THE ORNITHISCHIAN DINOSAUR *CAMPTOSAURUS PRESTWICHII* FROM THE UPPER JURASSIC OF ENGLAND

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ABSTRACT. The holotype of *Iguanodon prestwichii* Hulke, a reasonably complete skeleton from the Lower Kimmeridge Clay (Upper Jurassic, Lower Kimmeridgian) near Oxford, is redescribed and, because it is very similar to that of *Camptosaurus dispar* from the Upper Kimmeridgian of North America, is referred to the genus *Camptosaurus* as *C. prestwichii* (Hulke). The skeleton of *C. prestwichii* is more gracile and differs in a few other respects from those of *C. dispar*. *C. prestwichii* is the only undoubted species of *Camptosaurus* described from outside North America. The intramaxillary cavity of *Camptosaurus* probably housed a gland. Only the base of the paroccipital process of *C. prestwichii* is formed by the opisthotic, with the exoccipital forming the main occipital part. Documentation of an English species of *Camptosaurus* provides evidence for a land connection between Europe and North America some time during the early Late Jurassic, but the hypsilophodontid *Dryosaurus* may have used a different route between East Africa and North America.

PRESTWICH in 1879 announced the discovery of a skeleton of a new species of *Iguanodon* from the Lower Kimmeridge Clay (Upper Jurassic) at Cumnor Hurst near Oxford. The locality is Chawley Brick Pit, Hurst Hill, Cumnor, 2·5 miles west-south-west of the centre of Oxford (National Grid Reference SP 475 043). Prestwich (1880) provided a more detailed account of the geological occurrence of the specimen, which was named *Iguanodon prestwichii* by Hulke (1880, species name incorrectly given as *prestwichi* by most subsequent authors). The only description available of this reasonably complete skeleton is that given by Hulke (1880) who described most of the bones but only figured a few pieces of the skull, some teeth, the sacral centra, eight other vertebrae, and the proximal tarsals. Seeley (in Hulke 1880) considered that *I. prestwichii* represented a new genus, for which he subsequently (1888) erected the name *Cumnoria*. Lydekker (1888*a*) questioned the validity of the new genus and catalogued (1888*b*) the species as *I. prestwichii*. Lydekker (1889, 1890*a*) subsequently referred the species to the genus *Camptosaurus* Marsh (1885) as *Camptosaurus prestwichii* (Hulke). Gilmore (1909) redescribed the material of *Camptosaurus* from the Upper Jurassic of western North America and, after reviewing the description given by Hulke (1880), accepted *C. prestwichii* as a valid species of *Camptosaurus*.

In the intervening seventy years, *C.* (*Cumnoria*) *prestwichii* has received only a few passing mentions, with no restudy of the holotype. Consequently, almost a century later, the description given by Hulke (1880) still provides the only information available on this specimen. The specimen from the Lower Kimmeridge Clay (upper Lower Kimmeridgian, *Aulacostephanus pseudomutabilis* Zone, *c.* 141 m.y. ago, Van Hinte 1976) is important because it is a reasonably complete skeleton of an ornithopod dinosaur, a rare occurrence in the Middle and Upper Jurassic. Excellent material of ornithopod dinosaurs is known from the Morrison Formation (Upper Jurassic, Upper Kimmeridgian ≡ Lower Tithonian) of western North America (*C. dispar*, see p. 412), hypsilophodontids *Dryosaurus altus*, *Othnielia* Galton, 1977*a* (see Galton and Jensen 1973 as *Nanosaurus* ?*rex*)) and the Tendaguru Beds (Upper Kimmeridgian) of Tanzania (*D.* (= *Dysalotosaurus*) *lettowvorbecki* see Galton 1977*a*, *b*). A partial skeleton from the Upper Jurassic of Szechuan, China, was described as the iguanodontid *Sanpasaurus yaoi* Young (1944) but Rhozhdestvenskii (1967) showed that most of this material is that of a small sauropod dinosaur. The few other remains of ornithopod dinosaurs from the Middle and Upper Jurassic consist of single isolated bones (Steel 1969). Consequently, the material from Cumnor

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is the only associated skeleton of a non-hypsilophodontid dinosaur described from the Middle or Upper Jurassic outside North America. *Camptosaurus* is one of the few dinosaurian genera cited (Charig 1973; Galton 1977*b*) as occurring in the Upper Jurassic on both sides of the North Atlantic. If the Cumnor species is correctly referred to *Camptosaurus*, then the intercontinental distribution of this genus required the presence of a land route between western North America and southern England in the early part of the Late Jurassic.

Examination of the holotype of *I. prestwichii* resulted in the identification of all important pieces of bone apart from isolated pieces of neural arches and ribs. A redescription is needed for several reasons: Hulke (1880) provided an excellent description of the skull roof, braincase, jaws, and teeth, but additional cranial elements are now recognized, several of the bone identifications in the original description (one of the earliest for most of the bones of an ornithopod skeleton) are now found to be incorrect, and most of the bones of this skeleton have never been figured.

Unless noted to the contrary, the following references were used for comparative data on frequently cited ornithopod genera: Upper Jurassic, North America, *Camptosaurus* (Gilmore 1909), hypsilophodontid *Othnielia* Galton, 1977*a* (Galton and Jensen 1973 as *Nanosaurus ?rex*); East Africa, hypsilophodontid *Dryosaurus* (Janensch 1955); Lower Cretaceous, Europe, hypsilophodontid *Hypsilophodon* (Galton 1974*a*), iguanodontids *Ouranosaurus* (Taquet 1976), and *Iguanodon* (Hooley 1925); North America, *Tenontosaurus* (Ostrom 1970); Upper Cretaceous, North America, hypsilophodontid *Parksosaurus* (Parks 1926 as *Thescelosaurus warreni*), thescelosaurid *Thescelosaurus* (Gilmore 1915).

The reasons for referring *I. prestwichii* Hulke (1880) to the genus *Camptosaurus* rather than to the separate genus *Cumnoria* Seeley (1888) are discussed below (p. 431). In the comparative section, many references are made to the Morrison material of *Camptosaurus* Marsh (1885), five species of which were recognized by Gilmore (1909). Later, Gilmore (1925) recognized three species, the genotype *C. dispar*, the small *C. nanus*, and the large *C. amplus*. Gilmore (1925) noted that *C. medius* is perhaps a female *C. dispar*, and *C. browni* is probably a fully grown *C. medius*. Janensch (1955) noted that the characters used to distinguish *C. nanus* from *C. dispar* were probably juvenile features. The holotype of *C. amplus* is a pes of the carnivorous theropod *Allosaurus fragilis* (Bakker, pers. comm.; Gilmore 1909, pl. 17, cf. fig. 35, and Madsen 1976, pl. 53). The holotypes of four species of *Camptosaurus* (*C. dispar*, *medius*, *nanus*, *browni*) all came from Quarry 13 near Como, Wyoming (see Ostrom and McIntosh 1966; Gilmore 1909), and, given the range of individual variation shown by two species of *Dryosaurus* (Galton 1977*a*, *b*) and by *Hypsilophodon foxii*, it is reasonable to refer all the Morrison material to one species of *Camptosaurus*, *C. dispar* (Marsh 1879), and references to *Camptosaurus* given in the comparative section are to this American species.

Institution names have been abbreviated as follows: AMNH, American Museum of Natural History, New York; BMNH, British Museum (Natural History), London; CUM, Cambridge University Sedgwick Museum; HMN, Humboldt Museum for Naturkunde, East Berlin; OUM, University Museum, Oxford; USNM, United States National Museum, Washington DC; YPM, Peabody Museum, Yale University, New Haven.

DESCRIPTION AND COMPARISONS OF *CAMPTOSAURUS PRESTWICHII* (HULKE)

(based on specimen no. J330 in the University Museum, Oxford)

Skull

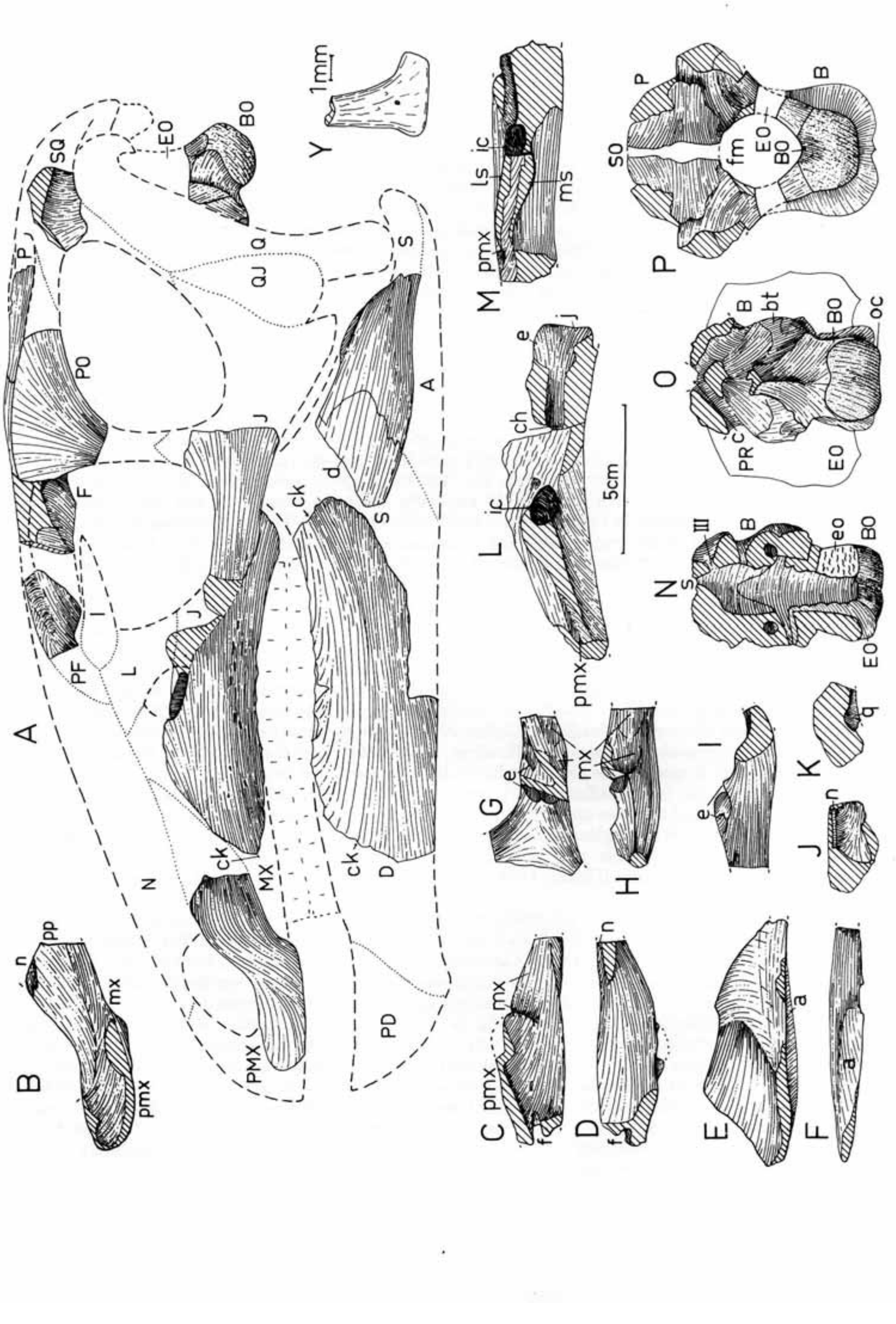
Apart from the braincase (text-fig. 1N–R; pl. 51, figs. 1–4), all the bones of the skull have separated at the sutures, and this presumably indicates that the animal was not an adult. The skull is long and low but broad (text-fig. 1A, S) rather than being proportionally higher and narrower as in all other ornithopod dinosaurus with the exception of *Camptosaurus*, *Ouranosaurus*, and some hadrosaurs (e.g. *Anatosaurus*, Lull and Wright 1942). However, the form of the individual bones is similar only to those of *Camptosaurus* (text-figs. 1A, 2A, B).

Dermal bones. The premaxilla (text-fig. 1A–D; pl. 52, fig. 16) is edentulous, and anteriorly there is a prominent foramen on the ventral surface (text-fig. 1D). This foramen appears to have opened on the lateral surface at the base of the anterior process, as does a comparable foramen in the premaxilla of *Camptosaurus* (Gilmore 1909, fig. 6). The massive posterior process overlapped the nasal dorsally (text-fig. 1A, B) and the maxilla fitted against its ventral surface, which has prominent sutural ridges at its base (text-fig. 1B, C; pl. 52, fig. 16). As in *Camptosaurus* (YPM 1880) and *Dryosaurus* (HMN dy 14), there is an anteriorly tapering groove on the medial surface (text-fig. 1B; pl. 52, fig. 16) which received a medial process of the maxilla and, as a result, the anterior end of the maxilla was probably expanded transversely, with an anteriorly projecting medial process as in *Camptosaurus* (YPM 1886), *Dryosaurus* (Janensch 1955, p. 11, fig. 2; YPM 1876), and the ornithopod *Priodontognathus* (CUM B53408, left maxilla, see Seeley 1875*a*, pl. 20, figs. 1, 2 for internal and external views). The posterior process of the premaxilla fitted into a groove on the antero-dorsal edge of the maxilla (text-fig. 1L, M; pl. 51, figs. 13, 14) as in *Camptosaurus* (USNM 5819; YPM 1886), *Dryosaurus*, *Iguanodon*, and *Ouranosaurus*. The antero-dorsal part of the maxilla is transversely constricted; dorsally, only the bases of the two sheets against which the anterior part of the lachrymal fitted are preserved. There is a well-defined sutural surface for the ectopterygoid on the jugal (text-fig. 1G, I; pl. 52, fig. 15) and, as the jugal is narrower than the maxilla (text-fig. 1I, L), the ectopterygoid also fitted against the postero-dorsal part of the maxilla.

About 15 mm above the maxillary tooth row, there is a prominent horizontal ridge with fine striations on the lateral surface (text-fig. 1A; pl. 52, fig. 7) which probably represents an attachment area for a muscle functionally analogous to the cheeks of mammals (Galton 1973*a*). Anteriorly, and also below this ridge, the lateral surface is pierced by several small foramina which pass obliquely backward. The foramina presumably unite within the maxilla and emerge postero-dorsally through a deep channel medial to the sutural area for the jugal (text-fig. 1L; pl. 52, fig. 14). Most of the maxilla is solid bone with a small fossa (text-fig. 1L, M; pl. 52, figs. 13, 14) immediately below the external antorbital fenestra (text-fig. 1A). The fossa opens dorsally and, in the left maxilla, this uncrushed oval aperture is 14 mm long and 10 mm wide, while the fossa is 11 mm deep with the walls progressively tapering inwards. In *Camptosaurus* (YPM 1886; Gilmore 1909, fig. 7) the fossa or intramaxillary cavity is proportionally much longer, extending a distance equal to a little more than four crown-widths posteriorly from the anterior border of the external antorbital fenestra, with the floor slightly above the most ventral line of the lateral foramina. Examination of several maxillae (USNM 5819; YPM 1886, 7417) indicates that these foramina do not pass into the intramaxillary cavity, and presumably they eventually pass into the postero-dorsal channel. Posteriorly the cavity appears to be completely closed off from the postero-dorsal channel by a narrow transverse bar of bone. Although the intramaxillary cavity of *Camptosaurus* is proportionally much larger, it also opens only dorsally.

The intramaxillary cavity is a remnant of the antorbital fenestra of thecodontians, which became enclosed by the maxilla. The large antorbital fenestra of thecodontians (Walker 1961; Ewer 1964) and the large intramaxillary cavity of lower ornithischians (Galton 1974*a*) probably acted as the area of origin of an anterior component of the pterygoideus musculature. However, Ewer (1964) notes that the original function of a small antorbital fenestra of thecodontians was probably to house a gland that might have been a nasal salt gland. The pit-like form of the intramaxillary cavity (text-fig. 1C) clearly precludes any function as an area of muscular attachment, and this also appears to be the case in *Camptosaurus*. The only structure which could have occupied such a cavity is a gland. The large antorbital fenestra and intramaxillary cavity of the ornithischian dinosaur *Hypsilophodon* may have provided an area of origin for an anterior component of the pterygoideus musculature (Galton 1974*a*) and, in addition, a gland probably occupied part of the cavity.

