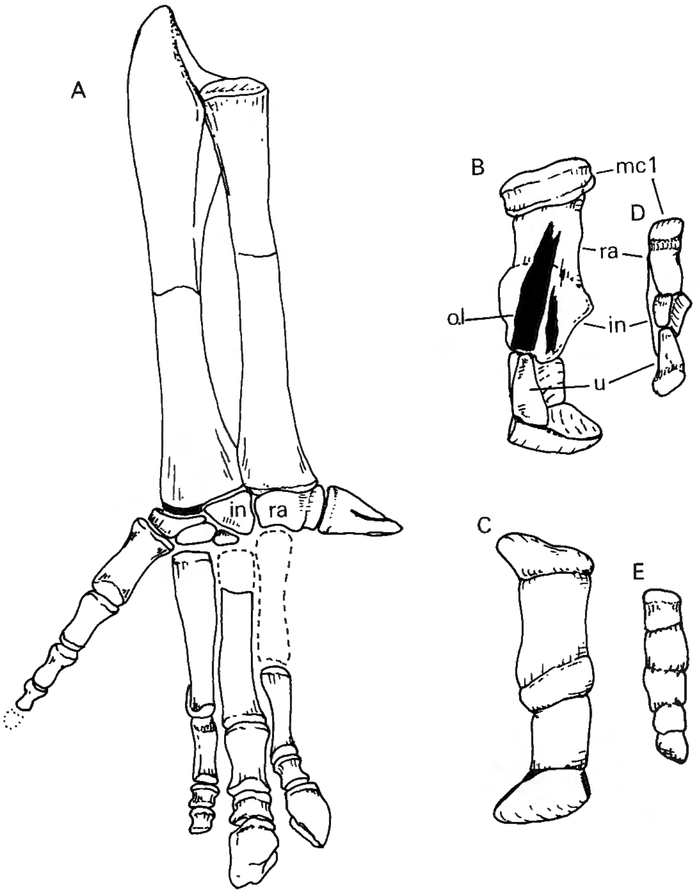


Fig. 50. – I. atherfieldensis. *BMNH R5764 (Holotype). A, Forearm and manus; D, carpus in lateral and E, medial views; B, C, carpus of* I. bernissartensis.

Fig. 51. – I. atherfieldensis. *IRSNB 1551. Metacarpals and phalanges in dorsal aspect.*

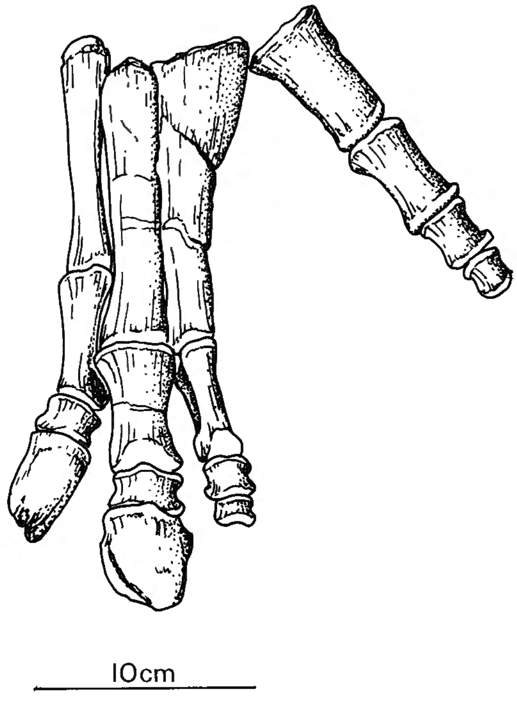
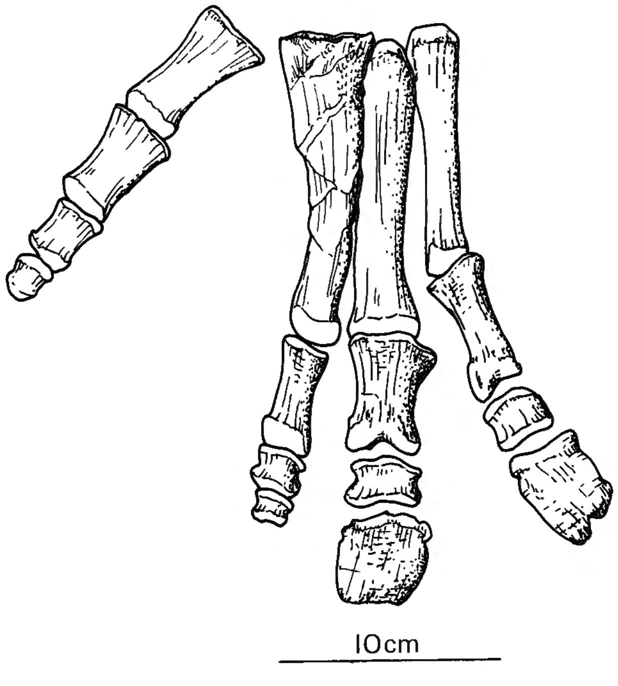


Fig. 52. – I. atherfieldensis. *IRSNB 1551. Metacarpals in ventral aspect. Partly disarticulated.*



The distal articular surface of metacarpal I is strongly convex convex dorsoventrally, very elongate horizontally and faces obliquely anteromedially. Beneath the articular surface, the anterior and posterior sides are slightly concave as they splay outwards over the surface of the carpus. The dorsal surface is very broad and bears a slightly everted edge forming a shoulder on the anterior surface, which clearly marks its junction with the radiale. Ventrally, the side of this metacarpal forms a broad shelf which curves smootly into the carpals beneath. The anterior (distal) surface is concave and forms the anterodorsal margin of the articular recess for metacarpal II. Proximally, the first metacarpal, along with carpal I, forms a lip which overlaps the distal end of the radius.

Metacarpal II is moderately well preserved in IRSNB 1551 (Fig. 51). In this form, this metapodial has a much more conventional structure than the first. It is a long, slender, somewhat transversely compressed rod, the proximal and distal ends of which are mildly expanded articular surfaces. The proximal end is slightly convex and articulates against a shallow depression on the carpus between the radiale and (?) carpal II. The medial surface of the shaft is smootly rounded, but laterally the surface is flattened and rugose where it was ligamentously bound to metacarpal III. The distal end of the shaft is tranversely compressed and bears a narrow convex articular surface (Figs. 51, 52).

Metacarpal III is the longest of the metapodials. The proximal and distal ends are expanded articular condyles, while the shaft between is moderately slender and subquadrangular in cross-section (Figs. 51, 52). The proximal articular end is rectangular and feebly convex, articulating against a shallow depression shared by carpals III and IV. Both the medial and lateral sides of the shaft are puckered for ligamentous attachment of metacarpals II and IV. The distal end has a well developed articular surface with a shallow intercondylar groove.

Metacarpal IV is only slightly shorter than metacarpal III. The proximal end is broad, quadrangular and slightly convex and articulates against carpals IV and V. Distally, the shaft is contracted and tapers toward its distal end. The medial surface, which lies against metacarpal III is raised and very rugose over much of its length, but this declines distally where the surface becomes smooth and slightly concave. The lateral surface, by comparison, is smooth and rounded and bears no ligaments scars. This distal articular surface is transversely compressed and slightly expanded anteroposteriorly into a narrow convex condyle.

In *I. atherfieldensis metacarpal V* is considerably shorter than metacarpal IV, and is quite robust. The proximal and distal ends are expanded, and between them the shaft is strongly contracted and slightly twisted along its length. The proximal end has an irregular more or less flat surface, slightly depressed at its centre, which is subcircular in outline, the ventral edge of which is flattened. The distal end is expanded with a broad, convex articular surface. From the characters it can be appreciated that these surfaces articulated rather loosely with the adjacent carpal V and also with its proximal phalanx.

THE DIGITS

Digit I was thought to have just a single phalanx in *Iguanodon* (HOOLEY, 1925; ROMER, 1956), in fact there were two in *I. bernissartensis*. This first or proximal phalanx is a thin oval disc which has an elongate ventral goove which caps the distal surface of metacarpal I. This phalanx was not preserved with either skeleton of *I. atherfieldensis*, this indicates either absence, non-ossification, or fusion to the ungual phalanx.

The ungual phalanx (Figs. 51, 52) is one of the most characteristic bones of the entire skeleton. It is a moderate sized slightly asymmetric conical structure; the broad base is depressed and its margin is rugose and everted for the attachment of ligaments and the tendons which controlled its movement. From its base, the sides of this bone contract and are slightly convex as they converge on the pointed apex. On the lateral edges of the anterior (dorsal) surface there are two narrow, moderately deep grooves, which represent the areas for the origin and growth of the horny ungual claw. This latter was in all probability an elongate and pointed structure, unlike the more hoof-like flattened ungual claws of digits II and III.

As a result of the fusion of metacarpal I to the carpus, this digit is set at an oblique angle to the main axis of the manus, directed anteromedially. When articulated, digit I is free to move in an oblique plane, and, when flexed, describes an arc transversely across the dorsal edge of the manus.

Digit II is composed of three phalanges (Figs. 50, 51). The proximal phalanx is a rather slender, slightly skewed bone, its proximal end is dorsoventrally expanded, roughly rectangular in end view and slightly concave, but more or less flat transversely. Proceeding along the shaft, the sides are flattened and in cross-section give a rhomboidal outline; the dorsolateral edge (adjacent to digit III) overhangs the ventrolateral edge quite markedly. Toward its middle, the shaft is contracted, but expands again toward the distal (articular) end. The articular surface of the distal end is strongly convex dorsoventrally, but only slightly so transversely; this surface is also notable because it is set at an angle to the rest of the shaft, away from digit III. The lateral surface of the proximal end of this phalanx is marked by rugosities which probably represent the scars of some ligaments which helped to bind this end against the side of metacarpal III. The second phalanx is an irregular, block-like bone; its proximal end is more strongly concave dorsoventrally than transversely and has a roughly triangular outline; the edges are thickened. Distally the sides are slightly contracted, before expanding for the distal articular surface. This distal surface is convex and also triangular, and is set at an angle to the proximal surface, directed anteromedially.

The ungual phalanx of *I. atherfieldensis* is quite characteristic. The proximal articular surface is roughly triangular in outline and bears a diagonal, concave depression. Distally, the bone tapers toward its distal end, becomes dorsoventrally flattened and terminates in a bluntly rounded point. The claw groove is unusual because it appears to be developed only along the anterolateral edge.

When articulated together, the phalanges of this digit display a prominent inward curvature, away from the longitudinal axis of the antebrachium and hand.

Digit III comprises three phalanges. The proximal surface is quadrangular in end view, concave dorsoventrally, but essentially flat transversely and has thickened edges. Distally, the sides of this phalanx are contracted and the ventral (flexor) surface is rugose, presumably showing the attachment area for the flexor tendon. The distal end is expanded and bears a well-developed articular surface, strongly convex anteroposteriorly, and divided by a shallow inter-condylar groove. The anterior extension of this articular surface shows that hyperextension of this digit could have occurred.

The second phalanx of the smaller form is a short, block-like element. The proximal surface is only slightly concave, but the distal surface is very broad and strongly convex dorsoventrally. The middle portion of the bone is flat ventrally and rounded dorsally.

The ungual phalanx is shorter and more blunt than that of digit II and is curved laterally, away from the latter. The proximal surface is broad, low and transversely grooved. Distally the sides are tapered and curve laterally. The nail groove is only well developed on the anteromedial edge. The ungual is flattened on its flexor surface, curved above and ends in a blunt, rugose and compressed edge. The ungual claw was obviously broad and hoof-like rather than laterally compressed and more sharply pointed as is usual in a grasping type of manus (*Hypsilophodon,* GALTON, 1974; *Deinonychus,* OSTROM, 1969a).

When articulated together, the phalanges of this digit show a slight lateral curvature, so that digits II and III appear to splay apart.

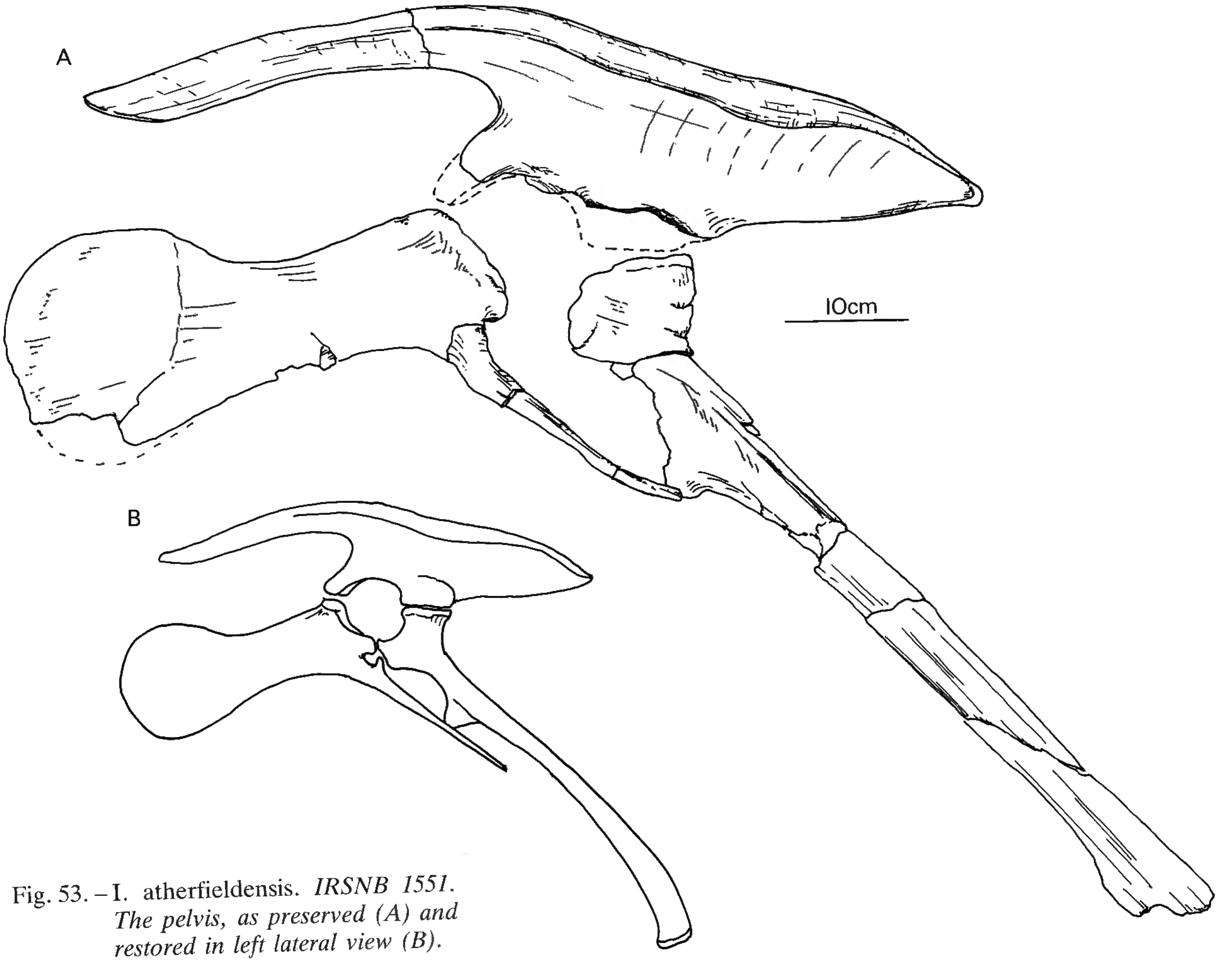


Fig. 53. – I. atherfieldensis. *IRSNB 1551. The pelvis, as preserved (A) and restored in left lateral view (B).*

Digit IV has three phalanges in *I. atherfieldensis* but only two are known in *I. bernissartensis.* In *I. atherfieldensis* all three of these are well preserved. The proximal phalanx is shorter and more slender than those of the previous two digits. The proximal end is transversely compressed, deep and slightly concave. Distally, the shaft is contracted with a transversely rounded dorsal (extensor) surface and a more or less flat ventral (flexor) surface; the sides are concave longitudinally and the flexor surface is heavily scarred as if for tendinous insertion. The distal end is expanded and has a well developed articular surface, with a slight intercondylar groove. The articular margin extends on to the extensor surface. The second phalanx is smaller and block-like, with moderately expanded articular ends. The third phalanx, unlike the previous digits, is not expanded to form a claw-bearing ungual. Its proximal surface is broad, slightly concave and smoothly articular. Distally, the sides taper slightly to a compressed, bluntly rounded distal end. The flexor surface is flat, but the extensor surface has a raised midline ridge on either side of which are lateral excavations. The distal surface is a rounded convex bulge; there is no evidence of a nail groove and, if a horny claw was borne on this digit, it would have been very small compared to those of digits I - III.

When articulated together the phalanges of this digit are more or less straight and run parallel to those of digit III, although they are much shorter than the latter.

Digit V is composed of three phalanges in both IRSNB 1551 and BMNH R5764. This count was confirmed by HOOLEY, who stated that:

> "... in the left hand this digit [V] was undisturbed and the phalanges were in position." (HOOLEY, 1925: p. 41)

All the phalanges of this digit have a very similar form although they become progressively smaller proximodistally. On each, the proximal end is moderately expanded and mildly depressed. Distally, the shaft is contracted but expands to a distal, convex articular surface. The flexor surface is flattened and the extensor surface transversely rounded.

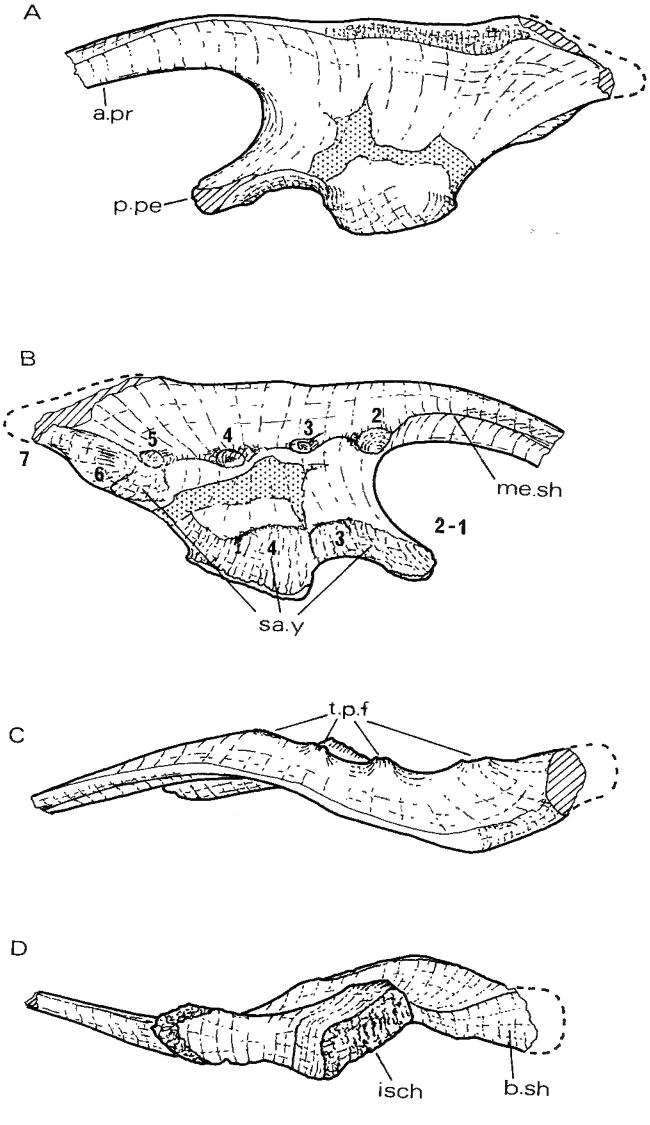
When articulated together the phalanges of the fifth digit are more or less straight and taper distally. This entire digit, including the metacarpal, diverges at an oblique angle from the middle three digits and is able to rotate across the wrist, on the oblique, convex articular facet of fifth carpal V.

The entire articulated manus can be seen to be a remarkably complex and specialized structure. The first digit is modified into an obliquely directed movable spine, which can rotate across the manus. The middle three digits (II - IV) are bound together proximally, into a single functional unit and this is turn is anchored onto the carpus by means of a deep socket which receives the proximal end of metacarpal I; the distal extremities of digits (II and III) splay outwards, and bear broad hoof-like unguals; each of these three digits can be hyperextended. The fifth digit is set at an oblique angle to the middle digits. The orientation of Carpal V ensures that this digit can rotate transversely across the hand and this, combined with the freedom of movement, between the proximal phalanges, suggests that this digit was probably a prehensile organ.

PELVIC GIRDLE

The anterior process of the *ilium* of *I. atherfieldensis* forms a long, tapering projection from the anterodorsal edge of the iliac blade (Fig. 53). This process is moderately thin and rounded along its dorsal edge, below which the sides are more or less flat. From its broad base, against the main blade, this

Fig. 54. – I. cf. atherfieldensis. *BMNH R6462. Left ilium in (A) lateral, (B) medial, (C) dorsal and (D) ventral aspects.*



process extends forward, tapering slightly along its length, and becomes curved outward and downward (away from the vertebral column and posterior ribs). It also becomes slightly twisted along its length, so that the lateral surface comes to face obliquely dorsolaterally toward its distal end. After gradually tapering for most of its length, this process becomes slightly expanded toward the distal end, before terminating in a bluntly rounded and compressed point. The medial surface of this process shows some variation in structure. In BMNH R5764 and R5347 the medial surface is very strongly buttressed at its base by a thick ridge, which develops from the buttressing around the facet for the transverse process of the first true sacral vertebra. This ridge extends forward along the anterior process in a shallow curve which progressively diminishes in size and rises toward the dorsal margin before disappearing near the distal end. This large ridge produces a broad ventral shelf on the anterior process. In other individuals the medial ridge is considerably less strongly developed (BMNH R6462 - Fig. 54) so that the ventral shelf is very poorly developed. The generalised ornithischian dinosaur *Hypsilophodon* (GALTON, 1974) also shows a considerable degree of variability in the structure of the anterior process within a single sprecies, which is comparable to that noted in *Iguanodon*.

The main blade of the ilium forms a deep vertical sheet of bone. The dorsal edge is transversely rounded, rugose and becomes thicker posteriorly. The lateral surface of the ilium below the dorsal edge is concave vertically and at the anterior end, it is rounded beneath the anterior process and ends abruptly at a sharp edge which marks the junction between medial and lateral surfaces. In lateral view, this margin forms a deep embayment beneath the anterior process and curves forward and downward to form the dorsal margin of the pubic peduncle. This latter is a moderately robust process, which has a triangular cross-section. From the dorsal margin of this process, the external surface is smooth and slopes away ventrolaterally to terminate at the sharp anterodorsal margin of the acetabulum; anteriorly, the surface is terminated at a blunt rugose end which was evidently capped by cartilage. Beneath the acetabular margin, the surface forms a deep, smoothly arched concave depression, the surface of which is rather uneven, but of a smooth texture. The medial surface of this process is more or less flat and its surface is marked by rugose striations which show the position of attachment of the anterior sacral ribs (Fig. 54). The distal end is rugose, blunt and contacts the pubis. However, the pubis is mostly supported by the large anterior end of the first sacral rib, which also braces the pubic peduncle of the ilium against the thrust from the head of the femur.

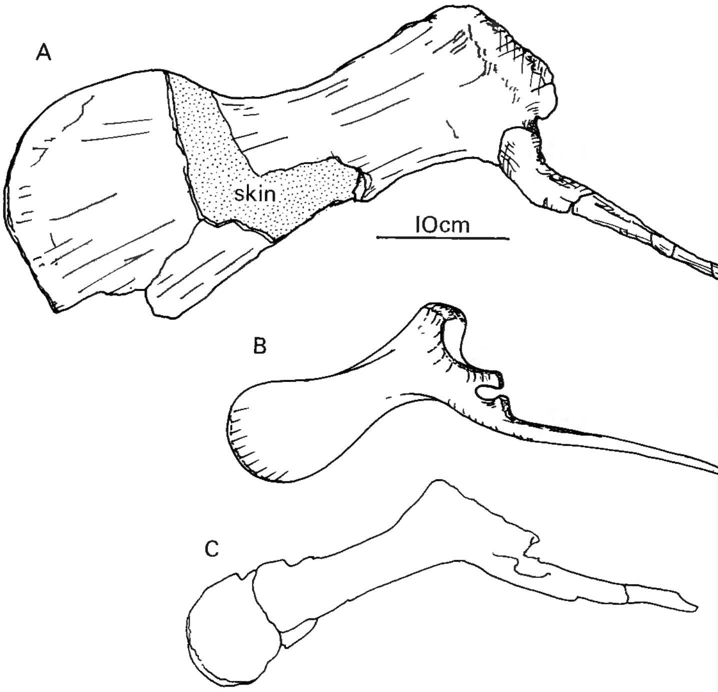


Fig. 55. – I. atherfieldensis. *IRSNB 1551. Pubis as preserved (A) and restored by reference to BMNH R5764 (B). C, an outline of the pubis of* I. bernissartensis *(IRSNB 1536).*

Extending backward from the pubic peduncle, the acetabulum, bordered dorsally by a sharp edge, forms a concave embayment beneath the main body of the ilium. Posteriorly, it terminates against the transversely expanded ischial tuber; the ventral surface of this tuber is abruptly truncated and is very rugose for attachment of the ischium. The anterior half of the lateral surface of the tuber is flattened, but posteriorly is more expanded so that these two areas are separated by a step (Figs. 54 A, D). Posterior to the ischial tuber, the ventral surface of the blade curves upwards and backward to meet the dorsal surface at a transversely expanded blunt point. In ventral view, this posterior ventral extremity can be seen to be reflected medially towards its hind end and a ridge is developed at its ventrolateral border so that a brevis shelf is enclosed between the two.

The medial surface of the iliac blade is quite complex in shape reflecting its rigid attachment to the sacrum. There is a pronounced ridge (Fig. 54) running along a line drawn between the ventral edge of the anterior process and the posterior tip of the blade. Above this ridge the ilium forms a broad, concave, obliquely inclined surface, which bears prominent fine radiating striations. Along the ridge there is a series of four, bluntly ended apophyses which serve as the sites of articulation of the transverse processes of the first four true sacral vertebrae. Immediately behind the most posterior of these, the surface of the ridge is heavily scarred by an elongate slightly irregular depression which serves as the area of attachment of the fused sacral rubs and transverse processes of the last two sacral vertebrae. Beneath the central part of this horizontal ridge there is a smooth expanse of bone which shows no sign of any form of osseus or muscular attachment. Beneath this area there is another rugose area which runs in a band along the ventromedial edge of the ilium from the internal surface of the pubic peduncle backward, to coalesce with the area for attachment of sacrals 5 and 6. This whole area is for attachment to the fused distal ends of the sacral ribs.

The *pubis*. The anterior pubic process has the form of a deep, laterally flattened blade (Figs. 53, 55). The anterior end is very expanded, with both lateral and medial surfaces marked by prominent striations for insertion of musculature for the hindlimb and abdomen. Passing backward, toward the acetabular margin, the dorsal edge of the anterior pubic process becomes thicker, more rounded and describes a smooth concave curvature; it is also slightly warped lengthways. This warp along the dorsal edge produces a very slight concave depression which has an oblique axis, passing backwards across the dorsal surface of the anterior pubic blade, toward the acetabulum (Fig. 55). This is most readily explained as an adaptation to accomodate the bulk of the dorsal part of the muscle running from the posterior dorsal vertebrae to the femoral head. At its proximal end, the anterior pubic process is broadly expanded and contacts the pubic peduncle of the ilium and the first sacral rib. The ventral border of the anterior pubic process is thin and describes a shallow concave arch ventrally and runs into the base of the post-pubic rod. The pubis forms the anteroventral margin of the acetabulum; this is a smooth concave depression which forms a broad, posteriorly directed articular surface in its anterior half, but becomes much narrower as it curves posteriorly. The lateral margins of the acetabular margin are strongly everted. The posterior end of the acetabular border is bluntly truncated where it meets the ischium, and forms a narrow process which overlies the obturator foramen. The latter is an elliptical opening, enclosed ventrally by the base of the post-pubic rod and posteriorly by a triangular process developed from the dorsal surface of the post-pubic rod. Between the latter process and the posterior acetabular margin there is a small gap, probably filled with cartilage in life. The posterior surfaces of these two processes are rugose and formed the area for attachment of the ischium; this was continued ventrally, on to the dorsal surface of the post-pubic rod for a short distance. The post-pubic rod forms a long, curved, tapering rod the proximal end of which is slightly flattened, and there is a shallow ridge which runs along its dorsal edge (BMNH 2194). In none of the specimens so far found has a complete post-pubic rod been preserved but, judging by the length of this same bone in the larger species, it probably terminated about mid-way along the shaft of the ischium.

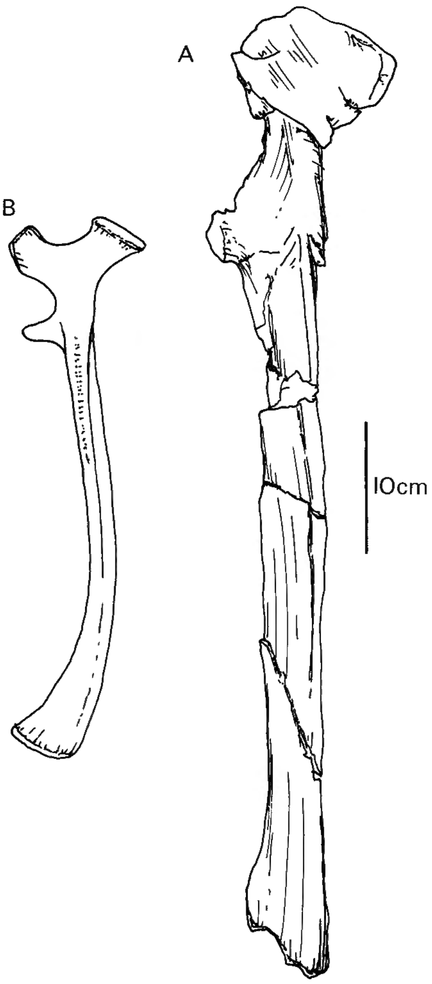


Fig. 56. – I. atherfieldensis. *IRSNB 1551. Ishium as preserved (A) and restored in lateral aspect from BMNH R2195.*

The *ischium* is a long J-shaped bone (Figs. 53, 56). The proximal end is broad and transversely flattened. The iliac head is broad, with an obliquely truncated surface, where it is attached to the ischial tuber of the ilium. Distally the shaft is laterally flattened and curves forward and downward, its posterior edge is rounded and describes a smooth concave curve. Proximally and on the anterior (acetabular) side of the head, the edge describes a smooth concave curve forming the ventral border of the acetabulum. Farther anteriorly, this margin broadens and develops a shallow articular surface just before it meets the acetabular portion of the pubis. At its junction with the pubis, the ischium forms a thick-edged deep plate; the ventral edge of this plate has a slight thickening for sutural attachment to the proximal end of the post-pubis, but becomes thin and sharp posteriorly as it curves backwards into the main shaft. Distal to the pubic

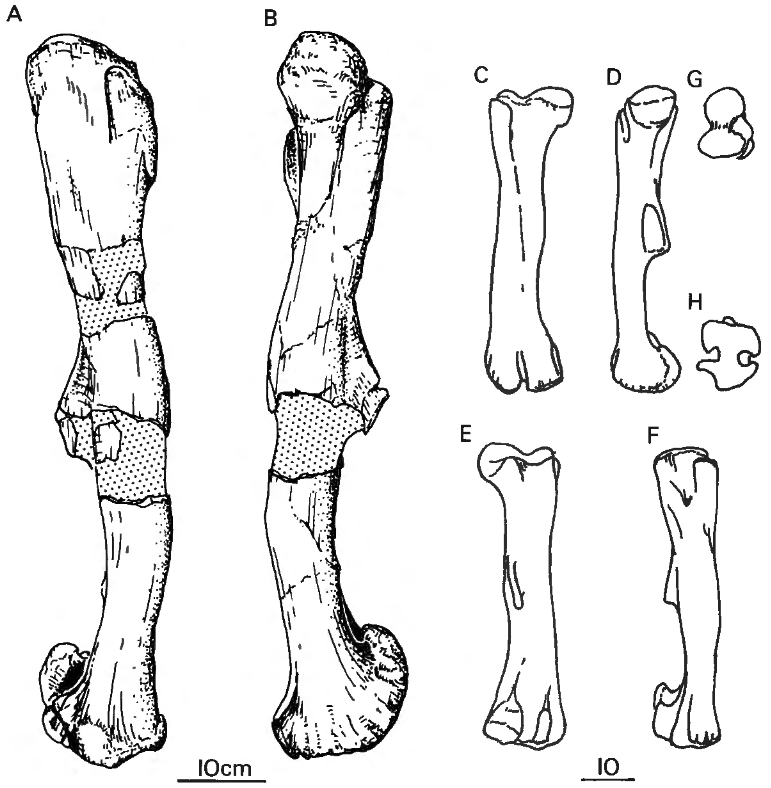


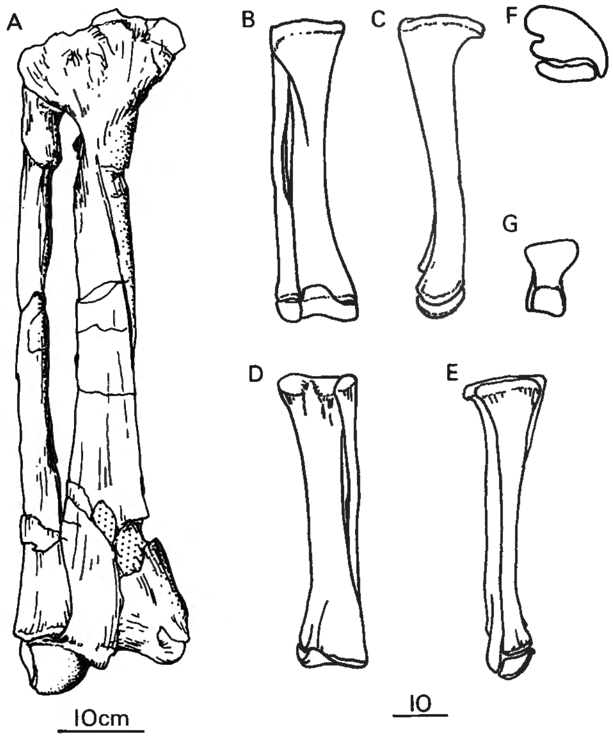
Fig. 57.
I. atherfieldensis. *IRSNB 1551. Femur (right) in lateral view (A) and medial view (B); and outlines of the right femur of BMNH R5764 in anterior (C), medical (D), posterior (E), lateral (F), proximal (G) and distal (H) aspects.*

process, the shaft of the ischium becomes thicker and also angular on its lateral surface but, as it does so, the anterior edge produces a thin leaf-shaped obturator process. This process curves medial to the post-pubic rod, which it presumably supports. Distally, the obturator process gives rise to a prominent ridge which descends the curved shaft of the ischium and, as it does so, curves from the anteromedial edge across to the posteromedial edge and thereby imparts a distinct twist to the axis of the shaft (Fig. 56). The external surface of the shaft is thick and angular proximally but, passing distally, this ridge becomes twisted forward, so that in cross-section the shaft has the outline of an aerofoil, with a thick rounded anterolaterally directed 'leading' edge and a sharp 'trailing' edge. Toward the distal end, the shaft becomes transversely flattened and anteroposteriorly expanded to give a footed end to the ischium. The medial surface of the footed distal end bears rugose striations, indicating its attachment to the adjacent ischium.

