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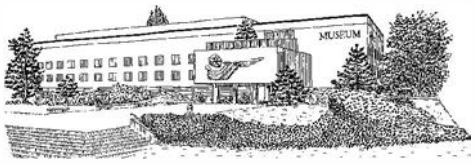


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# Notes on the remains of archosaurian reptiles, mostly basal sauropodomorph dinosaurs, from the 1834 fissure fill (Rhaetian, Upper Triassic) at Clifton in Bristol, southwest England

Peter M. GALTON[1]

**Abstract**

Many of the best preserved teeth and bones of archosaurian reptiles found in 1834 in an Upper Triassic Rhaetian fissure fill on Durdham Down in Clifton (now in Bristol), southwest England were destroyed in 1940. Based on an 1875 map, the site is positively identified as within Quarry Steps Quarry. This paper includes an annotated catalogue, copies of most of the illustrations from 1840 to 1908, and photos of important extant specimens. Most of the recognizable, mostly unassociated and incomplete bones have long been referred to the basal sauropodomorph dinosaur *Thecodontosaurus* RILEY & STUTCHBURY, 1836 (as *T. antiquus* MORRIS, 1843), with gracile and robust morphs of several of the appendicular bones as a sexual dimorphism. The deltopectoral crest of unassociated Clifton humeri is plesiomorphic for basal sauropodomorphs, being anteroposteriorly high and markedly asymmetrical in lateral view with a short edge distal to the very prominent apex. The apex is at 40% (measured perpendicular to long axis of humerus) of total length in gracile ones and +50% in robust ones of the same size. However, the former position is plesiomorphic for sauropodomorphs, the latter derived, and no other basal sauropodomorph species has such a marked dimorphism. The only partial skeleton from Clifton, which includes a forelimb and girdle, has a third humeral morph with a low symmetrical deltopectoral crest with a rounded apex at 25% of length. Whatever the status of the gracile and robust morphs, the characters of referred postcranial bones from Clifton cannot be used to distinguish the species of *Thecodontosaurus* RILEY & STUTCHBURY, 1836 that, along with *T. antiquus* RILEY & STUTCHBURY *vide* OWEN, 1842, may be a *nomen dubium*. However, *T. antiquus* is retained for the slender humeral morph pending the description of referred material from a Rhaetian fissure fill at Tytherington Quarry, Avon. In the humerus of *Pantydraco* (*Thecodontosaurus*) *caducus* (Upper Triassic/Lower Jurassic, Wales) the apex of the asymmetrical deltopectoral crest is at 40% of the length and the process is low, a morph that is not represented at Clifton. The Clifton forelimb and girdle is made the holotype of *Asylosaurus yalensis* n. gen. et sp. The manus shows lateral reduction, so phalangeal formula is 2-3-4-2-?1, and the humerus has a large medial tubercle (small in Welsh humerus). The other Clifton bones are identified as either: A. very basal Sauropodomorpha indet (could be *Asylosaurus* or *Thecodontosaurus*, includes slender morph bones); B. Anchisauria indet (more derived than A, includes robust morph bones); or C. basal Sauropodomorpha indet (could be A or B).

An ilium and two femora are very basal Theropoda (or possibly Dinosauriformes); other theropod remains include a small tooth crown with fine perpendicular denticles, a metacarpal I, a slender recurved manual ungual, and an astragalus. A dorsal centrum may be from an ornithischian dinosaur. *Rileyasuchus* KUHN, 1961 (type species *Palaeosaurus platyodon* RILEY & STUTCHBURY, 1840), a *nomen dubium*, is a heterodont crurotarsal phytosaur now represented by two teeth and two humeri. The denticles are angled slightly apically on the expanded mesial blade and perpendicular to the distal edge. *Palaeosauriscus* KUHN, 1959 (type species *Palaeosaurus cylindrodon* RILEY & STUTCHBURY, 1840) is based on lost teeth; it is Archosauria indet but may be a valid taxon based on the subcircular cross-section and fine, obliquely inclined denticles. A few bones are none of the above and are Archosauria indet (dentary with teeth, scapula-coracoid) and even Reptilia indet (?prootic, parietal, distal femur, tibia, metapodial).

**Key words**

Sauropodomorpha, Anchisauria, Theropoda, Phytosauria, *Asylosaurus, Palaeosauriscus, Rileyasuchus, Thecodontosaurus,* Upper Triassic, England, Anatomy, Taxonomy.

**Résumé**

**Notes sur les restes de reptiles archosaures, pour la plupart des dinosaures sauropodomorphes basaux, du remplissage, en 1834, de la fissure du Trias supérieur (Rhétien, Trias supérieur), à Clifton (Bristol), sud-est de l'Angleterre.-** Nombre de dents et d'os fossiles les mieux préservés de reptiles archosaures trouvés en 1834 dans le remplissage d'une fissure du Trias supérieur (Rhétien) de Durdham Down à Clifton (de nos jours à Bristol), dans le sud-ouest de l'Angleterre, ont été détruits en 1940. D'après une carte de 1875 le site est clairement identifié comme se trouvant dans la carrière de Quarry Steps. Ce travail inclut un catalogue commenté, des reproductions de la plupart des illustrations de 1840 à 1908, et des photos des spécimens restants les plus importants. La plupart des os que l'on peut reconnaître, incomplets et en grande partie non associés, ont longtemps été attribués au dinosaure sauropodomorphe basal *Thecodontosaurus* RILEY & STUTCHBURY, 1836 (comme *T. antiquus* MORRIS, 1843), avec des morphes gracile et robuste de plusieurs os appendiculaires interprétés comme du dimorphisme sexuel. La crête deltopectorale des humérus non associés de Clifton,

1. *Professor Emeritus, University of Bridgeport, Bridgeport, CT USA ; Curatorial Affiliate, Peabody Museum of Natural History, Yale University, New Haven, CT USA. 315 Southern Hills Drive, Rio Vista CA 94571-2153 USA ; E-mail : pgalton@juno.com, pgalton@bridgeport.edu*

qui est haute antéro-postérieurement et très asymétrique en vue latérale avec un bord distal court par rapport à l'apex proéminent, est plésiomorphe pour les sauropodomorphes basaux. L'apex est situé à 40% de la longueur totale (mesuré perpendiculairement à l'axe longitudinal de l'humérus) chez les formes graciles et à +50% chez les formes robustes de la même taille. Cependant, la première position est considérée comme plésiomorphe et la seconde comme dérivée pour les sauropodomorphes, et aucune autre espèce de sauropodomorphe basal ne présente un dimorphisme aussi marqué. Le seul squelette partiel de Clifton, qui comprend un membre antérieur et une ceinture, montre un troisième morphe huméral avec une crête deltopectorale symétrique basse portant un apex arrondi situé à un quart de la longueur. Quel que soit le statut des morphes gracile et robuste, les caractères des os postcrâniens rapportés de Clifton ne peuvent être utilisés pour distinguer l'espèce de *Thecodontosaurus* RILEY & STUTCHBURY, 1836 qui, avec *T. antiquus* RILEY & STUTCHBURY *vide* OWEN, 1842, pourrait être un *nomen dubium*. Néanmoins, *T. antiquus* est retenue pour le morphe huméral gracile en attendant la description du matériel rapporté provenant d'un remplissage de fissure du Rhétien de Tytherington Quarry, Avon. Chez l'humérus de *Pantydraco* (*Thecodontosaurus*) *caducus* (Trias supérieur/Jurassique inférieur, Pays de Galles), l'apex de la crête deltopectorale asymétrique est situé à 40% de la longueur et le processus est bas, correspondant à un morphe non représenté à Clifton. Le membre antérieur et la ceinture de Clifton deviennent l'holotype de *Asylosaurus yalensis* n. gen. et sp. La main montre une réduction latérale, de sorte que la formule phalangienne est 2-3-4-2-?1, et l'humérus possède un grand tubercule médial (petit chez l'humérus gallois). Les autres ossements de Clifton sont identifiés comme appartenant à : A, un Sauropodomorpha très basal indéterminé (qui pourrait être *Asylosaurus* ou *Thecodontosaurus*, incluant des os du morphe gracile) ; B, un Anchisauria indéterminé (plus dérivé que A, incluant des os du morphe robuste) ; ou C, un Sauropodomorpha basal indéterminé (qui pourrait être A ou B).
Un ilium et deux fémurs appartiennent à un Theropoda très basal (ou à un possible Dinosauriformes). D'autres restes incluent une petite couronne dentaire à fins denticules perpendiculaires, un métacarpien I, une phalange distale de la main mince et incurvée, et un astragale. Un centrum dorsal pourrait appartenir à un dinosaure ornithischien. *Rileyasuchus* KUHN, 1961 (espèce type *Palaeosaurus platyodon* RILEY & STUTCHBURY, 1840), un *nomen dubium*, est un phytosaure crurotarsal hétérodonte maintenant représenté par deux dents et deux humérus. Les denticules forment un angle léger apicalement sur la lame distal élargie et perpendiculaire au bord distal. *Palaeosauriscus* KUHN, 1959 (espèce type *Palaeosaurus cylindrodon* RILEY & STUTCHBURY, 1840) est basé sur des dents perdues ; il s'agit d'un Archosauria indéterminé qui pourrait être un taxon valide d'après la section transversale subcirculaire et de fins denticules inclinés obliquement. Un petit nombre d'ossements n'appartient pas aux taxons mentionnés plus haut et pourrait être rapporté à des Archosauria indéterminés (dentaire avec des dents, scapula-coracoïde), voire même à des Reptilia indéterminés (?prootique, pariétal, partie distale d'un fémur, tibia, métapode).

**Mots-clés**
Sauropodomorpha, Anchisauria, Theropoda, Phytosauria, *Asylosaurus, Palaeosaurisus, Rileyasuchus, Thecodontosaurus,* Trias supérieur, Angleterre, Anatomie, Taxonomie.

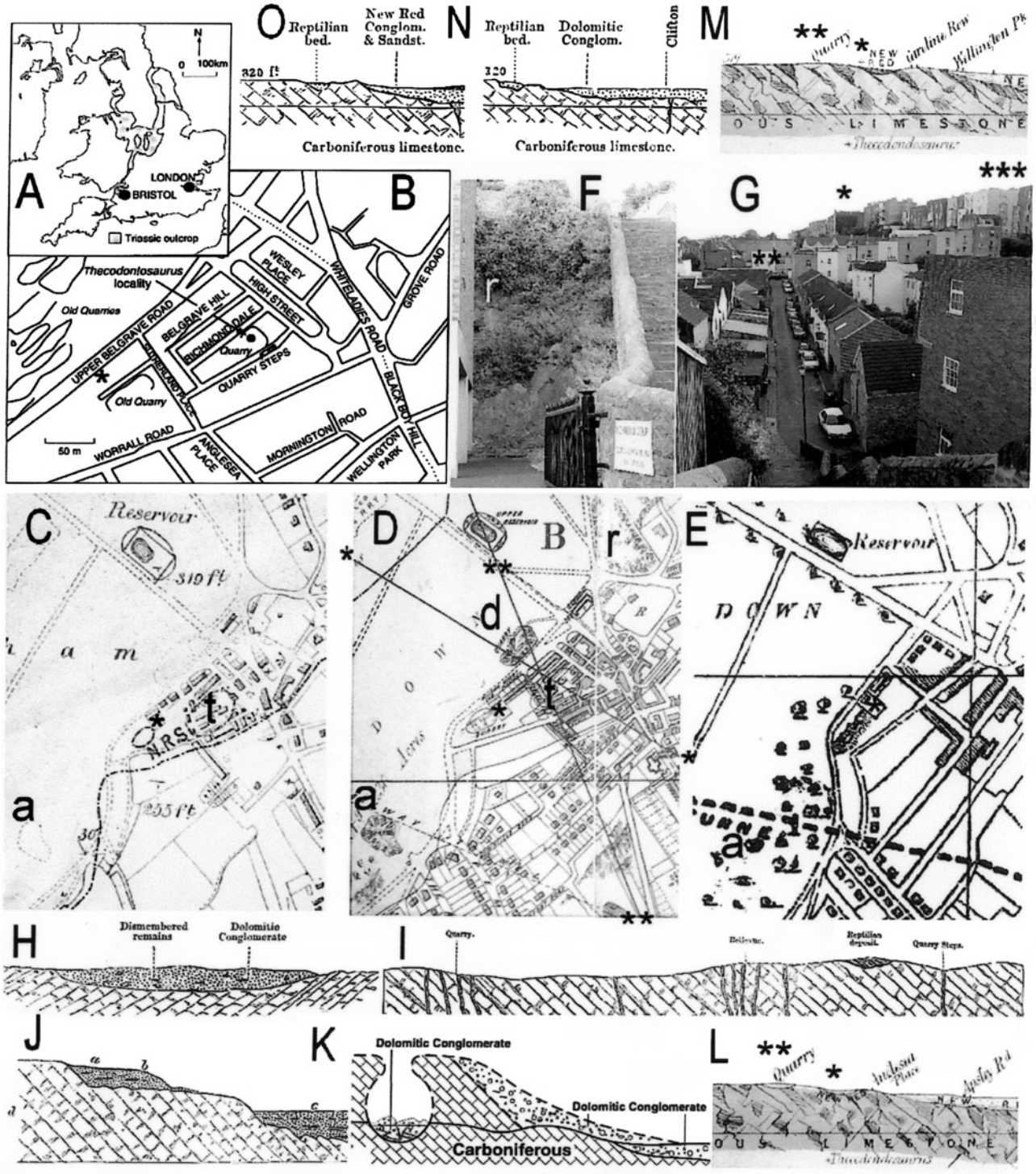
## Contents

## I. INTRODUCTION

Terrestrial reptiles are rare from the Upper Triassic of Britain, usually being represented by small bones coming mostly from Rhaetian fissure fills or cave breccia in the Lower Carboniferous limestone that formed an archipelago of low islands in the Mendips and parts of South Wales (FRASER, 1994, 2006). However, the remains of large dinosaurs are known from sedimentary beds near the base of the Westbury Formation (Rhaetian) in England and Wales on either side of the Severn Estuary (REYNOLDS, 1946 ; STORRS, 1994, 1999). These include a femur and partial skeleton of *Camelotia borealis* GALTON, 1985a, a basal sauropod (UPCHURCH *et al.*, 2007 ; YATES, 2007) with a femur 1000 mm long (GALTON, 1998a, 2005a), a dentary and teeth of the theropod *Megalosaurus cambrensis* (NEWTON, 1899) (GALTON, 1998a, 2005a), and columnar shafts of femora (length originally ~850 mm) of a stegosaurid ornithischian (GALTON, 2005a).

The first Triassic dinosaur to be described, although not recognized as such until much later, was discovered in 1834 in a heavily dolotomized cave breccia on the southeastern extremity of Durdham Down in Bristol (Fig. 1). Samuel STUTCHBURY (1789-1859) noted in 1836 that, during the first week of September 1834, a quarryman brought in to the Bristol Institution for the Advancement of Science, Literature and the Arts (precursor of the Bristol City Museum, for early history see BARKER, 1906 ; also TAYLOR, 1994 ; TAYLOR & TORRENS, 1987) one or two fragments of bone that, because he was away, were given to Dr. Henry RILEY (1797-1848 ; for short biographies see BENTON *et al.*, 2000 ; for STUTCHBURY see CRANE, 1983 ; BRANAGAN, 2004). Several other bones were brought in upon STUTCHBURY's return in early October when they "immediately engaged the men to work diligently upon the spot until a considerable number of fragments came into our possession - in a few days we had the pleasure of receiving Dr. (J. L. R.) AGASSIZ to whom they were shown", as well as to two others who made preliminary reports, viz., W. D. CONYBEARE (as ANON, 1834) and WILLIAMS (1835a, b, 1837) (also ANON, 1835).

A jaw with 21 teeth was described as *Thecodontosaurus* RILEY & STUTCHBURY, 1836a ("sheath-toothed reptile"). Other teeth were named *Palaeosaurus cylindricum* and *P. platyodon* by RILEY & STUTCHBURY (1836a, b, "ancient reptile", both *nomina nuda*) and as *P. cylindrodon* and *P. platyodon* by RILEY & STUTCHBURY (1837a ; also *nomina nuda*). RILEY & STUTCHBURY (1837a) figured a dorsal




vertebra in median section to show the concave ends of the centrum and the unique dorsal excavation by the neural canal. The teeth, along with the holotype dentary of *Thecodontosaurus*, were described and illustrated by RILEY & STUTCHBURY (1840) as *Paleosaurus cylindrodon* and *P. platyodon* (Figs 4A, D, 32H, Q). They also described various unassociated postcranial bones from Durdham Down, including the medially sectioned dorsal vertebra (Fig. 10D), without referring them to a particular taxon. They drew attention to similarities of the vertebrae and femur to those of crocodiles and *Megalosaurus*.

OWEN (1841, 1842a) redescribed the teeth from Durdham Down, figuring that of *Palaeosaurus platyodon* in 1841 (Fig. 32B) ; he used *Thecodontosaurus* RILEY & STUTCHBURY but listed *T. antiquus* RILEY &

STUTCHBURY without a reference in the list of species described in his report (1842a, p. 190). OWEN (1842a) attempted to assign the bones to particular taxa, and also noted resemblances of the femur to those of crocodiles and *Megalosaurus*. He did not refer the Durdham Down material to the Dinosauria OWEN, 1842a, which he erected for very large and more recent reptilian bones described from southern England, viz., *Megalosaurus* (Middle Jurassic, BUCKLAND, 1824), *Iguanodon* and *Hylaeosaurus* (Lower Cretaceous, MANTELL, 1825, 1833). Instead, OWEN (1841) referred *Thecodontosaurus* and *Palaeosaurus* to the "thecodonts" in the vernacular (with tooth of *Cladeiodon* OWEN, 1841 from Middle Triassic of English Midlands, now referred to crurotarsal rauisuchian *Bromsgroveia* (GALTON & WALKER, 1996a, b; BENTON & GOWER, 1997), and classified them in the Lacertilia (OWEN, 1842a). LYELL (1841, and in later books on geology) included copies of figures of the teeth of *Thecodontosaurus* and *Palaeosaurus platyodon* (latter also in PICTET, 1853).

MORRIS (1843, p. 211) listed the species *antiquus* as RILEY & STUTCHBURY, citing their paper of 1840 for the description. This was also the case in MORRIS (1854, p. 354), who did not attribute *Thecodontosaurus antiquus* to MORRIS (1843). Contemporary compilers of paleontological surveys (e.g. GIEBEL, 1847, p. 131 and references cited therein; BRONN, 1848, p. 1267) used *T. antiquus* without mentioning MORRIS (1843), instead citing RILEY & STUTCHBURY (1836b &/or 1840). However, *antiquus* is not used in these papers, or in any of the abstracts that I have seen (viz., RILEY & STUTCHBURY, 1836a-d, 1837a-c, 1841).

OWEN (1859) erected the Thecodontia as an independent order of the Subclass Sauria to which he referred "the most ancient of all Saurians" that had thecodont implantations, i.e., the marginal teeth were implanted in alveoli or sockets as against the acrodont or pleurodont teeth of modern lizards. He also added *Protorosaurus*, *Belodon* and *Bathygnathus* (now a protorosaur, a phytosaur and a pelycosaur, respectively) to the order but only *"Cladeiodon"* and *"Belodon"* remain in this group that is now referred to as the Archosauria (see PARRISH, 1997). OWEN (1861, p. 278) did refer to the "dinosaurian femur" but it was not until 1870 that HUXLEY clearly established the dinosaurian nature of the Triassic bones from Durdham Down, based on the form of a few figured bones (caudal vertebra with chevron, ilium, proximal tibia, Figs 11R, W, 21C, 28D), along with those of *Plateosaurus engelhardti* MEYER, 1837 from the Upper Triassic of Germany. HUXLEY (1870) figured a second dentary of *Thecodontosaurus*, which he referred to *T. platyodon* (RILEY & STUTCHBURY, 1840) based on the oblique angle of the denticles of the teeth (Figs 4G, N), and the tooth of *Palaeosaurus cylindrodon* (Fig. 32R), but he did not assign bones to either genus. COPE (1870, p. 122A) redescribed *Megalodactylus polyzelus* (now *Anchisaurus*, Lower Jurassic, Connecticut Valley; see GALTON, 1976), noting it as "a form of Dinosauria, not far removed in some points from *Palaeosaurus* of the English Trias." HUXLEY (1875, p. 434-436) provided extra information on the bones of the Thecodontosauria, noting that he described the ilium back to front in 1870, reidentified the ischium of RILEY & STUTCHBURY (1840, pl. 30, fig. 4) as a humerus, commented on the thick, not flattened distal end of the tibia, and calculated the proportions of the skeleton. HASSE (1878a, b) reported on the histology of *Thecodontosaurus* but the caudal vertebra (in Münich Museum, Germany; lost, MOSER,

Fig 1: The location of the *Thecodontosaurus* Quarry. A: key map showing the distribution of Triassic exposures in England and Wales and the location of Bristol, from BENTON *et al.* (2000). B-E: maps of the old quarries on Durdham Down in Clifton southwest of Redland (boundary line as …… in B) showing the location of the *Thecodontosaurus* find in 1834: * = western end of Belgrave (Bellevue of Moore, 1881) Terrace on Upper Belgrave Road; *-* = line of section L; **-** = line of section M; quarries: a = Avenue Quarry; d = quarry on Durdham Down on north side of Upper Belgrave Road; r = large quarry in Redland; t = *Thecodontosaurus* Quarry in Quarry Steps Quarry; modified from: B: BENTON *et al.* (2000); C: SANDERS (1862); D: LAVARS (1875) and E: WRIGHT (1874); for scale see B. F: partly overgrown quarry face visible to west (left) side of Quarry Steps, Clifton with reddish brown Rhaetian fissure fill material (r) in the limestone. G: view from top platform of Quarry Steps to show extent of the Quarry Steps Quarry (see B for roads, B-D for position of quarry). The backs of the houses on the edge of the quarry on Upper Belgrave Road (***) are visible along the top right half and the southwestern edge extended beyond the houses on Sutherland Place (**) to the far end of Belgrave Terrace (*, see maps B-E). H: S to N section to show position of Reptilia in conglomerate in Clifton, based on drawing made by STUTCHBURY when the remains were being removed, from ETHERIDGE (1870). I: W to E section at the edge of Durdham Down in Clifton to show fissure fills and *Thecodontosaurus* deposit: Quarry = Avenue Quarry; Bellevue = Belgrave Terrace; no scale given but from maps distance from "Bellevue" to Quarry Steps is about 180 m (197 yd), from MOORE (1881). J: section of *Thecodontosaurus* bed in Clifton by SANDERS, from MOORE (1881): a = Dolomitic Conglomerate; b = locality of *Thecodontosaurus*; c = Dolomitic Conglomerate; d = Carboniferous limestone. K: proposed model of the Clifton bone-bearing breccia as infill of a collapsed cavern, the upper portions, indicated by dashed lines, have been eroded; after HALSTEAD & NICOLL (1971), from BENTON *et al.* (2000). L-M: northwestern end of detailed sections (lines *-*, **-** on D), based on drawings by SANDERS, to show the *Thecodontosaurus* Quarry in Clifton: *, *Thecodontosaurus* = Quarry Steps Quarry (t in D); **, Quarry = one on Durdham Down on north side of Upper Belgrave Road (d in D); Caroline Row = now Worrall Road (see B, also for Anglesea Place and Wellington Park). N-O: northwestern end of NW to SE sections drawn by SANDERS to show the Reptilian bed (*Thecodontosaurus* Quarry) on Durdham Down; from ETHERIDGE (1870).

pers. comm.), which came from the Rhaetian of Ilminster in Somerset, is Reptilia indet.

MARSH (1882) allied *Thecodontosaurus* with *Anchisaurus* (*Amphisaurus*/*Megadactylus*) in the Anchisauridae MARSH, 1885, as did LYDEKKER (1888, 1890). LYDEKKER (1888, p. 175) illustrated the tooth of *Thecodontosaurus platyodon* (Fig. 32C) and listed a cast of the holotype dentary as *T. antiquus* MORRIS, 1843, noting that "this species name is commonly quoted as RILEY and STUTCHBURY, but it does not occur in either of their memoirs" (i.e. 1836a, 1840). LYDEKKER (1890) erected the Thecodontosauridae and catalogued some BMNH bones (by exchange from BCM, see next section for museum abbreviations) as being referable to either *T. platyodon* or *T. antiquus*. MARSH (1892) illustrated a braincase (Figs 5A, B) and the first associated specimen, a forelimb and girdle (Fig. 13A, both from BCM), as *T. platyodon*. SEELEY (1895) was the first to discuss the taxonomic affinities of specific bones using BCM specimen numbers, dividing them between *T. platyodon* and *Palaeosaurus cylindrodon.*

HUENE (1902) made a humerus (Figs 37C, D) of RILEY & STUTCHBURY (1840) the holotype of the non-dinosaurian phytosaur *Rileya bristolensis* but, on recognizing that the holotype tooth of *Palaeosaurus platyodon* was a phytosaur (HUENE, 1908a) (Figs 32E-G), he figured another tooth, two humeri, a radius and a metacarpal as *Rileya platyodon* (HUENE, 1908b; all figures also in HUENE, 1911, figure of humerus redrawn in 1920a, 1958) (Figs 32H-N, 37A, B, E-G, 38I, J). HUENE (1902) also reconstructed the ilium of *Thecodontosaurus* (Fig. 22K) and in 1905 re-erected the Thecodontosauridae. HUENE (1908a) provided a well illustrated detailed study of the best preserved teeth and bones (most BCM, a few YPM), referring the more common gracile bones to *T. antiquus* and the robust ones to *T. cylindrodon*. HUENE (1914a) did the same for specimens in the YPM and later provided the first skeletal reconstruction of *T. antiquus* (HUENE, 1932, p. 116, pl. 54, fig. 1; 1956, fig. 521) (Fig. 2A). KUHN (1959) erected *Palaeosauriscus* for *Palaeosaurus* (preoccupied, GEOFFROY SAINT-HILAIRE, 1838) and *Rileyasuchus* for *Rileya* (KUHN, 1961a; preoccupied, ASHMEAD, 1888).

GALTON (1973), who discussed the taxa of RILEY & STUTCHBURY (1836a, 1840), referred all of the non-phytosaurian bones to *Thecodontosaurus antiquus*. GALTON (1985b) illustrated and designated the left dentary (Fig. 4G) of HUXLEY (1870) as the neotype of *T. antiquus* because the holotype right dentary (Fig. 4A) was destroyed in November 1940 when the BCM was bombed. The teeth and/or braincase were figured by GALTON (1973, 1984a, 1985c, 1986a, 1990; also GALTON & BAKKER, 1985; GALTON & UPCHURCH, 2004) and YPM 2195 by GALTON & CLUVER (1976). The identification of bones of *Thecodontosaurus* from the Middle Triassic (Anisian/Ladinian) of the English Midlands by HUXLEY (1870) and HUENE (1908a, 1956) was based on misidentifications of bones of rauisuchian crurotarsal archosaurs and of dinosauriforms (GALTON, 1985d; GALTON & WALKER, 1996a, b).

An extremely large collection of isolated *Thecodontosaurus* bones in about 10 tonnes of rock was collected in 1975 by Robert T. G. SAVAGE (Geology Department, University of Bristol) from a Rhaetian mixed cave breccia or fissure fill in the Tytherington Quarry (UK National Grid Reference ST 660890) at Thornbury, Avon 16 km north of Bristol (MARSHALL & WHITESIDE, 1980; WHITESIDE, 1986; BENTON & SPENCER, 1995; SMITH, 2002; BENTON *et al.*, 2005). These remains, discovered by two amateur geologists Mike CURTIS and Tom RALPH, are preserved in a breccia composed of clasts of Carboniferous limestone in a sandy clay mixture (BENTON & SPENCER, 1995). The matrix is much softer than that from Durdham Down, being only partly dolomitized (SCHOUTEN, 2000), so the bones are more easily prepared mechanically free of matrix than those from Durdham Down. A small sample of these bones was described by WHITESIDE (1983), the histology by CHERRY (2002a, b), and the morphometrics by LEE (2002a, b); a detailed study of the bones will start once most of them are prepared free of matrix (YATES & BENTON, in prep.).

Kenneth A. KERMACK and Pamela L. ROBINSON, both of University College London, in 1952 discovered several partial skeletons of juvenile individuals, that they identified as *Thecodontosaurus,* from a Rhaetian/Lower Jurassic fissure fill at the Pant-y-ffynnon Quarry (UK National Grid Reference ST 047741) near Bonvilston (near Cowbridge, KERMACK, 1956), South Glamorgan, South Wales. The specimens were described as *Thecodontosaurus* sp. as part of the thesis of WARRENER (1983) who, as KERMACK (1984), published a description of the skull and a reconstruction of the skeleton (Fig. 2C).

The differences between appendicular bones from Durdham Down were discussed as a sexual dimorphism by GALTON (1997, also BENTON *et al.*, 2000), with the robust morph as the male (GALTON, 1997) or, more likely, as the female (GALTON, 1999). *Agrosaurus macgillivrayi* SEELEY, 1891 from the Upper Triassic or Lower Jurassic of Australia was shown by VICKERS-RICH *et al.* (1999) to be based on mislabeled Durdham Down material of *Thecodontosaurus antiquus* (BMNH 49984, see Appendix 6). They figured the bones of the holotype (see also HUENE, 1906; tibia BENTON *et al.*, 2000), as did GALTON (2000, fig. 15) who showed that *Agrosaurus* does not represent a herrerasaurid theropod as suggested by SERENO (1997).

It was long assumed that the teeth and bones from Durdham Down in the BCM were destroyed in November 1940 by bombing (ANON, 1941). However, this was not the case because other specimens were in storage and, in addition, some unprepared blocks were in the basement (ANON, 1961; TARLO, 1962). Many of these bones from Clifton on Durdham Down, plus some in other museums (ANSP,

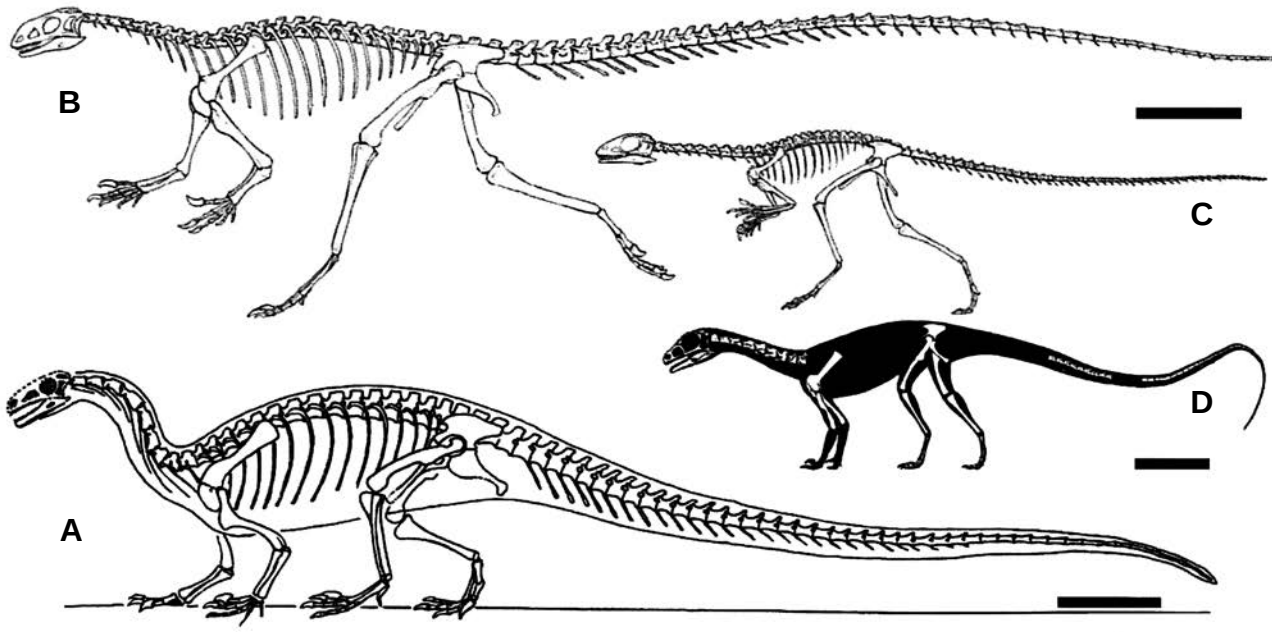



Fig. 2 : Reconstructions of the skeletons of basal sauropodomorph dinosaurs from Britain : an adult (A, B) and a juvenile (C, D) individual. A-B : mostly (except skull) based on bones from Clifton, many of which were destroyed in 1940, previously referred to *Thecodontosaurus antiquus*, and now mostly very basal Sauropodomorpha indet. A from HUENE (1932, pl. 54, fig. 1) and B modified after A and extant bones, from BENTON *et al.* (2000). C-D : based on the Welsh material of *Pantydraco caducus* : C, the dorsal vertebrae, forearm, manus, pubis, ischium and proximal femur restored, scapula based on misidentified ischium, modified after KERMACK (1984) from BENTON *et al.* (2000), and D from YATES (2003a), proximal scapula based on proximal ischium, distal scapula, distal humerus and proximal femur restored. Scale bars = 20 mm.

BMNH, YPM), were described by BENTON *et al.* (2000). However, the best BCM bones of *Thecodontosaurus* were destroyed and the only records are published illustrations, a few by RILEY & STUTCHBURY (1840), HUXLEY (1870) and SEELEY (1895) plus many by HUENE (1908a, b). However, HUENE (1908a, p. iv, vii) noted that he spent only 14 days in Bristol and that the artist was SHELLARD of Bristol. Consequently, the artist was probably unsupervised and this, along with unfamiliarity drawing bones, would account for the varying quality of the drawings. Richard OWEN (1804-1892) figured most of the reptiles discussed in his 1842a report in his *Palaeontographical Society Monographs* on British Fossil Reptilia and in his book on British Fossil Reptiles (OWEN, 1849-1884). However, no Triassic dinosaurs were described in the monographs, and only a copy of his 1842b paper on Middle Triassic labyrinthodonts was included at the end of the book. HUXLEY (1870) promised to provide full details and illustrations of the Durdham Down material, as a *Memoir of the Geological Society of London,* but these were never published. Correspondence from the BCM curator E. WILSON in early 1889 indicates that O. C. MARSH commissioned and received drawings of six specimens (including BCM 58, 96, 100 ; MCKEEVER, 1972, p. 79 ; YPM Archives Series I, Box No. 36, Folder No. 1530 ; microfilm reel 16, frames 762-772). However, unfortunately there are no unpublished illustrations of any bones from Clifton in the archives of R. OWEN at the BMNH (MCEWAN, pers. comm.), T. H. HUXLEY at Imperial College London (GORKCE, pers. comm.), or O. C. Marsh at the YPM (M. A. TURNER, B. NARENDRA, pers. comm.).

The Welsh material of *Thecodontosaurus* sp., briefly commented on by YATES (2001), was redescribed as *T. caducus* YATES, 2003a (Fig. 2D). GALTON (2005b) showed that the humerus of YPM 2195 represents a third morph from Clifton so *Thecodontosaurus antiquus* RILEY & STUTCHBURY *vide* OWEN, 1842a should be restricted to the type dentaries. In addition, because the humerus of the Welsh skeletons represents a fourth morph from Great Britain (GALTON, 2005b), *T. caducus* was made the type species of *Pantydraco* GALTON, YATES & KERMACK, 2007.

*Thecodontosaurus antiquus* was described as a medium sized prosauropod with a body length up to 2.5 m (with femoral length of 255 mm) (Fig. 2B ; BENTON *et al.*, 2000), a group of dinosaurs that were mostly herbivorous but which were probably also partly omnivorous (KERMACK, 1984 ; GALTON, 1984b, 1985c, 1986a, 1990 ; BARRETT, 2000 ; GALTON & UPCHURCH, 2004). Cladistic analyses of the Dinosauria indicate that *Thecodontosaurus* is a prosauropod (Fig. 3A) or a very basal sauropodomorph

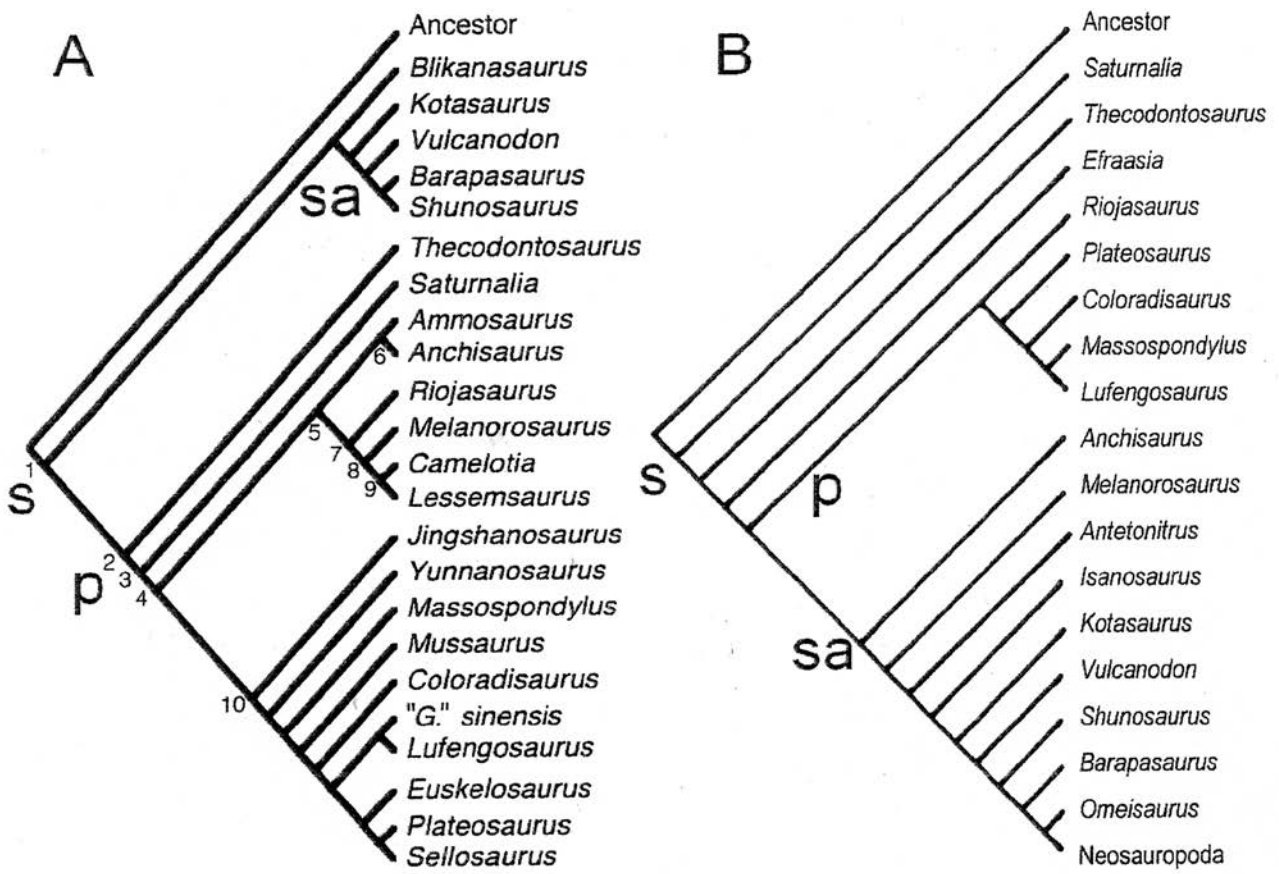



Fig. 3: Two recent cladistic analyses of basal Sauropodomorpha. A: One of the two most parsimonious trees found by a Heuristic analysis using PAUP 4.0 [SWOFFORD (1998), see GALTON & UPCHURCH (2004) for details]. The other most parsimonious tree is identical to that shown, except that *Massospondylus* and *Yunnanosaurus* have swapped positions. Tree statistics: Length = 279 steps; CI = 0.541; RI = 0.635; RCI = 0.355. From GALTON & UPCHURCH (2004), who provide a full discussion of the 136 characters, nodes and genera plus the character matrix. *Euskelosaurus* now *Plateosauravus* (see YATES, 2003c); "*G.*" *sinensis* = *Gyposaurus sinensis* of YOUNG (1941a, 1948); *Sellosaurus* = *Plateosaurus gracilis*; *Efraasia*, the genus to which most of the German Pfaffenhofen specimens are now referred (see YATES, 2003b), plots next to *Thecodontosaurus* (as in B) in UPCHURCH *et al.* (2007). B. Simplified cladogram of five most-parsimonious trees. Tree statistics: Length = 449 steps; CI = 0.5434; RI = 0.7288 after unstable *Blikanasaurus* has been pruned. After YATES & KITCHING (2003), who provide details on 212 characters, nodes and genera plus character matrix. p = Prosauropoda; s = Sauropodomorpha; sa = Sauropoda; 1-10: nodes referred to in text.

(Fig. 3B) (GALTON, 1990; SERENO, 1997, 1999; BENTON & STORRS in BENTON *et al.*, 2000; YATES 2001, 2003a, 2004, 2006. 2007; YATES & KITCHING, 2003; GALTON & UPCHURCH, 2004; UPCHURCH *et al.*, 2007). However, despite the recent description of the surviving material attributed to *T. antiquus* from Clifton, to which I contributed the section on the braincase and endocranial cast plus figures of some of the other bones (BENTON *et al.*, 2000, p. 83-86, figs 4-6, 8B-D, 17), and the preliminary description of the juvenile individuals of *Pantydraco* GALTON *et al.*, 2007 from Wales by YATES (2003a), a more detailed consideration is needed. With the recognition of the third humeral morph (YPM 2195) from Clifton (GALTON, 2005b, GALTON *et al.*, 2007), the taxonomic status of each of the specimens from Clifton that are currently referred to *Thecodontosaurus antiquus*, including the gracile and robust morphs of some of the long bones, needs to be reviewed. In order to do this, the majority of the published figures of this material (except most of those of extant specimens in HUENE, 1914a and BENTON *et al.*, 2000) are reproduced and discussed, along with photos of most of the previously described extant bones and several previously undescribed ones. A detailed description of YPM 2195, the holotype of the very basal sauropodomorph *Asylosaurus yalensis* gen. et sp. nov. (see character and systematic sections for details) is also provided; that of the Welsh material of *Pantydraco caducus* will be given elsewhere (KERMACK & GALTON, in prep.). In addition, teeth and bones of the other archosaurs from Clifton are described, including *Palaeosaurus platyodon* and *P. cylindrodon*, plus a few reptilian bones of uncertain affinities.

## II. MUSEUM ABBREVIATIONS

ACM: Amherst College Museum, Amherst, Massachusetts, USA; ANSP: Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; BCM: Bristol City Museum and Art Gallery, Bristol, UK (for institution and old specimen numbers); BGS: British Geological Survey, Keyworth, Nottinghamshire, UK (formerly Institute of Geological Sciences, Keyworth/ London and Geological Survey Museum/Museum of Practical Geology, London); BGS GSL: BGS, Geological Society of London Collection; BMNH: The Museum of Natural History [formerly British Museum (Natural History)], London, UK; BRSMG: specimens in Bristol City Museum and Art Gallery, Bristol, UK (for current specimen numbers); BRSUG: Department of Earth Sciences, University of Bristol, UK; GPIT: Institut für Geologie und Paläontologie, Universitat Tübingen, Germany; SMNS: Staatliches Museum für Naturkunde, Stuttgart, Germany; VMNH: Virginia Museum of Natural History, Martinsville, USA; WM: Wells Museum, Somerset, UK; and YPM: Yale University, Peabody Museum of Natural History, New Haven, Connecticut, USA.

## III. LOCALITY AND GEOLOGY

Early reports gave the location as Durdham Down near Bristol (Fig. 1A) but subsequently RILEY & STUTCHBURY (1840) gave it as Redland on the south-eastern extremity of Durdham Down (Fig. 1B). Robert ETHERIDGE (1870, p. 188, figs 4, 5), the next salaried BCM curator after STUTCHBURY, noted that the spot where the reptilian bones "were found is no longer recognizable or determinable, having been many years ago quarried away, and the site built upon. Fortunately, we have records of the exact position; and many years since, W. SANDERS ..... most accurately determined the site of the reptilian quarry on the eastern side of Durdham Down", showing it in two geological sections at 320 feet above mean sea-level (Figs 1N, O). William SANDERS (1799-1875) was a corn merchant and a keen amateur geologist who lived in Clifton and was deeply involved with the Bristol Institution, serving as its Honorary Curator in the 1860's. In 1835 he began, at his own expense, a detailed geological survey of 720 square miles around Bristol on a scale of 4 inches to the miles and he published the resultant map as 19 sections in 1862 (Fig. 1C); this work lead to the still ongoing Geological Survey's largescale survey of the whole country (CLARK, 2004). ETHERIDGE (1870, fig. 6) also reproduced a sketch, given him many years previously by STUTCHBURY, which shows the position of the bones in the conglomerate as they were being removed (Fig. 1H). Charles MOORE (1881, p. 67; 1815-1881, biography COPP *et al.*, 2000; SAVAGE, 2004), a noted local geologist who may also have spoken directly to STUTCHBURY, noted that "a few years since [1836], in drainage-works at the same spot [in Redland], this conglomerate was again crossed, and some other bones added to the series deposited" in the BCM (but there is no record of this in the Accessions Catalogue, CLARK, pers. comm.). A sketch section by SANDERS of the *Thecodontosaurus*-bed (Fig. 1J) was reproduced by MOORE (1881, fig. 2).

MOORE (1881), who fortunately gave more specific details, drew attention to Quarry Steps and to Quarry Steps Quarry (Figs 1B-H). From the platform at the top of the steps there is still visible, stretching behind the large mid- and late-Victorian houses on Upper Belgrave Road (Figs 1B, G), a long shallow quarry that is filled with small streets of workmen's houses and workshops built in the 1830's and 1840's (Fig. 1G), not the 1780's as thought by MOORE (1881, p. 72). This limestone quarry was evidently worked in the 1820s for building stone but, almost as soon as the bones were found, the quarry was exhausted and closed. MOORE (1881, p. 72) noted that, looking from the platform at the top of Quarry Steps "along the Down escarpment to the west, the eye takes in Bellevue Terrace [Figs 1B, G, I, on Upper Belgrave Road, see below], on the edge of the Down; and it is between these houses and the quarry, a distance probably of 200 yards [but on p. 73 it is to the end of the Terrace as about 300 yards], along the same face of limestone, and on the same horizon, that the deposit containing the Thecodontosaurian remains was found. Unfortunately the precise spot is unknown ..... and built over." Based on MOORE's account, BENTON *et al.* (2000, p. 79, 82) identified the *Thecodontosaurus* site as Quarry Steps Quarry, "off Belgrave Terrace" (UK National Grid Reference ST 572747; actually Upper Belgrave Road, Fig. 1B) in Clifton, Bristol. They noted that the "discovery site may still be seen behind a block of flats, and with an old set of stone steps (Quarry Steps) descending beside it [Fig. 1F]. The topotype quarry contains at least one fissure with a lithology similar to that of the bone-bearing matrix, but all the bones appear to have been quarried away." MOORE (1881, p. 72) noted that a few pounds of softer material from the edges of the fissure next to Quarry Steps, of especial interest because of its close proximity to the *Thecodontosaurus* deposit, yielded "numerous minute fragments of bone or teeth, one very small fish-tooth, an *Echinus* spine" (not "a low diversity fish fauna, represented by spines, scales and teeth, as well as an *Echinus* spine" as cited by BENTON & SPENCER, 1995, p. 88, presumably source of incorrectly cited "presence of unrolled fish teeth" on p. 90). This quarry cliff face (Fig. 1F) was selected by the Geological Conservation Review as one of 50 British fossil sites designated as Sites of Special Scientific Interest by the Nature Conservancy Council (BENTON, 1988; details in BENTON & SPENCER, 1995; BENTON *et al.*, 2000).

Despite the discussion by BENTON *et al.* (2000) on the locality and geology, there are still a few loose ends. There is no Bellevue Terrace on a current road map of

the area (Fig. 1B) but the last block of houses shown on Upper Belgrave Road is named Belgrave Terrace on the map in LAVERS (1875) (*, Fig. 1D); this is presumably the Bellevue Terrace of MOORE (1881). From the UK 1:2500 Ordinance Survey map, the far end of Belgrave (Bellevue) Terrace (*, Figs 1B-E, G) is about 180 m (197 yd) from the Quarry Steps platform and it borders the far end of a quarry face (Fig. 1B) that, before the very steep Sutherland Place was constructed (presumably from quarry debris, sometime after 1862 and before 1875; it has large depressions on either side of it, SCHOETEN, pers. comm.), was the western end of Quarry Steps Quarry. RILEY & STUTCHBURY (1840) gave the locality as Redland. However, the Quarry Steps and the adjacent Quarry are in Clifton (then in Somersetshire), not in Redland (then in Gloucestershire), with the county boundary at that time being located close to the edge of Durdham Down (...., Fig. 1B). A large quarry is shown nearby in Redland (r, Fig. 1D) by LAVARS (1875) but, as there are buildings and no quarry shown at the same spot by SANDERS (1862, sheet 6) (Fig. 1C), this is not the quarry. However, MOORE (1881, p. 72) thought that Quarry Steps and the *Thecodontosaurus* Quarry were in Redland, so presumably RILEY & STUTCHBURY (1840) made the same mistake that was repeated by subsequent authors (OWEN, 1841, 1842a, MORRIS, 1843, 1854; MOORE, 1881; LYDEKKER, 1888 as Gloucestershire; HUENE, 1908a; as near Clifton in ETHERIDGE, 1870).