The upper orbital margin is formed principally by the prefrontal and postorbital, parts of which are rugose, with only a small contribution from the frontal (text-fig. 1A, T, S; pl. 51, figs. 5, 6). The orbital part of the postorbital (text-fig. 1A, S) is similar to that of *Camptosaurus* (USNM 5473; Gilmore 1909, pl. 10; USNM 7421) and the continually smooth curve shown for the postero-dorsal part of the orbit (text-fig. 2A; Gilmore 1909, fig. 3) is inaccurate. A groove on the medial edge of the prefrontal probably fitted against the nasal (text-fig. 1J, T, S), and the posterior end fitted into the frontal (text-fig. 1A, T, U, W). The medial surface of the posterior process of the postorbital has a triangular sutural area (text-fig. 1T; pl. 51, fig. 6) for the squamosal, only a small part of which is preserved (text-fig. 1A, K). The postorbital and frontal have a broad and complex sutural surface (text-fig. 1S, T, X; pl. 51, figs. 5, 6), the details of which are the same as in *Camptosaurus* (USNM 7421), and both bones are overlapped by the parietal postero-laterally (text-fig. 1S, T). The skull roof (text-fig. 1S) is similar to that of *Camptosaurus* (Gilmore 1909, pl. 10). The postorbital and frontal together form a sutural surface for the expanded anterior end of the laterosphenoid (as in *Camptosaurus* USNM 5473 and *Hypsilophodon*), with the rest of the bone fitting against the parietal (text-fig. 1T; pl. 51, fig. 6).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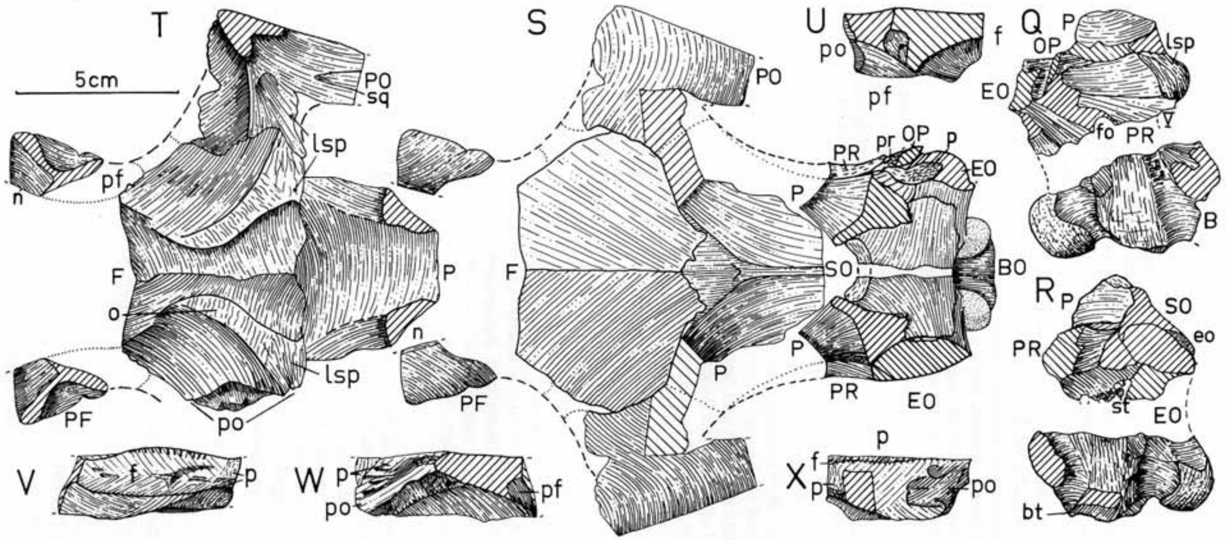


TEXT-FIG. 1. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303 × 0·5. Skull bones. A, reconstruction of skull in left lateral view with bones arranged in an appropriately distorted outline of the skull of *C. dispar* (after Gilmore 1909); B–D, right premaxilla in B, medial (see pl. 52, fig. 16); C, ventral and D, dorsal views; E, F, right surangular in E, medial and F, ventral views; G–I, left jugal in G, medial (see pl. 52, fig. 15); H, ventral and I, dorsal views; J, left prefrontal in medial view; K, right squamosal in medial view; L, M, maxillae in dorsal view, L, left (see pl. 52, fig. 14), M, right (see pl. 52, fig. 13); N–R, braincase, N, dorsal view of floor (see pl. 51, fig. 4), O, ventral view (see pl. 51, fig. 3); P, posterior view; Q, outline of right lateral view, compare with pl. 51, fig. 1; R, outline of left lateral view; S, dorsal view of posterior skull roof and braincase (see pl. 51, figs. 2, 5); T, ventral view of posterior skull roof (see pl. 51, fig. 6); U–X, right frontal in U, anterior; V, medial; W, lateral and X, posterior views; Y, stapes (× 4). For T, S, P, O, and N see also Hulke (1880, pl. 18, figs. 1–5). In all figures broken bone is indicated by mechanical shading. Abbreviations: A, angular; B, basisphenoid; BO, basioccipital; D, dentary; EO, exoccipital; F, frontal; I, infraorbital (= supraorbital); J, jugal; L, lachrymal; MX, maxilla; N, nasal; OP, opisthotic; PO, postorbital; PR, prootic; Q, quadrate; QJ, quadratojugal; S, surangular; SQ, squamosal; SO, supraoccipital. The same abbreviation in lower case indicates a sutural surface for that bone on another bone. bt, basisphenoid tubera; c, route of internal carotid artery; ch, channel; ck, ridges for attachment of cheeks; e, surface for ectopterygoid; f, combined foramen lacerum posterius and jugular foramen for internal jugular vein; fm, foramen magnum; fo, fenestra ovalis; ic, intramaxillary cavity; ls, lateral sheet; ms, medial sheet; o, surface for orbitosphenoid; oc, occipital condyle; pp, posterior process; s, sella turcica or pituitary fossa; st, stapes. III, oculomotor foramen; V, trigeminal nerve.

Braincase. A detailed description of the braincase (text-fig. 1Q, R, S; pl. 51, figs. 1–4) was given by Hulke (1880). The postero-lateral parts of the parietal fit closely on each side of the supraoccipital (text-fig. 1P, S; pl. 51, fig. 2) which is proportionately larger than it is in *Camptosaurus* (USNM 5473). As also in *Camptosaurus*, *Dryosaurus*, and *Hypsilophodon*, the supraoccipital is not excluded from the dorsal margin of the foramen magnum, as it is in *Iguanodon* (Dollo 1883*a*). The following features occur also in *Camptosaurus*: the postero-dorsal surface of the exoccipital lateral to the foramen magnum bears a prominent subcircular depression; ventrally the exoccipitals contribute to the lateral part of the occipital condyle (text-fig. 1P); and anterior tongue-like process of the basioccipital fits into a corresponding notch in the basisphenoid (text-fig. 1N, O; pl. 51, figs. 3, 4), and ventrally the process has a sharp median crest that arises out of a depression immediately anterior to the occipital condyle (text-fig. 1O). The flared-out antero-lateral part of the basioccipital is embraced by the massive buttress-like basisphenoid tubera (text-fig. 1O; pl. 51, fig. 3). Anteriorly the floor of the braincase has broken at the level of the posterior part of the sella turcica (text-fig. 1N, O) and more ventrally along the postero-laterally directed canals through which the internal carotid arteries passed to the pituitary fossa. Only the dorsal parts of these canals are preserved, and dorso-laterally it merges with the groove in which rami of the trigeminal and facial nerves passed ventrally after exiting from the braincase (text-fig. 1Q, R; pl. 51, fig. 1; see also Galton 1974*a*).

In nearly all ornithischians including *Camptosaurus* there is no trace of the suture between the exoccipital and the opisthotic, so the composition of the paroccipital process cannot be determined. This is the case on the left side (text-fig. 1R, S), but on the right the opisthotic is represented by a separate element which overlaps the antero-lateral part of the base of the paroccipital process and which is itself overlapped by the tapering dorsal part of the prootic (text-fig. 1Q, S; pl. 51, fig. 1). More ventrally the bone is broken, but the arrangement resembles that of the braincase of a juvenile hadrosaur described by Langston (1960) in which the main occipital part of the paroccipital process is formed by the exoccipital. In *Hypsilophodon*, the only other ornithischian for which information is available, the exoccipital is restricted to the lateral part of the occipital condyle. Anteriorly the prootic abutted against the dorsal part of the laterosphenoid and was itself slightly overlapped more ventrally (text-fig. 1Q; pl. 51, fig. 1). Breaks go through all of the cranial foramina, and the ventral borders of a few are preserved (text-fig. 1Q, R; pl. 51, figs. 1, 4). The dorsal part of the large foramen at the junction of the prootic and opisthotic is separated by a thin vertical septum. This area is similar to that of *Camptosaurus* and *Hypsilophodon* in which the anterior part is interpreted as the fenestra ovalis and the posterior and ventral parts as a combined foramen lacerum posterius and jugular foramen (Galton 1974*a*).

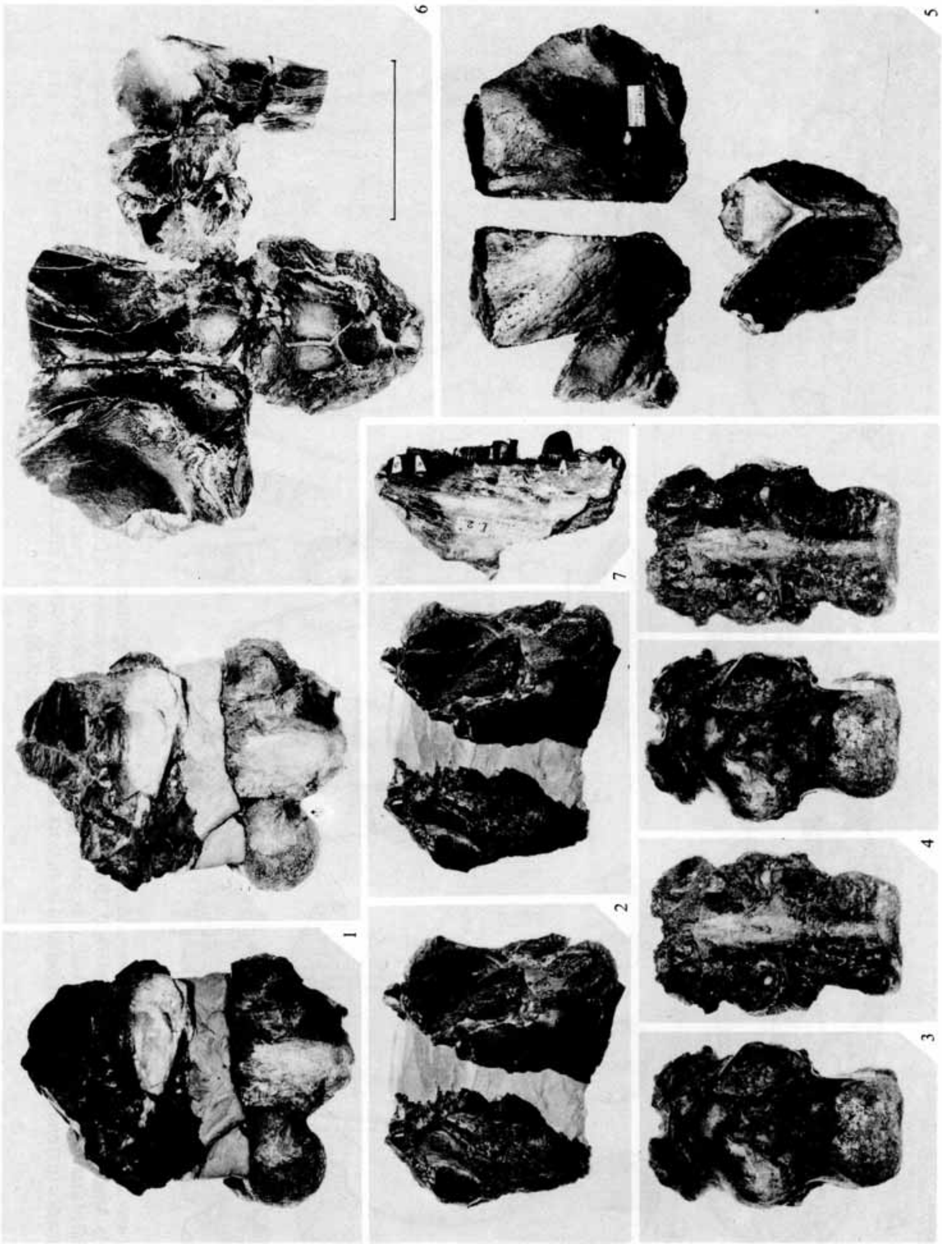
Mandible. The lateral surface of the dentary has a well-defined horizontal ridge (text-fig. 1A) which probably served as an attachment area for the cheeks (Galton 1973*a*). The medial view of the dentary (pl. 52, fig. 17) resembles that of *Camptosaurus* (Gilmore 1909, fig. 8), including the presence of a sutural area below the posterior six teeth which was probably for the antero-ventral part of the coronoid bone. The surangular (text-fig. 1A, E, F) is a sheet-like bone that was presumably overlapped antero-laterally by the dentary, which thickens ventrally to form a ventral surface, bordered laterally by a distinct edge, against which the angular fitted. A bevelled edge on the postero-lateral edge probably represents the posterior part of the insertion area of the M. adductor externus superficialis (see Ostrom 1961; Galton 1974*a*).

Dentition. The premaxilla is edentulous. The left maxilla has thirteen teeth and the left dentary has fourteen teeth, with two or three probably missing in each case, to give the same total count as for *C. dispar* (fourteen and fifteen or sixteen). Most of the teeth are broken, and only the crowns of incompletely erupted teeth are preserved. The original appearance of the dentary tooth row must have been as in *Camptosaurus* (Gilmore 1908, fig. 8). Several of the roots of functional teeth of the dentary show evidence of resorption adjacent to, and slightly above, the crown of the replacement teeth (pl. 52, fig. 7). In a study of tooth replacement in reptiles, Edmund (1960) found that all the teeth with 'odd' numbers in a numbered tooth series are replaced in sequence, followed by the 'even'

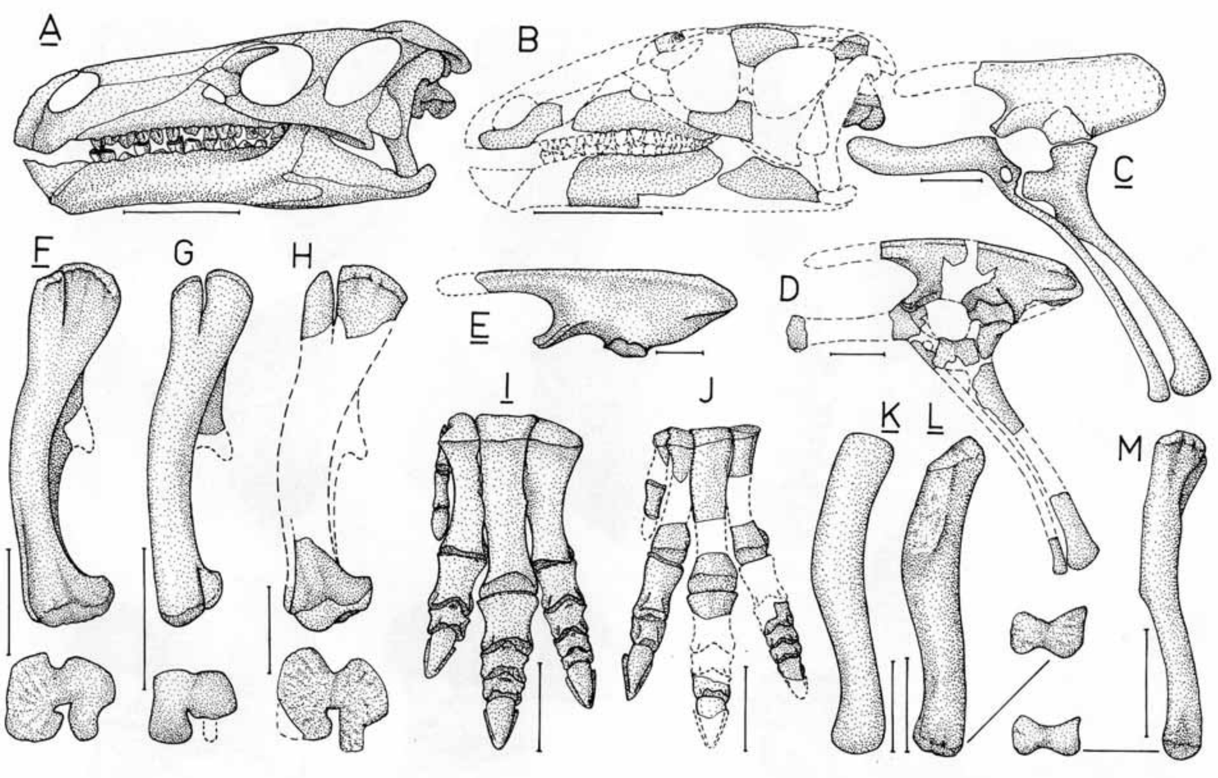
EXPLANATION OF PLATE 51

Cranial bones of *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303.