HIND LIMB

The proximal end of the *femur* is broad and saddle shaped; the head is large, globular and set on a neck at an angle to the shaft; it is separated from the greater trochanter laterally, by a narrow, waisted region (Fig. 57). This entire dorsal surface is of a uniform texture, being smooth but irregularly puckered, and was presumably entirely capped by cartilage. The greater trochanter is convex dorsally and anteroposteriorly expanded, its lateral surface is heavily scarred with vertical striation and there is a slightly raised ridge developed on its posterior edge. Wrapped around the anterolateral corner of

Fig. 58. – I. atherfieldensis. *IRSNB 1551. Tibia, fibula and proximal tarsals in anterior view (A). Outline lower leg bones of the holotype (BMNH R5764). B, anterior; C, medial; D, posterior; E, lateral; F, proximal; G. distal.*



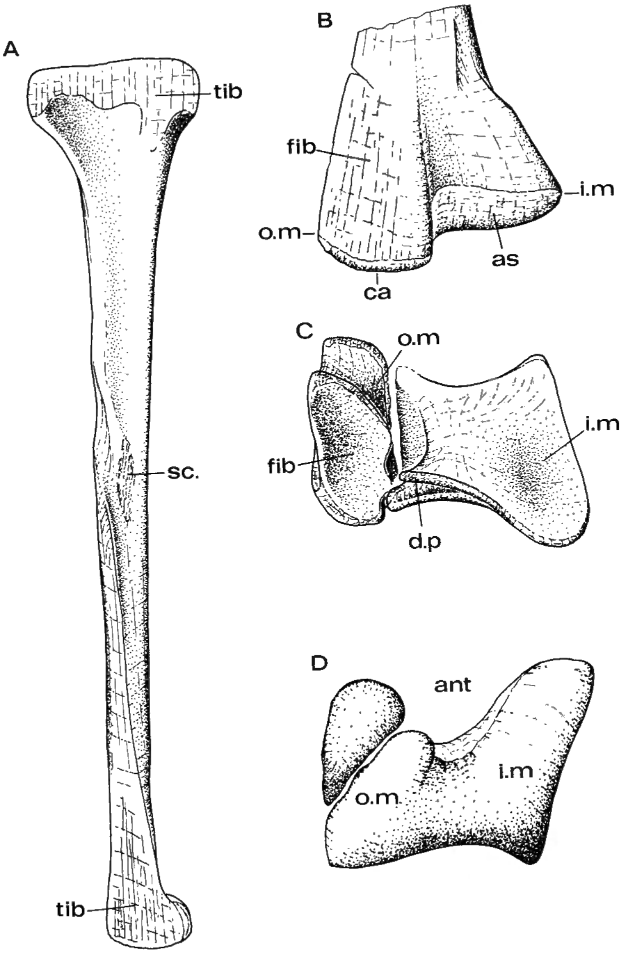


Fig. 59. – I. atherfieldensis. *(A) Fibula (left) medial view, BMNH R6464; (B) tibia, distal and anterior view, BMNH R6433; (C) astragalus and calcaneum, proximal view BMNH R5354: (D) Tibia and fibula distal view (Tibia BMNH R6433, fibula* Rivett *collection BMNH, unregistered).*

the greater trochanter, and separated from it by a deep, narrow cleft, is the flattened lesser trochanter. This has a thin posterior edge, a thickened rugose dorsal edge and a thicker, rounded anterior edge. From this anterior edge on the lesser trochanter there is a low slightly roughened ridge, which runs down and diagonally across the shaft of the femur toward the inner condyle; this gives the impression that the shaft has been twisted, the distal condyles having been rotated inwards 90° relative to the proximal head.

From the head, the shaft curves laterally and is anteroposteriorly contracted, producing a short neck from which the shaft descends more or less vertically. A short distance from the neck on the posteromedial side of the shaft there appears a slight ridge, and this develops into the 4th trochanter, which is of the crested type and lies in the middle of the shaft. Onto the surface, and around the base of this trochanter are the scarred areas for insertion of the massive femoral retractor and protractor muscles. Beneath the 4th trochanter, the shaft of the femur is curved towards the distal condyles, this curvature being anteriorly convex; the shaft in this region also has an oval cross-section. The distal articular surface is slightly expanded transversely, but considerably more expanded anteroposteriorly. The two condyles are separated anteriorly by a very deep, almost tubular intercondylar groove which is so deep that the lateral walls which enclose the groove almost meet above it. Ventrally, the two condyles are separated by a narrow waisted region, which appears as a slight concave depression in posterior view. Posteriorly, the condyles are extended backwards by large, heel-like buttresses which are themselves separated by a deep and very broad intercondylar groove. The inner condyle is considerably larger than the outer, which is laterally compressed; on the lateral surface of the latter condyle there is a prominent, rounded vertical ridge, separating the anterolateral surface of the condyle from the 'heel' region. The distal articular surface has the same smooth but irregular texture shown on the head, and was undoubtedly similarly capped by cartilage.

The proximal end of the *tibia* is broad and expanded and its surface is more or less flat transversely and slightly convex anteroposteriorly (Fig. 58). The posterior portions of both inner and outer condyles project backwards, and slightly downwards, overhanging the posterior surface of the shaft. The inner condyle is slightly larger than the outer and has a convex internal edge; posteromedially, these two condyles are separated by a narrow and deep intercondylar groove. The outer condyle has its lateral surface flattened with a small central condyle (BMNH R6431) and on to this surface rests the head of the fibula. Toward the anterior part of this fibular facet, the surface curves outward, wrapping around the anterior edge of the fibula to form the large cnemial crest. The edge of this crest faces laterally and its anterior surface is transversely rounded. Beneath the head of the tibia, the sides contract quite sharply into a very slightly sigmoid shaft. The cnemial crest which originates as a blunt ridge on the lateral surface (Fig. 59) swings medially across the anterior surface of the shaft before merging with the shaft; it continues as a slight ridge to the distal end, where it merges with the inner edge of the inner malleolus. The posterior surface of the tibial shaft is smoothly rounded transversely across most of its length. However, anteriorly the surface is more angular, with the oblique cnemial ridge and, lateral to this, another slight ridge which appears a short distance below the fibular facet and continues distally to form the lateral edge of the outer malleolus (BMNH R6431). The anterior surface of the mid-portion of the shaft between these ridges is flattened and becomes gradually broader distally, passing into the transversely expanded inner and outer malleoli.

The medial edge of the inner malleolus is broad and buttressed posteriorly by a thick ridge; its distal surface is anteroposteriorly expanded but is contracted laterally so as to be almost triangular in end view. This surface, which is convex anteroposteriorly extends on to the anterior surface and is heavily scarred for strong ligamentous attachment to the astragalus. In anterior view the outer malleolus is separated from the inner by a step and is less broad and thick than the latter. On its anterolateral side there is a flat striated facet, against which the distal end of the fibula was sutured. The posterior surface of this malleolus is slightly concave transversely and the lateral edge is thickened and rounded. The distal surface is convex and was firmly bound to the calcaneum, and is lower than the adjacent malleolus.

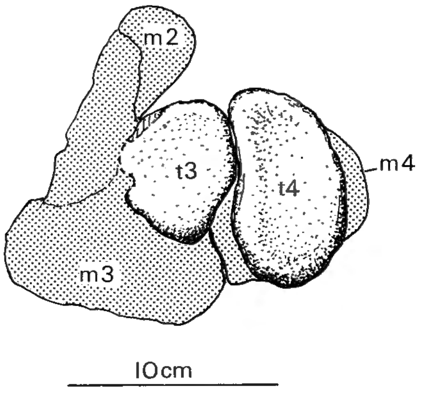
The *fibula* is a rather narrow, twisted bone attached to the lateral surface of the tibia. Its proximal end is transversely compressed and roughly crescent shaped in end view (Figs. 58, 59): its external surface is convex and its internal surface is concave. The proximal surface is more or less flat and bears signs which suggest that it was originally capped with cartilage. In lateral view, the proximal end is anteroposteriorly expanded with a more prominent posterior tongue-like process, which lies against the lateral tibial condyle. Internally, (BMNH R6464 - Fig. 59) the surface is vertically striated for ligamentous attachment to the external surface of the outer condyle and cnemial crest of the tibia. Descending from the proximal head, the anterior and posterior edges are thin and contract inwards to form the narrow, flat shaft which tapers toward its distal end. In external view, the shaft maintains a convex surface throughout its length. Internally, however, the surface is in places irregularly scarred and twisted. From the proximal end, the internal surface is at first smooth and slightly concave, but towards its middle the surface becomes irregularly scarred and the posterior edge is interrupted. From this point, the original posterior edge curves across the internal surface of the shaft, the latter becoming simultaneously thicker. This internal edge twists forward to form the sharp anteromedial edge of the flat facet on the distal end of the fibula which attaches to the anterolateral facet on the distal end of the tibia (Fig. 59). Distally, the fibula has a blunt expanded foot, the internal surface of which is flattened for attachment to the outer malleolus, and its external surface is swollen and bulges forward. The distal surface is convex, slightly rugose and articulates against a facet on the calcaneum.

The ankle of *Iguanodon* is typically dinosaurian with a hinge of the mesotarsal type between the proximal and distal tarsals. As a result of this, the proximal tarsals (astragalus and calcaneum) have become wrapped around, and rigidly bound to, the distal ends of the tibia and fibula and their distal surfaces form a single broad saddle shaped articular surface. The distal tarsals have the form of small flattened discs, resting on the proximal ends of the metatarsals; these provide (with the articular cartilages) a flattened articulating facet for the proximal tarsus and act as simple thrust pads.

The *astragalus* is the larger of the two proximal tarsals and caps almost the entire distal end of the tibia (Figs. 58, 59). Its proximal surface is excavated by two adjacent depressions for the two tibial malleoli. The medial of these is transverse, quite broad and its anterior lip has a dorsal extension or ascending process which increases the area of attachment to the malleolus. From the lateral edge of this lip, the proximal surface develops a rounded ridge running between the inner and outer malleoli, thereby separating the two adjacent facets. The lateral facet is steeply inclined and caps the medial side of the lateral malleolus and is confluent with the remainder of this facet on the calcaneum. The medial edge of the astragalus is moderately thick and convex ventrally. In ventral view, the astragalus is widest medially and tapers inwards laterally to a narrower waisted region which is saddle-shaped.

Most of the structure of the *calcaneum* (Figs. 58, 59) is known through an excellently preserved isolated calcaneum (BMNH R6493 - Fig. 59). In lateral view, the external surface is flattened; the ventral edge is convex, and the dorsal edge has two unequal recesses, separated by a broad projection. The ventral surface is slightly convex transversely and has an elongate rectangular shape; the surface is rather uneven but of a smooth rather than rough texture and was undoubtedly invested by cartilage. The dorsal surface bears two large concave depressions one behind the other and separated by an obliqueridge. The anterior of these depressions received the distal end of the fibula and, judging by the roughening of this surface, they were probably held together by connective tissue (ligaments). Behind this, the other depression is set at

Fig. 60. – I. atherfieldensis. *Distal tarsals as preserved (IRSNB 1551).*



a lower level than the former and is obliquely inclined, its long axis being directed anteromedially; this received the lateral and distal surfaces of the outer malleolus of the tibia. The medial surface of the calcaneum is rather compressed dorsoventrally and has a rough texture at its brief contact with the astragalus. The precise means of contact between astragalus and calcaneum is unclear.

There appear to be three flattened distal tarsals in *Iguanodon* (Fig. 60), as in *I. bernissartensis* (NORMAN, 1980). HOOLEY (1925) noted the presence of two tarsals in BMNH R5764; of these, only that referred to as the "outer tarsal" (distal tarsal III) remains, the other "inner tarsal" appears to have been mislaid.

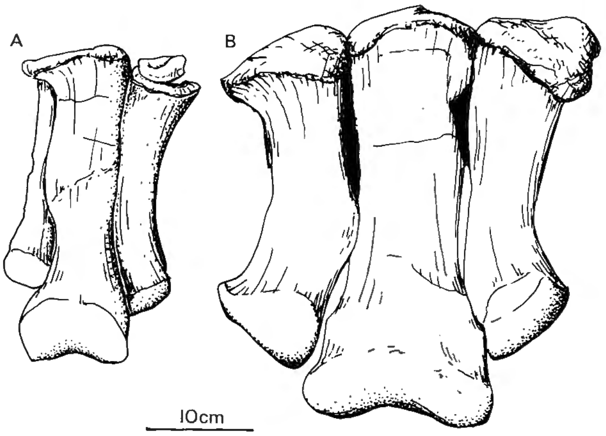
Distal tarsal II was apparently preserved in position in IRSNB 1551 and is an elongate oval and flattened bone, with one edge lightly indented. This bone, which corresponds to the "inner tarsal" described by HOOLEY (*op. cit.*) lay along the dorsal surface of metatarsal II. Its dorsal surface, which is depressed, articulated, via cartilages, against the inner edge of the astragalus, and its internal border is indented where it rests against distal tarsal III.

Distal Tarsal III is a smaller, more rounded disc of bone attached to the posterior dorsal surface of the third metatarsal. Its dorsal surface was slightly convex (BMNH R5764) and it appears to have articulated against the waisted middle region of the proximal tarsus.

Distal tarsal IV is quite a large thick disc of bone, roughly kidney-shaped. Its ventral surface bears a large convex bulge which fitted into a cup-shaped depression on the dorsal surface of metatarsal IV. The edges of this bone are thick and its dorsal surface, which articulated against the calcaneum, is depressed.

There are four *metatarsals*, all of which are tightly bound together into a single broad metapodial unit. Of these four, three (II, III and IV) are functional, that is they support phalanges, while the remaining one (I) is reduced to a splint bone and does not bear any phalanges. In the articulated foot, the third metatarsal is the largest and the second is the smallest; the fourth is only very slightly longer than the second (figs. 61-64).

Fig. 61. – *Comparative drawings of the left metatarsals of* I. atherfieldensis *(A) and* I. bernissartensis *(B).*



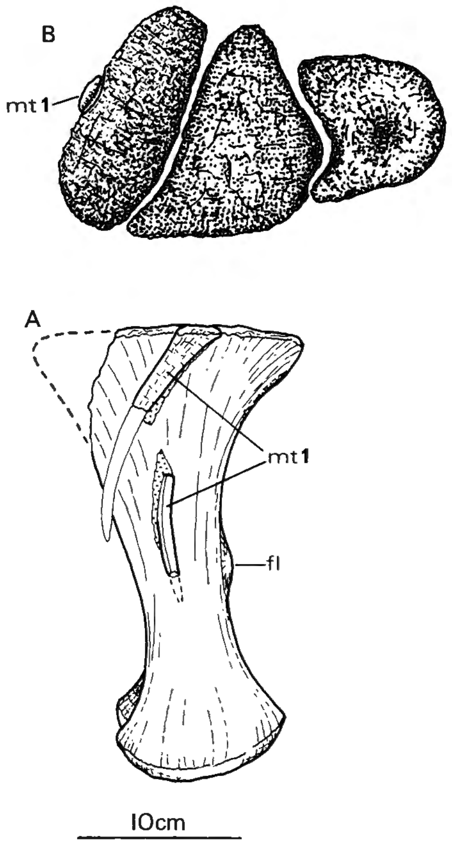


Fig. 62. – I. cf. atherfieldensis. *BMNH R1829. (A) medial view of metatarsal II, showing position of metatarsal I. (B) proximal view of metatarsals in articulation.*

Metatarsal I is present in neither BMNH R5764 nor IRSNB 1551, the two well-preserved skeletons of this species. However, the articulated hind foot (BMNH R1829) of an individual referable to this species, was found by S.H. BECKLES, in the Wealden Marls of the Isle of Wight; this was subsequently described by OWEN (1872) and shown to possess a rudimentary, style-like first metatarsal.

The proximal end to the first metatarsal is laterally flattened and closely pressed to the medial edge of the proximal surface of metatarsal II (Fig. 61); its surface is also rugose and was evidently involved in the proximal articular area. Below the head, the shaft is laterally flattened, curved and tapering. In this specimen, the proximal part of the shaft is obliquely inclined, pointing posteroventrally; the distal half of the shaft has broken away from the former and lies in a vertical position along the shaft of metatarsal II. On the basis of the position of this portion of the splint, OWEN reconstructed metatarsal I in a vertical position alongside metatarsal

II. However, since the proximal end of this splint is obliquely truncated and still lies flush with the edge of metatarsal II, it seems more probable that the natural position for this splint was the oblique one.

The proximal end of *Metatarsal II* is laterally compressed and anteroposteriorly expanded, so that the anterior edge forms a lip which overhangs the shaft below. Its proximal articular surface is more or less flat transversely and slightly convex toward the anterior lip (Figs. 61-64). Distally, the shaft is strongly contracted and laterally compressed, and curves forwards and outwards to the expanded distal articular end. The lateral surface presents a broad flat rugose area which is ligamentously bound to the adjacent surface of metatarsal III. About half-way down the shaft, there is a small lip, developed from the anterolateral edge of the shaft, which wraps around the medial edge of metatarsal III; this apparently served to more rigidly bind the second to the third metatarsal. Beneath this lip, the shaft curves medially, away from metatarsal III, and becomes strongly expanded anteroposteriorly. The distal articular surface is large, well-developed and faces obliquely inwards; it is convex anteroposteriorly, extending, on to the anterior surface, and more or less flat transversely. Posteriorly, there is a shallow intercondylar groove which probably acted like a pulley to guide the powerful flexor tendon.

Metatarsal III is the largest and most symmetrical of the metatarsals (Figs. 61-64). Its proximal end is expanded, and in end view is triangular (apex posterior) and flat. Its medial surface presents a broad flat surface for attachment to metatarsal II, and its anterodorsal edge is developed into a small, curved, finger-like process which wraps around the anterior edge of the latter. Beneath, the shaft is contracted in all aspects. The lateral surface has, near its anterior border, a low, rounded vertical ridge behind which there is a slight vertical depression. Both of these features carry strong, irregular surface markings which continue about half-way down the shaft. The ridge and groove arrangement ensure a close fit with the medial surface of metatarsal IV. About half-way down the shaft on the anterior medial surface, there is a shallow depression which receives the small lip-like process from metatarsal II. Distally, the shaft expands into a large, well-developed articular condyle. The articular surface extends well on to the anterior and posterior surfaces and is saddle-shaped, with a shallow inter-

Fig. 63. – I. atherfieldensis. *BMNH R5764 and IRSNB 1551. Restoration of pes in dorsal aspect.*

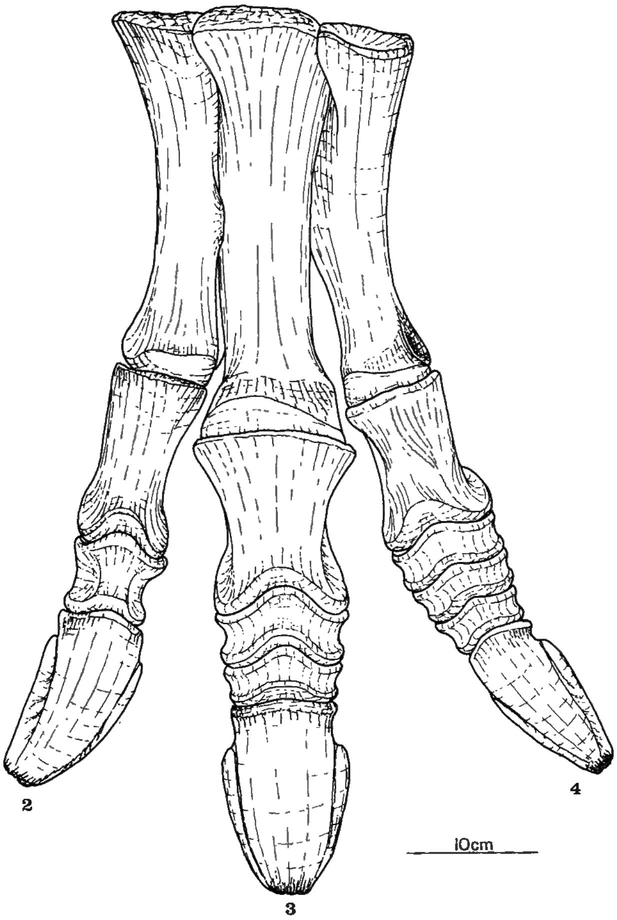
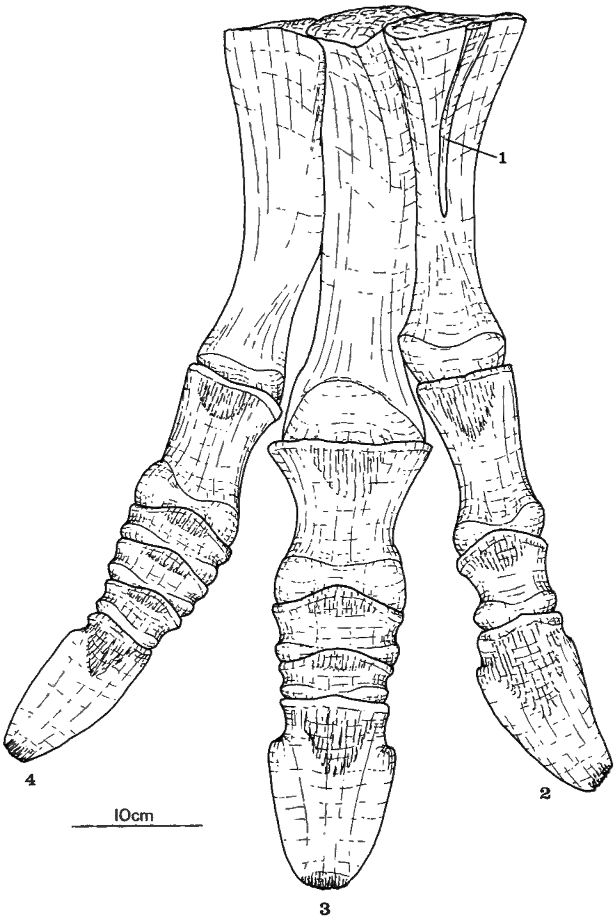


Fig. 64. – I. atherfieldensis. *BMNH R5764 and IRSNB 1551. Restoration of pes in ventral view.*



condylar groove. The shaft immediately above this surface is buttressed, especially on the anterolateral and anteromedial edges.

The proximal end of *Metatarsal IV* is expanded; its external surface is rounded, but it is concave medially where it is attached to metatarsal III. The proximal surface bears a moderately deep depression into which fitted distal tarsal IV. Beneath the proximal end, the shaft contracts and the external surfaces are rounded. On the internal surface, the concave depression descends the shaft and rapidly disappears, to be replaced by a stout vertical ridge which was bound by ligaments to metatarsal III. About half-way down the shaft this medial ridge subsides and the distal half of the shaft curves laterally (away from metatarsal III) to the anteroposteriorly expanded distal condyle. Like that of the second metatarsal, the distal articular surface faces obliquely outward, has a large convex articular surface and a small posterior intercondylar groove. Its lateral surface also possesses a rather deep pit for collateral ligaments, reminiscent of the very deep pits seen on the sides of theropod metatarsals.

THE DIGITS

The phalangeal count of the pes is 0, 3, 4, 5, 0 (Figs. 63, 64). The phalanges of the pes were reassembled for BMNH R5764 by HOOLEY (1925: fig. 8, VI). However, it is now clear from a study of this specimen and several others that this reconstruction was a composite of phalanges from both pes, several of which were misplaced. This explains the rather unusual arrangement of phalanges in digit IV, where the third phalanx is longer than the second — the "third phalanx" is in fact the second phalanx of digit II.

Digit II.

The *proximal* phalanx of this digit is the most slender of all three digits (Figs. 63-65). Its proximal end is depressed and roughly quadrangular in end view, although the dorsomedial corner is rounded and flattened. Distally, the shaft is waisted and re-expands distally to form the articular surface. The dorsal surface of the shaft is transversely rounded and the ventral surface more or less flattened. The distal articular surface is broad, with a slight shallow intercondylar groove, and the surface extends on to both extensor and flexor surfaces.

The *second* phalanx is considerably shorter than the first and, unlike all other distal phalanges, has strongly indented sides. Its proximal surface has two adjacent facets separated by a vertical, rounded ridge; dorsally, this ridge is continued as a small lip found in all the distal phalanges apart from the unguals. Distally, the shaft is flattened ventrally, and the articular surface is broad and has a slight intercondylar groove.

The *ungual* phalanx is a large, twisted and dorsoventrally flattened conical structure. Its proximal end is roughly rectangular and bears two adjacent articular depressions. Distally, the phalanx is dorsoventrally compressed with a blunt, flattened distal point; it is also curved both laterally and ventrally along its length. The nail groove is present and well-developed on the lateral surface, where it is supported by a shelf; medially, as a consequence of the twisting of the surface, the groove is less well marked.

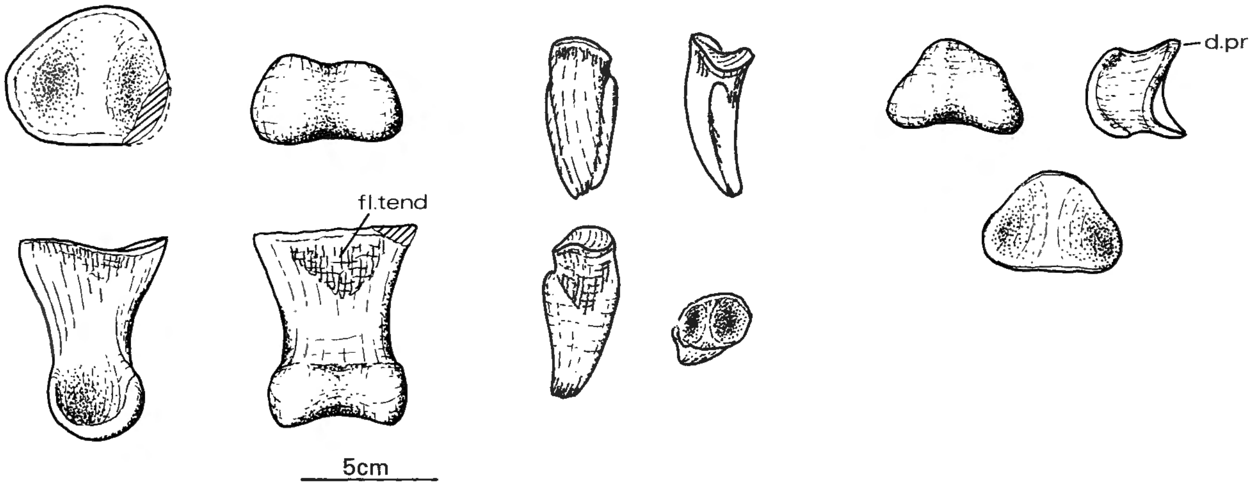
Digit III.

The proximal phalanx is considerably broader than that of digit II and is also shorter. Its proximal surface is broad and concave to receive the large distal condyle of metatarsal III. However, in most other respects this proximal phalanx resembles that of digit II.

Between the proximal phalanx and the ungual are two compressed phalanges similar to, although shorter and broader than, the second phalanx of digit II.

The ungual is a large, symmetrical hoof-like bone. From its broad and deep proximal end it curves

Fig. 65. – I. atherfieldensis. *Isolated pedal phalanges.*



forward and downward, becoming more dorsoventrally compressed and terminating in a broad extremely rugose edge. This is flanked on either side by a nail groove and its supporting shelf.

Digit IV.
The proximal phalanx is shorter than that of digit III but less broad and slightly twisted in comparison with the latter. The next three distal phalanges become progressively more compressed and narrower distally. The ungual phalanx has very similar characters to that of digit II, except that it has the opposite curvature to the latter, and tends to be very slightly narrower.

The epidermis

HOOLEY (1917, 1925) described several skin impressions found with the skeleton of BMNH R5764. These are of two types: small, irregular tubercles and considerably larger, flat polygonal tubercles. HOOLEY (1925) described both types of epidermal impression in detail. There are several fragments of matrix which were found near the ilium, dorsal ribs and on the manus (HOOLEY, 1917) and these all show characteristically low feebly convex, irregular small tubercles, showing that the skin was probably quite thin and pliable. The Belgian collection of *Iguanodon* was also inspected for evidence of skin impressions. The only ones found were on IRSNB 1551, and these consist of several small areas on the lateral surface of the anterior pubis (Fig. 55), and on several dorsal neural spines (Fig. 31). These are of the same type as those described above. HOOLEY (1925) also described some groups of larger, flat, polygonal tubercles, which he found in matrix attached to the ulna (*op. cit.*, pl. II, figs. 4, 5); this type of tubercle was not seen on any of the Bernissart specimens, although QUINET (1972, fig. 21) figured a skin impression of this type.

Comparative anatomy and systematic observations

Osteological comparisons are made below between *Iguanodon atherfieldensis* (Fig. 66) and four other well-described ornithopod dinosaurs: *I. bernissartensis, Camptosaurus dispar, Ouranosaurus nigeriensis, Hypsilophodon foxii* and the Hadrosauridae. These character lists are then used to review the systematics of these species of ornithopods.

a. IGUANODON BERNISSARTENSIS

The detailed anatomical similarities between *I. atherfieldensis* and this larger species are numerous and summarised in the generic diagnosis (page 3). However there are a number of autapomorphies of *I. bernissartensis*:
(i) an accessory palpebral
(ii) smooth convex margin to axis neural spine
(iii) sacrum with 7 true sacrals (+ 1 sacrodorsal)
(iv) humerus > 60% of length of femur
(v) intersternal ossification present
(vi) digital formula of manus: 2, 3, 3, 2, 4
(vii) pubis has narrow proximal part of shaft to anterior process.

In addition to these consistent characters there are several that may simply be size-related characters: neural spines short and broad; scapula stout and not expanded distally; pollex spike very large; ossified ligaments on carpus; greater number of teeth; greater degree of ossification of the occipital condyle and supraoccipital; rough parapophyseal facets; smaller orbit and shape of temporal fenestrae; depth of snout and lower jaw; quadrate straight.

Comments.
The significance of these differences are difficult to assess in terms of the taxonomic status of these two species; they are clearly open to two alternative interpretations. Firstly, and the view I adopted earlier (NORMAN, 1980), the osteological differences between the two morphotypes of *Iguanodon* can be regarded as sufficiently clear to enable them to be distinguished as what may be termed "osteological species". The implication of this interpretation is that since *I. atherfieldensis* and *I. bernissartensis* were undoubtedly sympatric contemporaries they may have exhibited some perhaps size-related or presently unknown ecological differences by which they were partitioned as biological species in their natural habitat. Certainly it has been proposed and observed that competition appears to be most intense among related species if sympatric distributions are maintained. Differences in behaviour (HUTCHINSON, 1959) size (ROSENZWEIG, 1966; SCHOENER, 1969, 1970) or combinations of these are necessary to decrease competition for similar resources. DODSON (1975, 1976) was able to demonstrate, with some confidence, that sexual dimorphism was present in lambeosaurine hadrosaurs and *Protoceratops* respectively. Both of these forms are notable for their development of cranial ornament (narial crests, horns or occipital frills) all of which proved crucial to the assignment of sexual morphs. The absence of such obvious visual display structures in *Iguanodon* sp. makes the identification of sexual types difficult. The osteological differences between *I. atherfieldensis* and *I. bernissartensis* do not readily correlate with sexual features, thus it seems most probable that the two species that are currently recognized are valid and that the differences in size etc., reflect ecological partitioning (cf. HUTCHINSON, 1959: *Diceros* vs. *Ceratotherium*).

The alternative viewpoint is that proposed initially by VAN BENEDEN (1881) and later elaborated by NOPCSA (1929) in which the two forms are regarded as sexual morphs of one species. NOPCSA suggested that the small species *I. atherfieldensis* represented a solitary, small male preserved with a herd of larger females (*I. bernissartensis*). The criteria for this assignment were derived from comparisons with North American hadrosaurids, which have since proved to be incorrect (cf. DODSON, 1975). While it is perfectly possible that these two species are sexual forms of a single species, unfortunately there seems to be no direct correlation between anatomical form and prospective sexual status in either specimen. I therefore regard them, for the time being, as separate species of the genus *Iguanodon.*

b. CAMPTOSAURUS DISPAR (Figs. 67-72)

Camptosaurus comes from the Upper Jurassic Morrisson Formation of Wyoming, and therefore predates both species of *Iguanodon.* Nevertheless *C. dispar* shows several synapomorphies with *Iguanodon* sp.

Characters shared with Iguanodon:

(i) elongation of snout using premaxillae, nasals, maxillae
(ii) general skull morphology
(iii) premaxillae edentulous and excavated laterally
(iv) mandibular bones very similar
(v) teeth in dentary and maxilla very similar
(vi) axial vertebral column very similar
(vii) scapula tall, expanded distally and proximally
(viii) humerus straight, low delto-pectoral crest, and longer than ulna
(ix) metacarpal I fused to carpus
(x) manus digits I and V divergent
(xi) ilium with deep and medially reflected post-acetabular blade
(xii) J-shaped, footed, ischium with proximal obturator process
(xiii) anterior pubic process laterally compressed
(xiv) femur curved distally, with crested 4th trochanter, and anterior intercondylar groove
(xv) small antorbital fenestra.

This character list is suggestive of a close relationship between *Camptosaurus* and *Iguanodon* sp. In particular, characters (v), (vii), (viii), (ix), (x) support the inclusion of *Camptosaurus* in the family Iguanodontidae.

Characters distinguishing Camptosaurus *from* Iguanodon:

(i) premaxillae have short postdorsal process
(ii) nasals divergent posteriorly
(iii) palpebral articulates *between* lachrymal and prefrontal
(iv) supraoccipital forms dorsal margin of the foramen magnum
(v) vertebral formula 9, 16(?), 4/5, 44+
(vi) axis neural spine not expanded anterodorsally
(vii) dorsal neural spines low, transverse processes long
(viii) crescent-shaped sternal bones
(ix) manus digital formula 2, 3, 3, 3, 1(+)
(x) pollex ungual not conical
(xi) posterior pubic rod = length of ischium
(xii) lesser trochanter of femur narrower
(xiii) digit I of pes has two phalanges (including an ungual claw)
(xiv) manus digits II-IV splayed apart.

These characters serve to clearly distinguish *Camptosaurus* from *Iguanodon* and substantiate its separate generic status.

c. OURANOSAURUS NIGERIENSIS (Figs. 67-72)

Ouranosaurus comes from the late Lower Cretaceous (Aptian) of Niger. As in the case of *Camptosaurus, Ouranosaurus* shows several synapomorphies with *Iguanodon,* as well as possessing its own distinctive characters.

Characters shared with Iguanodon:

(i) dentary and maxillary teeth very similar
(ii) general proportions of skull and lower jaw and articular relationships of bones
(iii) reduced antorbital fenestra
(iv) supraoccipital excluded from foramen magnum
(v) scapula tall expanded proximally and distally
(vi) humerus straight, low delto-pectoral crest, and longer than ulna
(vii) carpals co-ossified
(viii) metacarpal I fused to carpus
(ix) ungual of manus I is a conical spike
(x) femur curved distally, anterior intercondylar groove
(xi) iliac blade deep posteriorly and reflected medially
(xii) vertebral formula 11, 17, 6, 33(+)
(xiii) short posterior pubis
(xiv) anterior pubic process deep, transversely compressed
(xv) divergent manus digits I and V.

Many of these characters are also found in *Camptosaurus*: (i-iii), (v-viii), (xi), (xiv), (xv). This suggests very strongly that *Ouranosaurus* should also be included in the family Iguanodontidae.

Characters distinguishing Ouranosaurus *from* Iguanodon:

(i) premaxillae expanded transversely
(ii) nasals thickened posteriorly
(iii) palpebral articulates with lachrymal and prefrontal (*Camptosaurus*)
(iv) squamosal not extended posteroventral to the head of the quadrate
(v) longer diastema between predentary and 1st dentary tooth
(vi) axis neural spine not expanded anterodorsally (*Camptosaurus*)
(vii) neural arches fused to intercentrum in atlas
(viii) extreme elongation of neural spines of dorsal and sacral vertebrae
(ix) fused scapulo-coracoid
(x) pes, digit I absent
(xi) (?) posterior pubic symphysis.

The suite of characters above clearly distinguishes *Ouranosaurus* from *Iguanodon* and *Camptosaurus* at the generic level.

d. HYPSILOPHODON FOXII (Figs. 67-72)

A contemporary of *I. atherfieldensis,* and *I. bernissartensis, Hypsilophodon* is morphologically a rather generalized ornithopod. It shares only the most general of characters with *Iguanodon, Camptosaurus* and *Ouranosaurus* but will serve as a suitable comparator for systematic considerations (below).

Characters shared by Hypsilophodon *and the Iguanodontidae:*

(i) inset cheek teeth
(ii) cheek teeth crowns broad (laterally compressed) and form an interlocking battery with confluent wear facets
(iii) dentary crowns with thick enamel medially, maxillary crowns enamelled laterally
(iv) no external mandibular fenestra
(v) step between premaxilla and maxilla
(vi) slender 'loose' palpebral
(vii) maxillae meet in midline anteriorly (?)
(viii) skull pleurokinetic (NORMAN, 1984)
(ix) coronoid process developed on mandible
(x) curved sternal bones
(xi) divergent digit V in manus
(xii) obturator process on ischium.

Characters found in Hypsilophodon *and not in the Iguanodontidae:*

(i) short snouted triangular skull, orbits very large, frontals narrow and large orbital exposure (p)
(ii) large rectangular quadrato-jugal with foramen
(iii) medial ventral process on predentary (p)
(iv) no large median ridge on crowns of maxillary teeth
(v) "cursorial" hind limb proportions (p)
(vi) antorbital fenestra partly enclosed, large antorbital fossa
(vii) 5 premaxillary teeth
(viii) ossified tendons form sheeth around end of tail
(ix) narrow anterior pubic process
(x) straight ischium with obturator process midway along shaft
(xi) manus digital formula 2, 3, 4, ?2, ? (p)
(xii) small lesser trochanter and pendant 4th trochanter on femur
(xiii) metatarsal V retained (p).
[p = plesiomorphic or generalized ornithischian character.]