ETHERIDGE (1870, figs 4, 5), in the caption to SANDERS' sections, noted the "Reptilian Quarry on Durdham Down, 320 feet above mean sea-level" (same altitude repeated by BENTON *et al.*, 2000, p. 79), even though this was obviously not the case from the sections (Figs 1N, O). However, in the text ETHERIDGE (1870, p. 186) gave the altitude as 300 feet and, as MOORE (1881, p. 72) noted that the site was on the same horizon as the platform of Quarry Steps, the original altitude would have been about 300 feet. SANDERS (1862), showed two outliers of the Magnesian Conglomerate (as N.R.S., for New Red Sandstone) in the northern part of Clifton and these agree with the location of the two quarries shown by LAVARS (1875, topography based on UK Ordinance Survey Map) (Figs 1C, D). In both maps the more westerly location is shown as an open quarry but, as the area of the Quarry Steps Quarry is indicated by an outline with houses on it (t, Fig. 1D), this site was built over as was noted for the *Thecodontosaurus* quarry by ETHERIDGE (1870) and MOORE (1881). One problem with the geological sections of SANDERS (Figs 1N, O), those given by ETHERIDGE (1870, figs 4, 5), is that they could have passed through either quarry or even ones on Durdham Down to the west or north of Upper Belgrave Road (a, d, Fig. 1D). However, two more detailed sections based on the work of SANDERS (Figs 1L, M) are given by LAVARS (1875) and, as each section is indicated by a line on the map (*–*, **–**, Fig. 1D) with Quarry d (Fig. 1D) indicated as "Quarry" on both sections (Figs 1L, M), the *Thecodontosaurus* Quarry can be positively identified as the Quarry Steps Quarry based on SANDERS' original geological work rather than on hearsay published over 55 years later. SANDERS started his work on the geology of the Bristol area in 1835 (CLARK, 2004) so he undoubtedly would have visited the site with RILEY and/or STUTCHBURY when it was still a quarry and before it was built over.

A different location for the 1834 bone site is indicated by PERCEVAL (1908, p. 5), who noted that the "exposure of rock from which they were obtained used to be visible on the west side at the south end of Worrall Road. This exposure is represented in the maps that accompanied WRIGHT's Bristol Directories of the years 1870 to 1874. At page 111 of ARROWSMITH's Dictionary of Bristol, 1884, the locality is thus described: 'Reptilian remains were found some years ago in a dike of new red conglomerate, near Lower Belgrave Road Durdham Down.' The exposure in Worrall Road is no longer visible, having apparently been built over." Prior to 1878 at the latest (map in WRIGHT, 1878), Worrall Road was not straight (Figs 4C-E), like it is now, but had a southern part paralleling Lower Belgrave Road (latter now part of Upper Belgrave Road), so this alternative location would be the Avenue Quarry (a, Fig. 1D) of MOORE (1881; near north end of Avenue Road) (Quarry, Fig. 1I); no other quarry is show in this area by SANDERS (1862) or LAVARS (1875) (Figs 1C, D). This is presumably the "quarry (now infilled) near Worrall Road" given by KELLOWAY & WELCH (1993, p. 137) as the *Thecodontosaurus* quarry. HUENE (1908a, p. 191) also identified the Avenue Quarry as the discovery site but apparently misunderstood MOORE (1881, p. 74), who mentioned this quarry (Quarry, Fig. 1I) that produced Rhaetian fossils (teeth of *Saurichthys* and *Lophodus*, small palate identical with species from Holwell) from matrix washings at a location 680 yards away from Quarry Steps and terminating a transect of workings that produced fissures of different ages (Fig. 1I). PERCEVAL (1908) gave no reasons for identifying this quarry (Figs 1C, D, I), which was eventually filled in and never built on, as the reptile locality rather than the Quarry Steps Quarry.

The geological age assigned to the Durdham Down deposits at Clifton has varied considerably since the discovery of the bones. It was long equated with the Magnesian Conglomerate, which occurs very close by (Figs 1J, O; LEAN, 1888) and originally thought to represent the "lower division of the New Red Sandstone" (so Permian, RILEY & STUTCHBURY, 1840, p. 349; MORRIS, 1854, p. 351, 354). SANDERS (1862) had N.R.S. on his maps in the Bristol area (Fig. 1C), but WRIGHT (1876) noted that SANDERS considered it to be Triassic, and SANDERS (1850) himself commented on the improbability of there being any part of the Permian system in the Bristol district. ETHERIDGE (1870) equated both with the German Muschelkalk or Lower Keuper (Middle Triassic). However, HUENE (1908a-c) favored a still lower horizon, one equivalent to the German

Muschelkalk or Buntsandstein, based on the incorrect referral to *Thecodontosaurus* of bones (see GALTON & WALKER, 1996a, b; BENTON & GOWER, 1997) from what is now regarded as Middle Triassic in the English Midlands (beds Anisian, BENTON *et al.*, 1994).

MOORE (1859) studied the Carboniferous Limestone of the Mendip Hills in Somerset and showed that, in the region of Frome near Holwell, a fissure containing teeth of *Thecodontosaurus* and *Palaeosaurus* was associated with Triassic invertebrates so he deduced that the Durdham Down deposit was also Triassic. MOORE (1867, p. 455-456) briefly mentioned the same fissure fill deposit at Holwell as Rhaetic and, as it was lithologically identical and contained remains of the same reptiles as the fissure fill at Durdham Down, he inferred that the latter was Rhaetic rather than equivalent to the older Dolomitic Limestone. MOORE (1876) reported on the contents of a few fissure fills on Durdham and Clifton Downs, noting that the numerous remains of the Rhaetic fish *Saurichthys apicalis* and *Acrodus minimus* in a fissure near the Clifton end of the Suspension Bridge were identical to those of a Rhaetic fissure deposit containing *Thecodontosaurus* and *Palaeosaurus* in the Mendips (presumably Holwell; MOORE, 1859). BENTON *et al.* (2000, p. 80) cited MOORE (1867, 1881) as advocating a Rhaetic age and an extensive quote covering the Durdham and Clifton Down fissures was cited as MOORE (1867); the correct reference is MOORE (1876, p. 77-78) that is not listed. BENTON & SPENCER (1995, p. 88) also cited MOORE (1881) for a Rhaetic age for the Durdham Down fissure deposit, based on a reptile vertebra from Vallis Vale, and noted that he "later (according to H. H. WINWOOD) thought it to be 'Upper Keuper' after finding teeth of *Thecodontosaurus* at Ruishton near Somerset." However, MOORE (1881, p. 81) noted that the teeth of *Thecodontosaurus* from Durdham Down, which differed from those from Holwell in several respects, were identical with those he recently found in a section of variegated Keuper marls at Ruishton near Taunton in Somerset (details on site in MOORE, 1867, p. 468), so he thought that the age of the Bristol reptiles was probably equivalent to the middle of the Upper Keuper rather than Rhaetic. He also reported finding a dinosaurian vertebra in the Rhaetic of Vallis Vale at Hapsford near Holwell (MOORE, 1881, p. 67-68).

The recent literature on the age and geological origin of the deposit excavated by RILEY & STUTCHBURY (1840) is summarized by BENTON *et al.* (2000, p. 79-81), who conclude that it represent a Triassic (Rheatian) dolomitized cave breccia or fissure fill (not in Magnesian/ Dolomitic Conglomerate, STUTCHBURY, 1835; STORRS, 1994, p. 243) in Lower Carboniferous (Dinantian) marine limestone. As regards the Mercia Mudstone Group, WARRINGTON *et al.* (1980, p. 48) incorrectly noted that the "marginal facies ('Dolomitic Conglomerate') has yielded reptilian remains near Bristol (RILEY & STUTCHBURY, 1840; ETHERIDGE, 1870)." ROBINSON (1957) surveyed the Rhaetian-Lower Jurassic fissure deposits of southwestern England and South Wales but did not include the Durdham Down *Thecodontosaurus* site because she did not regard it as representing a fissure fill. However, TARLO (1959, 1962) noted that it evidently represented a fissure fill and HALSTEAD & NICOLL (1971) reinterpreted it as a collapsed cavern (Fig. 1K), most of which was eroded away since the Late Triassic except for the base, that was indicated by the shallow saucer-shaped depression illustrated by STUTCHBURY (Fig. 1H). However, the Clifton site would involve a much larger cavern than indicated (Fig. 1K) because the base was redrawn proportionally much shorter and more concave than in the original figure (Fig. 1H). In addition, MOORE (1881, p. 72, fig. 1) noted that the *Thecodontosaurus* bed occurred at the level of the platform of the Quarry Steps and indicated it as such (Fig. 1I). However, the original deposit probably extended deeper because, as noted above, MOORE (1881, p. 67) reported the discovery of additional bones during the excavation of a drainage ditch at the original site, presumably on the floor of the quarry. In addition, RILEY & STUTCHBURY (1837a, p. 91) noted that "In many instances, although the bed of dolomite is at this place near twenty feet thick, some of the bones were found even resting upon the carboniferous limestone itself" (Fig. 1H). The reddish brown Rhaetian deposit now exposed adjacent to the Quarry Steps on the quarry face of the grey Carboniferous limestone is all below the edge of the cliff and varies in vertical depth with a rounded eastern end (r, Fig. 1F), as in a cavern.

The only material of non-archosaurian reptiles from Clifton mentioned by BENTON *et al.* (2000; also BENTON & SPENCER, 1995) are two specimens of the small sphenodontid lepidosaur *Diphydontosaurus avonis* WHITESIDE, 1986 that were first identified as such by FRASER (1994, p. 223). The first is an isolated dentary (Fig. 34B, BRSMG Cb4714, *Clevosaurus* of HALSTEAD & NICOLL, 1971). The second is a partial articulated skeleton (Fig. 34A; BRSMG Cb4715), the "lizard" of ANON (1961), TARLO (1962) and HALSTEAD & NICOLL (1971, pl. 23B). This small partial articulated skeleton is significant because, as HALSTEAD & NICOLL (1971) noted, the animal either fell directly into the cavern or its mummified body was washed in. Either way, it would be difficult for this remarkable state of preservation to occur in any of the earlier proposed depositional environments for the Clifton deposits, viz., on a beach, alluvial fan or scree, or a "depression in the Palaeozoic land surface." As TARLO (1959) noted, this is the sort of preservation that is typical of cave or fissure deposits. A third specimen, a small piece of a maxilla (BMNH R14111), came from acid preparation of the matrix attached to the radius (see GALTON, 2000, figs 15H-J) of *Agrosaurus* (BMNH 49984, VICKERS-RICH *et al.*, 1999) (for identification of these three specimens as *Diphydontosaurus*, see Appendices 3, 6).

As regards evidence for other cave/fissure fill deposits

on Durdham Down, MOORE (1881, p. 74) noted a large lump of seemingly stratified yellow marl on the bottom of Avenue Quarry (a, Fig. 1D), which represented an alluvial infilling into a small limestone cavern, that was connected to one of the three fissure fill veins in the quarry wall (Fig. 1I). The contents of these fissures included Rhaetian remains, teeth of *Saurichthys* and *Lophus* and a small palate identical with a fish species from Holwell. In addition, a cavern/fissure in the Carboniferous limestone was discovered in 1842 in the middle of Durdham Down and it contained remains of Pleistocene animals including elephants, hippos, rhinos, deer, horse, bears, hyaena, fox and wolf (now in BCM; WILSON, 1886; PERCEVAL, 1908).

## IV. HISTORY OF SPECIMENS

Rev. David WILLIAMS (1835a, b, 1837) of Bleadon, Somerset reported the discovery of a small jaw fragment with replacement teeth from Durdham Down. WILLIAMS (1835c) noted that the substance of his short note (1835a, b) was fully ascertained at the Quarry and based on specimens "I collected with my own eyes and hammer, or from specimens brought me by the Quarrymen." The current location of the jaw and of the other bones is unknown but, according to STUTCHBURY (1836), there were no other bones and the rest of the report was based solely on BCM material. The jaw fragment was illustrated by RILEY & STUTCHBURY (1840) as *Thecodontosaurus* (Fig. 34D).

The ANSP material was donated by Thomas Bellerby WILSON (1807-1865), probably around 1848 (DAESCHLER, pers. comm.) (see Appendix 4 for list of specimens). SPAMER (pers. comm.) writes that, although WILSON was a physician in Newark, Delaware, he apparently never practiced, being wealthy enough to do what he pleased, and his house was stuffed to the rafters with all kinds of things related to natural history and other subjects. He donated many very significant collections of the mid-1800s that he purchased from around the world, as well as numerous books and money, being the Academy's greatest donor, but he wished to remain anonymous in his dealings. T. B. WILSON acquired collections through his brother back in the home country, Edward WILSON (1808-?, alive in 1865), who lived in Wales and served as his agent or broker, and these included some substantial specimens from the Bristol Institution. Many of the latter were plaster casts of prominent specimens like ichthyosaurs and plesiosaurs, which are still at the ANSP in their wooden frames as shipped. CLARK (pers. comm.) notes that T. B. WILSON acquired material for his brother through people at the Bristol Institution, including the curator Samuel STUTCHBURY and his brother Henry STUTCHBURY in London. Initially I assumed that the *Thecodontosaurus* material was obtained from the BCM and presumably listed in the records under the heading "duplicates", the Institution being a little short of cash at the time (as well as subsequently, TAYLOR, 1994). However, a couple of the ANSP specimens have, attached to the underside of the matrix, old flaking and worn hand written paper labels that read "Magnes. Conglomerate Bone of Paleosaurus Dr. (undecipherable - long name - not STUTCHBURY), Bristol. Old BCM labels read "Thecodontosaurus Durdham Down or Thecodontosaurus Quarry, Riley 1836". RILEY did give a couple of bones (but not 28) to his good friend Dr. J. CHANING PEARCE (died 1847) who donated them back to the BCM (BRSMG Cb4501, 4502, latter with label "Collected by Riley"). Although T. B. WILSON acquired a lot of specimens from the BCM, the ANSP collection of "28 bones of *Paleosaurus* and *Thecodontosaurus*" apparently came from the private collection of a Doctor in Bristol. Consequently they were obtained independently of the Bristol Institution, possibly directly from the quarrymen at the time of discovery, as suggested by BENTON *et al.* (2000) and STORRS (1997), respectively.

The BMNH purchased the holotype of *Agrosaurus macgillivrayi* SEELEY, 1891 in 1879 from Edward CHARLESWORTH after the dispersal of the collection of Samuel Long WARING of Norwood. However, as demonstrated by VICKERS-RICH *et al.* (1999; see Appendix 6, BMNH 49984), this material probably came from Durdham Down (i.e., Clifton), not the northeastern coast of Australia, but no earlier history of the specimen could be traced.

The history of the discovery of the BCM material at Clifton is given above (see Introduction). BCM specimens were donated to other museums by Edward WILSON (1848-1898), Curator at the Bristol Institution (and the Bristol City Museum after it was taken over by the Bristol City Council in 1894) from 1884 until his death. The BMNH received its material by exchange in 1888 (some of specimens listed in LYDEKKER, 1890, p. 247; see Appendix 6) but not also in 1889 (CHAPMAN, pers. comm. *contra* BENTON *et al.*, 2000). YPM 2195, which includes an associated shoulder girdle and forelimb, was presented to Othniel Charles MARSH of Yale College during his visit to Bristol in 1888, and the remaining specimens were acquired through exchange in 1889 and 1890 (see Appendix 7). MARSH (1892, p. 546) published a reconstruction of YPM 2195 (Fig. 13A) and drawings of a braincase (YPM 2192, Figs 5A, B), specimens for which he was "indebted to the trustees of the Bristol museum" (even though there were none, CLARK, pers. comm.). However, SEELEY (1895, p. 163) noted for these regions that "no example is known in this country in any museum" and that as "the Bristol Museum specimens came from a working long since closed, it would be interesting to learn the source from which these important new materials have been obtained." HUENE (1908a) went further, noting that the reconstructed girdle must have been partly from imagination because there were no coracoids other than those at the BCM.

As regards the reconstructed fore limb, HUENE (1908a) asserted that MARSH only had the material at the BCM to work on and the YPM specimen was not mentioned again in HUENE's description of the bones of the forelimb of *Thecodontosaurus*. The probable reason for HUENE's comments is that the photos he received in 1901 from the YPM (now in BCM Archives, Geology File No. 51) only included the side of YPM 2195 with most of the shoulder girdle (Fig. 6A), not of the other side (Fig. 6B) or of the scapular-coracoid fragment (Fig. 14L). YPM 2192 consists of blocks that were prepared at the YPM where the braincase was apparently first exposed (HUENE, 1908a, p. 192). In return for the YPM material from Clifton (see Appendix 7), the BCM received two United States Geological Survey Monographs (BCM accession records, CLARK, pers. comm.).

In 1926 and 1927, F. S. WALLIS wrapped and placed 166 BCM specimens of *Thecodontosaurus* into six storage boxes, with one bone being removed in 1932 (BCM Archives) and received as an exchange in December 1935 by the Wells Museum in Somerset (a partial femur, WM 1173, GILBERT, pers. comm.). In 1940, 92 specimens were destroyed by a direct hit on the BCM Geology and Natural History Gallery ; a femur (Figs 26A-H ; BRSMG *Ca7456/67) with burn marks was recovered in May 1941. Fortunately, the 165 specimens in storage were not hit and were unwrapped by M. L. K. CURTIS in 1959 (BCM Archives). In addition, John ATTRIDGE of Birkbeck College London in 1961 located some unprepared blocks in the BCM basement (ANON, 1961 ; TARLO, 1962).

## V. SPECIMEN NUMBERS

The specimen numbers of most of the postcranial bones figured by RILEY & STUTCHBURY (1840) (see Appendix 1) are preceded by an asterisk as the paralectotypes of *Thecodontosaurus antiquus* MORRIS, 1843 in BENTON *et al.* (2000, appendix 1, but no plate or figure numbers given and not listed as such in systematic section on p. 81-82). BRSMG *Ca7465/1♦ (see next paragraph for explanation) is the lost holotype dentary but the tooth BRSMG *Ca7449/4♦ (Fig. 32Q) is the lost holotype of *Palaeosaurus cylindrodon* RILEY & STUTCHBURY, 1840. None of the postcranial bones figured by RILEY & STUTCHBURY (1840) were specifically referred to *Thecodontosaurus*, *Paleosaurus cylindrodon* or *P. platyodon*. OWEN (1842a, p. 190) just wrote "*Thecodontosaurus antiquus* RILEY & STUTCHBURY", and MORRIS (1843, p. 211) only cited *Thecodontosaurus* RILEY & STUTCHBURY, 1836a, so the other bones illustrated by RILEY & STUTCHBURY (1840) are not paralectotypes of *T. antiquus* RILEY & STUTCHBURY *vide* OWEN, 1842a or of *T. antiquus* MORRIS, 1843.

Most of the referred specimens with old BCM numbers referred to *Thecodontosaurus antiquus* were tabulated in numerical order by BENTON *et al.* (2000, appendix 1), with the corresponding BRSMG number, whether specimen lost or not, and the figures in SEELEY (1895) and HUENE (1908a) ; ANSP, BMNH and YPM specimens were also tabulated in appendix 1 with the figures in HUENE (1908a, 1914a). Although BENTON *et al.* (2000, p. 77) noted that the "old (BCM) numbers are indicated in parenthesis after the first mention of the current BRSMG registration numbers", most specimens were described just using the BRSMG numbers. However, most of the best specimens, which were described using BCM numbers in the earlier papers, are now lost so where applicable both numbers are used for each specimen in this paper, e.g., BRSMG *Ca7487/85♦. The * indicates that this specimen was figured by RILEY & STUTCHBURY (1840, pls 29, 30 ; see Appendix 1 for an updated identification and the figure number for the copy in this paper), Ca7487 is the current BRSMG number (listed in numerical order with full details in Appendix 3), 85 is the old BCM number (listed in numerical order with current BRSMG number in Appendix 2), the ♦ indicates that it is lost (no ♦ means still in collection) and, where applicable, - indicates that it was described as an unnumbered specimen (♦ and - also used for other museums). Revised lists with full details are also given for the specimens in the ANSP, BMNH and YPM (Appendices 4, 6, 7). There are a few specimens in the BGS (Appendix 5 ; BENTON *et al.*, 2000 noted that these specimens could not be found after relocation of BGS to Keyworth) and a partial ?femur was exchanged to the Wells Museum, Somerset in 1935. For an explanation of [A], [B] and [C] after each specimen in Appendices 3-7, see below under Systematic paleontology.

## VI. BONES OF BASAL SAUROPOMORPH DINOSAURS

### VI.1. DESCRIPTION

The slender and robust morphs for girdle and limb bones from Clifton are discussed separately (see section : Cited evidence for bones from Clifton), as are the derived characters of the individual bones (see section : Characters and identifications).

#### VI.1.1. References

Unless indicated to the contrary, the following references were used in this paper for the genera and species of basal sauropodomorph dinosaurs (Fig. 3A) : *Anchisaurus polyzelius* (Lower Jurassic, eastern USA ; GALTON, 1976), *Camelotia borealis* (Upper Triassic, England ; GALTON, 1998a, 2005a), *Efraasia minor* (Upper Triassic, Germany, for systematics see YATES 2003b ; material from Pfaffenhofen and Ochsenbach : SMNS 11838, 12188-92, 12354, 12667, 12684, 17928, also SMNS 12216, 12668, 14881, previously described as *Efraasia*

*diagnostica*, *Palaeosaurus diagnosticus*, *Plateosaurus gracilis*, *P. minor*, *Sellosaurus gracilis*; HUENE, 1908a, 1932; GALTON, 1973, 1985b, 1999, 2001a; GALTON & BAKKER, 1985), *Euskelosaurus browni* (Upper Triassic, southern Africa; VAN HEERDEN, 1979), "*Gyposaurus*" *sinensis* (Lower Jurassic, China; YOUNG, 1941a, 1948), *Lufengosaurus huenei* (Lower Jurassic, China; YOUNG, 1941b, 1947, 1951), *Massospondylus carinatus* (Lower Jurassic, southern Africa; COOPER, 1981), *Melanorosaurus readi* (Upper Triassic, southern Africa; VAN HEERDEN & GALTON, 1997; GALTON *et al.*, 2005), *Pantydraco caducus* (Upper Triassic or Lower Jurassic, Wales; GALTON *et al.*, 2007; KERMACK & GALTON, in prep.; as *Thecodontosaurus* sp., WARRENER, 1983; KERMACK, 1984; as *T. caducus* YATES, 2003a), *Plateosaurus engelhardti* (Upper Triassic, Germany; for systematics see MOSER, 2003; HUENE, 1908a; SMNS 13200, HUENE, 1926; GALTON, 1990, 2001b; GALTON & UPCHURCH, 2004; SMNS, HUENE, 1932; GALTON, 2001b; MB HMN 25, JAEKEL, 1912-13; HUENE, 1932), *P. gracilis* (material from Heslach, Aixheim and Trossingen, SMNS 5175, GPIT 18318a, 18392, previously described as *P. gracilis* or *Sellosaurus gracilis*; HUENE, 1908a, 1915), *Riojasaurus incertus* (Upper Triassic, Argentina; BONAPARTE, 1972; BONAPARTE & PUMARES, 1986), *Saturnalia tupiniquim* (Upper Triassic, Brazil; LANGER *et al.*, 1999; LANGER, 2003; LANGER & BENTON, 2006), and *Yunnanosaurus huangi* (Lower Jurassic, China; YOUNG, 1942, 1951).

**VI.1.2. Dentary** (Figs 4A-U)

RILEY & STUTCHBURY (1840) described the holotype right dentary (Figs 4A, D) of *Thecodontosaurus*, the type genus of *T. antiquus* RILEY & STUTCHBURY *vide* OWEN, 1842a (=*T. antiquus* MORRIS, 1843), and just the anterior part was figured by HUENE (1908a) (Figs 4B, C, E, F). A left dentary (BRSMG C4529/2) was described by HUXLEY (1870) and HUENE (1908a) (Figs 4G, H, N, O), who both mistakenly thought it was the holotype, as did a BCM curator (WILSON, 1890, p. 365), but it is not (see discussion in BENTON *et al.*, 2000, p. 82). It is shown after I mechanical exposed the last tooth further in 1982 (Fig. 4I), prior to designating it as the neotype (GALTON, 1985b), an action necessitated by destruction of the holotype in 1940. The teeth (Figs 4A, B, E, F cf. 4G-I, N-T) were better preserved than in the holotype. It is fortunate that a cast was made in 1887 by the BMNH (as R1108, LYDEKKER, 1888, p. 175) because it shows the tooth crowns that were damaged by mechanical preparation of the neotype in 1992 (Figs 4J-L; description BENTON *et al.*, 2000, figs 3C-F, p. 82-83). Unfortunately no photographs were taken before preparation so the only photos of the complete teeth are the hand held shots I took in 1982 (Figs 4I, P-T; BENTON *et al.*, 2000, figs 4B, C). Note that the teeth were more recurved than shown by HUENE (1908a) and the obliquely inclined denticles extend further down the crown on the mesial (anterior) edge (Figs 4O cf. 4P-S). The last tooth (number 21) is incompletely erupted (Fig. 4T). The only other tooth is an incomplete and damaged crown (Fig. 4U).

**VI.1.3. Braincase** (Figs 5A-D)

The braincase YPM 2192 (Figs 5A-D) was described by HUENE (1908a, 1914a) and illustrated by MARSH (1892), GALTON (1973, 1990), GALTON & BAKKER (1985), GALTON & UPCHURCH (2004), and FEDAK & GALTON (2007). The originally complete right basipterygoid process is now damaged distally (BENTON *et al.*, 2000, figs 5B-D), a result of acid preparation in the late 1960's. Consequently, two of the photographs (Figs 5C, D) from HUENE (1908a) are included, the basis for the reconstruction of this process in my detailed figures and descriptions of it (and of the endocranial cast) in BENTON *et al.* (2000, p. 84-86, figs 5, 6).

**VI.1.4. Vertebrae and ribs**

**Cervical vertebrae** (Figs 6A, 7B-V)
The cervicals from Clifton were tentatively identified by comparisons with the articulated series C3-8 of *Pantydraco* (Fig. 7A) and *Plateosaurus* (see JAEKEL, 1913-14; HUENE, 1926; MOSER, 2003, pl. 15).
An anterior cervical (YPM 2195a, Figs 7B, C, on block with holotype of *Asylosaurus*) was figured by GALTON & CLUVER (1976; redrawn, BENTON *et al.*, 2000) as being almost complete. However, this vertebra is truncated by an obliquely inclined break (Figs 6A, 7D, F), so the anterior part bearing the prezygapophysis and parapophysis is missing, as is the diapophysis anterolaterally. Practically none of the neural spine is preserved and anteriorly the inter-prezygapophysial angle is visible (Fig. 7E). This angle is about the same distance anterior to the posteroventral corner of the centrum of a similar sized but much more complete C6 (Figs 7H, J, K). There is no trace of a posterior diapophyseal lamina on the side of the neural arch so this incomplete vertebra is probably C4 or C5. Part of the ventral median ridge is visible posteriorly on the centrum (Fig. 7F) and the posterior end surface is deeply concave.
HUENE (1908a) described an indeterminate posterior half of a centrum of an anterior cervical from Clifton (Fig. 7V). The two associated cervicals (HUENE, 1908a, pl. 77, fig. 1), described by HUENE (1914a, figs 37a, b) and BENTON *et al.* (2000, p. 86), are identified as C5 and C6 (Figs 7G-O) because the longer one lacks the small diapophyseal ridge that is present on the other neural arch. The bases of the prezygapophyses are connected posteriorly by a horizontal sheet of bone to form a "U shaped fossa" (Fig. 7K) as described for *Pantydraco caducus* by YATES (2003a, as *Thecodontosaurus caducus*). However, this fossa also extends posteriorly

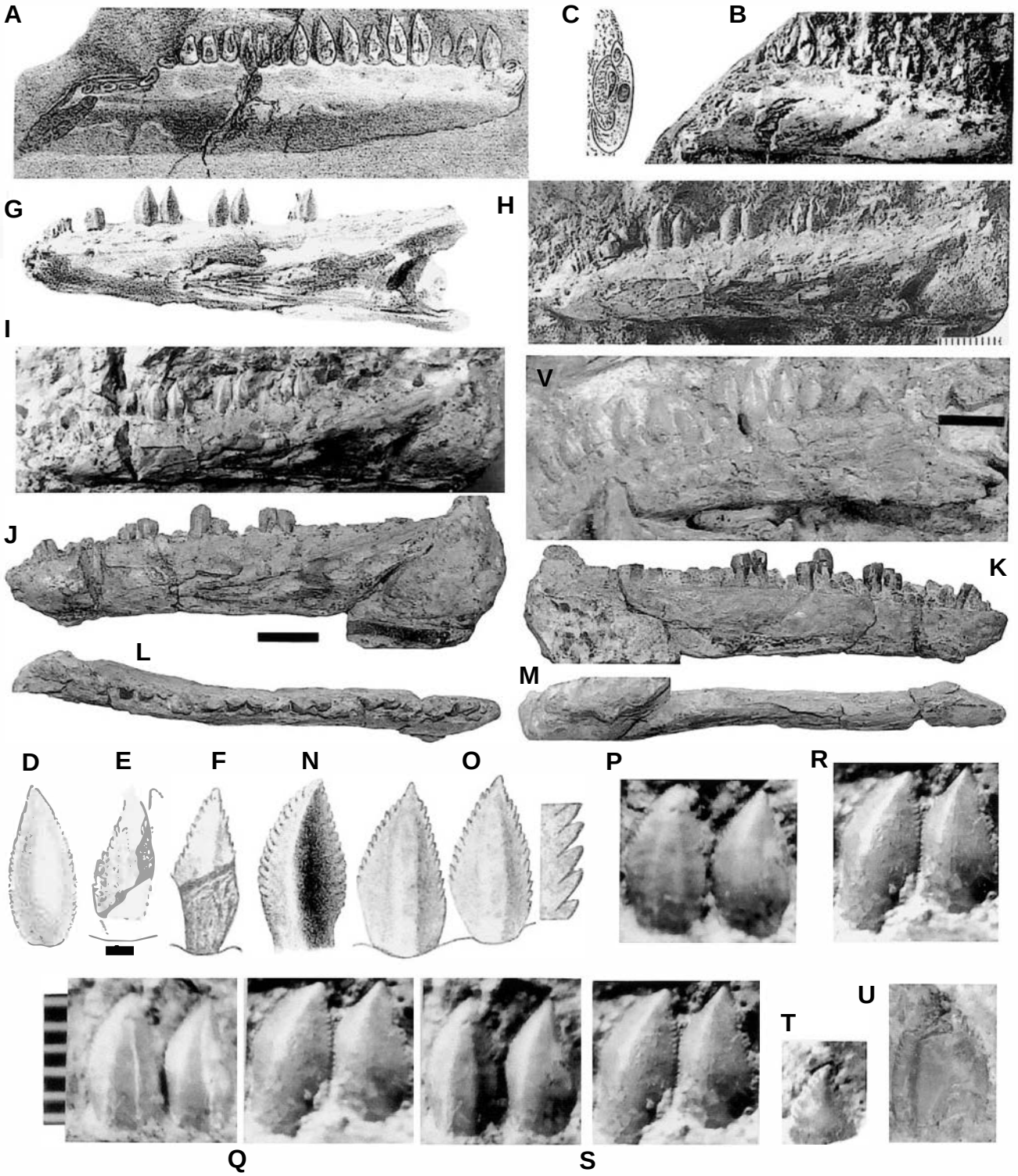



Fig. 4: Dentaries and teeth of basal sauropodomorphs from Clifton, Bristol (A-U) and South Wales (V). A-U: *Thecodontosaurus antiquus* RILEY & STUTCHBURY *vide* OWEN, 1842a. A-F: holotype right dentary BRSMG *Ca7465/1♦ A-C: bone in A, B: lateral view as A: originally preserved; B: anterior part and C: posterior sectional view of B; D-F: teeth (D restored) in labial (lateral) view. G-T: Neotype left dentary BRSMG Ca4529/2 (G-M) and teeth (N-T) in labial view: G, H: as originally preserved in lateral view and I: after further preparation of the last tooth in 1982; J-M: after mechanical preparation in 1992 in J: lateral; K: medial; L: dorsal and M: ventral views (BENTON *et al.*, 2000, figs 3C-F); N-T: teeth in labial view: N: tooth 5; O: teeth 5 and 6 with detail of 1 mm of edge; P, Q: teeth 5 and 6; R, S: teeth 8 and 9; T: tooth 21. U: isolated tooth BRSMG Ca4715a. V: left dentary in lateral view, BMNH P24, part of holotype of *Pantydraco caducus*. A, D from RILEY & STUTCHBURY (1840), B, C, E, F, H, O from HUENE (1908a), G, N from HUXLEY (1870); scale bars = 10 mm (next to J for A-C, G-M), 5 mm (V), 1 mm (next to E for D-F, N, O), and 1 mm subdivisions (Q for P-U).

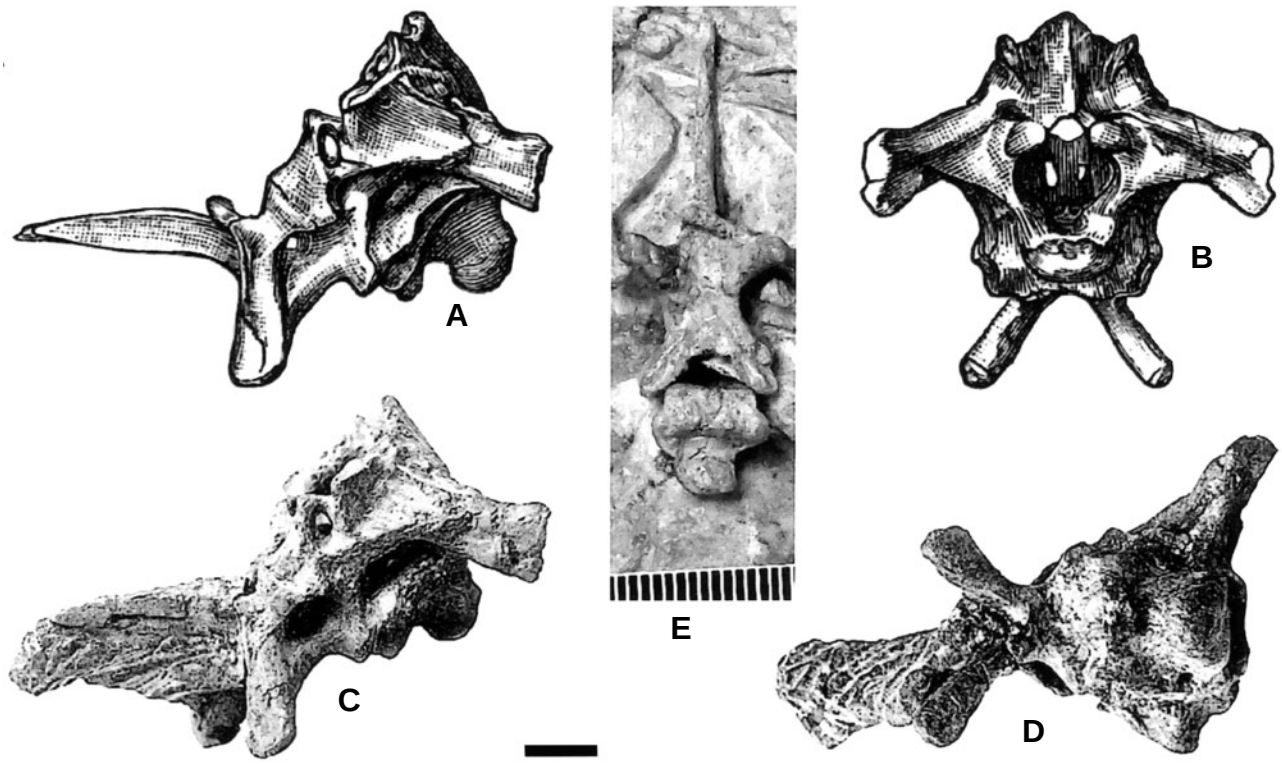



Fig. 5 : Braincases of very basal sauropodomorphs. A-D : braincase YPM 2192 from Clifton in A : lateral ; B : posterior ; C : left lateral (and slightly anterior) and D : ventral views (BENTON *et al.,* 2000, figs 5, 6). E : floor of braincase of a juvenile individual of *Pantydraco caducus,* part of holotype BMNH P24 from South Wales. A, B from MARSH (1892), C, D from HUENE (1908a) ; scale bar = 1 cm (A-D) and with 1 mm subdivisions (E).

into the adjacent part of the neural arch (Fig. 7I). There is a similar but much larger fossa in the neural arch above the base of the postzygapophyses (Figs 7G, K). The ends of the spindle-shaped centrum are amphicoelous, being strongly concave (Figs 7G, I, M), and there are indications of a small notochordal pit (Fig. 7I).

A long low neural arch (Figs 7P-T ; BENTON *et al.,* 2000, figs 7A, B) probably represents C4 or C5 ; the low ridge on the side of the prezygapophyses almost reaches the base of the postzygapophysis (Figs 7S, T). A posterior cervical has a proportionally shorter centrum that is damaged at both ends, revealing the concave surfaces, so only the base of the parapophysis is preserved, as is also the case for the diapophysis (Fig. 7U).

A posterior cervical rib (Fig. 8H) was identified by HUENE (1908a, p. 204, pl. 84), who commented on the inaccuracies of the drawing by SEELEY (1895) of this rib (Fig. 8I) ; the other cervical ribs (Fig. 8G) are dorsal ribs (see below).

**Dorsal vertebrae** (Figs 8A-C, 9, 10A-F)

The dorsal vertebrae are unknown for *Pantydraco caducus* so those from Clifton are tentatively identified by comparisons with the articulated series of *Efraasia* and *Plateosaurus* (see JAEKEL, 1913-14 ; HUENE, 1926, 1932 ; GALTON, 1973 ; MOSER, 2003, pl. 15).

Unfortunately, the dorsals of *Asylosaurus*, which are possibly articulated, are covered by the associated ribs and matrix (Figs 6B, 8D), but two adjacent vertebrae are partly visible and are probably from the middle of the series (Figs 8A-C).

The massive diapophyses of a dorsal identify this as an anterior dorsal (Fig. 9P ; BENTON *et al.,* 2000, fig. 7D). Two better preserved mid-dorsals are represented, one a bit more complete (Figs 9G-L ; BENTON *et al.,* 2000, p. 86 as mid-dorsal, figs 7H-K as D2 ; HUENE, 1908a, pl. 77, figs 7a, b as anterior dorsal, 1914a, figs 38a, b as a dorsal) than the other (Fig. 9T ; BENTON *et al.,* 2000, fig. 7G). The neural arch of another mid-dorsal has a complete diapophysis (Fig. 9A') and the proportional slenderness of the centrum in ventral view is visible in two others (Figs 9U-W, 10E, F). A few more complete dorsal vertebrae were exposed in lateral view up to the diapophysis and were identified by HUENE (1908a) as mid-dorsals (Figs 9B, E, F), D10 (Figs 9C, D) and D13 or 14 (Fig. 9A). However, two of these mid-dorsals are actually posterior ones because the two rib facets are close together (Figs 9C-F). Several other posterior dorsals are still preserved (Figs 9M-O, X-Z, 10A-D).

BENTON *et al.* (2000, p. 86, figs 7E, F) drew attention to "a horizontal face in front of the postzygapophyses," the hyposphene, a saurischian synapomorphy. However,

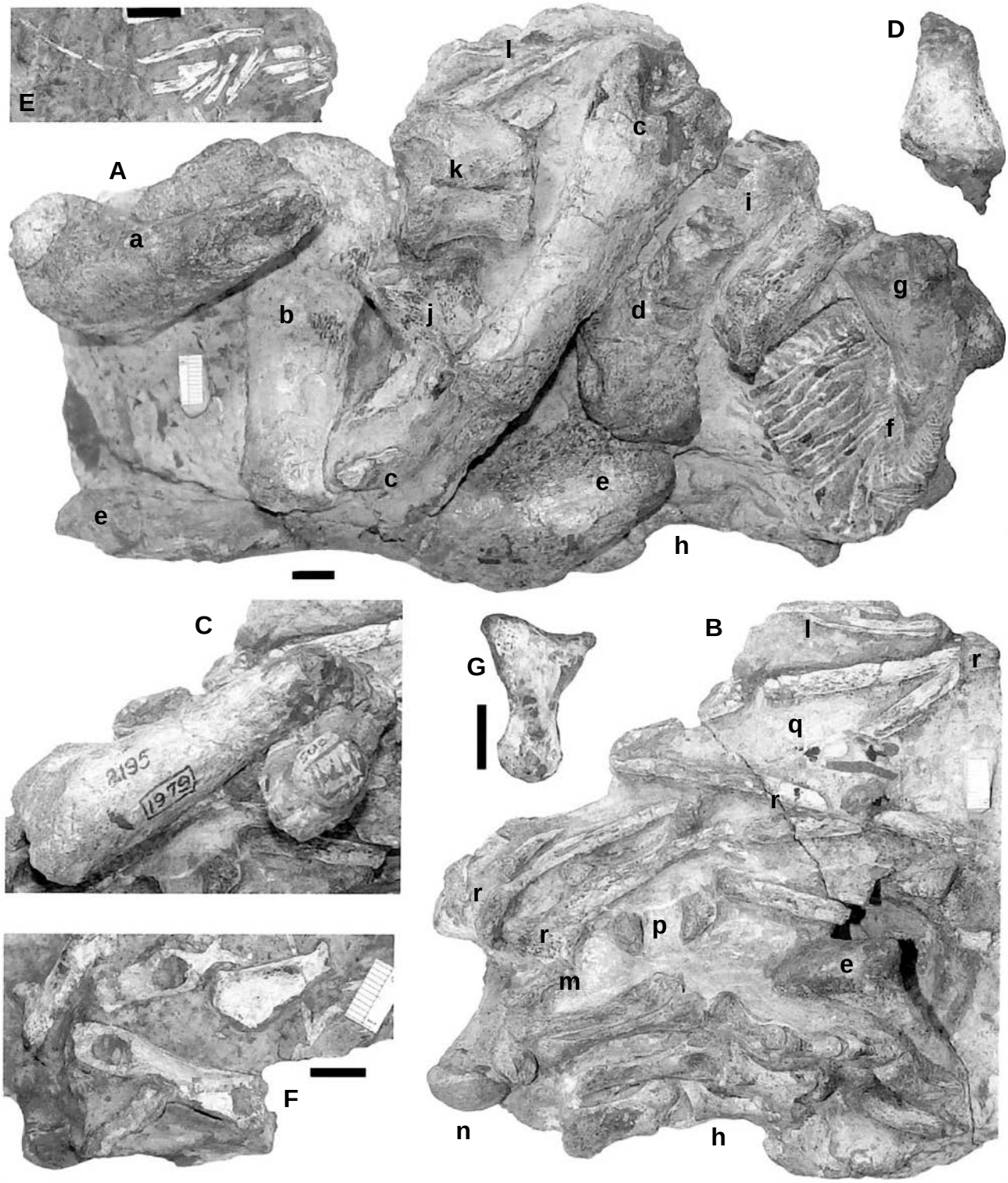



Fig. 6: Associated bones of very basal sauropodomorphs from Clifton. A-D: associated forelimb and girdle, dorsal ribs and other bones, YPM 2195, holotype of *Asylosaurus yalensis*, n. gen. et sp. A-C: main block at same magnification (~75%): A: main side and B: bone bearing part of other side; C: distal left femur repositioned using painted guidelines on B (in area q). D: distal right tibia in posterior view (has impression of rib on other side so probably from side B of block). E-G: YPM 56719: E: dorsal ribs and gastralia; F: disarticulated incomplete metacarpals and G: metacarpal V. a = distal right femur (Figs 25D-F) repositioned on block; b = right distal scapula blade (Figs 13B-D, 14I); c = left scapula blade (Figs 13E-G, 14J); d = proximal left humerus (Fig. 15N); e = right humerus (Figs 13A, I-K, 15A-M), bone in lateral view in A and proximal end in posterior view in B; f = fragment of shaft of left radius (Figs 17A-C); g = left ulna (Figs 13A, L-Q, 17A-G); h = digit I of left manus (Figs 13A, 19A-D, G, H); i = mid-cervical vertebra (Figs 7B-F); j = proximal caudal vertebra (Fig. 11A); k = proximal caudal vertebra (Figs 11B, C); l = gastralia (Figs 8D, F); m = left manus (Figs 13A, R, S, 19); n = distal left ulna (cf. g); p = ends of diapophyses of two dorsal vertebrae; q = attachment area for matrix with distal left femur shown in C (Figs 25A-C); r = dorsal ribs (Fig. 8D); scale bars = 10 mm.

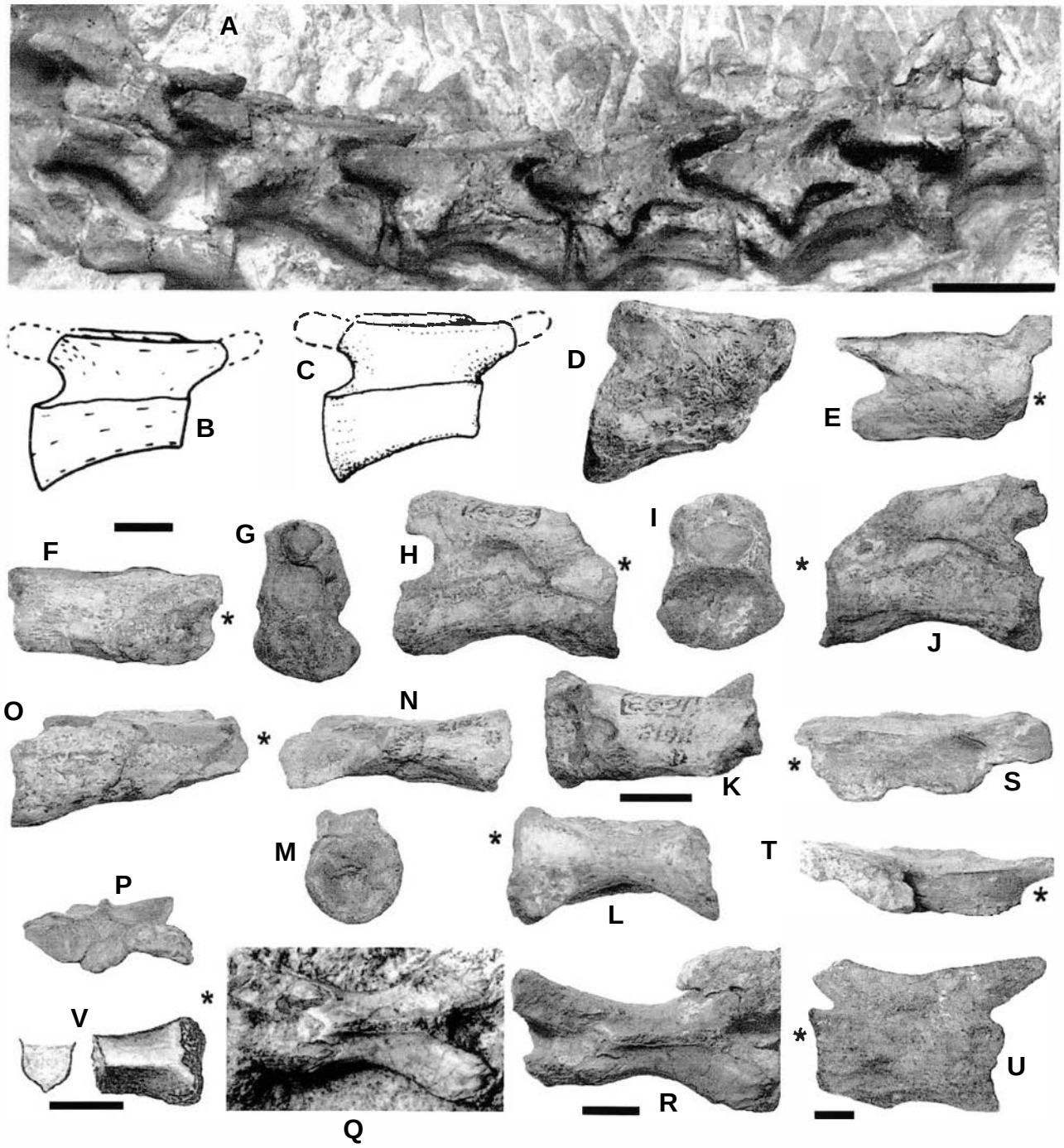



Fig. 7 : Cervical vertebrae of basal sauropodomorphs. A : *Pantydraco caducus* from South Wales, part of holotype BMNH P24, articulated cervicals 3-8 of a juvenile individual in left lateral view. B-U : from Clifton : B-T : anterior cervical vertebrae : B-F : YPM 2195a, *Asylosaurus yalensis* n. gen. et sp., part of holotype, C4 or C5 in B-D : right lateral, E : dorsolateral and F : ventral views. G-O : YPM 56720 : G-L : C6 in G : posterior ; H : right lateral ; I : anterior ; J : left lateral ; K : dorsal and L : ventral views ; M-O : C5 in M : posterior ; N : ventral and O : right lateral views. P-T : neural arch of C5, BRSMG Ca7467/- in P : posterior ; Q-R : dorsal view (Q in rock) ; S : left lateral and T : right lateral views (BENTON *et al.*, 2000, figs 7A, B). U : left lateral view of posterior cervical BRSMG Cb4726. V : posterior end of centrum of anterior cervical BRSMG Ca7472/16♦ in ventral view with cross-section. B from GALTON & CLUVER (1976), C from BENTON *et al.* (2000), V from HUENE (1908a) ; * = anterior end ; scale bars = 10 mm.