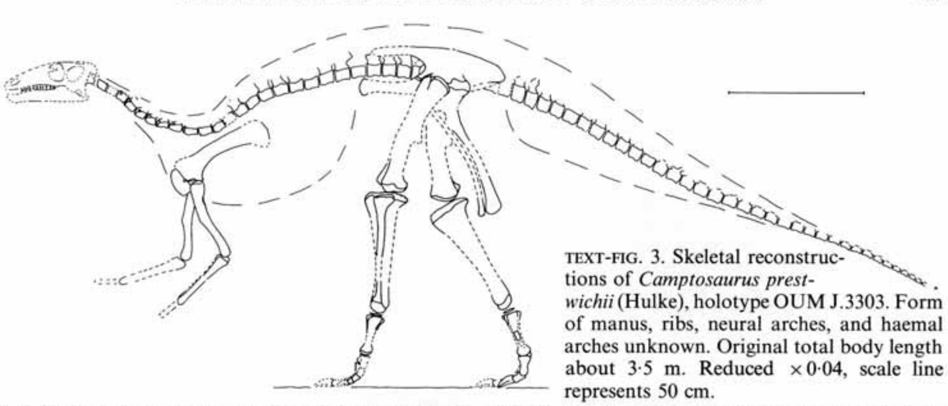
Fig. 1, braincase in right lateral view (cf. text-fig. 1Q), $\times\frac{2}{3}$.
Fig. 2, braincase in dorsal view (cf. text-fig. 1S), $\times\frac{2}{3}$.
Fig. 3, floor of braincase in ventral view (cf. text-fig. 1O), $\times\frac{2}{3}$.
Fig. 4, floor of braincase in dorsal view (cf. text-fig. 1N), $\times\frac{2}{3}$.
Fig. 5, frontals and parietals in dorsal view (cf. text-fig. 1S), $\times\frac{1}{2}$.
Fig. 6, frontals, parietal and left postorbital in ventral view (cf. text-fig. 1T), $\times\frac{1}{2}$.
Fig. 7, damaged right maxilla in lateral view (cf. text-fig. 1A), $\times\frac{1}{2}$.



GALTON and POWELL, dinosaur *Camptosaurus*



TEXT-FIG. 2. Comparison of *Camptosaurus dispar* (A, C, E, F, I, K, L; identifying letters underlined to facilitate comparisons) from Upper Jurassic of North America with *C. prestwichii* (OUM J.3303, B, D, H, J, M) from Upper Jurassic of England and '*C.*' *leedsi* (G, holotype BMNH R1993) from Middle Jurassic of England. A, B, skull; C, D, pelvic girdle; E, ilium; F–H, femur; I, J, pes; K–M, humerus. Views—left lateral (A–H, K–M), dorsal or anterior (I, J) and with distal end included (F–H, L, M). A, C, E after Gilmore (1909), K after Gilmore (1912), F, I, L holotype YPM 1877. Scale line represents 10 cm.



TEXT-FIG. 3. Skeletal reconstructions of *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303. Form of manus, ribs, neural arches, and haemal arches unknown. Original total body length about 3·5 m. Reduced ×0·04, scale line represents 50 cm.

and, in most cases, the waves of tooth replacement pass anteriorly, so that the replacement teeth of each series become progressively smaller passing anteriorly. This pattern is clearly seen in the right maxilla and in both dentaries (pl. 52, fig. 7; Hulke 1880, pl. 18, fig. 8) as is also the case in *Camptosaurus* (Gilmore 1909, fig. 8). In *Hypsilophodon* and other lower ornithopods (Galton 1973*b*), there is a shallow groove bearing a line of foramina, one per tooth position, for the access of replacement teeth (Edmund 1957), on the medial surface above the maxillary tooth row and below the dentary tooth row. Although these foramina are absent in the material figured by Gilmore (1909), this is probably due to damage, as they are well shown by other specimens (YPM 1886, 1889, 7416, 7417, 7419, 7421).

The teeth were well described by Hulke (1880) and are very similar to those of *Camptosaurus* (pl. 52, figs. 1–12). The crowns are roughly lozenge-shaped and the antero-posterior width is greater for dentary teeth than it is for maxillary teeth, whereas the reverse is true for the transverse thickness. The shiny enamelled surface of the elaborately sculptured side of the crown (lateral for maxilla, medial for dentary) merges smoothly into the matt surface of the root with a sinuous line as the only sign of the cingulum (pl. 52, figs. 3, 4, 7). On the plain side of the crown, only the denticulate half of the crown height is covered with a thin layer of enamel, which shows a few faint transverse ridges, and a few of the terminal denticles are prolonged into short ridges (pl. 52, fig. 1). The sides of the non-denticulate half of the crown of maxillary teeth show only a small degree of convergence toward the root, whereas in dentary teeth it is much more marked (pl. 52, figs. 3, 7–9). On maxillary teeth, the anterior and posterior edges of this half of the crown form distinct ridges, whereas only the posterior edge of dentary teeth forms such a ridge (pl. 52, figs. 3, 7–9). In dentary teeth, the medial surface of the upper end of this ridge has a series of extremely fine serrations (6 in 2 mm; pl. 52, figs. 7–9). Traces of these serrations are visible on the anterior ridge of a maxillary tooth and also in the corresponding positions on very well-preserved dentary and maxillary teeth of *Camptosaurus* (USNM 5819; YPM 7416) and *Iguanodon* (Owen 1861*a*).

The prominent vertical keel on the lateral surface of the maxillary teeth is proportionally closer to the posterior edge than it is in most specimens of *Camptosaurus* other than USNM 5818 (pl. 52, figs. 2, 3, 6). On the medial surface of dentary teeth this ridge is smaller and it is just posterior to the centre of the crown, as it is in *Camptosaurus* (pl. 52, figs. 7–12). There are no secondary vertical ridges posterior to this keel in maxillary and dentary teeth (pl. 52, figs. 2, 3, 7–9). This is also the case for some teeth of *Camptosaurus* (dentaries USNM 4281; YPM 1886, pl. 52, fig. 10) and in other teeth (pl. 52, figs. 6, 11, 12) the number of ridges in this position varies from one to four. Anterior to the prominent keel there are several ridges of different lengths (pl. 52, figs. 2, 3, 7–9). For maxillary and dentary teeth, the number of ridges reaching the base of the crown is 3 and 2 respectively (in *Camptosaurus* the numbers are 2, 3 or 4, and 2), the number reaching the middle of the crown is 5 and 2 (as against 3 or 4 and 2 or 3), and the number of short ridges is 1 and 1 (as against 1, 2 or 3, and 2).

The crowns of the teeth of *Iguanodon* show a wide range of variation (Owen 1855, 1861*a*, 1874; Galton and Jensen 1975, 1979*a*) but appear to differ in a few respects from those of *Camptosaurus*. In *Iguanodon* teeth only one side of the crown is enamelled (Owen 1854), it is more elaborately sculptured, and the free edge of the small, plate-like marginal denticles are minutely mammillated (Hulke 1880), whereas in OUM J.3303 and *Camptosaurus* the margin is even. The teeth of *I. hoggii* Owen (1874) from the upper part of the Lulworth Beds (Lower Cretaceous, Berriasian; Dodson *et al.* 1964; Hallam 1975) of Dorset are the most similar, but in this species the dentary tooth crowns are proportionally more elongate and there are two very prominent vertical ridges at one-third and two-thirds crown width, rather than one that is about in the centre (pl. 52, figs. 7–9). The maxillary teeth of the iguanodontid *Priodontognathus phillipsi* (Seeley 1875*a*; CUM B.53408; see Lydekker 1893, pl. 11, fig. 3; may be from Upper Jurassic of Yorkshire) are very different from those of *Camptosaurus*: in medial view the crown is subtriangular with only a hint of a central vertical thickening, the marginal denticles are proportionately large and the cingulum consists of two crescentic flanges with small denticles along the lower edge. In *Tenontosaurus* the dentary teeth have the prominent keel that is completely lacking on the maxillary teeth, whereas in *Dryosaurus* the prominent keel is equally well developed on both sets of teeth (Janensch 1955; YPM 1876).

Stapes. The proximal 4·5 mm of the left stapes is preserved in the ventral part of the large foramen between the prootic and the opisthotic (text-fig. 1Y).

The preserved part is boot shaped and the expanded footplate has a maximum diameter of 4·0 mm and the minimum diameter of the broken end of the shaft is 1·5 mm. Originally the stapes was probably a slender rod connecting the fenestra ovalis to the tympanum, which was supported by the paroccipital process and the quadrate as described for the hadrosaur *Corythosaurus* (Colbert and Ostrom 1958; Ostrom 1961). The stapes is also preserved in the hadrosaur *Anatosaurus* (Colbert and Ostrom 1958), the hypsilophodontid *Dryosaurus* (HMN dy B), the theropod *Dromaeosaurus* (Colbert and Ostrom 1958), the prosauropods *Anchisaurus* (Galton 1976*a*) and *Plateosaurus* (Colbert and Ostrom 1958), and the discovery of a stapes in a skull of the sauropod *Camarasaurus* is reported by King (1978). Its absence from most dinosaur skulls is presumably a function of its fragility, because the more robust ceratobranchials are also rarely preserved.

Vertebral column

No information is available concerning the original order of the vertebrae, all of which are crushed or broken to a varying degree (text-figs. 4–7). Many of the vertebrae are preserved only as centra, the measurements of which are given in Table 1. The vertebral count is estimated as 9 cervicals, 16 dorsals, 6 sacrals, and about 45 caudals (text-fig. 3).

Cervical vertebrae (text-fig. 4A–J). There are 7 cervicals in addition to the missing atlas and third cervical, so that the total count was probably 9 as in *Camptosaurus*, *Dryosaurus*, and *Hypsilophodon* rather than 10 or 11 as in *Iguanodon* (Dollo 1883*b*, 1884; Hooley 1925), 11 as in *Ouranosaurus*, and 12 as in *Tenontosaurus*. All the cervical centra show some degree of crushing and are opisthocoelous with a convex anterior surface and a concave posterior surface. A strong ventral keel that widens slightly anteriorly and more markedly posteriorly is present on cervicals four to nine. The parapophysis is very low on the axis, lies just below the neurocentral suture on the fourth and fifth cervicals, and is bisected by it on the remaining cervicals. The corresponding cervicals of *Camptosaurus* are opisthocoelous with the concavity either more strongly (USNM 5473) or more weakly developed (USNM 5474) and the centra are less angular in anterior view (Gilmore 1909).

EXPLANATION OF PLATE 52

Teeth and cranial bones of *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303 (1–4, 7–9, 14–16) and teeth of *C. dispar* (Marsh), holotype YPM 1877 (11) plus referred specimens YPM 7416 (5, 7, 12) and USNM 4281 (10). Maxillary teeth illuminated from below to show ornamentation more clearly.

Figs. 1–4, teeth of middle of right maxilla, × 2; 1, medial view of erupting crown; 2, lateral view of 1, 3, lateral view of fully erupted crown; 4, anterior view of 3.

Figs. 5, 6, teeth of right maxilla, × 2; 5, medial view; 6, lateral view.

Fig. 7, teeth on posterior part of right dentary in medial view, × 2; these teeth were the basis of the reconstruction by Hulke (1880, pl. 18, fig. 8).

Fig. 8, second tooth from posterior end of left dentary in medial view, × 2 (tooth a in Fig. 17).

Fig. 9, tenth tooth from posterior end of left dentary in medial view, × 2 (tooth b in Fig. 17).

Fig. 10, teeth on posterior part of right dentary in medial view, × 2.

Fig. 11, middle dentary tooth in medial view, × 1·5.

Fig. 12, tooth on right maxilla in medial view, × 2.

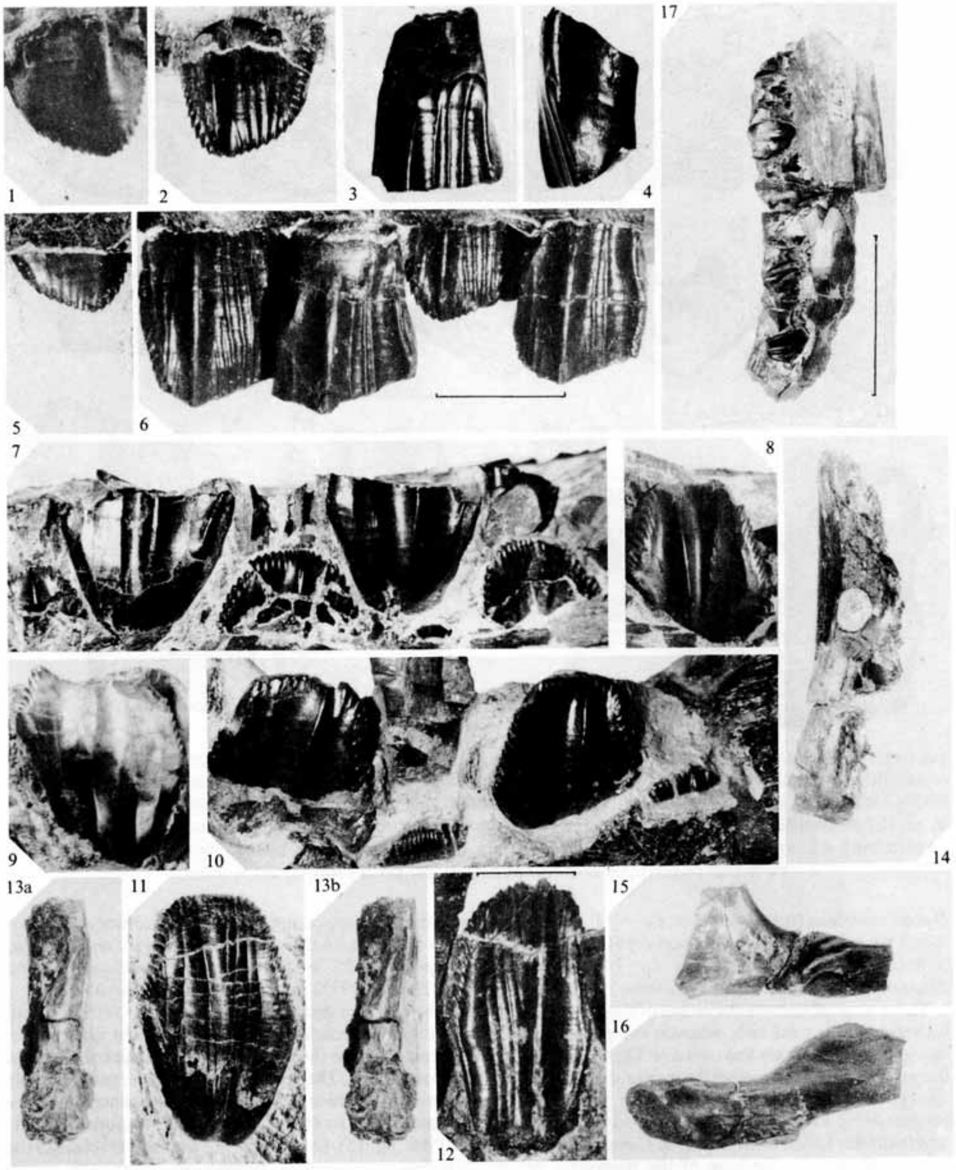
Fig. 13, stereophotographs of right maxilla in dorsal view (cf. text-fig. 1M), × 0·5.