Thus *Hypsilophodon* is recognized as a valid genus of ornithopod dinosaur.

e. HADROSAURIDAE (Figs. 67-72)

Hadrosaurs are a very distinctive group of ornithopods found in the Upper Cretaceous of the Americas and Eurasia which seem to have close affinities with the Iguanodontidae (NORMAN, 1984; TAQUET, 1975).

Characters shared by Hadrosaurids and Iguanodontids:

(i) elongate snout (premaxillae, nasals, maxillae)
(ii) supraoccipital excluded from foramen magnum (*Iguanodon* + *Ouranosaurus*)
(iii) 4th trochanter of femur crested and in middle of shaft (femur > tibia) (*Tenontosaurus*?)
(iv) anterior intercondylar groove on femur well developed
(v) deep anterior pubic process (*Tenontosaurus*)
(vi) premaxilla edentulous (*Tenontosaurus*)
(vii) paroccipital processes curved sharply downward behind quadrate head
(viii) lost one phalanx from manus digit III
(ix) reduced posterior pubis (*Iguanodon* + *Ouranosaurus* + *Tenontosaurus*)
(x) hatched-shaped sternals (*Iguanodon* + *Ouranosaurus*)
(xi) width between orbits > occipital width (? primitive).

Characters of the Hadrosauridae:

(i) broad premaxillary beak
(ii) reduced lateral exposure of maxilla
(iii) expansion of anterior end of jugal
(iv) no antorbital fenestra
(v) palpebral lost/fused to orbit margin
(vi) postorbital pouches
(vii) no quadrate foramen
(viii) long diastema between 'beak' and dentition

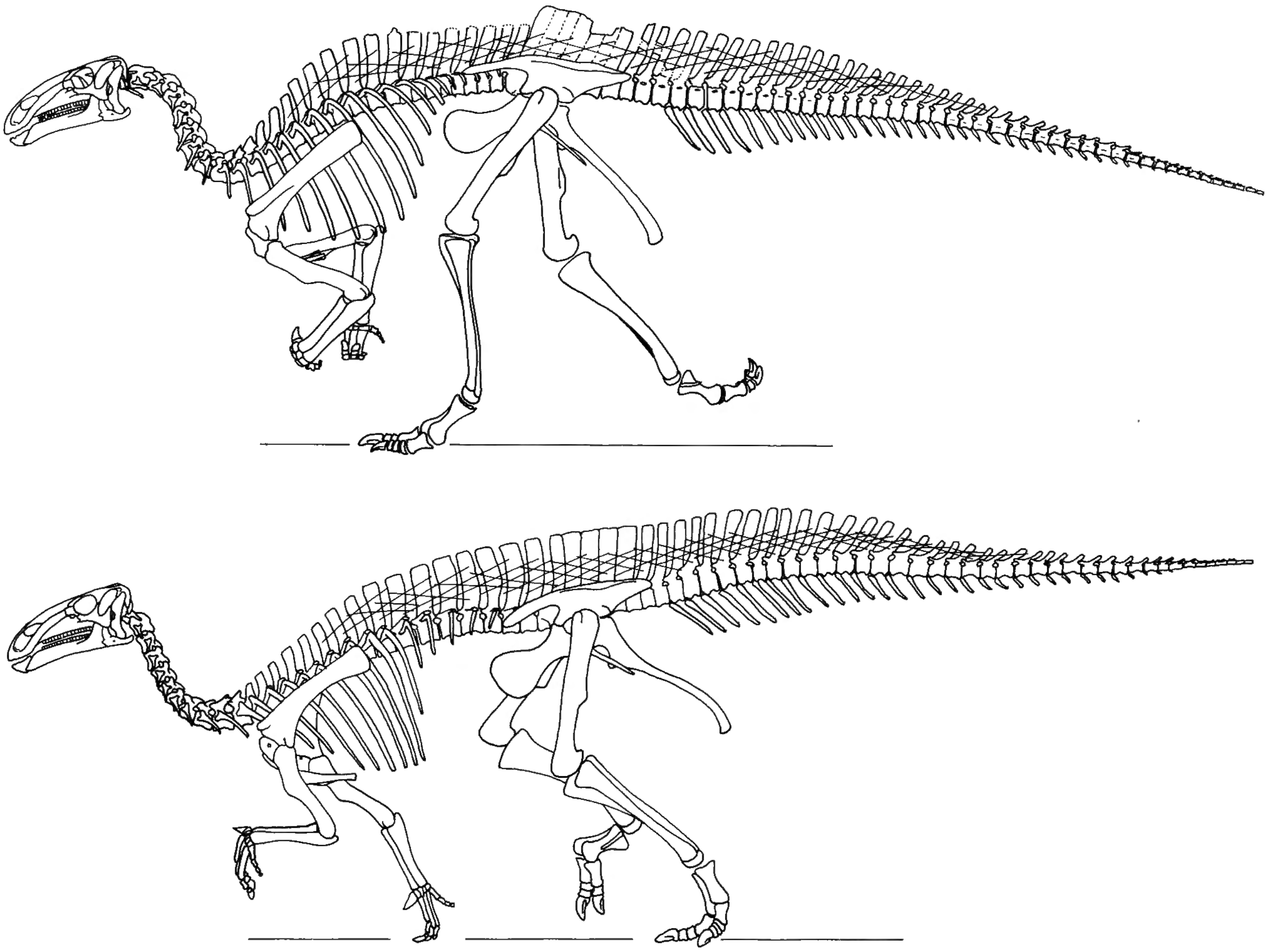


Fig. 66. – I. atherfieldensis. *Full skeletal restoration in bipedal pose. Based on IRSNB 1551, and in quadrupedal pose, from Gregory Paul.*

(ix) minimum of 3 teeth in each tooth family, tooth roots cemented together, maxillary and dentary tooth crowns diamond shaped with median primary ridge

(x) vertebral formula (average: 13, 19, 8, 50+)

(xi) dorsal vertebrae persistently opisthocoelous

(xii) scapula strongly curved with no anterior expansion of proximal end

(xiii) humerus sigmoid, prominent low delto-pectoral crest, equal to or > length of ulna

(xiv) two small carpal bones only

(xv) no digit I in manus (formula 0, 3, 3, 3, 3)

(xvi) ilium with 'antitrochanter' and low, narrow post-acetabular blade

(xvii) femur straight distally

(xviii) metatarsal I absent.

This extensive list of characters supports the proposition that the Hadrosauridae are a valid family of ornithopod dinosaurs.

f. SYSTEMATIC OBSERVATIONS

(i) *Hypsilophodon* in addition to its own characteristics (autapomorphies) shares several more general characters (synapomorphies) with both iguanodontids and hadrosaurids and can be regarded as the primitive sister-taxon of the latter (Node A - Fig. 74).

(ii) *Iguanodontids* and *hadrosaurids* share 11 synapomorphies (Node B - Fig. 74). However several of these characters appear sporadically elsewhere notably in *Tenontosaurus tilletti* OSTROM, 1970. *Tenontosaurus* (Fig. 73) is at present imperfectly known, although numerous skeletons of this species have been reported (OSTROM, 1970). Following DODSON (1980) *Tenontosaurus* is regarded as a hypsilophodontid and not an iguanodontid (GALTON, 1974). Hypsilophodontid characters of *Tenontosaurus* are: absence of primary ridge on maxillary teeth; large quadrato-jugal; (?) lack of contact between premaxilla and lachrymal; postacetabular blade deep with narrow (virtual) brevis shelf; ischium straight, with obturator process in middle of shaft; humerus sigmoid with prominent deltopectoral crest; no anterior intercondylar groove on

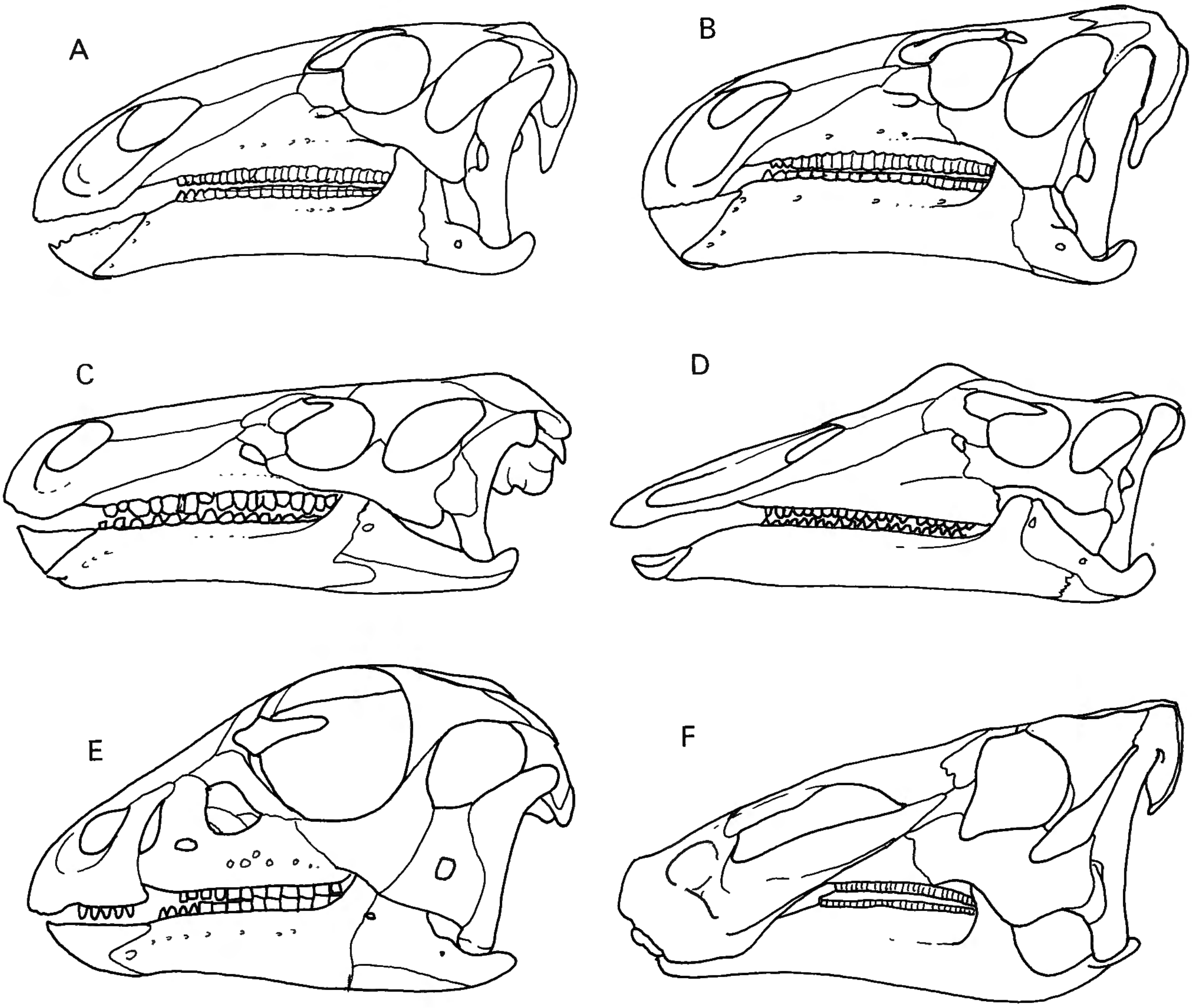


Fig. 67. – *Comparative outline drawings of ornithopod skulls of (A)* I. atherfieldensis, *(B)* I. bernissartensis, *(C)* Camptosaurus *(from* GILMORE, *1909), (D)* Ouranosaurus *(from* TAQUET, *1976), (E)* Hypsilophodon *(from* GALTON, *1974), (F)* Edmontosaurus *(from* LAMBE, *1922).*

femur; distal end of tail sheathed in ossified tendons; (?) unspecialized carpus. However, in addition to these characters, *Tenontosaurus* displays a suite of characters that are presumably size-related and appear in *parallel* to those seen in the Iguanodontidae and Hadrosauridae (Fig. 73): (i) no premaxillary teeth, (ii) crested 4th trochanter in middle of femur (femur > tibia), and a laterally compressed lesser trochanter; (iii) deep anterior pubic process and short posterior pubic process; (iv) phalanx lost in manus digit III.

(iii) The *Iguanodontidae* are a clade united by at least 10 synapomorphies (Node C - Fig. 74) — notably the possession of very similar teeth, shoulder girdles and forelimbs. *Iguanodon* and *Ouranosaurus* are placed as sister-taxa (Node D - Fig. 74) because of their shared possession of the conical pollex, vertebral formula, form of the occiput and short posterior pubis.

(iv) The *Hadrosauridae* (E - Fig. 74) are a well established clade placed here as the sister-family of the Iguanodontidae, rather than forming a simple transformational series from the grade group Iguanodontidae (*sensu* GALTON, 1974; TAQUET, 1975). The evolutionary assumptions that underlie this proposition are that (i) parallelism and convergence (as demonstrated in *Tenontosaurus*) occur in large-bodied ornithopods and are responsible for several anatomical features hitherto regarded, explicitly or implicitly, as being of value in determining phylogenetic relationships, (ii) that the specializations in the forelimb of iguanodontids (*sensu stricto*) in particular, are incompatible with the evolution of those of hadrosaurs and (iii) that *Ouranosaurus* is a specialized late iguanodontid which parallels in many respects the anatomical developments seen in hadrosaurs.

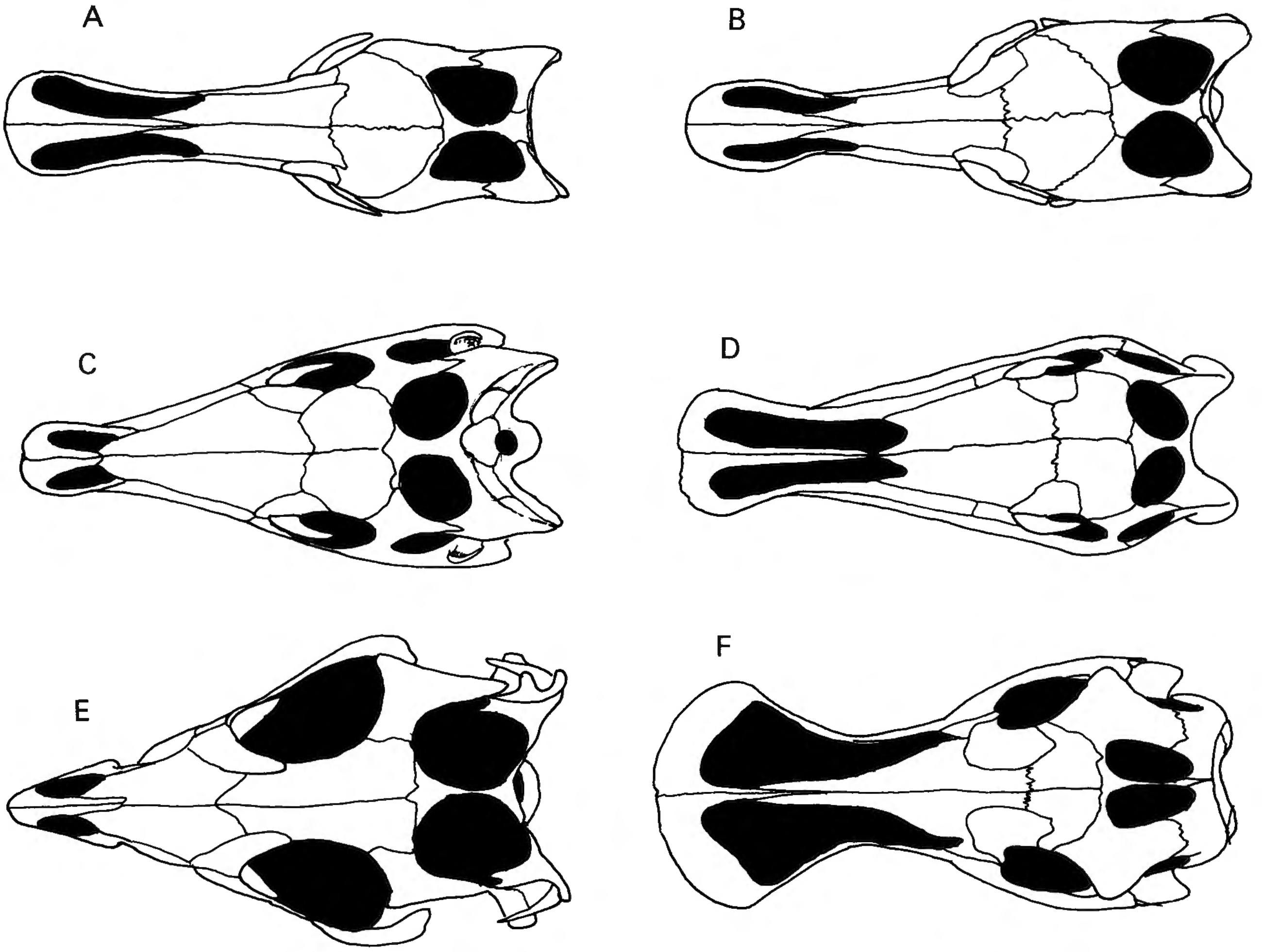
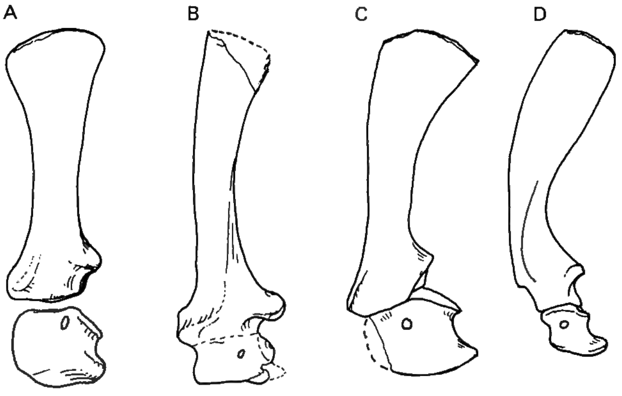


Fig. 68. – *Comparative drawings of ornithopod skulls dorsal views (A)* I. atherfieldensis, *(B)* I. bernissartensis, *(C)* Camptosaurus, *(D)* Ouranosaurus, *(E)* Hypsilophodon, *(F)* Edmontosaurus.

Fig. 69. – *Comparative pectoral girdles in lateral view. (A)* Camptosaurus, *(B)* Ouranosaurus, *(C)* Hypsilophodon, *(D)* Hadrosaurid *(after* LULL *and* WRIGHT, *1942).*



Skeletal myology

THE MUSCULATURE OF THE PECTORAL GIRDLE AND FORELIMB

In the past, attention has been focused on the musculature of the pelvis and hindlimb of the bipedal ornithischian dinosaurs (ROMER, 1927; LULL and WRIGHT, 1942; GALTON, 1969). This was stimulated by the unusual structure of the ornithischian pelvis. By contrast, the pectoral girdle of these dinosaurs and its musculature has, for the most part, been ignored save for a brief appraisal by LULL and WRIGHT (1942). The latter provided a brief description of the forelimb muscles of the hadrosaur *Anatosaurus*. However, the origins and insertions of the various shoulder muscles are difficult to trace.

In *Iguanodon,* the forelimb represents an interesting stage from a functional point of view, since the osteological evidence suggests that both *I. atherfieldensis* and *I. bernissartensis* were quite capable of using their forelimbs for weight support and quadrupedal progression (Fig. 66). Indeed, *I. bernis-*

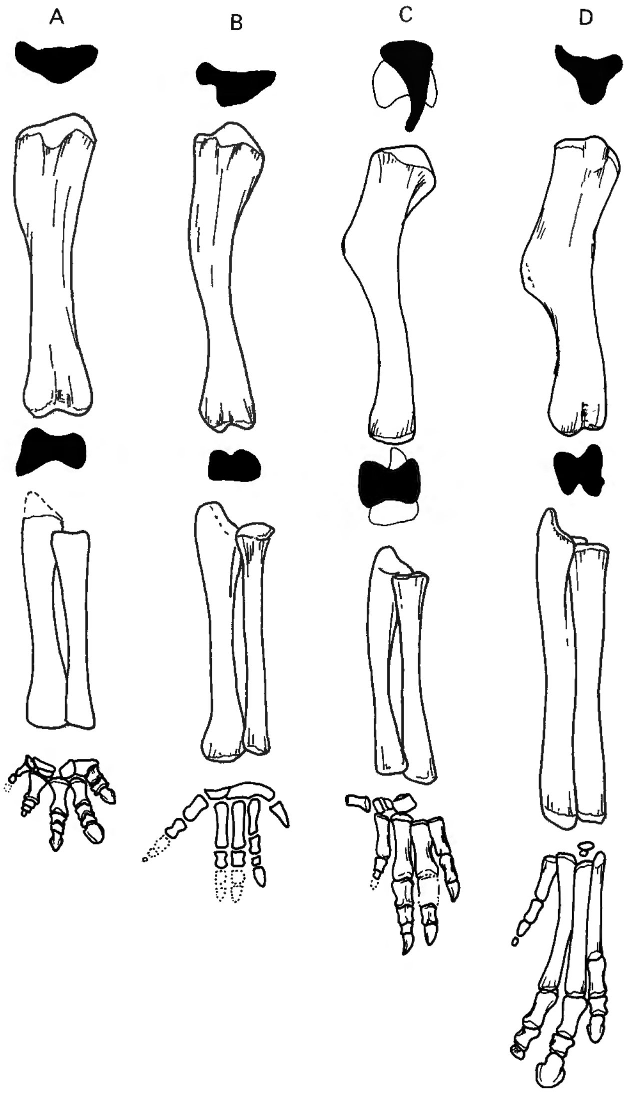


Fig. 70. – *Comparative forelimbs in lateral view. (A)* Camptosaurus, *(B)* Ouranosaurus, *(C)* Hypsilophodon, *(D)* Hadrosaurid.

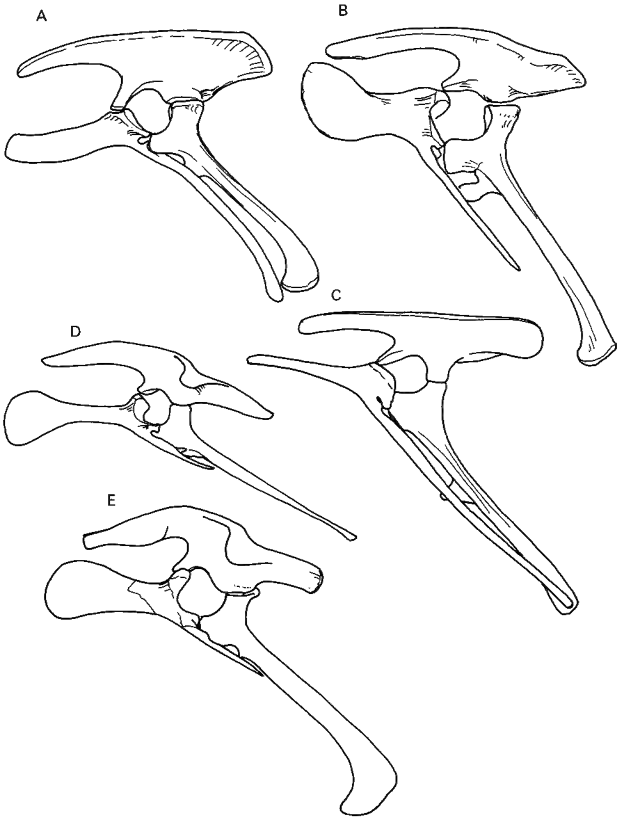
sartensis appears to be on the threshold between being a conventionally bipedal ornithopod and an obligate quadruped (NORMAN, 1980). However, these species have not yet developed the extremely massively constructed forelimb and the stout, frequently fused scapulo-coracoid, both of which seem to be characteristic of the obligate quadrupedal ornithischians (the ceratopians, stegosaurs and ankylosaurs). Nevertheless, the pectoral musculature of *Iguanodon* must have been sufficiently well developed to permit effective quadrupedal locomotion and weight support.

In order that the pectoral musculature of *Iguanodon* may be reconstructed, the various muscle scars on the pectoral girdle and forelimb have been compared to those found on the corresponding areas of the living crocodile. The reasons for this choice are two-fold. The crocodiles are arguably the nearest living relatives of ornithischian dinosaurs, apart from the birds, which are obviously too specialized for any fruitful myological comparisons. Secondly, the comparison is partly justified by the quite close correspondence in shape between the scapulae and humeri of these two archosaurs.

The muscles of the shoulder and the upper arm of the crocodile were first thoroughly described by FÜRBRINGER (1876). GREGORY and CAMP (1918) provided a detailed review of the identification of shoulder muscles in a variety of reptiles and mammals; this was augmented by ROMER (1922) in a detailed study of the homologies and functional aspects of the forelimb musculature in primitive vertebrates. The muscle terminology used in the following discussion is taken from GREGORY and CAMP (1918), with FÜRBRINGER's original terms included in parentheses; absence of parantheses indicates that FÜRBRINGER's terminology was the same.

Axial Musculature
- M. trapezius (cucullaris)
- M. levator scapulae (collo-scapularis superficialis)
- M. serratus superficialis (thoraci-scapularis superficialis)
- M. serratus profundus (collo-thoraci-scapularis profundus)
- M. rhomboideus
- M. costocoracoideus (sterno-costo-scapularis)

Fig. 71. – *Comparative pelves in lateral view. (A)* Camptosaurus, *(B)* Ouranosaurus, *(C)* Hypsilophodon, *(D)* Hadrosaurid.



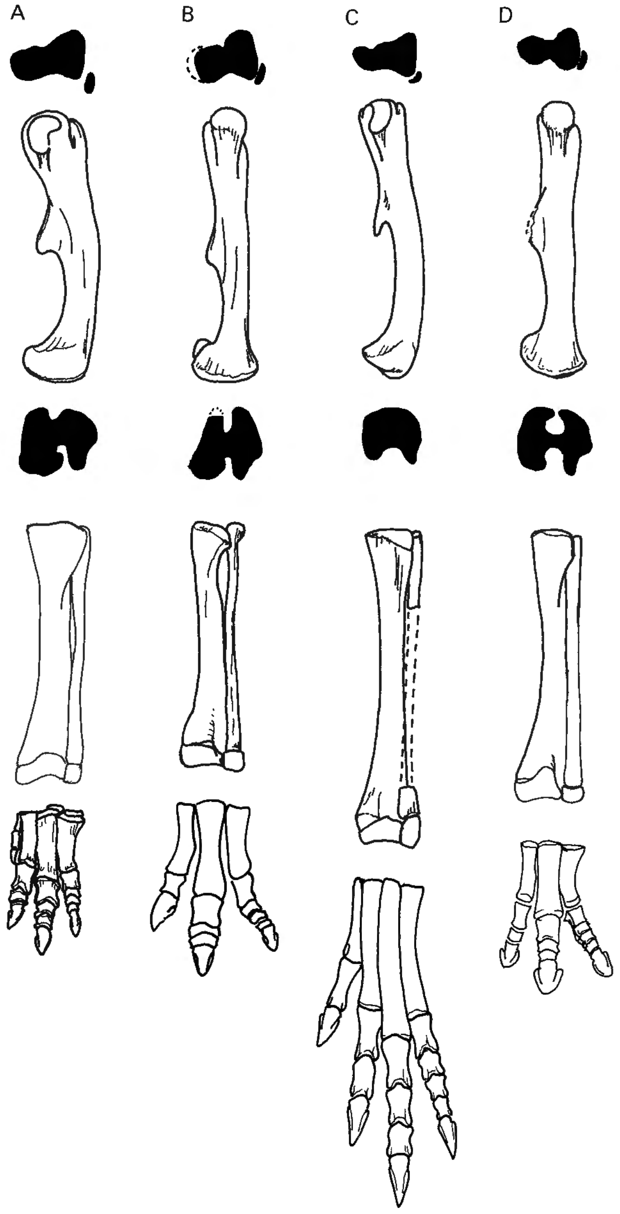


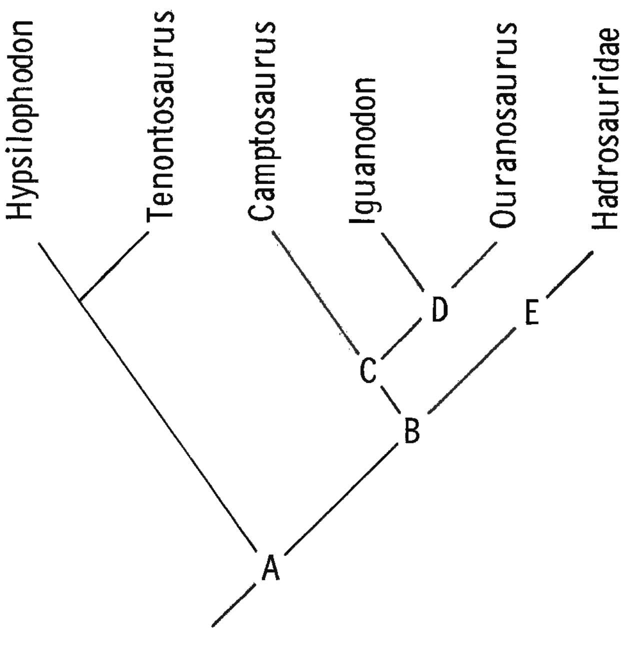
Fig. 72. – *Comparative hindlimbs. (A)* Camptosaurus, *(B)* Ouranosaurus, *(C)* Hypsilophodon, *(D)* Hadrosaurid.

Appendicular musculature
A. Dorsal muscles of the forelimb:
  M. latissimus dorsi (dorso-humeralis)
  M. teres major
  M. subcoraco-scapularis (subscapularis)
  M. scapulo-humeralis posterior (scapulo-humeralis profundus)
  M. dorsalis scapulae group:
    M. dorsalis scapulae (deltoides scapularis superior)
    M. deltoides clavicularis (deltoides scapularis inferior)
  M. scapulo-humeralis anterior
  M. triceps (anconaeus)
B. ventral muscles of the forelimb:
  M. pectoralis
  M. supracoracoideus
  M. coracobrachialis
  M. biceps (coraco-antebrachialis)
  M. brachialis (humero-antebrachialis inferior).

Axial musculature
(a) M. trapezius (cucullaris). This muscle typically arises from the fascia of the dorsal midline and runs diagonally backward and down to the anterior border of the scapulo-coracoid. Among crocodilians and other higher tetrapods (GREGORY and CAMP, 1918) its anterior portion reaches the skull. In crocodiles the more ventral part of this portion forms the M. sterno-mastoideus, inserting on the sternum (clavicle and its corresponding slip having been lost). The trapezius proper inserts on the anterior edge of the scapula, dorsal to the spine in crocodilians (FÜRBRINGER, 1876, T. XXVI, fig. 93 cu^{i}).
In *Iguanodon,* the origin of the trapezius was presumably along an aponeurosis over the neural spines of the posterior cervical and anterior dorsal vertebrae. Its area of insertion is not very clearly defined, but appears to have been confined to the proximal, anterior edge of the scapula, along the L-shaped, thickened buttress (scapular spine) of bone supporting the "clavicular facet" (Figs. 75A, 77 tra). The surface of this buttress is very rugose and probably represents a strong tendinous insertion.

(b) M. levator scapulae (collo-scapularis superficialis). This forms part of a group of lateral axial muscles originating from the ribs of the cervical and

Fig. 74. – *Cladogram of selected Ornithopoda based on the characters discussed in the text and modified from* NORMAN *(1984).*



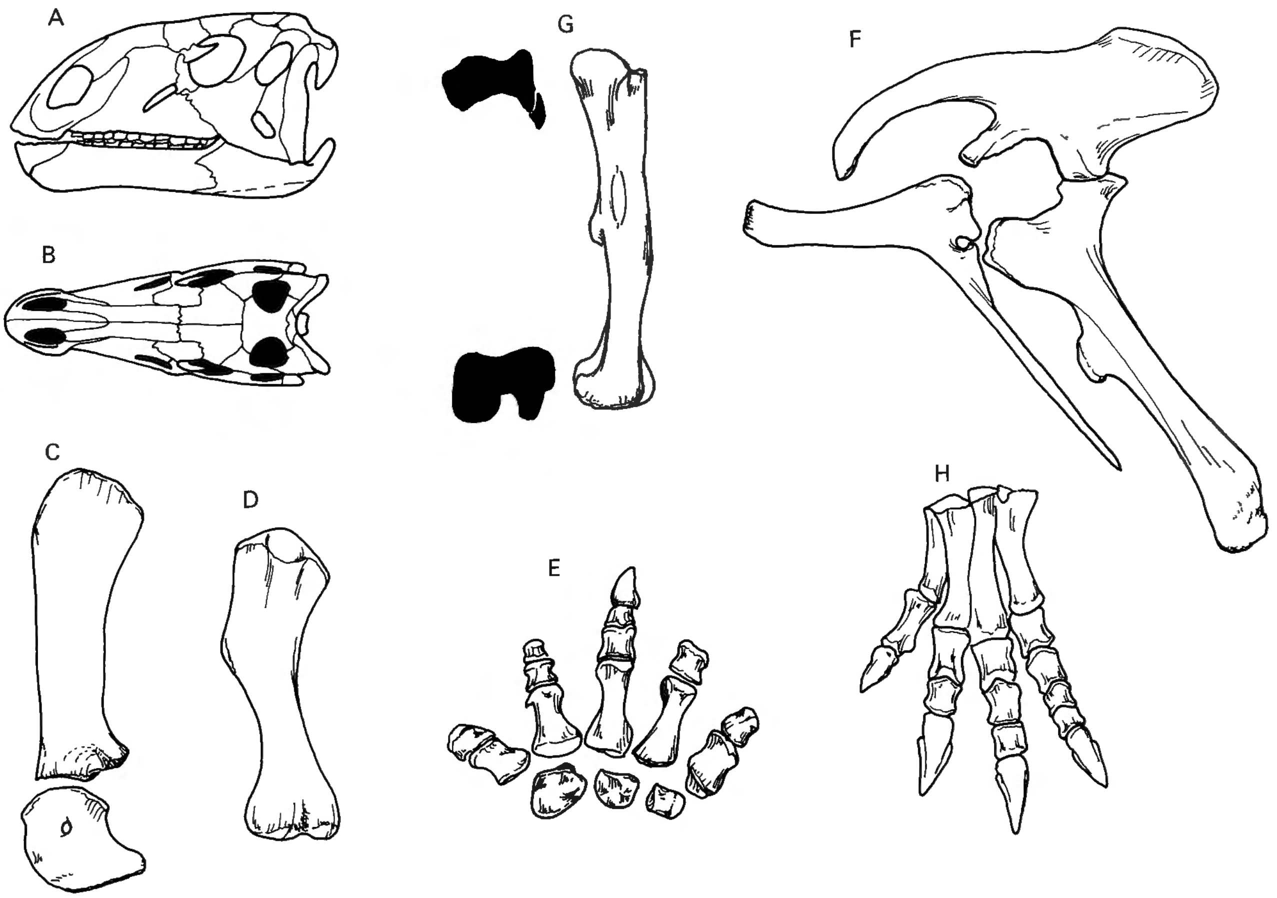


Fig. 73. – Tenontosaurus tilletti *OSTROM, 1970. (A) skull, lateral, (B) skull, dorsal, (C) pectoral girdle, (D) humerus, (E) manus, (F) pelvis, (G) femur, (H) pes. (From Dodson 1980).*

dorsal vertebrae; they insert mainly on the dorsal inner surface of the scapular blade. The most anterior member of this group, the levator scapulae, inserts along the anterior edge of the scapula in crocodiles (*op. cit.,* T. XXVL, fig. 93, cssp^{i}).
In *Iguanodon,* the anterior edge of the scapula, distal to the M. trapezius insertion, becomes sharp and rugose. This is very similar to the structure of the crocodilian scapula. This rugose edge is therefore interpreted as the probable area for insertion of the levator scapulae (Figs. 75A, B; 77, ls).

(c) M. serratus superficialis (thoraci-scapularis superficialis). This, the second of the lateral axial muscle group, arises from the distal ends of the ribs of the posterior cervical and anterior dorsal vertebrae in crocodiles. It inserts along the posterior margin of the scapular blade (*op. cit.,* T. XXVI, fig. 93, thssp^{i}).
In *Iguanodon,* the posterior edge of the distal part of the scapular blade is sharp, and heavily scarred on both lateral and medial surfaces. Since it is usual for portions of this group of muscles to insert on the medial surface of the scapula, the medial area is selected as that which most probably represents the insertion for this muscle (Figs. 75B, ser. s; 77).