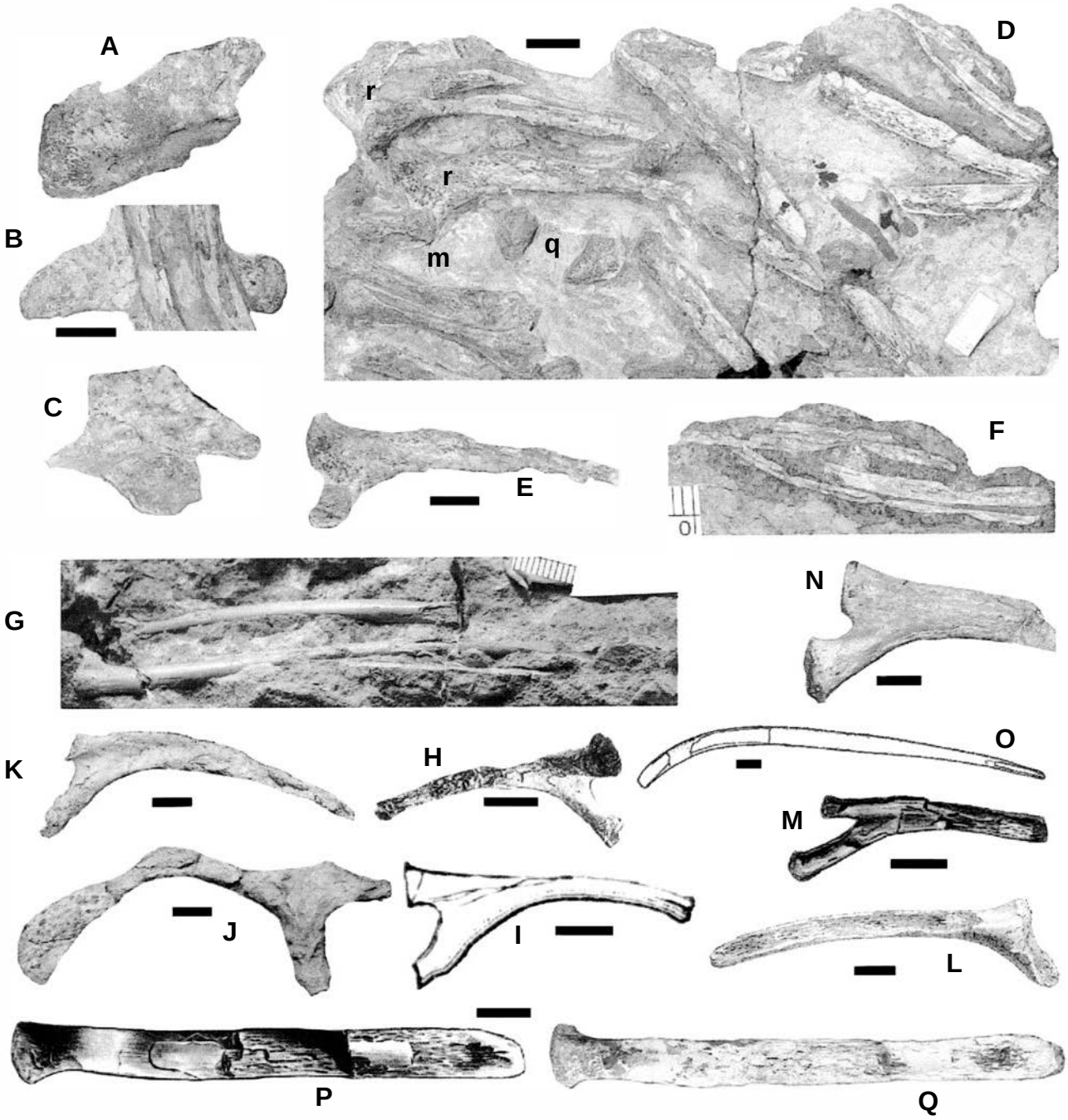



Fig. 8 : Basal sauropodomorph dorsal vertebrae, ribs and gastralia from Clifton. A-F : *Asylosaurus yalensis* n. gen. et sp., part of holotype YPM 2195. A-C : two adjacent anterior dorsal vertebrae in A, C : lateral and B : dorsal views ; D : anterior left dorsal ribs (m = manus ; q = two diapophyses ; r = dorsal ribs) ; E : proximal end of anterior left dorsal rib in posterior view (see D) and F : gastralia. G : shafts of three dorsal ribs, BRSMG Cb4196 (proximal cervical ribs, BENTON *et al.*, 2000, fig. 10A). H-I : posterior cervical rib in anterior view BRSMG Ca7457e/63♦, H : left and I : ?reversed as right. J : poorly preserved right anterior dorsal rib in anterior view, BRSMG Cb4180/58. K-N : proximal dorsal ribs, right (K-M) and left (N) in posterior (K, M) and anterior (L, N) views : K : BRSMG C4528/32 (BENTON *et al.*, 2000, fig. 10C) ; L : BRSMG *?Ca7503a/38♦ ; M : BRSMG Ca7477c/37♦ and N : BRSMG Cb4298. O : most of shaft of dorsal rib, BRSMG Cb4169/34. P-Q : distal end of dorsal rib shaft, BRSMG Ca7496/5. H, M, P from HUENE (1908a), I from SEELEY (1895) ; L from RILEY & STUTCHBURY (1840), O from BENTON *et al.* (2000) ; scale bars = 10 mm.

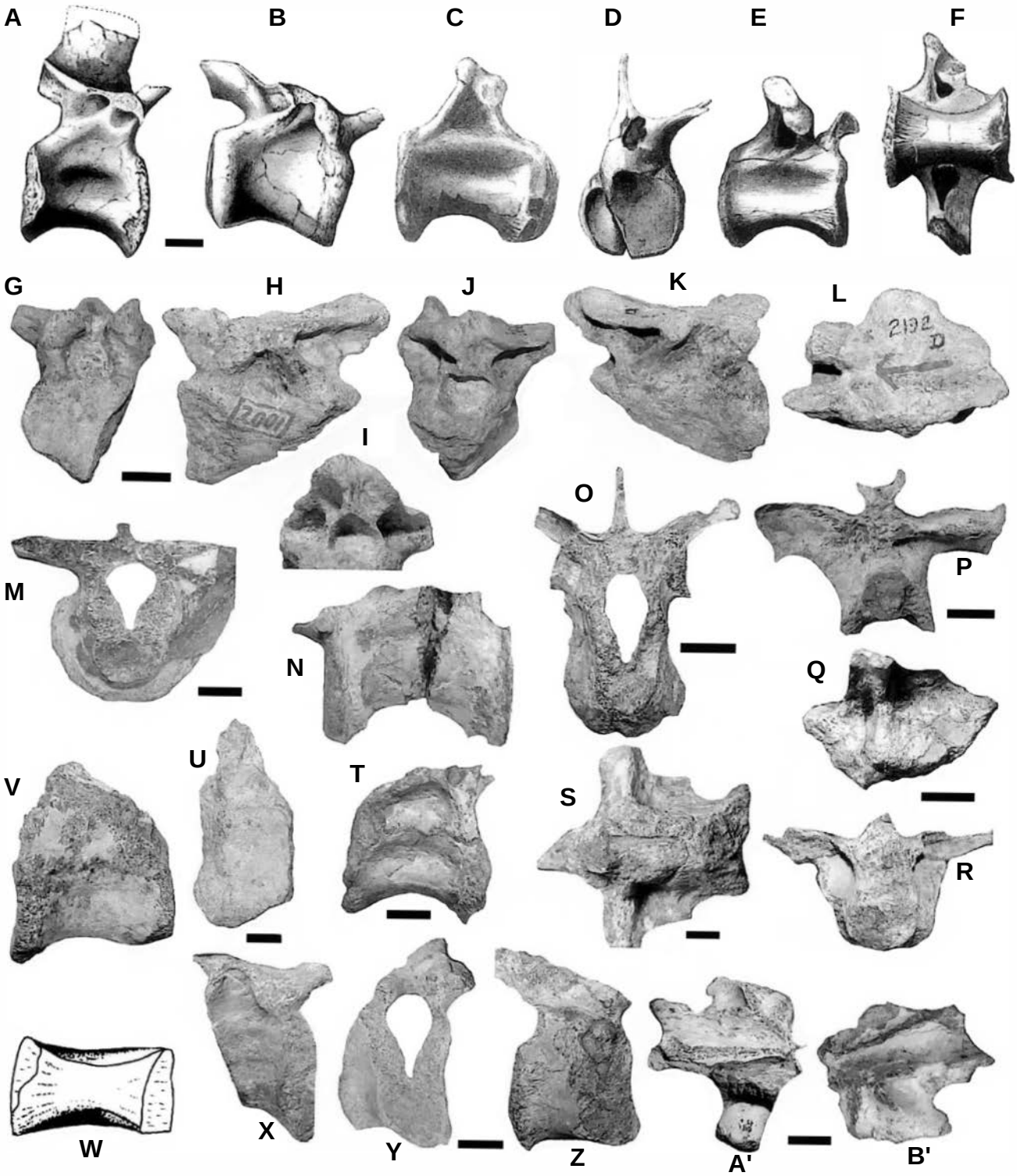



Fig. 9 : Basal sauropodomorph dorsal vertebrae from Clifton in right lateral (A-C, E, K, T, X, Z), ventral (F, S, W), posterior (D, , R, U), anterior (G, O, U), left lateral (H, N, Q, V, B'), posteroventral (I), dorsal (L, A'), and cross-sectional (M, O, Y) views. A : D13 or D14, BRSMG Ca7468/14♦. B : mid-dorsal, BRSMG Ca7469/13♦. C-F : posterior dorsals, C-D : BRSMG Ca7471/20♦ and E-F : BRSMG Ca7470/9♦ ; G-L : mid-dorsal YPM 56722 (BENTON *et al.,* 2000, figs 7H-K). M-O : posterior dorsals : M-N : BRSMG Cb4154/12 (BENTON *et al.,* 2000, figs 7N, O) ; O : BRSMG Cb4174a/41. P : anterior dorsal, BRSMG Cb4155/11 (BENTON *et al.,* 2000, fig. 7D as Cb4153). Q-S : posterior dorsals BRSMG Cb4153/15 (BENTON *et al.,* 2000, figs 7E, F as Cb4155) ; T-W : mid-dorsals : T : YPM 56719 (BENTON *et al.,* 2000, fig. 7G) ; U-W : BRSMG Cb4182/69 (BENTON *et al.,* 2000, figs 7L, M). X-Z : posterior dorsals X : BRSMG Cb4293 and Y-Z : ANSP 9865a ; A'-B' : mid-dorsal ANSP 9870c. A-F from HUENE (1908a), W from BENTON *et al.* (2000) ; scale bars = 10 mm.

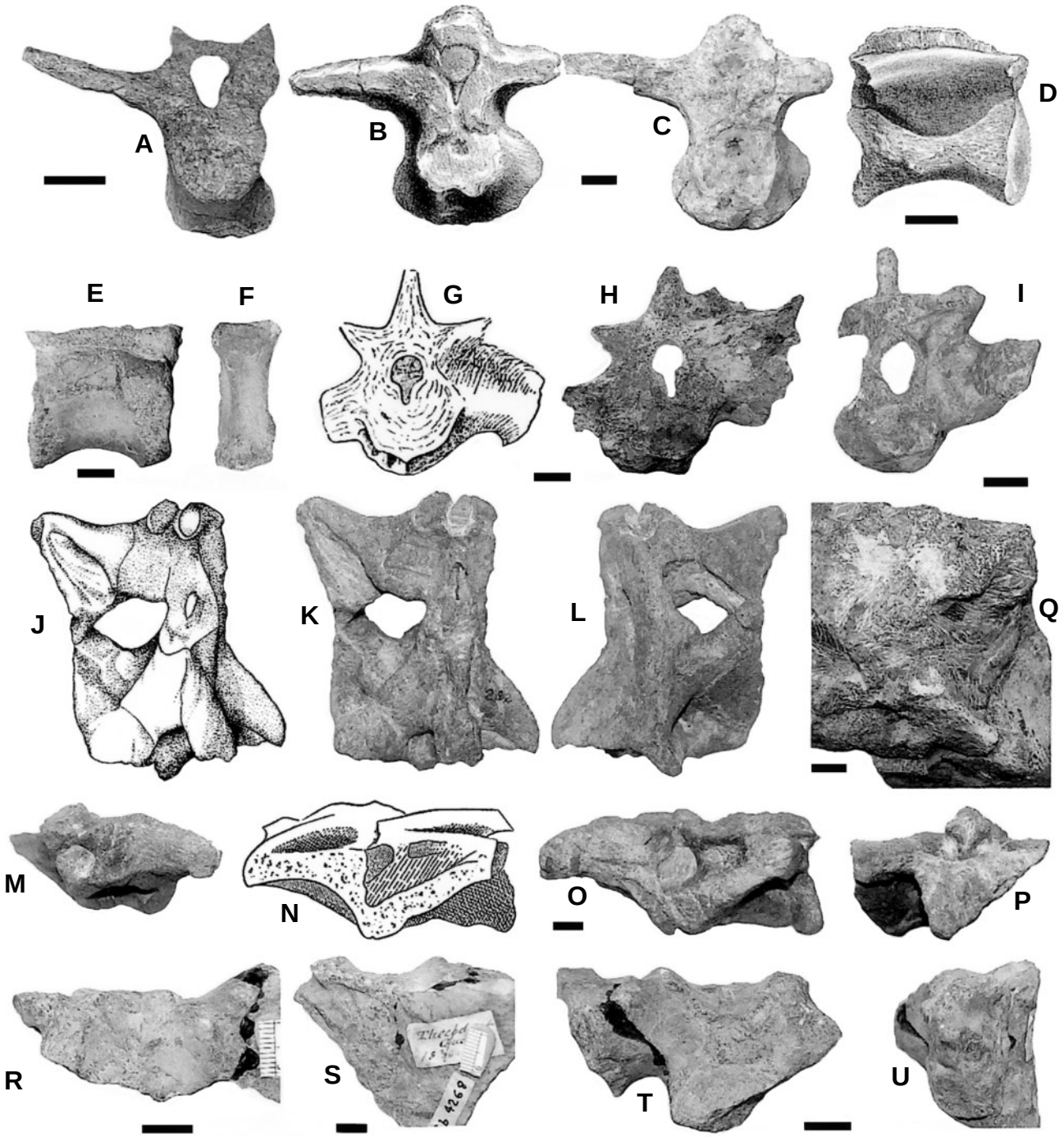



Fig. 10 : Basal sauropodomorph dorsal (A-F) and sacral (G-U) vertebrae from Clifton. A-D : posterior dorsal vertebrae : A-C : cross-sectional view of centrum and incomplete neural arch in anterior view, A : BRSMG Cb4221 ; B-C : BRSMG *C4533/8 ; D : sagittally sectioned vertebra with natural cast of neural canal, BRSMG *Ca7452/26♦ ; E-F : centrum and partial neural arch in E : right lateral and F : ventral views, BRSMG Cb4174b/41. G-H : cross-sectioned sacral 2 with left rib in anterior view, BMNH R1532 ; I : cross-sectioned sacral 2 with impression of rib in anterior view, BMNH R1553 ; J-Q : sacral vertebrae 1 and 2 : J-P : YPM 56733, in J-K : dorsal ; L : ventral ; M : anterior ; N-O : left lateral and P : posterior views (HUENE, 1914a, fig. 39 ; BENTON *et al.,* 2000, fig. 8) ; Q : YPM 56746, in dorsal view. R-U : incomplete sacral vertebra 1, BRSMG Cb4268, in R : dorsal ; S : posterior cross-sectional ; T : anterior ; and U : left lateral views. B, D from RILEY & STUTCHBURY (1840), G from HUENE (1908a), J from BENTON *et al* (2000), N from HUENE (1914a) ; scale bars = 10 mm.

the hyposphene, which is subvertical and immediately ventral to the postzygapophysis, is not visible on this vertebra (Figs 9Q-S) but it is present in others (Figs 9A, H-K, B'). The small corresponding subvertical accessory articular surfaces, the hypantra, are visible between the prezygapophyses (Figs 9G, L; BENTON *et al.,* 2000, figs 7J, K). The pleurocentral depression (groove, BENTON *et al.* 2000; "pleurocoel", GALTON, 1976), which is situated on the lateral aspect of the centrum adjacent to the neurocentral suture, is shallow on some dorsals (Figs 9B, H, K, V, X, Z, 10E) and deep on some of the more posterior dorsals (Figs 9A, C, N, T).

**Dorsal ribs and gastralia** (Figs 6B, 8E-G, J-Q)
The broken and slightly disarticulated mid-dorsal ribs of *Asylosaurus*, which are incompletely exposed except for one proximal part (Figs 6B, 8D, E), are similar to those of *Plateosaurus*.
The "tuberculum" of the cervical ribs (Fig. 8G) from Clifton of BENTON *et al.* (2000, fig. 10A) is very small so, compared to the complete series of ribs in *Plateosaurus* (JAEKEL, 1913-14, fig. 12a), these would be anterior ribs (C2-4). However, the Clifton ribs are very elongate, being twice the length of the known cervical centra, whereas they are shorter in *Pantydraco caducus* and, even in *Plateosaurus*, the ribs are only slightly longer than the centra. Also cervical ribs are slender, tapering very gradually to a point rather than expanding slightly at the distal end. Consequently, these ribs are reidentified as the distal parts of dorsal ribs. The appearance of a slight distal taper is due to twisting of the shaft and, although the most complete rib is incomplete proximally, it shows the beginning of an expansion.
A badly crushed anterior dorsal rib (Fig. 8J) was listed as a fragmentary ilium (BENTON *et al.,* 2000, p. 82, 93). The longitudinally sectioned distal part of a dorsal rib was identified by HUENE (1908a) as a distal half fibula (Figs 8P, Q; BENTON *et al.*, 2000, p. 104). However, the medulla is filled with cancellous bone as in a rib, not hollow as in a fibula (Figs 31C, D).
RILEY & STUTCHBURY (1840) figured the proximal end of an anterior right dorsal rib in anterior view (Fig. 8L, BRSMG *?Ca7503/38♦) and BENTON *et al.* (2000, p. 104, fig. 10C) incorrectly identified this specimen as BRSMG C4528/32 (HUENE, 1908a, pl. 77, fig. 3), a right rib in posterior view (Fig. 8K). Another proximal end of an anterior dorsal rib (Fig. 8M), and a more massive one from the middle of the series (Fig. 8N), are also similar to the much better preserved ones of *Plateosaurus*. There are also comparable partial rib shafts (Fig. 8O; YPM 56721, HUENE, 1908a, pl. 78, fig. 6, now in pieces). The proximal parts of the ribs are preserved fused to the ends of the transverse processes of posterior dorsal vertebrae (Figs 10A-C).
Pieces of a few gastralia or abdominal ribs are preserved in *Asylosaurus* (Figs 6A, B, 8D, F). They were illustrated by HUENE (1914a, fig. 54) for YPM 56719 (Fig. 6E) but most of them are broken longitudinally sectioned ribs and only a few very thin bones are gastralia.

**Sacral vertebrae** (Figs 10G-U)
The sacrum is not known in *Pantydraco caducus*. The form of S1 and S2 of the incomplete sacrum (Figs 10J-P; HUENE, 1914a, figs 39a, b; GALTON, 1999, figs 4F-H; BENTON *et al.*, 2000, fig. 8) are very similar to those of *Saturnalia, Efraasia* and *Plateosaurus,* especially in dorsal view (Figs 10J, K). This is also true for another partial sacrum (Fig. 10Q) of about the same size that, although not previously mentioned, is better preserved (but it needs additional preparation). There were probably three sacral vertebrae, as in most basal sauropodomorphs, based on the length of the distal extremities of sacral ribs 1 and 2 at 78 mm (Figs 10J-L, N, O) compared to the length of the articular facet (85 mm) for the ribs on the only well preserved "normal" sized ilium (HUENE, 1908a) exposed in medial view (Fig. 21C) (BENTON *et al.,* 2000). GALTON (1999) and BENTON *et al.* (2000) noted that the rugose surface on the posterior aspect of the centrum and rib of sacral 2 (Figs 10J, K, P) indicates the presence of a caudosacral, but this rugose surface may represent a break surface. However, the third vertebrae was probably a caudosacral, based on the proportions of sacral rib 2 that is only slightly longer than its centrum (Figs 10N, O), as in the three vertebrae sacra of *Plateosaurus gracilis* with a caudosacral (GALTON, 2001a; YATES, 2003b; also those of *Plateosaurus engelhardti,* GALTON, 2001b; YATES, 2003b). This rib is noticeably longer than the centrum of S2 in individuals of *Efraasia* with a dorsosacral as the third sacral (GALTON, 2001b; YATES, 2003b; also true for *Lufengosaurus, Massospondylus, Yuannosaurus*; GALTON, 1999, 2001a).
The anterior two thirds of S1 with much of both ribs is prepared almost in the round (Figs 10R-U). Three sacral vertebrae are transversely sectioned. The posterior part of S1 is preserved in anterior view with an impression of the posterior surface of the left sacral rib (Fig. 10I); parts of the articulated S2 are visible on the other side of the block. The ?S3 of HUENE (1908a) was reidentified as S2 in anterior view (Figs 10G, H) by GALTON (1999).

**Caudal vertebrae and chevrons** (Figs 6A, 11, 12)
There are only articulated series of mid and distal caudals for *Pantydraco* (Fig. 2D; YATES, 2003a) *contra* KERMACK (1984; also BENTON *et al.*, 2000) (Fig. 2C). Consequently, the Clifton proximal caudals are tentatively identified by comparisons with the partial articulated series of *Efraasia* (SMNS 17928; GALTON, 1973; also HUENE, 1932), *Plateosaurus gracilis* (SMNS 5715; HUENE, 1908a) and *P. engelhardti* (SMNS 13200; HUENE, 1926; MOSER, 2003, pl. 15; also JAEKEL, 1913-14).
The two proximal caudals (Figs 6A, 11A-C, ~10 and ~15, YPM 2195b,c) are tentatively included in the holotype individual of *Asylosaurus yalensis.*
The caudals from Clifton with the proportionally shortest

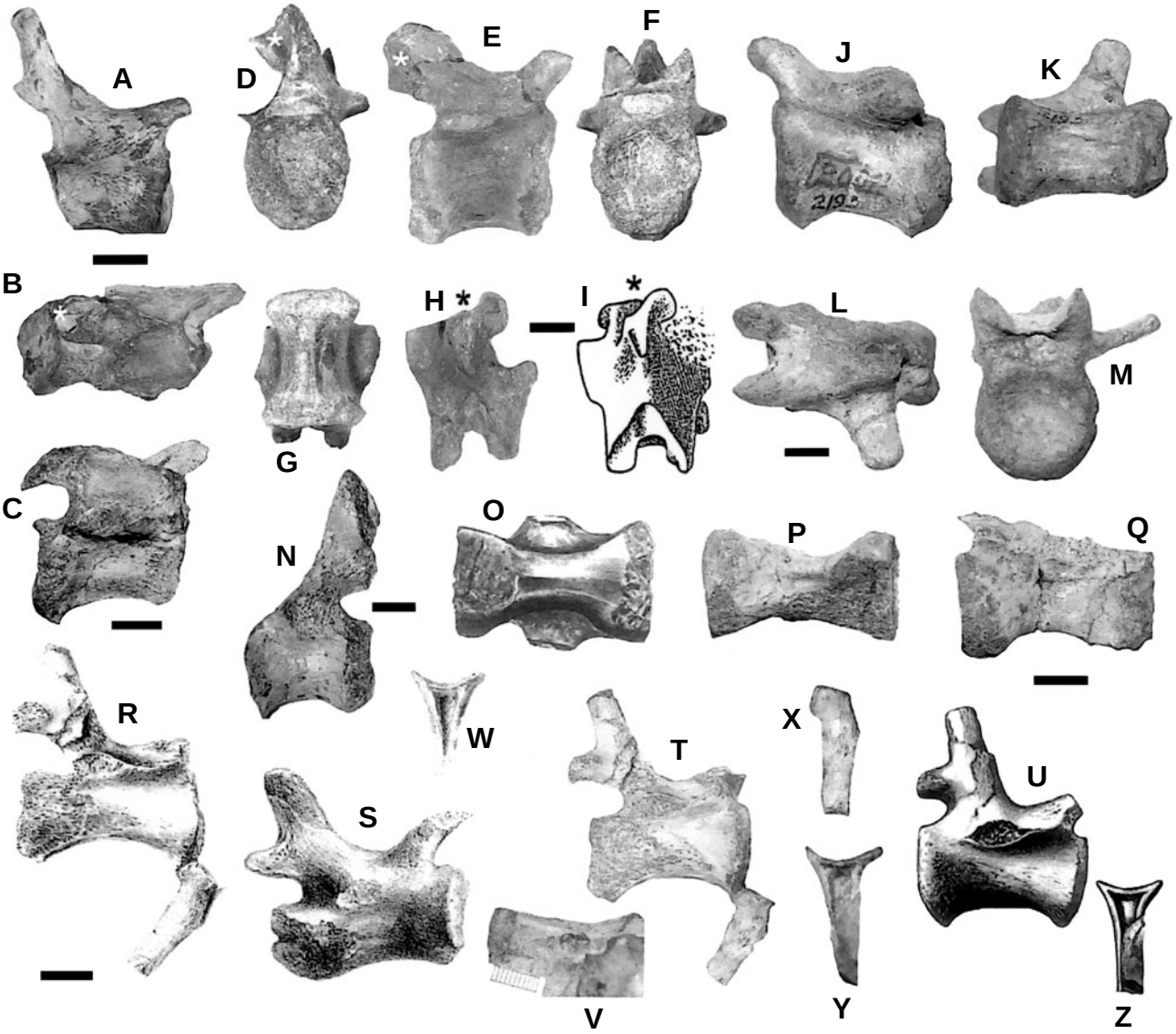



Fig. 11 : Very basal sauropodomorph caudal vertebrae and chevrons from Clifton. A-C : *Asylosaurus yalensis* n. gen. et sp., proximal caudals, YPM 2195b (A) and 2195c (B, C) in A, C : right lateral and B : dorsal views. D-I : proximal caudal BGS 54061a in D : posterior ; E : right lateral ; F : anterior ; G : ventral and H, I : dorsal views. J-M : proximal caudal YPM 2193 in J : left lateral ; K : ventral ; L : dorsal and M : anterior views (BENTON *et al.*, 2000, figs 9H-K). N : proximal caudal ANSP 9861a in left lateral view. O-Q : centrum and partial neural arch of anterior caudal vertebra, BRSMG Ca7475/22, in O-P : ventral and Q : left lateral views. R-V : mid-caudal vertebra (with articulated chevron, R, T), BRSMG *C4532a/17 in R-U : right lateral and V : ventral views (BENTON *et al.*, 2000, figs 9L, 10D, E). W-Z : chevron BRSMG C4532a/17 in W, Y, Z : anterior and X : right lateral views. I from HUENE (1914a), R, W from HUXLEY (1870), S from RILEY & STUTCHBURY (1840), U, Z from HUENE (1908a) ; * = interpostzygapophyseal space ; scale bars = 10 mm.

centra (Figs 11D-I, N) are identified as the most proximal caudals (~5). Judging from the proportionally more elongate centrum and the lower neural arch, the other proximal caudals are ~10-15 (Figs 11J-M, O-Q ; YPM 2193 a mid-caudal in BENTON *et al.,* 2000, p. 82, 106, figs 9H-K as YPM 2192).

A mid-caudal with the proximal part of an articulated chevron has been illustrated several times (Figs 11R-Z ; BENTON *et al.*, figs 9L, 10D, E). This vertebra still retains a distinct transverse process and BRSMG Ca7507a/23 (Fig. 12L) has a complete neural spine. There is a mid-caudal that is slightly more proximal in position (Fig. 12A) and two that are slightly more distal (Figs 12B, C). Three incomplete caudals with a chevron (Fig. 12Q) are probably from two-thirds length. Other distal caudals (Figs 12C-F, L) show that, passing more distally, the transverse process is lost (Figs 12D, E) and then the neural spine (Figs 12E, F). YPM 56736 is the best preserved of the

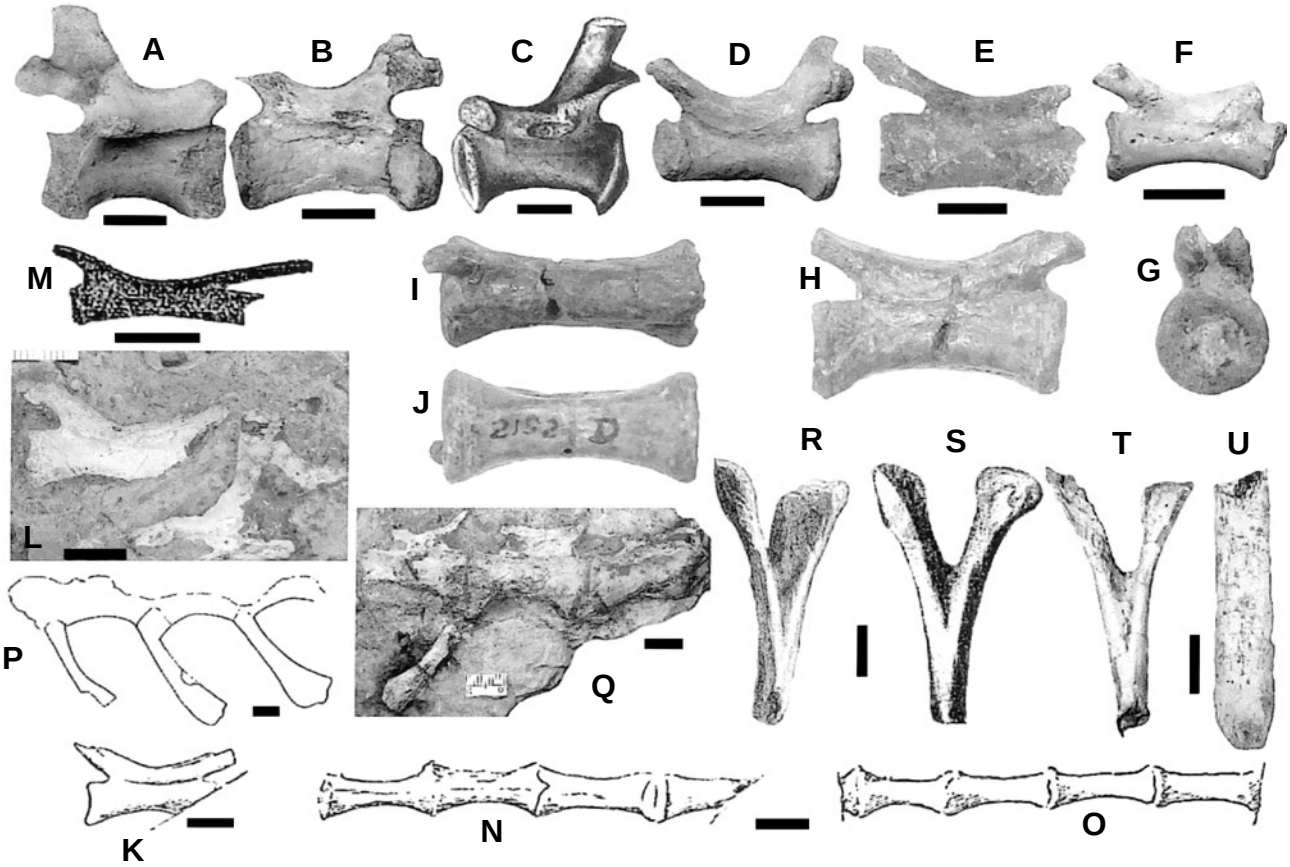



Fig. 12 : Caudal vertebrae and chevrons of basal sauropodomorphs from Clifton. A-O : mid (A-C) and distal (D-O) caudals (P, Q with chevrons) in right lateral (A, E, F, H, L, Q), left lateral (B-D, L, M, N), anterior (G), dorsal (I) and ventral (J, O) views. A : BRSMG Cb4301 ; B : BRSMG 4532b/17a ; C : BRSMG Ca7476b/59♦ ; D : BRSMG Cb4276 ; E : BMNH R1550b ; F : BMNH 49984a, a paralectotype of *Agrosaurus macgillivrayi* SEELEY, 1891 ; G-J : YPM 56736 (BENTON *et al.*, 2000, Figs 9N-Q, as YPM 2193, N is right lateral view) ; K-L : BRSMG Ca7507/23, K : distal caudal in right lateral view and L : block with distal caudal in right lateral view, mid-caudal neural arch in left lateral view and complete neural spine of more distal neural arch ; M : distal caudal YPM 56734♦ ; N-O : four very distal caudals, N : BRSMG Ca7509/20♦in mostly left lateral view and O : BRSMG Ca7508/20♦ in ventral view. P-Q : caudal vertebrae with articulated chevrons in left (P) and right (Q) lateral views : P : BRSMG Ca 7511/-♦ and Q : BRSMG Ca7510/18 (BENTON *et al.*, 2000, fig. 9M) ; R-T : proximal part of chevron BRSMG C4534/30 in anterior view ; U : distal part of chevron BRSMG Ca7466/35 in lateral view (or distal end of dorsal rib in lateral view). C, K, N-P from HUENE (1908a), M from HUENE (1914a), R from RILEY & STUTCHBURY (1840), S from HUENE (1908b) ; scale bars = 10 mm.

more distal caudals (Figs 12G-J ; BENTON *et al.*, 2000, figs 9N-Q as YPM 2193, note fig. 9N is right lateral view, not left). There were also two separate articulated series of four very distal centra in mostly lateral (Fig. 12N) and ventral views (Figs 12O). In a distal caudal (Fig. 12L) the postzygapophysis is shown unusually elongate and, if accurate, then this caudal (lost) may not be from a basal sauropodomorph.

The proximal part of a large proximal chevron (Fig. 12T) was figured by RILEY & STUTCHBURY (1840) (Fig. 12R), referred to the phytosaur *Rileya* by HUENE (1908b, 1911) (Fig. 12S), and returned to *Thecodontosaurus* by BENTON *et al.* (2000, fig. 10F). The distal part of a large proximal chevron (Fig. 12U) of HUENE (1908a, pl. 78, fig. 5) is only very slightly expanded distally ; BENTON *et al.* (2000, p. 104) listed it as ?distal chevron and it is probably the distal end of a dorsal rib. In mid (Fig. 12P) and more posterior parts of the tail (Fig. 12Q ; BENTON *et al.*, 2000, fig. 9M) the chevrons are anteroposteriorly wider distally as in *Plateosaurus*.

### VI.1.5. Pectoral girdle

**Scapula and coracoid** (Figs 6A, 13A-H, 14)

There are parts of both pectoral girdles (Figs 6A, B, 13A-H, 14I-M ; no sternum) and forelimbs of *Asylosaurus*, a reconstruction (Fig. 13A) of which was given by MARSH

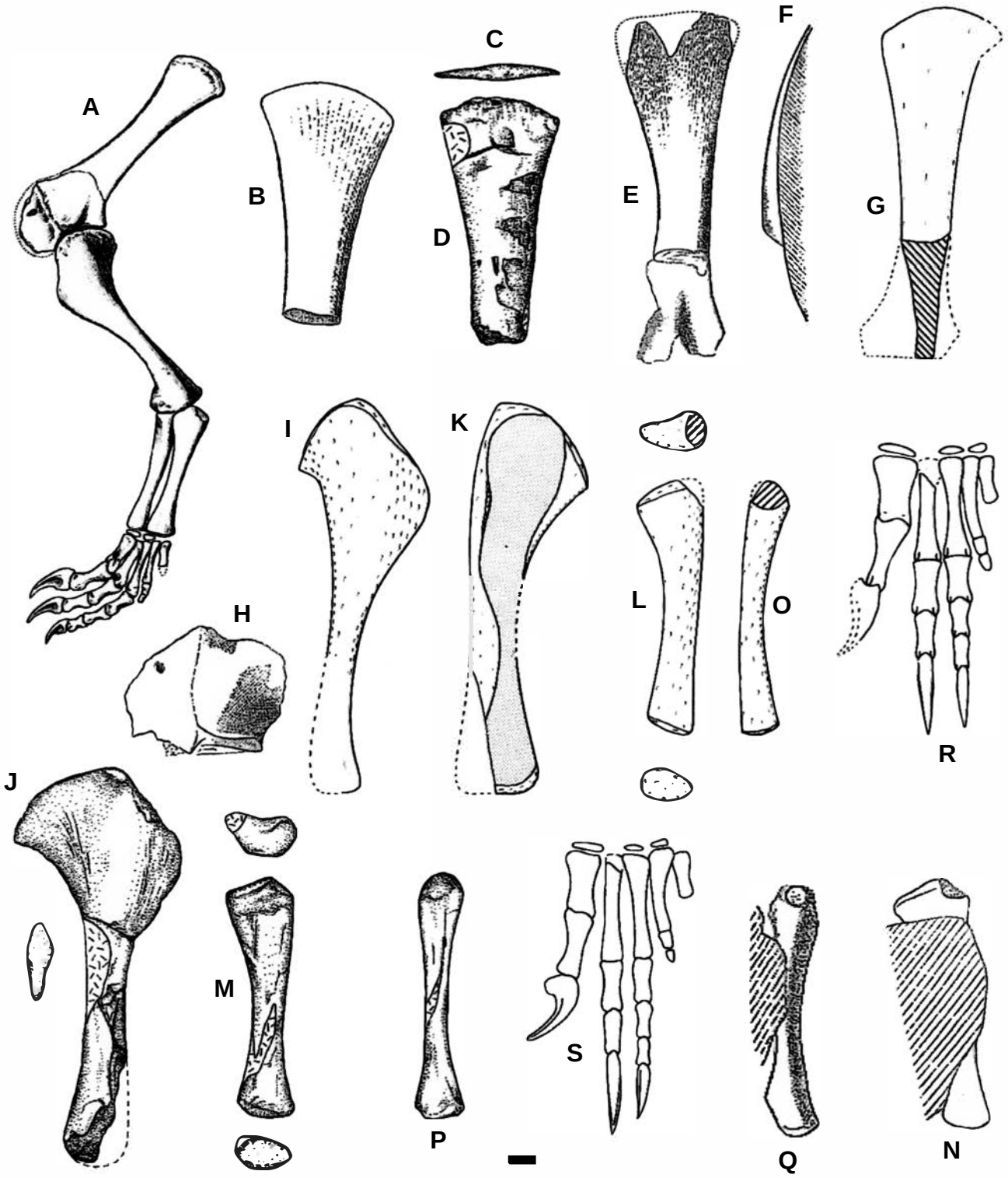



Fig. 13: Very basal sauropodomorph *Asylosaurus yalensis* n. gen. et sp., holotype YPM 2195 from Clifton, pectoral girdle and forelimb. A: reconstruction of articulated left girdle and limb in lateral view (proximal right scapula-coracoid in medial view, right humerus reversed, radius reconstructed). B-D: incomplete blade of right scapula in B, D: lateral and C: distal views. E-G: incomplete left scapula in E, G: lateral and F: anterior views. H: right proximal partial scapula and partial coracoid (with foramen) in medial view. I-K: right humerus in I: lateral; J: posterolateral (with posterior view of proximal end) and K: anterior views. L-Q: left ulna in L-N: lateral (L, M with ends) and O-Q: posterior views. R-S: reconstruction of right manus in dorsal (anterior) view. A from MARSH (1892), B, E, F, H, N, Q from HUENE (1914a), G, I, K, L, O, R from GALTON & CLUVER (1976), C, D, J, M, P, S from BENTON *et al.* (2000); scale bar = 10 mm (A) and 5 mm (B-S).

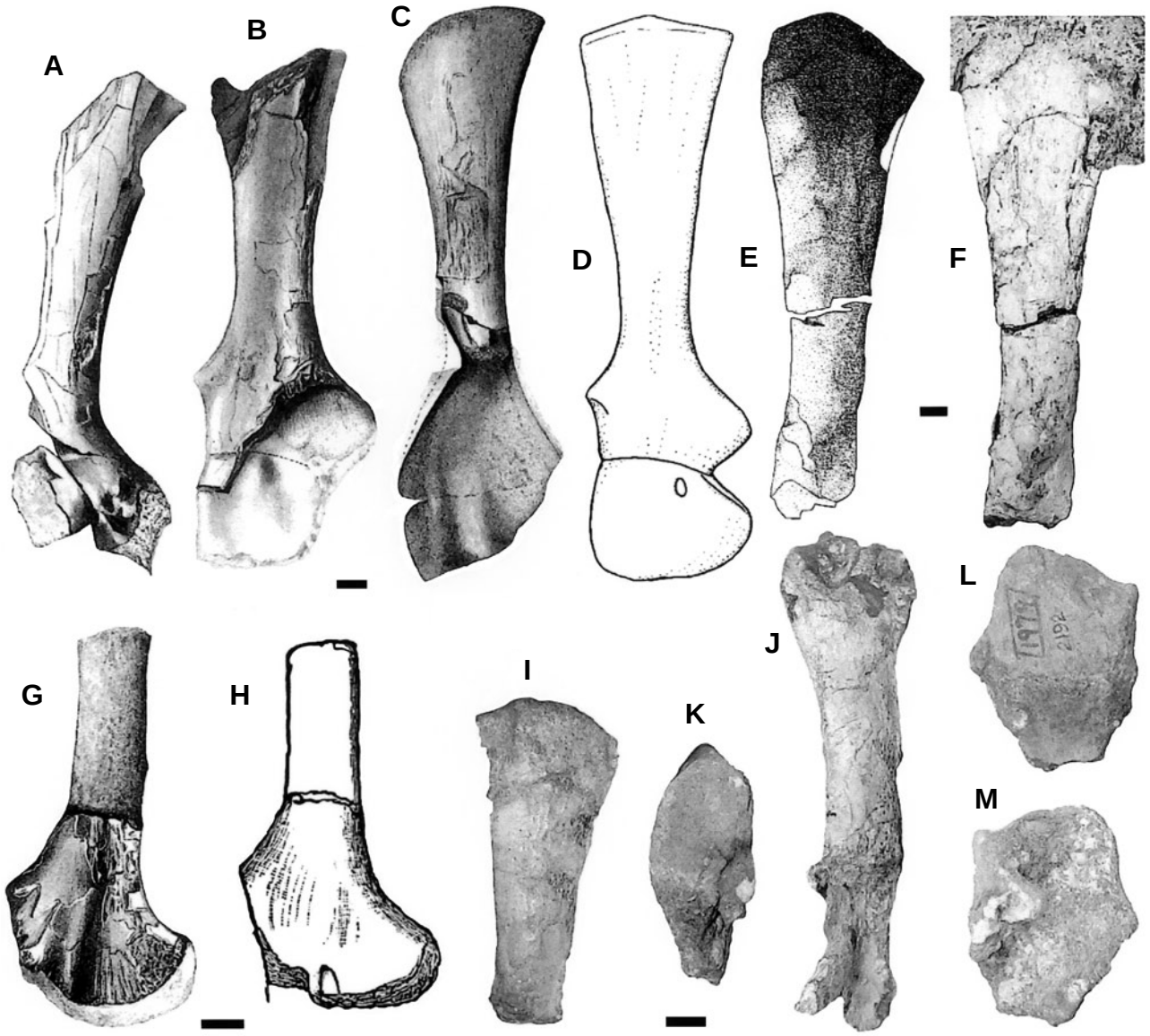



Fig. 14 : Incomplete pectoral girdles of basal sauropodomorphs from Clifton. A-D : Incomplete left scapula and coracoid in lateral view (with ventral part as impression of medial surface in B and C) : A : BRSMG Ca7480/90♦ ; B : BRSMG Ca7479/89♦ ; C : BRSMG Ca7478/92♦ and D : reconstructed girdle based on B and C. E-F : left scapula blade in lateral view, BRSMG Ca7481/91. G-H : medial view of right scapula (with impression of blade), BRSMG Ca7458/97♦. I-M : *Asylosaurus yalensis* n. gen et sp., part of holotype YPM 2195 : I, J : blades of scapulae in lateral view : I : distal right and J : left, incomplete at ends ; K-M : right proximal scapula and adjacent part of coracoid in K : posterior ; L : medial and M : lateral views (cf. Figs 13A, H). A-C, G from HUENE (1908a) D, E from BENTON *et al.* (2000), H from SEELEY (1895) ; scale bars = 10 mm.

(1892 ; most of bones also figured by HUENE, 1914a ; GALTON & CLUVER, 1976 ; BENTON *et al.*, 2000) (Figs 13B-S). The distal scapular blade (Figs 13B-D ; maximum and minimum widths 43 and 22 mm) figured in lateral view by BENTON *et al.* (2000, fig. 11B, "right or left?") is the right (Fig. 14I). The left scapula is more complete, with an estimated length of about 150 mm. BENTON *et al.* (2000, p. 90) noted that "incomplete scapulae are the only elements of the pectoral girdle surviving" but this is incorrect because part of the right coracoid is preserved with the separated proximal end of the scapula (Figs 14K-M ; see Appendix 7). The well preserved surface (Fig. 14L) was illustrated as the left in lateral view (Figs 13A, H) by MARSH (1892) and HUENE (1914a). However, judging from the curves, it is the right in medial view and this is confirmed by the more dorsal position of the coracoid foramen (Fig. 14L) compared to its position on the lateral surface (Fig. 14M).

BENTON *et al.* (2000, p. 91) used the illustration in HUENE (1908a) of the scapula and coracoid of BRSMG Ca7479/89♦ (Fig. 14B) from Clifton, along with that of BRSMG Ca7478/92♦ (Fig. 14C, scapula length including proximal impression 170 mm), as the basis for a reconstruction for *Thecodontosaurus antiquus* (Fig. 14D). They noted that the distal scapula blade is unknown in both specimens but it was present in the latter (Fig. 14C) and looks nothing like the reconstruction (Fig. 14D), that was presumably based on this one and/or the only other specimens with this end preserved (YPM 2195, Figs 14I; BRSMG Ca7481/91, Figs 14E, F). The distal end of the almost complete blade of the latter is less clearly preserved (Fig. 14F) than previously illustrated (Fig. 14E; BENTON *et al.,* 2000, fig. 11A). One corner is more acute and, because it would point posteriorly (cf. Fig. 14C), this is another left scapula rather than a right as identified by HUENE (1908a, pl. 80, fig. 1; also BENTON *et al.,* 2000, p. 105, fig. 11A). The coracoidal foramen should also be more anterior and slightly more ventral in position than shown in the reconstruction (Fig. 14D cf. Figs 14B, H, L, M). Judging from the surface contours (Fig. 14G), and a groove that would be dorsomedial to the coracoid foramen (Fig. 14H), BRSMG Ca7458/97♦ was a right proximal scapula in medial view (HUENE, 1908a as left lateral; BENTON *et al.,* 2000, p. 105 as left).

### VI.1.6. Fore limb

**Humerus** (Figs 6A, B, 13A, I-K, 15, 16)

HUENE (1914a, p. 80) mentioned that only a small part of the proximal end of the right humerus of *Asylosaurus* is preserved (Figs 6A, 15N), but did not mention or figure the other almost complete humerus that was figured by GALTON & CLUVER (1976) and BENTON *et al.* (2000) as the left. However, it is the right (Figs 6A, 13I-K, 15A-M), with the proximal "right' as a left (Figs 6A, 15N), and the complete humerus was correctly reversed, so the deltopectoral crest is positioned laterally, in the reconstruction of the left fore limb by MARSH (1892) (Fig. 13A). In addition, very little of the radius is preserved (Figs 17A-C), so the left "articulated forelimb" of BENTON *et al.* (2000, p. 82, 91, 92, fig. 13) is an ulna articulated with an almost complete manus. The deltopectoral crest is anteriorly directed (Fig. 15C) and low with a symmetrical rounded outline with the apex at about 25% of humeral length (measured perpendicular to length) (Figs 13A, I, J, N; similar crest in BMNH R1542, Figs 15O, P) and there is a large process medial to the head (Figs 13A, I, J, 15C-F, I-K; shown too small in Figs 13I, K). In both humeri the proximal width is 54 mm, head to apex of crest is 61 mm, and maximum length of right is 150 mm. Distally the transversely expanded end is anteroposteriorly crushed and incomplete laterally (Figs 15C, L, incorrectly shown as intact bone in Fig. 13J; too narrow in Fig. 13K).