Fig. 14, left maxilla in dorsal view (cf. text-fig. 1L), × 0·5.

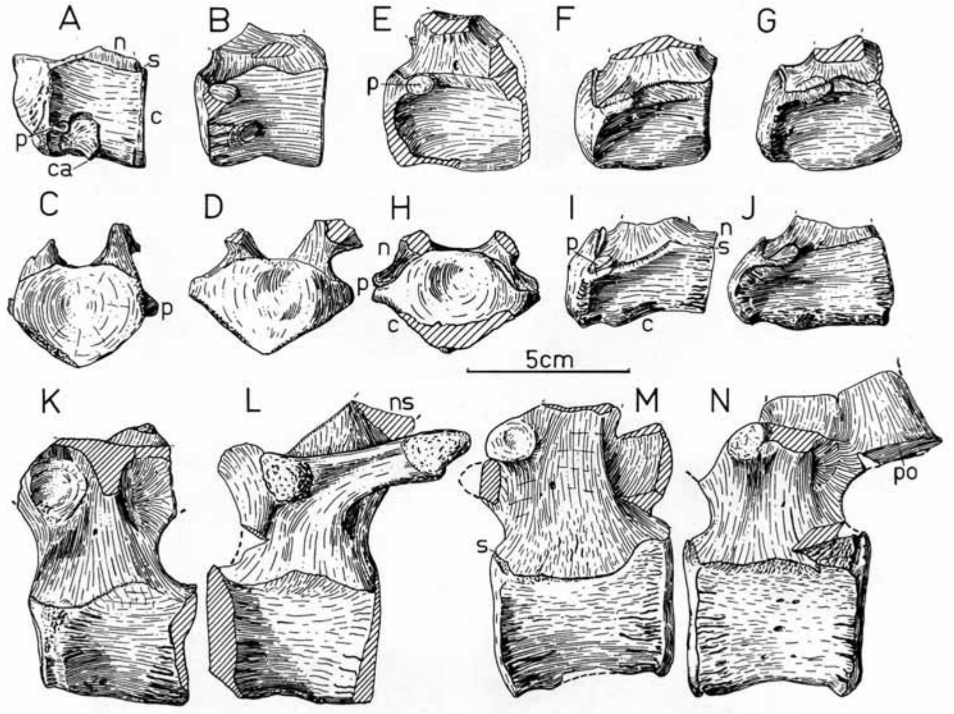
Fig. 15, left jugal in medial view (cf. text-fig. 1G), × 0·5.

Fig. 16, right premaxilla in medial view (cf. text-fig. 1B), × 0·5.

Fig. 17, posterior part of left dentary in medial view, × 0·5. For teeth a and b see Figs. 8 and 9.



GALTON and POWELL, dinosaur *Camptosaurus*

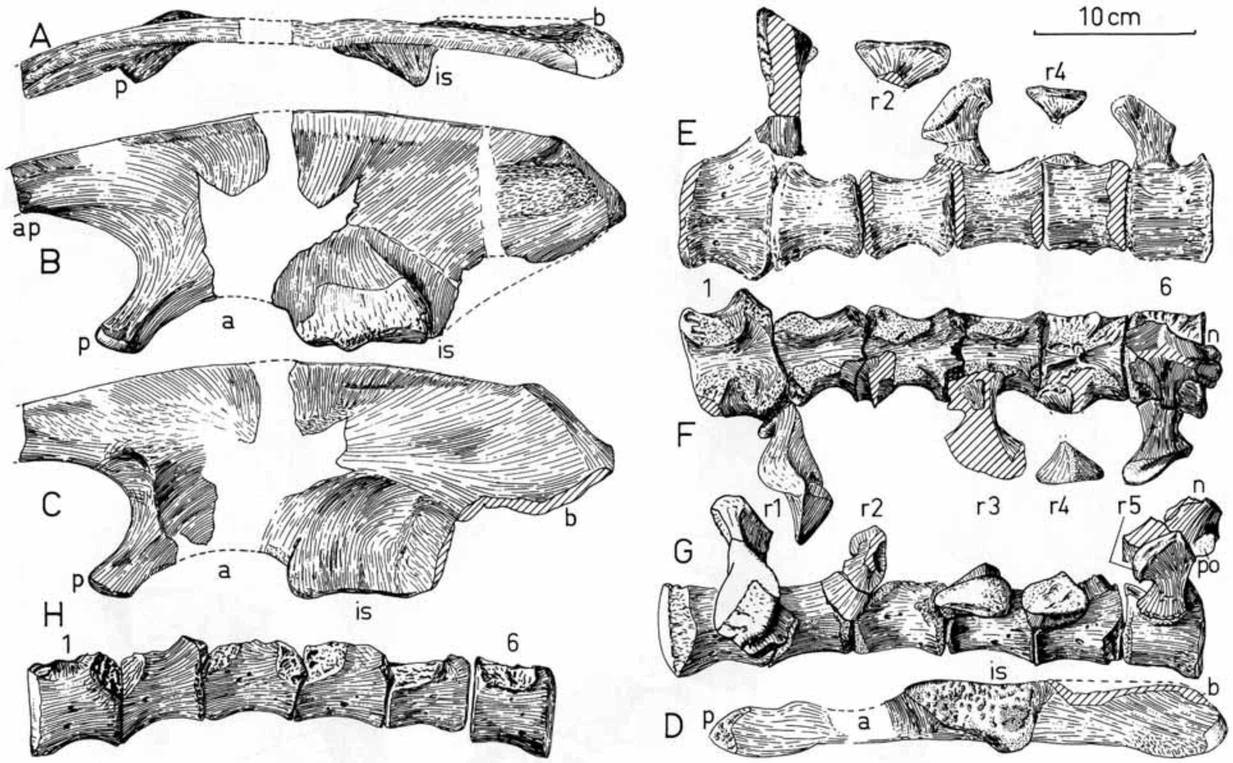


TEXT-FIG. 4. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303 × 0·5. A–J, cervical vertebrae: A, second (axis) with proximal end of left rib (displaced and with medial surface exposed); B, C, fourth; D, E, fifth (see also Hulke 1880, pl. 19, figs. 1–4); F, sixth; G, H, seventh; I, eighth; J, ninth; K–N, dorsal vertebrae: K, fifth; L, seventh; M, ninth; N, twelfth. Views—left lateral (A, B, E–G, I–N), anterior (D, H), and posterior (C). Abbreviations: c, centrum; ca, capitulum; ch, facet for centrum; d, diapophysis; n, neural arch; ns, neural spine; p, parapophysis; po, postzygapophysis; pr, prezygapophysis; s, suture.

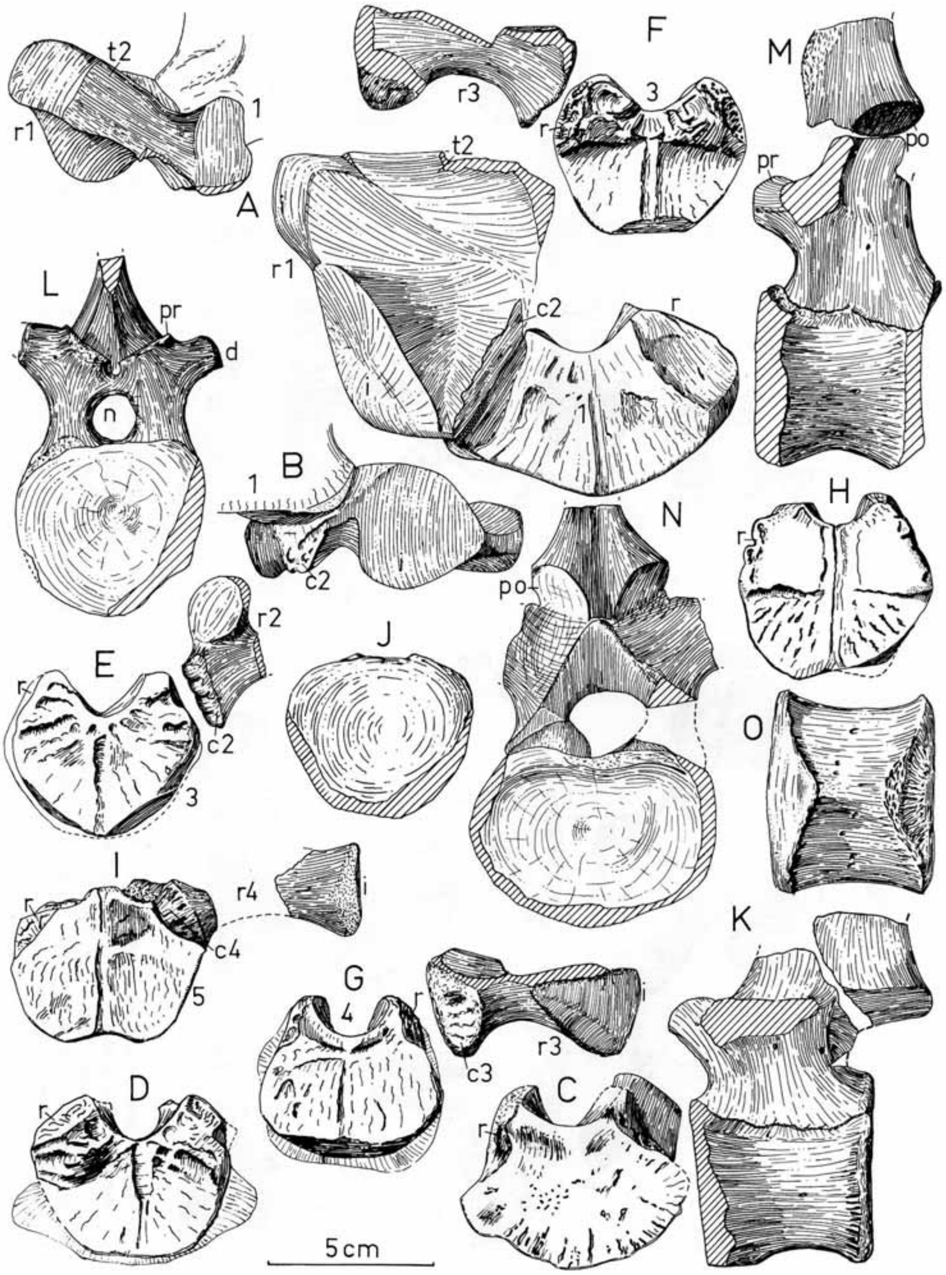
Dorsal vertebrae (text-figs. 4K–N, 6K–N). If the sacro-dorsal vertebra supporting the anterior surface of the first sacral rib is included as a functional part of the sacrum, then there are 16 dorsal vertebrae as in *Camptosaurus* (Gilmore 1925) whereas there are 14 or 15 in *Hypsilophodon*, 15 in *Dryosaurus*, *Tenontosaurus*, and *Thescelosaurus*, 16 or 17 in *Iguanodon* (Dollo 1883*b*, 1884; Hooley 1925), and 17 in *Ouranosaurus*.

The degree of convex curvature of the anterior surface of the centrum decreases in the first two vertebrae and increases in the next two, whereas the posterior surface becomes progressively less concave. The ventral keel becomes progressively less concave. On the fourth dorsal centrum and on the succeeding centra the concavity of the posterior surface is slightly greater than that of the anterior surface. The ventral keel becomes progressively less pronounced on the first five centra posterior to this, the ventral surface is rounded and the centra becomes progressively more massive. The first four dorsals are represented only by centra, but the fifth is more complete and is similar to the third dorsal of *Camptosaurus* (Gilmore 1909, fig. 15). On the seventh dorsal (text-fig. 4L) the parapophysis is at the base of the transverse process, whereas on the ninth, twelfth, and thirteenth dorsal vertebrae it is completely on the transverse process. The fourteenth dorsal is similar to the thirteenth of *Camptosaurus* (Gilmore 1909, fig. 16). In dorsal vertebra fifteen and sixteen the base of the transverse process is higher on the neural arch.

Sacrum (text-figs. 5E–H, 6A–J, 7A–E). The sacrum as a functional unit has six vertebrae with a massive sacro-dorsal anteriorly and a sacro-caudal posteriorly. The rib of the sacro-caudal contacted the ilium but the adjacent



TEXT-FIG. 5. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303 × 0·25. A, B, left ilium; C, D, right ilium; E–G, sacral vertebrae and ribs; H, restoration of sacral centra. Views—left lateral (B, G, H), medial (C), dorsal (A, F), and ventral (D, E). For dorsal and ventral views of sacral centra 1 to 5 see also Hulke (1880, pl. 36, figs. 1, 2). Abbreviations: a, acetabulum; ap, anterior process; b, brevis shelf; c, surface for centrum; ch, facet for chevron; d, diapophysis; i, surface for ilium; is, surface for ischium; n, neural arch; p, public peduncle; po, postzygapophysis; pr, prezygapophysis; r, surface for sacral rib; r1–5, sacral ribs 1 to 5; s, suture; t, transverse process; t2, transverse process of second sacral vertebra; 1–6, centra of sacral vertebrae 1 to 6.


A
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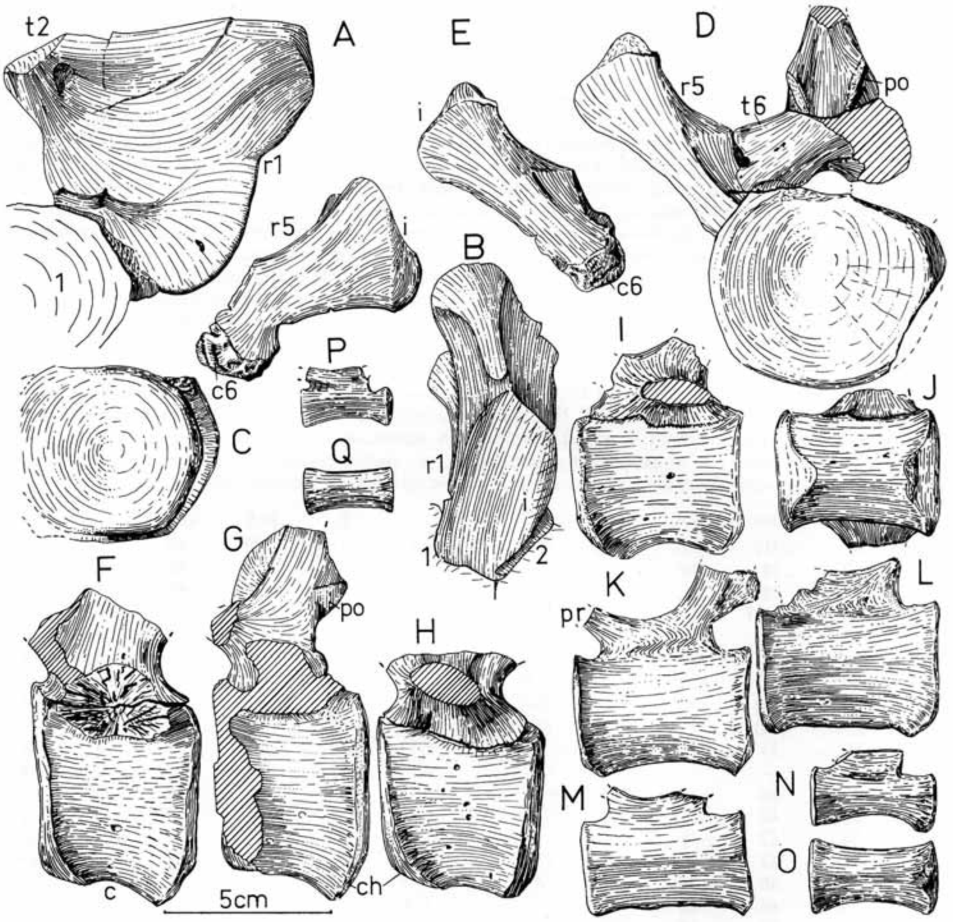


TEXT-FIG. 7. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303 × 0·5. A–E, sacral vertebrae and ribs; A, B, left sacral rib; C, D, sixth sacral vertebra and left fifth sacral rib; E, left fifth sacral rib; F–Q, caudal vertebrae: F, second; G, third; H, fourth; I, J, ninth; K, fourteenth; L, seventeenth; M, twentieth; N, O, thirtieth; P, Q, thirty-fourth. Views—anterior (A, C), posterior (D, E), left lateral (F–I, K–N, D) and ventral (O, Q). For G see also Hulke (1880, pl. 19, fig. 9), for abbreviations see text-fig. 4. For caudals 18, 30, and 35 see also Hulke (1880, pl. 19, figs. 11–13).