(d) M. serratus profundis (collo-thoraci-scapularis profundus). The third and last member of this group arises from the transverse processes of the cervical vertebrae, and inserts on the inner and upper surface of the scapula and suprascapula in crocodiles (*op. cit.,* T. XXVI, fig. 91, cthspr).
In *Iguanodon,* this muscle probably inserted in a similar area on the distal inner surface of the scapular blade, an area which shows many sub-parallel rugose striations. It may also have inserted on the medial surface of the suprascapula, if this bone was originally present (Fig. 75B, ser. p).

(c) M. rhomboideus. Crocodiles are the only living reptiles in which the rhomboideus muscle is developed. It arises from the fascia above cervical vertebrae eight and nine and inserts on the anterior portion of the dorsal inner surface of the suprascapula (*op. cit.,* T. XXVI, fig. 91, rh). Since this muscle is also present in birds, it seems probable that it was present in stem-archosaurs. Therefore, although there is no direct evidence from muscle scars on the scapula or suprascapula of *Iguanodon,* this muscle may nevertheless have been present.

(j) M. costo-coracoideus (sterno-costo-scapularis). In crocodiles this muscle originates along the anterior margin of the sternal ribs, and inserts along the posterior margin of the coracoid and the lateral borders of the sternal plate.

This muscle appears to have been present and well developed in *Iguanodon,* judging by the conspicuous, depressed, crescent-shaped muscle scar found on the posteromedial edge of the coracoid. It presumably had a similar arrangement to that in crocodiles and originated from the cartilaginous sternal ribs and the lateral borders of the adjacent sternal bones (Fig. 75D, cc).

Dorsal muscles of the forelimb

(a) M. latissimus dorsi (dorso-humeralis). Typically, this muscle arises from the fascia of the external surface of the dorsal ribs and its fibres converge anteriorly to an insertion near the head of the humerus. This insertion is in common with that of the closely related M. teres major.

In *Iguanodon,* the origin of the latissimus dorsi was probably from the dorsal fascia of the rib cage. However, the common tendinous insertion is very well marked as an oval rugose patch on the dorsal surface of the humerus. This scar is situated distal to the head of the humerus, on the dorsomedial surface of the shaft (Figs. 76A, ld - tm; 77, ld).

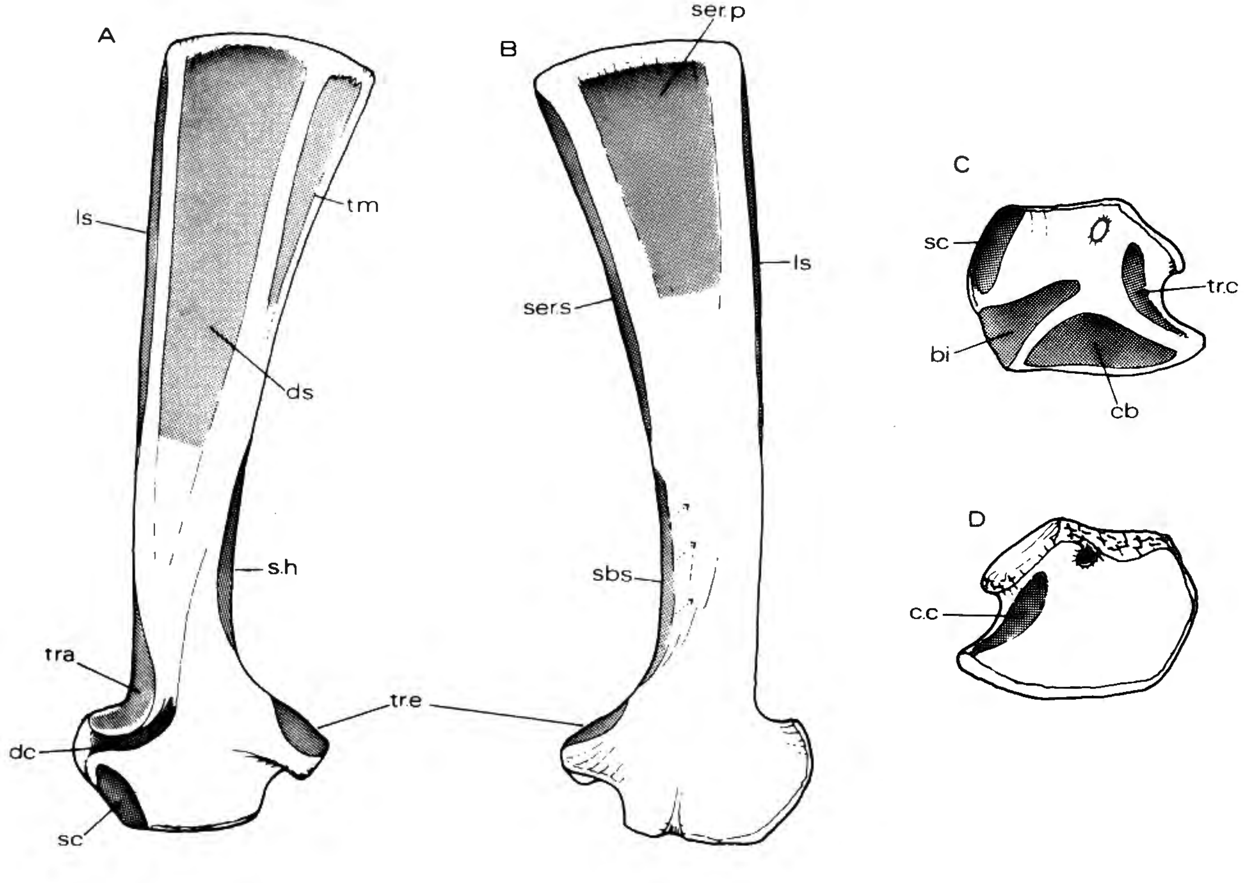
(b) M. teres major. As has been noted by ROMER (1922), the fibres of the latissimus dorsi run close to the posterior upon it. This derived muscle, the equivalent of the mammalian teres major, joins a common tendon to insert with the latissimus dorsi on the dorsal surface of the humerus.

In *Iguanodon,* the external surface of the scapula has, on its posterodistal surface, a broad triangular area which is available for, and probably served as an area for origin of, the M. teres major. This muscle, as suggested above, inserted onto the dorsal surface of the humerus by a common tendon with the latissimus dorsi, (Figs. 75A, 77, tm).

(c) M. subcoraco-scapularis (subscapularis). This muscle arises from most of the medial surface of the scapula, and inserts on the medial edge of the humerus, medial and adjacent to the articular head.

In *Iguanodon,* the posterior edge of the scapular blade is prominently scarred along either side of a sharp, bevelled edge. The more dorsal part of the inner posterior surface was presumably occupied by the M. serratus superficialis. However, ventral to this there is an area on the posteromedial edge of the shaft, adjacent to the prominent scar for origin of the M. scapulo-humeralis posterior. It seems reasonable to suppose that this area represents at least a part of the area of origin for the subcoraco-scapularis. The medial shoulder of the proximal end of the humerus is heavily scarred as if by tendinous insertion (BMNH R6614) and this

Fig. 75. – I. atherfieldensis. *A restoration of the muscular attachments on the pectoral girdle. (For abbreviations see page 371-372.) (A) scapula lateral, (B) scapula medial, (C) coracoid lateral, (D) coracoid medial.*

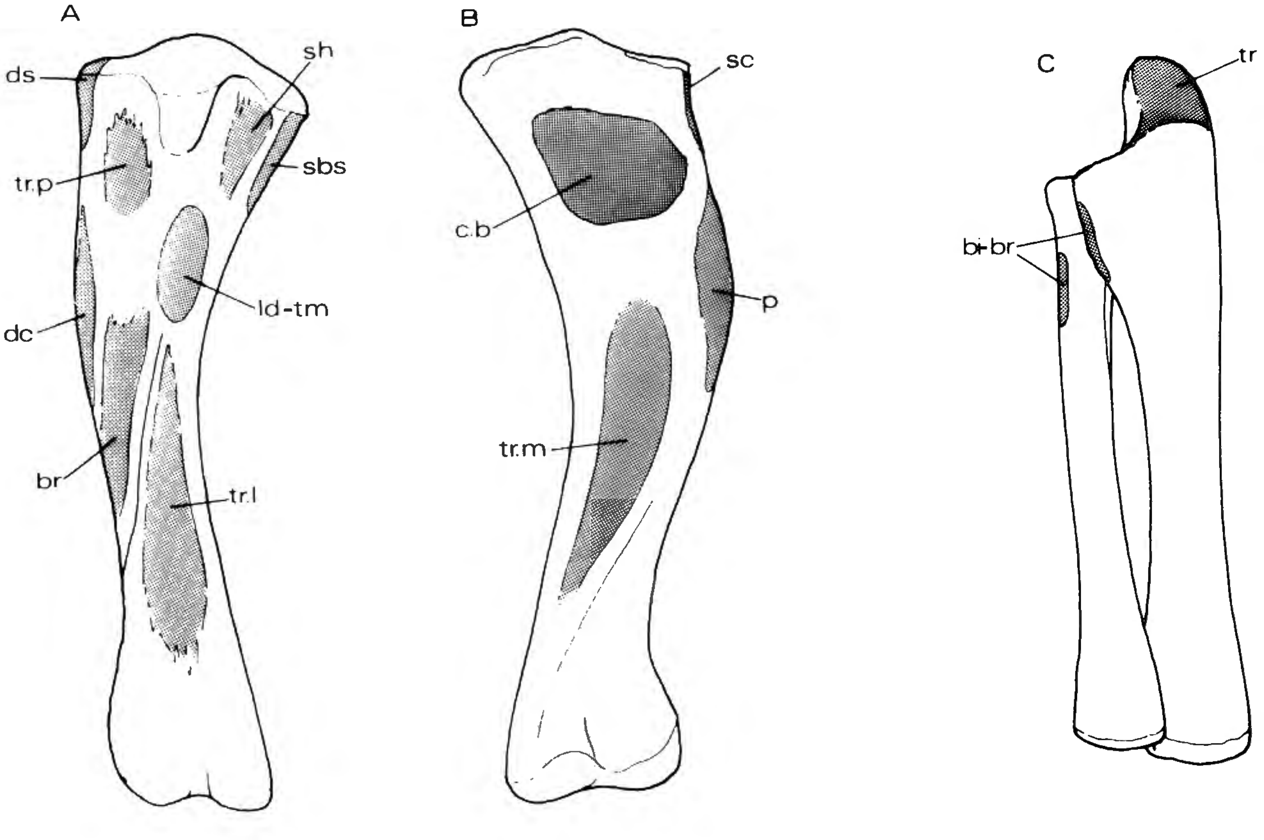


most probably represents the area for insertion of the above muscle (Figs. 75B; 76A, sbs).

(d) M. scapulo-humeralis posterior (scapulohumeralis profundus). In crocodiles, this muscle originates from the posterior edge of the lower third of the scapular blade, on the lateral, rather than the medial side (*op. cit.,* T. XXVI, figs. 90, 93, shpr). This muscle inserts on the proximal end of the humerus adjacent to the insertion of the subcoraco-scapularis, on the medial edge of the proximal end of the humerus (*op. cit.,* T. XXVII, fig. 102, shpr^{i}). In *Iguanodon,* several scapulae (BMNH 36505, R2848) possess a very well-defined scarred area, in a position exactly homologous to the area for origin of the scapulo-humeralis posterior in crocodiles, on the postero-lateral edge of the proximal end of the blade. The humeral insertion of this muscle is less well defined. On the dorsal surface of the humerus, lateral to the scarred area interpreted as the area for insertion of the subcoraco-scapularis, there is an ill-defined area of lightly striated bone which may represent the area for insertion of this muscle (Figs. 76A; 77, sh).

(e) Deltoid group (dorsalis scapulae). In crocodiles, the deltoid muscle forms a broad sheet of fibres, running from the dorsal and anterior portions of the girdle, to the proximolateral area of the shoulder of the humerus. It is divisable into two sheets: the M. dorsalis scapulae (deltoides scapularis superior) from the upper external surface of the scapula (*op. cit.,* T. XXVI, fig. 93, dss^{o}); and the M. deltoides clavicularis (deltoides scapularis inferior). The latter is derived from an origin on the clavicle and interclavicle but, since the clavicle is absent in crocodiles, this muscle has shifted its origin to the anteroventral border of the scapula (hence FÜRBRINGER's more appropriate terminology — *op. cit.* T. XXVI, fig. 93, dsi^{o}). The M. dorsalis scapulae inserts on the dorsolateral surface of the humerus, near the proximal head and medial to the delto-pectoral crest. The M. deltoides clavicularis inserts on the dorsolateral surface of the deltopectoral crest, adjacent and dorsal to the pectoralis muscle (*op. cit.,* T. XXVI, fig. 93, dss^{i}, dsi^{i}).
In *Iguanodon,* the M. dorsalis scapulae undoubtedly originated from the major part of the broad antero-external surface of the scapula (Fig. 75A, ds). It would have inserted either on the lateral shoulder of the head of the humerus, which is rugose and scarred, or alternatively from the dorsolateral surface of the shaft, near to the head, similar to the situation in crocodilians, as this area also shows some low striation (Figs. 75A; 76A; 77, ds). The second part of the complex, the M. deltoides clavicularis, probably originated from the raised rugose buttress on the scapula of *Iguanodon* (Figs. 75A, 77 dc) as this occupies an approximately homologous position to the scapular spine in croco-

Fig. 76. – I. atherfieldensis. *A restoration of the muscular attachments on the forelimb. (A) humerus posterior, (B) humerus anterior, (C) radius and ulna lateral. (For abbreviations see page 371-372.)*



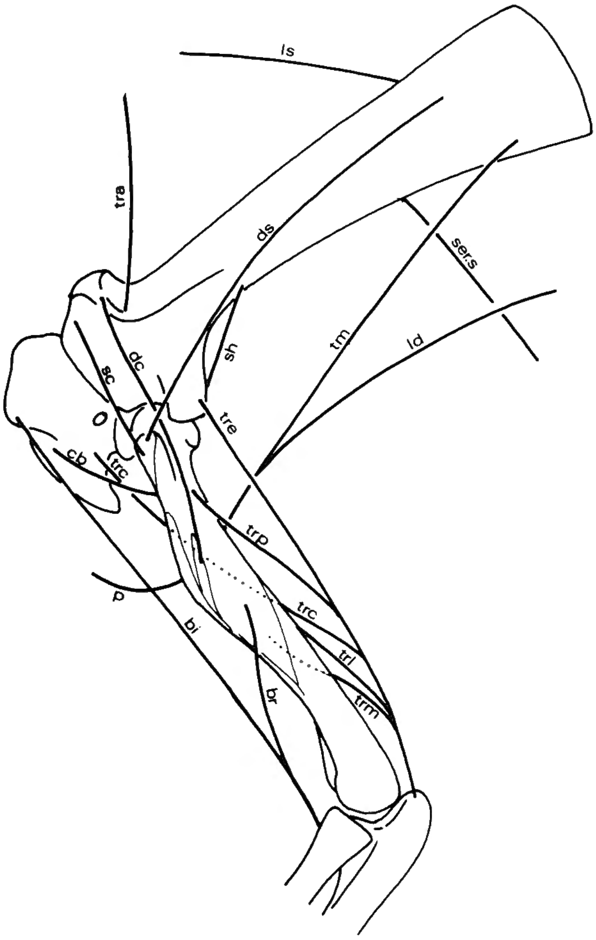


Fig. 77. – I. atherfieldensis. *Restoration of the lines of action of the principal shoulder muscles.*

diles, which serves as the origin of this muscle in these forms, (*op. cit.*, T. XXVI, fig. 93, Sp.S). This muscle was evidently powerful, since its insertion on the humerus is very heavily scarred, lying along the dorsolateral edge of the deltopectoral crest, and slightly separate from the more lateral and ventrally positioned scar for the pectoralis muscle.

(f) M. scapulo-humeralis anterior. This muscle is absent from crocodiles, and its presence in *Iguanodon* cannot be identified with any certainty. Indeed it may have been absent, since it is also absent in birds. Had it been present, it would undoubtedly have had a very similar position to that occupied by the M. deltoides clavicularis, at least judging by its position in *Spenodon* (FÜRBRINGER, 1900), originating from the anterior edge of the proximal end of the scapula and inserting on the lateral surface of the shaft of the humerus.

(g) M. triceps (anconaeus). This muscle is the principal extensor of the forearm and has a single massive tendinous insertion on the olecranon of the ulna. This muscle is subdivided into a number of slips — five in the crocodile. Two of these originate from the pectoral girdle, while the remaining three originate from the shaft of the humerus. FÜRBRINGER noted that this degree of differentiation was found in some birds, but not in lizards or *Sphenodon*. It seems likely that this rather complex form of triceps musculature was present in the earliest archosaurs. Therefore it does not seem too unreasonable to suppose that this arrangement was also present in ornithischian dinosaurs.

The two pectoral origins of the triceps can be identified in *Iguanodon* with some confidence. (i) M. triceps scapulare laterale externum. As in crocodiles, this head of the triceps originated from the strong buttress immediately above the glenoid. In *Iguanodon*, the surface of the homologous buttress is similarly heavily scarred as if for this muscle (Figs. 75A, B; 77, tre). (ii) M. triceps coraco-scapularis. This head aries below the glenoid from the postero-external surface of the coracoid (Fig. 75c, trc). In *Iguanodon*, this precise area is marked by a well-developed, depressed, crescent-shaped muscle scar.

The humeral origins of the three heads of the triceps are much less clearly developed: (i) M. triceps humeralis lateralis. It is suggested that this muscle had an extensive origin from the dorsal surface of the shaft of the humerus, as in crocodiles (*op. cit.*, T. XXVL, fig. 93, ahl°). This head appears to be indicated by numerous, low rugose striations, which extend down the dorsal surface of the distal half of the shaft, toward the intercondylar groove. This is immediately posterior to the scar for insertion of the combined tendon of the latissimus dorsi and teres major (Figs. 76A; 77, trl). (ii) M. triceps humeralis posticus. In crocodiles, this slip originates from the dorsolateral surface of the shaft, between the insertions of the teres major and subcoracoscapularis (*op. cit.*, T. XXVI, fig. 93, ahp°). In *Iguanodon* this area is available and bears numerous low striations (BMNH R6614) suggestive of muscular attachment. This slip is therefore tentatively identified on this basis (Figs. 76A, 77 trp). (iv) M. triceps humeralis medialis. The last of the three humeral heads, this slip arises from the internal edge of the humerus and wraps around onto the ventral (flexor) surface. The curvature of the humerus in *Iguanodon* seems to be moulded as if to accommodate this muscle; however, there are few indications of muscular insertion, so that its presence is largely conjectural (Figs. 76B, 77 trm).

The olecranon process of the ulna is very large and well formed in *Iguanodon*, indicating that the triceps was a powerful muscle. However, this correlation does not always hold true, since the olecranon process in crocodiles is virtually absent, despite the fact that the triceps is a large and powerful muscle.

Ventral Muscles of the forelimb

(a) M. pectoralis. This muscle undoubtedly originated, as in all vertebrates, from the ventral midline of the chest region. In *Iguanodon,* this area would have included the sternal bones and perhaps also the anterior sternal ribs. Typically, this muscle inserts along the proximolateral edge of the humerus, on the prominent deltopectoral crest. In *Iguanodon,* this crest is very well-developed and toward its distal end is thickened and bears a very rugous raised area, which faces ventrally. This most probably represents the insertional area for the pectoralis muscle, and indicates from its size that this was one of the most powerful muscles in the forelimb (Figs. 76B; 77, p).

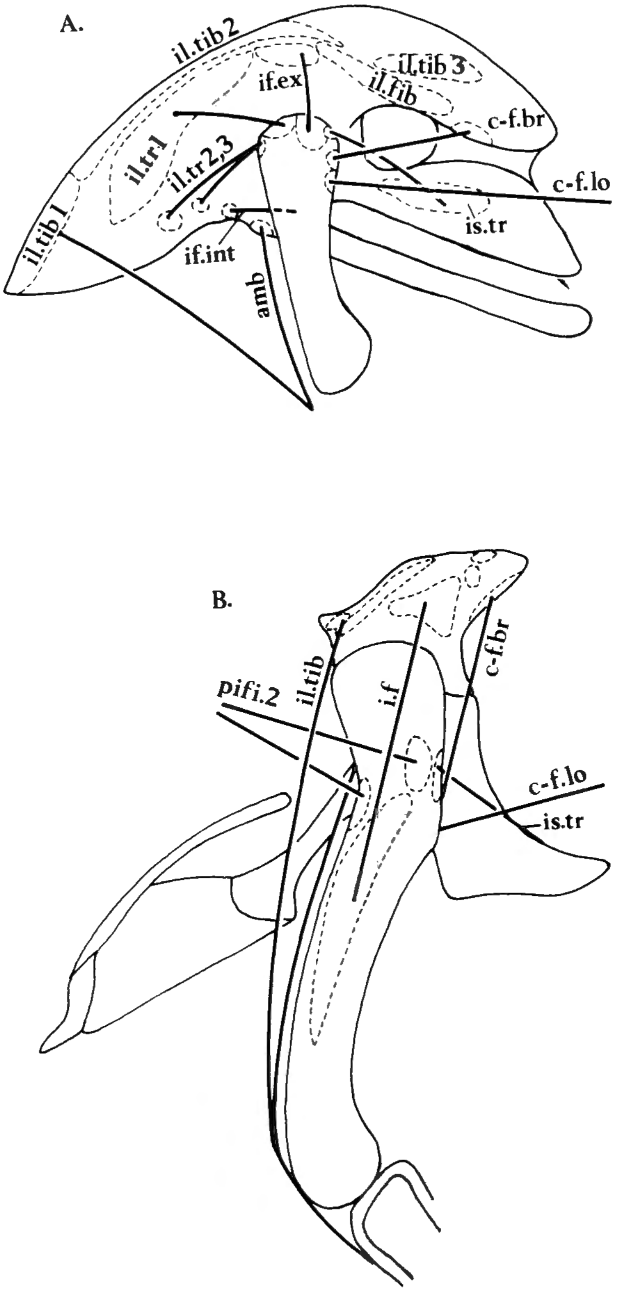
(b) M. supracoracoideus. In crocodiles, this muscle takes its origin along the lower edge of the scapula and continues onto the anterior and inner surface of the coracoid; it inserts on the delto-muscle (*op. cit.,* T. XXVI, fig. 88 sps).
In *Iguanodon,* the supracoracoideus probably took its origin from the broad depressed area beneath the scapular spine, and along the thickened anterior edge of the coracoid. Its insertion cannot be clearly defined, but was probably confined to the heavily scarred proximal part of the delto-pectoral crest, adjacent to the presumed area of insertion of the M. dorsalis scapulae (Figs. 75a, C; 77, sc).

(c) M. coracobrachialis. This arises from the extensive lateral surface of the elongate crocodilian coracoid, below the glenoid; it inserts over a broad area on the ventral surface of the humerus, just below the articular head (*op. cit.,* T. XXVI, fig. 93, obb^{o}; T. XXVII, fig. 102, cbb^{i}).
The coracoid of *Iguanodon* is considerably smaller than that of the crocodile. However, the surface of the coracoid beneath the glenoid forms a broad depressed triangle, between the biceps ridge and the posterior hook-like process. This surface bears shallow, radiating striations and in all probability it served as the site of origin for the M. coracobrachialis. It is suggested that the area of insertion of this muscle was the broad depressed area on the ventral surface of the humerus. There are no clearly defined markings, but this may perhaps indicate that this was for a large fleshy muscular insertion which would leave little tangible evidence of its presence (Figs. 75C; 79, cb).

(d) M. biceps (coraco-antebrachialis). The biceps muscles originates from a small area below and anterior to the coracoid foramen in crocodiles. It inserts in a double tendon on the proximal ends of both radius and ulna, sharing this tendon with the brachialis muscle [*op. cit.,* T. XXVII, fig. 102].
On the coracoid of *Iguanodon,* between the areas for origin of the supracoracoideus and coracobrachialis, there is a diagonal, raised rigde. This quite prominent feature is tentatively interpreted as the probable area for origin of the biceps muscle. Its insertion on the radius is however well defined, as a small area of rugose markings on the dorsal surface of the proximal end of the shaft; an additional tendon most probably inserted on to the adjacent dorsal crest of the ulna (Figs. 75C; 77, bi).

(e) M. brachialis (humero-antebrachialis inferior). In crocodiles, this muscle originates along the lateral edge of the humerus, distal to the delto-pectoral crest. This muscle inserts, with the biceps, by a pair of common tendons, on the proximal ends of the radius and ulna.

Fig. 78. – *(A) A restoration of some of the principal pelvic muscles of the chick (*Gallus*). From* Romer *(1927). (B) A restoration of some of the principal pelvic muscles of the crocodile. From* Romer *(1923). (For abbreviations see pages 371-372.)*



In *Iguanodon,* the probable area of origin of the brachialis appears to be moderately well defined (BMNH R6614). From the deltopectoral crest, a low ridge continues distally down the lateral edge of the shaft, marking the lateral extent of the origin of this muscle. Dorsal and medial to this feature, the surface of the shaft bears low relief, faint striations, which pass up the shaft medial to the deltopectoral crest. These striations are delimited medially by another low ridge, which extends diagonally across the shaft proximomedially, from a junction with the former low, lateral ridge. This second ridge serves to separate the brachials from the area of origin of the M. triceps humeralis lateralis. The precise proximal extent of this muscle cannot be determined (Fig. 76, br). The insertions of this muscle were presumably identical to those of the biceps (Figs. 76A; 77, br).

Discussion

From the evidence available, it would appear that the musculature of the pectoral girdle and forelimb of *Iguanodon,* as here interpreted, was of a reasonably conventional archosaurian pattern — conforming in most details with that seen in the living crocodile. However, it should be added that the shoulder musculature could only be interpreted through a comparison with the crocodile, so that these proposed similarities may be more apparent than real.

The primary difference between these two forms lies in the construction of the ventral part of the girdle. In crocodiles, the coracoid has the form of an elongate, broad plate, expanded at each end, and thickened along the scapular suture. Its ventromedial edge is bound to the median sternum by connective tissue and so forms a rigid brace across the chest between the scapula and sternum. In *Iguanodon* the coracoid, by contrast to that of crocodiles, is proportionately smaller and has a rounded, saucer-shaped appearance. This was not firmly bound to the sternum medially, since the latter is absent, but was most probably connected to its opposite by a flexible, cartilaginous sternal plate.

This difference in structure probably indicates that the coracobrachial (adductor) musculature of *Iguanodon* was less well developed than it is in crocodiles, since this would be expected to have dwindled along with the coracoid, from which these muscles originated. The significance of this difference in girdle construction can be related to the ancestry of the Ornithischia as a whole. At present, the fossil evidence indicates that the most primitive ornithischians ware small, agile bipeds, judging by the skeletons of the known Late Triassic ornithischians: *Lesothosaurus* (THULBORN, 1972) and the rather specialized contemporary *Heterodontosaurus* (SANTA-LUCA, 1980). In these, and all subsequent ornithopods, the coracoids are small, saucer-shaped and not braced against an ossified sternum. This alteration from the rigidly braced girdle seen in the more primitive euparkeriid thecodontians (*Euparkeria* EWER, 1965) probably occurred to permit the forelimb to perform the greater range of movements which were made possible once the forelimb had been freed of its primitive weight-supporting function. In addition, the medial bracing was no longer necessary since the stresses across the chest created during quadrupedal walking were no longer present. During the evolution of the Ornithischia, several lines appear to have reverted to quadrupedalism: the ceratopians, stegosaurs and ankylosaurs. Theoretically, at least from the line of reasoning being developed here, this reversion would present some functional problems for these forms. The forelimbs and girdles of these secondarily quadrupedal forms, having, initially evolved toward a rather "free" system as a result of the primitive condition of bipedality, would need to be reinforced secondarily so that they could once more effectively support and transmit the body weight. This implies a general improvement not only in the musculature, but also in the strength of the pectoral girdle. Indeed, several improvements can be seen in the forelimb of these quadrupedal forms. (i) The coracoid becomes proportionately much larger than in typical ornithopods; this in all probability increased the power and leverage of the various coraco-brachial muscles, which are important forelimb adductors. (ii) The coracoid and scapula show a strong tendency to fuse together, unlike the ornithopods (except *Ouranosaurus*), where they are persistently separate; this fusion naturally increases the strength of the combined scapulocoracoid to enable it to withstand the stresses created by the various shoulder muscles and also the increased thrust exerted on the glenoid by the forelimb. This thrust must have been considerable in all the quadrupedal forms, since the stegosaurs and ankylosaurs bore heavy armour and the advanced ceratopians possessed an exceptionally large, heavy skull. (iii) The usually paired sternal bones (single in some ankylosaurs) are large and well developed on either side of the ventral midline and presumably helped to reinforce the sternal region in the absence of a true sternum, as well as providing origin for the powerful pectoral muscle. In ornithopods the sternal bones, although present, are usually not very large structures. (iv) The forelimb, especially the humerus, became very massive and developed a huge delto-pectoral crest. This not only increased the strength of the forelimb, but also allowed for insertion of the larger, more powerful, shoulder muscles. In ornithopods the humerus in particular is much more slender in appearance, and is clearly not as well adapted for weight support.

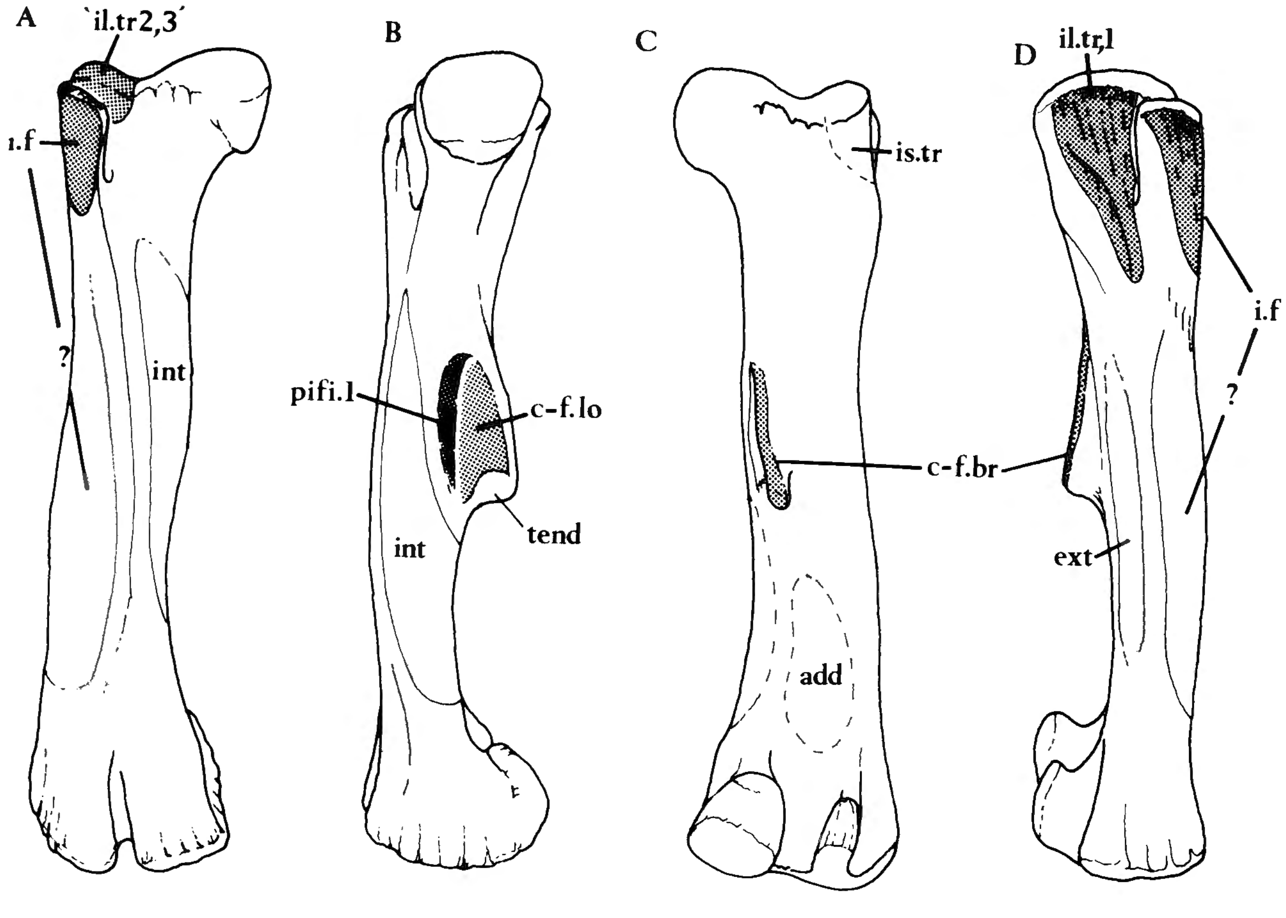
In *Iguanodon,* the forelimb and pectoral girdle are clearly not as specialized for weight support as they are in the obligate quadrupedal ornithischians. More especially, the coracoid is not much larger than in most ornithopods, and there is no fusion between the scapula and coracoid, even in the largest specimens of *I. bernissartensis.* However, despite this, there is osteological evidence which indicates that *I. bernissartensis,* in particular, was able to assume a quadrupedal stance and walk in that manner; indeed adult individuals may well have been obliged to do so. Evidently then, the musculature and construction of the shoulder region of *Iguanodon* was sufficient to permit limited quadrupedal walking. But I suspect that the coracobrachial musculature was rather weak, since the coracoid was quite small, and that in conjunction with this, the ventromedial (sternal) portion of the girdle was also weak; the latter factor has resulted in the appearance of the apparently pathological formation of an "intersternal ossification" in large adult individuals. This is most readily explicable as an adaptation for counteracting the stresses across the sternal area, which are produced when walking quadrupedally (NORMAN, 1980).

THE MUSCULATURE OF THE PELVIC GIRDLE AND HINDLIMB

The structure of the pelvic girdle and hindlimb of *Iguanodon* is similar to that of most ornithopod dinosaurs. It was in 1883 that the musculature of the pelvis of any ornithischian dinosaur was first considered. In this, and a subsequent paper (DOLLO, 1883, 1888a) the significance of the prominent 4th trochanter of the femur of *Iguanodon,* and its relationship to the caudifemoral musculature were discussed. Subsequently, several other papers dealt, rather briefly, with the structure and musculature of the dinosaurian pelvis (ABEL, 1922, 1927; HEILMANN, 1926; VON HUENE, 1907; NOPSCA, 1918). Several important papers by ROMER were directly or indirectly involved with various aspects of the musculature of the pelvis of dinosaurs. These included descriptions of the pelvic musculature of the crocodile (ROMER, 1923), saurischian dinosaurs (ROMER, 1923a) and later (ROMER, 1927) on the development of the thigh musculature of the chick. As a result of the information gained from these papers, ROMER was able to produce a rational interpretation of the musculature in ornithischian pelves (ROMER, 1927a); in particular, he provided very useful detailed "dissections" of the restored musculature of the pelvis of the ornithopod *Thescelosaurus* (*op. cit.,* figs. 15-18).

Since this classic work, the pelvic musculature of the ceratopian *Chasmosaurus* and the hadrosaur

Fig. 79. – I. atherfieldensis. *Areas of muscle insertion on the femur. (A) anterior (dorsal), (B) medial, (C) posterior (ventral), (D) lateral. (For abbreviations see pages 371-372).*



Anatosaurus have been described briefly by RUSSELL (1935) and LULL and WRIGHT (1942) respectively; both of these accounts added little, since they followed ROMER's original interpretations. Much more recently, excellent newly prepared material of *Hypsilophodon* has permitted GALTON (1969) to reconstruct the pelvic musculature of this small ornithopod in remarkable detail. In doing so, he has provided a review of the original conclusions of ROMER on the very similar ornithopod *Thescelosaurus.* While for the most part GALTON followed closely ROMER's original restorations, several modifications were made regarding some muscle insertions, and the novel suggestion was made that the ornithischian anterior pubic process not only provided support for the lateral abdominal musculature, but that it also anchored some femoral protractors. Along with this new proposal, the ornithopod abdomen was envisaged as an elongate, deep structure hanging between the legs, thereby aiding balance about the hips in these bipedal forms.

As had already been noted, the pelvic girdle of *Iguanodon* is, in most of its characters, similar to that of *Thescelosaurus* and *Hypsilophodon,* and its musculature can be derived quite readily from these more anatomically primitive forms. The reconstruction of the musculature of *Iguanodon* follows that used by ROMER. It has been derived from that of its two closest living relatives, the crocodiles and birds: the former are classified as archosaurs, as are the dinosaurs, while the latter are very probably derived from theropod dinosaurs (OSTROM, 1976; THULBORN and HAMLEY, 1981).