BENTON *et al.* (2000, p. 90) correctly noted the dinosaurian form of the isolated Clifton humeri, including the "distinct twist to the shaft, as seen in ANSP 9880, and a subrectangular deltopectoral crest, seen in BMNH R1541", even though these bones are a partial femur of a basal sauropodomorph and a phytosaurian humerus (Figs 37G-I; incorrectly listed as *Thecodontosaurus antiquus,* BENTON *et al.,* 2000, p. 82, 106). Other listed partial "humeri" are an incomplete right scapula (BMNH R1543) and a proximal left ischium (BMNH R1550b, Fig. 24K). The proximal humerus of YPM 56724 (Figs 16H-J) is the left figured in posterolateral and anteromedial views, not the right in posterior and anterior views (BENTON *et al.,* 2000, figs 11D, E, also all of anterior edge of deltopectoral crest is incomplete; HUENE, 1908a, pl. 83, fig. 1 in matrix; HUENE, 1914a, fig. 48 inverted as distal left humerus of YPM 2195).

BENTON *et al.* (2000, fig. 11F) based the restoration of the Clifton humerus (Fig. 16G) on the figures of HUENE (1908a) of BRSMG Ca7477a/37♦ (Fig. 16D) and Ca7512/93♦ (Fig. 16K). The contribution from the latter, a proximally incomplete large humerus originally at least 220 mm long with a distal width of ~60 mm, appears to have been minimal (cf. Fig. 16G), and I suspect that this humerus was illustrated upside down. As regards the former, HUENE (1908a, p. 205) noted that only the lateral part of the proximal edge was missing on this 165 mm long humerus with 17 mm as the minimum thickness of the shaft, which appears straight because it thickens equally on both sides towards the 35 mm wide distal end. HUENE (1908a) partly restored the deltopectoral crest of this humerus (Fig. 16D) after that of BRSMG *Ca7453/66♦ (Fig. 16F). However, earlier figures show the anterior edge of the deltopectoral crest of *Ca7453/66♦ without a step (Fig. 16E) and that of Ca7477/37♦ as incomplete (Fig. 16C). No other deltopectoral crest from Clifton shows such a step (Figs 13A, I, 15A, B, O, 16A-C, H, I) so the accuracy of this restored outline (Fig. 16G), which is unique for a basal sauropodomorph, cannot be confirmed. In the isolated humeri the deltopectoral crest is large, being anteroposteriorly high and markedly asymmetrical in side view, being hatchet shaped with a short edge distal to the very prominent apex (Figs 15V, 16H-J). The apex is at about 40% (measured perpendicular to long axis of humerus) in gracile humeri (Figs 15Q, R, 16C-F) and +50% in robust ones (Figs 15S-U, 16A, B). There is a large process medial to the head (Figs 15Q, S, V, 16A-D). Distally the bone is transversely expanded (shown too narrow for YPM 2195, Fig. 13K cf. Figs 15C, D) and the intercondylar fossa is deeper anteriorly than posteriorly (Figs 15W, X).

**Radius** (Figs 13A, 17A-C, 18A-O).

The radius is represented in *Asylosaurus* by part of the edge of the shaft as it crosses the adjacent ulna (Figs 17A-C). Although not indicated as such, it was restored by MARSH (1892) (Fig. 13A), presumably after that of *Anchisaurus* (YPM 1883).

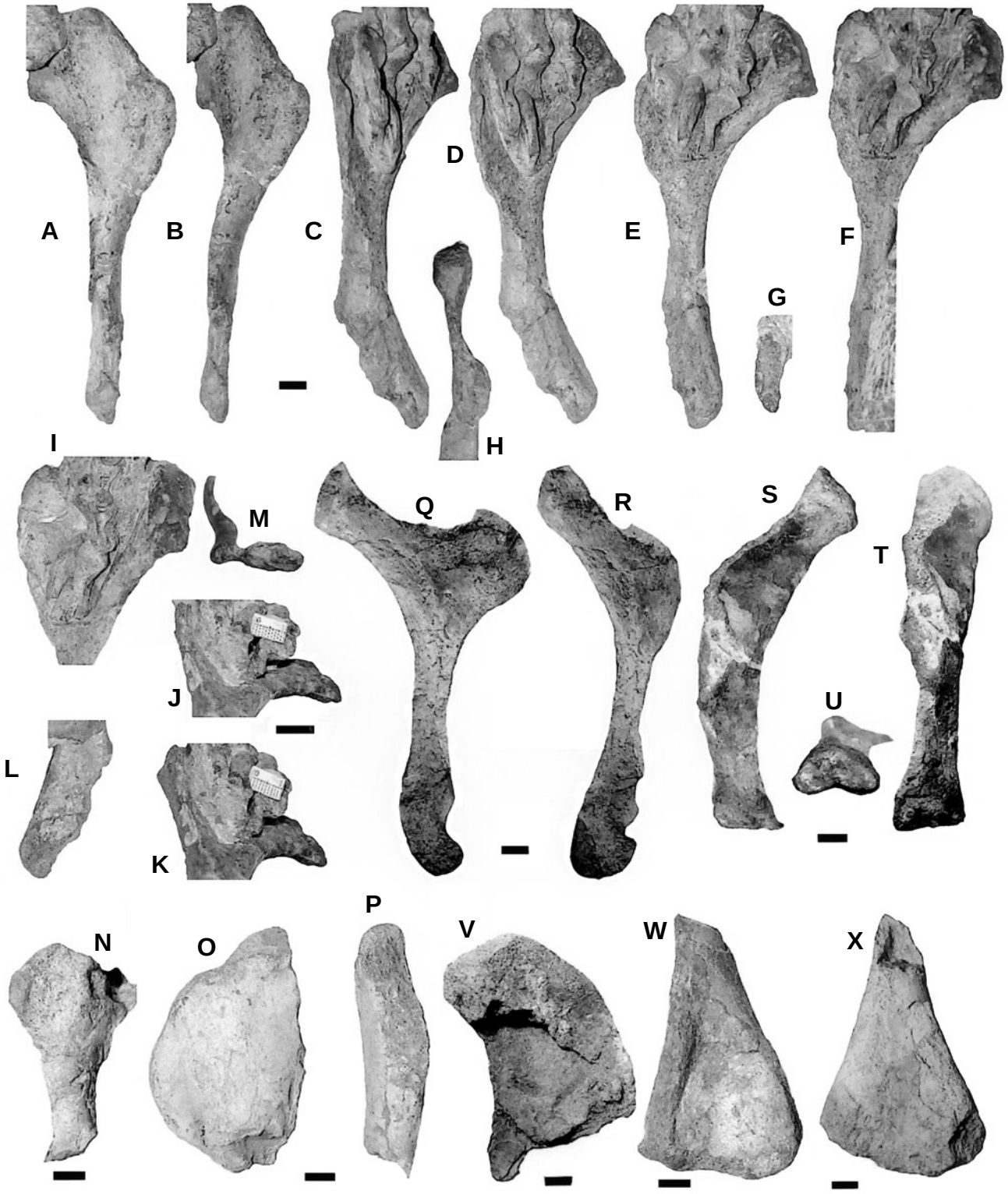



Fig. 15 : Basal sauropodomorph humeri from Clifton. A-P : *Asylosaurus yalensis* n. gen. et sp. from Clifton, A-N : part of holotype, YPM 2195, A-M : right humerus, A-F : complete bone in A : lateral, B : lateral and slightly anterior ; C : anterior ; D : anterior and slightly medial ; E : anteromedial and F : medial views. G : proximal end in proximomedial view. H-K : proximal part in H : anterolateral (overlapping matrix blocked out on inside of deltopectoral crest) ; I : medial ; J : distomedial and K : distomedial (slightly more medial) views. L-M : distal part in L : posterior and M : distal (with outline of deltopectoral crest) views. N : incompletely visible proximal half of left humerus in anterior view ; O-P : referred specimen BMNH R1542, incomplete proximal left humerus in G : lateral and H : posterior views. Q-R : BRSMG Cb4265, gracile left humerus, ?*Thecodontosaurus antiquus*, in Q : medial and R : posteromedial views ; S-U : incomplete robust right humerus, lacking most of deltopectoral crest and distal end, in S : anteromedial ; T : anterior and U : distal views. V : BRSMG Cb4189/78, proximal left humerus in medial view. W : BRSMG Cb4188/94, distal left humerus in anterior view ; X : BRSMG Cb4185, distal right humerus in posterior view. Scale bars = 10 mm.


Fig. 16: Basal sauropodomorph right (A-G) and left (H-L) humeri from Clifton (A-K) and South Wales (L) in medial (I) and medial and slightly anterior (A-G), lateral (H, L) and anterior (J, K) views. A-B: robust humerus BRSMG Ca7464/118♦; C-G: gracile humeri, ?*Thecodontosaurus antiquus*: C-D: BRSMG Ca7477a/37♦; E-F: BRSMG Ca*7453/66♦; G: reconstruction based on D and K (given as right in anterolateral view but actually anteromedial); H-K: robust humeri: H-J: YPM 56724 (BENTON *et al.*, 2000, figs 11D, E); K: BRSMG Ca7512/93♦ (?shown upside down); L: *Pantydraco caducus,* referred humerus BMNH P19/7♦. A, C from SEELEY (1895), B, D, F, K from HUENE (1908a), E from RILEY & STUTCHBURY (1840), G from BENTON *et al.* (2000), L from GALTON *et al.* (2007); scale bars = 5 mm (L) and 10 mm.

HUENE (1908a) figured a radius from Clifton that could be the right in medial view or the left in lateral view (Fig. 18A; length, proximal and distal widths 115, 30, 30 mm). However, the distal end is very massive and convex so it could be an inverted left ulna in lateral view. A radius, incomplete at both ends (Figs 18B-H), was figured as that of the phytosaur *Rileya* (Figs 18B-D) by HUENE (1908b) but returned to *Thecodontosaurus* by BENTON *et al.* (2000, p. 79, figs 14C-F). However, compared to the larger radii of *Plateosaurus* (SMNS 13200; HUENE, 1926, 1932), the ends of BRSMG Ca7504/52 are proportionally more massive so this referral may be incorrect. No complete proximal end is known. Distal left (Figs 18I-M; HUENE, 1906, figs 88a-d; GALTON, 2000, figs 15H-J) and right (Figs 18N, O) radii are well preserved, resembling those of *Efraasia* and *Plateosaurus*. HUENE (1906, p. 148) noted that on the distal end on the ulna side there is a beaked, sharp projection and the whole radius curves rather forwards (to dorsum of hand) so right and left are easily distinguished this way.

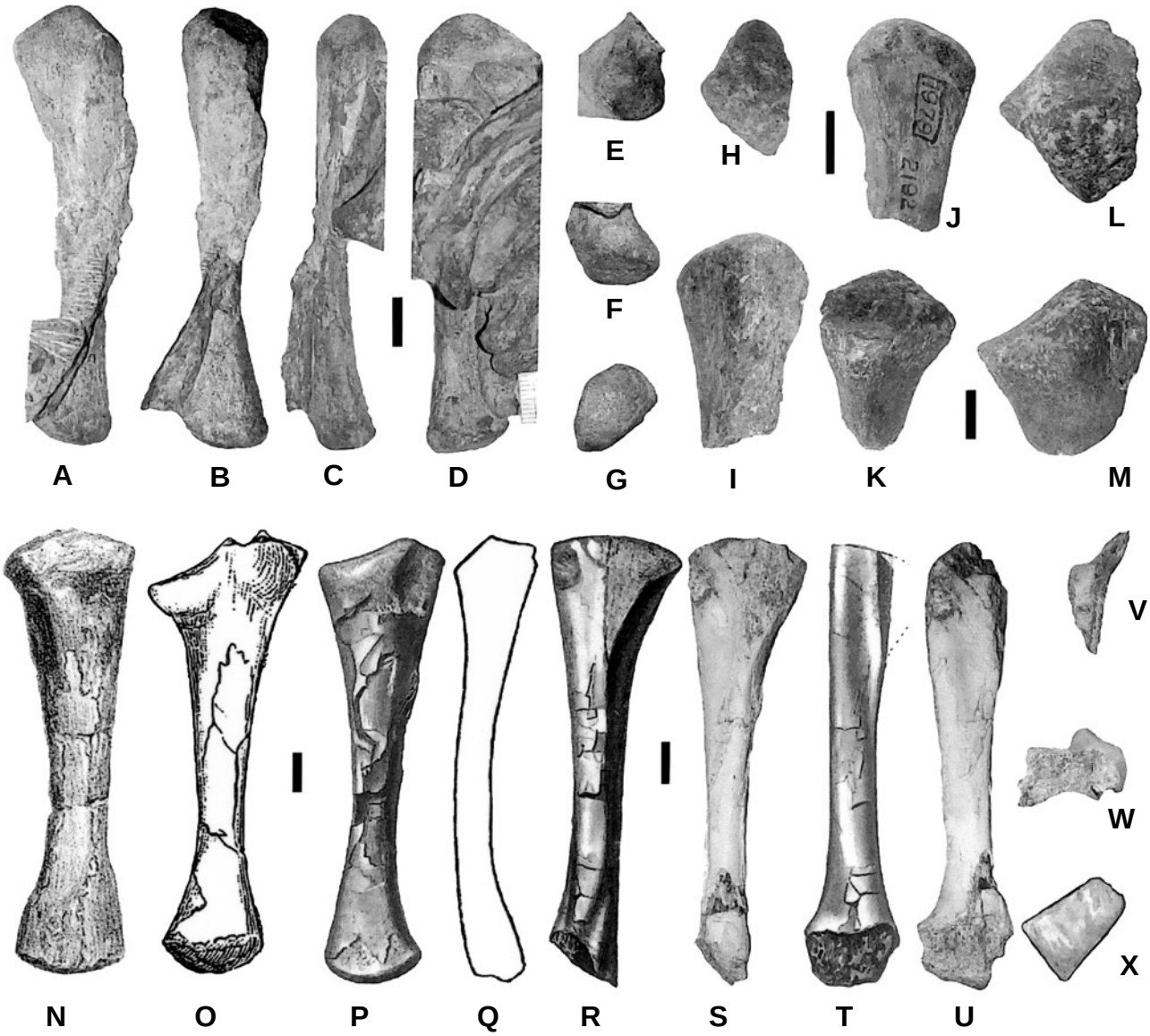



Fig. 17: Very basal sauropodomorph ulnae from Clifton. A-J: *Asylosaurus yalensis* n. gen. et sp., part of holotype YPM 2195, A-G: left ulna in A: lateral; B: posterolateral; C: posterior; D: medial; E: proximal and slightly lateral; F: proximal and G: distal views; H-J: right ulna, medial half of proximal end in H: proximal; I: medial and J: posterolateral views. K-M: YPM 56735, proximal part of left ulna in K: anterior; L: proximal and M: lateral views (HUENE, 1914a, fig. 49). N-Q: BRSMG *Ca7459/46♦, left ulna in N-P: lateral and Q: posterior views. R-X: BRSMG Ca7486/79, ?left ulna (probably slender metatarsal III) in R-S: anterior; T-U: medial; V, X: proximal and W: distal views (BENTON *et al.*, 2000, figs 14A, B). N from RILEY & STUTCHBURY (1840), O from SEELEY (1895), P-R, T, X from HUENE (1908a); scale bars = 10 mm.

**Ulna** (Figs 6B, 13A, L-Q, 17)

The almost complete left ulna of *Asylosaurus* (Figs 13L-Q, 17A-G; length, proximal and distal widths 95, ~24, 19.2 x 12.9 mm) is bowed in anterior view (shown too straight Fig. 13P; also bowed in BRSMG Ca7459/46♦, Fig. 17Q) as in *Efraasia* and *Plateosaurus*. MARSH (1892) and BENTON *et al.* (2000) illustrated a small olecranon process on the ulna (Figs 13A, M) whereas HUENE (1914a) indicated a broken surface (Fig. 13N), as did GALTON & CLUVER (1976) who reconstructed it larger (Fig. 13L). This area is plainly eroded (Figs 17A-F), as is also the case in YPM 56735 (Figs 17K-M; not indicated as such by HUENE, 1914a, fig. 49). HUENE (1914a) suggested that the olecranon process of YPM 56735 (Figs 17K-M) was probably extended by a cartilaginous cap; this may be the case because in *Plateosaurus* this extension is represented by a separate ossification on both proximally pathologic ulnae of the current mounted


Fig. 18 : Basal sauropodomorph bones from Clifton. A-O : radii : A : BRSMG Ca7487/85♦, right radius in medial view (or left in lateral view or inverted right ulna in lateral view). B-H : right radius BRSMG Ca7504/52, B-C : distal end in B : anterior and C : medial views, D-H : complete bone in D-E : posterior [with ends (D, E) and cross-section (D)] ; F : anterior ; G : medial and H : lateral views (BENTON *et al.*, 2000, figs 14C-F). I-M : distal left radius, BMNH 49984b, a paralectotype of *Agrosaurus macgillivrayi* SEELEY, 1891, in I : posterior ; J : distal ; K : lateral ; L : anterior and M : medial views. N-O : distal right radius BRSMG Cb4298 in N : medial and O : anterior views. P-R : gracile metacarpals : P : metacarpal IV in side view, BRSMG Ca7484/56♦ ; Q-R : right metacarpal I in palmar view, BRSMG *Ca7463/88♦ ; S-B' : robust metacarpals : S-T : metacarpal II, S : ANSP 9864 in side view and T : ANSP 9875 in dorsal view ; U-B' : metacarpal III : U-Y : with pieces of bone on either side, BRSMG Ca7482/80, in U, V, X : dorsal and W, Y : side views ; Z : BRSMG Ca7483/82♦ in side view ; A'-B' : BRSMG Cb4174c/41 in side views. A, P, R, U, Z from HUENE (1908a), B-D from HUENE (1908b) ; Q from RILEY & STUTCHBURY (1840), V from BENTON *et al.* (2000) ; scale bars = 10 mm.

skeleton in Berlin (Galton, 2001b, fig. 27). Also the proximal end of the ulna of *Saturnalia* shows evidence of two additional olecranon ossifications compared to those of other basal sauropodomorphs (LANGER *et al.*, 2007, fig. 8). A sectioned piece of bone is identified as the medial part of the proximal right ulna (Figs 17H-J ; YPM 2195d, see Appendix 7 re. 2192 on bone).

A fairly complete left ulna (Figs 17N-Q ; length, proximal and distal widths 128, 37, 27 mm) was described by RILEY & STUTCHBURY (1840, as tibia) and HUENE (1908a, pl. 82, fig. 3 in lateral view, not posterior), who also figured a less complete one (Figs 17R-X ; BENTON *et al.*, 2000, figs 14A, B). However, the latter does not correspond with the other two ulnae and it is probably a slender metatarsal II.

**Articulated manus** (Figs 6B, 13A, R, S, 19)

Apart from reconstructions (Figs 13A, R, S) and poor illustrations of the articulated manus as preserved (HUENE, 1914a, fig. 46 ; BENTON *et al.*, 2000, figs 12A, B), the manus of *Asylosaurus* has not been well illustrated so a stereo photo and several other photos are provided (Figs 6B, 19).

**Carpus** - The transverse width of distal carpal I at 11.7 mm (by 11.5 mm) is less than the width of metacarpal I at 16.6 mm (Figs 19A, D, F). The sectioned edges of two other distal carpal bones are visible in articulation as thin plates (Figs 19A-D, F). HUENE (1914a) noted that three other carpals were disarticulated, one lying beside the distal end of metacarpal IV and two adjacent to the lateral edge of digit IV. However, the former represents the two phalanges of digit IV (Fig. 19P) and the other two are the ends of the diapophyses of two dorsal vertebrae (q, Figs 6B, 8D, close to end of digit IV).

**Metacarpals** - Metacarpal I is transversely slender (Figs 13R, S, 19A-D, H). The proximal end is subtriangular in outline. Distally there is no extensor depression and the lateral condyle projects the furthest so the phalanx is directed mediodistally. The length and widths proximally, at mid-shaft and distally in mm are 30.9, 16.6 by ~8, 12 and ~13. Metacarpals II-IV (Figs 19A-E) are slender and proximally each overlaps the next one laterally ; the lengths and proximal and distal widths in mm are : II : ~40.5, -, 9 ; III : 40.5, -, 9 ; IV : 38.3, 6.5, 6.5 ; V : 19, 8 (by 5), 6. All of the proximal end of metacarpal II is missing and distally the lateral extensor depression is prominent ; it is less marked on III and even less so on IV (medial ones not visible) that is damaged so the distal width looks as if it is only ~4 mm. Metacarpal V is short, the proximal end is slightly expanded transversely, and the distal end is gently rounded (Fig. 19E).

**Phalanges** - Phalanx 1 of digit I proximally has a prominent extensor process and a flexor "heel" (Figs 19A-D, G), the long-axes of its articular surface are twisted at about 45° to each other, and it is narrow in dorsal view (Fig. 19H), so its transverse width matches that of metacarpal I. The transverse widths are 12.5 mm proximally and ~7 mm distally with a narrow waist inbetween. Digits II and III are subequal in length (Fig. 13R) and proximally the first phalanx has a semicircular dorsal edge without the prominent extensor process that is present on the other phalanges, including the unguals (Figs 19K-O). The length and proximal depth in mm are for ungual I : 17.4, 32.2 (Figs 19G-J), II : 13.7, 28.6 (Figs 19L, M) and III : 9.8, 23 (Figs 19N, O). Although very short, consisting of only two phalanges (not none as described by HUENE, 1914a), digit IV is complete and the very small terminal phalanx, which is subconical and tapers to a rounded point (Figs 13A, R, S, 19P), is very reduced.

BENTON *et al.* (2000) noted that the phalangeal formula of YPM 2195 is 1-2-3-1-0. However, metacarpal V has a rounded articular end (Figs 19A, D-F) that probably bore one small tapering phalanx that was not reconstructed by GALTON & CLUVER (1976) or BENTON *et al.* (2000) (Figs 13R, S). In addition, the ungual or terminal phalanx should be included in the count so the phalangeal formula was probably 2-3-4-2-1 as reconstructed by MARSH (1892) (Fig. 13A).

**Isolated metacarpals** (Figs 6F, G, 18P-B')

The disarticulated manus of YPM 56719 consists of poorly preserved and very incomplete metacarpals (Fig. 6F) and a complete metacarpal V (Fig. 6G ; length 26.7 mm) similar to that of YPM 2195 (Fig. 19F, length 19 mm).

A bone that, because of its length, was identified by RILEY & STUTCHBURY (1840) as a metapodial (Fig. 18Q), was illustrated by HUENE (1908a) as phalanx 1 of digit I of the right pes in plantar view (Fig. 18R ; phalanx, BENTON *et al.*, 2000, p. 105). However, this bone is not a phalanx of the pes but probably a right metacarpal I in palmar view, as indicated by the proportionally large ends and the asymmetrical form of the bone (but not twisted so not phalanx 1 of digit I of basal sauropodomorph manus). Proximally the medial corner is angular and the lateral one is indented by a longitudinal depression for metacarpal II. The articular condyles are obliquely inclined mediodistally. This metacarpal I is slender as in *Asylosaurus* (Figs 13R, S, 19A-D) ; there is also a slender metacarpal IV (Fig. 18P).

The other metacarpals from Clifton appear to be more robust than those of *Asylosaurus*. HUENE (1908a) identified the metacarpals of BRSMG Ca7482/80 (Fig. 18U) as III with fragments of II and IV on either side, as did BENTON *et al.* (2000, fig. 14, in caption as dorsal view so left but IV not shown) (Fig. 18V). However, "metacarpals II and IV" appear to be odd pieces of bone (Figs 18W-Y) and the central bone is probably metacarpal II, the most robust metacarpal in the manus of basal sauropodomorphs, in dorsal view (Fig. 18X). Two other robust second metacarpals are known (Figs 18S, T), as are a couple of slightly more slender third metacarpals (Figs 18Z, A', B'). The concave outline caused by the

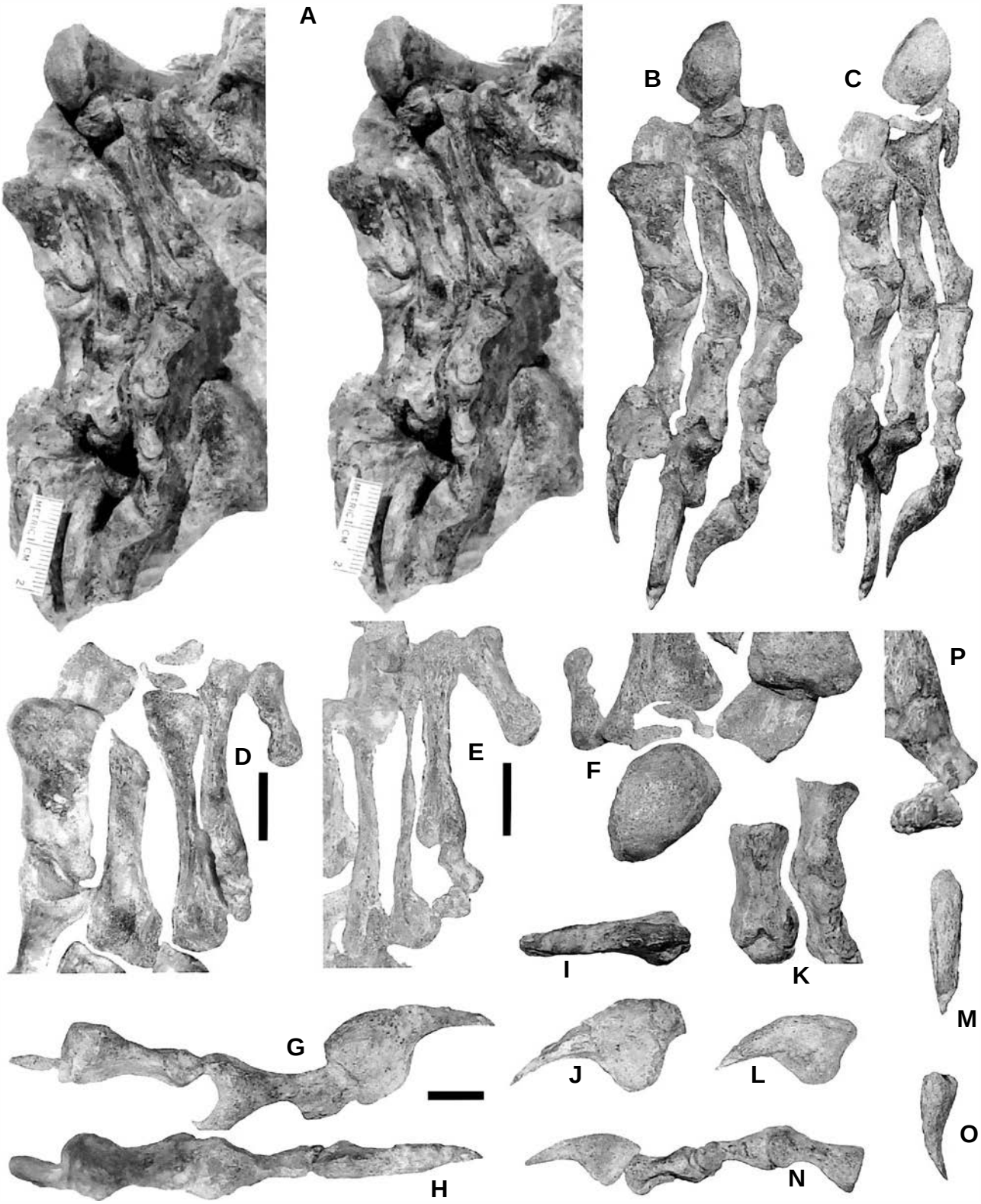



Fig. 19: Very basal sauropodomorph *Asylosaurus yalensis* n. gen. et sp. from Clifton, YPM 2195, articulated left manus, part of holotype. A-C: manus (with distal end of ulna) in A: anterior (dorsal) view (stereo photo); B: anterior and slightly medial and C: anteromedial views. D-E: carpus and metacarpus in D: anterior and E: anterolateral views. F: proximal metacarpals, carpals and distal ulna, metacarpals in anterior and slightly medial view (inverted). G-J: digit I: G-H: carpal and complete digit in G: medial and H: dorsal views; I-J: ungual phalanx in I: dorsal and J: lateral views. K: digits II and III, phalanges 1 and 2, in dorsal view. L-M: digit II, ungual phalanx in L: lateral and M: dorsal views. N-O: digit III: N: phalanges in lateral view and O: ungual phalanx in dorsal and slightly lateral view. P: digit IV, end of metacarpal and phalanges in anterior (dorsal) view. Scale bars = 10 mm.

prominent extensor pit of BRSMG Cb4174 is on the dorsum (Figs 18A', B') so the side view is given upside down in BENTON *et al.* (2000, fig. 14G).

**Isolated manual phalanges** (Figs 20A-S, X-C').
YPM 56745 (Figs 20F-J) is a manual phalanx with a prominent extensor process (Figs 20F, H, J), which is presumably why BENTON *et al.* (2000, p. 93) identified it as phalanx 2 of digit II or III. However, it is phalanx 1 of digit I because of the basal sauropodomorph character of the prominent flexor "heel" (Figs 20F-H) and the apparent medial twisting around its long axis. It is slender in dorsal view with a markedy constricted middle part (Fig. 20H), as in *Asylosaurus* (Figs 13R, S, 19H).
A proximal phalanx (Figs 20A-E), originally figured by RILEY & STUTCHBURY (1840) (Fig. 20A), was identified as phalanx 1 of digit I of the manus by HUENE (1908a, p. 206-207, fig. 224, pl. 81, fig. 7 with no caption, in text as 46) (Fig. 20D). BENTON *et al.* (2000, figs 14I, J) correctly noted that this phalanx is straight in ventral view, not twisted so the articular ends are at 45° to each other as in *Asylosaurus* (Figs 13R, S) and other basal sauropodomorphs, so they concluded that it must be from another digit of the manus. Given the prominent extensor process (Figs 20A, B), it is probably phalanx 2 of digit II or III.
RILEY & STUTCHBURY (1840) illustrated a large ungual phalanx (Fig. 20K) that was subsequently identified as from the pes (Fig. 20L) by HUENE (1908a). However, compared to unguals from articulated pes of other basal sauropodomorphs (see HUENE, 1908a, 1926, 1932; GALTON & CLUVER, 1976; GALTON, 1971, 1973, 1976; COOPER, 1980; same references for manus) and presumed pedal unguals from Clifton (Figs 20M-O, T-V), this ungual (Fig. 20K) has a proportionally much deeper proximal end, with a large and deep flexor process, and a greater degree of distal curvature and taper, features characteristic of the ungual of digit I of the manus of basal sauropodomorphs. BENTON *et al.* (2000, p. 105 as claw phalanx) identified these drawings (Figs 20K, L) as the same bone. However, this is incorrect because one (Fig. 20K), with a preserved length of 65 mm, is ungual I whereas the second (Fig. 20L) at 58 mm is ungual II. RILEY & STUTCHBURY (1840) illustrated another recurved ungual phalanx (Fig. 20P) that was subsequently figured obliquely, preserved alongside a metatarsal III, as a pedal ungual (Fig. 31F, HUENE, 1908a; BENTON *et al.*, 2000, fig. 18Q). However, this is a manual ungual, possibly from digit II (Figs 19P-R, 31F-H), as is another one (Fig. 20W; BENTON *et al.*, 2000, fig. 14K as possibly I). The best preserved manual ungual is massive and undoubtedly from the left digit I (Figs 20X-C').

### VI.1.7. Pelvic girdle

**Ilium** (Figs 21, 22, 23A-E)
Most of the ilia from Clifton were destroyed in 1940. However, RILEY & STUTCHBURY (1840, as a coracoid) (Fig. 21A), HUXLEY (1870) (Fig. 21C), SEELEY (1895) (Figs 22C, F), and HUENE (1908a) (Figs 21D-G, 22D, E, G-J) illustrated six ilia, the basis for an earlier reconstruction (Fig. 22K; HUENE, 1902), so it is one of the better illustrated bones. The reliability of the figures of HUENE (1908a) varies but fortunately he also included a photograph of one block (BRSMG Ca7457/63♦) that bore three of the ilia (Figs 21E-G). SEELEY (1895) figured two ilia on this block as the lateral surface of the left (Fig. 22F) and a mostly natural impression from the internal surface of the right (Fig. 22C). HUENE identified both as left ilia (Figs 21E, F, 22D, G) from individuals of different sizes and possibly species. However, as seen from the photo (Fig. 21F), one shows the outside of the posteroventral part of the ischial peduncle (cf. Figs 21I-K), not the medial one (cf. Figs 21C, K), so SEELEY (1895) was correct. Impressions and some bone of the attachment areas for the sacral ribs are visible along the middle of the bone, as is the obliquely striated attachment area for axial muscles along the dorsal margin (cf. Fig. 21C). The more acute tapering shape of the posterior end is determined by preservation of the ventral edge of the medial shelf (cf. Figs 21C, K), rather than of the more ventrolaterally situated brevis shelf part of the postacetabular process of the subvertical body of the ilium (cf. Figs 21C, E, I-K, 22F). The ventral part of the third ilium is a right but it is very incomplete and represented by bone in medial view (Figs 21G, 22E).
BENTON *et al.* (2000) redrew the figure of an ilium from HUENE (1908a) in which the pubic and especially the ischial peduncles look strange (Figs 21D, 22J). HUENE was only in Bristol 14 days (HUENE, 1908a, p. iv, vii) so the artist, SHELLARD of Bristol, probably drew the bone without supervision. As mentioned by SEELEY (1895), but not by HUENE (1908a) or BENTON *et al.* (2000), an ilium was illustrated by HUXLEY (1870, pl. 3, fig. 7), although the anterior part was described as posterior and *vice versa* (corrected, HUXLEY, 1875, p. 434; LYDEKKER, 1888, p. 174). A comparison of the pattern of cracks (Figs 21C, D) clearly shows that this is the same ilium, viz., BRSMG Ca7460/57♦. Given the confirmed accuracy of other figures on the same plate, e.g., those of the neotype dentary of *Thecodontosaurus antiquus* (Figs 4G-I), the proximal articular surface of the right tibia BRSMG C4531/77a (Figs 28D, E), and the sacrum of the rauisuchian crurotarsal archosaur *Bromsgroveia* (GALTON & WALKER, 1996a, figs 1I, J, 4E, 5A, C, D; BENTON & GOWER 1997, figs 5, 6), the figure (Fig. 21C) of HUXLEY (1870) should be used rather than that of HUENE (1908a) (Figs 21D, 22J).
BENTON *et al.* (2000) figured the posterior ramus of a right ilium (ANSP 9870) in lateral and dorsal views (Figs 22A, B) as extremely massive and transversely expanded, a unique form for a basal sauropodomorph. However, the form is normal if the posterior ramus is reidentified as the pubic process in medioventral and dorsal views,

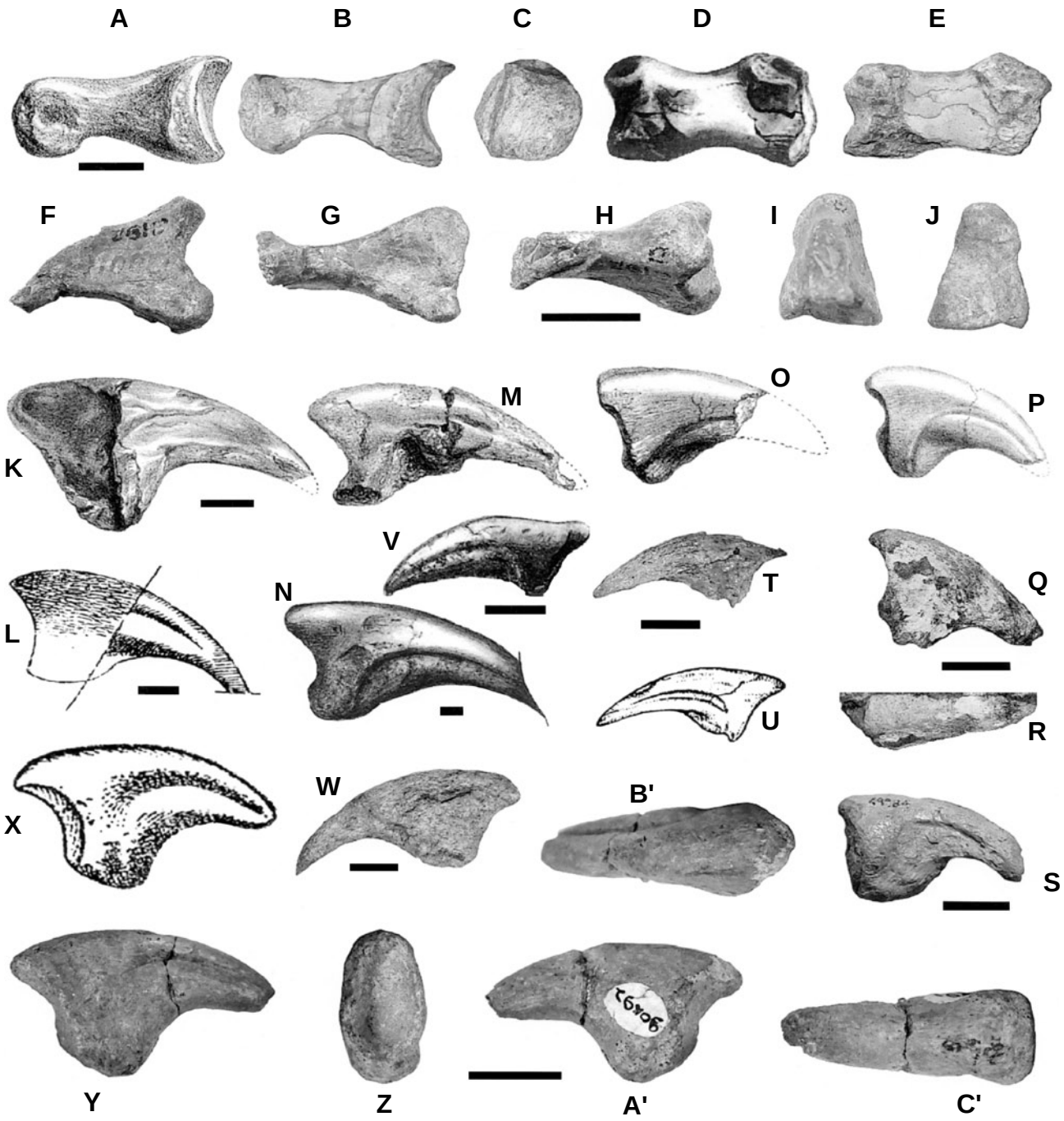



Fig. 20 : Basal sauropodomorph phalanges from Clifton from manus (A-L, P-S, W-C') and pes (M-O, T-V) from digits I (F-K, M, N, X-C'), II (A-E, L, O-R, W), III (V) and IV (T, U), unguals mostly in side view (K-Q, S-Y). A-E : phalanx 2 of digit II or III, BRSMG *Ca7485/46b in A, B : side ; C : proximal and D, E : palmar views (BENTON *et al.*, 2000, figs 14I, J). F-J : *Asylosaurus yalensis*, n. gen. et sp., YPM 56745, referred right manual digit I, phalanx 1 in F : medial ; G : palmar ; H : dorsal ; I : distal and J : proximal views. K-L : manual unguals : K : I, BRSMG *-/-♦ and L : II, BRSMG *Ca7454/87♦ ; M-O : pedal unguals : M-N : I, BRSMG *Ca7455/86♦ and O : II, BRSMG *-/-♦. P-R : manual ungual I, BRSMG *Ca7451a/81 in P-Q : side and R : dorsal views. S : left manual ungual I in medial view, BMNH 49984c, a paralectotype of *Agrosaurus macgillivrayi* SEELEY, 1891. T-U : pedal ungual IV, ANSP 9861b. V : pedal ungual III, BRSMG Ca7476/59♦. W : sectioned manual ungual II, BRSMG Cb4187/84 (BENTON *et al.*, 2000, fig. 14K). X-C' : left manual ungual I, GSM 90792, in : X-Y : medial ; Z : proximal ; A' : lateral ; B' : dorsal and C' : palmar views. A, K, M, O, P from RILEY & STUTCHBURY (1840), D, L, N, V from HUENE (1908a), U from BENTON *et al.* (2000), X from HUENE (1914a) ; scale bars = 10 mm.

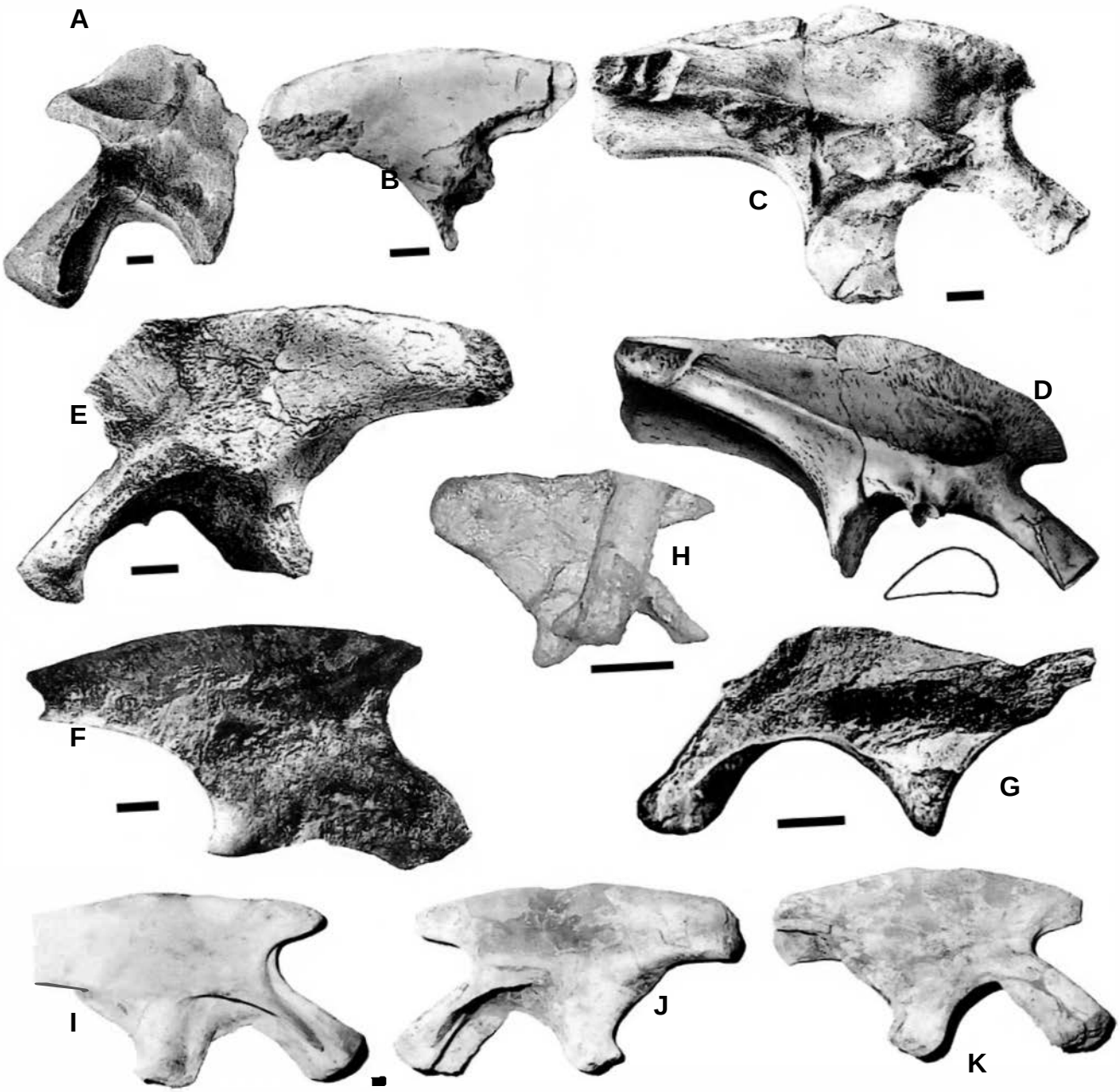



Fig. 21 : Basal sauropodomorph ilia. A-G : from Clifton, left (A, C-E) and right (B, F, G) ilia in lateral (A, B, E, F) and medial (C, D, G) views. A : anterior half, BRSMG *Ca7450/61♦ (cf. Fig. 22H) ; B : posterior half, BMNH R1540 ; C-D : BRSMG Ca7460/57♦ (D with outline of distal end of pubic peduncle ; cf. Fig. 22J) ; E : BRSMG Ca7457a/63♦ (cf. Figs 22F, G) ; F : BRSMG Ca7457b/63♦ (mostly as impression of medial surface in lateral view, cf. Figs 22C, D) ; G : BRSMG Ca7457c/63♦ (cf. Fig. 22E). H : *Pantydraco caducus* from South Wales, right ilium in lateral view, BMNH P77/1. I-K : *Efraasia minor* from Upper Triassic of Germany, right SMNS 12354e (I) and left SMNS 12354 (J, K) in lateral (I, J) and medial (K) views. A from RILEY & STUTCHBURY (1840), C from HUXLEY (1870), D-G from HUENE (1908a) ; scale bars = 10 mm.

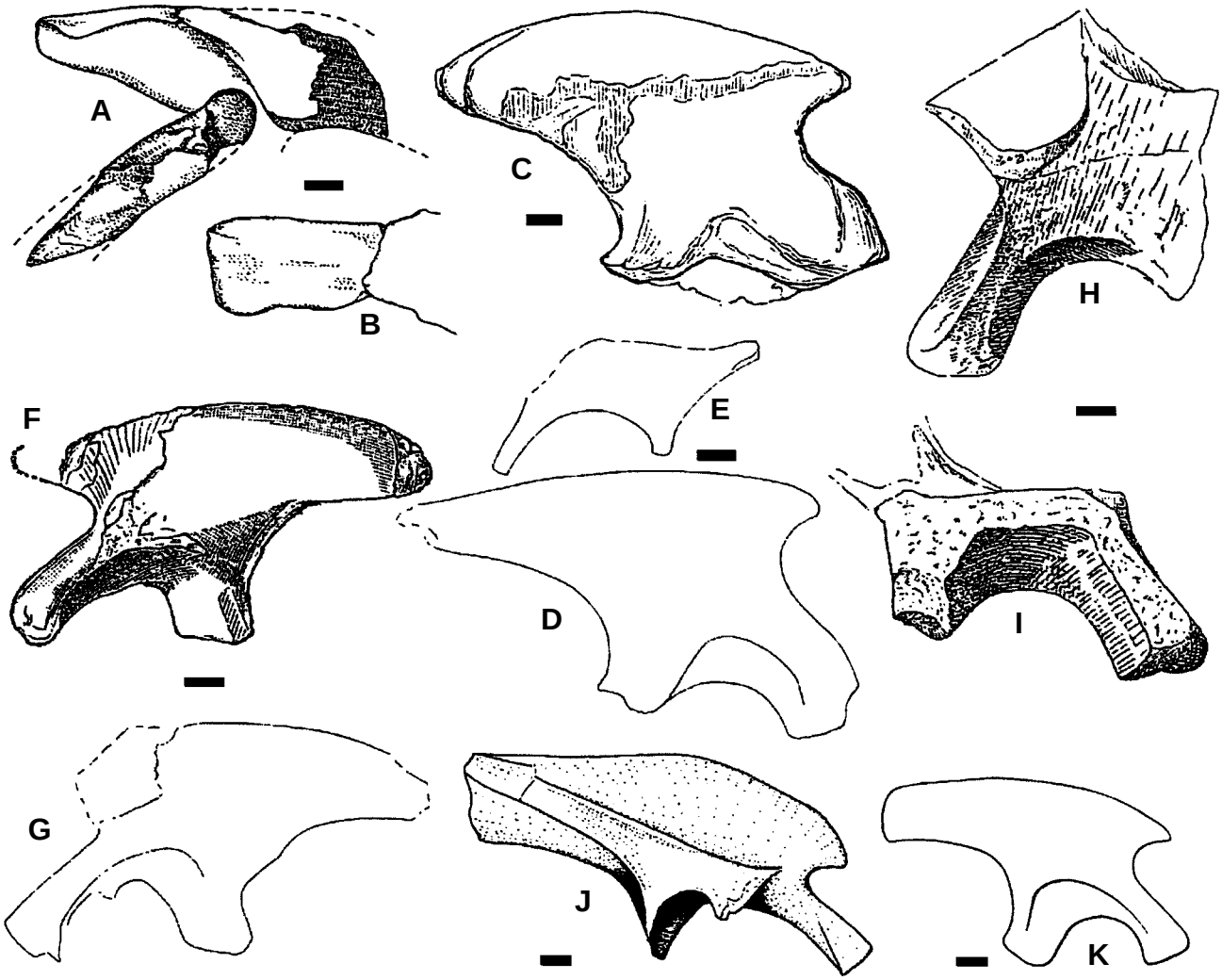



Fig : 22 : Basal sauropodomorph ilia from Clifton in ventromedial (A), dorsal (B), lateral (F, G-I, K) and medial (C-E, J) views. A-B : ANSP 9870a,b : A : anterior third of right ilium (with distal half of left ischium in medial view) and B : pubic peduncle (cf. Figs 23A-C). C-D : left ilium BRSMG Ca7457b/63♦(cf. Fig. 21F) figured as C : internal impression of left ilium and some bone in lateral view (C) and as lateral view of right ilium (D). E : BRSMG Ca7457c/63♦, acetabular region of right ilium (cf. Fig. 21G). F-G : BRSMG Ca7457a/63♦, left ilium with impression of internal surface of base of anterior process (cf. Fig. 21E). H : BRSMG *Ca7450/61♦, partial left ilium (cf. Fig. 21A). I : BRSMG Ca7506/60♦, partial right ilium. J : BRSMG Ca7460/57♦, left ilium (cf. Figs 21C, D). K : reconstruction of right ilium based on BRSMG specimens. A, B, J from BENTON *et al.* (2000), C, F from SEELEY (1895), D, E, G-I from HUENE (1908a), K from HUENE (1902) ; scale bars = 10 mm.

because in basal sauropodomorphs this process is wide and squared off in dorsal view (Figs 21D, 23C). The obliquely inclined lateral and medial surfaces are almost at right angles to each other, meeting at a rounded edge that extends anterolaterally from the broken base of the anterior process (Figs 23C, E). The lateral edge forms the acetabular margin, the posterior part of which is obscured by matrix (Figs 23D, E). Little of the pubic peduncle is visible in medioventral view (Fig. 23A), so the ventral outline (Fig. 22A) given by BENTON *et al.* (2000) was reconstructed from the opposite side (Fig. 23B). In medial view (Fig. 23B), the bone is also broken diagonally across the base of the ischial process and there is an impression of part of the lateral surface of the body of the ilium.