TEXT-FIG. 6. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303 × 0·5. A–J, centra and ribs of sacral vertebrae; A, dorsal view of left first sacral rib and posterior view of same rib and centrum of first sacral vertebra; B, ventral view of left first sacral rib; C, D, second sacral centrum; E, third sacral centrum and base of second left sacral rib; F, third sacral centrum and third left sacral rib; G, fourth sacral centrum and third left sacral rib; H, fourth sacral centrum; I, fifth sacral centrum and fourth sacral rib; J, fifth sacral centrum; K–N, dorsal vertebrae; K, fifth; L, fourteenth; M–N, sixteenth; O, centrum of third caudal vertebrae. Views for C–O: anterior (C, E, G, I, L), posterior (D, F, N, H), left lateral (K, M) and ventral (O). For abbreviations see text-fig. 5.

surfaces of the last two sacral centra are gently concave and were not co-ossified. The sacral count varies in several genera of ornithopods, being either six of seven in *Camptosaurus* (USNM 2210; YPM 1877a; USNM 4282), *Hypsilophodon*, *Iguanodon*, and *Tenontosaurus*. Ostrom (1970) notes that the degree of fusion of the sacral vertebrae varies in different specimens of *Tenontosaurus*.

The form of the sacral centra resemble those of *Camptosaurus* (USNM 2210; YPM 1877a; Gilmore 1909) in most respects. The first centrum has a median ventral keel, which is more strongly developed anteriorly, the second has a much weaker median keel, the third to fifth have a median longitudinal groove, and the sixth is gently convex with a ventrally protruding rim. The facets for the first four sacral ribs are intervertebral, with the fifth borne completely on the last sacral vertebra. The neural canal of the first four centra is transversely wide, with that of the last two constricted (text-fig. 5F) as in *Camptosaurus* (YPM 1877a). The sacral centra do not show the well-defined peg-and-notch articulation of some of the specimens of *Camptosaurus*, but the slight development of such an articulation between sacrals two and three and three and four approaches the condition in USNM 2210 (Gilmore 1909). The form of the ribs and their interrelations to the centra and the ilium is shown, but unfortunately little information is available concerning these ribs in *Camptosaurus*. Part of the transverse process of the second sacral vertebra is attached to the large first sacral rib which, judging from the figures in Gilmore (1909, figs. 17, 39), is similar to that of *Camptosaurus*.

TABLE 1. *Camptosaurus prestwichii*, OUM J.3303, measurements of vertebral centra in mm. C, caudal vertebra; CE, cervical vertebra; D, dorsal vertebra; HA, maximum height at anterior end; HP, maximum height at posterior end; L, maximum length; S, sacral vertebra; WA, maximum width at anterior end; WP, maximum width at posterior end; ( ), measurement approximate; +, measurement a minimum value as eroded; a, measured from floor of neural canal to ventral edge; b, includes chevron facet.

	L	HA	WA	HP	WP
CE2	42	(31)	(32)	(30)	(28)
CE4	42	28	44	31	40
CE5	45	28	50	33	41
CE6	44	31·5	51	32	46
CE7	45	31	53	33	(43)
CE8	46	35	54	(32)	(50)
CE9	50	(27)	(58)	(32)	(51)
D1	53	(33)	(55)	(30)	(51)
D2	(51)	(30)	44	—	(44)
D3	50	35	40	—	39
D4	—	—	—	—	45
D5	51·5	36	34	38	+38
D6	55	40	(32)	—	(35)
D7	54	42	+38	(40)	+38
D8	58	42	40	(44)	(37)
D9	57	46	(36)	46	(45)
D10	58	46	44	49	47
D11	55	50	44	(52)	48
D12	55	50	52	51	57·5
D13	59	52	(53)	(53)	61
D14	55	54	58	55	70
D15	54	56	68	56	(65)
D16	55	55	64	52	74
S1	55	53[a]	(66)	46	71
S2	54	43[a]	67	37[a]	(62)
S3	(55)	37[a]	57	39[a]	58
S4	52	38[a]	54	47[a]	58
S5	51	46[a]	57	50[a]	58
S6	48	53	59	59	70
C1	45	—	—	—	—
C2	51	(60)	60	65	59
C3	46	55	54	62[b]	51
C4	51	55[b]	50	55[b]	46
C5	51	52[b]	46	51[b]	46
C6	46	48[b]	45	48[b]	42
C7	52	48[b]	44	—	41
C8	55	49[b]	43	49[b]	38
C9	53	45[b]	(38)	45[b]	41
C10	53	45	40	45	40
C11	51	43	42	43	42
C12	50	41	43	40	(43)
C13	53	40	43	41	41
C14	53	37	39	39	41
C15	53	36	40	39	39
C16	53	36	36	39	—
C17	54	37	36	38	(36)
C18	54	34	38	36	(34)
C19	53	32	37	34	33
C20	50	29	32	31	31
C21	49	28	30	30	27
C22	50	29	(29)	30	28
C23	48	27·5	30	—	(28)
C24	47	25	29	28	26
C25	46	25	27	25	25
C26	44	23	27	—	—
C27	43	(22)	(27)	(20)	24
C28	40	18	23	19	23
C29	41	20	(21)	19·5	22
C30	38	18	23	18	22
C31	37	16·5	(22)	(16)	(19)
C32	33	14	18	13	17
C33	30·5	13	17	12	15
C34	27	12	15	11	13
C35	25	11	13	10	12
C36	—	10	11·5	—	—

Caudal vertebra (text-figs. 6O, 7F–Q). Remains of thirty-six caudals are preserved (text-fig. 3) and the original count was probably at least forty-five, as Gilmore (1909) estimated for *Camptosaurus*. Several progressive changes are observable in the series. The centra become progressively lower but, allowing for distortion from crushing and breaks, the length remains approximately the same until about caudal twenty-two and then decreases (Table 1). The second caudal shows a sutural area on the neural arch and centrum for the transverse process; on the third caudal this is just on the neural arch, and on the fourth caudal it is further on the arch. As in *Camptosaurus*, the transverse processes become progressively smaller, being vestigial on the twelfth and absent on the thirteenth caudal. The anterior and posterior surface of the anterior centra are equally concave but, posterior to the fifteenth, the posterior surface is more concave. On the first twelve centra the anterior chevron facet is slightly larger than the posterior one but, posterior to this, the reverse is the case; posterior to caudal twenty, only the posterior remains. The antero-ventral end of the posterior chevron facet is single anterior to caudal eight and double from there on posteriorly. Posterior to caudal fifteen, there is a lateral longitudinal ridge along the middle of the centra, the ends of which change from circular to approximately hexagonal in outline.

TABLE 2. *Camptosaurus prestwichii*, OUM J.3303, measurements of appendicular skeleton in mm.

	L	WP	WD
Humerus	297	83	64
Radius	—	46	36
Ulna	—	58	41
Femur	—	124	122
Tibia	—	161	143
Fibula	—	82	44

	WP	PA	PT	WD	DA	DT
MT I (left)	23	45	23	—	—	—
MT I (right)	21	40	21	—	—	—
MT II	—	81	31	—	53	44
MT III	—	68	48	—	47	58
MT IV	57	49	47	59	52	47

DA, antero-posterior diameter of distal end; DT, transverse diameter of distal end; L, maximum length; MT, metatarsal; PA, antero-posterior diameter of proximal end; PT, transverse diameter of proximal end; WD, maximum width of distal end; WP, maximum width of proximal end.

Appendicular skeleton

Pectoral girdle and fore-limb (text-fig. 8). The scapula is longer than the humerus as in *Camptosaurus*, *Dryosaurus altus* (Shepherd *et al.* 1977), *Ouranosaurus*, *Tenontosaurus*, and *Iguanodon* rather than being subequal as in *Othnielia*, *Hypsilophodon*, and *Dryosaurus lettowvorbecki*, or shorter as in *Thescelosaurus* (Galton 1974*b*). The incomplete dorsal end may have been posteriorly expanded as in *Camptosaurus*. Medially there is a foraminal groove which, according to Gilmore (1909), is only present in *Camptosaurus* and *Laosaurus* but which is also present in *Hypsilophodon*, *Ouranosaurus*, and *Iguanodon*. The coracoid has a foraminal notch as in *Camptosaurus* (Gilmore 1909; USNM 4282), rather than a complete foramen as in most other ornithopods. However, this is a variable feature in *Camptosaurus*, because in YPM 1877 the foramen is complete. A notch is present in some specimens of *Iguanodon* (Dollo 1882*a*; Hooley 1925).

A pair of incomplete bones may be part of either the pectoral girdle or the sternum. Each bone (text-fig. 8E–H) is triangular in section with a rounded end which, judging from its texture, was originally covered with cartilage. The thick edge is moderately flat with diagonally inclined striations. The paired sternal bones are known in only a few ornithopods, and there are two distinct patterns: either two thin crescentic plates together forming a shield-like structure, or two long, rod-like bones set at right angles to each other with contact between the median part of the thinner, transversely expanded, anterior end. The first pattern occurs in *Dryosaurus* (Gilmore 1925 as *Laosaurus*; Janensch 1955), *Othnielia*, *Hypsilophodon*, *Parksosaurus*, and *Tenontosaurus*. The second pattern occurs in *Camptosaurus* (YPM 1877), *Ouranosaurus*, *Iguanodon* (Dollo 1882*b*), and the hadrosaurs (Lull and Wright 1942). However, the paired bones described here are probably not sternal bones because they are proportionally too small and do not resemble any part of the sternal bones of either pattern. Sternal ribs are known for very few ornithopods. These are formed from ossified cartilage in *Othnielia*, *Hypsilophodon*, and *Thescelosaurus*, but in *Parksosaurus* the third and fourth sternal ribs are large pieces of bone. A third possibility to be considered is that these bones are clavicles, for which there is a distinct facet on the antero-ventral part of the scapula in most ornithischians. However, this is considered unlikely because in *Leptoceratops*, the only ornithischian for which a clavicle has been described (Brown and Schlaikjer 1940), it is rod-like and pointed at both ends. The paired bones are not sacral ribs, because these are all acounted for (text-fig. 5E–G) and they do not correspond to any cranial element. Although the form is not the same as those of *Parksosaurus*, the paired bones are tentatively identified as the anterior end of a left and right sternal rib.

The humerus (text-fig. 8L–O) is a little crushed and it has a low deltopectoral crest as in *Camptosaurus* (text-fig. 2K, L), *Dryosaurus* (Janensch 1955; Shepherd *et al.* 1977), and *Othnielia* but, because of its slenderness, it looks more like that of the hypsilophodontids *Dryosaurus* and *Othneilia*. The humerus is more slender than those of *Ouranosaurus*, *Iguanodon*, *Tenontosaurus*, and *Thescelosaurus*. The incompletely preserved radius and ulna (text-fig. 8P–Z) are also slender. The only identifiable element from the manus is a small piece (text-fig. 8I–K) that is tentatively identified as the ventro-lateral corner of the proximal end of metacarpal II. Hulke (1880) considered that the metacarpals were slender, a feature Gilmore (1909) noted was more suggestive of *Iguanodon* than of *Camptosaurus*, but this was based on pieces now identified as the radius. The measurements of the bones of the pectoral girdle and limbs are given in Table 2.

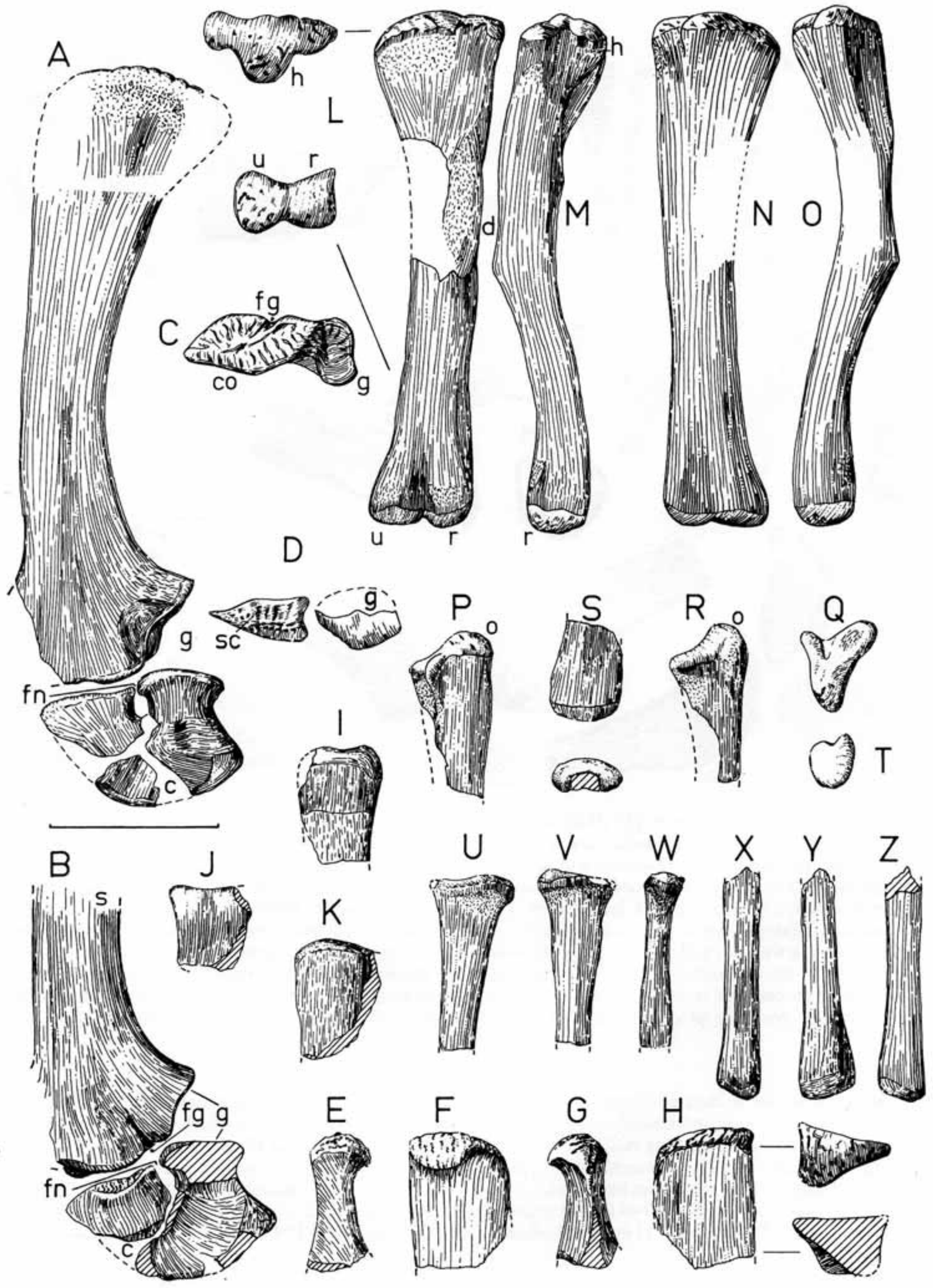
Pelvic girdle and hind-limb. The incomplete pelvic girdle resembles that of *Camptosaurus* (text-fig. 2C–E). The ilium (text-fig. 5A–D) has a deep blade, a massive ischiadic head, and a narrow brevis shelf. The pubis (text-fig. 9A–H) has a deep blade-like anterior process, and probably a long subacetabular part. Because of the expanded form of the distal end, which has a flat medial surface, the post-pubic rods were probably long with united distal ends. The ischium (text-fig. 9I–O) has a proximally placed obturator process. The flat medial surfaces of the bar-shaped distal ends were united to each other. The massiveness of the distal end of the ischium is intermediate between those of YPM 1888a (text-fig. 2C) and AMNH 6120 (Gilmore 1909, pl. 19).