The following classification of pelvic muscles has been taken from ROMER (1927a).

Axial Muscles
A. Dorsal : M. dorsalis trunci and caudae
B. Ventral: M. obliquus abdominis internus, and externus
  M. transversus abdominis
  M. rectus abdominis
  M. ilio-caudalis
  M. ischio-caudalis

Appendicular Muscles
A. Dorsal:
  (i) To the lower leg:
    M. triceps femoris - M. ilio-tibialis (Including M. sartorius of birds), M. ambiens, M. femoro-tibialis
    M. ilio-fibularis
  (ii) To the femur:
    M. pubo-ischio-femoralis internus (M. ilio-femoralis internus (?) M. ilio-trochantericus II and III of birds)
    M. ilio-femoralis (M. ilio-femoralis externus, M. ilio-trochantericus I of birds)
B. Ventral:
  (i) To the lower leg:
    M. pubo-tibialis
    M. pubo-ischio-tibialis
    M. flexor tibialis externus (M. caudo-ilio-flexorius of birds)
    M. flexortibialis internus (M. ischio-flexorus of birds)
  (ii) To the femur:
    M. caudifemoralis longus and brevis (M. caudo-ilio-femoralis of birds)
    M. adductor femoralis (M. pubo-ischio-femoralis of birds)
    M. pubo-ischio-femoralis externus (M. obturator internus of birds)
    M. ischio-trochantericus (M. ischio-femoralis of birds).

The studies of both ROMER and GALTON have been used as the basis for interpreting the surface markings on several specimens of *Iguanodon.* These include ilia: BMNH R5764, R6462; pubes: BMNH R6460, R6463, R5764; IRSNB 1551; ischia: BMNH 2169, IRSNB 1551 (and others, unregistered); and femora: BMNH R5764, R6611.

Axial musculature

(a) M. dorsalis trunci and caudae. Typically, these dorsal muscles run down either side of the vertebral column, above the transverse processes and caudal ribs. Both of these blocks of muscle have areas of insertion along the medial surface of the ilium in all reptiles. In only birds, and perhaps ankylosaurs, are the M. dorsalis trunci and caudae completely separated by the ilia.

In *Iguanodon,* the M. dorsalis trunci probably inserted along the medial surface of the anterior process of the ilium (fig. 80, d. trunci); in several specimens, this area above the medial shelf bears numerous longitudinal striations which suggest such an insertion. The M. dorsalis caudae likewise probably originated from the broad, obliquely inclined, medial surface of the posterior half of the ilium, since this area bears a fine radiating pattern of low striations (Fig. 80, d. caudae).

(b) The ventral axial muscles. The complex mesh formed by the oblique and transverse lateral abdominal muscles, present in crocodiles and birds, cannot be identified with any certainty in *Iguanodon.* In recent reptiles and birds they, for the most part, arise from sheets of connective tissue and muscles bordering the abdominal cavity and thus leave little evidence of their presence on the skeleton. The only evidence which might indicate the presence of these muscles in *Iguanodon* is to be found along the ventral edge of the anterior pubic process: this is sharp-edged and bears surface markings on the medial and lateral surfaces which can be most readily explained as areas for insertion of these muscles (Fig. 80, lat. abd). In *Hypsilophodon,* GALTON (1969) found evidence which suggested that the lateral abdominal muscles inserted along the ventral edge of the anterior pubic

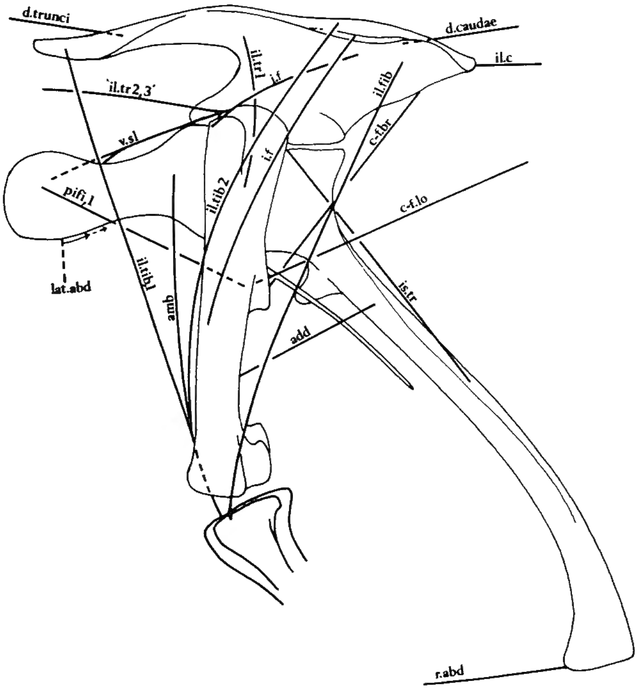


Fig. 80. – I. atherfieldensis. *Restoration of the lines of action of the principal pelvic muscles. (For abbreviations see pages 371-372).*

and posterior pubic processes. It would seem logical that a similar arrangement existed in *Iguanodon,* in order to support the undoubtedly bulky abdomen. If, as seems likely, this was the case, then these muscles would have transferred their origins from the distal end of the posterior pubic rod on to the adjacent ischium, which is considerably longer and more robust.

The M. rectus abdominis is a very large median sheet of muscle, which in reptiles originates from the posterior edge of the sternal plate and the distal ends of the thoracic ribs. It inserts along the posterior edge of the pubis and the surface of the M. ischio-caudalis. In birds, this muscle has a similar disposition, arising along the posterior margin of the sternum and inserting on the distal ends of the pubes and the interpubic ligament (GEORGE and BERGER, 1966). In *Iguanodon,* although the origins of this muscle are uncertain from the evidence available, it seems likely that a similar muscle was present, and arose from the anterior sternal region. Its insertion would have been on the large distal foot of the ischium (Fig. 80, r. abd); the post-pubic rod was considerably shorter than the ischium and was in any case far too slender to have supported what must have been a very long and powerful muscle.

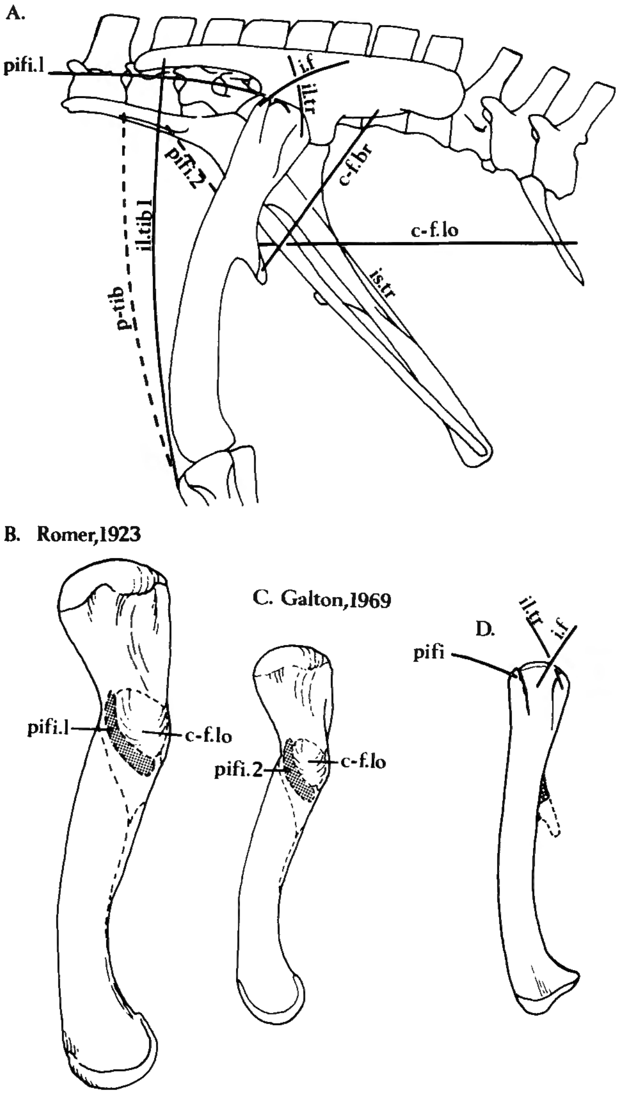
The M. ilio-caudalis arises from part of the posterodorsal edge of the ilium in crocodiles, and inserts on the undersides of the caudal ribs and centre of the anterior caudal vertebrae. The situation was probably very similar in *Iguanodon* (Fig. 80, il. c), since the hind end of the ilium is thickened and rugose, and the anterior caudal ribs are noticeably broad, with rugose dorsal and ventral surfaces (IRSNB 1561).

The M. ischio-caudalis arises from the posteroexternal angle of the ischium in crocodiles, and inserts on the distal ends of the chevrons. In *Iguanodon,* the corresponding muscle probably arose from the distal, footed end of the ischial symphysis and likewise inserted on the distal ends of the chevrons.

Appendicular Musculature: Dorsal

(a) M. triceps femoris. Collectively, this group of muscles form the major extensor of the lower leg. The group consists of three muscles. (i) M. iliotibialis. This originates along the dorsal margin of the ilium, and is divided into three parts in crocodiles and birds (ROMER, 1927). These all insert, via a common patellar tendon, on to the cnemial crest

Fig. 81. – *Pelvic and limb mucles of: (A)* Hypsilophodon *(after GALTON, 1969), (B) crocodile femur (after ROMER, 1923), (C) crocodile femur (after GALTON, 1969), (D)* Hypsilophodon *femur (after GALTON, 1975).*



of the tibia. In *Iguanodon,* the dorsal margin of the ilium bears a very prominent longitudinal scarred edge, which is interpreted as the main area of origin of this muscle. On the anterior process, there is an area which was most probably for a separate portion, the M. ilio-tibialis I (equivalent to the "sartorius" of birds - Fig. 80 il. tib. 1); this is separated from the main body of the ilio-tibialis (the M. iliotibialis II - Fig. 80, il. tib 2) by a line running diagonally across the anterior process. A very similar arrangement was first noted in *Thescelosaurus* and hadrosaurs by ROMER (1927). (ii) M. ambiens. As ROMER was able to show, this muscle always originates from the proximal preacetabular region of the pubis. Indeed ROMER (1927a, fig. 9) illustrated the pubis of a specimen of *Iguanodon* (BMNH 2194) which showed such an area bearing rugose markings as if for origin of this muscle. This muscle would have inserted on the cnemial crest of the tibia (Fig. 80, amb). The presence of an ambiens tendon that crossed the distal end of the femur, to insert on the external head of M. gastrocnemius, has been proposed by both ROMER and GALTON, since this tendon is present in both crocodiles and birds. (iii) M. femoro-tibialis. In crocodiles and birds this muscle tends to develop a number of heads, filling all the available space on the femur. ROMER (*op. cit.*) identified three possible areas of origin for this muscle in *Thescelosaurus,* and an exactly similar situation was described by GALTON for *Hypsilophodon.* In the latter the origins of the three heads of this muscle were described and formally identified as M. femoro-tibialis 1, 2 and 3: equivalent in position to M. femoro-tibialis (Vastus) lateralis, M. femoro-tibialis (Vastus) medialis, and M. femor-tibialis (Vastus) internus respectively, in birds (CRACRAFT, 1976; OWRE, 1967). In *Iguanodon,* a more or less similar arrangement seems to have been present; areas for the origin of at least two of the three heads of this muscle have been tentatively identified. M. femor-tibialis seems to have originated from a heavily scarred area on the lateral surface of the femur (Fig. 79, ext) — in an almost exactly similar position to that of the M. femoro-tibialis externus in crocodiles (ROMER, 1923). This origin is particularly well shown on BMNH R6610, as a heavily scarred, slightly depressed, elongate area on the lateral surface of the shaft. Anterior (dorsal) to this, there is a smoother area of the shaft, which was probably occupied by a portion of the M. ilio-femoralis externus. M. femoro-tibialis 2 covers the majority of the anteromedial surface of the femoral shaft, and is bounded laterally by a prominent diagonal ridge, which runs across the length of the shaft, from the base of the lesser trochanter to the medial (tibial) condyle (Fig. 79 A, B, int). It was presumably limited medially by the 4th trochanter and associated structures. M. femoro-tibialis 3 cannot be identified with any certainty in *Iguanodon,* but probably occupied the posteromedial area of the shaft, beneath the 4th trochanter; in all probability, these last two divisions (M. femoro-tibialis 2 and 3) formed a single muscle, equivalent to the crocodilian M. femorotibialis internus.

In summary, from the surface markings on the femur of *Iguanodon* it would seem that the M. femoro-tibialis had a "crocodilian" rather than an "avian" construction as has been suggested in the more primitive forms *Thescelosaurus* and *Hypsilophodon.*

(b) M. ilio-fibularis. This muscle was only tentatively identified in both *Thescelosaurus* and *Hypsilophodon,* since no clear indication of a muscular origin is preserved. However LULL and WRIGHT (1942) proposed an origin on the ilia of hadrosaurs, immediately behind the "antitrochanter", and both *Thescelosaurus* and *Hypsilophodon* (GALTON, 1969) were restored with this muscle in an homologous position. In *Iguanodon,* as with the latter forms, there is no clear site or origin of this muscle, and its origin is placed by default on the posterolateral corner of the iliac blade (Fig. 80, il. fib.). This muscle would have inserted on the lateral surface of the proximal end of the fibula.

(c) M. pubo-ischio-femoralis internus. In crocodiles, this muscle consists of two parts, the M. puboischio-femoralis internus 1 and 2. The former arises from the medial surface of the ilium and the ventral surfaces of the sacral ribs (ROMER, 1923: pl. XX, fig. 2; pl. XXIV, fig. 2). From this origin it wraps around the anterior edge of the ilio-pubis to insert on the medial side of the shaft of the femur, adjacent to the area for insertion of the M. caudi-femoralis longus (*op. cit.,* pl. XXV). In birds, what appears to be the homologous muscle — M. iliofemoralis internus — arises from the anteroventral edge of the ilium and inserts on the medial surface of the shaft of the femur below the head (Fig. 78A, if. int). In both these instances, these muscles serve to protract the femur.

The second part of this muscle, the M. pubo-ischiofemoralis internus 2, arises in crocodiles from the ventral surface of the transverse processes of the posterior dorsal vertebrae and passes diagonally backward and downward to insert at two sites on the lateral surface of the proximal end of femur (ROMER, 1923: pl. XX, fig. 1; pl. XXV). In birds the homologue of this muscle is less obvious. I consider it most probable that it is the avian iliotrochanterici 2 and 3 (ROMER, 1927). These muscles arise from the anteroventral margin of the ilium, above and forward of the M. ilio-femoralis internus, and insert via a common tendon on the proximal end of the shaft of the femur (Fig. 78, il. tr. 2, 3). However, this homology is doubtful, since the reptilian muscle serves to protract the femur, while the avian muscles retract the femur — since the latter insert above the axis of rotation of the femoral head.

Discussion

Both ROMER (1927a) and GALTON (1969) considered the presence of the M. pubo-ischio-femoralis internus (M. ilio-femoralis internus) in *Thescelosaurus* and *Hypsilophodon* respectively, and came to slightly different conclusions. ROMER concluded that in *Thescelosaurus,* the avian muscle M. Ilio-femoralis internus was present. This muscle, he proposed, had an origin similar to that of the crocodilian M. pubo-ischio-femoralis internus 2 i.e. from the transverse processes of the posterior dorsal vertebrae; however its insertion was placed on the greater trochanter. In this position, this muscle, must have changed from a femoral protractor to a retractor. This is a rather fundamental change for a typical reptilian and avian femoral protractor, and therefore seems at least questionable from a functional point of view.

GALTON (1969) in his re-interpretation of this musculature came to rather similar conclusions to ROMER. However, the better preserved material of *Hypsilophodon* allowed additional conclusions to be drawn. The lateral surface of the greater trochanter of the femur in *Hypsilophodon* has two quite distinct muscle insertions, separated by a sinuous vertical ridge. Initially (*op. cit.,* p. 17) he concluded that the "M. pubo-ischio-femoralis internus 1", inserted on the posterior of these two areas, however, later (*op. cit.,* p. 37, fig. 1, 4, 9) this insertion was transferred to the anterior surface on the greater trochanter — in agreement with ROMER's original restorations. In addition, GALTON suggested that, since this muscle ran from its origin on the posterior dorsal vertebrae, over the anterior pubic process and on to the greater trochanter, it was reasonable to suppose that a ventral slip, the "M. pubo-ischio-femoralis internus 2" gained an origin from the lateral surface of the anterior pubic process and inserted farther down the shaft, below the head of the femur. The presence of this latter slip, and/or the M. pubo-tibialis, explained the prominent surface markings on the lateral surface of the anterior pubic process in *Hypsilophodon.* Later, GALTON (1975) appears to have altered his opinions concerning the insertion of the main body of the M. pubo-ischio-femoralis internus. This he transferred to the lesser trochanter of the femur (Fig. 81, D); unfortunately the reasons for this change were not explained.

The restoration of the main body of the M. pubo-ischio-femoralis internus inserting on either the lesser or greater trochanter presents the same functional problems noted above in ROMER's restoration. In addition, the nomenclature used by GALTON (1969) is rather confusing. The main portion of this muscle, as restored by GALTON, arose from the centra of the posterior dorsal vertebrae and inserted on the greater trochanter. This corresponds very closely with the M. pubo-ischio-femoralis internus 2 of crocodiles. However this muscle was described as the M. pubo-ischio-femoralis internus 2, but this was given an insertion which is more typical of the M. pubo-ischio-femoralis internus 1 of crocodiles (M. ilio-femoralis internus of birds). Indeed, ROMER's and GALTON's nomenclature are obviously at variance, even though GALTON used ROMER's original accounts (compare Figs. 81B, C). Clearly then, the published accounts of the structure of the M. pubo-ischio-femoralis internus do not provide a completely unambiguous account of this important muscle complex.

One of the most immediate problems concerning this muscle in ornithischians is the obviously fundamental change in function that is proposed: from protracting the femur in crocodiles and birds, to that of retracting the femur in ornithischians. In this connection, there are two small muscles present in the avian pelvis which have not so far been considered in any muscular restorations. These are two heads of the M. ilio-trochantericus, II and III. In birds, they arise from the anteroventral edge of the ilium and insert together on the anteroexternal corner of the greater trochanter of the femur (Fig. 78A). These muscles have a very similar line of action to that of the "M. pubo-ischio-femoralis internus 1" of GALTON and the "M. ilio-femoralis internus" of ROMER, as they would likewise have retracted the femur. I therefore consider it possible that in the ornithischian pelvis, the muscle(s) which arose from the ventral surfaces of the transverse processes of the posterior dorsal vertebrae, and inserted on the greater trochanter of the femur were more functionally homologous with the M. ilio-trochantericus (pars II and III) of the avian pelvis, than with any other crocodilian or avian muscle. As ROMER pointed out (1923b), the ilia of ornithischians and birds differ in that the pre-acetabular extension is formed by the dorsal spine alone in the former, while in the latter it involves the entire front edge of the blade. According to ROMER, this difference was a result of the ventral expansion of the dorsal spine of the avian ilium. However, this hypothesis seems less parsimonius, in view of the apparent theropod origin of birds (OSTROM, 1976). Thus in ornithischians dinosaurs, the area of the iliac blade normally occupied by the heads of the ilio-trochanterici is absent, so that an origin of these heads more anteromedially, from the sides of the posterior dorsal vertebrae, or ventral surface of the anterior process, seems most probable.

There still remains the question of whether or not a portion of the true femoral protractor part of the M. pubo-ischio-femoralis internus remained.

A thorough search through the collections of the British Museum (Nat. Hist.) has failed to reveal any femora which show obvious areas for insertion an equivalent of the crocodilian M. pubo-ischio-femoralis internus 2. However, it does seem likely that a slip, equivalent to the M. pubo-ischio-femoralis internus 1 (M. ilio-femoralis internus of birds) was indeed present. In crocodiles, this muscle inserts on the medial surface of the shaft of the femur, adjacent to the large depression for the tendon of the M. caudi-femoralis longus (Fig. 81B); it has a similar insertion on the medial side of the shaft of the femur in birds. In *Iguanodon,* this area of insertion is well-defined and lies on the medial side of the shaft of the femur, at the base of the prominent 4th trochanter (Fig. 79B, pifi 1). The adjacent area on the medial surface of this trochanter was for insertion of the M. caudi-femoralis longus — as in crocodiles. The surface markings on this area of insertion are predominantly diagonal, in an anterodorsal direction (toward the anterior pubic process). The origin of this muscle is not clearly marked in *Iguanodon,* but can be deduced with a reasonable degree of confidence. In crocodiles, this muscle arises from the medial (internal) surface of the ilium, and wraps around the anterior edge of the pelvic blade, before descending steeply to its femoral insertion. In birds, this muscle (M. ilio-femoralis internus) arises from the proximal area of the ventral surface of the pre-acetabular blade, close to the M. ambiens origin. In ornithischians (*Hypsilophodon*) GALTON demonstrated that the lateral surface of the anterior pubic process bore prominent surface markings, suggestive of muscle insertion; these, he suggested, could have been for either a ventral slip of the M. pubo-ischio-femoralis internus ("1") or alternatively for the M. pubo-tibialis. As the M. pubo-tibialis is absent in both birds and crocodilians, its presence would seem to be improbable in ornithischian dinosaurs — the implication being that this muscle was absent in the archosaurs generally. It is suggested that a portion of the M. pubo-ischio-femoralis internus took its origin from the lateral surface of the anterior pubic process. In *Iguanodon,* the lateral surface of the anterior pubic process bears numerous radiating striations, which could seem to indicate the origin of such a muscle (Fig. 80 pifi. 1). This muscle is very favourably placed as a femoral protractor, and would greatly augment the action of the M. ilio-tibialis 1 and the M. ilio-femoralis externus, the only other significant femoral protractors.

Apart from the areas for origin of the M. ambiens and the M. pubo-ischio-femoralis internus on the anterior pubic process of *Iguanodon,* there also appears to be another area on the dorsomedial edge of this process; this is especially well shown on two pubes (BMNH R6460, R6463). This muscle, which may have been a ventral slip of the M. Ilio-trochantericus II and III or (less probably) a slip of the M. pubo-ischio-femoralis internus, wrapped around the embayed dorsal margin of the anterior pubic process and passed backwards to insert on the greater trochanter (Fig. 80, v. sl). From such a position, this proposed slip would have been able to exert a turning couple to retract the femur that would have been more effective than that of the dorsal part of this muscle, especially when the femur was fully protracted.

(d) M. ilio-femoralis. ROMER (1927a) proposed that ornithopods possessed the avian subdivisions of this muscle: an anterior portion, the M. ilio-trochantericus 1, and a posterior portion, the M. ilio-femoralis externus. On the basis of ROMER's work, GALTON proposed a similar arrangement in the pelvis of *Hypsilophodon.* (i) M. ilio-trochantericus 1. This muscle arose, as in *Thescelosaurus,* from the lateral surface of the ilium, anterior to the area occupied by the M. ilio-femoralis externus. On the basis of ROMER's work, GALTON proposed a similar arrangement in the pelvis of *Hypsilophodon.* (i) M. ilio-trochantericus 1. This muscle arose, as in *Thescelosaurus,* from the lateral surface of the ilium, anterior to the area occupied by the M. ilio-femoralis externus. In *Iguanodon,* this muscle arose from a slightly depressed area beneath the thickened dorsal edge of the ilium. This area extends backwards to above the middle of the acetabulum, and forwards along the anterior process; it is quite well demarcated on an ilium (BMNH R6462, Fig. 80, il. tr. 1). The area of insertion of this muscle is uncertain but, judging by the situation in birds (Fig. 78A), it was probably on the lateral surface of the greater trochanter, posterior to the lesser trochanter (Fig. 79D). In several femora this surface is heavily marked by a fan-like arrangement of striations, which spread out toward the dorsal edge of the greater trochanter from a pit-like depression, adjacent to the base of the lesser trochanter. (ii) M. ilio-femoralis externus. ROMER deduced that this muscle probably originated from the "antitrochanter", a prominent swollen boss on the lateral surface of the ilium in hadrosaurs. Consequently, he restored this muscle as originating from an homologous area on the ilium of *Thescelosaurus;* he suggested that its insertion was on the lesser trochanter of the femur. The reasons for this are unclear, as ROMER (1927a) suggested that this insertion on the lesser trochanter correspond to that in saurischians (ROMER, 1923a). However, in his work on saurischians, the M. ilio-femoralis was reconstructed inserting, as in crocodiles, on the anteroexternal surface of the femoral shaft, and the M. pubo-ischio-femoralis internus 2 was inserted on the lesser trochanter (*op. cit.,* figs. 5, 6). In birds, the M. ilio-femoralis externus arises from the ilium above and slightly posterior to the acetabulum, and inserts on the posteroexternal surface of the greater trochanter (ROMER, 1927, fig. 5a).

In *Iguanodon,* the arrangement of this muscle is by no means clear. It probably arose from the iliac blade, above and behind the acetabulum, as in both crocodiles and birds. As ROMER suggested, the muscle most probably inserted on the lesser trochanter of the femur (Fig. 80, if; Fig. 79, A, D). There are two main reasons for this proposition. Firstly, the striations on the surface of the lesser trochanter are directed towards the presumed area of insertion of this muscle, and may indeed reflect the primary line of action of this muscle. Secondly, such an insertion may help to explain the development of the lesser trochanter in dinosaurs. The lesser trochanter arises from the anteroexternal surface of the femur, and in most cases terminates at a level slightly below that of the greater trochanter. The M. ilio-femoralis externus seems to be the only muscle that can possibly gain on advantage from this arrangement. In this case, the lesser trochanter increases the moment of the force which this muscle can exert to protract the femur. The formation of this process may well have been essential in the early ornithischians which, because the anterior pubic process was very short (CHARIG, 1972; SANTA-LUCA, 1980) and clearly lacked the principal pubic femoral protrators; they must have relied on the M. ilio-tibialis 1, and the rather mechanically inefficient M. pubo-femoralis internus 1, which was wrapped around the rudimentary anterior pubic process. This could explain the great development of the lesser trochanter in forms such as *Lesothosaurus* (THULBORN, 1972), and *Heterodontosaurus* (SANTA-LUCA, 1980) and its gradual diminution in the Ornithopoda culminating with the hadrosaurs, in which the lesser trochanter is much thinner and splint like. In these latter forms, protraction was presumably greatly augmented by the musculature of the hypertrophied anterior pubic process.

In addition to the insertion of this muscle on the lesser trochanter there is a very well defined muscle scar on the lateral surface of the femoral shaft, directly beneath the lesser trochanter. At first this area was supposed to be for a head of the femortibial complex. However, its position on the shaft, separating the two principal (internal and external) heads of the femoro-tibialis — as in crocodiles — and its unusually strong development, suggested otherwise. This area may have provided for insertion of another portion of the M. ilio-femoralis externus, which corresponded very closely with that for the M. ilio-femoralis in crocodiles (ROMER, 1923).

Appendicular Musculature: Ventral

(a) M. pubo-tibialis. Since this muscle is absent in both crocodiles and birds, it seems probable that it is absent in all archosaurs.

(b) M. pubo-ischio-tibialis. This muscle is reduced to a slip in crocodiles, and is lost in birds, as was probably the case in ornithischians.

(c) M. flexor tibialis internus. In crocodilians there are three heads to this muscle; on the medial surface of the posteroventral corner of the ischium, on the ventral margin of the acetabulum, and on the posterior corner of the ilium. These insert via a double tendon on the proximal end of the tibia and external head of the M. gastrocnemius. The M. ischio-flexorius is the only part present in birds originating near the middle of the lateral surface of the ischium. ROMER proposed a typically avian arrangement in *Thescelosaurus*; this muscle, it was suggested, originated from a small projection on the dorsolateral surface of the ischium. No indication of an homologous projection could be found on any ischia of *Iguanodon.*

(d) M. flexor-tibialis externus. This muscle arises from the posterior corner of the ilium in crocodiles, and from the caudal vertebrae in avians — as the M. caudo-ilio-flexorius. It inserts on the medial surface of the head of the tibia. This muscle, identified as the M. ilio-flexorius, was restored by ROMER in *Thescelosaurus* but its area of origin cannot be identified in *Iguanodon.*

(e) M. caudi-femoralis longus. This muscle probably originated from the sides and ventral surfaces of the anterior caudal vertebrae, as it does in crocodiles; in these forms, it inserted by a thick tendon on to the medial surface of the femoral trochanter. This tendon is connected to the head of the fibula by a thin tendon present also in birds and lizards. In *Iguanodon,* the 4th trochanter of the femur is very large and of the crested type. Its medial surface is very rugose and corresponds to the area of insertion of this large muscle in crocodiles (Figs. 79B; 80c-f. lo). This area is therefore identified as the area of insertion of the M. caudi-femoralis longus; it is bounded anteromedially by the probable area for insertion of the M. pubo-ischio-femoralis internus 1.

(f) M. caudi-femoralis brevis. In crocodiles, this muscle arises mainly from the posteroventral surface of the ilium, and inserts along the elevated surface of the femoral trochanter, adjacent to the depression for the M. caudi-femoralis longus. In *Iguanodon,* as was suggested for *Hypsilophodon* by GALTON (1969), this muscle arose from the brevis shelf and adjacent ventral surfaces of the sacral ribs. It inserted along the elevated crest of the 4th trochanter of the femur (Figs. 79C; 80, c-f. br). As pointed out by GALTON, the elevated 4th trochanter improved the leverage exerted by the M. caudi-femoralis brevis during the initial phases of femoral retraction (*op. cit.,* p. 41).

(g) M. adductor femoralis. This muscle has two heads, that originate on the outer surface of the ischium and insert on the ventral surface of the femur in crocodiles. ROMER (1927a) restored *Thescelosaurus* with two heads of this muscle on the shaft of the ischium. In *Iguanodon,* there is a very well marked area on the lateral surface of the shaft of the ischium. This appears to have been the area of origin of a large single-headed M. adductor femoralis. Its area of insertion is not clearly defined but was probably on the distal ventral (posterior) surface of the shaft of the femus, below the 4th trochanter (Figs. 79C; 80, add).

(h) M. pubo-ischio-femoralis externus. This muscle in ornithischians is probably more correctly equivalent to the M. obturator internus of birds. Both ROMER and GALTON identified this muscle as arising from the adjacent areas of, and ligaments between, the posterior pubic rod and ischial shaft, in *Thescelosaurus* and *Hypsilophodon.* In *Iguanodon,* the posterior pubic rod had undergone substantial reduction compared to those of hypsilophodontids and this probably reflects a similar decrease in size of this muscle. It is conceivable that this muscle simply transferred its origin to the ischium distally, but no muscle scars have been discovered which prove that such was the case.

(i) M. ischio-trochantericus. This is a relatively small muscle in crocodiles, which arises from the posteromedial surface of the ischium. Its insertion is by a tendon on the outer dorsal edge of the femur, close to its head. In birds, this muscle originates from the lateral surface of the ischium, but has a similar insertion to the crocodile. In *Iguanodon,* this muscle probably arose from the posterior edge of the shaft of the ischium behind a low ridge marking the posterior limit of the M. adductor femorais. It probably inserted in the usual position on the posterior (ventral) edge of the freater trochanter of the femur (Figs. 79C; 80, is. tr).

Additional comments

(a) *M. pubo-ischio-femoralis internus.* GALTON's (1975) restoration of the femoral muscles of *Hypsilophodon* (Fig. 81D), showed the M. pubo-ischio-femoralis internus inserting upon the lesser trochanter. Unfortunately, no reasons for the change (from an insertion on the greater trochanter) were given, but I think there are two considerations which suggest that this new restoration is unlikely. Firstly, there seems to be no functional advantage in this change; the lesser trochanter is at the same level as, or slightly lower than, the greater trochanter; therefore no extra leverage would have resulted from this new position. Secondly, the surface markings on the lesser trochanter are orientated posterodorsally, toward the dorsal margin of the iliac blade, in all ornithopod femora so far seen; this seems to be a fair — albeit not conclusive — indication of the direction of the principal line of action of the muscle inserting on this process (the M. ilio-femoralis externus).

(b) *Muscles associated with the 4th trochanter.* DOLLO (1883, 1888a) first demonstrated that the 4th trochanter of the femur in *Iguanodon* was the area for insertion of the caudi-femoral muscles. This was agreed by ROMER (1927a), and not until JANENSCH (1955) was any more consideration given to this particular structure. JANENSCH (*op. cit.*) noted that in the ornithopod *Dysalotosaurus* the 4the trochanter possessed, near its base, a prominent concave depression. This, he suggested, was too large to have been for a muscle insertion and he proposed that it housed a mucous gland. However, JANENSCH did point out that this depression, which was dorsal to the 4th trochanter in *Dysalotosaurus,* corresponds quite closely with a small elongate depression, adjacent to the depression which accommodates the M. caudi-femoralis longus on the crocodilian femur (see Fig. 81B). This smaller area was occupied by the M. pubo-ischio-femoralis internus 1, and JANENSCH suggested that the prominent depression may have accommodated this muscle in *Dysalotosaurus.* GALTON (1969) reconsidered the previous interpretations of the probable function of the 4th trochanter and its associated structures in *Hypsilophodon* and other ornithopods. He rejected JANENSCH's mucous gland interpretation because the depression which was supposed to have housed the gland was strongly marked by muscle scars and concluded that this depression was for insertion of a large tendon of the powerful M. caudi-femoralis Longus, instead of the M. pubo-ischio-femoralis. JANENSCH's primary reason for suggesting that the latter muscle inserted on this area was that it was so widely separated from the 4th trochanter in *Dysalotosaurus.* However, GALTON considered that the unusual position of this depression in *Dysalotosaurus* and *Dryosaurus* was "secondary" and that it was equivalent to the large depression at the base of the 4th trochanter in crocodilians.

In view of the proposal above that the M. pubo-ischio-femoralis internus 1 was well developed and inserted along the anterior edge of the depression at the base of the 4th trochanter in *Iguanodon,* this area was reinvestigated in *Hypsilophodon* and *Dysalotosaurus.*

In *Hypsilophodon,* the 4th trochanter and associated structures are well preserved in one particular specimen, BMNH R193 (GALTON, 1969, figs. 8, 9, 10). On the lateral surface of the large, pendent, 4th trochanter there is a very clearly defined area of insertion which was most probably for the

M. caudi-femoralis brevis. This area is separated, as in *Iguanodon,* by a sharp, sinuous edge, from the medial surface. Towards the tip of the trochanter, the latter bears a depressed area for a (?) gastrocnemial tendon. Proximal to this area, there is another slightly raised, rugose surface; this was interpreted as an additional area of insertion of the M. caudi-femoralis brevis (*op. cit.,* fig. 10, D). However, this might equally well be interpreted as the area of insertion of the M. caudi-femoralis longus since it is separated from that of the M. caudi-femoralis brevis by a sharp ridge, and it corresponds in position to a similar scar on the 4th trochanter of *Iguanodon* and *Dysalotosaurus.* At the base of, and anterior to, the 4th trochanter, there is a large depressed area of scarred bone which was interpreted by GALTON as the area of insertion of the M. caudi-femoralis longus. This depression is shaped rather like a thumbprint, and is deepest at its ventral edge and becomes shallower dorsally. The muscle scars do no yield any definite evidence upon the line of action of the muscle which acted on this area. In posterior view, the 4th trochanter curves medially, so that this muscle scar is not visible, indicating a curved, but by no means impractical, path for the caudi-femoral muscle. In proximomedial view, along the approximate path of the M. pubo-ischio-femoralis internus 1, the depressed muscle scar presents a large area for insertion, bounded by the prominent ventral edge of the depression.

In *Dysalotosaurus,* the 4th trochanter and associated areas are moderately well preserved in one specimen BMNH R8350. Although the major part of the distal end of the 4th trochanter is missing, the area of insertion of the M. caudi-femoralis brevis is discernible on the lateral surface of the trochanteric crest, as in *Hypsilophodon.* The medial surface of the 4th trochanter is better preserved and exhibits very well developed striations and scarring. This appears to correspond to the scarring found on the medial surface of the 4th trochanter in *Iguanodon* and interpreted as the area of insertion of the M. caudi-femoralis longus. Separated from the 4th trochanter by a short interval is a very deep depression, which is heavily scarred. This depression possesses a steep ventral (distal) edge and becomes progressively shallower dorsally (proximally) as it merges with the rounded shaft. In posterior view, the medial edge of this depression can be seen, and in proximomedial view, the whole depression can be seen, bounded by the steep curved distal edge. Many of the striations around the proximal edge of the depression radiate outwards and upwards (proximally) from the depression.