As indicated by the better preserved specimens (Figs 21B, C, E, 22F, G, 23B-E), the form of the ilia from Clifton is similar to that of other basal sauropodomorphs, including *Efraasia* (Figs 22I-K) from the Upper Triassic of Germany. The main body is a low subvertical sheet with a small triangular anterior process and an elongate tapering posterior (postacetabular) process, the truncated end of which varies from rounded (Figs 21E, 22F, G) to more squarish in outline (Fig. 21C). BMNH R1540, a previously unillustrated partial ilium from Clifton, has a rounded posterior end (Fig. 21B). The acetabulum

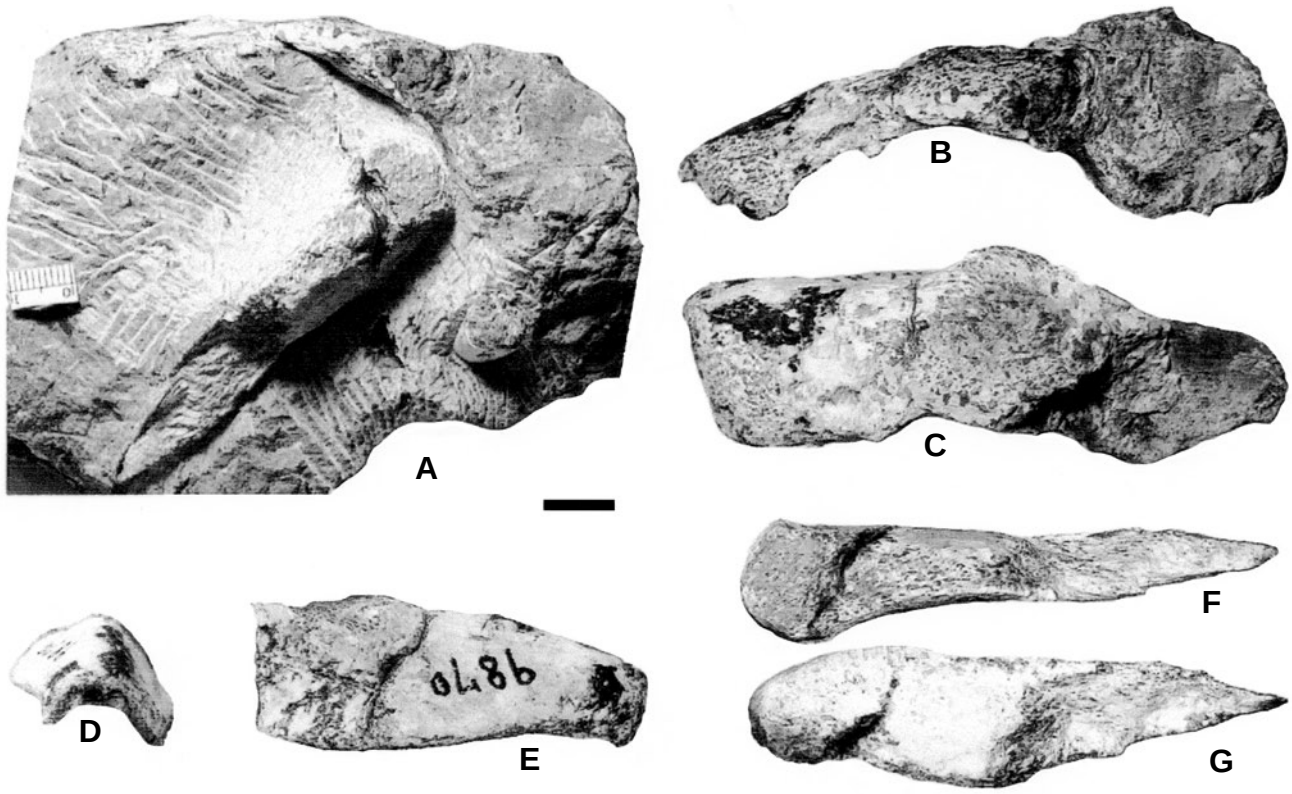



Fig: 23: Basal sauropodomorph from Clifton, ANSP 9870a,b. A: anterior two thirds of right ilium in ventromedial view and distal half of left ischium in medial view (cf. Fig. 22A); B-E: right ilium: B-C: acetabular region with impression of part of medial surface of body in B: medial and C: dorsal views (cf. Fig. 22B); D-E: pubic peduncle in D: anterior and E: lateral views. F-G: distal left ischium in F: medial and G: posterodorsal views. Scale bar = 10 mm.

is partly backed by bone in some ilia (a plesiomorphic character) and roofed by a prominent supra-acetabular flange that extends anteriorly onto the massive pubic peduncle (Figs 21E, 22F, G, 23C-E); this peduncle is not "delicate and slender in relation to those of other prosauropods" (BENTON *et al.*, 2000, p. 93, based on a distally incomplete peduncle). The ischial peduncle is massive but, depending on the angle of view and how much of it is exposed, it can appear small in medial view (Figs 21D, 22J cf. Fig. 21C). The extensive rugose surface for articulation with the sacral ribs is visible medially (Figs 21C, F) and, posterior to the ischial peduncle, this surface is borne by a medially protruding shelf that ascends diagonally to end almost level with the dorsal edge (Fig. 21C) as in *Efraasia* (Fig. 21K) and *Plateosaurus*; the adjacent part of the post-acetabular process forms a large brevis shelf (Fig. 21C).

**Pubis** (Figs 24N-R)

HUENE (1908a) figured two proximal parts (Figs 24N-P). Although incomplete ventromedially, so much of the margin of the obturator foramen is missing, these foramina obviously differed considerably in size. BENTON *et al.* (2000, figs 15E, F) identified the broad pubic apron of the most complete pubis as a left exposed in anterodorsal view. However, the anteromedial part curves outwards, as correctly indicated by the shading, so it is a right in posteroventral view (Figs 24Q, R). There are two other less complete pubic aprons (ANSP 9859, 9865, latter ?scapula fragment of BENTON *et al.*, 2000, p. 82, 106).

**Ischium** (Figs 22A, 23A, F, G, 24A-M)

The proximal ischium of RILEY & STUTCHBURY (1840) is the incomplete right humerus BRSMG Ca7512/93♦ (Figs 16E, F). The partial humerus of BENTON *et al.* (2000, p. 106) is the only well preserved proximal ischium (Fig. 24L). The most complete ischium, incomplete at both ends, is exposed in ventrolateral view (Fig. 24M). The distal ischium of HUENE (1908a; BENTON *et al.*, 2000, p. 82 as probable proximal ischium, p. 105 as ?ischium) is the proximal end of a basal theropod femur (Figs 36H-J, see below). BENTON *et al.* (2000, p. 94) noted that a "small portion of what appears to be the proximal end of the ischium remains articulated to the ilium/acetabulum of ANSP 9870. The ischium head is small and the shaft narrow, and otherwise similar to that of anchisaurids."

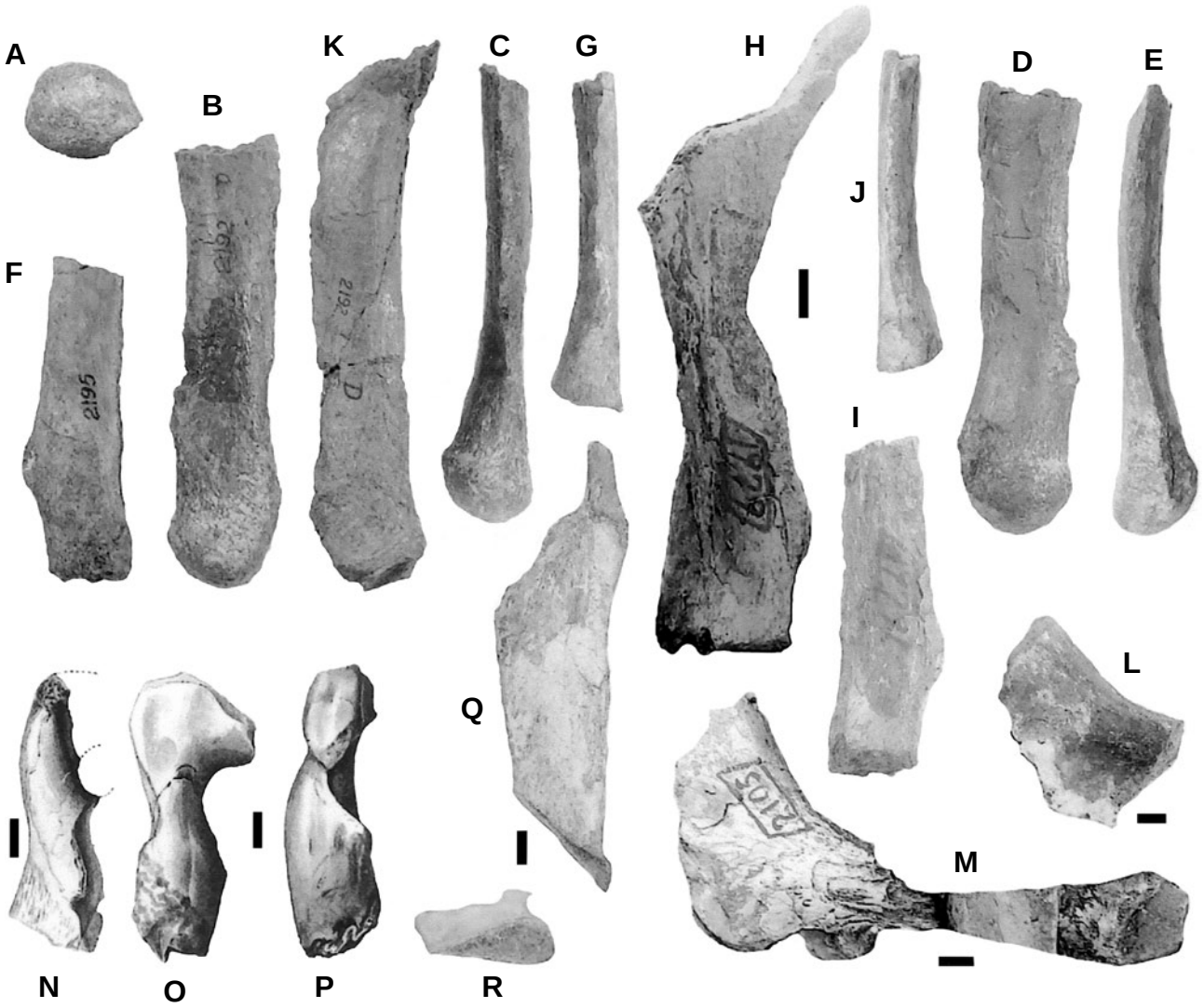



Fig. 24: Basal sauropodomorph ischia (A-M) and pubes (N-R) from Clifton. A-K: distal left (A-J) and right (K) ischia: A-E: YPM 56726; F-J: YPM 2195e and K: YPM 56725 in: distal (A), posterodorsal (B, F, K), lateral (C, G), anteroventral (D, H, I) and medial (E, J) views. L: proximal left ischium BMNH R1550b in ventrolateral view. M: distally incomplete left ischium YPM 56747 in ventrolateral view. N-P: proximal pubes: N: BRSMG Ca7488/101♦, right in anterodorsal view; O-P: BRSMG Ca7489/100♦, left in O: lateral and P: posteroventral views. Q-R: incomplete right pubis BRSMG Cb4267 in Q: posteroventral and R: distal cross-sectional views (BENTON *et al.*, 2000, figs 15E, F as left in anterodorsal and distal views). N-P from HUENE (1908a); scale bars = 10 mm.

This bone is also listed and figured as the associated femur (fe, BENTON *et al.*, 2000, p. 106, fig. 15A), but it is the distal end of a left ischium (Figs 22A, 23A, F, G).

HUENE (1908a) illustrated two isolated distal ischia exposed in dorsal view. These bones, which were fully prepared sometime after 1901, were briefly described but not illustrated by BENTON *et al.* (2000, p. 94). One has more of the shaft preserved and, as this includes a part of the anterodorsal region arching up towards the ilium, this is a right (Fig. 24K; HUENE, 1908a, pl. 83, fig. 2 in matrix). The other one, the distal end of which is complete, is a left (Figs 24A-E; HUENE, 1908a, pl. 83, fig. 3 in matrix). There are also two less complete distal left ischia (Figs 22A, 23A, F, G, 24F-J; also YPM 56739). In lateral (Figs 24C, G) and medial views (Figs 24E, J), the distal ischium is thin; the cross section is oval with the medial edge sharper than the lateral one (anterior and posterior edges of BENTON *et al.*, 2000, p. 94). At about 50 mm from the distal end the edge is lost laterally whereas medially the contact edge thickens to form an elongate triangular shaped rugose area. The bone also more than doubles in thickness and the rounded end becomes more subcircular in outline, being slightly wider than deep (Fig. 24A). However, the thickest parts

are not in contact with each other, being separated by a cleft about 20 mm long and Λ-shaped in dorsal and ventral views (Figs 24B, K) that is not present in ischia of other basal sauropodomorphs. The distal left ischium YPM 2195e, that lacks the distal end (Figs 24F, G, I), was originally more complete proximally as indicated by a photo taken prior to further preparation (Fig. 24H) that was sent by the YPM to HUENE in 1901 (BCM Archives, Geology file No. 51).

### VI.1.8. Hind limb

**Femur** (Figs 6A, C, 25-27)

The form of the femora from Clifton (Figs 25-27) is plesiomorphic for basal sauropodomorphs in being sigmoidal in anterior and lateral views, strongly broadened proximally with the head directed anteromedially and merging smoothly with the lateral margin of the shaft, the anterior (=lesser trochanter) is a low ridge (Figs 25G,

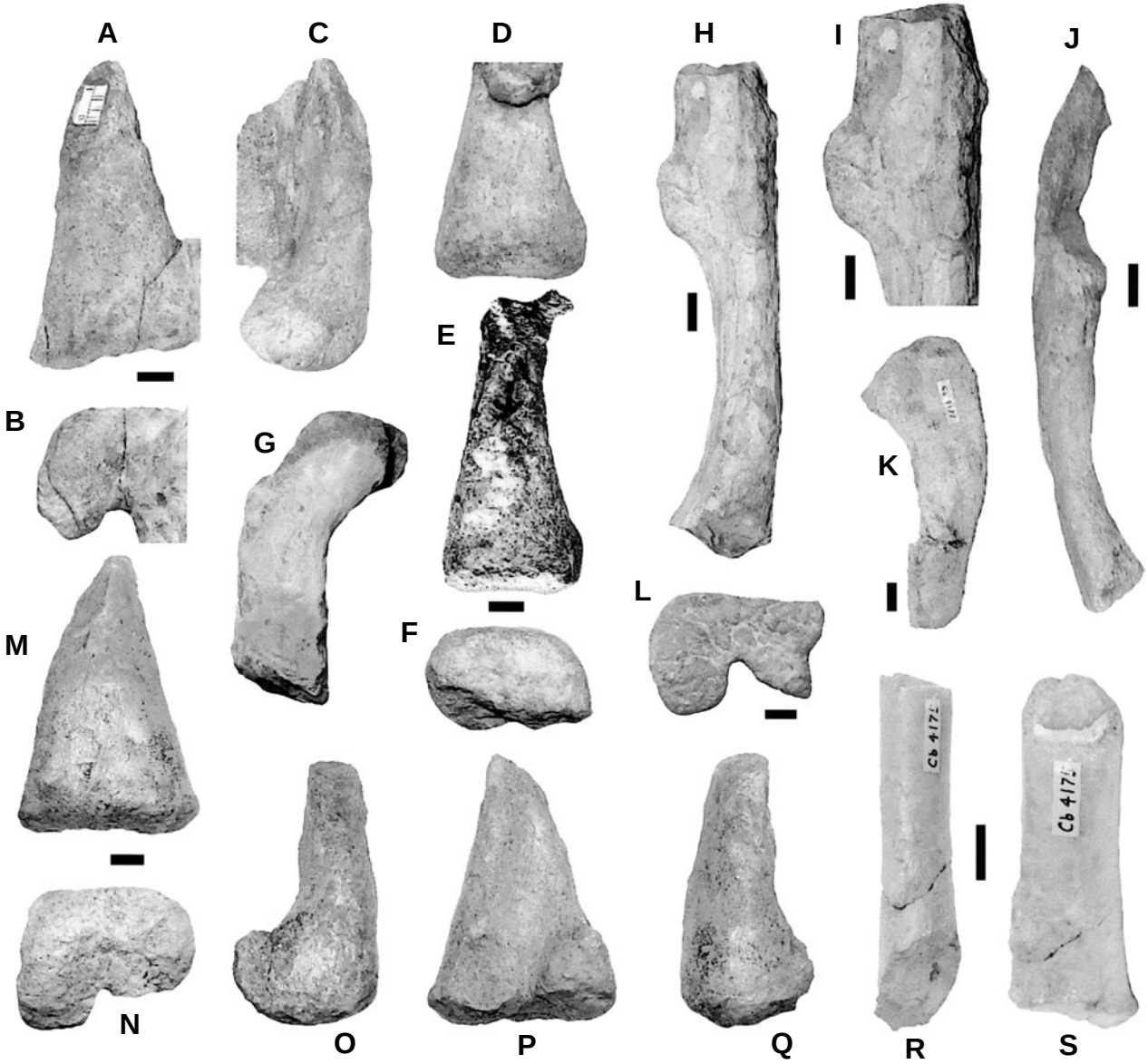



Fig. 25: Basal sauropodomorph femora from Clifton. A-F: *Asylosaurus yalensis* n. gen. et sp., distal femora: A-C: right femur YPM 2195f in A: anterior; B: distal and C: lateral views; D-F: left femur YPM 2195g in D-E: anterior and F: distal views. G: proximal right femur, BRSMG Cb4190/99, in anterior view. H-I: right femur BRSMG Cb4183/72 lacking both ends in lateral view: H: bone as preserved and I: detail of proximal part with fourth trochanter. J: much of shaft of a small femur, BMNH R1545, in side view. K: proximal left femur, BRSMG Cb4177/49,74 in anterior view. L: distal left femur YPM 56727 in distal view. M-Q: distal left femur, BMNH R1594, in M: anterior; N: distal; O: medial; P: posterior and Q: lateral views. R-S: distal shaft of ?left femur, BRSMG Cb4175/44 in R: ?lateral and S: ?posterior views. E from HUENE (1908a) as a gracile femur, along with A-C, R, S. Scale bars = 10 mm.

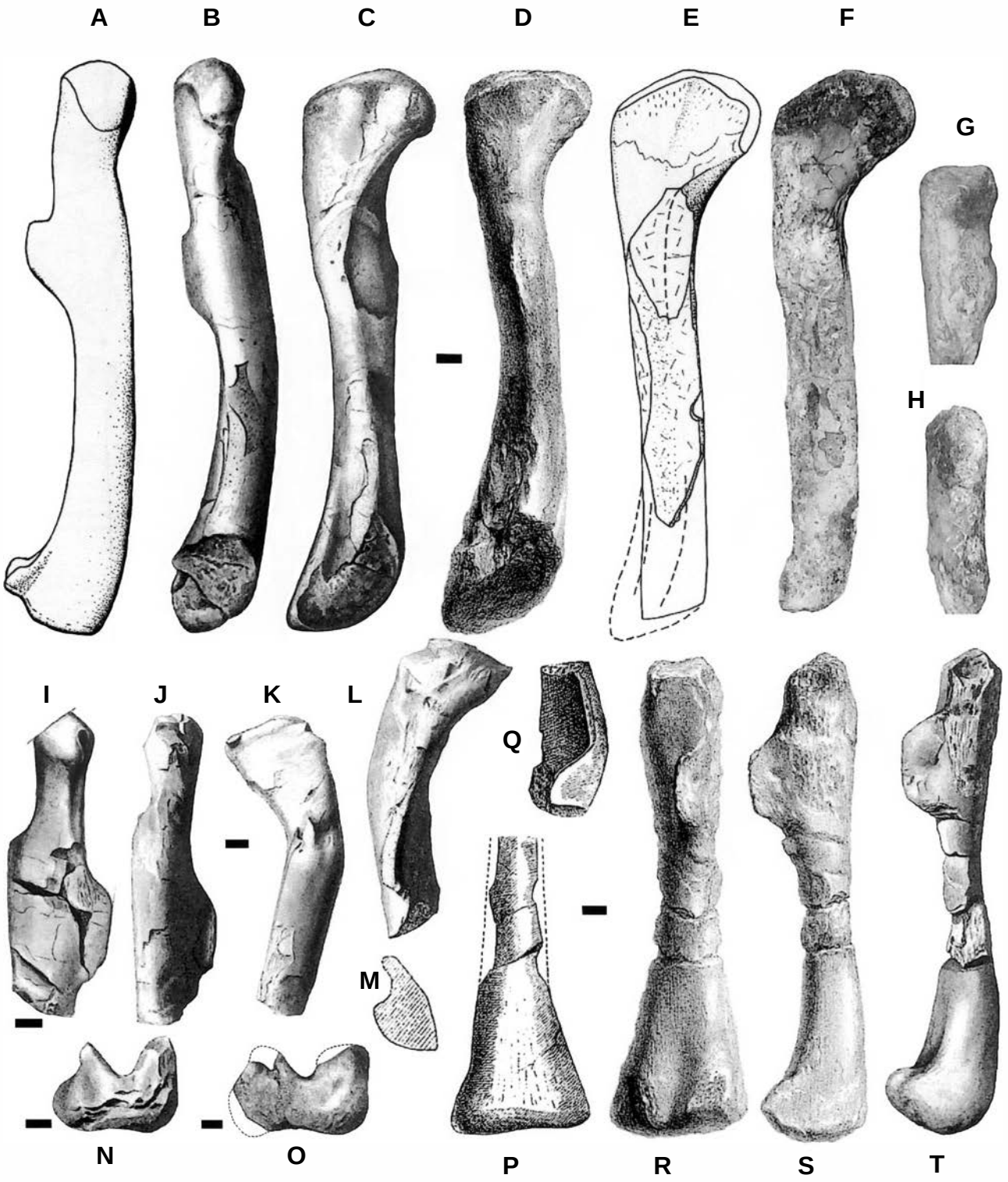



Fig. 26 : Basal sauropodomorph femora from Clifton, robust (A-H, O-T) and gracile (I-N) forms of HUENE (1908a). A-H : left femur BRSMG *Ca7456/67 in : A-B : medial view : A : restored and B : as originally preserved with medial condyle incomplete distally ; C-F : posterior view in C-D : as originally preserved and E-F : current damaged state after being rescued from ruins with burn marks in 1941 ; G-H : proximal part in G : medial and H : lateral views. I : proximal part of right femur BRSMG Ca7477b/37♦ in medial view. J-M : proximal part of left femur BRSMG Ca7491/68♦ in J : lateral ; K : anterior ; L : posterior and M : distal (of broken end) views. N : left femur BRSMG Ca7493/70♦ in distal view. O-T : proximally incomplete left femur BRSMG Ca7492/69I♦ in O : distal ; P : anterior ; Q-R : posterior and S-T : medial views. In N and O the extensor groove is on lower edge ; A, E from BENTON *et al.* (2000), B, C, I-Q, T from HUENE (1908a), D, R, S from RILEY & STUTCHBURY (1840) ; scale bars = 10 mm.

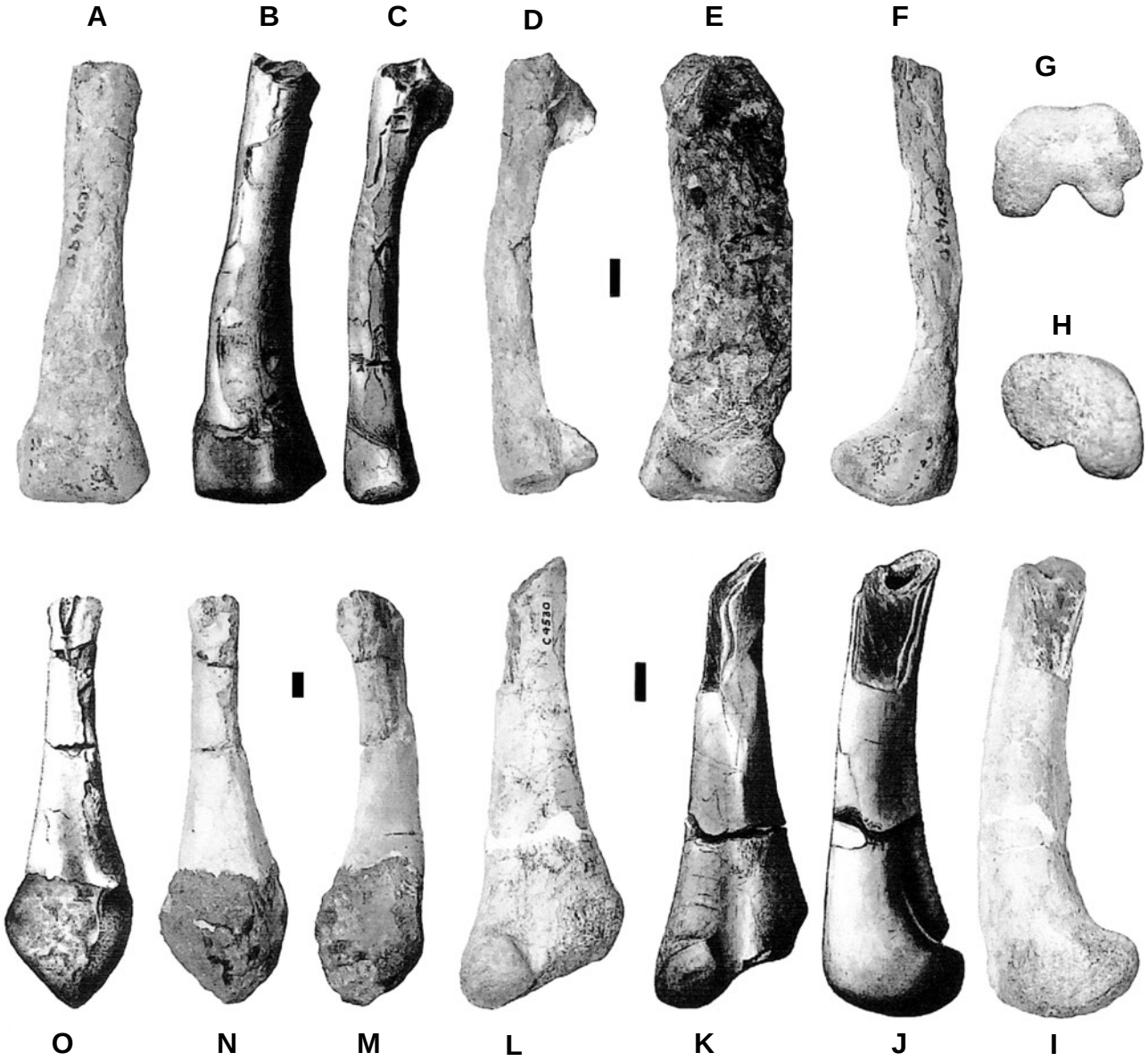



Fig. 27 : Basal sauropodomorph femora from Clifton, gracile form in HUENE (1908a). A-G : BRSMG Ca7490//71, distal part of left femur with part of fourth trochanter in A, B : anterior ; C, D : lateral ; E : posterior ; F : medial and G : distal views (BENTON *et al.*, 2000, figs 16C-H). H-L : distal part of right femur BRSMG C4530/73 in H : distal ; I, J : medial and K, L : posterior views. M-O : BRSMG Ca7494/69a-II, distal left femur to base of fourth trochanter, in M : medial and N, O : posterior views. B, C, J, K, O from HUENE (1908a) ; scale bars = 10 mm.

26I, J), and the fourth trochanter is proximally placed well above mid-length (base at 43% of length, Figs 26B-D ; HUENE, 1908a, p. 210) and in the middle of the posterior surface of the shaft (Figs 26C, D, L, R).

BENTON *et al.* (2000, p. 94) reconstructed the femur (Fig. 26A) of BRSMG *Ca7456/67, basing it on data from HUENE (1908a) (Figs 26B, C) and what remains of the specimen, viz., the proximal end, a sectioned part of the adjacent shaft and a natural mold of the rest of the bone (Figs 26E, F). The form of the fourth trochanter, which looks as though it is drawn upside down, is unique for a basal sauropodomorph (and for any other dinosaur). However, the complete fourth trochanter, which is known in several Clifton specimens (best Figs 24H, I, also Figs 26B, I, J, L, Q-T, 27C, D), looks to be longer and the proximal edge is more gradually curved than reconstructed (Fig. 26A) ; it is shown more accurately in the drawing of the skeletal of an adult individual (Fig. 1B ; BENTON *et al.*, 2000, fig. 19). BENTON *et al.* (2000, p. 94, 96) noted that this femur was “formerly complete”

prior to 1940. However, it is shown as distally incomplete in earlier illustrations (Figs 26B-D) and HUENE (1908a) noted that it was almost complete, lacking merely a piece of the condyle at the distal end, and it was the largest femur at 255 mm long (with smallest ones a third smaller). Although not indicated on the illustrations (Figs 26B-D), he also noted that below and laterally beside the fourth trochanter, the shaft was restored in plaster (area now missing, Fig. 26F). Distally the outline of the reconstructed medial condyle (Fig. 26A) resembles the smaller lateral condyle of basal sauropodomorphs, including a femur from Clifton (Fig. 27D), rather than the usual more massive medial condyle of basal sauropodomorphs (Figs 25O, 26S, 27F, I) and other dinosaurs. This end was possibly based on the somewhat misleading medial view of BRSMG *Ca7492/69I♦ given by HUENE (1908a) (see Fig. 26S cf. Fig. 26T).

**Tibia** (Figs 6D, 28, 29A-G, 30A-P)
The figures of the best preserved tibia BRSMG *Ca7462/76♦ (Figs 28A, B, length 180 mm, proximal end 50 x 30 mm) differ somewhat but they are the same bone because SEELEY (1895, p. 153) noted that "the tibia figured in 1840 still remains the only complete specimen." The tibia of *Agrosaurus* (Figs 29A-F, length 180 mm; SEELEY, 1891, figs 1-5; HUENE, 1906, figs 86a-e; GALTON, 2000, figs 15A-F; BENTON *et al.,* 2000, figs 17A-D but note A, medial and C, lateral views) is now a second complete tibia from Clifton. The referral of this tibia to *Thecodontosaurus antiquus,* rather than to the Herrerasauridae (SERENO, 1997), is discussed by GALTON (2000). The ends are well preserved but the middle part of the shaft is crushed and some of the outer cortical layer is missing. SEELEY (1895, p. 153) noted that "the expansion of the proximal end appears to be relatively greater" in BMNH 49884 than in BRSMG *Ca7462/76♦ (Figs 28A, B; gracile form of HUENE, 1908a); in the latter "the notch at the distal end appears to be about a line with the cnemial crest, while in *Agrosaurus* it is obviously lateral and on the fibular side." YATES (2003a, p. 18) noted that BMNH 49884 "is aberrant and unlike all other tibias (sic) assigned to *T. antiquus*", but he did not give any other details. This tibia (Figs 29A-F) is the only possibly definable bone of BMNH 49984 (cf. Figs 12F, 18I-M, 20S) so it is designated as the lectotype of *Agrosaurus macgillivrayi* SEELEY, 1891.
The proximal tibia is well preserved in BRSMG Ca4531/77a (Figs 28D-K; BENTON *et al.,* 2000, figs 18A-E but note A, lateral and D, medial views) and YPM 56731 (Figs 28N, O, HUENE; 1908a, pl. 89, fig. 5 photo in medial view in matrix, 1914a, fig. 50 inaccurate proximal view; distal 15 mm ground off at some time to give histological cross section); it is a bit crushed in YPM 56730 (Figs 28L, M; originally with a damaged shaft, HUENE, 1908a, pl. 89, fig. 3 as left, bone now freed of matrix and half its original length).
The 160 mm long poorly preserved left fibula (BRSMG Ca7502/42♦) of SEELEY (1895, fig. 6) is a poorly preserved tibia (HUENE, 1908a, p. 212). The distal right tibia in matrix (YPM 56732) of HUENE (1908a, pl. 89, fig. 4; BENTON *et al.*, p. 82, 106 as distal right tibia) is a crushed proximal half of a metatarsal. A distal left tibia (Figs 30A-J; BENTON *et al.,* 2000, figs 18F-J) is not well preserved but it shows the notched end for the ascending process of the astragalus.
A distal left tibia with the astragalus attached (Figs 30K-P) was illustrated by HUENE (1908a, pl. 89, figs 2a, b as right; 1914a, fig. 51) and BENTON *et al.* (2000, figs 18K-O). Distally the posterolateral edge of the tibia is broken (Figs 30M, N; HUENE, 1908a, pl. 89, fig. 2a) but even so it was still unexpanded laterally, as is also the case in *Efraasia*, whereas it is broader in *Massospondylus* and *Plateosaurus*. The posterolateral corner of a similar distal right tibia (YPM 2195h) is broken and the anterior width is 26.2 mm wide (Fig. 6D) as against 25.6 mm for YPM 56731 (Fig. 30N).

**Fibula** (Figs 29H, 31A-E)
The fibula is poorly represented, one supposedly complete fibula (BRSMG Ca7502/42♦; SEELEY, 1895, fig. 6) being a poorly preserved tibia (HUENE, 1908a, p. 212). The most complete fibula (length 125 mm) has most of the shaft, but the ends are damaged (Figs 31C, D; BENTON *et al.,* 2000, fig. 18P), and another one is very poorly preserved (Fig. 31E). The proximal part of a large fibula (Figs 31A, B) was one of the first bones brought in by workers to the Bristol Institution (STUTCHBURY, 1836); another one is less well preserved (Fig. 29H; fibula BENTON *et al.*, 2000, p. 82) and might be a proximal metatarsal. The protruding end of the proximal fibula of HUENE (1908, pl. 84, Fib.) is more probably the proximal end of a metatarsal in anterior view. The distal half fibula (Figs 8P, Q) of HUENE (1908a; BENTON *et al.,* 2000, p. 104) is a longitudinally sectioned distal end of a dorsal rib (see above).

**Tarsals** (Figs 30K-W)
An astragalus is attached to a left distal tibia (Figs 30K-P; HUENE, 1908a, pl. 89, figs 2a, b as right; 1914a, fig. 51; BENTON *et al.*, 2000, figs 18K-O, in O the anteroposterior line across lateral part of astragalus is a crack). The ascending process of the astragalus is clearly seen keying into the tibia (Figs 30K-N, P), a character of the Sauropodomorpha. The associated calcaneum (Figs 30Q-T) of HUENE (1914a) is the ventral part of the distal articular surface of a phalanx (?pedal, Figs 30U-W).

**Metatarsals** (Figs 29I-R, 30X, 31F-Y)
A small, articulated right pes (Fig. 31Y; phalanges of BENTON *et al.*, 2000, p. 106), probably originally complete, now consists of the distal ends of metatarsals I, II and III plus the adjacent phalanges (digit I complete but ungual mostly in matrix, specimen needs further preparation).

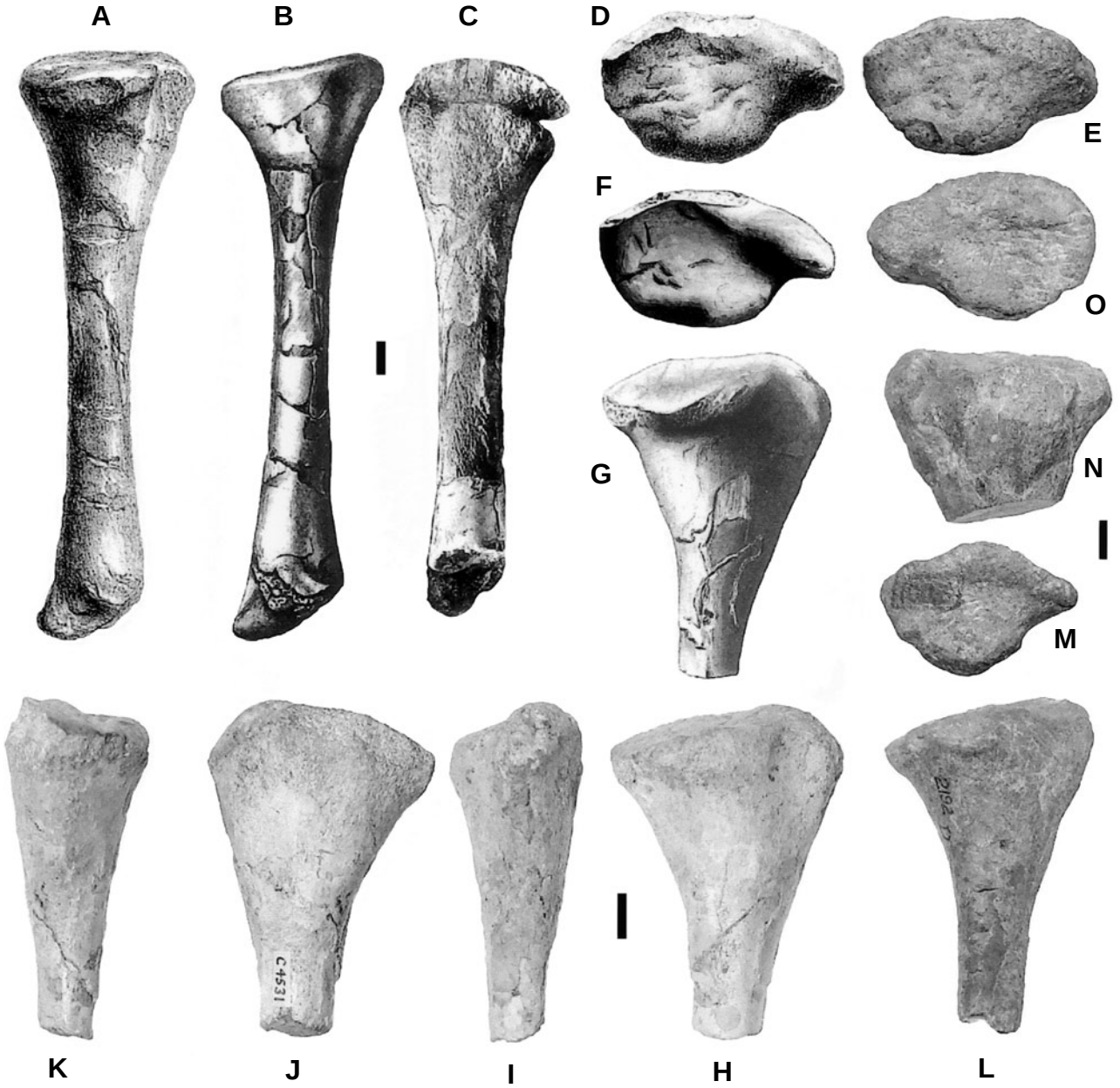



Fig. 28 : Basal sauropodomorph tibiae from Clifton. A-B : right tibia (gracile form, HUENE, 1908a), BRSMG *Ca7462/76♦, in lateral view. C : BRSMG Ca7457d/63♦, right tibia (robust form HUENE, 1908a), slightly incomplete distally, in medial view. D-K : proximal right tibia BRSMG C4531/77a in D-F : proximal ; G, H : lateral ; I : anterior ; J : medial and K : posterior views (BENTON *et al.*, 2000, figs 18A-E but A : medial and D : lateral views). L-M : proximal right tibia YPM 56729 in L : lateral and M : proximal views. N-O : proximal left tibia, YPM 56730, in N : lateral and O : proximal views (medial view, HUENE, 1908a, pl. 90. fig. 5). A from RILEY & STUTCHBURY (1840), B, F, G from HUENE (1908a), D from HUXLEY (1870) ; scale bars = 10 mm.

Three bones have been described as the proximal end of metatarsal I. The first (Fig. 30X, lost ; HUENE, 1914a, with distal tibia and astragalus, Figs 30K-P) is based on part of the articular end of a very small indeterminate bone. The second is very narrow (Fig. 31W ; ?compressed or incompletely exposed) and, because of the diagonal ridge (Fig. 31V), it may be a distal right metatarsal IV in anterior view ; the third may be correctly identified (Fig. 31X).

HUENE (1908a) described a slender distal metatarsal II as a right but, based on the articular surface facing mediodistally, it is a left (Figs 31K-R ; but K may go


Fig. 29 : Basal sauropodomorph lower hind limb bones from Clifton. A-G : BMNH 49984, *Agrosaurus macgillivrayi* SEELEY, 1891, A-F : lectotype left tibia in A : anterior ; B : lateral ; C : proximal ; D : posterior ; E : distal and F : medial views ; G : paralectotype BMNH 49984e, transversely compressed proximal right tibia in medial view. H : proximal right fibula, ANSP 9869, in lateral view. I-R : metatarsals. I-J : proximal metatarsal II, BGS 54061b in I : side and J : proximal views. K-M : distally incomplete right metatarsal III, ANSP 9860, in K : medial ; L : anterior and M : proximal views. N-O : right metatarsal III lacking ends, ANSP 9856, in N : anterior and O : proximal views. P-R : left metatarsal II lacking distal end, ANSP 9867, in P : lateral ; Q : proximal and R : anterior views. S-X : pedal phalanx 2 of digit III or IV, BRSMG Ca7501, in S-T : dorsal ; U-V : proximal and W-X : side views (BENTON *et al.*, 2000, figs 14I, J). S, U, W from HUENE (1908a) ; scale bars = 10 mm.

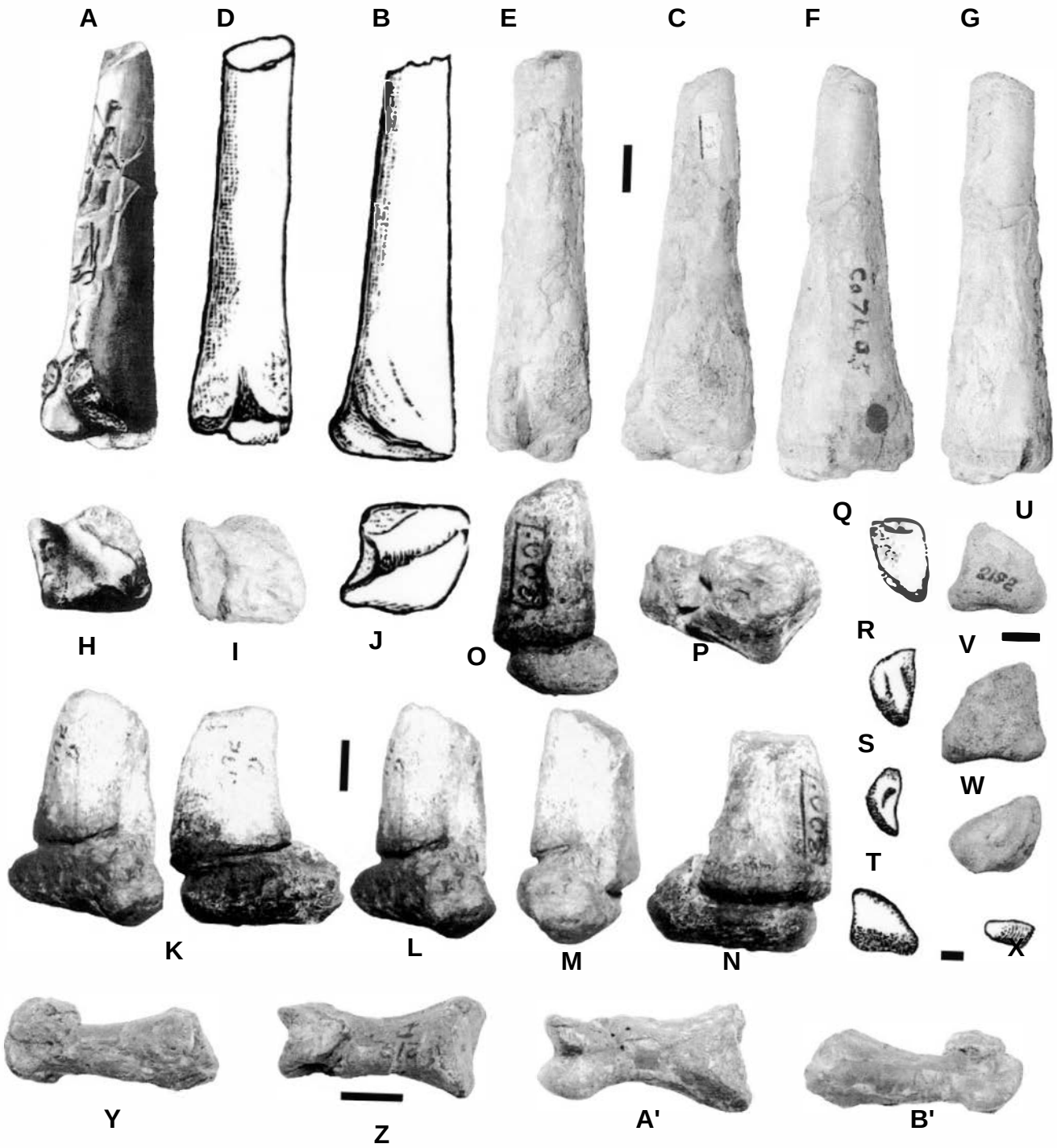



Fig. 30 : Lower hind limb bones of basal sauropodomorphs from Clifton. A-J : distal right tibia BRSMG Ca7495/53 in A-C : anterior ; D-E : lateral ; F : posterior ; G : medial and H-J : distal views (BENTON *et al.*, 2000, figs 18F-J). K-X : YPM 56731 : K-P : distal left tibia with articulated astragalus in K : anterolateral (stereo pair) ; L : anterior ; M : lateral ; N : posterior ; O : medial and P : proximal views (BENTON *et al.*, 2000, figs 18K-O) ; Q-W : supposed left calcaneum figured in Q : dorsal ; R : lateral ; S : medial and T : distal views is actually an incomplete distal articular end of a pedal phalanx shown in U : distal ; V : ventral and W : side views ; X : supposed metatarsal I, ♦, in proximal view. Y-B' : pedal phalanx 1 of digit I, YPM 56723 in Y, B' : side ; Z : dorsal and A' : ventral views. A, H from HUENE (1908a), B, D, J from SEELEY (1895), Q-T, X from HUENE (1914a) ; scale bars = 1 mm (Q-T, X), 5 mm (U-W) or 10 mm.