The pelvic girdle of *Dryosaurus* (Galton 1977*a*, *b*) is similar to that of the Cumnor ornithopod, but the posterior part of the ilium is low, the brevis shelf is wide, and the anterior process of the pubis is more rod-like. In *Othnielia*, *Hypsilophodon*, and *Thescelosaurus* (Galton 1974*b*) the anterior process is even more rod-like and the distal part of the ischium is dorso-ventrally flattened and laterally expanded. In *Tenontosaurus* the dorsal margin of the ilium shows a distinct step, so the posterior part of the blade is deep, and the distal part of the ischium is more blade-like. In *Ouranosaurus* the pubis is proportionally much longer and the ilium smaller. In *Iguanodon* the ilium is similar in some specimens (Lydekker 1890*b*) and the anterior process of the pubis is comparably expanded (Dollo 1882*a*) or extremely large (Dollo 1882*a*; Hooley 1925). In *Iguanodon* (Dollo 1882*a*), *Ouranosaurus*, and *Tenontosaurus* the post-pubic rod is much shorter than the ischium.

Most of the bones of the hind-limb are represented (text-figs. 10–13), but only the ends of the long bones and of the metatarsals are preserved. The femur (text-fig. 10A–F) has a well-developed distal anterior intercondylar groove as in *Camptosaurus* (text-fig. 2F, H). This groove is deeper than it is in most femora of *Dryosaurus* (for range of variation see Galton 1977*a*, *b*). In *Othnielia* and *Hypsilophodon* there is no such groove, in '*Camptosaurus*' *leedsi* it is small (text-fig. 2G), in *Thescelosaurus* it is broad but shallow, and in *Ouranosaurus* and *Iguanodon* (Owen 1855; Galton and Jensen 1979*a*) it is very deep with the edges overhanging the groove. The massive femur of *Cryptodraco* Lydekker, 1889 (type species *Cryptosaurus eumerus* Seeley, 1875*b*; CUM J.46882) from the Oxfordian (Upper Jurassic) of Great Grandsen, seven miles east of St. Ives, Huntingdonshire, has a greater trochanter that is only half the antero-posterior width of the head, and distally the anterior intercondylar groove is shallow. The ends of the fibula and tibia (text-figs. 10G–L, 11A, J–L) are of the standard ornithopod pattern. The proximal end tapers more, so the tibia was probably more slender than that of *Camptosaurus*.

The astragalus and calcaneum (text-fig. 11A–I) are of the standard ornithopod pattern (cf. Galton 1974*a*). The pronounced depression on the anterior surface of the ascending process is also present on the astragali of *Camptosaurus* (YPM 1877) and *Dryosaurus* (YPM 1884). A large, cushion-shaped bone (text-fig. 13A–D) is similar to the large distal tarsal (fused II and III) of *Camptosaurus* (YPM 1877) and *Dryosaurus* (YPM 1884).

TEXT-FIG. 8. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303 × 0·5 (E–K) and × 0·25. A–D, scapula and coracoid A, left in lateral view; B, right in medial view; C, sutural surface of right scapula; D, sutural surfaces of right coracoid; E–H, proximal end of a left sternal rib in E, medial view; F, ventral view; G, lateral view; H, dorsal view with anterior end and posterior cross section; I, K, proximal end of ?second metacarpal in I, ?dorsal view; J, proximal end and K, ?medial view; L–O, left humerus in L, anterior view with proximal and distal ends; M, lateral view; N, posterior view; O, medial view; P–S, left ulna, P, proximal end in lateral view; Q, proximal end; R, as P in dorsal view; S, distal end in lateral view with distal view; T–Z, left radius, T–W proximal end in, T, proximal; U, medial; V, lateral and W, posterior (or ventral) views; X–Z, distal end in X, anterior (dorsal), Y, lateral and Z, posterior (ventral) views. Abbreviations: c, coracoid; co, surface for coracoid; d, deltopectoral crest; fg, foraminal groove; fn, foraminal notch; g, glenoid cavity; h, head; o, olecranon process; r, radial condyle; s, scapula; sc, surface for scapula; u, ulnar condyle. Scale line represents 5 cm (E–K) or 10 cm.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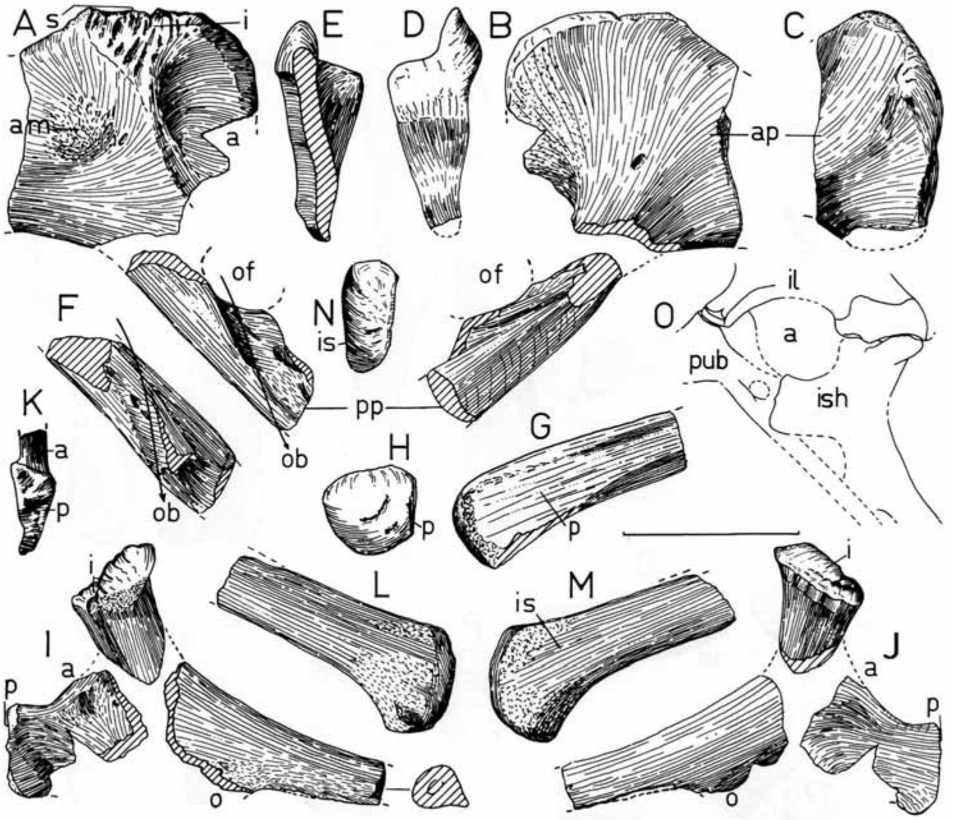


TEXT-FIG. 9. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303. A–H, pubis × 0·5, A, acetabular part of left pubis in lateral view; B, as A in medial view; C, proximal end of right anterior pubis (prepubic process) in lateral view; D, as C, proximal end; E, reverse of D to show cross-section; F, dorsal view of anterior part of posterior pubis (postpubic rod); G, distal end of posterior process in medial view; H, distal end of posterior process; I–N, left ischium × 0·25, I, proximal end in lateral view; J, as I in medial view; K, proximal view of surface for pubis; L, distal end in lateral view; M, as L in medial view; N, distal end; O, reconstruction of acetabular region of pelvic girdle, compare with A, I and text-fig. 5B. Abbreviations: a, acetabulum; am, area of origin of M. ambiens (see Galton 1969); ap, anterior process; i, sutural surface for ilium; is, sutural surface for ischium; ish, ishium; o, obturator process; ob, route of obturator nerve and blood vessels; of, obturator foramen; p, sutural surface for pubis; pp, posterior process (postpubic rod) of pubis; s, sutural surface for first sacral rib. Scale line represents 5 cm (A–H) or 10 cm.

The pes is similar to that of *Camptosaurus* (text-figs. 2I, J, 11M, 12, 13). The proximal end of metatarsal I (text-figs. 12M, 13E) is proportionally more massive than it is in *Camptosaurus*, in which the complete bone is either short (text-fig. 2I) or long (Gilmore 1909, fig. 35). Metatarsals II and IV (text-fig. 13F–H, L) are very incomplete. Metatarsal III is reasonably complete (text-fig. 13I–K) and the ratio of the maximum antero-posterior width over the maximum length is between 0·4 (maximum value assuming no shaft lost) to 0.35 (more probable value) as against 0·39–0·46 for the more massive metatarsal III of *Camptosaurus* (USNM 4277; YPM 1877, 6801, 7355). This ratio is 0·15 in *Hypsilophodon*, 0·26 in *Dryosaurus* (YPM 1884), 0·27 in *Ouranosaurus*, and

0·34–0·51 in *Iguanodon* (Owen 1858; Dollo 1883*b*). The proximal end of metatarsal IV is less expanded transversely than is that of *Camptosaurus* (text-fig. 2I, J).

Most of the phalanges are represented and these are tentatively identified as shown (text-figs. 12, 13M–S). A small phalanx (text-fig. 12C–G) is similar to the first phalanx of digit I of *Camptosaurus* (text-fig. 2I, J) so this digit was reduced. In *Othnielia*, *Hypsilophodon*, *Tenontosaurus*, and *Thescelosaurus* this phalanx is longer than the first phalanx of digit II whereas in *Dryosaurus* (Galton 1977*a*, *b*; Shepherd *et al.* 1977), *Ouranosaurus* and *Iguanodon* (Dollo 1882*a*, 1883*b*) this digit is represented only by a vestigial metatarsal. The first phalanges of digits II and III are slightly more slender than are those of *Camptosaurus*. The width is greater than the length for the third and fourth phalanges of digit IV (text-fig. 12A, B, H–J) and this is also the case in *Camptosaurus* and *Iguanodon* (Dollo 1882*a*; Hooley 1925 in which phalanges 2 and 3 are incorrectly transposed). The reverse is true in *Othnielia*, *Dryosaurus* (Galton 1977*a*), *Hypsilophodon*, *Tenontosaurus*, and *Thescelosaurus*.

EUROPEAN SPECIES OF *CAMPTOSAURUS*

The four species of ornithopod dinosaurs from Europe that have been referred to the genus *Camptosaurus* Marsh (1885) are listed below and discussed in descending stratigraphical order.

Camptosaurus inkeyi Nopcsa (1900), Upper Cretaceous of Comitat Hunyad, Transylvania, Hungary; holotype, a dentary with part of angular.

C. valdensis Lydekker (1889), Lower Cretaceous (Wealden) of Isle of Wight, England; holotype, a left femur (BMNH R167); referred specimen, a dentary (BMNH R180).

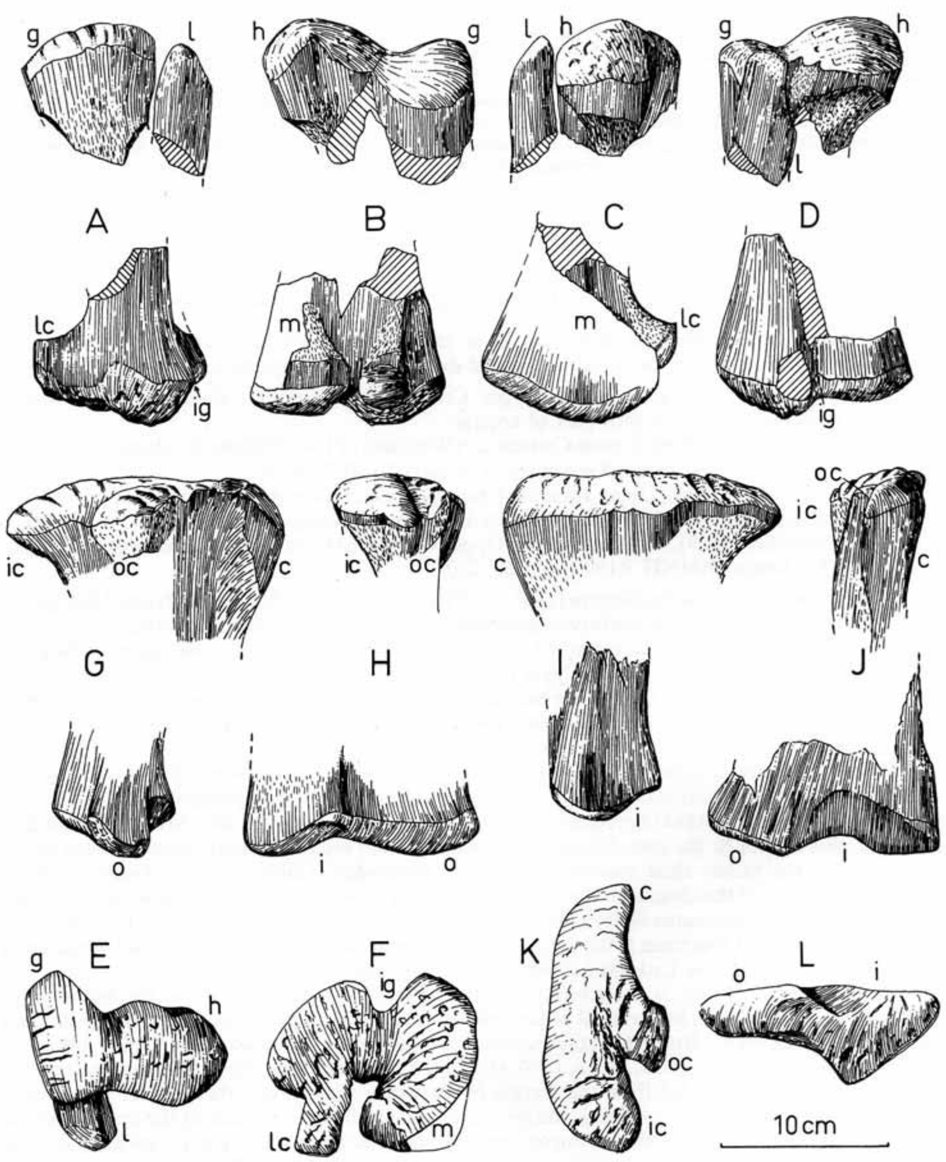
C. prestwichii Hulke (1880), Upper Jurassic (Lower Kimmeridgian) of Cumnor Hurst near Oxford, England; holotype, skeleton OUM J.3303 described above (text-figs. 1–13).

C. leedsi Lydekker (1889), Middle Jurassic (Upper Callovian) from near Peterborough, England; holotype, a left femur (BMNH R1993, text-fig. 2G).

1. *C. inkeyi* was described by Nopcsa (1900, p. 579) in a footnote. Gilmore (1909) listed the species as *C. ?inkeyi* but noted that the dentary as described was quite unlike those of the American species. However, a fuller description was promised, so he left the final disposition of this species to Nopcsa. The citation of *Camptosaurus* from the Upper Cretaceous of Europe by Steel (1969) and Charig (1973) is based on this specimen, which has never been figured and is probably lost. However, Nopcsa (1904) noted that the holotype of *C. inkeyi* is another specimen of *Rhabdodon* (= *Mochlodon*), the common iguanodontid from the Upper Cretaceous of Transylvania.