In conclusion, it would appear that the evidence concerning the detailed musculature on, and around the base of, the 4th trochanter is consistent with that in crocodilians, the M. caudi-femoralis brevis probably inserted on the external surface of the distal part of the 4th trochanter. If GALTON's proposal that the 4th trochanter became a prominent structure in order to increase the lever arm of the M. caudi-femoralis brevis during initial phases of femoral retraction is correct, then this muscle would *not* have been expected to extend on to the medial side of the base of the 4th trochanter in *Hypsilophodon,* since its mechanical advantage would be considerably less in this position. M. caudi-femoralis longus probably inserted on the medial surface of the 4th trochanter, as in crocodilians, so that these two muscles were separated by the trochanteric crest. This certainly seems to have been the case in *Iguanodon* and perhaps also in *Dysalotosaurus* and *Hypsilophodon.* However, there remains the problem of the depression near the base of the 4th trochanter. In *Iguanodon,* this area bears well-developed striations which are directed toward the anterior process, the presumed area of origin of the M. pubo-ischio-femoralis internus, the latter being an important ornithopod protractor muscle. In *Hypsilophodon* and *Dysalotosaurus,* the equivalent area is differentiated as a large concave area adjacent to the 4th trochanter. The size and definition of this depression is suggestive of a very powerful muscle, possibly the M. caudi-femoralis longus of GALTON. However, its orientation, shape and positioning in *Dysalotosaurus* are suggestive of its being for the M. pubo-ischio-femoralis internus 1. If this is correct, the large size of this muscle scar may confirm the importance of this muscle in femoral protraction and adduction.

(c) *The functional significance of the anterior pubic process.* It also seems necessary to pass a few comments on the evolution and functional significance of the ornithischian anterior pubic process. CHARIG (1972) very perceptively proposed that the ornithischian pubis had undergone a backward rotation in response to a change in limb posture, which took place among early archosaurs: from the "semi-erect" condition, shown by living crocodilians when walking, to the "fully-erect" state, with the limbs held vertically beneath the body (as seen in some advanced thecodontians, all dinosaurs and birds). The consequence of this change in posture of the hind limb, it was suggested, was that the typically anteroventrally directed pubis was unable to act as an origin for effective pubic hind limb protractor muscles. This "problem" was solved in several ways: (i) by the development of bipedality in theropod saurischian forms, thereby swinging the pubis forwards and upwards into a more mechanically favourable position; (ii) by the development of a long anterior process of the ilium in ornithischians. This process permitted hind limb protraction to be accomplished by an anterior division of the M. ilio-tibialis, as accurs in birds. As a result of this change, the functionally redundant pubis swung backwards to lie against the ischium in the typical (primitive) ornitischian state; and (iii) by limitation of femoral swing in sauropodomorphs.

The primitive ornithischian condition with the backwardly directed pubis is shown in several early ornithischians: *Lesothosaurus* (THULBORN, 1972) and *Heterodontosaurus* (SANTA-LUCA, 1980) and *Scelidosaurus* (CHARIG, 1972). Coupled with this character is the presence of a long anterior process on the ilium, and also a rudimentary anterior pubic process. Many later ornithischians (although not all) developed a large anterior ramus to the pubis. In the less anatomically specialised forms, such as the hypsilophodontids, this ramus is narrow and rod-like, while in the larger and more specialized forms (iguanodontids, hadrosaurids) the process becomes deeper and plate-like. The secondary development of an anterior pubic ramus appears, because of its position, to be a functional replacement for the typical reptilian pubis. However, the reasons for its development and persistent absence in some ornithischian lineages are still puzzling. CHARIG (*op. cit.*, p. 140) noted these problems. He suggested that the anterior pubic process may have resulted from a concomitant change to bipedality; this resulted in a less effective line of action of the anterior portion of the ilio-tibialis muscle, since the anterior process of the ilium would have swung upwards, away from the hindlimb. As a result, the anterior pubic process evolved to provide increased leverage for a new protractor muscle — suggested as derivable from the ambiens muscle. However, CHARIG was unable to reconcile this theory with the presence of an anterior pubic process in the large quadrupedal ceratopians and stegosaurs, and suggested that the development of this process may alternatively have been related to a factor such as large size in ornithischians.

CHARIG's first explanation for the functional reasons behind the development of the anterior pubic process is very elegant, and it can be expanded in order to explain the situation in the rather anomalous stegosaurs and ceratopians. The effect of size seems unlikely to have governed the development of the anterior pubic process, as the large ankylosaurs appear to be able to manage without one, as does the large individual of *Scelidosaurus* (total length approximately 3 m) yet small ornithopods possess long anterior pubic processes (*Hypsilophodon*). It could be argued that the (?) supporting function of the anterior pubic process had been replaced by the huge overhanging iliac blades in the ankylosaurs, but similar broadly expanded ilia are present in ceratopians and stegosaurs.

Primitive ornithischans. In these forms the anterior pubic process is short, but never absent; most probably, it served as the area of origin for the M. ambiens and the M. pubo-ischio-femoralis internus 1. The latter had migrated from its primitive position on the internal surface of the ilium, to the dorsal and lateral surfaces of the adjacent anterior pubic process. In this connection, it is interesting to note that small tubercles have been noted on the lateral surface of the prepubic process of *Heterodontosaurus* which were tentatively identified as origins for heads of the M. pubo-ischio-femoralis internus (SANTA-LUCA, *et al.*, 1976). The very well-preserved pubes of *Scelidosaurus* (BMNH R6704, R1111) and these show a quite rugose dorsal edge to the anterior ramus, and a lightly striated lateral surface; which are directed toward the femoral shaft. It seems likely therefore that, even though the principal protractor of the femur was the M. ilio-tibialis 1 in promitive forms, the action of this muscle was augmented by the M. pubo-ischio-femoralis internus 1. The latter had presumably transferred its origin to the small anterior pubic process to increase its effectiveness as a protractor, rather than as an adductor and partial protractor as it is still in crocodilians, and probably was in some "semi-erect" thecodontians. The subsequent evolution of the anterior pubic process was almost certainly governed by the posture adopted by later lineages.

Ornithopods: these forms are typically bipedal and have, as a rule, a well-developed, rod-like or flattened anterior pubic process. This afforded a greatly increased area for attachment of the femoral protractor musculature of this process, and also increased the leverage which these muscles could exert on the femur. This reduced the dependence on the anterior process of the ilium, which had now become less advantageously positioned since it had swung upwards in these bipedal forms.

Ankylosauria: show no development of an anterior pubic process, and are obligate quadrupeds. It seems probable that these forms were quite early departures from the primitive ornithischian stock. The anterior pubic process is primitively absent, and the main protractor muscles, probably the M. ilio-tibialis 1, arose from the ventral surface of the broad, overhanging anterior iliac blade. The quadrupedal gait removed the necessity of developing an anterior pubic process. Thus the entire pubis almost completely disappeared in these forms, as its functions were performed by the ilium and ischium.

Ceratopia and Stegosauria: both of these suborders of the Ornithischia are typically quadrupedal and possess deep, flattened anterior pubic processes. According to the model above, these forms should not possess an anterior pubic ramus. However, both of these groups appear to have been primitively bipedal and to have become quadrupedal secondarily; the great disparity in length between fore and hind limbs in very suggestive of bipedal forebears. The ceratopians are almost certainly derived from forms like the small bipedal psittacosaurs, but the ancestry of the stegosaurs is less clear. The anterior pubic process was probably developed during the primitive (bipedal) stage of the evolution of these two groups, and was presumably retained by the later secondarily quadrupedal forms.

(d) *Some persistent problems in restorations of the pelvic musculature of ornithischians.* As might be expected from its anatomical structure, the musculature of the pelvis of *Iguanodon* is quite closely comparable to that of birds. The principal areas of doubt and ambiguity arise where homologous structures are lacking in ornithischians, namely the anterior process of the ilium and the anterior pubic ramus. In the case of the anterior process of the ilium, ROMER (1923b) proposed that this structure had the form of a prolongation of the primitive dorsal iliac spine, whereas in birds the entire anterior edge of the iliac blade was expanded. ROMER assumed that the condition in birds was derived from the ornithischian condition by hypertrophy of the ventral edge of the ornithischian dorsal spine. However, recent work suggests that this interpretation is in need of review, as evidence now suggests that birds and theropod dinosaurs had a far closer ancestry than did either with the Ornithischia (OSTROM, 1974). The function of the musculature which arose from beneath the anterior process of the ilium in ornithischians presents one problem. Ornithischians almost certainly evolved from thecodontians with a semi-erect posture. The latter, judging by their anatomy, were not greatly different from modern Crocodylia and in all probability their pelvic musculature was of a similar plan. In these forms, as with recent crocodilians, the M. pubo-ischio-femoralis internus 2, arose from the centra of the posterior dorsal vertebrae and passed backward across the ambayed area beneath the dorsal edge of the ilium, to insert on the lateral surface of the femoral shaft, below the head of the femur. This muscle was probably a very important factor in the gradual evolution of an erect limb posture in archosaurs. As a result of its position, this muscle naturally protracts the femur. However, there are in addition two other important functions performed simultaneously with this: adduction and rotation. *Adduction* is achieved because the muscle has an oblique orientation; that is, it passes diagonally backward and outward from its origin near the midline, to insert on the outer surface of the femur. Contraction therefore not only draws the femur forwards, but also inwards, into a more erect position. *Rotation* is achieved as a consequence of the position of the insertion of this muscle on the lateral surface of the shaft of the femur. These last two functions were essential prerequisites for the subsequent development of the ability to attain an erect, vertical limb posture, as found in some thecodontians and dinosaurs.

Once the dinosaurian limb posture had been achieved, several consequential changes in the form of the hind limb occur. The femur develops a more of less straight shaft, an inwardly turned head is supported by a short neck, and lateral to this, the prominent greater and less trochanters are developed. These changes imply some reorganization of the musculature inserting near the proximal end of the femur.

The following suggestions are purely speculative, but serve to indicate one possibility of the functional reorganization of some of the pelvic muscles which took place in the change from the thecodontian "crocodiloid" to dinosaurian pelvic and hind-limb structure.

M. ilio-femoralis. As a consequence of the forward rotation of the femur which took place with the change from "semi-erect" to "fully-erect" limbs, the M. ilio-femoralis insertion came to lie on the dorsal surface of the anteroventrally directed shaft rather than in its original dorsal position on a laterally directed femur. As a result, this muscle became a femoral protractor rather than an abductor or elevator; it ran along the dorsal surface of the femoral shaft, over the 'pulley' formed between the greater trochanter and the femoral head, and backwards to its origin on the lateral surface of the ilium, above and behind the acetabulum. To increase the effectiveness of this femoral protractor, the 'dinosaurian' lesser trochanter was developed. This increased the leverage exerted by this muscle and caused the muscle, or a slip thereof, to alter its insertion to a more proximal position. Certainly, as pointed out previously, the muscle scar striations seem to indicate that the muscle which inserted on the lesser trochanter came from the area on the ilium which was probably occupied by this muscle. The large size of the lesser trochanter in early ornithischians (*Lesothosaurus*) is another feature which can be tentatively correlated with the elaboration of M. ilio-femoralis. In these forms, the backward rotation of the pubis has 'removed' some of the principal pubic femoral protractor muscles, so that the M. ilio-femoralis would become, in theory at least, a very important protractor. Hence the larger and more prominent the lesser trochanter, the greater the leverage (moment arm) of this muscle. In this respect the lesser trochanter appears to be crest-like, and is not separated from the greater trochanter in *Heterodontosaurus* (SANTA-LUCA, 1980).

M. pubo-ischio-femoralis internus 2. The change in orientation of the femoral shaft and development of the femoral trochanters also radically altered the function of this muscle. In the femur of the fully erect dinosaurs, the torsion of the shaft has twisted the essentially lateral surface of the femur in thecodontians into an anterior surface. The M. pubo-ischio-femoralis internus would therefore be expected to have an insertion on the dorsal surface near the proximal end of the shaft. However, no such insertion can be identified in ornithischian femora. It seems possible that this muscle had in fact transferred its origin to the dorsal margin of the greater trochanter. This is quite feasible if the lesser trochanter was, as has been suggested, associated with the M. ilio-femoralis, since the upward migration of the ilio-femoral muscle would have 'forced' the M. pubo-ischio-femoralis 2 upwards on to the adjacent greater trochanter. As a result of the displacement of this muscle, it would have undergone a complete change of function. It now inserted above the centre of the femoral head and therefore acted to retract the femur; its ability to adduct the femur was lost, and the original rotatory component now merely served to clamp the femoral head into the acetabulum. The loss of this extremely important femoral protractor must presumably have been compensated for by the development of the anterior process of the ilium, which provided an origin for an equivalent of the avian "sartorius", and also by the "new" protractor function of the M. ilio-femoralis, which inserted on the lesser trochanter.

OSSIFIED TENDONS

The presence of ossified tendons on either side of the neural spines of the dorsal vertebrae is a character which is found in all Ornithischia and some birds (personal observation). These structures have, for a long time, puzzled palaeontologists, and have provoked several papers concerning their arrangement, structure and probable function.

Their arrangement was first described by DOLLO (1887a) using some of the well-preserved *Iguanodon* skeletons from Bernissart (IRSNB 1551, 1561). In these specimens, the ossified tendons are preserved as a rhombic lattice along either side of the neural spines of the dorsal, sacral and caudal vertebrae. DOLLO noted that these structures were truly bony — not artefactual remains — and homologized them with the dorsal epaxial muscles, which OWEN had earlier described in a similar rhombic lattice arrangement in *Apteryx australis*. He also added the proposal that these tendons supported the vertebral column against the force of gravity. DOLLO could use this explanation for those ossified tendons lying along the dorsal vertebra, but he was unable to use it for those which lay above the caudal vertebrae. In the latter case, DOLLO had reconstructed *Iguanodon* in an upright, bipedal posture, so that most of the tail rested on the ground, which seemingly obviated the need for such tendons in this region (cf. NORMAN, 1980). DOLLO therefore suggested that these tendons served to brace the tail against the pull of the powerful caudi-femoral musculature (*op. cit.*, 261-262).

MOODIE (1928, 1929) was the first to investigate the detailed structure of ossified tendons, using fragments, from the hadrosaur *Anatosaurus annectens* and the ankylosaur *Ankylosaurus*. Cut sections of these specimens revealed that their structure was surprisingly uniform.

> "The arrangement of Haversian systems is strikingly regular, and there is no evidence of stellate cells, or bundles of tissue, so characteristic of recent tendons. Osteoid tissue, so abundant in the skeletal parts of fossils reptiles, is strikingly absent from the fossil tendons. There is an interesting similarity in the histology of the ossified tendons and pathological fossil bone in the tendency of both to the production of fairly perfect Haversian systems."
>
> (MOODIE, 1928: 2)

Opinions of the function of these tendons have been principally of two kinds, both concerning hadrosaurian biology. The first was that of OSBORN (1912). BROWN (1916) and others since LEIDY (1859), who considered that hadrosaurs were essentially aquatic. For this mode of life, the ossified tendons were conceived of as a system of braces along either side of the tail, which aided the powerful lateral flexures of the tail during swimming (COLBERT, 1951). The second view was that hadrosaurs were primarily terrestrial (OSTROM, 1964). The latter reviewed, in some detail, the probable biology of hadrosaurs and the function of their ossified tendons. He concluded that the lattice arrangement of ossified tendons was functionally equivalent, in terms of its potential mechanical properties, to the supporting struts of a cantilevered bridge. This suggested that the development of ossified tendons was primarily a terrestrial adaptation, to prevent excessive sagging of the vertebral column. The aquatic adaptations of hadrosaurs (the allegedly weebed hand, and the deep tail) would have allowed these animals to migrate across coastal plains and swamps in their normal habitat, where limited swimming capabilities would be an advantage. These proposals were further enlarged upon by GALTON (1970) who advocated, even more strongly, the anatomical features suggestive of terrestrial locomotion in hadrosaurs, and many other ornithopods. More recently the function of ossified tendons has been considered in relation to the function of the tail in sauropod dinosaurs, considering whether it might have been used for swimming, as a whip-lash in defence, or merely normally held off the ground (COOMBS, 1975). In this context, the discussion of the function of ossified tendons seems singularly inappropriate, since saurischian dinosaurs do not possess ossified tendons along the vertebral column. Indeed, the functions of the ossified tendons of the Ornithischia seem to be achieved by at least two different mechanisms in the Saurischia. Both the lumbering sauropoda and the more agile theropods possess hyposphene-hypantra articulations between vertebrae and rugose areas along the anterior and posterior edges of the neural spines, which were bound together by powerful ligaments. These served to bind the neural spines together in much the same way as did the ossified tendons running along the sides of the neural spines in ornithopods. OSTROM (1969, 1969a) described another method of backbone strengthening in the theropod *Deinonychus.* In this form, the zygapophyses and chevrons of the distal caudal vertebrae are greatly lengthened and form a sheath of bony rods around the tail, greatly strengthening it. This development has been correlated with an improvement in balancing in this animal, associated with being able to pursue and capture moving prey, and also with the ability to stand on one leg, while striking its grey with the other, the foot of which bore a massive sickle-shaped talon. This same problem of improving the balancing ability in a fleet-footed animal, was solved in similar fashion by the ornithopod *Hypsilophodon.* GALTON (1971) described a sheath-like arrangement of ossified tendons surrounding the distal end of the tail in this form; he proposed that this served as a dynamic stabilizer, useful for an animal which, from its anatomical construction, was probably a fast runner.

However, COOMBS did pass several comments pertinent to the problems of the functional significance of the ossified tendons of ornithischians. Firstly, he proposed that these structures did not add rigidity to the vertebral column, because they could easily bend through any arc assumed by the vertebrae; and secondly, that they were ossified to reduce the stretching which occurs in long tendons. These factors he correlated with either swimming, or holding the tail clear of the ground, in hadrosaurs, and with the ability to swing a heavy tail club in some ankylosaurs.

General considerations

There are a few general facts regarding the structure and probable function of the ossified tendons, which should be stated prior to any functional considerations.

(i) In those forms in which the lattice of ossified tendons is well developed (hadrosaurs and iguanodontids), the vertebral column of naturally preserved, articulated specimens is nearly always straight in the region occupied by these tendons (Figs. 1; BROWN, 1916, pl. 13, fig. 2).

(ii) The ossified tendons in the lattice are rather loosely attached to the neural spines of the vertebral column. That is to say that even the least disturbed skeletons of hadrosaurs show some evidence of displacement of their ossified tendons. This suggests that they were not firmly bound to each of the neural spines that they lie across. It has also been noticed that in *Iguanodon atherfieldensis* at the most, only one end of any ossified tendon is fused to a neural spine. Those which are fused, are fused against the neural spines of the sacral vertebrae; the latter seems to act as an area of anchorage for ossified tendons from the dorsal and caudal regions. The free ends of the ossified tendons are usually blunt, rounded and slightly flattened.

(iii) MOODIE's work on the histology of ossified tendons reveals one obvious point of functional significance. These tendons functioned as tensile rods; this accounts for the remarkably uniform Haversian systems and for the absence of large vascular spaces, Volkmann's canals and bundles of osteoid tissue, since these would be natural foci of stress concentration in a stressed rod. This factor also accounts for the structure of the lacunae (MOODIE, 1928, fig. 46) which are shallow biconvex discs, aligned along the axis of stress, again minimising stress concentrations.

(iv) The ossified tendons are usually most numerous immediately around the sacrum, and become less numerous anterior and posterior to this area. Notable exceptions to this condition are forms like *Hypsilophodon* and *Tenontosaurus* (OSTROM, 1970) which possess a sheath of tendons around the distal end of the tail.

(v) In none of these forms possessing ossified tendons is there any indication that the vertebral column has lost any particular range of movement. The articular surfaces of the centra, and the zygapophyses, are all well developed.

Functional considerations

There are very strong reasons for suggestion that most ornithopods normally held their vertebral column more or less horizontally, especially when moving (LULL and WRIGHT, 1942; OSTROM, 1964; GALTON, 1970; NORMAN, 1980). In such a position, the long vertebral column is supported at its middle by the pelvis; there must therefore have been, a great tendency for the column to sag at either end, caused by the sheer length of the vertebral column and the combined weight of the hypaxial musculature and viscera. In the large Ornithopoda, this effect must have been considerable requiring, in theory, extremely powerful epaxial muscles. As OSTROM pointed out (*op. cit.*) this problem appears to have been solved by the lattice of ossified tendons, which provides a perfect cantilever system to support the vertebral column against the effects of gravity; this parallels the arrangement in theropods, which instead used powerful intervertebral ligaments. Thus, the general principle concerning the support of the vertebral column has been established. However, exactly how and under what conditions the ossified tendon system operated in the living ornithopod has not been considered in any great detail.

Support and locomotion. These two functions are intimately associated in the living animal and must be considered together in the ornithopod. A natural consequence of locomotion in bipedal ornithopods (and the majority of animals) is that forward propulsion is accompanied by an alternate rise and fall of the centre of gravity with each stride. This oscillatory effect implies certain functional requirements of the vertebral column and its supporting system in all bipedal ornithopods, and especially those of moderate to large size (iguanodontids and hadrosaurids). From a mechanical point of view it is probably best to visualise the bipedal ornithopod as a slightly flexible, horizontal beam (the vertebral column) balanced at its centre on a telescopic strut (the hindlimb). During the normal locomotory cycle, this simplified system would travel forwards, as the telescopic strut alternately extends and retracts. The balance point (fulcrum, at the acetabulum) during this sequence, describes a simple sine wave. Considered at a fixed point, the balance point oscillates in a vertical plane, as does the horizontal beam. However, due to the inertia of the beam, its distal ends rise and fall momentarily later than the centre; in other words, the oscillations of the ends of the beam would be out of phase with those at the centre. Therefore in life the oscillations encountered during walking imply that the vertebral column of ornithopods was impelled to flex in the vertical plane in order to accomodate 'out of phase' oscillations of the ends of the vertebral column. A vertebral column which was rigidly clamped by a trellis of ossified tendons would therefore be totally impracticable, since it would cause considerable jarring of the vertebral column, as it lacks the elasticity essential to any dynamic system. In *Iguanodon,* as had already been pointed out, the ossified tendons appear to have been fused to the neural spines of vertebrae (usually sacral) at one end alone, the remaining end being free and available for some form of flexible attachment. However, LULL and WRIGHT (1942) and OSTROM (1964) stated that the ossified tendons of hadrosaurs

> "... attached at their anterior end to the base of a neural spine and extended backward an upward to a posterior attachment near the crest of another neural spine some 4 to 10 vertebrae caudad."
>
> (OSTROM, 1964: 992)

In view of the above considerations this seems an extremely unlikely arrangement. Unfortunately, no adequate hadrosaurian material has been available for an examination to determine whether or not the findings reported above are accurate.

The problem which remains concerns the mode of attachment of the free end of the ossified tendons to the vertebral column. In COOMBS' view, this would be through a muscle. An alternative is that the free end of the ossified tendons inserted on the neural spines of the vertebrae by means of short natural tendons. These short tendons would provide a restricted amount of elasticity to the otherwise inextensible ossified tendons, which was necessary to this system, and they would also provide a powerful elastic recoil. In this way the vertebral column could become a self-bracing system, which is more economical than one supported by muscle. Indeed, the horse and other ungulates have a very roughly comparable adaptation to provide support for their large, heavy heads. This relies on a very powerful band of elastic connective tissue, the *ligamentum nuchae,* stretched between the occiput of the skull and the tips of the neural spines. This structure reduces the bulk of muscle otherwise necessary to support the head, and also reduces the amount of metabolic energy which would have been needed to maintain the head in its normal position.

If muscles were attached to the ossified tendons instead, there would be several inconsistencies. Firstly, the musculature for the caudal ossified tendons in *Iguanodon atherfieldensis* would have been situated toward the distal end of the tail, since the majority of these tendons insert against the sacral neural spines. These would therefore have added considerable bulk and weight to the end of the tail, the very structure which COOMBS supposes they were trying to raise from the ground! It would seem that a similar large bulk of muscles would have been present above the shoulder and anterior dorsal region which, although not entirely unreasonable, seems a little impractical for such an animal. In addition, there is the problem of the metabolic energy drain that these muscles would create. In the large hadrosaurids and iguanodontids, the tensile stresses acting along the spine must have been very considerable and would have necessitated a large bulk of powerful epaxial muscles to resist these stresses, so that all postures, whether while stationary or while moving, would have involved considerable, continuous strain on these muscles. It is rather difficult to visualize the musculature involved in lateral undulation associated with ossified tendons of such great length; also, the action of these muscles would have been extremely inefficient as a result of the great length of the ossified tendons, and their extremely low angle of insertion on the neural spines. In this respect, their ability to produce lateral undulations of the tail seems extremely dubious.

In the aquatic environment, the mechanical problems of weight support are removed by displacement. In this state, the entire vertebral column in the large ornithopods is buoyed up and the ossified tendon lattice would have 'relaxed' because the longitudinal tensile stresses had been removed. Thus it is conceivable that in this situation the tail might be used as a sculling organ. This action could have been powered by residual epaxial muscles inserting on the caudal ribs. However, as OSTROM (1964) pointed out, the ossified tendons would not only brace the tail, but would effectively limit the amount of lateral flexibility in the tail, as well and the amplitude and frequency of undulation — crocodiloid caudal undulation seems extremely improbable. If, as has been suggested, the ossified tendons had muscular ends, these could not have been of much use in sculling, because the tendons are far too long and insert at very low angles on the neural spines to provide sufficient lever arms to flex the vertebral column. The lever arms of these muscles would be very small even if the ossified tendons were attached to the tips of the caudal ribs because of the great length of the ossified tendons. In any case, the fore and hindlimbs could have been used very effectively as paddles for swimming, without necessarily needing the added propulsion from the tail.

In some ankylosaurs, ossified tendons are found near the tail club and may have prevented the tail from suffering whip-lash damage after striking an object, by stiffening the region of the tail proximal to the club. Alternatively, they might be associated with the muscles which swung the tail club, as proposed by COOMBS (1974, 1979).

In conclusion, the ossified tendon lattice of hadrosaurids, iguanodontids and in fact most ornithopods formed a supporting framework of tensile rods, which were attached by natural tendons to the neural spines on at least one of their ends. This arrangement conferred on the vertebral column the dynamic properties necessary to permit normal "oscillatory" locomotor movements. This system has the advantage of being self-supporting and does not require the expenditure of considerable quantities of metabolic energy associated with a system supported by muscles, since energy can be stored and released in the collagenous portion of each tendon. It is not necessary to suppose that *all* of the epaxial musculature was reduced to the condition of ossified tendons in these large ornithopods, only a comparatively small number of epaxial muscles seem to become ossified, probably in response to the proportionate reduction in longitudinal stresses. The positioning of the majority of ossified tendons against the neural spines, makes it less likely that the ornithopod tail was an effective swimming organ; they would have restricted lateral movements of the tail and could not have provided the power for such movements. The sheaths of ossified tendons found around the distal end of the tail in *Tenontosaurus* (OSTROM, 1970) and *Hypsilophodon* (GALTON, 1971, 1974) probably served to hold the distal end of the tail rigid in these forms, and may well have been attached to more proximally placed epaxial and hypaxial muscles; these could have served to clamp the distal end of the tail rigidly when they were contracted, to form a rigid stabilizer or dynamic counterbalance for rapid changes of direction when running at speed.

Notes on the excavations at Bernissart: 1878-1881

DE PAUW (1902) and CASIER (1960, 1978) have alluded to the existence of detailed plans of the excavations at Bernissart made between 1878 and 1881. Many of these plans are still preserved in the archives of the Royal Institute of Natural Sciences, Brussels and have made possible the reconstruction of details of the excavations.

The popular interpretation of Bernissart and its fossils among palaeontologists from Britain and the United States in particular is summarised very effectively by COLBERT.

> "The bones were not contained within the regular stratified beds of the coal mine, but rather were deposited in unstratified clays that cut *through* the layered shales and coals. In short, the fossils were within a *cran,* a deep pit or filled fissure, extending down through the sediments. Did this remarkable concentration of bones through such a depth of sediments signify a long period of time during which many dinosaurs died and were buried in accumulating muds? One might think so, but careful work by M. DE PAUW and his assistants would seem to indicate that within the coal mine of Bernissart there was preserved an ancient ravine — a narrow, deep gully in the Cretaceous landscape, into which, within a comparatively short span of years, many iguanodonts had slipped and fallen and died, to be buried in deep deposits of mud brought in by flooding waters after heavy rains. The painstaking digging and mapping that were done in the mine revealed this detail in an ancient landscape; it was possible to delineate the banks of the Cretaceous ravine, and to discern the inwash of sediments that had filled it — all quite distinct from the regular layers of coal and shale that were being mined far beneath the surface of the earth."
>
> (COLBERT, 1968: 58)

This general view has been elaborated and embellished, particularly in popular books on dinosaurs, to the point where it is regarded as *fact* that the herd of *Iguanodon* was stampeded [by carnivores or a forest fire and fell into the ravine at Bernissart *en masse* (e.g. HALSTEAD, 1975)]. Such interpretations do not accord with the facts so far as they are

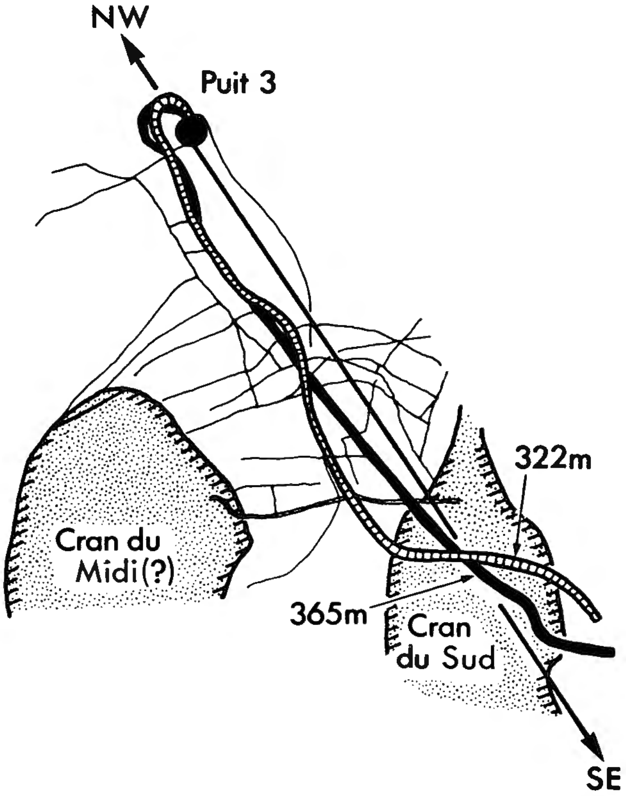


Fig. 82. – *(Above) Bernissart and its excavations. Plan drawing of the excavations at 322 metres (cross-hatched) and 356 metres (black line).*

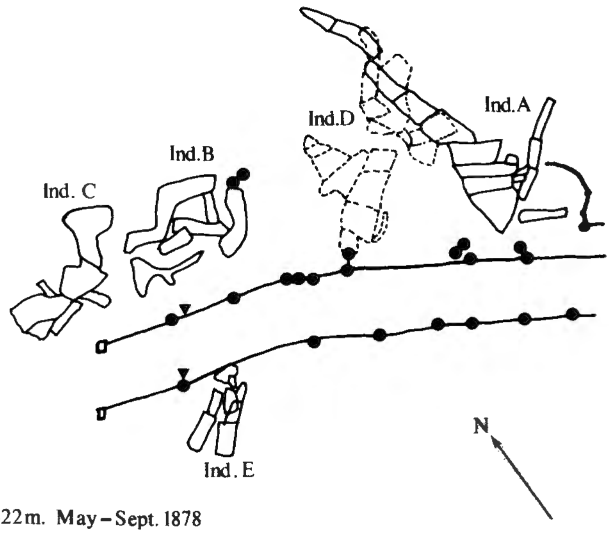
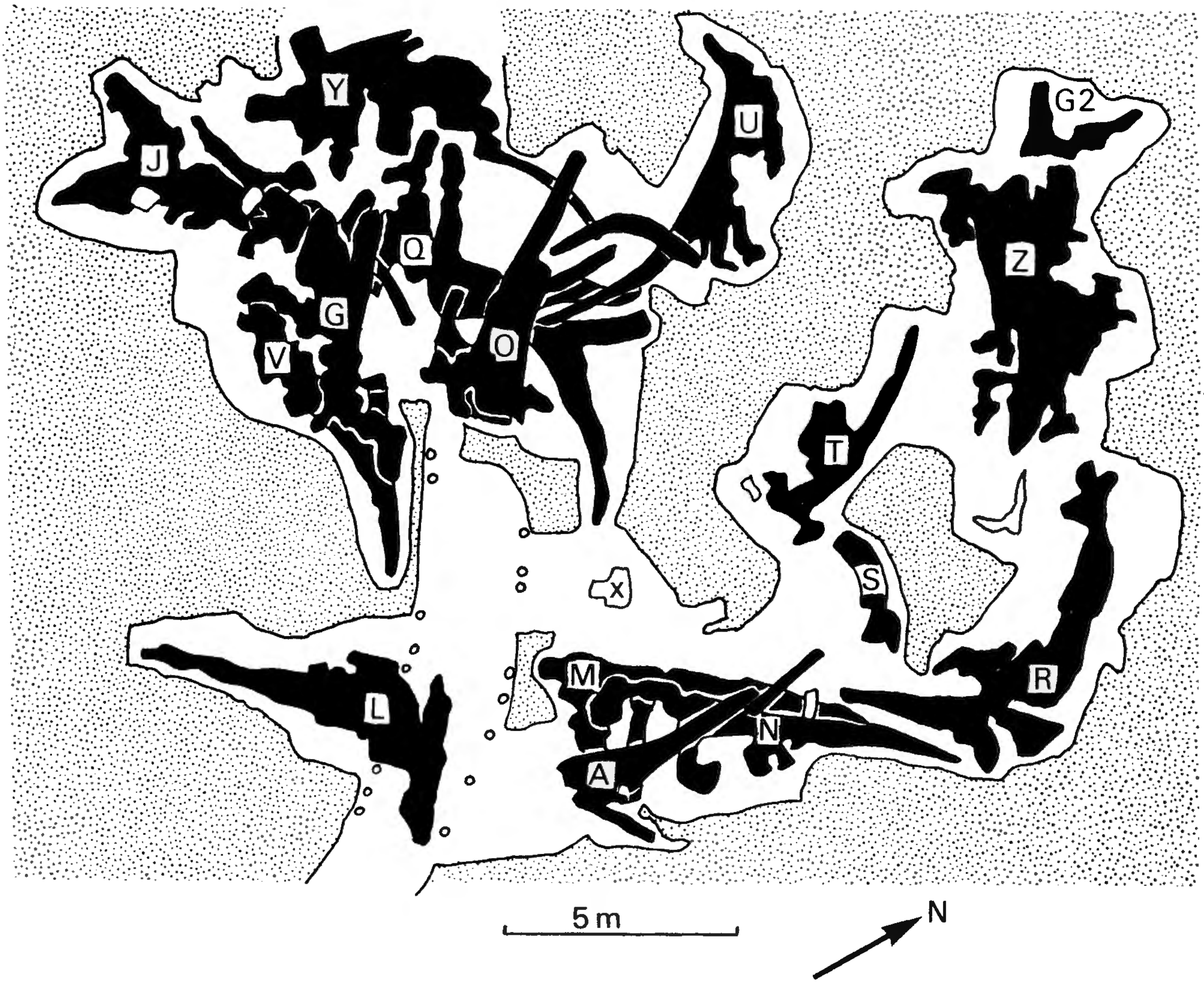


Fig. 83. – *(Above) First phase of excavations: 1978, prior to the earth movements which flooded the galleries. Five skeletons partially excavated. "Ind A" was prepared and mounted in 1878/9 (IRSNB 1716) (Adapted from original archive documents IRSNB).*

Fig. 84. – *(Below) Plan layout of the full extent of the first phase of excavation at 322 metres showing the distribution of the skeletons* in situ. *(Adapted from original archive documents IRSNB).*



known, as was stated as early as 1878. The archive material confirms that neither the views of COLBERT (1968) nor others are correct.