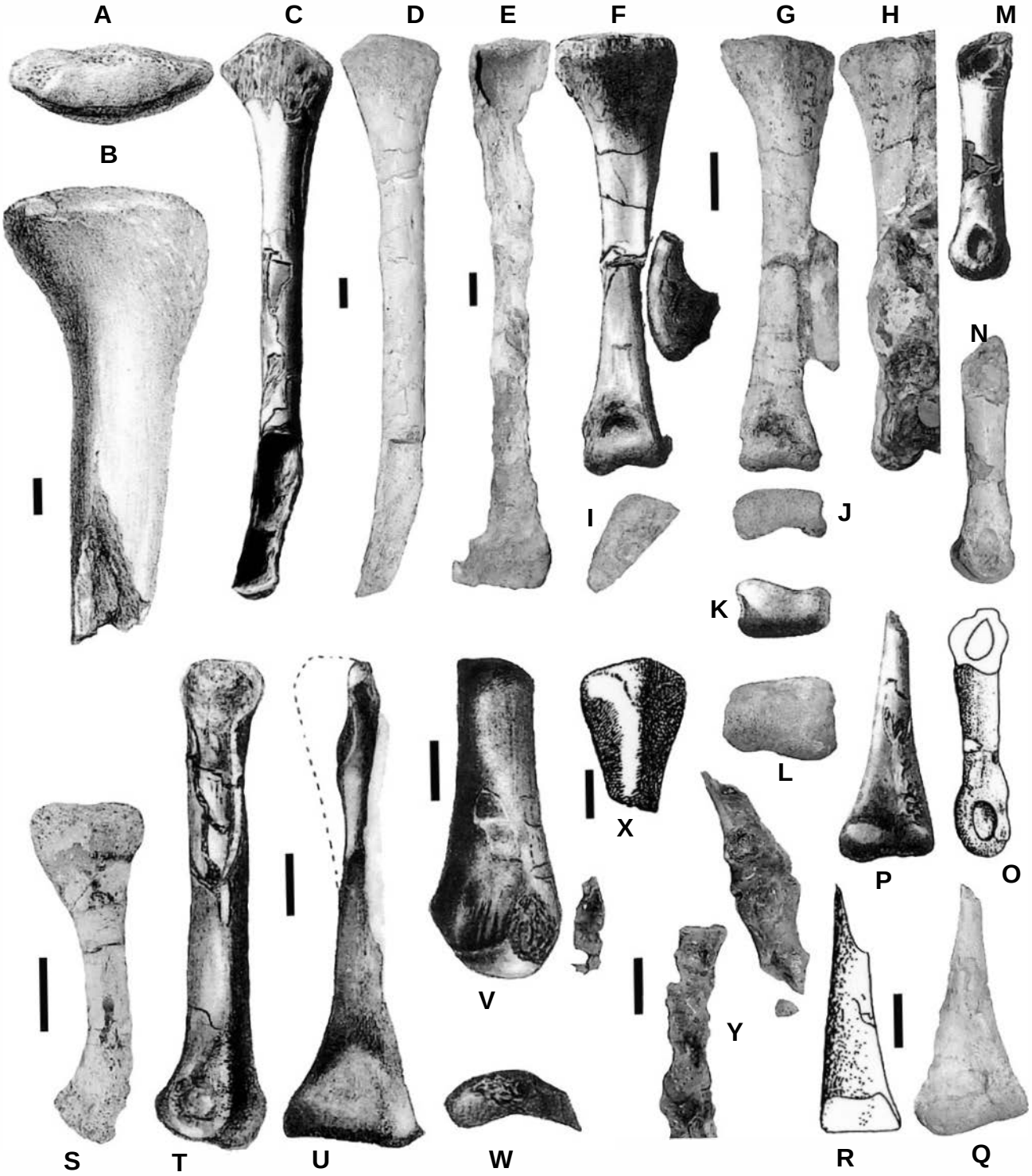



Fig. 31 : Lower hind limb bones of basal sauropodomorphs from Clifton. A-B : proximal part of right fibula BRSMG *-/-♦ in A : proximal and B : lateral views. C-D : right fibula BRSMG Ca7497/47 in lateral view (BENTON *et al.*, 2000, fig. 18P). E : fibula BRSMG Cb4242 in side view. F-K : BRSMG *Ca7451a,b/81, gracile left metatarsal III of HUENE (1908a) (b, and manual ungual phalanx II, a, Figs 20P-R) in F, G : anterior ; H : lateral ; I : proximal and J-K : distal views (K went with P so drawn inverted but should go with F) (BENTON *et al.*, 2000, fig. 18Q). L-R : left metatarsal II, BRSMG Ca7499/55, in L : distal ; M-O : medial and P-R : posterior views. S : metatarsal IV, BRSMG Cb4179, in side view. T-U : robust right metatarsal III of HUENE (1908a), BRSMG Ca7498/83♦, in T : lateral and U : posterior views. V-W : distal right metatarsal IV, BRSMG Ca7500/-♦, in V : anterior and W : distal views (drawings inverted). X : proximal end of metatarsal I, BRSMG Ca7503b/38♦, in ?medial view. Y : articulated incomplete right pes, BMNH R1552, in dorsal view. A, B from RILEY & STUTCHBURY (1840), C, F, K, M, P, T-X from HUENE (1908a), O, R from BENTON *et al.* (2000) ; scale bars = 10 mm.

with J, see below). BENTON *et al.* (2000, p. 82, 105, figs 18R, S) listed this bone as a distal metatarsal but described it as a possible pedal phalanx (Figs 31O, R), commenting on the broad roller-like distal end with a laterally placed ligament pit, but this bone is much too elongate to be a phalanx. There is also a left metatarsal II that is incomplete distally (Figs 29P-R) and the ?radius (Figs 17Q-X) may be another slender metatarsal II (see above). HUENE (1914a, p. 80, fig. 41) mentioned a caudal vertebra and a metatarsal in the BGS and illustrated the former (Figs 11D-I); because these two bones are on the same small piece of matrix, the latter is presumably the proximal part of metatarsal II shown (Figs 29I, J) with both sides gently concave to give an hourglass shaped articular surface (Fig. 29J, also Fig. 29Q).

The slender right metatarsal III of HUENE (1908a; BENTON *et al.*, 2000, fig. 18Q) is complete but it is a left (Figs 31F-J). Judging from the photos of the distal end (Figs 31J-L), K looks more like J than it does L, so HUENE (1908a, pl. 90, fig. 3b) goes with metatarsal III rather than II. HUENE (1908a, p. 213, as II) referred an almost complete and robust right metatarsal III (Figs 31T, U) to *Thecodontosaurus cylindrodon*, the robust morph, and there is another similar but less complete one (Figs 29K-M).

In addition to the possible distal metatarsal IV (Figs 31V, W, see above under I), the metacarpal impression of BENTON *et al.* (2000, p. 82) is probably a longitudinally sectioned metatarsal IV (Fig. 31S).

**Pedal phalanges** (Figs 20M-O, T-V, 29S-X, 30Y-B')

The phalanx figured by HUENE (1908a, p. 207, pl. 80, fig. 3; three phalanges of BENTON *et al.*, 2000, p. 106) as from the manus (text) or pes (caption) is probably a right pedal phalanx 1 of digit I (Figs 30Y-B'). The small phalanx (Figs 29S-X) is probably phalanx 2 of pedal digit III or IV. Compared to manual unguals (Figs 19G, J, L, 20K, L, P-S, X-C'), pedal unguals (Figs 20M-O, T-V) are not as deep proximally, do not have as prominent a flexor process, and are less recurved. The pedal unguals are probably from digits I (Figs 20M, N), II (Fig. 20O), III (Fig. 20V) and IV (Figs 20T, U).

### VI.2. SEXUAL DIMORPHISM IN BASAL SAUROPODOMORPHS

#### VI.2.1. Other than from Clifton

The interpretation of the gracile and robust morphs from Clifton as representing a sexual dimorphism was supported by purported evidence of a sexual dimorphism in the much better represented material of the basal sauropodomorph *Plateosaurus* from the Upper Triassic of Germany. A morphometric analysis by WEISHAMPEL & CHAPMAN (1990) of the femora of *Plateosaurus* from the quarry at Trossingen indicated the presence of one species, *P. engelhardti* (see MOSER, 2003; not *P. longiceps* as suggested by GALTON, 2001b) with two cluster groups that were interpreted as an individual variation, probably sexual (see also GALTON, 1997, 2001a). However, MOSER (2003) noted that the observed variations are not due to biological variability but are the result of diagenetic influences on the morphology. GOW *et al.* (1990) suggested that a Trossingen skull of *Plateosaurus engelhardti* (and also a large one of basal sauropodomorph *Massospondylus carinatus*, Lower Jurassic, southern Africa), with a thicker dorsal orbital rim and a deeper maxilla posteriorly is a male and the other more lightly built skulls are females (see GALTON, 1997, fig. 1). However, these differences in the skull of *Plateosaurus*, which do not correlate with the femoral differences, probably represent individual variations (GALTON, 1997, 2001a; probably also true for *Massospondylus*, not discussed by SUES *et al.*, 2004). From a study of long bone histology of many bones of *Plateosaurus engelhardti*, SANDER & KLIEN (2005, p. 1801; for more details see KLEIN & SANDER, 2007) conclude that "growth stage assignment and skeletochronology ….. indicate that growth rate and final size varied strikingly in individuals of the species *P. engelhardti.*" Sexual dimorphism is rejected "because terminal body size shows a unimodal distribution, albeit with a high standard deviation, and not a bimodal distribution expected for sexual dimorphs."

GALTON (1999) suggested that the two and three vertebrae sacra of the basal sauropodomorph *Sellosaurus gracilis* (Upper Triassic, Germany) represent a sexual dimorphism. This suggestion was subsequently modified to a sexual dimorphism of the three sacral vertebrae sacrum of *S. gracilis* with one sex having a dorsosacral and the other a caudosacral (GALTON, 2001a). However, YATES (2003b) referred individuals with the former sacral type to *Efraasia minor* (HUENE, 1908a) and those with the latter type to *Plateosaurus gracilis* (HUENE, 1908a), whereas MOSER (2003) argued that all these sacra have a caudosacral. However, although most of the specimens referred to *Efraasia minor* have a dorsosacral (see GALTON 2001a; YATES, 2003b), SMNS 12667 (holotype of *Palaeosaurus diagnosticus* HUENE, 1932, type species of *Efraasia* GALTON, 1973) probably had a caudosacral, the rib of which attached to the unoccupied posterior part of the medial shelf of the ilium (GALTON, 2001a; not discussed by YATES, 2003b). The caudosacral of *Plateosaurus* represents a homeotic transformation or "frame shift" to the plesiomorphic condition (GALTON & UPCHURCH, 2000; GALTON, 2001a) and this is probably also the case for SMNS 12667. However, given the similarities and the lack of differences from the other specimens of *Efraasia minor* from Pfaffenhofen and Ochsenbach (see YATES, 2003b; also HUENE 1908a, 1932), the sacral difference of SMNS 12667 probably represents an individual variation and the 1:6 ratio is not indicative of a sexual dimorphism (see GALTON, 2001a for figures).

### VI.2.2. Cited evidence for dimorphism in Clifton bones

**Introduction**

OWEN (1842a) referred most of the appendicular bones from Durdham Down to *Palaeosaurus platyodon* (but no characters given), as did SEELEY (1895) who noted similarities to those of *Zanclodon quenstedti* (Upper Triassic, Germany; now *Plateosaurus*, GALTON, 2001b), a species that was incorrectly assumed to have carniverous teeth as in the earlier type species *Z. laevis* (Middle Triassic, Germany; see GALTON, 2001b). Apart from two phytosaur humeri (Figs 37A-I), HUENE (1908a) divided the bones into two different species. He noted that *Thecodontosaurus*-like teeth were associated with the more lightly built *Plateosaurus poligniensis* from France (see HUENE, 1908a; GALTON, 1998b) whereas teeth of a carnivorous form were associated with the more heavily built *Plateosaurus reingeri* from Germany (see HUENE, 1908a; GALTON, 2001b). Based on this comparison, the more common and more lightly built bones from Durdham Down were referred to *Thecodontosaurus antiquus* (including YPM 2195, HUENE, 1914a) whereas the less common but more heavily built ones were referred to *T. cylindrodon* (used instead of *Palaeosaurus cylindrodon*, *Palaeosaurus* being preoccupied, but HUENE did not want to erect a new genus; *Thecodontosaurus* sp. of WEISHAMPEL *et al.*, 1990, p. 67; WEISHAMPEL *et al*., 2004, p. 521). However, the teeth of carnivorous form were probably shed by a predatory or scavenging theropod and were removed from the holotype of *Plateosaurus reinigeri* by GALTON (1985e); this taxon and *P. poligniensis* are *nomina dubia* but the bones are probably referable to *Plateosaurus engelhardti* (GALTON, 2001b; MOSER, 2003).

GALTON (1973) included the referred bones of *Thecodontosaurus cylindrodon* in *T. antiquus*. Unfortunately, only a few of the bones involved remain in the BCM collection. The discussions of GALTON (1997) and BENTON *et al*. (2000) of the characters of these bones, which include the scapula, humerus, femur, tibia, fibula and metatarsal II, were uncritically based on the summary comparisons of HUENE (1908a, p. 214-215), who listed most of the specimens he referred to each taxon. BENTON *et al.* (2000) noted that the possibility of two species cannot be ruled out but, in the absence of any distinguishing characters other than relative proportions, all the material from Clifton was referred to *T. antiquus*. They ruled out allometric variation (growth-related shape change) because the gracile and robust forms are essentially of the same size (*contra* BENTON & SPENCER, 1995 with *T. cylindrodon* as adult individuals of *T. antiquus*), as well as individual variation, because there were two morphs, not a continuum of forms, which left sexual dimorphism as an explanation for the differences. They noted that the only evidence for two species, rather than a sexual dimorphism, is that robust individuals appear to be much rarer than gracile ones: nine elements to 44 from the data in HUENE (1908a, p. 214-215). GALTON (1997) suggested that the robust morphs might represent males that are usually more robust and larger in living species of amniotes (reptiles, birds, especially mammals). GALTON (1999, 2001a) subsequently noted that, based on anatomical evidence from the theropod dinosaurs *Syntarsus rhodesiensis* (Lower Jurassic, southern Africa; RAATH, 1977, 1990) and *Tyranosaurus rex* (Upper Cretaceous, western USA; CARPENTER, 1990; LARSON, 1994) and histological evidence from *Syntarsus rhodesiensis* (RAATH, 1977; CHINSAMY, 1990), the robust morph probably represents the female as in many living amniotes (especially birds, see GALTON, 1999 for references).

As noted earlier in this section, there is no convincing evidence for sexual dimorphism in the abundant, well preserved and often articulated specimens of *Plateosaurus engelhardti* from several mass burial sites in Germany (Ellingen, MOSER, 2003; Halberstadt, JAEKEL, 1912-13; HUENE, 1932; Trossingen, HUENE, 1908a, 1926, 1932; GALTON, 2001b; MOSER, 2003) and Switzerland (Frick, GALTON, 1986b; SANDER, 1992). The detailed histological work on specimens from Frick and Trossingen cited above is especially important in this regard (SANDER & KLEIN, 2005; KLEIN & SANDER, 2007). There is no evidence for dimorphism in any other species of basal sauropodomorph and, in addition, PADIAN *et al*. (2005) have questioned the evidence for nearly all examples of sexual dimorphism in dinosaurs, including the gracile and robust morphs in several much better represented saurischians. A study of *Alligator* and *Rhea* showed that the bones giving the most consistent morphological and morphometric determination of sexual dimorphism were those adjacent to the cloaca, viz., the posterior edge of the ischium and the chevrons (POWELL, 2000), neither of which have been cited for *Thecodontosaurus*. Consequently, the evidence cited by HUENE (1908a) for gracile and robust morphs of certain appendicular bones from Clifton needs to be critically examined bone by bone. It should be noted that, in the absence of two morphs for a given bone (as with the radius, ulna, metacarpals, pubis, phalanges), HUENE (1908a, p. 215) referred them to *Thecodontosaurus antiquus*, the more common slender morph, even though no supporting evidence was provided. In addition, a robust humerus (Figs 16H-J; YPM 56724) is in the wrong list and a robust metatarsal (Figs 31T, U; BRSMG Ca7498/83♦) is not included. Consequently, the ratio of robust to gracile appendicular bones is 11 to 34 from the data in HUENE (1908a) rather than nine to 44 as cited by BENTON *et al*. (2000). In the captions to the plates, two caudal vertebrae (YPM 2193, Figs 11J-M, HUENE, 1908a, pl. 77, fig. 4; BRSMG Ca7457f/63♦, HUENE, 1908a, pl. 84, V.c.) were referred to the robust *T. cylindrodon* and the rest to *T. antiquus*, but no differences were given.

**Scapula** (Figs 14A-C, E-H)

HUENE (1908a) noted that the robust form of scapula from Clifton, represented by one almost complete blade (Figs

14E, F), is larger, stouter, less curved and its narrowest part is relatively more distal in position compared to those of the more common gracile form (Figs 14A-C). However, the variations within these scapulae, which are all basal Sauropodomorpha indet, appear to be comparable to those resulting from preservational differences and size and individual variations in a taphonomic population of *Plateosaurus engelhardti* from a single quarry at Trossingen (SMNS, GPIT; HUENE, 1908a, 1926, 1932). HUENE (1908a) also noted that, compared to BRSMG Ca7478/92♦ (Fig.14C, gracile), the other scapulae (all gracile; Figs 14A, B, G, H) seemed to widen out more at the coracoidal end. However, this is based on an impression of the medial surface and, without the specimen, it is not possible to tell if this is a valid difference.

**Humerus** (Figs 15Q-U, 16A-F H-J)
The humerus referred by SEELEY (1895) to *Thecodontosaurus antiquus* became the holotype of the crurotarsal phytosaur *Rileya bristolensis* HUENE, 1902 (Figs 37A-F). However, SEELEY (1895) also stated that the remaining humeri, those he referred to *Palaeosaurus*, appear to represent more than one species, but he gave no further details. HUENE (1908a, p. 205, 215, list 215) noted that the robust form of humerus (Figs 16A, B, BRSMG Ca7464/118♦ as *T. cylindrodon*; Figs 16H-J, YPM 56724 as robust in text and illustration, gracile in table in HUENE, 1908a, as *T. antiquus* in HUENE, 1914a, fig. 48; BENTON *et al.*, 2000, figs 11D, E) has a relatively broader proximal part with the deltopectoral crest reaching further down than in the other humeri; in gracile forms [Figs 16C-F, H-J; BRSMG Ca7477/37♦ (Figs 16C, D) gracile in figure and table but robust in text, HUENE, 1908a] the deltopectoral crest projects less anteriorly and extends less distally along the relatively thicker shaft. The massiveness of the deltopectoral crest of the robust humerus (Figs 16A, B) is not a function of size because it is about the same size as BRSMG Ca7477/37♦ (Figs 16C, D) and smaller than BRSMG *Ca7453/66♦ (Figs 16E, F) (SEELEY, 1895).

**Ilium** (Figs 21E, F, 22C, D, F G)
HUENE (1908a, p. 215) listed the ilium BRSMG Ca7457/63♦ as *Thecodontosaurus cylindrodon* (so robust morph) but he did not indicate which of the three ilia on this block was the robust one and no differences from the ilia of *T. antiquus* were given. However, in the caption, HUENE (1908a, pl. 84) referred "Il. Sin. Innen" (Figs 21F, 22D) to *T. cylindrodon* but, as discussed above, this is a poorly preserved right ilium in lateral view with impressions of the medial surface (Fig. 22C), as originally identified by SEELEY (1895).

**Femur** (Figs 25A-C, F-H, K, Q, 26A-H, J-T, 27)
Based on photos (now in BCM Archives, Geology file No. 51) sent by the YPM in 1901, HUENE (1908a, p. 211, 215) cited three small gracile femora and one robust femur. The gracile distal ends are YPM 2195f (right, photo cf. Fig. 25C; Figs 25A-C), YPM 2195g (slightly smaller left, photo Fig. 25E; Figs 25D-F) and YPM 56727 (Fig. 25F); the robust one is YPM 56728 (very poorly preserved).
HUENE (1908a) noted that robust femora (Figs 25, S, 26A-H, O-T) have a somewhat smaller anterior (=lesser) trochanter, the lengthwise axis of the fourth trochanter is slightly bent (versus a straight ridge) so it is larger and stronger, the distal part of the shaft is straighter, and the distal end is distinctly broader transversely compared to gracile femora (Figs 25A-I, L, 26J-N, 27). He did not figure the lesser trochanter for a robust femur or the fourth trochanter for a gracile femur but the complete fourth trochanters appear to be comparably large (Figs 26S, T cf. Figs 25H, I). One of the two figured robust femora does appear to have a straighter distal shaft (Figs 26S, T) but, because the longitudinal curve of the anterior edge is partly concave rather than being continuously convex as in other femora of basal sauropodomorphs, this is the result of poor repair of the breaks of the shaft distal to the fourth trochanter. The curvature of the distal shaft of the most complete robust femur (Fig. 26B) is comparable to that of the best preserved gracile femur (Fig. 25H). The transverse broadness of the distal end of the robust femur (Fig. 26O) was probably the result of anteroposterior compression. The differences in size, individual variation, completeness and preservational factors such as the plane of crushing are sufficient to account for the differences mentioned by HUENE (1908a) (cf. the differences in femora of *Plateosaurus engelhardti* from Trossingen, HUENE, 1908a, 1926, 1932; WEISHAMPEL & CHAPMAN, 1990; MOSER, 2003; SANDER & KLEIN, 2005; KLEIN & SANDER, 2007).

**Tibia** (Figs 28A-O)
HUENE (1908a) noted that the robust tibia (Fig. 28C) has a somewhat stronger shaft (cf. slender, Figs 28A, B) but the proximal end is transversely narrower and the condyles are shaped differently compared to the other tibiae (Figs 28D-O). No proximal view of this tibia was given but SEELEY (1895, p. 154) noted that the cnemial crest is "defined by a small superior cavity, which is continued downward by the fibular groove on the external aspect." However, this surface is damaged (?one reason proximal end narrower) and the transverse narrowing could be the result of compression, as could the supposedly more massive shaft. Although HUENE and SEELEY agree that the tibia was exposed in lateral view, it looks more like the medial view; HUENE (1908a, pl. 89, fig. 3) also misidentified a right tibia (YPM 56730) in medial view as a left in lateral view (cf. real lateral view, Fig. 28N).

**Fibula** (Figs 8P, Q, 31C, D)
Based on its association with the robust tibia (Fig. 28C), HUENE (1908a, p. 216, pl. 84, Fib) identified a robust

proximal fibula on block BRSMG Ca7457/63♦, but he cited no anatomical differences from the gracile fibulae BRSMG Ca7496/5 (distal end of dorsal rib, Figs 8P, Q) and BRSMG Ca7497/47 (Figs 31C, D). However, there were three ilia on this block (Figs 21E-G), so at least two individuals are represented, and the obliquely exposed bone was probably a proximal metatarsal.

**Metatarsal III** (Figs 31F-K, T, U)
HUENE (1908a) correctly recognized a gracile metatarsal III (Figs 31F-K; BENTON *et al.*, 2000, fig. 18Q) and a robust one (Figs 31T, U; described by HUENE, 1908a, p. 213 as metatarsal II of *Thecodontosaurus cylindrodon*).

From the above discussion of the characters cited by HUENE (1908a) for the unassociated appendicular bones from Clifton, it is apparent that gracile and robust morphs are not recognizable for the scapula, ilium, femur, tibia, and fibula but are for the humerus and metatarsal III.

## VI.3. CHARACTERS AND IDENTIFICATIONS

### VI.3.1 Introduction

Most of the extant recognizable basal sauropodomorph dinosaur bones from Durdham Down at Clifton in the ANSP, BMNH, BRSMG and YPM are listed by anatomical region in BENTON *et al.* (2000, p. 82; same list in GLUT, 2001, p. 545) as the hypodigm of *Thecodontosaurus antiquus* MORRIS, 1843. However, because the neotype is an isolated dentary and there are three different forms of basal sauropodomorph humerus from Clifton (GALTON, 2005b; GALTON *et al.*, 2007), with one as part of the holotype of *Asylosaurus yalensis* n. gen. et sp. (see Systematic section), material from Clifton that can be confidently referred to *Thecodontosaurus antiquus* RILEY & STUTCHBURY *vide* OWEN, 1842a from Clifton is restricted to the type dentaries (GALTON, 2005b) and, tentatively following past practice, the slender humeral morph (GALTON *et al.*, 2007). The few bones with derived characters that match those of the holotype (YPM 2195) of *Asylosaurus yalensis* are referred to that taxon. The remaining unassociated sauropodomorph bones from Clifton fall into one of three groupings as either very basal Sauropodomorpha indet, Anchisauria indet (Anchisauria *sensu* UPCHURCH *et al.* 2007) or basal Sauropodomorpha indet (see Systematic section for details, indicated in Appendices 3-7 as [A], [B] or [C]).

### VI.3.2. Dentaries of *Thecodontosaurus antiquus* RILEY & STUTCHBURY *vide* OWEN, 1842 (Figs 4A-T)

The type dentaries shows the following synapomorphies of, firstly, the Sauropodomorpha (Fig. 3A), viz., the anterior end is deflected ventrally (Figs 4J, K, M), the tooth crowns overlap in lateral view (Figs 4G-K, P-S), and the tooth serrations are oriented at 45° apically to the crown long axis (Figs 4D-F, N-S) and, secondly, of the Prosauropoda, viz., there is a ridge on the lateral surface of the dentary (Figs 4A, G-J) and the first tooth is inset posteriorly (Figs 4A, G-L); the teeth are plesiomorphic in all being recurved in lateral view (Figs 4A, B, D-I, N-T), whereas at node 3 (Fig. 3A) the middle and posterior teeth become lanceolate or unrecurved [alternatively this character is a synapomorphy for Sauropodomorpha that reverses in *Thecodontosaurus* (GALTON & UPCHURCH, 2004)]. A short and deep dentary, with a maximum dorsoventral depth that is greater than 20% of its length, is listed by YATES (2003a) as a derived character for *Thecodontosaurus antiquus* (Figs 4G-K) and *Pantydraco* (as *T. caducus*, Fig. 4V), with the dentary less than 40% of total mandibular length in the latter in which the mandible can be reconstructed. However, a short and deep dentary also occurs in *Saturnalia tupiniquim* LANGER *et al.*, 1999 (Upper Triassic, Brazil). *Thecodontosaurus antiquus* is a very basal sauropodomorph but, with three humeral morphs (gracile, robust, *Asylosaurus yalensis*), postcranial bones from Clifton cannot be identified with certainity as *Thecodontosaurus antiquus* (GALTON, 2005b; GALTON *et al.*, 2007). However, the slender morph has long been referred to *T. antiquus.* A large number of bones (in BRSUG) of a basal sauropodomorph have been found at the Tytherington Quarry, Avon just north of Bristol (see WHITESIDE, 1986; BENTON & SPENCER, 1995; BENTON *et al.*, 2005). A small sample of the bones was described by WHITESIDE (1983) and only one taxon of basal sauropodomorph is represented, one with the slender humeral morph, and the character list for *T. antiquus* in the cladistic analyses of YATES (2003a, 2004, 2006, 2007; YATES & KITCHING, 2003) is mostly based on bones from this quarry (GALTON *et al*, 2007). Consequently, *T. antiquus* RILEY & STUTCHBURY *vide* OWEN, 1842a is provisionally accepted as a valid taxon, the diagnosis of which awaits description of the referred bones from Tytherington Quarry by YATES & BENTON (in prep.).

### VI.3.3. *Asylosaurus yalensis* n. gen. et sp.

Based on the delicate form and structure of the distal expansion, the scapula of YPM 2195 (Figs 13B, E, H) was referred by HUENE (1914a) to *Thecodontosaurus antiquus*, the gracile form. He discussed and figured the associated forearm and manus but, rather surprisingly, the complete humerus was not even mentioned. The rounded apex of the deltopectoral crest of this humerus is proximally placed, with the apex at about 25% (measured perpendicular to long axis of humerus) of humeral length (Figs 13A, I, J, 15A-F), as against 40% in *Pantydraco caducus* (Fig. 16L). In both the crest is anteroposteriorly low in lateral view (Figs 13A, I, J, 15A, B, 16L) but in YPM 2195 it forms a symmetrical triangle, with the

edges on either side of the gently rounded apex being equal in length. In *Pantydraco caducus* (crest low, Fig. 16L) and in other basal sauropodomorphs (crest high), including the gracile and robust morphs from Clifton, the deltopectoral crest is sub-quadrangular or hatchet shaped with an angular apex (at 40% and +50% of humeral length) followed by a short and steeply inclined distal edge (Figs 15Q, 16A-F, H, I). A derived character for YPM 2195 (and the other Clifton humeri) compared to *Pantydraco caducus* is the strongly projecting medial tubercle of the proximal humerus (posteromedial corner of bone, Figs 13A, I-K, 15A-F; shown too small for YPM 2195 in Figs 13I, K cf. Fig. 15D) compared to the plesiomorphic small tubercle in *Pantydraco caducus* (YATES, 2003a; GALTON *et al*., 2007).

At node 3 (*Saturnalia*, Fig. 3A) the deltopectoral crest terminates at or below the mid-length of the humerus [Reversed at node 6 (Anchisauridae) and "*Gyposaurus*" *sinensis*, GALTON & UPCHURCH, 2004]. In the three most complete gracile Clifton humeri the apex of the deltopectoral crest is at about 40%, as in *Pantydraco caducus*, but the crest extends further anteriorly (Figs 15G, 16C-F). In the two robust Clifton humeri, the anterior extensions are even more pronounced and the complete crest, and even the apex, clearly extended beyond 50% of humeral length (Figs 15S, T, 16A, B).

Based on the form of the deltopectoral crest (anteroposteriorly low, symmetrical outline, proximal position of rounded apex at 25% of humeral length) and the large size of the medial tubercle adjacent to the head, the humerus shows that YPM 2195 represents a new taxon, *Asylosaurus yalensis* n. gen. et sp., distinct from *Pantydraco caducus* (with low but asymmetrical crest with apex at 40%, small medial tubercle). The deltopectoral crest is hatchet shaped, projecting well anteriorly with the apex at 40% or +50% of length, in most other basal Sauropodomorphs.

The transverse width of distal carpal I is less than the width of metacarpal I (Figs 19A, D, F) and there are no ossified proximal carpals, plesiomorphic characters for basal Sauropodomorpha. As noted by GALTON (1973), metacarpal I (and its proximal phalanx) are transversely slender (Figs 13R, S, 19A-C, H), a plesiomorphic character for basal sauropodomorphs that is also present in *Efraasia*, and it is not short and robust, a derived character of node 4 (Fig. 3A; GALTON & UPCHURCH, 2004). Metacarpals II-IV are also slender (Figs 19A-E), the plesiomorphic condition as in *Efraasia* and *Anchisaurus*, rather than broad as in other basal sauropodomorphs. Phalanx 1 of digit I has a proximal "heel" (Fig. 19G) and the long-axes of its proximal and distal articular surface are twisted at about 45° to each other (Figs 19A-C, H), synapomorphies of basal sauropodomorphs. It is also plesiomorphic for basal sauropodomorphs in being narrow in dorsal view (Fig. 19H), so its transverse width matches that of metacarpal I as in *Efraasia*, rather than being broad, a derived character of node 4 (Fig. 3A). The structure of the manus of *Asylosaurus* is that of a very basal Sauropodomorpha.

Unfortunately, the phalanges of digits IV and V are rarely completely preserved in the manus of basal sauropodomorphs (see GALTON & CLUVER, 1976, fig. 7). The phalangeal formula for *Asylosaurus yalensis* at 2-3-4-2-?1 (Fig. 13A) is derived in showing lateral reduction compared to the condition in *Efraasia*, *Massospondylus* and *Lufengosaurus* at 2-3-4-3-2 and especially *Plateosaurus* at 2-3-4-3-3 or even 2-3-4-4-2 (GALTON & CLUVER, 1976, fig. 7). For the phalangeal formula, BENTON & STORRS (in BENTON *et al.*, 2000, p. 107, character 30) gave a plesiomorphic state "based on outgroup comparisons with a wider group of dinosaurs and dinosauromorphs", but further on noted that "*Scleromochlus* and *Herrerasaurus* are included as postulated outgroups of the crown-group clade" for the plesiomorphic state of 2-3-4-1/2-0/1 (0) as against 2-2-2-2-1 (1), the derived state (BENTON *et al.*, 2000, p. 107). However, it is coded as character state uncertain for *Scleromochlus* (BENTON, 1999) and it ignores the lateral reduction that occurred within basal sauropodomorphs (*Asylosaurus*, *Massospondylus*, *Lufengosaurus*), comparable but less extreme to that which occurred in bipedal theropods (RAUHUT, 2003, p. 97), as distinct from the distal reduction that affected digits II-V in quadrupedal sauropods (2-2-2-2-1).

### VI.3.4. Braincase (Figs 5A-D)

Based on overall similarities to the braincases of *Pantydraco* (WARRENER, 1983; KERMACK, 1984), *Efraasia*, *Anchisaurus*, and *Plateosaurus*, YPM 2192 (Figs 5A-D) is referred to the basal Sauropodomorpha, even though braincase characters have not been utilized to diagnose this group. Node 4 (Fig. 3A) is characterized by a separate opening for the vena cerebralis media (above foramen for cranial nerve V; separate opening absent in YPM 2192, the plesiomorphic condition, Figs 5A, C). The derived character "elongate and slender basipterygoid processes" is listed by YATES (2003a; GALTON, 1973; BENTON *et al.*, 2000) for this braincase (Figs 5A-D) and that of *Pantydraco* (Fig. 5E; KERMACK, 1984, figs 6-9; also in *Efraasia minor*, GALTON & BAKKER, 1985, fig. 4A). However, this braincase is not referable to *Pantydraco* (KERMACK & GALTON, in prep.). It is very basal Sauropodomorpha and comparisons with material from Tytherington Quarry may show that it is referable to *Thecodontosaurus antiquus*.

### VI.3.5. Vertebrae and ribs

**Cervical vertebrae** (Figs 7B-R)

YATES (2001, 2003a) characterized the epipophyses of anterior cervicals (C3-5), which form flat plates that

overhang the posterior margins of the postzygaopohyseal facets but do not form raised ridges on the dorsal surface of the postzygapophysis, as an autapomorphy for *Thecodontosaurus*. This is true for the holotype of *Pantydraco* (Fig. 7A) but the only cervicals from Clifton with this region preserved, C4 or 5 (Figs 7P-T) and C6 (Figs 7G, H, J), have plesiomorphic epipophyses that form a raised ridge atop the postzygapophysis. There is no trace of an autapomorphic pneumatic fossa close to the neurocentral suture on any of the Clifton cervicals (Figs 7H, J, O) that is comparable to those on C6-8 of *Pantydraco* (WEDEL, 2007, fig. 10; pseudopleurocoel YATES, 2003a, fig. 12).

YATES (2003a) noted that *Pantydraco* (as *Thecodontosaurus caducus*) also differs from all other basal sauropodomorphs, with the exception of *Riojasaurus incertus*, in not having mid-cervical centra that are at least three times as long as wide (Fig. 7A). The character "elongate cervical centra" is a derived state that occurs in the Anchisauridae (convergent Eusauropoda and at Node 6, the Plateosauria, Fig. 3A, reversed in *"Gyposaurus" sinensis*; alternatively a synapomorphy at node 4 convergently acquired in eusauropods and reversed in *Riojasaurus* and *"G." sinensis*; GALTON & UPCHURCH, 2004). The centra of cervicals from Clifton have the derived state with this ratio more than 3.0 (Figs 7G-O), so they cannot be referred to *Pantydraco*. The anteriorly incomplete centrum of C4 or 5 (Fig. 7D, YPM 2195a), which is tentatively included in the holotype individual of *Asylosaurus yalensis*, was probably proportionally elongate as in most other basal sauropodomorphs. If this referral is correct, then the other cervicals with elongate centra from Clifton (Figs 7G-O) could be from *Asylosaurus yalensis* or, alternatively, they could be Anchisauria indet.

**Dorsal vertebrae and sacrum** (Figs 9, 10)

In anterior dorsals of basal sauropodomorphs the centra are elongate (length: height ratio greater than 1.0) and there is no prezygapophyseal lamina. On these characters, and the overall similarity of form to those of *Efraasia*, *Anchisaurus*, *Massospondylus*, and *Plateosaurus*, the isolated dorsal vertebrae (Figs 9, 10A-F) are regarded as basal Sauropodomorpha indet.

RILEY & STUTCHBURY (1837a, p. 94) reconstructed a series of six articulated dorsal vertebrae with amphicoelous centra that were hourglass-shaped in longitudinal section because of the extensive excavation dorsally by the neural canal. William BUCKLAND (in RILEY & STUTCHBURY, 1836c, p. 352) "was particularily struck by the singular structure of these vertebrae, as indicating in the animal a nervous power of the most extraordinary character." In the median section of an incomplete dorsal vertebra (Fig. 10D), the neural canal is preserved as a natural cast and it is deepest at mid-length where the centrum is extensively excavated. RILEY & STUTCHBURY (1840, p. 353; also 1837a, p. 92 as one third) noted that "the vertical diameter of the canal would, in the middle of each vertebra, be at least one-half more than at either of its points of junction with the next vertebrae." They also figured a posterior dorsal in transverse section with a keyhole-shaped neural canal, with the centrum excavated by its ventral part (Figs 10B, C). A similar situation is visible in some other incomplete posterior dorsals (Figs 9M, O, Y, 10A) and in sacrals 1 and 2 (Figs 10G-I). OWEN (1842a, c) commented on the peculiar ventricose excavations of the dorsal centra so the depth at the middle was greater than at the ends. The sacral centra are only slightly excavated in the sauropod dinosaur *Dicraeosaurus* (Upper Jurassic, Tanzania), in which most of the sacral enlargement of the spinal canal is bordered by the neural arch (JANENSCH, 1939, fig. 2), as is also the case in stegosaurian ornithischian dinosaurs (LULL, 1910, 1917), but the centra are more extensively excavated in the middle sacrals (S2-5) of the ornithopod ornithischian dinosaur *Dryosaurus* (JANENSCH, 1939, fig. 6b). As in sauropods such as *Dicraeosaurus*, in which the sacrum includes five rather than three vertebrae as in basal sauropodomorphs, the central excavation (Fig. 10D) was presumably part of the enlargement for the dorsosacral plexus so it probably only affected the last one or two dorsal vertebrae, not six as illustrated by RILEY & STUTCHBURY (1837a, p. 94). As first suggested for stegosaurian dinosaurs by LULL (1910, 1917), the enlarged dorsosacral plexus was for the innervation of the large hindlimbs and tail (see GIFFIN, 1991 for full discussion of the so called "sacral brain" of dinosaurs). This region is rarely visible in centra of basal sauropodomorphs but the keyhole shape of the neural canal in transverse section, with excavation of the centrum in posterior dorsal and anterior sacral vertebrae, may be an autapomorphy for these Clifton vertebrae.

The form of S1 and S2 is similar to those of *Saturnalia*, *Efraasia* and *Plateosaurus*, especially in dorsal view (Figs 10J, K, Q, R). In particular, there is a strong constriction between the sacral rib and transverse process of the first primordial sacral vertebra, a plesiomorphy for basal Sauropodomorpha (YATES & KITCHING, 2003). The third vertebra as a caudosacral is plesiomorphic for basal Sauropodomorpha but the derived state, with the third vertebra as a dorsosacral, occurred several times, as did reversals to the plesiomorphic condition (including *Plateosaurus*) (GALTON & UPCHURCH, 2000, GALTON, 2001a), so the Clifton sacral vertebrae are basal Sauropodomorpha indet. It should be noted that the incomplete sacrum with three vertebrae described as *Thecodontosaurus* from the Middle Triassic of the English Midlands by HUXLEY (1870) and HUENE (1908a), the presumed BCM specimen that SEELEY (1895, p. 147) could not locate, is actually in the Warwickshire Museum in Warwick. The third vertebra is a dorsosacral and it is referred to the rauisuchian crurotarsal archosaur *Bromsgroveia walkeri* GALTON, 1985c (GALTON & WALKER, 1996a; BENTON & GOWER, 1997).

**Caudal vertebrae** (Figs 11, 12A-Q)
YATES (2003a) characterized the caudals of *Thecodontosaurus* (as *T. antiquus* and *T. caducus*) by two autapomorphies. Firstly, by the shortness (less than 30 % of length of neural arch) and extreme posterior position of the neural spines (versus more than 30 % with posterior margin anterior to the postzygapophyses) on proximal and mid-caudals, so they fill the U-shaped interpostzygapophyseal space (also in *Efraasia*) that is present in most dinosaurs. Secondly, by the reduction (proximal quarter of tail) or loss of the ventral furrowing of the centra (versus prominent furrowing for at least proximal two thirds of tail). However, it should be noted that at least the proximal quarter of the tail of *Pantydraco* is missing (Fig. 2D; YATES, 2003a). The neural spine is short and posteriorly situated in Clifton proximal caudals (Figs 11A, E, N) but, where this region is visible, a U-shaped interpostzygapophyseal space is present and it is not obliterated in any caudal vertebra from Clifton (*, Figs 11B, H, I; BRSMG Ca7475a/22); this is also true for *Pantydraco caducus* (KERMACK & GALTON, in prep.) and *Efraasia* (SMNS 12667-9, 12684). The degree of ventral furrowing of proximal (Figs 11K, O, P) and mid-caudal centra (Fig. 11V) from Clifton appears to be reduced and in a proximal caudal it is lost completely, so it is transversely convex with a median ridge (Fig. 11G); the latter may be an autapomorphy for this vertebra. The caudal vertebrae from Clifton are probably all very basal Sauropodomorpha indet.
In mid-caudals the anterior edge of the transverse process continues as a sharp ridge across the side of the neural arch to the middle of the notch bordered by the prezygapophysis (Figs 11R, T, U, 12A); this ridge is also visible on some proximal caudals (Figs 11E, Q; region abraded YPM 2195b, c, Figs 11A, C) and may be an autapomorphic character for Clifton caudals; it is not present on mid-caudals of *Pantydraco caducus* (WARRENER, 1983).

**VI.3.6. Pectoral girdle** (Figs 14A-H)
Based on their similarity to those of *Asylosaurus* and other basal sauropodomorphs, the scapular-coracoids are regarded as basal Sauropodomorpha indet.

**VI.3.7. Fore limb**
**Humerus** (Figs 15Q-X, 16A-K)
The deltopectoral crest is low and gently rounded in lateral view with a proximally situated apex in BMNH 1542 (Figs 15O, P) that is referred to *Asylosaurus yalensis*. The other isolated humeri from Clifton are more derived because the deltopectoral crest is hatchet shaped, being anteroposteriorly high and asymmetrical in side view with the apex at 40 % of humeral length (measured perpendicular to humeral length) in gracile humeri (Figs 16A-F) and +50 % in a robust one (Figs 16A, B). Previously unillustrated humeri from Clifton include a gracile (Figs 15Q, R; length 130 mm) and a robust one (Figs 15S-U; preserved length 157 mm; YPM 56724 probably also robust, Figs 16H-J, as is BRSMG Cb4189/78, Fig. 15V). The difference between the two humeral morphs could represent a sexual dimorphism in a taxon more derived than *Pantydraco caducus* and *Asylosaurus yalensis* but, given the lack of evidence for dimorphism in any other species of basal sauropodomorph, including the very well represented *Plateosaurus engelhardti* (see above, SANDER & KLEIN, 2005; KLEIN & SANDER, 2007), this possibility is considered very unlikely. Following past practice, the slender morph of the humerus is tentatively referred to *Thecodontosaurus antiquus*. The robust humeri are Anchisauria indet *sensu* UPCHURCH *et al.* (2007). The distal humeri are transversely broad (Figs 15W, X), as in *Asylosaurus* (Fig. 15C, D; shown too narrow Fig. 13K), *Efraasia* and *Anchisaurus*, so these are basal Sauropodomorpha.

**Fore arm** (Figs 17K-Q, 18I-O)
The isolated distal radii are similar to those of other basal sauropodomorphs (Figs 18I-O). The beaked sharp projection distally on the dorsal ulnar corner may be a plesiomorphic character for the group as it also occurs in *Efraasia*, *Anchisaurus*, *Massospondylus* and *Plateosaurus*. A complete ulna (Figs 17N-Q) and a proximal end (Figs 17K-M) are probably basal sauropodomorph because they resemble those of *Asylosaurus* (Figs 17A-G), *Efraasia* and *Plateosaurus*.

**Metacarpals and phalanges** (Figs 18P-B', 20)
Slender metacarpals I (Figs 18Q, R) and IV (Fig. 18P) resemble those of *Asylosaurus* (Figs 19A-E) and *Efraasia* so they are very basal Sauropodomorpha indet. The remaining metacarpals (Figs 18S-B') are more robust so they are Anchisauria indet.
Phalanx 1 of digit I is transversely narrow with a prominent waist and flexor heel (Figs 20F-J), as in *Asylosaurus yalensis* (Figs 19A-C, G, H), so it is tentatively referred to this taxon. The isolated ungual phalanges of the manus (Figs 20K, L, P-S, W-C') are more robust than those of digits I and II of *Asylosaurus yalensis* (Figs 19G, J, L) and *Efraasia*, so they are regarded as Anchisauria indet.

**VI.3.8. Pelvic girdle**
**Ilium** (Figs 21A-G, 22, 23)
BENTON *et al.* (2000) noted that the posterior blade in several ilia of *Thecodontosaurus antiquus* has a distinctly squared termination (Fig. 21C), a supposed autapomorphy compared to the usual rounded termination in other basal sauropodomorphs. However, YATES, (2003a) noted that this is a plesiomorphic character as it is also present in the basal saurischian *Guiabasaurus* (Upper Triassic, Brazil; BONAPARTE *et al.*, 1999), Neotheropoda (e.g. *Dilophosaurus*, WELLES, 1984) and *Efraasia* (Figs 21J, K; SMNS 12354, 12667). YATES (2001) noted that *Pantydraco* (as *Thecodontosaurus caducus*) lacks certain autapomorphies of *T. antiquus*,

such as a short, dorso-ventrally deep, preacetabular blade of the ilium that "projects cranially (versus a downcurved preacetabular process in *T. antiquus*)" (YATES, 2003a, p. 4). However, these autapomorphies of *T. antiquus* are presumably based on the ilium figured by BENTON *et al.* (2000, fig. 15C; BMNH R1539) that is not from a basal sauropodomorph but is possibly Theropoda indet (Figs 35A-E, see below).

An ilium with an acetabular foramen is characteristic for Dinosauria and, as described above, the overall form of the Clifton ilia (Figs 21A-G, 22, 23A-E) is that of a basal sauropodomorph (see Figs 21I-K). The acetabulum is partly backed by bone in some ilia (Figs 21E, F, 22C, D, F. G) and not in others (Figs 21A, C, D, G, 22E, H-J). The large medial sheet of bone backing the acetabulum of very basal sauropodomorphs is lost at node 4 [Fig. 3A; reversed in *Euskelosaurus*, convergent in Sauropoda, GALTON & UPCHURCH, 2004)]. These ilia show no autapomorphies (*contra* BENTON *et al*, 2000; YATES, 2001, 2003a). The ilia with an acetabulum partly backed with bone are very basal Sauropodomorpha indet whereas those with a full opening are Anchisauria indet. However, some of the former may belong to *Asylosaurus yalensis* so the ilium in this taxon was probably plesiomorphic for a basal sauropodomorph and rather different from that of *Pantydraco* (Fig. 21H).

**Pubis** (Figs 24-P)

The broad pubic apron (Figs 24M-P) is characteristic of Sauropodomorpha but the obturator foramen is variable in size (Figs 24M-O). Basal Sauropodomorpha are characterized by a large foramen but there are multiple reversals and, in addition, this character is polymorphic in *Plateosaurus engelhardti* from Trossingen, Germany (SMNS, GPIT). The pubes are identified as basal Sauropodomorpha indet.

**Ischium** (Figs 24A-L)

The distal ischia (Figs 24A-K) differ from that of *Anchisaurus*, in which the taper is more gradual in side view, the distal cross-section is subtriangular, and there is a larger vertical sutural surface that extends almost to the distal end. However, in both, the width of the distal end of the ischium only slightly exceeds the depth. In *Pantydraco caducus* the depth exceeds the width and this difference is much greater in *Saturnalia*. The character state for *Thecodontosaurus antiquus* in the cladistic analysis of GALTON & UPCHURCH (2004; also UPCHURCH *et al*., 2007) is based on the previously unillustrated distal shafts from Clifton (Figs 24A-K). At node 3 (Fig. 3A) the distal end of the ischium is expanded dorsoventrally, the condition in *Thecodontosaurus* (Reversed *Anchisaurus* and Convergent Sauropoda, alternatively a synapomorphy of the Sauropodomorpha that reverses in *Anchisaurus* and *Thecodontosaurus*). At node 4 the distal end of the ischium is triangular in outline (Reversed *Camelotia* and *Plateosaurus*, Convergent *Vulcanodon*, alternatively a synapomorphy of Sauropodomorpha that reverses in *Camelotia*, *Plateosaurus*, *Thecodontosaurus* and Eusauropoda). The distal left ischium YPM 2195e (Figs 24F-J; distally incomplete) is similar to the others from Clifton (Figs 23F, G, 24A-E, J, L) that are tentatively referred to *Asylosaurus yalensis*.

**VI.3.9. Hind limb**

**Femur** (Figs 25-27)

As described above, the form of the Clifton femora is that of a basal sauropodomorph. The anterior (=lesser trochanter) is a low ridge (Figs 25K, 26I, J) but there is a prominent knob proximally (Figs 25K, 26K), a possible autapomorphy for Clifton femora with this region preserved.

Two distal femora of slightly different sizes (Figs 6A, 25A-C, right YPM 2195f, ~20-25% larger than left YPM 2195g, Figs 6B, 25D-F; see Appendix 7) are associated with the holotype individual of *Asylosaurus yalensis* and anteriorly both lack an extensor groove, so this surface is gently convex (Figs 25B, F). This is also the case in a few other Clifton distal femora (Figs 25N, 27H) and in those of *Pantydraco*, *Saturnalia* and *Efraasia*. YATES (2003a) coded this character state as plesiomorphic for *Thecodontosaurus antiquus* and *T. caducus* (now *Pantydraco*) so these Clifton femora are very basal Sauropodomorpha indet. However, other distal femora from Clifton have a shallow extensor depression (Figs 26N, O, 27G) so they represent a more derived basal sauropodomorph, Anchisauria indet (UPCHURCH *et al*., 2007), not *Asylosaurus* or *Thecodontosaurus*. The other femora from Clifton in which this surface is not exposed (Figs 26A-H) or preserved (Figs 25G-K, 26I-M, 27M-O) are basal Sauropodomorpha indet.