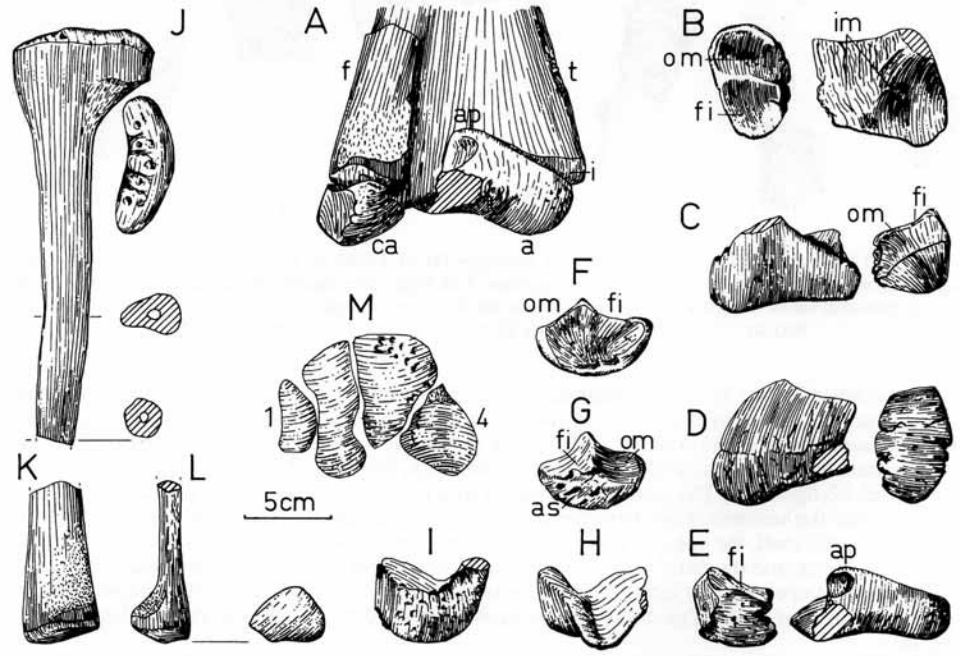
2. *C. valdensis* was described by Lydekker (1889), but the type femur was only recently figured by Galton (1974*a*) who concluded that it is from a large individual of *Hypsilophodon foxii*. Galton (1974*a*) followed Owen (1864) in regarding the mandibular ramus as that of a juvenile *Iguanodon*. However, this cannot be the case, because the posterior teeth are on the antero-medial edge of the coronoid process rather than medial to it as in *Iguanodon* (Galton 1976*b*). Galton (1976*b*) provisionally referred this dentary to the iguanodontid *Vectisaurus valdensis*, but now refers it to the hypsilophodontid *Valdosaurus* Galton (1977*a*, type species *Dryosaurus ?canaliculatus* Galton, 1975; an additional referred specimen is the *Dryosaurus*-like ilium (BMNH R2150) from the Wealden of Sussex that was figured by Lydekker (1888*a*) as *Hylaeosaurus*).

3. *C. prestwichii* (Hulke) is described above (text-figs. 1–13). The skeleton is the holotype of *I. prestwichii* Hulke (1880) but referral of this species to the genus *Iguanodon* is incorrect because it shows many differences from the other species of that genus. In *Iguanodon* (Dollo 1882*a*, *b*, 1883*a*, *b*, 1884; Owen 1855, 1858, 1861*a*, 1874; Hooley 1925; Casier 1960) the skull is tall and narrow, the supraoccipital is excluded from the margin of the foramen magnum, there are 21 to 23 tooth positions in each jaw (18 in a juvenile), the teeth are unenamelled on one side of the crown and the sculpturing on the other side is more complex, and the posterior teeth of the dentary are medial to the coronoid process rather than being on its anterior edge (see Galton 1976*b*). There are 10 or 11 cervicals and 17 or 16 dorsal vertebrae, the posterior process of the pubis is much shorter than the ischium, the anterior intercondylar groove at the distal end of the femur is tunnel-like with the sides overhanging it anteriorly, and metatarsal I is reduced to a splint with no phalanges (for contrasting situations in OUM J.3303 see p. 434).

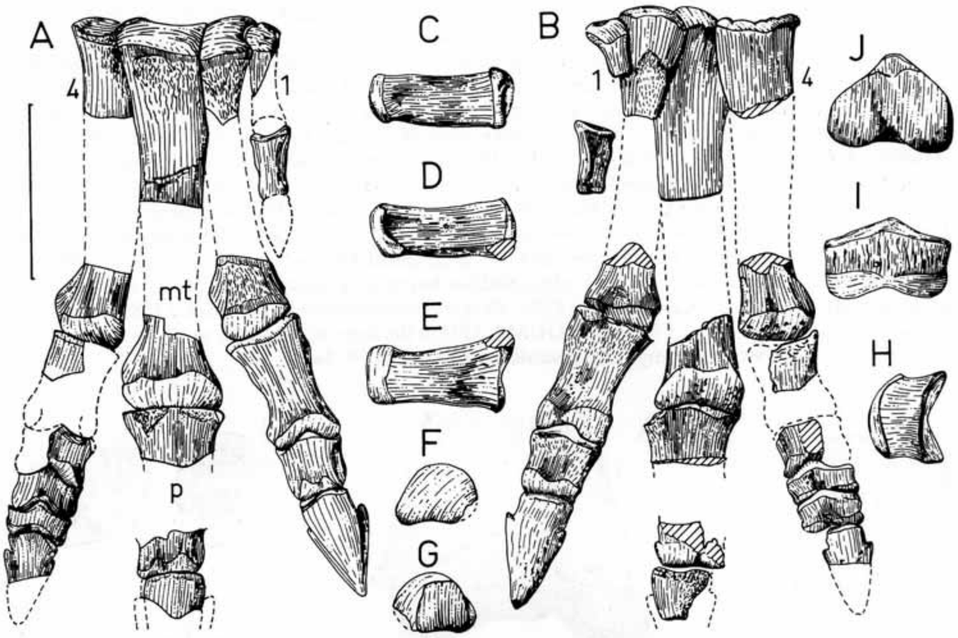


TEXT-FIG. 10. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303 × 0·25. Right femur (A–F) and tibia (G–L) in lateral (A, G), posterior (B, H), medial (C, I), anterior (D, J), proximal (E, K), and distal views (F, L). For abbreviations see text-fig. 11.

The skeleton described as *I. prestwichii* by Hulke (1880) is readily distinguishable from the corresponding parts of the other ornithopod taxa described from the Upper Jurassic and the Lower Cretaceous of England. *Cryptosaurus eumerus* Seeley (1875*b*), the type species of the iguanodontid genus *Cryptodraco* Lydekker (1889), is based on a femur (CUM J.46882) from the Oxfordian (p. 428) that has a very narrow greater trochanter (half antero-posterior width of head) and distally the anterior intercondylar groove is broad and very shallow (cf. text-fig. 10E, F). The maxilla (CUM B53408) of *Priodontognathus phillipsii* (Seeley 1875*a*) may have come from the Upper Jurassic of Yorkshire and the teeth are very different from those of OUM J.3303 (see p. 420). Two ornithopods are described from the upper part of the Lulworth Beds of Dorset (= Middle Purbeck Beds, Lower Cretaceous, Berriasian, Dodson *et al.* 1964, Hallam 1975), *I. hoggii* Owen (1874) in which the dentary teeth have two prominent vertical ridges, and the fabrosaurid *Echinodon becklessii* Owen (1861*b*) in which the teeth lack secondary vertical ridges and are borne on a slender dentary and a maxilla with an almost flat lateral surface (Galton 1973*a*, 1978). *Hypsilophodon foxii* Huxley (1869) from the Wealden of the Isle of Wight differs from OUM J.3303 in the form of the skull, teeth, humerus, pelvic girdle, femur, and pes (see comparative section and Galton 1974*a*).



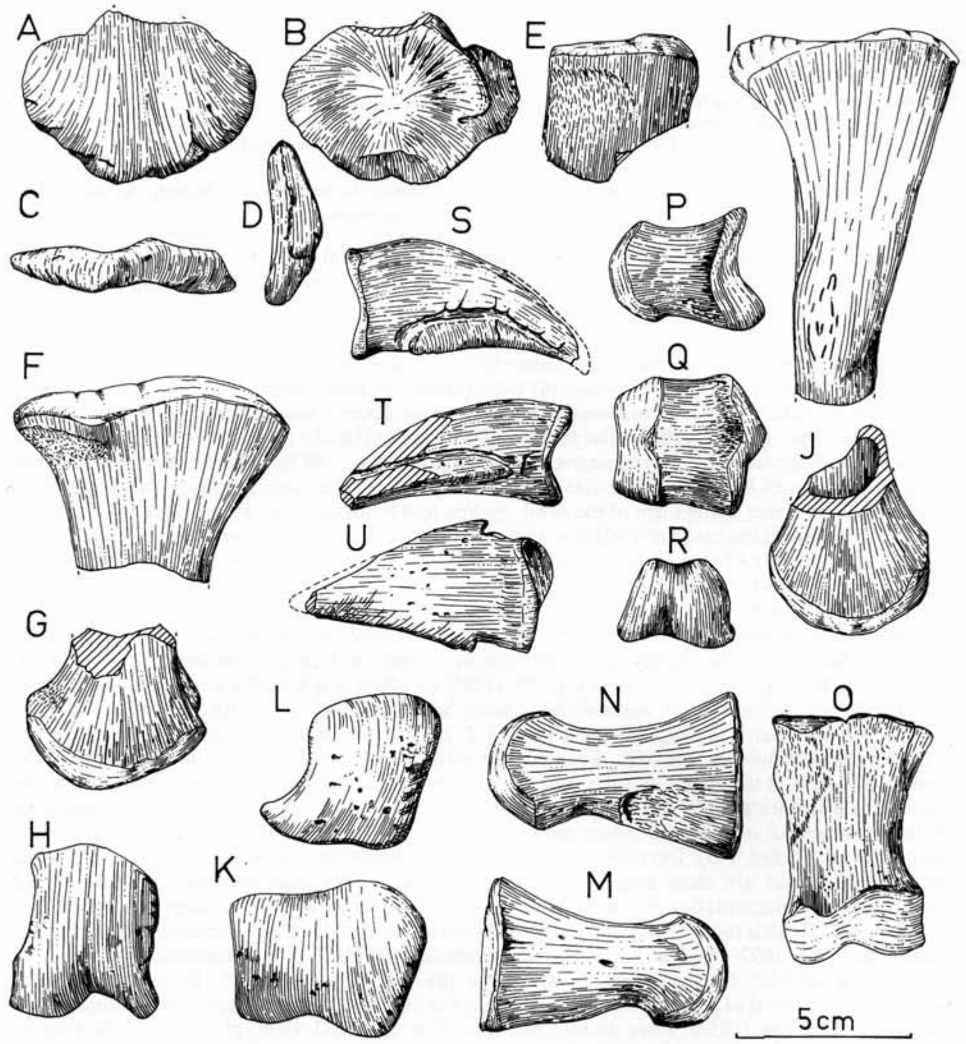
TEXT-FIG. 11. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303 × 0·25. Right hind-limb: A, distal end of tibia and fibula with proximal tarsals in anterior view; B–E, proximal tarsals in B, proximal; C, posterior; D, distal and E, anterior views; F, G, calcaneum and H, I, astragalus in lateral (F, H) and medial (G, I) views, J–L, fibula J, proximal part with end view and cross section; K, distal part in anterior view; L, as K in medial view with end view; M, proximal ends of metatarsus. For A, B, D, and F see also Hulke (1880, pl. 20, figs. 3–6). Abbreviations: a, astragalus; ap, ascending process; as, surface for astragalus; c, cnemial crest; ca, calcaneum; f, fibula; fi, surface for fibula; g, greater trochanter; h, head, i, inner malleolus; ic, inner condyle; ig, intercondylar groove; im, surface for inner malleolus; l, lesser trochanter; lc, lateral condyle; m, medial condyle; mt, metatarsal; o, outer malleolus; p, phalanx; t, tibia; 1–4, digits 1 to 4.



TEXT-FIG. 12. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303. A, B, right pes (ends of metatarsals spaced a bit too far apart, see text-fig. 2); C–G, phalanx 1 of digit I in C, lateral; D, medial; E, ventral; F, distal and G, proximal views; H–J, phalanx 4 of digit IV in H, medial, I, ventral and J, distal views. For abbreviations see text-fig. 11. Scale line represents 10 cm (A, B ×0·25) or 5 cm (C–J ×0·5).

The skeleton OUM J.3303 is very similar to those of *Camptosaurus dispar* (see note p. 412) from the Upper Jurassic of North America, and the similarities are listed in the diagnosis of the genus *Camptosaurus* (p. 437). The skull is low and broad, the outlines of the bones are similar (text-fig. 2A, B) and the maxilla and dentary each bear about sixteen teeth, the form of which is very similar in both species (pl. 52, figs. 1–12). The vertebrae are similar with the same number in each region. The scapula is longer than the humerus, which has a low deltopectoral crest (text-fig. 2K–M). The ilium is deep with a narrow brevis shelf, the anterior process of the pubis is evenly expanded and blade-like, the post-pubic rod is long, and the distal part of the ischium is rod-shaped (text-fig. 2C, D). Distally the femur has a well-developed anterior intercondylar groove (text-fig. 2F, H). In the pes, the phalanges of digit I are reduced and the width of the third and fourth phalanges of digit IV is greater than the length (text-fig. 2I, J).

The differences between *Camptosaurus dispar* and *C. prestwichii* are listed (p. 438) and given below (Table 3). There are differences in the proportion of the skulls and of the individual bones (text-fig. 2A, B) but these are less than those shown within the genus *Iguanodon* (see Dollo 1883*b*, 1884; Casier 1960; Hooley 1925). The small size of the intramaxillary cavity of *C. prestwichii* is an important character, but the difference in the maxillary teeth is minor and could be an individual variation of the English specimen. The difference in the outline of the anterior end of the centra of cervical vertebrae four to nine is a valid difference. *C. prestwichii* is more gracile than the very massive *C. dispar* (text-fig. 3; figures of skeletons in Gilmore 1909, 1912) and this is reflected in the more slender form of the limb bones and in particular the humerus, tibia, and metatarsals (text-fig. 2I–M). Numerous species of



TEXT-FIG. 13. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303. Right pes × 0·5. A–D, medial distal tarsal in A, proximal; B, distal; C, posterior and D, medial views; E, proximal end of metatarsal I in medial view; F, proximal part of metatarsal II in medial view; G, distal part of metatarsal II in medial view; H, as G in distal view; I, proximal part of metatarsal III in medial view; J, distal part of metatarsal III in medial view; K, as J in distal view; L, distal end of metatarsal IV; M–O, phalanx 1 of digit II in M, lateral; N, medial and O, ventral views; P–R, phalanx 2 of digit II in P, medial; Q, ventral and R, distal views; S–U, ungual phalanx of digit II in S, lateral; T, medial and U, ventral views.

TABLE 3. Comparison of skeletal characters of *Camptosaurus dispar* and *C. prestwichii*.

Character	*C. dispar*	*C. prestwichii*
Intramaxillary cavity	Large	Small
Number of secondary ridges reaching middle of maxillary tooth crown anterior to prominent keel	3 or 4	5
Anterior end of cervical centra 4 to 9	Less angular, rounded ventrally	Subrhomboidal
Peg-in-notch articulation between sacral centra	Weakly to strongly developed	Weakly developed
Long bones	Robust	Slender
Anteroposterior expansion of proximal end of metatarsals I, II, and III	I reduced, II and III much expanded	I not reduced, II and III slightly expanded

Iguanodon have been described from the Lower Cretaceous of western Europe (see Steel 1969), but Ostrom (1970) concluded that there were only two or three morphological—if not valid taxonomic—entities, which include a smaller and slender *Iguanodon* (e.g. single *I. mantelli* skeleton in Brussels, see Dollo 1882*a*, 1884; Casier 1960; *I. atherfieldensis* Hooley, 1925) and a larger more robust *Iguanodon* (e.g. several skeletons of *I. bernissartensis*, see Dollo 1882*a*, 1883*a*; Casier 1960). These two osteological types of *Iguanodon*, regarded as male and female of the same species by Nopcsa (1929), show more differences in the form of the skull, girdles, and limbs than do skeletons of *C. prestwichii* and *C. dispar*. Given the range of variation within the ornithopod genus *Iguanodon*, we consider that the differences shown (Table 3) do not justify recognition of the genus *Cumnoria* Seeley (1888) for *I. prestwichii* Hulke (1880) which instead is referred to the genus *Camptosaurus* Marsh (1885) as *C. prestwichii* (Hulke).