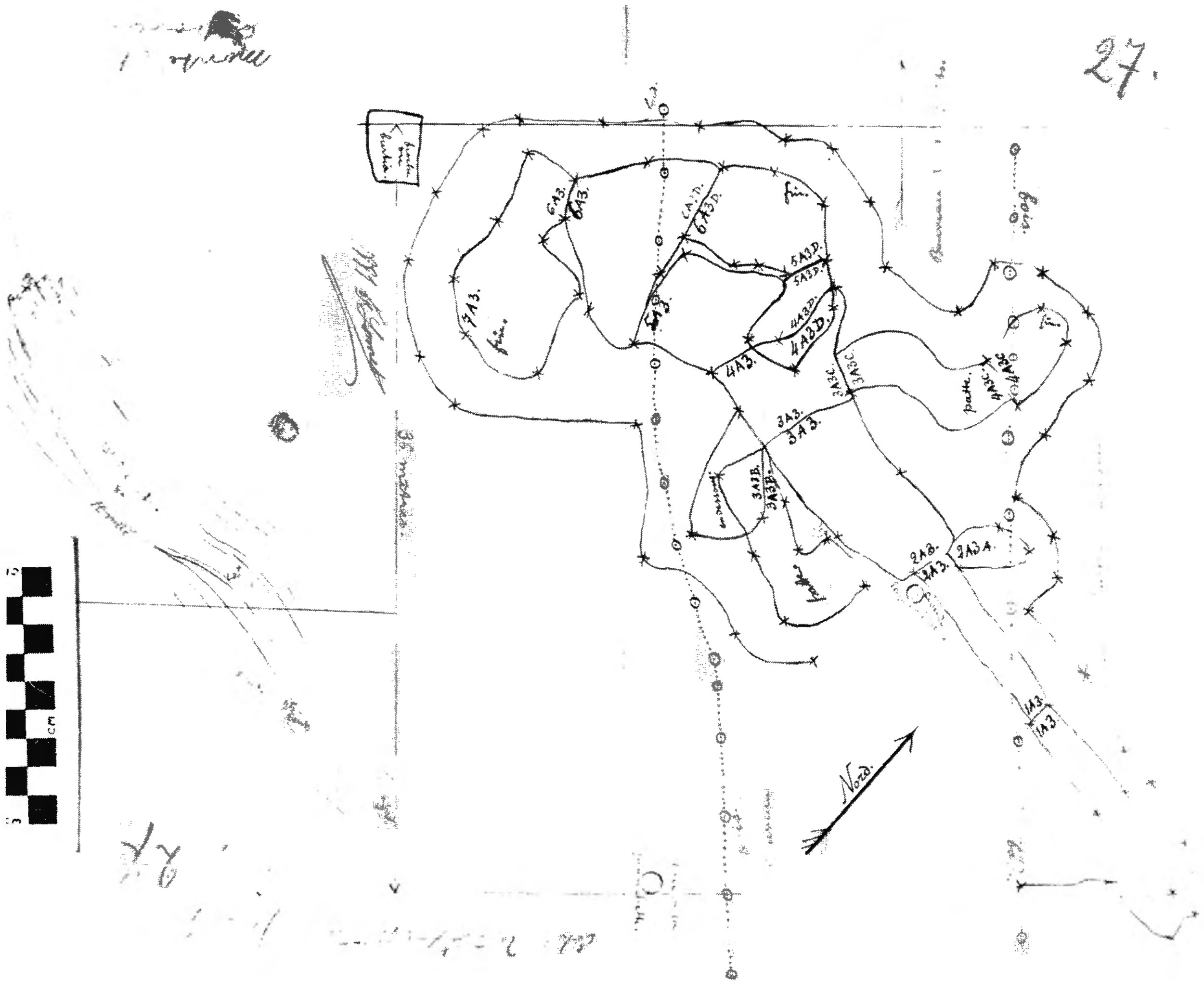
FURTHER DETAILS OF THE EXCAVATIONS

A general plan view of the Cran du Sud* (Fig. 82) reveals that the two galleries from which fossils were collected ran WNW-ESE (at a depth of 322 metres) and NW-SE (at 356 metres). Within these galleries there were, respectively, 60 metres and 8 metres of fossiliferous sediment (CORNET and SCHMITZ, 1898 — after SOHIER unpublished archive drawings). The fossils were apparently recovered from three areas and were documented with varying degrees of completeness by SONNET and DE PAUW. Since interest would have undoubtedly been most intense shortly after the first discoveries, the first area to be excavated received the most detailed attention, it also yielded the greatest number of specimens and consequently allows the most complete retrospective reconstruction.

1st series of excavations

In October 1878 the first excavations at 322 metres depth had to be abandoned because of flooding after an 'earthquake' in August (DE PAUW, 1902). At this time plans of the excavations reveal that at least five separate skeletons of *Iguanodon* had been discovered (Fig. 83) although only that of "A" (Fig. 83, Ind. A - IRSNB 1716) had been excavated completely. Between October and April of 1878/9, individual "A" was prepared and mounted in the museum workshop (la Chapelle St Georges) see CASIER (1968: pl. V, right). This was one of the earliest mounted skeletons of associated dinosaur remains.

Fig. 85. – *Original plan drawing of a skeleton as preserved at Bernissart, prior to removal from the mine. (See Fig. 89-A3).*



---

* DELMER and VAN WICHELEN (1980) have discovered that the renowned Cran from which the fossils were recovered was the *Cran du Sud* and not the *Cran du Midi* as it has been called in all previous literature.

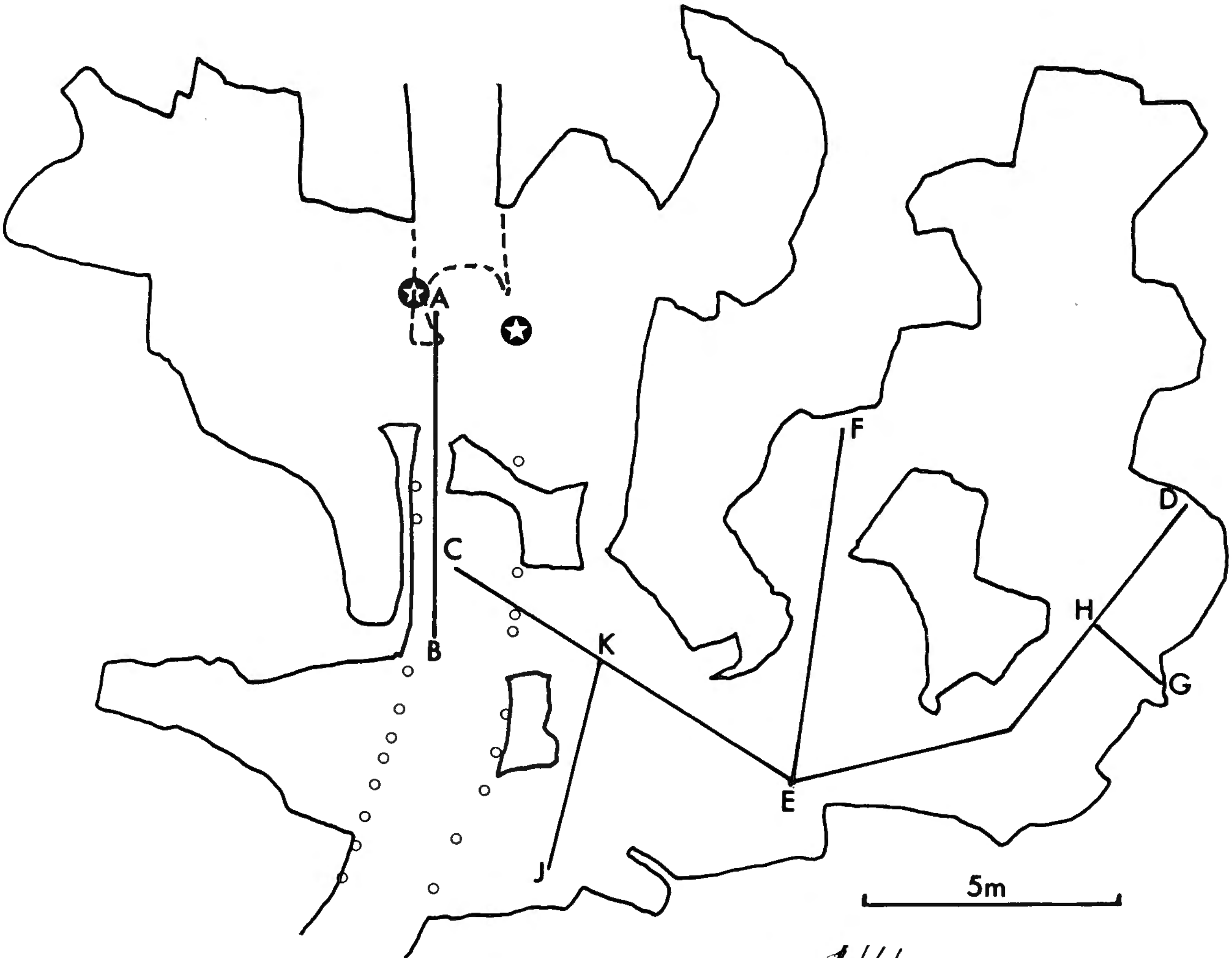
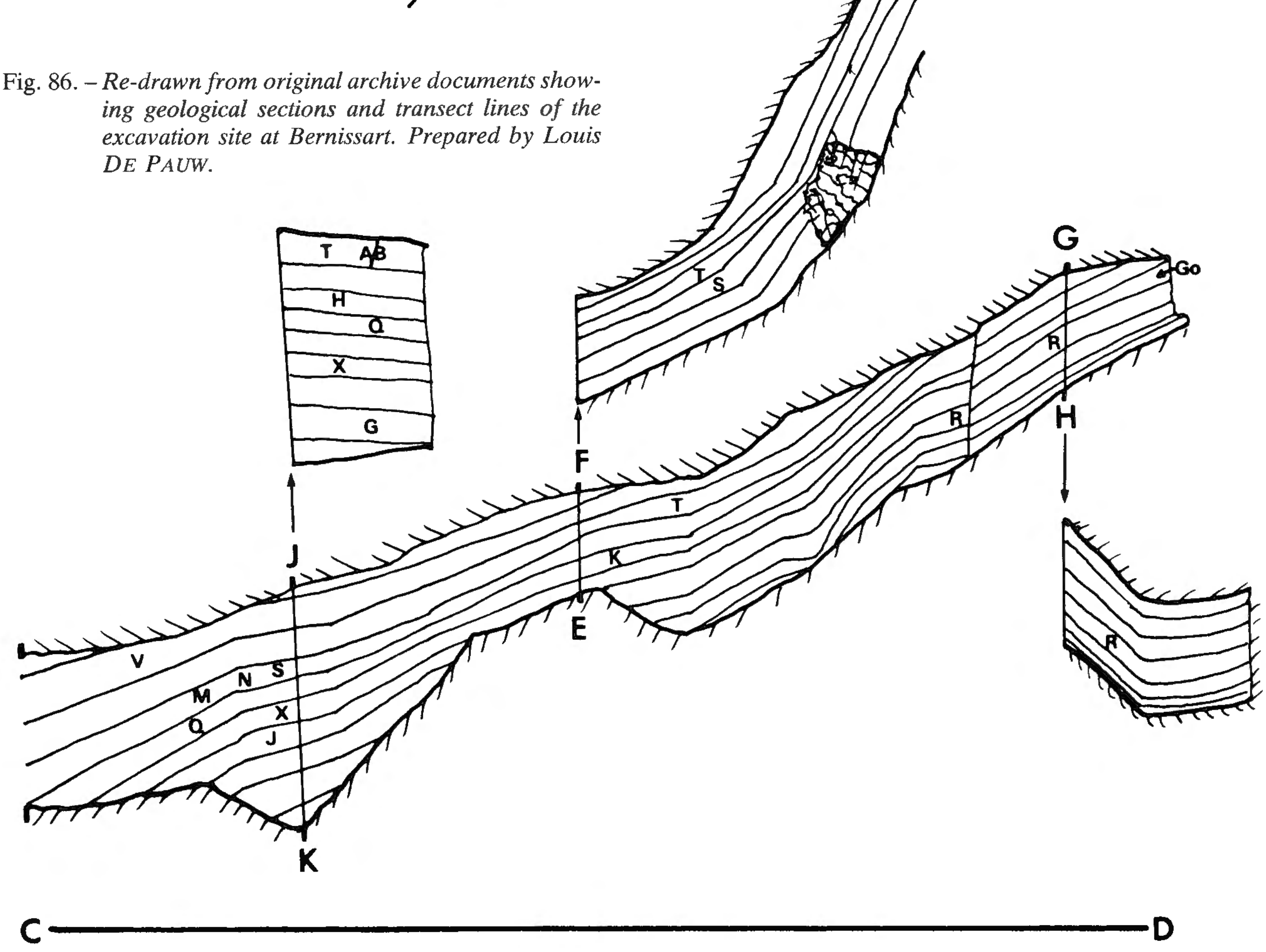


Fig. 86. – *Re-drawn from original archive documents showing geological sections and transect lines of the excavation site at Bernissart. Prepared by Louis* De Pauw.



From May 1879 onwards, excavations proceeded with considerably greater success resulting in the removal of 14 more or less complete and 4 partial skeletons of *Iguanodon,* 2 *Bernissartia* (Fig. 84, Be - a dwarf crocodile) skeletons, 1 *Goniopholis* skeleton (Fig. 84, Go - a crocodile), 2 turtles (Fig. 84, Ch) and innumerable fish and other remains that were not recorded on the plans. A comprehensive series of plans of the excavation of each skeleton produced by SONNET and DE PAUW (Fig. 85) has made it possible to construct a plan view of this 1st Series of excavations with the skeletons *in situ* (Fig. 84). In addition to this, there are some geological sections which record the stratigraphic levels from which the fossil remains were recovered (Fig. 86). It is evident from the records that (a) the sediments were clearly stratified (*contra* COLBERT, 1968) and (b) that some beds were essentially without fossils while others were abundantly fossiliferous with the dinosaur skeletons being found in several discrete layers (four according to DE PAUW (1902). Crude vertical geological sections were prepared along the transect lines A-B, C-K-E-H-D, J-K, E-F and G-H (Fig. 86). Included in these sections are letters "M", "N", "S". In general, the letters seem to correspond to the letter code used to identify individual skeletons (see Fig. 84). Unfortunately, however, this does not seem always to be the case. For example, "J" refers, apparently, to "ossements J" which includes individuals "O" and "U" (Fig. 84) yet it is not clear whether "O" on another section refers to "ossements O" [unknown indivudal (S)] or really to individual "O" ("ossements J")! The use of similar letters to identify both individual skeletons and/or apparent layers of accumulated skeletons unfortunately adds uncertainty to the interpretation of these otherwise remarkable records. This confusion simply reflects the difficulty of excavation such a concentrated accumulation of fossils. Indeed it is a testament to the diligence of DE PAUW and his team that the records are as good as they are. While it is not possible to use the letter codes with any great confidence to obtain information on the sequence of deposition of the skeletons, it is nevertheless possible to distinguish a taphonomic (?) pattern from the relative orientation of the various skeletons (Fig. 87A, B). Fig. 87A illustrates all the skeletons from Fig. 1 which have similar bodily orientations (O-U-A-R-T-Z). Figure 87B shows what may perhaps be two patterns L-M-N and J-G-V-Q-F-Y-S. The general point is that the carcasses of the dinosaurs *may* have been aligned by the predominant current direction when they were buried. As an additional observation, just as "M" and "N" (Fig. 87B) are clearly closely associated *in situ* (see CASIER, 1960: pl. III), so are "O" and "U" (Fig. 87A); there is also circumstantial evidence from the original plan drawings that "T", "Z" and "R" (Fig. 87A) are closely associated; there is, however no definite proof of any association between "O" - "U" and "T" - "Z" - "R", as proposed here on the basis of similarity of orientation.

2nd series of excavations

After the excavations of this first concentration of fossils, the tunnel was extended in an ESE direction across the Cran, passing through an area where the stratified sediments, were almost horizontal, there are no archive records of large vertebrate remains from this area. On the 22nd October, 1879, another crocodile skeleton (*Goniopholis*) was recovered in the gallery at a distance of some 38.4 metres from the entrance to the cran (Fig. 88A Go). A further eight well-preserved *Iguanodon* skeletons were recovered between 38-60 metres from the original entrance to the Cran before reaching its opposite side. Detailed plans of the recovery of each dinosaur skeleton are excellent, but there are no records of any attempt to chart the geology of these deposits, or the relative stratigraphic position of each skeleton. However, since the skeletons were separated by distances of several metres in some cases, it is probable that they were derived from separate stratigraphic levels; CORNET and SCHMITZ (1898 - after SOHIER) indicate steeply inclined beds on both sides of the Cran. It is a curious fact that the skeletons show the same pattern of orientation as in the 1st series.

3rd series of excavations

By 1881 a new gallery had been extended into the Cran du Midi at a depth of 356 metres; at this level, the fossiliferous sediments seem to have been extremely restricted (7-8 metres). Within this region three more articulated skeletons were recovered (Fig. 89). Again, clear plans of the skeletons are preserved (Fig. 85), but the stratigraphic details are unclear.

GEOLOGICAL IMPLICATIONS

As early as 1870 CORNET and BRIART published a paper which represented the first attempt to provide a rational explanation for the presence of "Cran" or "puits naturels" that had been encountered on numerous occasions during mining in the Mons basin. Their conclusion was that these phenomena were created by dissolution of subterranean limestone and the production of caverns into which overlying sediments had subsided. The first review of the discoveries at Bernissart was published by DUPONT (1878), after a visit to the excavations in the June of that year; having reviewed the fauna, DUPONT discussed the geological nature of the "Cran du Midi" (= Cran du Sud) and concluded that it represented a ravine.


A
G2
U
O
Z
T
R
A
B
Y
J
Q
G
V
F
S
M
L
N

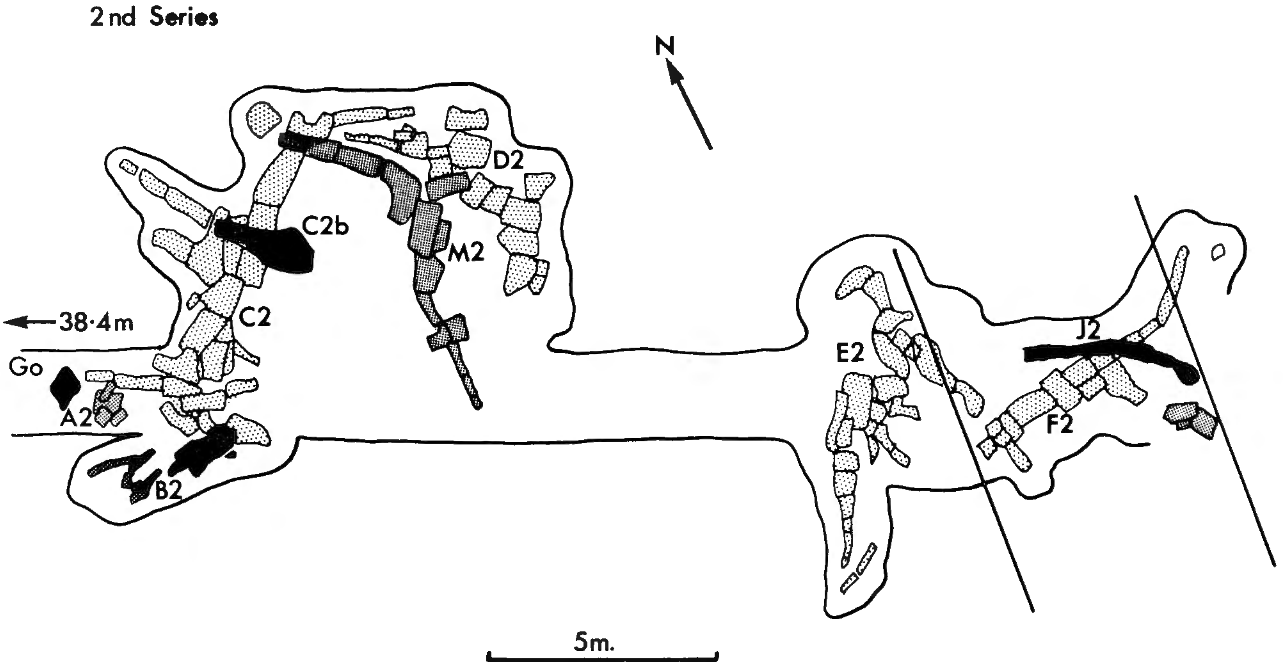
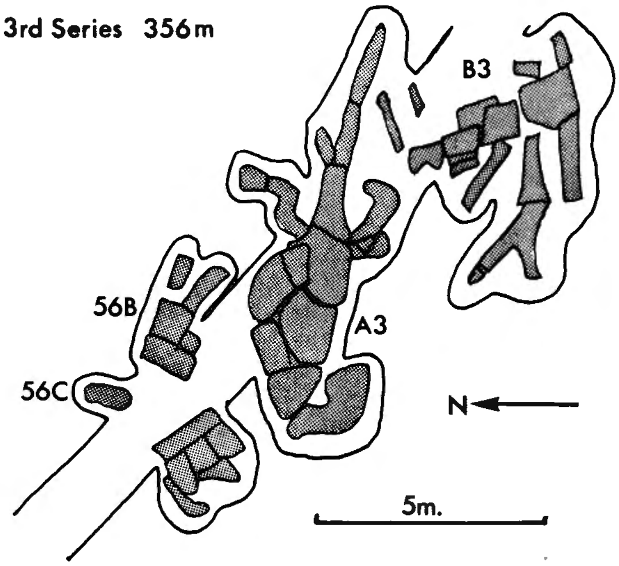


Fig. 88-89. – *Drawings of the second and third phases of the excavations at 322 metres and 356 metres depth respectively. Distribution of the skeletons indicated. Not all of the letter/number coded individuals are now identifiable in the collections. (Adapted from original archive documents IRSNB).*



> "La crevasse de Bernissart nous apparaît ainsi comme l'une des vallées latérales de la grande vallée longitudinale du Hainaut dont le remplissage s'effectua pendant la période crétacée. Elle était traversée par une rivière qui venait de déverser dans la vallée centrale et où se developpaient de nombreux poissons en temps ordinaire, sur les bords marécageux du cours de l'eau; croissaient d'abondantes fougères au milieu desquelles vivaient des tortues et des petits lézards, et les gigantesques Iguanodons, attirés sans doute par une abondante nourriture, venaient s'y enbourber et y périr."
>
> (Dupont, 1878: 406)

He did this despite the fact that Cornet (1878) and Arnould (1878) had already suggested that it represented a typical "puit naturel". The views of Dupont were, however, not seriously challenged until two decades later following the publication of the first museum guide in which Dupont (1897) not only reaffirmed his views that the "Cran du Midi" was a valley, but also provided an illustration of the presumed valley. This publication provoked a series of severely critical papers refuting Dupont's proposal (Cornet and Schmitz, 1898; Van Den Broeck, 1898; De Pauw, 1898; Van Den Broeck, 1899; Van Ertborn, 1902 and De Pauw, 1902). The consensus of these papers was that the fine-grained, highly stratified sediments, the articulated nature of the fossils and the characteristics of the irregular mass of sediment of either side of the stratified region of the cran were inconsistent with the river-valley proposal. It was argued that the fossiliferous sediments were probably deposited in a lacustrine or marshy environment which had undergone post-depositional deformation as a result of collapse into a subterranean cavern. The most recent review of the occurrence and geological nature of the "puits naturels" of the Valenciennes-Mons coal field, which includes Bernissart, is that of Delmer and Van Wichelen (1980); their conclusions are that Cornet and

Fig. 87. – *Galleries at 322 metres depth with skeletons separated into groups showing similar orientations, which may have some taphonomic significance. (Adapted from original archive documents IRSNB).*
◁

BRIART (1870) were probably correct. The underlying cause of the "puits" is understood to be through the dissolution of subterranean gypsum evaporites, interstratified with or beneath the coal-bearing Palaeozoic limestone, causing subsidence of the overlying strata. The displacements seem to result in a lozenge of material (usually circular or elliptic in plan view) falling abruptly; these falls generate seismic shock waves that have apparently regularly been recorded in this area. Indeed such a local collapse may have caused the 'earthquake' of August 1878 which was witnessed by DE PAUW.

CONCLUSION

As a consequence of the considerations above, several statements may be concerning the fossil locality at Bernissart, which correct frequently published assertions on the nature of the site.

(i) The sedimentary environment was marshy or lake-like rather than that of a river-valley.

(ii) There was no pit, chasm or ravine at Bernissart at the time of deposition of the sediments. Nevertheless during Wealden times the Bernissart site may have been somewhat lower topographically than the surrounding countryside because of subterranean dissolution; if this was the situation, then it might explain the preferential accumulation of fossils at Bernissart.

(iii) There was no single catastrophic event which led to the accumulation of fossils. The mine records indicate at least in the case of the dinosaurs that there were four separate depositional layers. This is tentatively supported by taphonomic evidence revealed in the reconstruction of the excavation site.

(iv) There is no clear evidence of a herd of *Iguanodon* at Bernissart. This is not to say that *Iguanodon* was not capable of living in herd-like aggregations, but merely that we cannot prove so from the evidence at Bernissart.

Summary

The osteology of the skull and lower jaw of *I. atherfieldensis* is described in considerable detail on the basis of the fragmentary, disarticulated skull of the holotype (BMNH R5764) and the complete but unprepared skull of the referred skeleton (IRSNB 1551). By comparison with *I. bernissartensis* (NORMAN, 1980) the skull of *I. atherfieldensis* is generally more slender and lightly built. The only consistent osteological differences, apart from those which can be considered to be size-related, are in the structure of the palpebral and the supraoccipital.

The postcranial skeleton of *I. atherfieldensis* is described completely and is, again by comparison with *I. bernissartensis,* of gracile proportions. Two proatlases are preserved in the referred specimen (IRSNB 1551). Compared with *I. bernissartensis,* the dorsal vertebrae have lower, more elongate centra and have taller more slender neural spines, there are six sacral vertebrae; the pectoral girdle and forelimb are considerably smaller and do not show such extreme weight-supporting adaptations (no intersternal ossification or ossified ligaments in the carpus, slender 1st phalanx on digit II) and the digital formula is 2, 3, 3, 3, 3, compared with 2, 3, 3, 2, 4 in *I. bernissartensis*; in the pelvis and hindlimb, the pubis has a deeper and more laterally compressed anterior process and the 1st metatarsal is narrow.

The suite of anatomical differences between *I. atherfieldensis* and *I. bernissartensis* can be used to define them as *osteological species;* however, this begs the question of their validity as *biological species.* The position is regarded as unresolvable in this paper. Fossil species have been "proved" to be sexual morphotypes in only a few instances (cf. DODSON, 1975, 1976) in these cases cranial ornamentation proved to be crucial to the analysis. In the absence of such well-marked visual clues, or osteological characters that can be unequivocally attributed to sex, it is argued that the two species of *Iguanodon* may exhibit size-related niche partitioning by analogy with closely sympatric species of living mammal.

The comparative anatomy and systematics of *Iguanodon, Camptosaurus, Ouranosaurus, Hypsilophodon* and hadrosaurids is analysed. *Iguanodon, Camptosaurus* and *Ouranosaurus* form a clade, the Iguanodontidae rather than a paraphyletic group. *Hypsilophodon* is the sister-taxon of the Iguanodontidae + Hadrosauridae and the latter are regarded as sister-families.

Myological reconstructions of the forelimb and hindlimb are attempted. The forelimb myology represents the first attempt to reconstruct this musculature in any ornithopod. The hindlimb musculature is compared and contrasted with previous accounts by ROMER and GALTON on related genera, and the evolution of ornithischian hip anatomy and musculature is reviewed. The structure and function of ossified tendons is reconsidered and a much more dynamic rôle is proposed.

Archive material concerning the excavations at Bernissart reveals that considerable numbers of plan drawings were made of the original excavations; these show details of the excavations that have hitherto not been published and contribute to the debate concerning the nature of formation of the fossil site at Bernissart. There was no ravine at Bernissart in Wealden times; the fossils were not formed as a result of a single 'catastrophe', there appear to have been at least 4 periods of deposition; the large number of *Iguanodon* preserved at Bernissard neither 'proves' nor 'disproves' that *Iguanodon* lived in herds; the 'Cran' or 'puit naturel' was formed by subterranean solution of evaporites to form caverns into which the superincumbent strata collapsed.

References

ANDREWS, C.W., 1897. Note on the cast of the brain of *Iguanodon.* [Ann. Mag. nat. Hist. (6) XIX: 585-591, 1 text-fig., pl. XVI.]

ARNOULD, G., 1878. *Bassin houiller du couchant de Mons - mémoire historique et descriptif.* 210 pp., 6 pls. Mons: Hector Manceaux.

BENEDEN, P.J. VAN, 1878. Sur la découverte de reptiles fossiles gigantesques dans la charbonnage de Bernissart, près de Péruwelz. (Bull. Acad. r. Belg. XLV: 578-579.)

BENEDEN, P.J. VAN, 1881. Sur l'arc pelvien chez les dinosauriens de Bernissart. [Bull. Acad. r. Belge. Ch. Sci. (3) 1: 600-608.]

BOULENGER, G.A. [in BENEDEN, P.J. VAN], 1881. Sur l'arc pelvien chez les dinosauriens de Bernissart. [Bull. Acad. r. Belge. Ch. Sci. (3) 1: 600-608.]

BROECK, E. VAN DEN, 1899. Nouvelles observations relatives au gisement des Iguanodons de Bernissart. [Bull. Soc. Belge Géol. Pal. Hydrol. XIII (1899): 6-11, 175-181.]

BROECK, E. VAN DEN, 1898 (1899). Les coupes du gisement de Bernissart - caractères et dispositions sédimentaires de l'argile ossifère du Cran aux Iguanodons. [Bull. Soc. Belge Géol. Pal. Hydrol. XII (1898): 216-243.]

BUCKLAND, W., 1829. On the discovery of bones of *Iguanodon* in the Ironsand formation of the Wealden formation in the Isle of Wight and the Isle of Purbeck. [Trans. geol. Soc. Lond. (2) 3: 425-432 (1835).]

CASIER, E., 1960. *Les Iguanodons de Bernissart. A la mémoire de Louis Dollo (1857-1931).* Brussels, Inst. r. Sci. nat. Belge, pp. 134. Goemaere: Brussels.

CASIER, E., 1978. *Les Iguanodons de Bernissart. A la mémoire de Louis Dollo (1857-1931).* Brussels, Inst. r. Sci. nat. Belge, pp. 166: Hayez.

CHARIG, A.J., 1972. The evolution of the archosaur pelvis and hindlimb: an explanation in function terms. *In* K.A. Joysey and T.S. Kemp (Eds.), *Studies in vertebrate evolution (essays presented to Dr. F.R. Parrington, F.R.S.)*: 121-155. Edingburgh: Oliver and Boyd.

COLBERT, E.H., 1968. *Men and dinosaurs.* 283 pp. Evans Brothers: London.

COLBERT, E.H. and OSTROM, J.H., 1958. Dinosaur stapes. (Am. Mus. Novit. 1900: 20 pp., 11 figs.)

COOMBS, W.P., 1975. Sauropod habits and habitats. (Palaeogeogr., Palaeoclimatol., Palaeoecol. 17: 1-33.)

COOMBS, W.P., 1978. Forelimb muscles of the Ankylosauria (Reptilia: Ornithischia). (J. Paleont. 52: 642-657.)

CORNET, L.-F., 1878. Sur la rencontre d'ossements d'*Iguanodon* dans un accident du terrain houiller de Bernissart. (Ann. Soc. Géol. Belg. V: 112-114.)

CORNET, L.-F. and BRIART, A., 1870. Notice sur les puits naturels du terrain houiller. [Bull. Acad. r. Belg. (2^{ième} ser.) t. XXIX: (5).]

CORNET, J. and SCHMITZ, R.-G., 1898 (1899). Note sur les puits naturels du terrain houiller du Hainaut et sur le gisement des Iguanodons de Bernissart. [Bull. Soc. Belge Géol., Pal., Hydrol. XII (1898): 301-318, 196-206.]

CRACRAFT, J., 1971. The functional morphology of the hindlimb of the domestic pigeon, *Columba livia.* [Bull. Am. Mus. nat. Hist. 144 (3): 171-268.]

CUVIER, G., 1825. *Recherches sur les Ossements Fossiles.* 3rd Edn. Vol. 5 (2), pp. 547, 23 pls.

DE PAUW, L.-F., 1898 (1899). Observations sur le gisement de Bernissart. [Bull. Soc. Belge Géol., Pal., Hydrol. XII (1898): 206-216.]

DE PAUW, L.-F., 1902. Notes sur les Fouilles du charbonnage de Bernissart. Découverte, solidification et montage des iguanodons, pp. 1-25, Etterbeek - Brussels.

DODSON, P., 1975. Taxonomic implications of relative growth in lambeosaurine hadrosaurs. [Syst. Zool. 24 (1): 37-54.]

DODSON, P., 1976. Quantitative aspects of relative growth and sexial dimorphism in *Protoceratops.* (J. Paleont. 50: 929-940.)

DODSON, P., 1980. Comparative osteology of the American ornithopods *Camptosaurus* and *Tenontosaurus.* (Mém. Soc. géol. Fr., N.S. 1980, 139: 81-85.)

DODSON, P. and MADSEN, J.H., 1981. On the sternum of *Camptosaurus.* (J. Paleont. 55: 109-112.)

DOLLO, L., 1882. Première note sur les dinosauriens de Bernissart. (Bull. Mus. r. Hist. nat. Belg. 1: 55-80 pls. IV-VI.)

DOLLO, L. 1882a. Deuxième note sur les dinosauriens de Bernissart. (Bull. Mus. r. Hist. nat. Belg. 1: 205-211, pl. XII.)

DOLLO, L., 1883. Note sur la présence chez les oiseaux du «Troisième trochanter» des dinosauriens et sur la fonction de celui-ci. (Bull. Mus. r. Hist. nat. Belg. II: 13-20, pl. 1 / Bull. biol. Fr. Belg. XV: 47-52.)

DOLLO, L., 1883a. Troisième note sur les dinosauriens de Bernissart. (Bull. Mus. r. Hist. nat. Belg. II: 85-126, pls. III-V.)

DOLLO, L., 1883b. Quatrième note sur les dinosauriens de Bernissart. (Bull. Mus. r. Hist. nat. Belg. II: 223-252, pls. IX, X.)

DOLLO, L., 1884. Cinquième note sur les dinosauriens de Bernissart. (Bull. Mus. r. Hist. nat. Belg. III: 129-146, pls. VI, VII.)

DOLLO, L., 1887. Note sur les ligaments ossifiés des dinosauriens de Bernissart. (Arch. Biol. VII, 249-264, pls. VIII, IX.)

DUPONT, E., 1878. Sur la découverte d'ossements d'*Iguanodon,* de poissons et de végétaux dans la fosse Sainte-Barbe du Charbonnage de Bernissart. [Bull. Acad. r. Belg. XLVI (2): 387.]

DUPONT, E., 1897. *Musée Royal d'Histoire naturelle de Belgique. Guide dans les collections. Bernissart et les Iguanodons.* Brussels: Polleunis and Centerick.

ERTBORN, BARON O. VAN, 1902. *Le Musée de Bruxelles et les Iguanodons de Bernissart.* 7 pp. Anvers: Buschmann.

FITZINGER, L.J., 1843. *Systema reptilium.* Vienna, 106 pp.

FÜRBRINGER, M., 1876. Zur vergleichenden Anatomie der Schultermuskeln. Thiel III. (Morph. Jb. 1: 636-816, pls. XXII-XXVII.)

FÜRBRINGER, M., 1900. Zur vergleichenden Anatomie der Schultermuskeln. Thiel IV. (Jena. Z. Med. Naturw., pp. 215-817, pls. XIII-XVII.)

GALTON, P.M., 1969. The pelvic musculature of the dinosaur *Hypsilophodon* (Reptilia: Ornithischia). (Postilla 131: 1-64.)

GALTON, P.M., 1974. The ornithischian dinosaur *Hypsilophodon* from the Wealden of the Isle of Wight. [Bull. Brit. Mus. nat. Hist. Geol. 25 (1): 1-152, 2 pls., 64 figs.]

GALTON, P.M., 1975. English hypsilophodontid dinosaurs (Reptilia: Ornithischia). [Palaeontology 18 (4): 741-751.]

GALTON, P.M. and JENSEN, J.A., 1979. Remains of ornithopod dinosaurs from the Lower Cretaceous of North America. (Brigham Young Univ. Geol. Stud. 25: 1-10.)

GALTON, P.M. and POWELL, H.P., 1980. The ornithischian dinosaur *Camptosaurus prestwichii* from the Upper Jurassic of England. (Palaeontology 23: 411-443.)

GEORGE, J.C. and BERGER, A.J., 1966. Avian Myology: London, Academic Press, p. 500.

GILMORE, C.W., 1909. Osteology of the Jurassic reptile *Camptosaurus,* with revision of the species of the genus and description of two new species. (Proc. U.S. Natn. Mus. 36: 197-332.)