**Tibia and astragalus** (Figs 28, 29A-G, 30A-P)

The ascending process of the astragalus keys into a notch in the distal tibia (Figs 28A-C, 29B, E, 30A-E, H-N, P), a plesiomorphic character of the Sauropodomorpha (CHARIG *et al*., 1965). Distally the posterolateral edge of the tibiae is unexpanded laterally (Figs 6D, 29A, D, E, 30B, C, F, H-J, N, P), as is also the case in *Efraasia*, whereas it is broader in *Massospondylus* and *Plateosaurus*. The Clifton tibiae with a distal end (Figs 6D, 29A-F, 30A-P) are very basal Sauropodomorpha indet. Those in which the distal end is not shown in anterior or posterior views (Figs 28A-C), or in which it is missing (Figs 28D-O), are basal Sauropodomorpha indet.

**Metatarsals and phalanges** (Figs 20A-E, M-O, T-V, 29H-X, 30Y-B')

The hour-shaped proximal articular surface of metatarsal II (Figs 29J, Q) is a synapomorphy present in *Pantydraco* and *Efraasia* (YATES & KITCHING, 2003) so these bone are very basal Sauropodomorpha indet. This is also true for slender metatarsals II and III (Figs 29N-R, 31F-K) as this occurs in only a few very basal sauropodomorphs

(*Pantydraco*, *Saturnalia*, *Efraasia*); the robust third metatarsals (Figs 29K-M, 31T, U) are Anchisauria indet and the remaining metatarsals (Figs 31L-S, V) are basal Sauropodomorpha indet. The isolated pedal phalanges (Figs 20A-E, M-O, T-V, 29S-X, 30Y-B') are comparable to those of *Pantydraco*, *Efraasia*, *Massospondylus* and *Anchisaurus* so they are identified as basal Sauropodomorpha indet.

## VI.4. Systematic paleontology

### Order Saurischia Seeley, 1888
### Suborder Sauropodomorpha Huene, 1920b
### Genus *Thecodontosaurus* Riley & Stutchbury, 1836a
### *Thecodontosaurus antiquus* Riley & Stutchbury *vide* Owen, 1842a
### Figs 4A-T

1836a. *Thecodontosaurus* Riley & Stutchbury, p. 398.
1842a. *Thecodontosaurus antiquus* Riley & Stutchbury. - Owen, p. 190
2005b. *Thecodontosaurus antiquus* Riley & Stutchbury *vide* Owen, 1842a. - Galton, , p. 61A
2007. *Thecodontosaurus antiquus* Riley & Stutchbury *vide* Owen, 1842a. - Galton *et al*., p. 123, fig. 1L.
For other synonomies see Benton *et al.* (2000, p. 81).

**Etymology:** Greek *theka* = "socket" + Greek *odous* = "tooth" + Greek *sauros* = "lizard"; Latin *antiquus* = "old, ancient".
**Distribution:** Upper Triassic (Rhaetian) of Western Europe.
**Holotype:** right dentary with teeth, BRSMG *Ca7465/1♦ (Figs 4A-F), destroyed in 1940.
**Neotype:** left dentary with teeth, BRSMG C4529/2 (Figs 4G-T), designated by Galton (1985b, p. 15).
**Horizon and type locality:** Upper Triassic (Rhaetian) fissure fill in Quarry Steps Quarry off Upper Belgrave Road in Clifton, Bristol, England (UK National Grid Reference ST 572747; Figs 1A-G).
**Diagnosis:** as in *Pantydraco caducus*, the dentary is short and deep, with a maximum dorsoventral depth that is greater than 20% of its length, and teeth are plesiomorphic in all being recurved in lateral view. Based on the type Clifton material, *Thecodontosaurus antiquus* has no autapomorphies or a unique combination of characters and the diagnosis awaits description of the referred material from Tytherington.
**Referred material**: Following past practice, the slender humeral morph (Figs 15Q, R, 16C-G) from Clifton is tentatively referred to this taxon (Galton *et al*., 2007). There are 1000's of bones (in BRSUG) of the slender morph in the monospecific basal sauropodomorph assemblage from the Tytherington Quarry, Avon north of Bristol (UK National Grid Reference ST 660890). The character list for *Thecodontosaurus antiquus* in the cladistic analyses of Yates (2003a, 2004, 2006, 2007; Yates & Kitching, 2003) is mostly based on bones from this quarry (Galton *et al*., 2007) (also true for many characters for *Thecodontosaurus*, Langer & Benton, 2006). *T. antiquus* Riley & Stutchbury *vide* Owen, 1842a is provisionally accepted as a valid taxon, the complete diagnosis of which awaits description of the referred bones from Tytherington Quarry by Yates & Benton (in prep.).

### *Asylosaurus* n. gen.
### *Asylosaurus yalensis* n. sp.
### Figs 6A-D, 7B-F, 8A-F, 11A-C, 13, 14I-M, 15A-N, 17A-J, 19, 24F-I, 25A-F

**Etymology:** Greek *asylos* = unharmed, safe from violence or *asylon* = refuge, sanctuary + *sauros* = lizard; *yalensis* = of Yale College (now University), where O. C. Marsh took specimen so it was unharmed in air raids on BCM in November, 1940.
**Distribution:** Upper Triassic (Rhaetian) of England.
**Holotype:** YPM 2195, an associated partial skeleton consisting of dorsal vertebrae, ribs and gastralia, pectoral girdle, right and proximal left humeri, articulated left forearm (radius very incomplete) and manus (Figs 6A, B, 8A-F, 13, 14I-M, 15A-N, 17A-G, 19); also YPM 2195a-g, disarticulated bones on block tentatively referred to holotype individual (or species for femora), viz., vertebrae (cervical ~4 or 5, caudals ~10 and ~15), proximal medial part of right ulna, distal left ischium, 2 distal femora: larger right and smaller left, distal right tibia (Figs 6D, 7B-F, 11A-C, 17H-J, 24F-J, 25A-F, for details see Appendix 7).
**Hypodigm:** proximal left humerus (BMNH R1542, Figs 15O, P), manual phalanx 1 of digit I (YPM 56745, Figs 20F-J), ischia (YPM 56725, 56726, 56739, Figs 24A-E, K).
**Horizon and type (only) locality:** as for types of *Thecodontosaurus antiquus* (see above).
**Diagnosis:** autapomorphies: deltopectoral crest symmetrical in lateral view with the gently rounded apex at 25% (measured perpendicular to long axis of humerus) of humeral length, manus with lateral reduction so phalangeal formula 2-3-4-2-1, distally the thickest parts of the ischia are separated by a cleft that is Λ-shaped in dorsal view; plesiomorphies: low deltopectoral crest (also in *Pantydraco caducus* but apex asymmetrical at 40% of humeral length) with large medial tubercle adjacent to head (also in most basal sauropodomorphs, small in *P. caducus*), distal tarsal I transversely narrower than metatarsal I (occurs in no other basal sauropodomorph) and transversely narrow metacarpals I (and phalanx 1, also in *Efraasia minor*) and II-IV (also in *E. minor* and *Anchisaurus polyzelus*).

**Very basal Sauropodomorpha indet [A]**
These bones have characters that are plesiomorphic for the

very basal Saropodomorpha (*Saturnalia tupiniquim, Pantydraco caducus, Asylosaurus yalensis, Efraasia minor*) and lack the derived condition that is present in this bone in the Anchisauria *sensu* UPCHURCH *et al.* (2007), i.e. *Ammosaurus major, Anchisaurus polyzelus, "Gyposaurus" sinensis, Coloradisaurus brevis, Plateosaurus engelhardti, Riojasaurus incertus, Lufengosaurus huenei, Massospondylus carinatus, Euskelosaurus browni* (now *Plateosauravus cullingworthi*, see YATES, 2003c), and *Yunnanosaurus huangi* (cf. Figs 3A, B).

**Braincase** - YPM 2192 (Figs 5A-D), very plesiomorphic in lacking a separate opening for the vena cerebralis media above the trigeminal foramen so very basal Sauropodomorpha indet. It has elongate basipterygoid processes but it is not referable to *Pantydraco caducus* (KERMACK & GALTON, in prep.) and, depending on the Tytherington material, it may prove to be *Thecodontosaurus antiquus*.

**Cervical vertebrae** - if the referral of the proportionally elongate but anteriorly incomplete centrum (length: height ratio +3.0) of C4 or 5 (Figs 7B-F) to *Asylosaurus yalensis* is correct then the other elongate cervicals (BRSMG Ca7467/-, Figs 7P-T; YPM 56720, Figs 7G-O) could be from *Asylosaurus yalensis* or, alternatively, they could be Anchisauria indet; the cervicals of *Pantydraco caducus* are proportionally short (ratio less than 3.0).

**Posterior dorsal and sacral vertebrae** - the keyhole shape of the neural canal in transverse section, with excavation of the centra in posterior dorsals and anterior sacral vertebrae, may be an autapomorphy: ANSP 9865a (Figs 9Y, Z), BMNH R1532 (Figs 10G, H), BMNH R1533 (Fig. 10I), BRSMG Ca7452/26♦ (Fig. 10D), BRSMG C4533/8 (Figs 10B, C), BRSMG Cb4154/12 (Figs 9M, N), BRSMG Cb4174a/41 (Fig. 9O), BRSMG Cb4221 (Fig. 10A); probably sacrals 1 and 2: YPM 56733 (Figs 10J-P), YPM 56746 (Fig. 10Q).

**Caudal vertebrae** - the neural spine is short and posteriorly situated on the neural arch and the degree of ventral furrowing of proximal and mid-caudal centra is reduced or lost as in *Pantydraco caducus* and *Efraasia minor*: BGS 54061a (Figs 11D-I), BMNH R1550b (Fig. 12E), BMNH 44984a (Fig. 12F), BRSMG Ca4532a/17 (Figs 11R-Z), BRSMG Ca4532b/17 (Fig. 12B), BRSMG Ca7476/59♦ (Fig. 12C), BRSMG Cb4276 (Fig. 12D), BRSMG Cb4301 (Fig. 12A), YPM 2193 (Figs 11J-M).

Possible autapomorphies: proximal centrum rounded ventrally with a median ridge in BGS 54061a (Fig. 11G). In mid-caudals the anterior edge of the transverse process continues as a sharp ridge across the side of the neural arch to the middle of the notch bordered by the prezygapophysis (Figs 11R, T, U, 12A, B); this ridge is also visible on some proximal caudals (Figs 11E, Q); this ridge is not present on mid-caudals of *Pantydraco caducus* (WARRENER, 1983).

**Metacarpals** – slender: BRSMG Ca7463/88♦ (I, Figs 18Q, R), Ca7484/56♦ (IV, Fig. 18P).

**Ilia** – acetabulum partly backed by bone: BRSMG Ca7457a,b/63♦ (Figs 21E, F, 21C, D, F. G).

**Femora** – lack extensor groove distally: BMNH R1544 (Figs 25L-P), BRSMG Ca4530/73 (Figs 27H-L).

**Metatarsals** – slender: ANSP 9856 (III, Figs 29N, O), ANSP 9867 (II, Figs 29P-R), BRSMG Ca7451b/81 (III, Figs 31F-K).

**Anchisauria indet [B]**

Bones with characters that are derived with respect to group A but plesiomorphic with respect to those of Sauropoda, Anchisauria *sensu* UPCHURCH *et al.* (2007; for genera see A).

**Humeri** – robust: BRSMG Ca7464/118♦ (Figs 16A, B), BRSMG Cb4243 (Figs 15S-U), ?BRSMG Cb4189/78 (Fig. 15V), YPM 56724 (Figs 16H-J).

**Metacarpals** – robust: ANSP 9864 (II, Figs 18S), ANSP 9875 (II, Fig. 18T), BRSMG Ca7482/80 (III, Figs 18U-Y), BRSMG Ca7483/82♦ (III, Fig. 18Z), BRSMG Cb4174c/41 (III, Figs 18A', B').

**Manual phalanges** – more robust than those of manus of *Asylosaurus* and *Efraasia*: BGS 907924 (Figs 20X-C'), BMNH 49984c (Fig. 20S), BRSMG Ca7451a/81 (Figs 20P-R), BRSMG Ca7454/87♦ (Figs 20K, L).

**Ilia** – acetabulum not backed by bone: BRSMG Ca7450/61♦ (Figs 21A, 22H), BRSMG Ca7457c/63♦ (Figs 21G, 22E), BRSMG Ca7460/57♦ (Figs 21C, D, 22J), BRSMG Ca7560/60♦ (Fig. 22I).

**Femora** - have a distal extensor groove: BRSMG Ca7490/71♦ (Figs 27A-G), BRSMG Ca7492/69I♦ (Figs 26O-T), BRSMG Ca7493/70♦Fig. 26N).

**Metatarsal III** – robust: ANSP 9856 (Figs 29K-M), BRSMG Ca7498/83 (Figs 31T, U).

**Basal Sauropodomorpha indet [C]**

The remaining sauropodomorph bones that lack the characters of Sauropoda but cannot be referred specifically to group A or B (see Appendices 3-7 as [C]).

## VII. THEROPODA INDET

**Tooth** (Figs 32V, W)

Although not mentioned or figured by SEELEY (1891), VICKERS-RICH *et al.* (1999) or GALTON (2000), there was a tooth included in the holotype of *Agrosaurus* (BMNH 49984e). It was near the ungual phalanx on the underside of the small block with the distal radius (GALTON, 2000, fig. 15J, on bottom angle of block). This small tooth (Figs 32V, W, since destroyed during acid preparation) was described by HUENE (1906, p. 148, figs 90a, b) as being badly damaged, 8.4 mm long and 3.3 mm broad at the base, transversely narrow and rather recurved. The concave posterior edge is very finely serrated, the denticles forming long sharp points perpendicular to the edge with seven denticles in 1 mm (Fig. 32W). This tooth is very different from the three other tooth-types from Clifton,

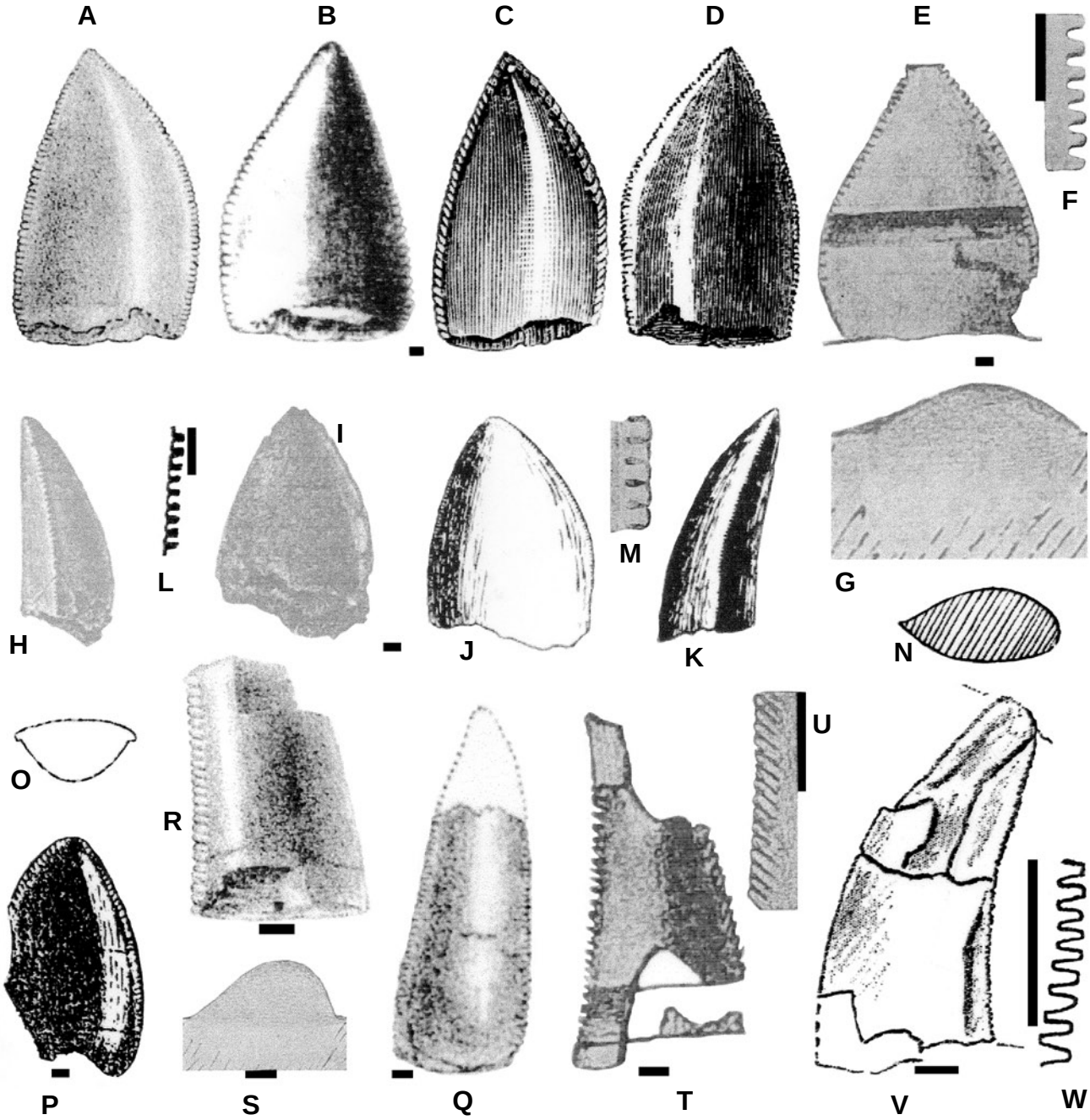



Fig. 32: Teeth of carnivorous archosaurs from Clifton (A-N, Q-W) and Coombe Hill (O-P). A-N: heterodont crurotarsal phytosaur *Rileyasuchus* (*Palaeosaurus*) *platyodon*: A-P: *Palaeosaurus platyodon* RILEY & STUTCHBURY, 1840: A-G: holotype BRSMG *Ca7448/3 in A-E: medial (lingual) view; F: detail of serrations on mesial (anterior) edge and G: cross sectional view of root. H-N: referred tooth BMNH R16119 in H: mesial; I-J: lingual and K: distal (posterior) views; L-M: detail of serrations on L: distal and M: mesial edges, and N: cross-section of base of crown. O-P: *Palaeosaurus stricklandi* DAVIS, 1881, holotype BGS GSL4498 in: O: cross sectional view at lowest level of complete crown and P: lingual view. Q-U: *Palaeosauriscus* (*Palaeosaurus*) *cylindrodon* (RILEY & STUTCHBURY, 1840), holotype BRSMG *Ca7449/4♦ in Q, R, T: side view; S: cross section of base of crown and U: detail of serrations of distal edge. V-W: Theropoda indet, BMNH 49884e♦ in V: side view with W: detail of serrations on distal edge. A, Q from RILEY & STUTCHBURY (1840), B from OWEN (1841), C from LYDEKKER (1888), D from ZITTEL (1890), E-I, M, S-U from HUENE (1908a), J-L, N from HUENE (1908b), O, P from DAVIS (1881), R from HUXLEY (1870), V, W from HUENE (1906); scale bars = 1 mm.

viz., *Thecodontosaurus* (Figs 4D-F, O-U), *Rileyasuchus* (*Palaeosaurus*) *platyodon* (Figs 32A-N, 33A-D, I-L), and *Palaeosauriscus* (*Palaeosaurus*) *cylindrodon* (Figs 32N-T), as well as the teeth of the holotype of the theropod dinosaur *Megalosaurus cambrensis* (NEWTON, 1899; GALTON, 2005a, figs 10A-H) from the Rhaetian of South Wales and referred teeth from the Rhaetian of Somerset (GALTON, 1998a, 2005a, figs 10I-O). Given its recurved and transversely narrow form, it is definitely Theropoda indet; it represents a small form.

**Metacarpal I** (Figs 35F-I)

The unidentified limb bone BMNH R1549 of BENTON *et al.* (2000, p. 82, 106) is a left metacarpal I in dorsal view (Figs 35F-I). In crurotarsal archosaurs and ornithischian dinosaurs metacarpal I has a more or less symmetrical distal end, with both distal condyles developed sub-equally. As in all saurischians except *Herrerasaurus* (SERENO, 1994), the distal end of this metacarpal I is pronouncedly asymmetrical, the medial condyle being positioned more proximally than the lateral condyle, so the articular surface faces mediodistally rather than

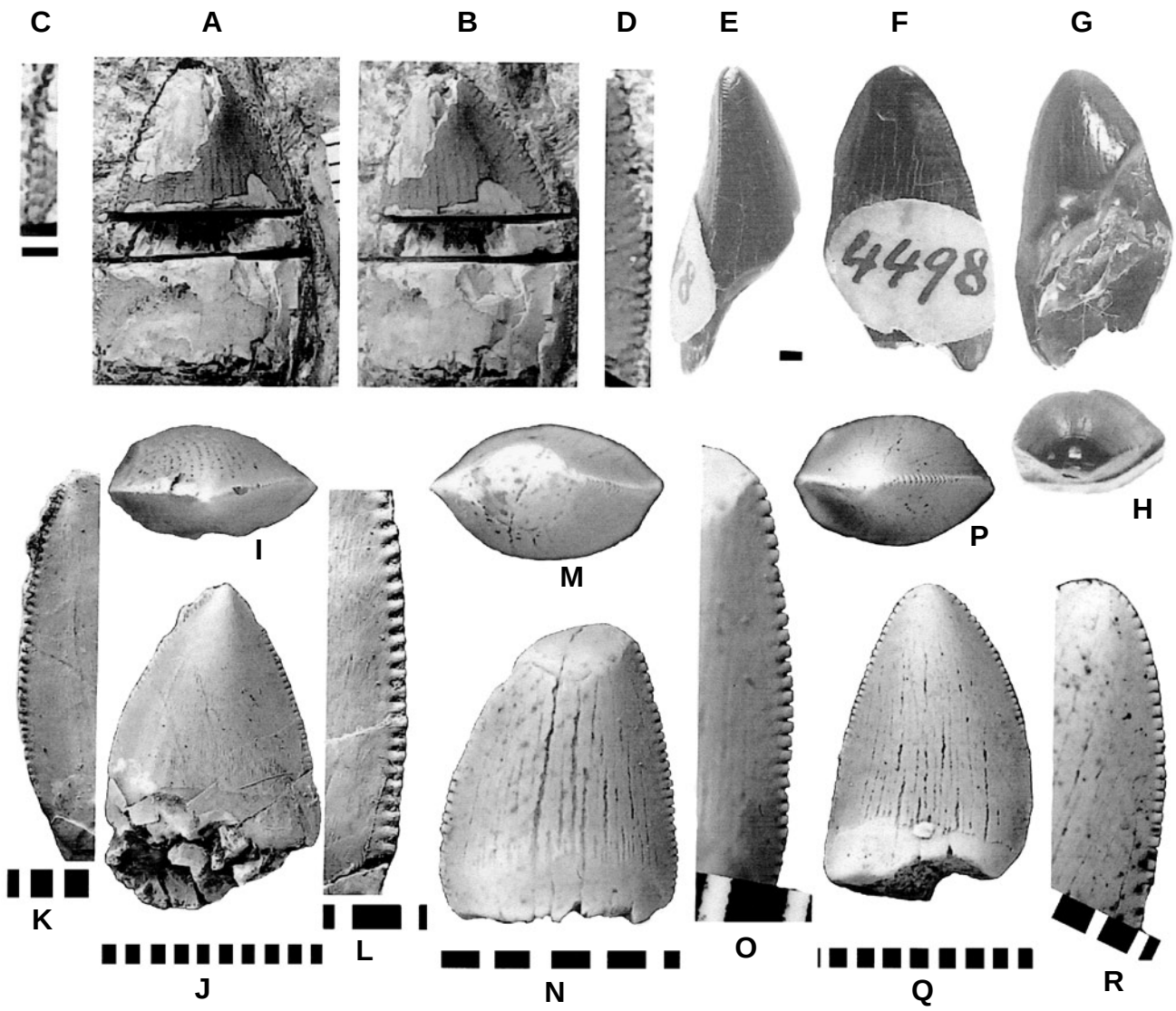



Fig. 33: Teeth of heterodont crurotarsal phytosaur *Rileyasuchus* (*Palaeosaurus*) *platyodon* from Clifton (A-D, I-L), Coombe Hill (E-H) and Somerset (M-R): A-D: *Palaeosaurus platyodon* RILEY & STUTCHBURY, 1840, holotype BRSMG *Ca7448/3 in A, B: lingual view with details of C: distal and D: mesial edges. E-H: "*Palaeosaurus*" *stricklandi* DAVIS, 1881, holotype BGS GSL4498 in: E: mesial; F: lingual; G: labial (buccal, lateral) and H: apical views. I-R: *Rileyasuchus platyodon*, referred teeth: I-L: BMNH R16119 in I: apical and J: lingual views with details of serrations on: K: mesial and L: distal edges. M-R: associated teeth BMNH R1695: M-O: BMNH R1695a in M: apical and N: lingual views with O: detail of serrations on mesial edge; P-R: BMNH R1695b in P: apical and Q: lingual views with detail of serrations on R: mesial edge. Scale bars = 1 mm (C, D-H) or ruler subdivisions in mm.

strictly distally (RAUHUT, 2003). The extensor pit on the distal dorsal surface is deep (Figs 35F-I) as in theropods, rather than shallow or non-existent as in sauropodomorphs including basal forms such as *Asylosaurus* (Figs 19A-D), *Efraasia, Anchisaurus, Massospondylus* and *Plateosaurus*, so this metacarpal I is Theropoda indet; it represents a large form. It should be noted that the deep depression allows for hyperextension of phalanx 1 and the extensor tendons attach to the proximodorsal process of phalanx 1, not into the extensor pit of the metacarpal as suggested by RAUHUT (2003, p. 99).

**Ungual phalanx of manus** (Fig. 34H)
An ungual phalanx of the manus on block BRSMG Ca7487c/85♦ has a deep proximal end but the claw supporting part is more slender and recurved (Fig. 34H, distal end as impression) than those of basal sauropodomorphs (Figs 19G, J, L, N, 20K, L, P, Q, S, X, Y). This ungual is tentatively identified as Theropoda indet.

**Ilium** (Figs 35A-E)
One of the few surviving ilia from Clifton, BMNH R1939 (Figs 35A-D), was referred to *Thecodontosaurus antiquus* by LYDEKKER (1890, p. 247) and BENTON *et al.* (2000, p. 82, 106, described p. 93, fig. 15C) (Fig. 35E). However, this referral is questionable because it is very different from the other well preserved ilia from this site (Figs 21B, C, E, 22F, G) and, in addition, from those of other basal sauropodomorphs (Figs 21I-K; HUENE, 1908a, 1926, 1932; YOUNG, 1951; BONAPARTE 1972; COOPER 1981; GALTON, 1986b, 1990, 1999, 2001a, b). This ilium is proportionally much deeper transversely, with the body being anteroposteriorly and transversely concave (Figs 35A-C), so the anterior process faces dorsolaterally (Fig. 35D). The acetabulum is transversely wide and much of it is backed by bone that has a concave ventral edge so it was open inferiorly (Figs 35A, B, D). Unfortunately, the dorsal and posterior limits are not preserved so the original height and length are unknown. The pubic peduncle is distally incomplete. The inferior edge of the post-acetabular process angles up very steeply and starts to become more horizontal (as indicated by the natural cast) well above the ventral edge of the anterior process, a unique configuration. However, this edge probably follows the more lateral part of the process so the presence or absence of a brevis shelf and a more medial shelf for the sacral ribs cannot be determined (Fig. 35A cf. Figs 21E, I, I,-K35J-N, P-R).
This ilium is very different from the others from Clifton and it is clearly not that of a basal sauropodomorph. The overall form is similar to that of the dinosauriform *Marasuchus* (Fig. 35M; Middle Triassic, Argentina; SERENO & ARCUCCI, 1994) except that BMNH R1939 has an open acetabular foramen (Figs 35A, E), commonly regarded as a derived character of Dinosauria (Figs 35P-S; NOVAS, 1996) that is absent in dinosauriform ilia (Figs 35M-O). The Clifton ilium probably lacked the long postacetabular process of the basal theropod *Agnosphitys* (Figs 35J-L; FRASER *et al.*, 2002 as Dinosaurimorpha; LANGER, 2004 as Dinosauria; YATES, 2006 as Theropoda) from the Upper Triassic fissure fill at Cromhall Quarry, Avon, England. A perforate acetabulum is present in herrererasaurid theropod dinosaurs (Figs 35P-R) and the preserved part of BMNH R1539 is similar to the ilium of *Herrerasaurus* (Figs 35R, S, Upper Triassic, Argentina; NOVAS, 1994). The lateral ridge passing anterodorsally to the base of the preacetabular process resembles that of the herrerasaurids *Chindesaurus* (Fig. 35P, Upper Triassic, western USA; LONG & MURRY, 1995; a basal theropod, LANGER, 2004) and *Staurikosaurus* (Fig. 35Q, Upper Triassic, Brazil; GALTON 2000). A perforate acetabulum may occur convergently within the crurotarsal Rauisuchia (e.g. *Poposaurus gracilis*, Upper Triassic, western USA; see LONG & MURRY, 1995) but this is disputed by ALCOBER & PARRISH (1997, p. 555). It is very unlikely that this ilium (Figs 35A, E) is rauichian because there is no trace of any supraacetabular buttress, rugosity, ridge or swelling (see LONG & MURRY, 1995; GOWER, 2000; NESBITT, 2005, fig. 5) and the most recent record of the group is Norian (GOWER, 2000). BMNH R1539 is probably from a herrerasaurid or basal theropod dinosaur, much less likely as a dinosauriform, and it is about the correct size to go with the femur YPM 56744 (Fig. 36), the affinities of which are discussed in the next section.

**Femur** (Fig. 36)
HUENE (1902, fig. 76; 1908b, pl. 6, figs 2a, b; 1911, figs 31.2a,b) described two caudal vertebrae of YPM 2192 from Clifton that he referred to the phytosaur *Rileya platyodon* HUENE, 1902. This identification was based on very poor photos (supplied by YPM in 1901, BCM Archives, Geology File 51) and, on seeing the specimen in 1911, HUENE (1914a, fig. 55) reidentified one caudal (Fig. 9T, now YPM 56719) as a dorsal vertebra of *Thecodontosaurus.* According to BENTON *et al.* (2000, p. 79), he did this for both caudals but this is incorrect; HUENE (1914a, figs 56a-e) reidentified the second caudal as the proximal end of a right femur of *Thecodontosaurus* (Figs 36B', C', E'-G', now YPM 56744). This femur was originally part of YPM 2192 (now YPM 56719) that included a disarticulated and incomplete metacarpus (Fig. 6F), so it was not part of the block with the complete manus (YPM 2195) as implied by HUENE (1914a).
Although it is a proximal left femur (Figs 36A-F), it is not that of a basal sauropodomorph (cf. Figs 25J, K, 26A-L; GALTON, 1976, 1990; GALTON & UPCHURCH, 2004; HUENE, 1908a, 1926, 1932; for melanorosaurids see VAN HEERDEN & GALTON, 1997; GALTON *et al.*, 2005). Thus the proximal end is narrow anteroposteriorly, not broad as in basal sauropodomorphs, the anterior (=lesser) trochanter is a massive process, not a low ridge or at most a thin sheet (melanorosaurids), and the base of the fourth

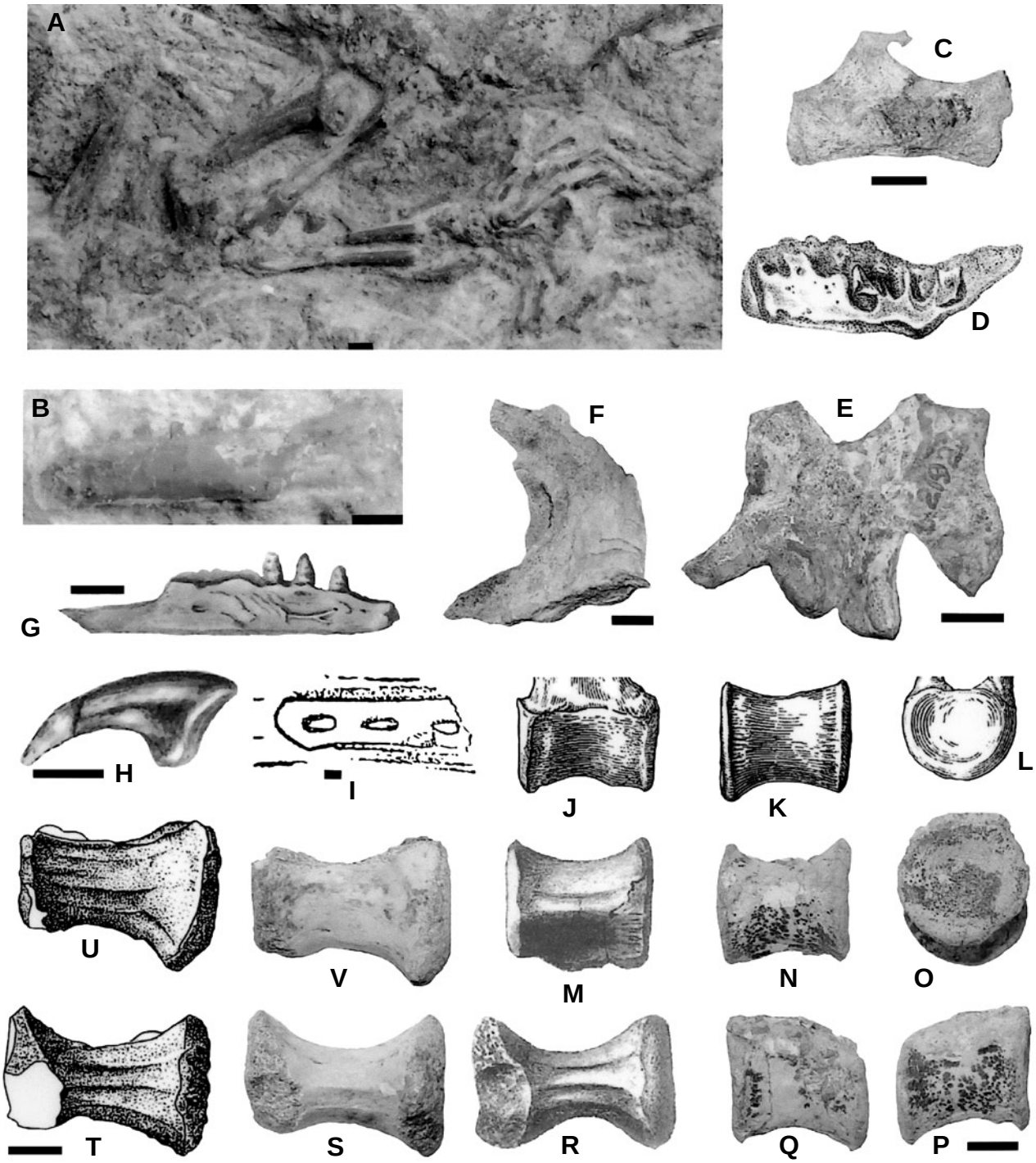



Fig. 34: Bones from Clifton (A-I, M-V) and Upper Jurassic of Tanzania (J-L). A-B: Sphenodontid lepidosaur *Diphydontosaurus avonis*: A: BRSMG Cb4715, articulated skeleton showing part of vertebral column and hind limbs and B: BRSMG Cb4714, left dentary in lateral view. C: Theropoda indet, BRSMG Cb4199, right astragalus in anterior view. D: Archosauria indet, fragment of jaw in medial view with alveolar septa and a replacement tooth, WILLIAM's Collection -♦. E-F: Reptilia indet, YPM 56719, ?sidewall bone of braincase in medial view and F: BRSMG Cb4251, left parietal in dorsal view. G: Archosauria indet, BRSMG Ca7487b/85♦, anterior part of left dentary in medial view. H: Theropoda indet, BRSMG Ca7487c/85♦, manual phalanx with impression of tip, in side view. I: Archosauria indet, YPM 2195i♦, jaw piece with three alveoli in medial view. J-L: Ornithopod ornithischian dinosaur *Dryosaurus lettowvorbecki*, centrum of posterior dorsal vertebra in J: left lateral; K: ventral and L: anterior views. M-Q: Ornithischia indet, BRSMG Ca7474/16b, centrum of posterior dorsal vertebra in M-N: ventral; O: anterior; P: right lateral and Q: left lateral views (BENTON *et al.*, 2000, figs 9A-D). R-V: Reptilia indet, BRSMG Ca7473/16, proximal caudal centrum in R-T: ventral and U-V: left lateral views (BENTON *et al.*, 2000, figs 9E-G). D from RILEY & STUTCHBURY (1840), I from HUENE (1914a), G, H, M, R from HUENE (1908a), J-L from JANENSCH (1955), T, U from BENTON *et al*. (2000); scale bars = 1 mm (A, B, I) and 10 mm (D unknown).

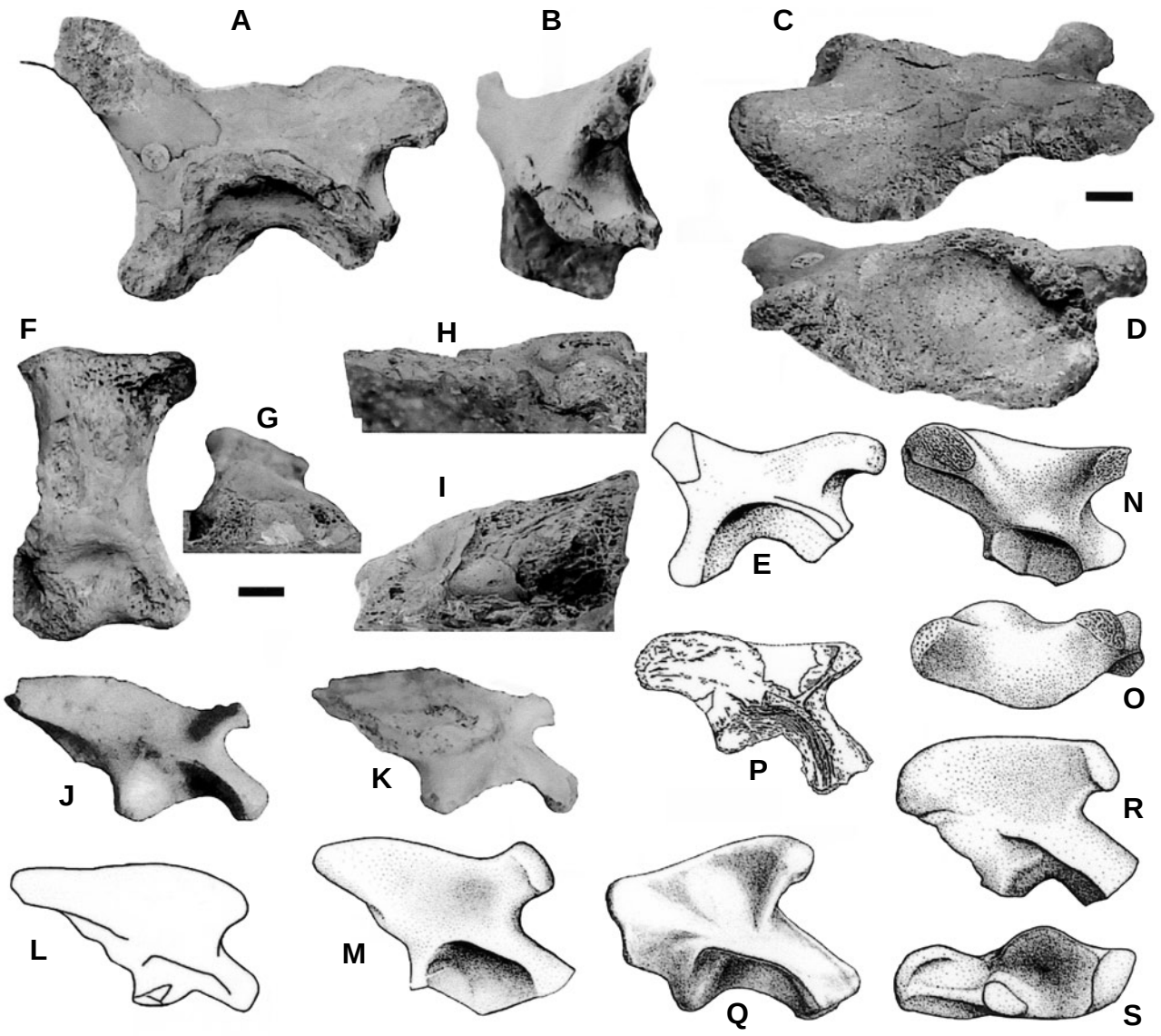



Fig. 35: A-I: Basal theropods from Clifton. A-E: right ilium, BMNH R1539, in: A, E: lateral; B: anterior; C: dorsal and D: ventral views. F-I: right metacarpal I, BNMH R1549, in: F: dorsal (anterior); G: distal; H: lateral and I: medial views. J-S: left (K) and right ilia of dinosauriformes (M-O) and herrerasaurian or basal theropods (J-L, P-S) from the Upper Triassic of England (J-L), Argentina (M, R, S), Poland (N, O), USA (P) and Brazil (Q) in lateral (J, L-N, P-R), medial (K), dorsal (O) and ventral (S) views. J-L: *Agnosphitys cromhallensis* FRASER *et al.*, 2002 from Cromhall Quarry, Avon, England: J-K: VMNH 1745, holotype left ilium in J: lateral (reversed so right) and K: medial views; L: restoration of right ilium in lateral view. M: *Marasuchus*; N-O: *Silesaurus*; P: *Chindesaurus*; Q: *Staurikosaurus* and R-S: *Herrerasaurus*. E from BENTON *et al.* (2000), L from FRASER *et al.* (2002), M from SERENO & ARCUCCI (1994), N, O from DZIK (2003), P, from CASE (1927), Q from COLBERT (1970), R, S from NOVAS (1992); scale bars = 10 mm (A-I), rest not to same scale.

trochanter is very proximally situated rather than being at a third to half of femoral length. Another similar but less complete and anteroposteriorly compressed left proximal femur (Figs 36H-J) was described as a distal ischium by HUENE (1908a; ?distal ischium BENTON *et al.*, 2000, p. 105). These femora resemble those of basal theropods in these respects and, in addition, there is a fossa trochanterica, a longitudinal groove passing transversely across the proximal end (Figs 36B, D, E, H), as in the Upper Triassic basal theropod *Alwalkeria* (India) and the herrerasaurids *Staurikosaurus* (Brazil) and some individuals of *Herrerasaurus* (Argentina) (LANGER, 2004, figs 2.7, 2.8). However, this femur differs from those of basal theropods and herrerasaurids because proximally the anterior trochanter does not form an apex, rather it merges with the shaft, there is no trochanteric

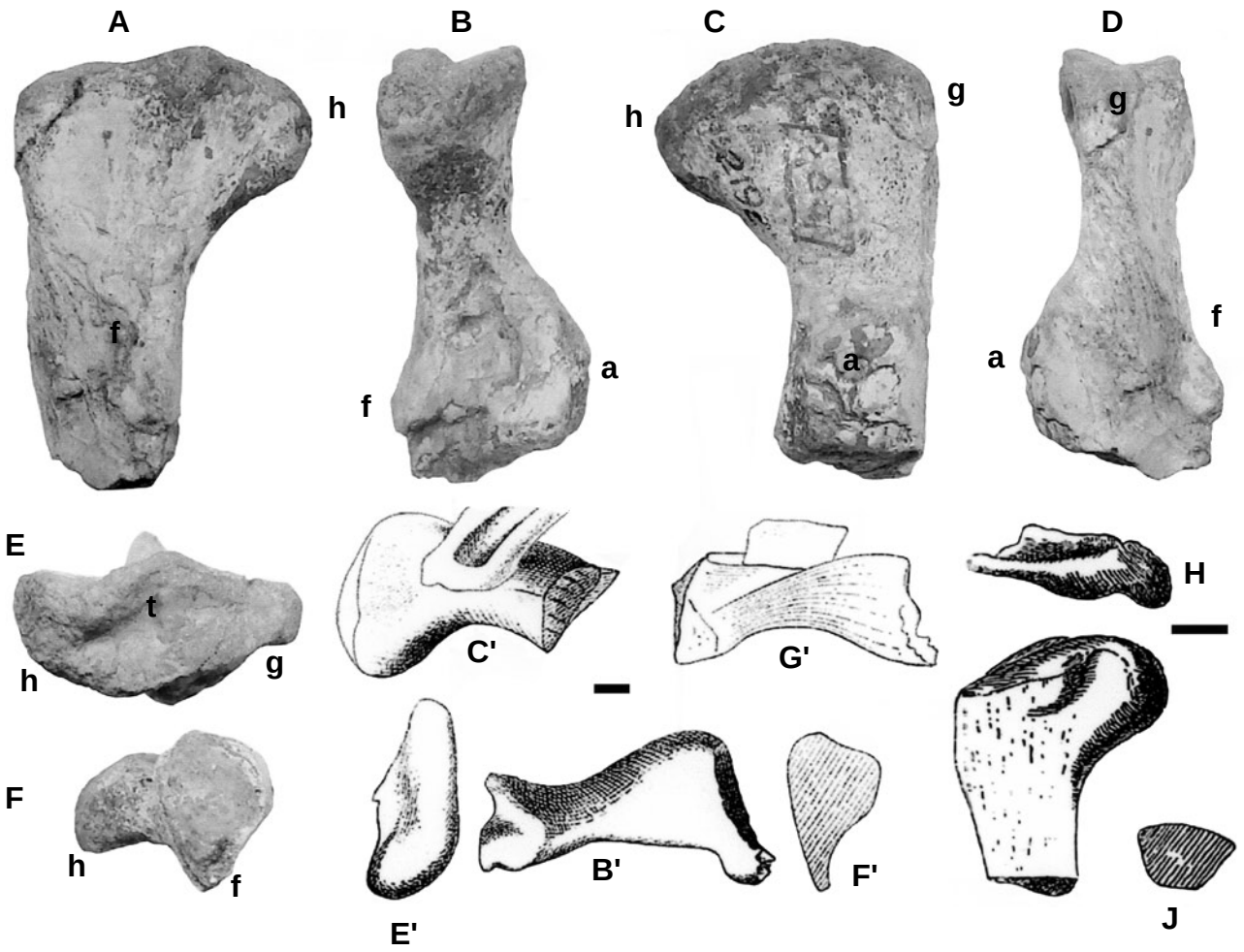



Fig. 36: Basal theropod femora from Clifton. A-G: proximal left femur YPM 56744 free of matrix (A-F) and as illustrated by HUENE (1914a) (B', C', E'-G') with matrix and end of rib in A: posterior; B, B': medial; C, C': anterior; D: lateral; E, E': proximal; F, F': distal and G': posteromedial views. H-J: proximal right femur BRSMG Ca7513/77b♦ in H: proximal; I: posterior and J: distal cross sectional views. a = anterior or lesser trochanter; f = fourth trochanter; g = greater trochanter; h = head; t = fossa trochanterica; scale bars = 10 mm.

shelf as in *Herrerasaurus*, and the base of the fourth trochanter is very proximally placed so it overlaps the lesser trochanter rather than being close to its distal end (see LONG & MURRY, 1995; LANGER, 2004; LANGER & BENTON, 2006). The ilium and femora (Figs 35A-E, 36) may be Herrerasauria GALTON, 1985d *sensu* LANGER, 2004, the sister group to *Eoraptor* + Theropoda.

**Astragalus** (Fig. 34C)

The anterior aspect of the right astragalus (Fig. 34C, transverse width 36 mm) is poorly preserved, especially the body. The full height of the anterior process is not known but it was certainly not less than that of the astragalar body, the condition in ornithischians, basal sauropodomorphs, herrerasaurids and some theropods ("ceratosaurid" tarsus of WELLES & LONG, 1974; NOVAS, 1989; RAUHUT, 2003). In contrast to the situation in basal sauropodomorphs, it is anteroposteriorly thin rather than broad with an almost flat top (see NOVAS, 1989, fig. 4; FRASER *et al.*, 2002, fig. 8). In herrerasaurids it is a small centrally located process that keys into the tibia (NOVAS, 1989) and in the Upper Triassic theropods *Coelophysis* (western USA) and *Liliensternus* (Germany) it is a more anteriorly situated but still a stout short process. A taller (twice height of body) anteroposteriorly thin anterior process is given as a possible apomorphy for the Coelurosauria by RAUHUT (2003). This astragalus is identified as Theropoda indet.

## VIII. ORNITHISCHIA INDET (Figs 34M-Q)

A centrum was described as that of an anterior caudal of *Thecodontosaurus antiquus* by HUENE (1908a) (Fig.

34M, with posterior end on left) and by BENTON *et al.* (2000, p. 88, figs 9A-D, orientation reversed in text so C left lateral view, not right), who noted that it "has a notably platycoelous, spool-shaped centrum ... (and) no chevron facet is evident." However, this centrum (Figs 34M-Q) is slightly amphicoelous, is from a dorsal vertebra rather than a proximal caudal, and it does not resemble the vertebral centra of any basal sauropodomorph. However, the form of the side and ventral edges is very similar to those of centra of dorsal vertebrae of ornithischian dinosaurs such as "fabrosaurids" (SANTA LUCA, 1984, fig. 1) and ornithopods (*Dryosaurus*, Upper Jurassic, western USA and Tanzania, Figs 34I-K; JANENSCH, 1955; GALTON, 1981, figs 1C-F, 2M, N, R, 4C; *Camptosaurus*, Upper Jurassic, western USA and England; GALTON & POWELL, 1980, figs 4K-M). This centrum is tentatively identified as Ornithischia indet.