A few other specimens described from the Upper Jurassic of Europe have been referred to *C.* (*Iguanodon*) *prestwichii*. Lydekker (1886) figured a tooth as *I. prestwichii* but this is incorrect, because the drawing is reproduced from Dollo (1885) in which it is labelled as an *Iguanodon* tooth from the Lower Cretaceous (*I. mantelli* from text). Sauvage (1888, pl 12, fig. 5; 1897–1898, p. 7, figs. 11, 12) illustrated a fragmentary tooth of *I. prestwichii* from the Upper Jurassic (Upper Portlandian) of Boulogne-sur-Mer, France. The sides of the crown diverge from the root, the prominent keel is in the centre and the root shows a resorption area on the ornamented side of the tooth. This is a dentary tooth and it may be from the left side. Four ridges reach the base of the crown on the ornamented side, so the ridges are more numerous and pronounced than on teeth of *C. prestwichii* (pl. 52, figs. 7–9). The unworn base of the other side of the crown has two centrally located vertical ridges that are close together and continue on to the adjacent part of the root. In *Camptosaurus*, ornamentation on this side of the tooth is restricted to a few short terminal ridges (pl. 52, figs. 1, 5). This tooth is identified as iguanodontid, generically and specifically indeterminate.

Sauvage (1888, 1897–1898) also referred five vertebrae from the Upper Jurassic of Boulogne-sur-Mer to *I. prestwichii*. A caudal vertebra (Sauvage 1897–1898, pl. 7, figs. 7–12) was classified by Nopcsa (1928) as that of a theropod dinosaur and is the holotype of the coelurid taxon *Caudocoelus sauvagei* von Huene (1932). Four sacral vertebrae (Sauvage 1897–1898, pl. 7, figs. 2–6) may be iguanodontid but the material is generically and specifically indeterminate. It should be noted that the material figured by Sauvage (1897–1898, pl. 7, figs. 2–12) was destroyed in World War II.

Sauvage (1897–1898, pl. 7, fig. 1) also referred two associated sacral centra (Geological Service of Portugal Collections) from the Kimmeridgian of Porto-de-Mós (Leira), Portugal, to *I. prestwichii*. However, Lapparent and Zbyszewski (1957, p. 51) note that the vertebrae are those of a juvenile plated dinosaur (*Dacentrurus* (= *Omosaurus*) *lenneri*).

von Huene and Maubeuge (1954) described a partial camptosaurid pubis from the Upper Jurassic (Rauracien) of Fours à Chaux d'Haudainville, near Verdun, France. The anterior process is much more dorso-ventrally expanded and plate-like with more divergence between the dorsal and ventral edges than there is in *Camptosaurus* (text-fig. 2C, D). The expanded form of the anterior process is more similar to that of *Ouranosaurus* and the robust form of *Iguanodon* (see Dollo 1882*a*; Casier 1960). This pubis is identified as iguanodontid, generically and specifically indeterminate.

4. *Camptosaurus leedsi* Lydekker (1889) is based on a left femur (text-fig. 2G) from the Oxford Clay that was referred to the Oxfordian (Upper Jurassic) by Galton (1975). However, Hoffstetter (1957) noted that the bone-bearing layer is the lower Oxford Clay, which is of Upper Callovian (Middle Jurassic) age. This femur differs from that of *Camptosaurus* (text-fig. 2F–H) in several respects: the greater trochanter is much less massive, the fourth trochanter is more proximally placed, distally the anterior surface does not sweep out to form a wider anterior end and the anterior intercondylar groove is much more shallow. This femur should not be referred to the genus *Camptosaurus* and it probably represents a new genus.

SYSTEMATIC PALAEONTOLOGY

Order ORNITHISCHIA
Suborder ORNITHOPODA
Family IGUANODONTIDAE
Camptosaurus MARSH, 1885

Type species. Camptonotus dispar Marsh, 1879, p. 501.

Type locality. Quarry 13 near Como Bluff, Albany County, Wyoming, U.S.A.

Known distribution. Upper Jurassic of western U.S.A. and England; Lower Cretaceous of western U.S.A.

Diagnosis. Skull low and wide, large posterior process to premaxilla, small antorbital fenestra, small contribution of frontal to orbital margin, surpaoccipital borders foramen magnum, premaxilla edentulous, fifteen or sixteen functional teeth in each maxilla and dentary, and one replacement tooth per alveolus; teeth lozenge-shaped with prominent vertical keel more strongly developed on maxillary teeth than on dentary teeth, several secondary vertical ridges on sculptured surface of crown with anterior and posterior ridges bordering the non-deniculate half of maxillary tooth crown, posterior ridge on equivalent part of dentary teeth. Nine cervicals, sixteen dorsals, and six or seven sacral vertebrae; cervicals 4–9 opisthocoelous; variable development of peg-and-notch articulation between sacral centra. Scapula longer than humerus, which has a poorly developed deltopectoral crest. Deep ilium with long anterior process and narrow brevis shelf. Pubis with a deep evenly expanded anterior process and elongate posterior process that reaches end of ischium. Ischium with proximally placed obturator process and bar-shaped distal part with dorso-ventrally expanded end. Femur curved, longer than tibia with pendant fourth trochanter extending on to distal half of shaft and distally a well-developed anterior intercondylar groove. Pes robust with four digits, first being rudimentary. The width is greater than the length in phalanges 3 and 4 of digit IV of pes.

Camptosaurus dispar (Marsh)

1879 *Camptonotus dispar* Marsh, p. 501, pl. 3.
1879 *Camptonotus amplus* Marsh, p. 503.
1885 *Camptosaurus dispar* (Marsh), Marsh, p. 169.
1885 *Camptosaurus amplus* (Marsh), Marsh, p. 169.
1894 *Camptosaurus medius* Marsh, p. 85.
1894 *Camptosaurus nanus* Marsh, p. 85, pl. 5, fig. 3.
1909 *Camptosaurus browni* Gilmore, pp. 230–297.

Type species. Camptonotus dispar Marsh, 1879, p. 501, pl. 3.

Type specimens. Holotype YPM 1877 (partial skeleton), paratypes YPM 1877a (partial sacrum), YPM 1878 (pelvic girdle and forelimb).

Type locality and horizon. Morrison Formation (Upper Jurassic, Upper Kimmeridgian ≡ Lower Tithonian) of Quarry 13 near Como, Albany County, Wyoming, U.S.A.

Known distribution. Upper Jurassic of Wyoming, Utah, and Colorado.

Diagnosis. Large intramaxillary cavity, posterior process of premaxilla reaches prefrontal, three or four secondary ridges reach middle of tooth crown anterior to prominent keel. Centrum of cervical three platycoelous, ventral edge of anterior end of cervical centra four to nine gently rounded. Well ossified carpus, radiale and metacarpal I fused, five short and stocky digits. Massive long bones and pes.

Camptosaurus prestwichii (Hulke)

1880 *Iguanodon prestwichii* Hulke, pp. 433–456, pls. 18–20.
1888 *Cumnoria prestwichii* (Hulke), Seeley, p. 698.
1889 *Camptosaurus prestwichii* (Hulke), Lydekker, p. 259.

Type species. Iguanodon prestwichii Hulke, 1880, p. 433.

Holotype. OUM J.3303 (almost complete skeleton).

Type locality and horizon. Lower Kimmeridge Clay (upper Lower Kimmeridgian *Aulacostephanus pseudomutabilis* Zone, Upper Jurassic), Chawley Brick Pit, Hurst Hill, Cumnor, 2·5 miles WSW. of the centre of Oxford, England (National Grid reference SP 475 043).

Known distribution. Upper Jurassic of England.

Diagnosis. Small intramaxillary cavity, five secondary ridges reach middle of tooth crown anterior to prominent keel. Anterior end of cervical centra 4–9 subrhomboidal in outline. Slender long bones and pes.

Camptosaurus depressus Gilmore

Type species. Camptosaurus depressus Gilmore, 1909.

Holotype. USNM 4753 (partial skeleton).

Type locality and horizon. 'Calico Canyon' near Buffalo Gap Station, South Dakota, from Lakota Sandstone (Lower Cretaceous, ?Aptian).

Diagnosis. Ilium low with shallow acetabulum and narrow preacetabular notch. Sacrals with rounded ventral surfaces. Anterior end of pubis broad. (The validity of this species is provisionally accepted, but the type material needs to be fully described.)

PALAEOBIOGEOGRAPHICAL IMPLICATIONS

The similarities between the dinosaurian faunas of the Morrison Formation of the western interior of North America and the Tendaguru Beds of Tanzania, East Africa, can be accounted for only by assuming the presence of a land connection between the two areas some time during the Late Jurassic (Galton 1977*a*, *b*). Western Europe and North America are presumed to have been connected at this time (Charig 1973; Colbert 1974; Cox 1974) but faunal evidence for this is slight.

The Morrison stegosaur *Stegosaurus* was reported from the Oxford Clay (Upper Callovian, Middle Jurassic) from near Peterborough, England, but *Stegosaurus priscus* Nopcsa, 1911 is regarded by Hoffstetter (1957) as a juvenile of *Omosaurus durobrivensis* Hulke, 1887, the type species of the genus *Lexovisaurus* Hoffstetter, 1957. Lydekker (1890*a*) referred *Omosaurus armatus* Owen, 1875 from the Kimmeridge Clay of Swindon to *Stegosaurus* but Lucas (1902) subsequently made it the type species of the genus *Dacentrurus*. Both *Lexovisaurus* and *Dacentrurus* differ in many respects from the

Morrison *Stegosaurus* (see Hoffstetter 1957; Steel 1969). Galton (1976*c*) referred the Morrison theropod dinosaur *Stokesosaurus clevelandi* Madsen, 1974 to the Middle Jurassic English genus *Iliosuchus* von Huene, 1932 but this was incorrect (Galton and Jensen 1979*b*). *Apatosaurus* and *Brachiosaurus*, two genera of Morrison sauropods, are described from the Kimmeridgian of Portugal by Lapparent and Zbyszewski (1957), but these generic referrals are probably incorrect (J. S. McIntosh, pers. comm.). *Cteniogenys antiquus* Gilmore, 1928 is the only Morrison lizard known and Seiffert (1973) described a new species, *C. reedi* from the Lower Kimmeridgian of Portugal. However, only upper and lower jaws are available for comparison and these are very similar to those of *Kuehneosaurus* Robinson, 1962 from the Upper Triassic of England (Estes, in press).

From the above review, it is apparent that there is little faunal evidence for a land route between the western interior of North America and western Europe during the late Middle or early Late Jurassic. This situation is rectified to a certain extent by the description given above of the reasonably complete skeleton from England that is referred to the Morrison genus *Camptosaurus* as *C. prestwichii* (Hulke). However, the land route was probably available for a relatively short period of time, because the maximum extent of Jurassic seas was reached during the Callovian, Oxfordian, and Kimmeridgian, when between a quarter and a third of the total continental area was covered (Hallam 1969, 1975). The continental area showing most submergence was western Europe and northern Africa and, because of this, it was suggested (Galton 1977*a*, *b*) that the Morrison–Tendaguru connection was probably via Central and South America rather than via Europe as commonly assumed (Charig 1973; Colbert 1974; Cox 1974).

Two genera of ornithopod dinosaurs from the Morrison Formation (Upper Kimmeridgian, about 138 m.y. van Hinte 1976) of the western interior of North America have an intercontinental distribution: *Camptosaurus* and *Dryosaurus*. The anatomy of *Camptosaurus prestwichii* from the Lower Kimmeridgian (about 141 m.y. van Hinte 1976) of England differs in several respects from that of the slightly more recent *C. dispar* (text-fig. 2; table 3). This is not the result of a growth difference, because the limb bones of *C. prestwichii* are proportionately more slender than those of the smaller individual (humerus length 143 mm *v.* 297 mm) of *C. dispar* illustrated by Gilmore (1909, 1912) as *C. nanus*. The difference in build probably represents a relatively short-term evolutionary change because both a gracile and a massive species of *Iguanodon* lived together in the Early Cretaceous of western Europe (Casier 1960). The difference in the sacral centra may represent evolutionary divergence resulting from the more recent occurrence of the Morrison species. However, the reduction in size of the intramaxillary cavity, with additional ossification lateral to the tooth row, is an advanced character for an ornithopod (see Galton 1974*a*). Consequently, it is surprising that this reduction occurs in *C. prestwichii* rather than in the more recent *C. dispar*. The anatomy of the Morrison hypsilophodontid *Dryosaurus altus* is extremely similar to that of *D. lettowvorbecki* from the Tendaguru Beds (Upper Kimmeridgian) of Tanzania, East Africa (Galton 1977*a*, *b*).

The higher degree of evolutionary divergence of the two species of *Camptosaurus* is probably not a function of distance, because their Upper Jurassic positions are only half as far apart as were those of *Dryosaurus* (see maps in Cox 1974; Galton 1977*a*, *b*; Hallam 1977), but it may be that the two species of *Camptosaurus* were isolated from each other for a longer period of time than was the case for the species of *Dryosaurus*. The North Atlantic epicontinental seaway was a barrier to gene flow for *Camptosaurus*; on the basis of evidence from marine molluscs, this was established by the Pliensbachian (183 m.y.) at the latest and persisted throughout the Jurassic (Hallam 1977). If the Morrison–Tendaguru connection was via South America, then the Central Atlantic, linking the Pacific to Tethys, was a barrier for *Dryosaurus*. Hallam (1977) notes that the Central Atlantic was probably represented in the latest Aalenian and early Bajocian by a well-developed epicontinental seaway which later became restricted or intermittently closed until the Mid Callovian, but that true oceanic crust was not created in the Central Atlantic, by the movement apart of North America and South America plus Africa, until late Callovian or, more definitely, Oxfordian times (149 m.y.). It is apparent that the excessively long times involved (40 m.y. for *Camptosaurus*, 10 m.y. for *Dryosaurus*) indicate that the dispersal of these genera did not occur prior to the origin of the seaways. A land route across the North Atlantic epicontinental seaway was probably available for the dispersal of *Camptosaurus* some time in the Oxfordian (144 m.y.) and for *Dryosaurus* across the western end of the Central Atlantic some time in the Kimmeridgian.

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Note added in press. The results of additional research by the senior author are relevant to some of the contents of this paper. A 366-mm long femur from the Geological Survey of Portugal Collections, very similar to those of *Camptosaurus dispar*, is described from the Kimmeridgian of Portugal (Galton, in press *a*, *b*). The holotype femur of *Camptosaurus leedsi* (p. 437) is redescribed and made the type specimen of a new ornithopod genus (Galton, in press *b*). The holotype femur of *Cryptodraco eumerus* (pp. 428, 433) is also redescribed (Galton, in press *b*); because of its close similarity to the femur of the nodosaurid ankylosaur *Hoplitosaurus marshii* (Gilmore 1914), *Cryptodraco* is transferred to the ankylosaurian family. Nodosauridae (Galton, in press *b*, *c*). *Priodontognathus phillipsii* (pp. 413, 420, 433) is also transferred to the Nodosauridae because the teeth are similar to those of the nodosaurid *Sauropelta edwardsi* Ostrom, 1970 (Galton, in press *c*).

GALTON, P. M. in press *a*. *Dryosaurus* and *Camptosaurus*, intercontinental genera of Upper Jurassic ornithopod dinosaurs. *Mem. Soc. Geol. Fr.* (N.S.), **59** (139).

——in press *b*. European Jurassic ornithopod dinosaurs of the families Hypsilophodontidae and Camptosauridae. *Neues Jb. Geol. Paläont. Mh.*

——in press *c*. Armored dinosaurs (Ornithischia: Ankylosauria) from the Middle and Upper Jurassic of Europe. *Paläont. Z.*

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