GREGORY, W.K. and CAMP, C.L., 1918. Studies in comparative myology and osteology. No. III. (Bull. Am. Mus. Nat. Hist. 38: 447-563.)

HOLL, F., 1829. Handbuch der Petrefactenkunde. Pt. 1. (Quedlinberg: Leipzig, 232 pp.)

HOOLEY, R.W., 1912. On the discovery of remains of *I. mantelli* in the Wealden beds of Brightstone Bay, Isle of Wight. (Geol. Mag. n.s. 9: 444-449.)

HOOLEY, R.W., 1912(b). On the discovery of remains of *Iguanodon mantelli* in the Wealden beds of Brightstone Bay, Isle of Wight, and the adaptation of the pelvic girdle to an exact position and bipedal progression. [Rep. Brit. Assoc. Adv. Sci., Portsmouth LXXXI. 390 (1911) / Geol. Mag. (5), VIII, 520-521 (1911).]

HOOLEY, R.W., 1917. On the integument of *Iguanodon bernissartensis* (Blgr) and of *Morosaurus becklesii* (Mantell). [Geol. Mag. (6) VI: 148-150, pl. X.]

HOOLEY, R.W., 1925. On the skeleton of *Iguanodon atherfieldenses* sp. nov., from the Wealden shales of Atherfield (Isle of Wight). (Q. Jl. geol. Soc. Lond. 81: 1-61.)

HOPSON, J.A., 1975. The evolution of cranial display structures in hadrosaurian dinosaurs. (Paleobiology 1: 21-43.)

HULKE, J.W., 1871. Note on a large reptilian skull from Brook, Isle of Wight, probably dinosaurian and referable to the genus *Iguanodon.* (Q. Jl. geol. Soc. Lond. XXVII: 199-206, pl. XI.)

HULKE, J.W., 1882. Description of some *Iguanodon*-remains, indicating a new species, *I. seelyi.* (Q. Jl. geol. Soc. Lond. XXXVIII: 135-144, pl. IV.)

HUTCHINSON, G.E., 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? (Amer. Nat. 93: 145-159.)

HUTCHINSON, G.E., 1965. *The ecological theater and the evolutionary play.* Yale Univ. Press: New Haven.

HUXLEY, T.H., 1870. On the classification of the Dinosauria, with observation on the Dinosauria of the Trias. (Q. Jl. geol. Soc. Lond. XXVI: 32-50.)

JANENSCH, W., 1955. Der Ornithopode *Dysalotosaurus* der Tendaguruschichten. (Palaeontographica, Suppl. 7, Erste Reihe, III: 105-176.)

LAMBE, L.H., 1920. The hadrosaur *Edmontosaurus* from the Upper Cretaceous of Alberta. (Mem. Canada Geol. Surv. 120: 1-79.)

LULL, R.S. and WRIGHT, N.E., 1942. Hadrosaurian dinosaurs of North America. (Spec. paper Geol. Soc. Am. 40: 1-242.)

LYDEKKER, R., 1888. Note on a new Wealden iguanodont and other dinosaurs. (Q. Jl. geol. Soc. Lond. XLIV: 46-52, 3 figs., pl. III.)

LYDEKKER, R., 1889. Notes on new and other dinosaurian remains. [Geol. Mag. (3) VI: 352-356, figs. A-D.]

MACARTHUR, R.H., 1958. Population ecology of some warblers of north eastern coniferous forests. (Ecol. 39: 599-619.)

MANTELL, G.A., 1925. Notice on the *Iguanodon,* a newly discovered fossil reptile, from the Sandstone of Tilgate Forest, in Sussex. (Phil. Trans R. Soc. CXV: 179-186, pl. XIV.)

MANTELL, G.A., 1927. Illustrations of the Geology of Sussex: with figures and descriptions of the fossils of Tilgate Forest. 92 pp. + 20 plates. Lupton Relfe: London.

MANTELL, G.A., 1829. A tabular arrangement of the organic remains of the county of Sussex. [Trans. geol. Soc. Lond. (2) III (1): 201-216.]

MANTELL, G.A., 1834. Discovery of the bones of the *Iguanodon* in a quarry of Kentish Rag (a limestone belonging to the Lower Greensand formation) near Maidstone, Kent. (Edinb. New. Phil. J. XVII: 200-201.)

MANTELL, G.A., 1835. Notice of the discoevery of the remains of the *Iguanodon* in the Lower Greensand formation of the South-East of England. (Am. J. Sci. XXVII: 355-360, 420.)

MANTELL, G.A., 1838. The Wonders of Geology; or a familiar exposition of geological phenomena; being the substance of a course of lectures delivered at Brighton ... From notes taken by G.F. Richardson. 1st Ed. 2 vols. 8°, Relfe and Fletcher: London.

MARSH, O.C., 1881. Classification of the Dinosauria. (Am. J. Sci. XXI: 423.)

MEYER, J. VON, 1832. Palaeologica zur Geschichte der Erde und ihrer Geschöpfe, pp. 560, 8° Frankfurt am Main, 1832.

Milner, A.R. and Norman, D.B., 1984. The biogeography of advanced ornithopod dinosaurs (Archosauria: Ornithischia) - a cladistic vicariance model. 3rd Symp. Mesozoic Terrestr. Ecosyst. (Eds.) Reif, W.E. and Westphal, F., Tübingen: Attempto Verlag.

Nopsca, F.B., 1929. Sexual differences in ornithopodous dinosaurs. (Palaeobiologica 2: 187-200.)

Norman, D.B., 1977. *On the anatomy of the ornithischian dinosaur Iguanodon.* (Ph. D. Thesis: University of London, U.K.)

Norman, D.B., 1980. On the ornithischian dinosaur *Iguanodon bernissartensis* from the Lower Cretaceous of Bernissart (Belgium). (Mém. Inst. r. Sci. nat. Belg. 178: 105 pp.)

Norman, D.B., 1984. On the cranial morphology and evolution of ornithopod dinosaurs. [Symp. zool. Soc. Lond. (1984) No. 52: 521-547.]

Norman, D.B., 1984a. A systematic reappraisal of the reptile Order Ornithischia. 3rd Symp. Mesozoic Terrestr. Ecosyst. (Eds.) Reif, W.E. and Westphal, F., Tübingen: Attempto Verlag.

Owen, R., 1841. Report on British Fossil Reptiles, part II. [Rep. Br. Ass. Advmt. Sci XI: 60-204 (1841).]

Owen, R., 1855. Monograph on the fossil Reptilia of the Wealden and Purbeck formations. Part II. Dinosauria (*Iguanodon*). (Wealden). [Palaeontogr. Soc. (Monogr.) VIII: 1-54, pls. I-XIX.]

Owen, R., 1874. Monograph on the Reptilia of the Wealden and Purbeck formations. Supplement No. V *Iguanodon.* [Palaeontogr. Soc. (Monogr.) XXVII: 1-18, pls. 1, 11.]

Owre, O.T., 1967. Adaptations for locomotion and feeding in the anhinga and the double-crested cormorant. (Ornith. Monogr. 6: 1-138.)

Ostrom, J.H., 1970. Stratigraphy and paleontology of the Cloverly formation (Lower Cretaceous) of the Big Horn Basin of Wyoming and Montana. (Bull. Peabody Mus. nat. Hist. 35: 1-234.)

Ritgen, F.A., 1828. Versuch einer natürlichen Eintheilung der Amphibien. [Nova Acta Acad. Caesar. Leop. Carol. 14 (1): 247-284.]

Romer, A.S., 1922. The locomotor apparatus of certain primitive and mammal-like reptiles. (Bull. Am. Mus. nat. Hist. 46: 517-606.)

Romer, A.S., 1923. Crocodilian pelvic muscles and their avian and reptilian homologues. (Bull. Am. Mus. nat. Hist. 48: 533-552.)

Romer, A.S., 1923a. The pelvic musculature of the saurischian dinosaurs. (Bull. Am. Mus. nat. Hist. 48: 605-617.)

Romer, A.S., 1923b. The ilium in dinosaurs and birds. (Bull. Am. Mus. nat. Hist. 48: 141-145.)

Romer, A.S., 1927. Development of the thigh musculature of the chick. (J. Morph. 43: 347-385.)

Romer, A.S., 1927a. The pelvic musculature of ornithischian dinosaurs. (Acta Zool. Stockh. 8: 225-275.)

Romer, A.S., 1956. Osteology of the Reptiles. 722 pp., 248 figs. Chicago: University of Chicago Press.

Rozenweig, M.L., 1966. Community structure in sympatric Carnivora. (J. Mamm. 47: 602-612.)

Rozhdestvenskii, A.M., 1952. "A new Mongolian iguanodont." (C.R. Acad. Sci. URSS 84: 1243-1246, 3 figs. [In Russian].)

Rozhdestvenskii A.K., 1966. "New iguanodonts from Central Asia. Phylogenetic and taxonomic relationships between late *Iguanodontidae* and early *Hadrosauridae.*" (Paleont. Zh. 1966 (3): 103-116, 4 figs., 1 table [In Russian].)

Santa-Luca, A.P., 1980. The postcranial skeleton of *Heterodontosaurus tucki* (Reptilia: Ornithischia) from the Stormberg of South Africa. (Ann. S. Afr. Mus. 79: 159-211.)

Santa-Luca, A., Crompton, A.W. and Charig, A.J., 1976. A complete skeleton of the Late Triassic ornithischian *Heterodontosaurus tucki.* (Nature, Lond. 264: 324-328.)

Schoener, T.W., 1969. Size patterns in West Indian *Anolis* lizards. I. Size and species diversity. (Syst. Zool. 18: 386-401.)

Schoener, T.W., 1970. Size patterns in West Indian *Anolis* lizards. II. Correlations with sizes of particular sympatric species - displacement and convergence. (Amer. Nat. 104: 155-174.)

Seeley, H.G., 1883. On the dorsal region of the vertebral column of a new dinosaur (indicating a new genus *Sphenospondylus*) from the Wealden of Brook in the Isle of Wight, preserved in the Woodwardian Museum of the University of Cambridge. (Q. Jl. geol. Soc. Lond. XXXIX: 55-61, Figs. 1-3.)

Seeley, H.G., 1888. The classification of the Dinosauria. (Rep. Br. Ass. Advmt. Sci 57th meeting at Manchester, 1887: 698-699.)

Seeley, H.G., 1888a. On the classification of fossil animals commonly named Dinosauria. [Proc. Roy. Soc. 43 (260): 165-171.]

Synder, R.C., 1954. The anatomy and function of the pelvic girdle and hindlimb in lizard locomotion. (Am. J. Anat. 95: 1-46.)

Taquet, P., 1975. Remarques sur l'évolution des iguanodontidés et l'origine des hadrosauridés. (Coll. int. Cent. natn. Rech. scient. 218: 503-511.)

Taquet, P., 1976. Géologie et paléontologie du gisement de Gadoufaoua (Aptien du Niger). (Cahiers Paléont. Cent. natn. Rech. scient. 1976, pp. 191, 24 pls.)

Wever, E.G., 1978. *The reptile ear, its structure and function.* Princeton: University Press.

Appendix I

A catalogue of skeletal remains of *Iguanodon* sp. in the collections of the Institut Royal des Sciences Naturelles de Belgique updated and amended from CASIER (1960, 1978).

Registered number [letter code]	Notes and comments
IRSNB 1534 [Q]	*Holotype - I. bernissartensis* BOULENGER, 1881. Mounted skeleton, lacking: distal portions of digits II-IV of right manus, the distal phalanges of digits III-IV of left pes, the right ilium and an "intersternal ossification". Figured extensively in NORMAN (1980). Mounted 1882/3.
IRSNB 1535 [N]	*Paratype - I. bernissartensis.* Skeleton displayed "en gisement", lacking distal portions of both hindlimbs and many ribs. Skull figured by DOLLO (1883, pl. IX), CASIER (1960, pl. XII). Assembled in 1905.
IRSNB 1536 [A3]	*Paratype - I. bernissartensis.* Mounted skeleton lacking only distal end of tail. Figured extensively in NORMAN (1980). Mounted in 1888. (Skull sectioned sagittally).
IRSNB 1551 [T]	*I. atherfieldensis* HOOLEY, 1925 (*non. I. "mantelli"* VON MEYER, 1832). Mounted skeleton, well-preserved, lacking portion of tail. Figured DOLLO (1882) and CASIER (1960: pl. XIX), as "*I. mantelli*". Mounted in 1884.
IRSNB 1558 [N/A]	Distal end of left radius and ulna and left manus. Well-preserved, lacking only phalanx 3 of digit V. Figured NORMAN (1980: Figs. 59, 60, 78, 80). Also includes entire right forelimb. Assembled in 1905.
IRSNB 1561 [L]	*Paratype - I. bernissartensis.* Mounted skeleton, lacking distal portions of right radius and ulna, manus, and distal portions of right tibia, fibula and pes. Skull figured DOLLO (1923) and NORMAN (1980, pls. I, II). Mounted in 1886. (Skull partly disarticulated).
IRSNB 1562 [E2]	*Paratype - I. bernissartensis.* Mounted skeleton almost complete but poorly preserved. Mounted in 1890. (Skull transected).
IRSNB 1639 [R]	*Paratype - I. bernissartensis.* Mounted skeleton almost complete but poorly preserved. Mounted in 1905.
IRSNB 1657 [D2]	*Paratype - I. bernissartensis.* Mounted skeleton, skull poorly preserved. Both hindlimbs imperfect, tail missing. Mounted in 1905.
IRSNB 1680 [J]	*Paratype - I. bernissartensis.* Skeleton displayed "en gisement". Skull obliquely fractured, remainder of skeleton rather poorly preserved. Portions of left hindlimb and right forelimb missing. Assembled in 1891.
IRSNB 1709 [N/A]	*I. bernissartensis.* Forearm and manus embedded in matrix exposed on upper surface. The lower surface is encased in a plaster jacket in which can be seen iron rods for reinforcement, as described previously.
IRSNB 1710 [N/A]	*I. bernissartensis.* Distal part of tibia and right pes. Displayed as preserved in partial articulation. [Also carries original ref. nos.: 1737-023D].
IRSNB 1711 [N/A]	*I. bernissartensis.* Portion of tail preserved in articulation and displayed "en gisement". Assembled in 1905.
IRSNB 1712 [N/A]	*I. bernissartensis.* Major portions of two articulated feet and distal ends of the crus and tarsus. Assembled in 1905.
IRSNB 1713 [Z]	*Paratype - I. bernissartensis.* Mounted skeleton (imperfectly preserved). - Right manus and distal ends of hindlimbs missing. Mounted in 1904.
IRSNB 1714 [G]	*Paratype - I. bernissartensis.* Mounted skeleton. Pectoral girdle imperfect, forelimbs missing (except right humerus). Right hindlimb imperfect, distal end of tail missing. Mounted in 1904.
IRSNB 1715 [C2]	*Paratype - I. bernissartensis.* Skeleton notable for the degree of pyritic decay. Hindlimbs imperfectly preserved. Mounted in 1905.
IRSNB 1716 [A/B]	*Paratype - I. bernissartensis.* Part skeleton comprising the articulated tail, posterior portions of the pelvis, distal portions of left femur and hindlimb. This was the first skeleton to be excavated systematically and mounted. The anterior portion was undoubtedly destroyed during initial gallery construction. Mounted Nov. 1878.
IRSNB 1722 [M]	*Paratype - I. bernissartensis.* Skeleton displayed "en gisement", lacking skull and anterior cervical vertebrae. Assembled in 1905.
IRSNB 1723 [V]	*Paratypes - I. bernissartensis.* Skeleton (part) displayed "en gisement". Skull missing as are the forelimbs and distal end of the tail. Assembled 1905.
IRSNB 1724 [Y]	*Paratype - I. bernissartensis.* Skeleton displayed "en gisement". Skull missing, forelimbs imperfect. Assembled in 1905.
IRSNB 1725 [O]	*Paratype - I. bernissartensis.* Displayed "en gisement". Skeleton moderately well preserved, skull poor. This individual is unusually preserved having been dorsoventrally flattened. It is also interesting to note that this skeleton and IRSNB 1726 [U] have been inverted when compared to the original plans (see Fig. 9). Assembled in 1905.
IRSNB 1726 [U]	*Paratype - I. bernissartensis.* Skeleton displayed "en gisement". Dorsal vertebrae poorly preserved, as is the pectoral girdle. This is a smaller than usual (sub-adult?) individual. Assembled in 1905.
IRSNB 1727 [B3]	*Paratype - I. bernissartensis.* Skeleton displayed "en gisement". Skull missing as are parts of the pectoral girdle and the manus. Sternal bones figured by DOLLO (1885b). Assembled in 1905.
IRSNB 1728 [B2]	*Paratype - I. bernissartensis.* Skeleton displayed "en gisement". Lacks most of pectoral girdle and forelimbs, right hindlimb and distal end of tail. Assembled in 1905.
IRSNB 1729 [M2]	*Paratype - I. bernissartensis.* Skeleton displayed "en gisement". Skull badly crushed and disarticulated. Pelvis and right forelimb imperfect. This also appears to be a subadult individual. Figured by NORMAN (1980, Figs. 44, 46). Assembled in 1905.

IRSNB 1730 [F2]	*Paratype - I. bernissartensis.* Skeleton displayed "en gisement". Lacks skull and anterior vertebrae and parts of pectoral girdle. Another sub-adult individual. Figured in NORMAN (1980, Fig. 85). Assembled in 1905.
IRSNB 1731 [F]	*Paratype - I. bernissartensis.* Skeleton displayed "en gisement". Skull quite well preserved externally (CASIER, 1960, pl. XII). Dorsal vertebrae mostly missing as is pelvis and tail. Assembled in 1905.
IRSNB 1733 [X]	*I. bernissartensis.* Fragmentary forearm and right manus.
IRSNB 1723 [J2]	*I.* cf. *bernissartensis.* Poorly preserved series of caudal vertebrae "en gisement". Assembled? 1905.
IRSNB 1735 [N/A]	*I.* cf. *bernissartensis.* Ungual and distal phalanges of single pedal digit. (Note that this was found with IRSNB 1731 [F]).

Unregistered collections

"A"	*I.* cf. *bernissartensis.* Phalanges of pes, femoral fragment, sternal bone (possibly associated with 1716 [A/B]).
"C"	*I. bernissartensis.* Several cervical vertebrae, both humeri, sternal bones, distal radius and ulna, portions of manus, left scapulo-coracoid, part of ilium, various indeterminate fragments.
"D"	*I.* cf. *bernissartensis.* Fragments of the pes, ribs and zygapophyses.
"E"	*I.* cf. *bernissartensis.* Acetabular fragment of the left pubis, and portions of pubic rami. Indeterminate fragments.
"2F bis"	*I.* cf. *atherfieldensis.* Ilium, ischium, pubis, tibia, metatarsal and ulna.
"G2"	*I. bernissartensis.* Large scapulo-coracoid, humerus, fragments of radius and ulna, sternal bone, rib fragments, caudal vertebrae, fragments of pes. [Note: "found alongside Z"]
"H"	*I. bernissartensis.* Partial skeleton including fragments of skull, cervical vertebrae, dorsal vertebrae and rib fragments, some caudal vertebrae, parts of pectoral girdle and forelimb. [Note: proximal phalanx of digit I of manus figured in NORMAN (1980, Fig. 61, e-h)], fragments of hindlimb and the pes.
"K"?	[labelled "K3"]. Indeterminate fragments, possibly represents fragments found near individuals "M" and "N" (1722 and 1535 respectively).
"P"	*I.* cf. *bernissartensis.* Parts of hindlimbs and left and right pes and some indeterminate fragments [possibly represents fragments found overlying individual [G] (1714) referred to in excavation plans].
"R"	[Found with [R]-1639]. Humerus, radius and ulna, distal ends of tibia and fibula, fragments of vertebrae. Probably referable to "Rbis" of excavation plan 10.
"S"	*I. bernissartensis.* Partial skeleton consisting of moderately well preserved series of dorsal vertebrae, the sacrum, fragments of pelvis and anterior caudal vertebrae. [Figured in NORMAN (1980, Figs. 34-39)].
"Z"	*I. bernissartensis.* Partial skeleton comprising part skull, cervical vertebrae, dorsal ribs, fragments of the pelvis and limb bones. [This is apparently not referable to IRSNB 1713 - "Z", but represents another individual for which there are no excavation records].

[Note: Some additional material was collected from the coal tips ("terril") at Bernissart and includes several caudal vertebrae, ossified tendons and a small tooth crown which seem referable to *I. atherfieldensis.* There is no proof of association of this material with "2Fbis".]

GENERAL COMMENT

From the catalogue above it is possible to deduce that at a conservative estimate 37-38 individuals of the genus *Iguanodon* were collected from the locality at Bernissart; of these, there are at least 3 "sub-adult" specimens of *I. bernissartensis,* although these are all rather poorly preserved. There are also at least 2 specimens of *I. atherfieldensis,* with possibly even a third collected from the coal tips. The remainder all appear to be full-sized presumably adult specimens of *I. bernissartensis.*

Appendix 2
Skeletal measurements

I. *I. atherfieldensis* IRSNB 1551 (T)

	length (mm)	width (mm)	height (mm)
Skull	540	—	—

Cervical Vertebrae	length (mm) ventral	width (mm) anterior	height (mm) anterior	height neural spine (mm)	width neural spine (mm)
C_2—crushed	—	—	—	—	
C_3	55	54p	—	slight crest	—
C_4	62	61p	47e	"	—
C_5	62	46	47e	"	—
C_6	—	41	48e	"	—
C_7	68e	56	47e	—	—
C_8	61e	—	—	—	—
C_9	68e	72p	—	—	—
C_{10}	75	55	52e	—	—
C_{11}	—	—	—	—	—

Dorsal Vertebrae	length (mm) ventral	width (mm) anterior	height (mm) anterior	height neural spine (mm)	width neural spine (mm)
D_1	68e	59	52	21	—
D_2	70e	—	60e	—	—
D_3	80e	58	60e	—	—
D_4	—	—	—	—	—
D_5	—	—	—	—	—
D_6	—	—	—	—	—
D_7	71	—	59e	—	—
D_8	—	—	—	180	—
D_9	76	71p	63	200e	77
D_{10}	78	—	75	220	80e
D_{11}	80	63p	70e	220	80e
D_{12}	80	69	77	220	80e
D_{13}	79e	73	80e	—	—
D_{14}	82e	72e	—	—	—
D_{15}	88e	—	—	240e	80
D_{16}	70e	—	84p	240e	—
D_{17} (sacrodorsal)	80e	—	—	240e	—

Sacrum	length (mm) ventral	width (mm) anterior
S_1	—	crushed
S_2	—	"
S_3	—	"
S_4	77	slight ventral sulcus
S_5	80	" " "
S_6	77	slightly convex ventrally

Caudal Vertebrae	length (mm) ventral	width (mm) anterior	height (mm) anterior	height neural spine (mm)	length of chevron (mm)
Ca_1	68	102	81	—	artificial
Ca_2	72	92	85e	artificial	25 (style-like)
Ca_3	73	80e	90e	230(e)	24(e) (spatulate)
Ca_4	79	79e	84e	240(e)	22+
Ca_5	76	70e	85e	240(e)	265
Ca_6	—	70e	70(e?)	250	250
Ca_7	crushed	—	—	—	—
Ca_8	"	—	—	—	—
Ca_9	"	—	—	—	—
Ca_{10}	—	—	—	—	—
Ca_{11}	—	—	—	—	—
Ca_{12}	72	62	68(e)	20(e)	—
Ca_{13}	72	61	68(e)	—	—
Ca_{14}	74(e)	61	66(e)	165	—
Ca_{15} (last caudal rib)	76	61	68(e)	—	—
Ca_{16}	broken	60	65(e)	—	—
Ca_{17}	70	60	63(e)	—	115
Ca_{18}	—	60	—	—	—
Ca_{19}	72(e)	—	—	—	100
Ca_{20}	72	57	60	10(e)	95
Ca_{21}	73	58	56	75	85
Ca_{22}	70	57	54	75	65
Ca_{23}	72(e)	59	54	75	5(+e)
Ca_{24}	74	58	52	—	3(+e)
Ca_{25}	74	54(e)	51(e)	—	—
Ca_{26}	72	50(+)	—	—	—
Ca_{27}	70	53	—	—	—
Ca_{28}	70	56	50	—	—
Ca_{29}	70	52	46	—	—
Ca_{30}	—	—	—	—	—
Ca_{31}	72	51	42	—	—
Ca_{32}	72	50	4	—	—
Ca_{33}	70	50	4	—	—

Pectoral Girdle and Forelimb

			length (mm)	width proximal (mm)	width midlength (mm)	width distal (mm)
Scapula	R		610(e)	200	90	140(e)
	L		600(e)	180	85	140
Coracoid	R		120	N/A	160	N/A
	L		120	N/A	170	N/A
Humerus	R		440(e)	135	50	—
	L		430(e)	140	50	110
Radius	R		crushed	—	—	—
	L		345(e)	65(e)	—	—
Ulna	R		incomplete	—	—	—
	L		"	—	—	—
Metacarpals	R	II	115	—	—	—
		III	153	24	—	37(e)
		IV	135	34	—	25(e)
		V	66	43	—	31
	L	II	125	25	—	22
		III	155	24	—	35
		IV	155(e)	—	—	22
		V	67	41	—	30

Pelvic Girdle and Hindlimb

		length (mm)	height (mm)	length (postacetabular) (mm)
Ilium	R	700	140	200
	L	—	—	210
Ischium	R	—	—	—
	L	750(+)	—	—

		length (anterior ramus-mm)	width (distally-mm)	width (minimum-mm)
Pubis	R	—	202	104
	L	40	190	100

		length (mm)	width (proximal-mm)	width (distal-mm)	width (minimum-mm)
Femur	R	760	190	150	107
	L	—	—	160	—
Tibia	R	710	20(e)	197	75
	L	660(+)	—	180	75
Fibula	R	—	—	—	
	L	—	—	—	
Metatarsals	R II	200	—	—	
	R III	280	—	—	
	R IV	220	—	—	
	L II	190	—	—	
	L III	270	—	—	
	L IV	210	—	—	

II. *I. bernissartensis* Holotype IRSNB 1534 (Q)

Dorsal Vertebrae (examples)	length ventral (mm)	width (mm) anterior	height (mm) anterior
D_6	93	98	134
D_{10}	98	104	148
D_{16}	86	162	140(e)

Caudal Vertebrae	length ventral (mm)	width (mm) anterior	height (mm) anterior	length (mm) neural spine
C_1	92	170(e)	142	310
C_4	87	130(e)	140(e)	280
C_{10}	98	120(e)	123	230
C_{15}	104	106	106	180
C_{20}	100	97	86	110
C_{27}	98	90	84	60(+)
C_{37}	86	72	67	v. short prong
C_{43}	82	60	45	”

Pectoral Girdle and Forelimb

		length (mm)	width (mm) proximal	width (mm) distal	width (mm) minimum
Scapula	R	970	370	210	15(e)
	L	920	375	210	16
Coracoid	R	380	—	—	280
	L	370	—	—	280
Humerus	R	790	240	160	130
	L	820	230	160	125
Radius	R	490	95	55	65
	L	530	—	—	—
Ulna	R	640	120(+)	75	>8(e)
	L	650(e)	130	75	—
Metacarpals	R II	145	—	—	—
	III	—	—	—	—
	IV	—	—	—	—
	V	80	65	65	—
	L II	140	40	50	—
	III	190	60	60	—
	IV	190	70	55	—
	V	90	—	55	—

Pelvic Girdle and Hindlimb

		length (mm)	height (mm)	length (mm) postacetabular
Ilium	R	—	—	—
	L	1030+[110e]	250	310(+)

		length (mm)	width (mm) proximal	width (mm) distal	width (mm) minimum
Ischium	R	1240(e)	380	—	—
	L	1210	360	120	—
Pubis	R	470	170	93	—
	L	480	180	97	—
Femur	R	1030	270	240	155
	L	1020	260	240	160
Tibia	R	910	360	250	122
	L	900	380	250	133
Metatarsals	R II	270	210	100	—
	III	340	190	140	—
	IV	290	130	110	—
	L II	270	200	100	—
	III	340	170	140	—
	IV	264	100(e)	90+	—

Three partial "subadult" specimens

III. *I. bernissartensis* IRSNB 1726 (U)

Vertebrae	length (mm) ventral	height (mm) anterior
C_9	80	—
C_{10}	80	—
C_{11}	80	—
D_5	90	—
$D_{14/15}$	90	110p
Ca_1	80	100
Ca_5	80	90p
Ca_{14}	75	75
Ca_{20}	85	70
Ca_{30}	73	50
Ca_{41}	53	30

Appendicular skeleton

			length (mm)	width (mm) proximal	width (mm) distal	width (mm) minimum
Humerus	L		500	180	120	—
Radius	L		360(e)	—	—	—
Metacarpals	L	II	90	—	35	—
		III	150	45	—	—
		IV	—	—	40	—
Ilium			75+ [est 85 max]	—	—	—
Femur	L		73(?+)	—	—	—
Tibia	L		65(e)	270(e)	170(e)	100(e)
Metatarsal II			20(e)	—	—	—

IV. *I. bernissartensis* IRSNB 1729 (M2)

Vertebrae	length (mm) ventral	height (mm) anterior
C_5	84	—
C_7	85	—
D_5	92	—
D_7	94	neural spine - 290 mm long
Ca_{10}	82	80(e)
Ca_{14}	85	85

Appendicular skeleton

			length (mm)	width (mm) proximal	width (mm) distal	width (mm) minimum
Scapula	L		830(e)	320	180	140
Coracoid	L		280	—	—	190
Humerus	L		60(+)	200	130	90
Radius	L		480	80	90	55
Ulna	L		550(e)	—	90	60
Metacarpals	L	II	125	33	46	—
		III	170	45(e)	50e	—
		IV	165(+)	—	50e	—
		V	—	—	—	—
	R	II	130	40	45	—
		III	170	35(e)	50(e)	—
		IV	170	55	45	—
		V	85	50(e)	50(e)	—

V. *I. bernissartensis* IRSNB 1730 (F2)

Vertebrae	length (mm) ventral	height (mm) anterior	width (mm) anterior
D_{13}	82	72	72
D_{15}	87	—	100(e)
D_{16}	90	—	110(e)
Ca_3	78	85	—
Ca_4	78	80(e)	—
Ca_5	79	79	—
Ca_{10}	82	75	—
Ca_{13}	81	68	72
Ca_{18}	84	61	—
Ca_{21}	84	60	—
Ca_{29}	74	52	—
Ca_{35}	62	42	—

Appendicular skeleton

			length (mm)	width (mm) proximal	width (mm) distal
Humerus	R		530(e)	170	110
Metacarpals	L	II	100	40(e)	30
		III	145	30	40
		IV	150	50	40
		V	7–	—	—
	R	II	105	40(e)	—
		III	140	40	40(+)
		IV	—	—	—
		V	—	—	—
Pubis	R		38	72	150(e)
Metatarsals	R	II	235	85	—
		III	280	105	—
		IV	200(e)	85(e)	—
	L	II	220(+)	—	—

Appendix 3: Index of Abbreviations

A	Articular
a	primary ridge
acet	acetabulum
add	M. adductores
a.fo	adductor fossa
Al	alveolus
al.p	alveolar parapet
amb	M. ambiens
An	Angular
ant	anterior
a.o.ca	antorbital canal
a.pr	anterior process
ar	articular surface
ar.pal	arteria palatinus
as	astragalus contact
a.sh	anterior shelf
a.zyg	anterior zygapophysis
b	secondary ridge
bi	M. biceps
bi-br	insertions of M. biceps and branchialis
Bo	Basioccipital
br	M. brachialis
bs	surface for basioccipital
b.sh	brevis shelf
Bsp	Basisphenoid
c	tertiary ridge
ca	capitulum
cal	calcaneal contact
ca.rib	caudal rib
cb	M. coraco-brachialis
cc	M. costo-coracoideus
c.f.br	M. caudi-femoralis brevis
c.f.lo	M. caudi-femoralis longus
Co	Coronoid
D	Dentary
de	depression
dc	M. deltoides-clavicularis
D.caudae	M. dorsalis-caudae
dia	diapophysis
dp	dorsal process
ds	M. dorsalis scapulae
d. trunci	M. dorsalis trunci
Ec	Ectopterygoid
Ecf	ectopterygoid facet
es	surface for exoccipital
Ex	exoccipital
ext	M. femoro-tibialis externus
F	Frontal
fa	facet
fib	fibular contact
fi.c	fibular condyle
fl	flange
fl.tend	flexor tendon
fm	foramen magnum
for	foramen
fs	frontal suture
4th.tr	fourth trochanter
gl	glenoid
gr	groove(s)
gt	greater trochanter
i	ilium.
if.ext	M. ilio-femoralis externus
if.int	M. Ilio-femoralis internus
ic	Intercentrum
if.	M. ilio-femoralis
il	iliac contact
il.c	M. ilio-caudalis
il.fib	M. ilio-fibularis
il.tib 1	M. ilio-tibialis 1
il.tib 2	M. ilio-tibialis 2
il.tib 3	M. ilio-tibialis 3
il.tr1	M. ilio-trochantericus 1
il.tr2,3	M. ilio-trochantericus 2,3
im	inner malleolus
int	M. femoro-tibialis internus
isch	ischial facet
is.tr	M. ischio-trochantericus
jp	jugal process
Ju	Jugal
ju	jugal process of lachrymal
La	Lachrymal
la	lachrymal process
la.du	lachrymal duct
lat.abd	lateral abdominal muscles
ld	M. latissimus dorsi
ld-tm	insertions
lig	ligament scars
lp	lachrymal process
ls	M. levator scapulae
l.t	lesser trochanter
l.t.fen	lateral temporal fenestra
max	maxillary suture
mc1	metacarpal 1
me	Meckel's canal
Me.sh	medial shelf
mpp	median posterior premaxillary process
Mx	maxilla
N	Nasal
na	neural arch
na.s	nasal suture
nc	nasal cavity
ncs	neuro-central suture
nm	narial margin
ns	neural spine
nsr	neural spine recess
nub	nubbin
obt	obturator process
obt.for	obturator foramen
od	odontoid
ol	ossified ligaments
om	outer malleolus
Op	Opisthotic
Orb	orbital cavity
ot	ossified tendon
P	Parietal
p	M. pectoralis
Pa	Palpebral
paf	palpebral facet
Pal	Palatine
Par	Prearticular
par	parapophysis
pas	paroccipital suture
pat	Proatlas
Pd	Predentary

Pf	Prefrontal
p.i.f.i.1	M. pubo-ischio-femoralis internus 1
p.i.f.i.2	M. pubo-ischio-femoralis internus 2
Pmx	Premaxilla
pmg	Premaxillary groove
P.ob	Postorbital
pob.s	postorbital suture
Pp	Pleurosphenoid
p.pe	pubic peduncle
Pro	Proötic
ps	parietal suture
p.sh	posterior shelf
Psp	Parasphenoid
Pt	Pterygoid
p.t.fen	post-temporal fenestra
p.tib	M. pubo-tibialis
pt.pr	basiopterygoid process
pts	pterygoid suture
pu	pubic contact
p.zyg	posterior zygapophysis
Q	Quadrate
qc	quadrate cotylus
Q-j	Quadrato-jugal
qu	quadrate notch
r	rib
r.abd	M. rectus-abdominis
rep.cr	replacement crown
res	resorption facet
rf	rib facet
ri	ridge
sa.s	sacral suture
sa.y	sacral yoke facets
sbs	M. subcoraco-scapularis
sc	scar
sc	M. supracoracoideus
sd	sacrodorsal
ser.p	M. serratus profundis

ser.s	M. serratus superficialis
sh	shelf
sh	M. scapulo-humeralis
so	Supraoccipital
so.s	supraoccipital suture
Sp	Splenial
sp	surface for prefrontal
spal	surface for palpebral
Sq	Squamosal
sr	sacral rib
Sur	Surangular
sut	sutural surface
Sym	symphysis
t.gr	tooth groove
tib	tibial contact
ti.c	tibial condyle
tm	M. teres major
tpf	tranverse process facet
tr	M. triceps (insertion)
tra	M. trapezius
tr.c	M. triceps coraco-scapularis
tr.e	M. triceps scapulare lateralis externum
tr.f	transverse fluting
tr.l	M. triceps humeralis lateralis
tr.m	M. triceps humeralis medius
tr.p	M. triceps humeralis posticus
tu	tuberculum
u	ulnare
V	Vomer
vas.imp	vascular impressions
vcm	vena cerebralis media
vid	cidian canal
vp	ventral process
v.par	vena parietalis
vs	vomerine suture
vsl	ventral slip of M. ilio-trochantericus 2,3

Contents