## IX. CRUROTARSI: PHYTOSAURIA INDET

***Rileyasuchus* (*Palaeosaurus*) *platyodon***

The names *Palaeosaurus cylindricum* and *P. platyodon* of RILEY & STUTCHBURY (1836a, b) and *P. cylindrodon* and *P. platyodon* of RILEY & STUTCHBURY (1837a) are *nomina nuda*. The two teeth from Clifton were subsequently described and figured as *Paleosaurus cylindrodon* RILEY & STUTCHBURY, 1840 (Fig. 32Q) and *P. platyodon* RILEY & STUTCHBURY, 1840 (Fig. 32A), so *Paleosaurus* is used by BENTON *et al.* (2000) instead of *Palaeosaurus*. However, *Paleosaurus* was probably a typographical error, given the use of *Palaeosaurus* by RILEY & STUTCHBURY (1836a, b, 1837a) and STUTCHBURY (MS), and it was recognized as such by subsequent authors. *Palaeosaurus* is used in RILEY & STUTCHBURY (1841, abstract of 1840) and OWEN (1841, p. 266, 267), in footnotes for *Thecodontosaurus* and *Palaeosaurus*, cited "Geol. Transactions, 1836, p. 349" and "Loc. cit. p. 352" and the pagination refers to RILEY & STUTCHBURY (1840, p. 349-357; same true for OWEN, 1842a, p. 153, 154, 1861, p. 276), not the earlier abstract (RILEY & STUTCHBURY, 1836a, p. 397-399). HUXLEY (1870, p. 42, 43) used *Palaeosaurus* and referred to "their well known memoir*" but miscited the title in the footnote. MORRIS (1843, p. 209, 1854, p. 351) referred to the figures in RILEY & STUTCHBURY (1840, pl. 29, figs 4, 5) for *Palaeosaurus cylindrodon* and *P. platyodon*, as did LYELL (1841, p. 100 for *P. platyodon*), SEELEY (1895, p. 145), HUENE (1908a, p. 240, 241, 1908b, p. 228, 1914b, p. 12, 1932, p. 72) and KUHN (1933, p. 24, 1939, p. 57). Consequently, BENTON *et al.* (2000) are the first primary workers to use *Paleosaurus* RILEY & STUTCHBURY, 1840. However, according to article 33.3.1 of the ICZN (1999), "when an incorrect subsequent spelling is in prevailing usage and is attributed to the publication of the original spelling, the subsequent spelling and attribution are to be preserved and the spelling is deemed to be a correct original spelling." Consequently, *Palaeosaurus* should continue to be used, not *Paleosaurus*.

A phytosaurian humerus (Figs 37A-F) from Clifton was described as *Rileya bristolensis* HUENE, 1902. However, HUENE (1908b) regarded the tooth of *Palaeosaurus platyodon* (Figs 32E-G, 33A-D) as that of a phytosaur and, as *Palaeosaurus* was preoccupied (GEOFFROY SAINT-HILAIRE, 1833), the tooth and humerus became *Rileya platyodon* (RILEY & STUTCHBURY, 1840). *Palaeosauriscus* KUHN, 1959 was proposed to replace *Palaeosaurus* (preoccupied, GEOFFROY SAINT-HILAIRE, 1833) and *Rileyasuchus* KUHN, 1961a to replace *Rileya* (preoccupied, ASHMEAD, 1888).

BENTON *et al.* (2000) cited STEEL (1970, p. 25) as the first designator of the type species of the genus *Palaeosaurus* RILEY & STUTCHBURY, 1840 as *P. platyodon* RILEY & STUTCHBURY, 1840 (same type species in WHITE, 1973; GLUT, 1997, 2002). They regarded this as a surprising decision, because *P. cylindrodon* has page priority, but it makes sense because the holotype of *P. platyodon* is a phytosaurian tooth, as recognized by HUENE (1908b), whereas the tooth of *P. cylindrodon* is generally regarded as indeterminate (CHARIG *et al.*, 1965; GALTON, 1973; GALTON & WALKER, 1996a; BENTON *et al.*, 2000; but see below). However, OWEN (1841, p. 267, pl. 62A, fig. 7; text only 1842a, p. 154) figured the larger tooth and noted that RILEY and STUTCHBURY (1840) "have founded upon it the genus *Palaeosaurus*, and distinguish it by the specific name of *platyodon*, from the second tooth which they refer to the same genus under the name of *Palaeosaurus cylindrodon*." Although RILEY & STUTCHBURY (1840) did not specify the type species, OWEN (1841, 1842a) did and, as first revisor of the genus, this has clear priority over KUHN (1939, p. 57), who designated *Palaeosaurus cylindrodon* RILEY & STUTCHBURY, 1840 as the type species of *Palaeosaurus* RILEY & STUTCHBURY, 1840. *Palaeosauriscus* KUHN, 1959 was erected for *Palaeosaurus* RILEY & STUTCHBURY, 1840 *non Palaeosaurus* GEOFFROY SAINT-HILAIRE, 1833 but KUHN did not specify the type species that, based on his earlier work (KUHN, 1939), was for him *Palaeosaurus cylindrodon* RILEY & STUTCHBURY, 1840. This is confirmed by KUHN (1965, p. 22), who listed the genotype as *Palaeosauriscus cylindrodon*. Consequently, the holotype tooth of *Palaeosaurus platyodon* RILEY & STUTCHBURY, 1840, the type species of *Palaeosaurus* RILEY & STUTCHBURY, 1840 (both *nomina dubia*) as specified by OWEN (1841, 1842a), is that of a heterodont crurotarsal phytosaur (Figs 32A-G, 33A-D); it is quite distinct from the holotype tooth of *Palaeosaurus cylindrodon* RILEY & STUTCHBURY, 1840, the type species of *Palaeosauriscus* KUHN, 1959 (Figs 32Q-U, see below) following KUHN (1939, 1965). Rather than erecting a new genus for a *nomen dubium*, the indeterminate phytosaur tooth from Clifton will be referred to as *Rileyasuchus platyodon* (RILEY & STUTCHBURY, 1840) following KUHN (1933, 1961a, b),

even though the phytosaurian affinities of the holotype humerus (Figs 37A-F) are uncertain (see below).

**Teeth** (Figs 32A-N, 33A-D, I-L).

RILEY & STUTCHBURY (1840, p. 352) described "a single tooth 7/10ths of an inch long and 5/10ths broad (18 x 12.7 mm), carinated ?laterally and finely serrated at right angles to the axis; this tooth approaches more nearly in form and serrations to the upper portion of the tooth of *Megalosaurus*." They named it *Palaeosaurus platyodon*, based on the more flattened form of the tooth (Fig. 32A). The holotype tooth was described and figured (Fig. 32B) by OWEN (1841, p. 267). A description of the histology of *Palaeosaurus* is included in the section on *Thecodontosaurus* but later a similar description was given for *Thecodontosaurus* (OWEN, 1842a, p. 153-154). Given the sectioned tooth of *Palaeosaurus platyodon* (Figs 33A, B), it is reasonable to assume that both histological descriptions pertain to *Palaeosaurus*. OWEN (1841, p. 267) noted that the tooth "is sub-compressed and traversed by two opposite finely serrated ridges, its length is five lines; its breadth at the base two lines" and measured "9 lines in length and 5 lines in breadth (1 line = 1/12 inch so 19 x 10.6 mm). It is compressed, pointed, with opposite trenchant and serrated margins." HUXLEY (1870, p. 43) noted that RILEY & STUTCHBURY (1840) attached the name of *Palaeosaurus platyodon* "to a single specimen of a broadly lanceolate tooth, with serrations at right angles to the axis ... The description of the teeth of *Thecodontosaurus* is perfectly accurate; but I can see no important difference, in the direction of the serrations or otherwise, between these teeth [Figs 4G, N] and the tooth called *Palaeosaurus platyodon*, which, I suspect, may belong simply to a larger *Thecodontosaurus*." The denticles were shown obliquely inclined (Fig. 32C) by LYDEKKER (1888, fig. 33 as *Thecodontosaurus platyodon* following HUXLEY, 1870). However, in a footnote, LYDEKKER (1890, p. 247) noted that the "serrations are made too oblique" in his earlier figure (but used in subsequent BMNH publications, e.g. ANON, 1896, fig. 18D and as recently as SWINTON, 1958, fig. 53). SEELEY (1895), who also considered this representation to be inaccurate, stated that the serrations are at right angles to the cutting-margin as shown in the good figure of ZITTEL (1890) (Fig. 32D).

HUENE (1908a, p. 240), who recognized the tooth as that of a phytosaur (HUENE, 1908b), described what he thought was the type tooth (Figs 32E-G) as "broad, flat, with a somewhat constricted base, the shape being similar to the top half of a broad, lance-like leaf. The entire anterior and posterior edges show fine, but not deep Palisadenkerbung; there are a good 3 denticles per mm. The length of the tooth crown is 17 mm and the maximum width 12.5 mm. In the center of the area that was probably cut out by R. OWEN for a thin section, half of the thickness of the tooth crown, which is embedded in matrix, equals 4 mm, and about 2 mm below the apex 2 mm; the side obscured is probably the flatter one" (translation, HUNGERBÜHLER).

Available drawings (Figs 32A-F) of the tooth vary as regards the outline (but note that reversed in Figs 32B, D) and the form of the serrations, despite the fact that only one tooth is supposedly involved (Figs 33A-D). However, this tooth may not be the holotype because STUTCHBURY (MS) listed "No. 1 Flattened tooth with two cutting edges serratures at right angles to the axis of the tooth. Identical with *Palaeosaurus platyodon.* [No.] 4 Do- Do-" (with No. 4 listed immediately underneath No. 1). This indicates that originally there were three teeth of *Palaeosaurus platyodon* and this would explain why STUTCHBURY allowed one of them (probably No. 1 or 4, not the holotype) to be sectioned by OWEN. The third tooth could be the recently catalogued BMNH R16119 figured by HUENE (1908a,b, 1911; see below). The holotype was probably on exhibition and destroyed in 1940 but, following the BCM catalogue and HUENE (1908a), BRSMG *Ca7448/3 (Figs 33A-D) is regarded as the holotype of *Rileyasuchus* (*Palaeosaurus*) *platyodon* (RILEY & STUTCHBURY, 1840).

The exposed surface of the holotype tooth (Figs 33A, B) is slightly concave vertically and gently convex transversely so it is the lingual (medial) surface (cf. Figs 32H-K, 33E, F, J, N, Q). The tooth, which is strongly asymmetrical mesiodistally (anteroposteriorly) with an expanded mesial (anterior) blade, is a mid- to posterior dentary tooth of a heterodont phytosaur (gen. et sp. indet.) (HUNGERBÜHLER, pers. comm., see HUNGERBÜHLER, 2000). As regards the angle of the serrations, a point of disagreement in previous descriptions, the ones on the mesial edge are slightly angled apically (Figs 33B, D) whereas the distal ones are perpendicular to the edge (Figs 33A, C). Another tooth of *Rileyasuchus* (*Palaeosaurus*) *platyodon* (Figs 32H-N, 33I-L) from Clifton, figured by HUENE (1908a, figs 264a-c, 1908b, pl. 6, figs 1a-c, 1911, figs 31.1a-d), shows a similar asymmetry of the serrations (Figs 33K, L). This tooth is also from the posterior part of the maxilla or dentary of a heterodont Phytosauria indet.

STUTCHBURY (MS) listed "No. 2. Conical tooth fluted similar to young crocodile" but unfortunately this tooth was not catalogued or described and is presumed lost; it may have been another phytosaur tooth.

The only other illustrated tooth of a heterodont phytosaur from England was collected in 1841 from the Rhaetian bone bed of Coomb Hill, between Gloucester and Tewkesbury (4 miles to south, near Cheltenham) by Mr. DUDFIELD. This water worn tooth, briefly described by STRICKLAND (1842, p. 587) as a portion of a tooth with two finely serrated edges from a saurian allied to *Palaeosaurus*, was described in more detail (Figs 32O, P) as the holotype of *Palaeosaurus stricklandi* DAVIS, 1881, a *nomen dubium*. This tooth (Figs 33E-H) is Phytosauria indet (HUNGERBÜHLER, pers. comm), as are two other very similar teeth of different sizes (Figs 33M-R) from the Rhaetian of Somerset that were catalogued

as *Palaeosaurus platyodon* by LYDEKKER [1890, p. 247; donated by Prof. JÄGER in 1889, cited as from "Upper Triassic (?Lower Keuper) of Somersetshire"]; presumably these are the "teeth in the BMNH (hitherto unfigured)" from Durdham Down cited by BENTON *et al.* (2000, p. 80). However, LYDEKKER (1890, p. 247) cited specimens from Durdham Down as from the "Upper Triassic (Lower Keuper) bone-bed near Bristol." and earlier (LYDEKKER, 1888, p. 175) as being in Gloucestershire, the location of Redland, the supposed site of the *Thecodontosaurus* quarry (see section on Locality and geology). Consequently, BMNH R1695 probably came from another unspecified locality in Somerset rather than from Clifton on Durdham Down.

**Humerus** (Figs 37A-I)
A humerus split between two slabs (Figs 37C, D; BRSMG *Ca7461/95♦,96♦) was described by RILEY & STUTCHBURY (1840; also SEELEY, 1895, p. 158) and it is the holotype of *Rileya bristolensis* HUENE, 1902 (Fig. 37E; also Fig. 37A as holotype of *Rileya stutchburi* HUENE, 1920a), the type species of *Rileyasuchus* KUHN, 1961a (*Rileya* preoccupied, ASHMEAD, 1888). This figure or other versions of it (Figs 37B, F) were given by HUENE (1908b, 1911, 1920a, 1958). This specimen was recognized as "broadly phytosaurian" but incorrectly listed as *Thecodontosaurus antiquus* by BENTON *et al.* (2000, p. 79, 105, but not on p. 82). The more concave edge is medial and, as the proximal part shows no evidence of a deltopectoral crest (cf. Figs 37J, K), it is a right humerus with the proximal part exposed in posterior view (Figs 37A-C); the distal part is exposed in anterior view on the counterpart (Figs 37D-F). The two ends of this 170 mm long bone are equally expanded and in the same plane; the head is missing proximally and the entepicondyle external to the lateral condyle is incomplete. BENTON *et al.* (2000) noted that the latter is unfortunate because the presence or absence of an entepicondylar groove, a distinguishing feature of a phytosaurian humerus, cannot be determined. The overall form of the humerus is phytosaurian but the identification is uncertain (cf. Figs 37J, K; HUNGERBÜHLER, pers. comm.). Indeed, WESTPHAL (1976, p. 116) suggested that *Rileya* might be a "Pseudosuchian (?*Stagonolepis*)", i.e. an aetosaur. An entepicondylar groove is present in the humerus of aetosaurs and, as also in most phytosaurs, the ends of the humerus are expanded to a much greater degree than in the Clifton humerus (WALKER, 1961; LONG & MURRY, 1995); the same is true for the humerus of rhynchocephalians (LONG & MURRY, 1995, fig. 16). Given the presence of phytosaur teeth and the absence of any other evidence for aetosaurs or rhynchocephalians at Clifton, it is best to regard the humerus BRSGM *Ca7461/95♦,96♦ as that of Phytosauria indet with *Rileya bristolensis* HUENE, 1902, *Rileyasuchus* KUHN, 1961a and *Rileyasuchus platyodon* (RILEY & STUTCHBURY, 1840) as *nomina dubia*.

HUENE (1908b) also described a similar but larger right humerus (estimated length ~190 mm) exposed in posterior view (Figs 37G-I). It was incorrectly listed as *Thecodontosaurus antiquus* by BENTON *et al.* (2000, p. 82, 106, used in description of humerus of *T. antiquus*, p. 90). This humerus, which is also probably Phytosauria indet, may have had a natural association because, preserved alongside it, is a long thin bony sheet, possibly part of the distal blade of a scapula (Fig. 37I).
Only one other bone of a possible phytosaur has been reported from the United Kingdom. It is a proximal left femur from the Rhaetian of Wigston, Leicestershire, England (Figs 37L-R), collected by Edward WILSON and presented in 1887, which was referred to *Phytosaurus* or *Mystriosuchus* by HUENE (1911). However, this femur, which has a solid shaft (Fig. 37M), is Phytosauria indet or even Crurotarsi indet.

## X. ARCHOSAURIA INDET

***Palaeosauriscus* (*Palaeosaurus*) *cylindrodon***
Unfortunately the holotype tooth of *Palaeosaurus cylindrodon* RILEY & STUTCHBURY, 1840 was destroyed in 1940 so only earlier descriptions and figures are available. RILEY & STUTCHBURY (1840, p. 352) noted that "The portion of this tooth which has been preserved, is about 5/10ths of an inch in length, and 2/10ths in breadth: the edge is finely carinated" (Fig. 32Q; 1.27 x 0.5 mm) ... and that the species, from the form of the tooth, "may be called *P. cylindrodon*." OWEN (1841, 1842a, p. 156) wrote that the portion of the tooth of *P. cylindrodon* preserved "shows that the crown is sub-compressed and traversed by two opposite finely serrated ridges, as in the *Thecodontosaurus*; its length is 5 lines; its breadth at the base 2 lines (1 line = 1/12 inch so 1.06 x 0.42 mm). HUXLEY (1870, p. 43) said that in a solitary tooth of more elongated conical form "termed *Palaeosaurus cylindrodon*, on the other hand, the direction of the serrations is really at right angles to the axis of the tooth; and in its form, also, the tooth more resembles that of *Megalosaurus*, being elongated, with the posterior margin straight or slightly concave, while the anterior contour is convex. The sharp posterior median ridge of the tooth extends for the whole length of the crown, and is strongly serrated throughout. The anterior serrated ridge is visible in what remains of the upper part of the crown; but I am unable to trace it in the lower half of the front face of the enamel" (Fig. 32R). HUENE (1908a, p. 241) as *Thecodontosaurus cylindrodon* noted that "The original is a tooth fragment only ... preserved without apex and base. The tooth is slender, very attenuated, somewhat curved. The side exposed from the matrix is high-vaulted. There are sharp anterior and posterior edges showing very fine, high, and obliquely directed 'Palisadenkerbung'; there are 8 denticles per 1 mm. The maximum preserved length is

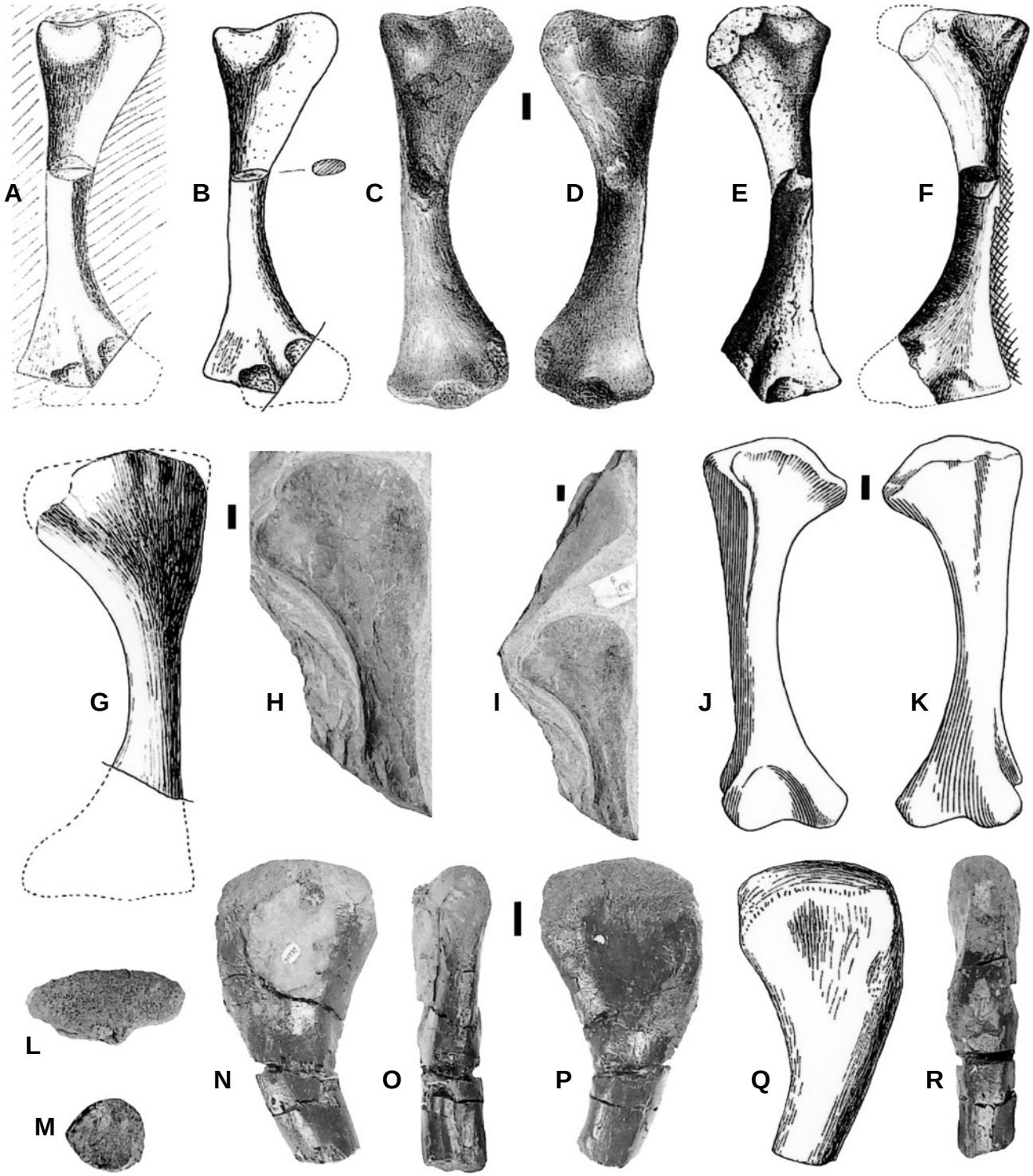



Fig. 37: Phytosauria indet humeri from Clifton [(A-I) *Rileyasuchus* (*Palaeosaurus*) *platyodon* (RILEY & STUTCHBURY, 1840)] and a femur from Wigston (L-R). A-K: humeri from Clifton (A-I) and India (J-K). A-F: holotype of *Rileya bristolensis* HUENE, 1902, type species of *Rileyasuchus* KUHN, 1961a, BRSMG *Ca7461/96♦ (A-C) and counterpart *Ca7461/95♦ (D-F): A-C: proximal right humerus in posterior view with impression of anterior surface of distal part and D-F: distal right humerus in anterior view with impression of posterior surface of proximal part; G-I: proximal part of right humerus BMNH R1541 in posterior view (with part of blade of scapula in I). J-K: *Parasuchus hislopi* from Maleri Formation (Upper Triassic) of India, right humerus (left reversed) in J: anterior and K: posterior views. L-R: BGS 90737 from Rhaetian of Wigston, Leicestershire, England, proximal left femur in: L: proximal; M: distal cross-sectional; N: posterior; O: medial; P-Q: anterior and R: lateral views. A from HUENE (1920a), B from HUENE (1958), C, D from RILEY & STUTCHBURY (1840), E from HUENE (1902), F, G from HUENE (1908b), J, K from CHATTERJEE (1978); Q from HUENE (1911); scale bars = 10 mm.

14 mm (posterior edge); at two points in 6 mm distance from each other (the total length of the preserved anterior edge) the width measures 6 mm at the basal point, 4 mm at the apical point. Such teeth are not found in parasuchians [phytosaurs], and it is most likely that the tooth derives from a theropod. The tooth must have originated from a not very large individual" (translation, HUNGERBÜHLER). In the caption to the figures (Figs 32S-U) it is noted that the tooth was the original of R. OWEN, Odontography, i.e. OWEN (1841).

BENTON *et al.* (2000, p. 104; but not included on p. 82) incorrectly indicated the tooth of *Palaeosaurus cylindrodon* (BRSMG *Ca7449/4♦ of HUENE, 1908a, fig. 266) as a paralectotype of *Thecodontosaurus antiquus* MORRIS, 1843.

An obvious problem is that the descriptions and illustrations differ from each other much more than do those for the holotype of *Rileyasuchus* (*Palaeosaurus*) *platyodon*. However, there were at least two teeth because STUTCHBURY (MS) listed "No. 7. Tooth, incurved, with one cutting edge serrated, resembles *Palaeosaurus cylindrodon* but differs from the latter having [i.e. that has] two cutting edges." This might be the tooth (Fig. 32R) described by HUXLEY (1870) in which, as quoted above, the lower half of the anterior edge lacked a serrated ridge (in other tooth or teeth the anterior edge is shown completely serrated, Figs 32Q, T). All accounts agree that the teeth were cylindrical in form (hence name), so obviously not from *Thecodontosaurus antiquus* (Figs 4D-F, N-T), *Rileyasuchus platyodon* (Figs 32A-D, 33A, B), the Clifton theropod (Figs 32V, W), or *Megalosaurus cambrensis* (Rhaetian of south Wales, Aust Cliff and Somerset; NEWTON, 1899; GALTON, 1998a, 2005a). The difference in serrations could be a function of tooth position. The figures of HUXLEY (1870) and HUENE (1908a, also text) agree in the obliqueness and fineness of the serrations but differ on their length (Figs 32R, T, U). HUNGERBÜHLER (pers. comm.) notes that the tooth form of the referred teeth does not fall readily into one of the tooth types of phytosaurs and the denticles are too long and too oblique. However, he adds that the lingual side was possibly phytosaur-like flat (Fig. 32S), but the absence of a clear outline of the lingual side might be the result of HUENE (1908a) simply distinguishing the tooth (dark shade) from the matrix (light shade) by an imaginary straight line. If asymmetrical, then the tooth proportion of height to length is too slender to be typical phytosaurian. The denticles are very fine but the spacing comes close to the extreme observed in the phytosaurian range that is 6 per mm. The vaultedness seems to preclude a theropod origin (*contra* HUENE, 1908a). The tooth form and the obliqueness of the very fine serrations would also seem to preclude any known theropod dinosaur.

The teeth (Figs 32Q-U) are not typical indeterminate carnivorous archosaurian teeth as commonly presumed (CHARIG *et al.*, 1965; GALTON, 1973; GALTON & WALKER, 1996a; BENTON *et al.*, 2000) because several archosaurian groups (theropods, typical prosauropods, phytosaurs) can be safely excluded. In addition the teeth are potentially diagnostic on the basis of the cylindrical shape with the obliquely inclined (45° to cutting edge), long and very fine denticles (8 per mm). Consequently, *Palaeosauriscus cylindrodon* (RILEY & STUTCHBURY, 1840) is tentatively regarded as a valid taxon, not a *nomen dubium*, even though it is Archosauria indet because the group it belongs to is not apparent at the moment.

**Jaw framents** (Figs 34D, G, I)

Three partial jaws are identifiable only as Archosauria indet based on the Rhaetian age and the non-marine environment that eliminates the other reptilian groups with a thecodontian implantation. The fragmentary jaw with a replacement tooth, described by WILLIAMS (1835a, b, 1837) from Clifton and figured by RILEY & STUTCHBURY (1840) as *Thecodontosaurus* (Fig. 34D), cannot be located. WILLIAMS (1835a, p. 112) noted that "the form is triangular, the point sharp, and the margin on each side regularily crenated from the apex downwards." From this description and the illustration (Fig. 34D), it would appear that the denticles were perpendicular to the edge, as in a carnivorous form, rather than apically inclined as in *Thecodontosaurus*. Most of a dentary in medial view (Fig. 34G) was figured as *Thecodontosaurus* by HUENE (1908a) but, as it lacks synapomorphies of the Sauropodomorpha (ventral deflection of anterior end of bone, overlap of the teeth in lateral view), it is not *Thecodontosaurus*. It might be theropod as it was on the same block as a theropod ungual (Fig. 34H; HUENE, 1908a, pl. 82, fig. 2). A very small jaw piece figured with three alveoli (Fig. 34I) by HUENE (1914a, p. 80) is possibly also Archosauria indet. The three openings are probably on the medial surface of the bone and represent foramina for the access of replacement teeth into the alveoli. Unfortunately, this cannot be confirmed because the jaw piece, originally on the main block of YPM 2195, was prepared away sometime after 1911.

**Postcrania**

**Caudal vertebra** (Figs 34R-V)

BENTON *et al.* (2000, p. 88, figs 9E-G) noted that an anterior caudal centrum (Figs 34R-V) has three longitudinal ridges along the ventral surface that, because they are unusual for a dinosaur, may not be from *Thecodontosaurus antiquus*. I agree with this suggestion but, as no alternative identification is evident, this distinctive centrum is tentatively regarded as Archosauria indet.

**Scapulacoracoid** (Figs 38A, B)

The "neural spine" of BENTON *et al.* (2000, p. 106) appears to be a poorly preserved right scapula-coracoid with the base of the scapular blade preserved, the more proximal part of the scapula and the partial coracoid being represented by an impression of the medial surface

and the most medial layer of bone. It is not referable to the Dinosauria or Phytosauria but it may be Archosauria indet (?Crurotarsi).

## XI. REPTILIA INDET

Illustrations of a few interesting bones of uncertain affinity from Clifton are provided in the hope that comparisons with more complete material will result in a more positive identification.

**Possible skull bones** (Figs 34E-F)
These include a partial left parietal (Fig. 34F) and a peculiar bone (Fig. 34E) that is preserved as a thin layer of almost flat compact bone in internal view with the inner cancellous bone removed. The very irregular outline, not resembling any appendicular bone, is suggestive of a bone from the sidewall of the braincase (?prootic), but it is difficult to identify it positively as part of either a skull or a vertebra.

**Limb bones** (Figs 38C-K)
These include a small distal humerus (Figs 38E-G), the shaft of which includes cancellous bone (Fig. 38E), and a small proximal metapodial (Figs 38H-I) with a shaft that is clearly hollow (Fig. 38H). BENTON *et al.* (2000, p. 79, 105) refer a small metacarpal (Figs 38I, J), originally referred to the phytosaur *Rileya* by HUENE (1908b, pl. 6, figs 7a, b, 1911, figs 31.7a,b), to *Thecodontosaurus.* This small flattened bone appears to be too slender waisted to be from a basal sauropodomorph but, as it does not match any metapodial of the associated manus or pes of phytosaurs or aetosaurs (e.g. CHATTERJEE, 1978, figs 11e, 13d; LONG & MURRY, 1995, figs 44, 50G, 53A, 55, 109), it is regarded as Reptilia indet. The massive large humerus (or possibly tibia; Figs 38C, D), with poorly preserved expanded ends, is clearly not dinosaurian and is also Reptilia indet.

## XII. FAUNAL DIVERSITY AT CLIFTON QUARRY

The Rhaetian archosaurian fauna from Clifton includes three humeral morphs representing dinosaurs with a body length of ~2-3 m. The humeri of *Asylosaurus yalensis* (Figs 15A-N) and the slender morph (?*Thecodontosaurus antiquus*, Figs 15Q, R, 16C-F) are very basal sauropodomorphs whereas the robust morph (Figs 15S-U, 16A, B, H-J) is a more derived basal sauropodomorph (Anchisauria *sensu* UPCHURCH *et al.*, 2007). These animals were presumably omnivorous to herbivorous (BARRETT, 2000) as was a fourth humeral morph (Fig. 16L), that of *Pantydraco caducus* from South Wales, another very basal sauropodomorph from the area adjacent to the Severn Estuary of Britain (GALTON *et al.*, 2007). The ecological niches of these herbivorous species presumably overlapped with partitioning possibly being a function of size differences and different degrees of omnivory. This high diversity of smaller basal sauropodomorphs is unique to southwestern Britain. *Camelotia borealis*, a partial skeleton from the Rhaetian of Somerset, is a very large and presumably completely herbivorous basal sauropod (UPCHURCH *et al.*, 2007; YATES, 2007) with a femur 1000 mm long (GALTON, 1998a, 2005a). The shaft of a large femur from the Rhaetian bone bed at Aust Cliff, Avon near Bristol is probably also referable to *Camelotia* (GALTON, 2005a).
The only possible record from Clifton of an ornithischian dinosaur, that was probably fully herbivorous, is one small dorsal centrum (Figs 34M-Q); columnar stegosaurid femoral shafts (original length ~900 mm), that are straight in anterior and lateral views and slightly wider transversely than antero-posteriorly, represent another large herbivore from the Rhaetian of Aust Cliff (GALTON, 2005a).
The remains of carnivorous theropod dinosaurs are very much rarer than those of sauropodomorphs at Clifton, being represented by a few postcranial bones that probably represent two taxa, a basal theropod (?Herrerasauridae indet or possibly Dinosauriformes indet) (Figs 35A-E, 36; 3 bones) and a more derived theropod taxon (Figs 34B, 35F-I; 2 bones). The one small theropod tooth with fine serrations (Figs 32V, W) is rather different from those of the large theropod *Megalosaurus cambrensis* from the Rhaetian of south Wales and Somerset (GALTON, 2005a).
Heterodont phytosaurs, which were primarily aquatic carnivores, are represented by teeth (*Rileyasuchus platyodon*, Figs 32A-N, 33A-D, I-L; 3 originally, STUTCHBURY, MS) and two humeri (Figs 37A-H).
The enigmatic *Palaeosauriscus* (*Palaeosaurus*) *cylindrodon*, the rarest element of the fauna, was represented by at least two very small teeth (STUTCHBURY, MS; Figs 32Q-U) but the affinities and habitat (terrestrial or aquatic) of this small carnivorous or possibly pisciferous (based on circular cross section of teeth) form are unknown.
Several more reptilian elements of unknown affinities are represented by skull bones (5, Figs 34C-E, G), vertebrae (2, Figs 34L-U), a scapula-coracoid (Figs 38A, B) and limb bones (4, Figs 38C-K).
The only definite non-archosaurian reptiles from Clifton are three specimens of the very small herbivorous sphenodontid lepidosaur *Diphydontosaurus avonis* WHITESIDE, 1986 (dentary, Fig. 34B; partial maxilla BMNH R14111, VICKERS-RICH *et al.*, 1999; partial articulated skeleton, Fig. 34A, HALSTEAD & NICOLL, 1971, pl. 23B). The predominance of archosaurs from Clifton is real, not due to selective collecting, because every scrap of bone appears to have been collected (350 catalogued specimens, Appendices 3-7), and this is in contrast to the much greater abundance of non-archosaurs from other Rhaetian fissure deposits in southwestern Britain (for details see FRAZER, 1994, 2006). However, the bones from these quarries are very small compared to

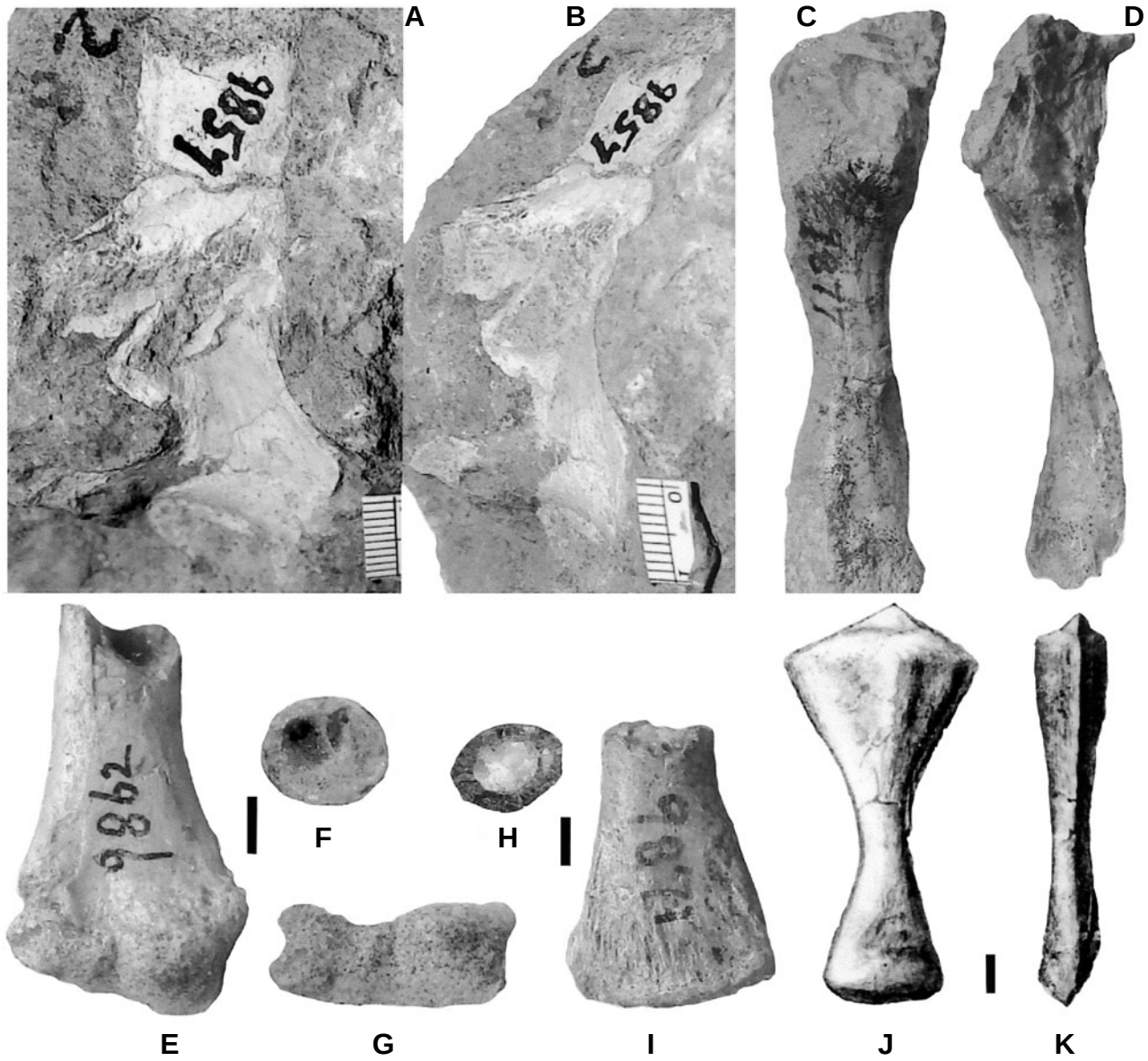



Fig. 38: Reptilian bones from Clifton. A-B: Archosauria indet, ?Crurotarsi, incomplete left scapula-coracoid ANSP 9875 in A: lateral and B: anterolateral views. C-D: humerus (or tibia) ANSP 9877 in C: anterior or posterior and D: side views. E-G: distal left humerus ANSP 9862 in E: proximal; F: posterior and G: distal views. H-I: distal part of metapodial ANSP 9871 in H: proximal and I: anterior or posterior views. J-K: metacarpal BRSMG Ca7505/102♦ in J: anterior or posterior and K: side views, from HUENE (1908b). Scale with 1 mm subdivisions (A, B); scale bars = 10 mm (C, D) and 5 mm (E-K).

most of those from Clifton, that are usually disarticulated and incomplete, so there may have been a bias in preservation based on sorting by size before the remains reached the cave at Clifton.

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**Appendix 1 : BRSMG/BCM numbers for RILEY & STUTCHBURY (1840)**

The BRSMG/BCM numbers and figure numbers in this paper are given for the specimens illustrated by RILEY & STUTCHBURY (1840) ; for full details see Appendix 3. SEELEY (1895) noted that the previously figured vertebrae were BCM 17-19, 25, 27 and 38. However, BENTON *et al.* (2000, appendix 1) do not list BCM 19 and only BRSMG *Ca4532a/17 (mid-caudal vertebra) is indicated as figured by RILEY & STUTCHBURY (1840, pl. 29, fig. 8) (Fig. 11S). BRSMG Ca7510/18 is three caudals (Fig. 12Q), which do not correspond to any of the figures in RILEY & STUTCHBURY (1840) ; this is also true for BRSMG Cb4163a,b/25 (two dorsal vertebrae) and Cb4164a,b/27 (two caudal vertebrae). BRSMG *Ca7503/38♦ is a metatarsal (Figs 31V, W) and ribs, one of which might have corresponded to RILEY & STUTCHBURY (1840, pl. 29, fig. 10) (Fig. 8L).

**RILEY & STUTCHBURY, 1840, pl. 29 :**

**figs 1, 2**, *Ca7465/1♦, right dentary and detail of a tooth, holotype of *Thecodontosaurus* RILEY & STUTCHBURY, 1836a and *T. antiquus* RILEY & STUTCHBURY *vide* OWEN, 1842a (= *T. antiquus* MORRIS, 1843) (Figs 4A, D).

**fig. 3**, William's Collection♦, jaw fragment with tooth (Fig. 34D).

**fig. 4**, *Ca7499/4♦, tooth, holotype of *Palaeosaurus cylindrodon* RILEY & STUTCHBURY, 1840 (Fig. 32Q).

**fig. 5**, *Ca7448/3, tooth, holotype of *Palaeosaurus platyodon* RILEY & STUTCHBURY, 1840 (Fig. 32A).

**fig. 6**, *Ca7452/26♦, posterior dorsal vertebra (Fig. 10D).

**fig. 7**, *C4533/8, cross-section of posterior dorsal vertebra (Fig. 10B).
**fig. 8**, *Ca4532a/17, mid-caudal vertebra (Fig. 11S).
**fig. 9**, *C4534/30, large proximal chevron (Fig. 12R).
**fig. 10**, *?Ca7503/38♦, proximal right dorsal rib (Fig. 8L).
**fig. 11**, *Ca7450/61♦, incomplete large left ilium (Fig. 21A).

**Riley & Stutchbury, 1840, pl. 30:**
**figs 1, 1a**, *Ca7461/95♦,96♦, left humerus on slab split into two parts (Figs 37C, D).
**fig. 2**, *Ca7462/76♦, right tibia (Fig. 28A).
**fig. 3**, *Ca7456/67, left femur (Fig. 26D).
**figs 4, 4a**, *Ca7492/69I♦, proximally incomplete left femur (Figs 26R, S).
**fig. 5**, *Ca7453/66♦, incomplete right humerus (Fig. 16E).
**fig. 6**, *Ca7459/46♦, left ulna (Fig. 17N).
**figs 7, 7a**, *-/-♦, large right proximal fibula (Figs 31A, B).
**fig. 8**, *Ca7485/46b, manual phalanx 2, digit II or III (Fig. 20A).
**fig. 9**, *****Ca7463/88♦, right metacarpal I (Fig. 18Q).
**fig. 10**, *****-/-♦, manual ungual phalanx I (Fig. 20K).
**fig. 11**, *Ca7455/86♦, pedal ungual phalanx I (Fig. 20M).
**fig. 12**, *-/-♦, pedal ungual phalanx II (Fig. 20O).
**fig. 13**, *Ca7451a/81, manual ungual phalanx II (Fig. 20P).

**Appendix 2: BCM numbers with corresponding BRSMG numbers**
For full details on specimens, see Appendix 3 under BRSMG number.

**1♦**, *Ca7465, right dentary.
**2**, C4529, left dentary.
**3**, *Ca7448, tooth.
**4♦**, *Ca7449, tooth.
**5**, Ca7496, distal dorsal rib.
**6**, Cb4151, anterior cervical vertebra.
**7**, Cb4152, indeterminate vertebra.
**8**, *C4533, posterior dorsal vertebra.
**9♦**, Ca7470, mid-dorsal vertebra.
**11**, Cb4153, anterior dorsal vertebra.
**12**, *Cb4154, posterior dorsal vertebra.
**13♦**, Ca7469, mid-dorsal vertebra.
**14♦**, Ca7468, posterior dorsal vertebra.
**15**, Cb4155, posterior dorsal vertebra.
**15a**, Cb4156, dorsal vertebra.
**16♦**, Ca7472, partial centrum of anterior cervical vertebra.
**16**, Ca7473, proximal caudal centrum.
**16b**, Ca7474, proximal caudal centrum.
**17**, *Ca4532a,b, mid-caudal vertebra and associated chevron, slightly more distal caudal vertebra.
**18**, Ca7510, 3 associated mid-caudal vertebrae and a chevron.
**20♦**, Ca7471, dorsal vertebra.
**20♦**, Ca7509, 4 very distal caudal vertebrae.
**21♦**, Ca7508, 4 very distal caudal vertebrae.
**22**, Ca7475, proximal caudal vertebra.
**23**, Ca7507, 3 caudal vertebrae.
**25**, Cb4163a,b, 2 dorsal vertebrae.
**26♦**, *Ca7452, posterior dorsal vertebra.
**27**, Cb4164a,b, 2 caudal vertebrae.
**28**, Cb4165, cervical vertebra, limb bone.
**29**, Cb4166, caudal vertebra.
**30**, *C4534, large proximal chevron.
**31**, Cb4167, vertebra, dorsal ribs, fibula.
**32**, C4528, proximal dorsal rib.
**33**, Cb4168, dorsal rib, ?proximal fibula.
**34**, Cb4169, dorsal rib shaft.
**35**, Ca7466, distal dorsal rib.
**36**, Cb4170, dorsal rib shaft.
**37♦**, Ca7477a-c, proximal rib, right humerus, proximal right femur.
**38♦**, *Ca7503, a, dorsal ribs, b, proximal metatarsal I.
**39**, Cb4172, dorsal rib shaft.
**40**, Cb4173, dorsal rib.
**41**, Cb4174a,b, 2 posterior dorsal vertebrae, metacarpal III.
**42♦**, Ca7502, left fibula.
**44**, Cb4175, shaft of femur.
**46♦**, *Ca7459, left ulna.
**46b**, *Ca7485, manual phalanx 2, digit II or III.
**47**, Ca7497, right fibula.
**48**, Cb4176, ?longitudinally sectioned knee.
**49**, Cb4177, proximal left femur (with 74), 2 vertebrae.
**50**, Cb4178, mid-caudal centrum, slender long bone.
**52**, Ca7504, right radius.
**53**, Ca7495, distal right tibia.
**54**, Cb4179, sectioned metacarpal II.
**55**, Ca7499, distal left metatarsal II.
**56♦**, Ca7484, metacarpal IV.
**57♦**, Ca7460, left ilium.
**58**, Cb4180, anterior dorsal rib.
**59♦**, Ca7476a,b, distal caudal vertebra, right humerus, proximal right femur, proximal dorsal rib.
**60♦**, Ca7506, partial right ilium.
**61♦**, *Ca7450, partial left ilium.
**62**, Cb4181, partial left ilium.
**63♦**, Ca7457a-g, 3 ilia, distal fibula, left tibia, ribs, caudal vertebra..
**66♦**, Ca7453, partial right humerus.
**67**, *Ca7456, left femur.
**68♦**, Ca7491, proximal left femur.
**69**, Cb4182, incomplete mid-dorsal vertebra.
**69I♦**, Ca7492, distal left femur.
**69a (=69II)**, Ca7494, distal right femur.
**70♦**, Ca7493, distal left femur.
**71**, Ca7490, distal right femur.
**72**, Cb4183, right femur lacking ends.
**73**, C4530, distal right femur.
**74**, Cb4177 (with 49), proximal left femur.
**75**, Cb4184, proximal left femur.
**76♦**, *Ca7462, right tibia.
**77**, Cb4185, distal humerus.
**77a**, C4531, proximal right tibia.
**77b♦**, Ca7513, proximal femur.
**78**, Cb4186, dorsal vertebra, proximal tibia.
**79**, Ca7486, left ulna.
**80**, Ca7482, metacarpal II.
**81**, *Ca7451a,b, manual ungual II, right metatarsal III.
**82♦**, Ca7483, metacarpal II.
**83♦**, Ca7498, right metatarsal III.
**84**, Cb4187, manual ungual phalanx II.
**85♦**, Ca7487a-c, radius, theropod dentary, theropod manual ungual.
**86♦**, *Ca7455, pedal ungual phalanx I.
**87♦**, *Ca7454, manual ungual phalanx I.
**88♦**, *Ca7463, phalanx, metatarsal IV.
**89♦**, Ca7479, left scapula, coracoid.

**90♦**, Ca7480, left scapula.
**91**, Ca7481, left scapula blade.
**92♦**, Ca7478, left scapula, coracoid.
**93♦**, Ca7512, distal humerus.
**94**, Cb4188, proximal tibia.
***95♦, *96♦**, Ca7461, split left humerus.
**97♦**, Ca7458, proximal left scapula.
**98**, Cb4189, distal humerus.
**99**, Cb4190, proximal right femur.
**100♦**, Ca7489, proximal left pubis.
**101♦**, Ca7488, proximal right pubis.
**102**, Ca7505, metacarpal.
**103**, Cb4191, partial neural arch.
**106,** dorsal ribs, now BMNH R1536-38.
**108**, Cb4192, distal dorsal rib.
**110**, Cb4193, distal dorsal rib.
**115**, Cb4194, distal dorsal rib.
**116**, Cb4195, distal dorsal rib.
**117**, Cb4196, 3 dorsal ribs.
**118♦**, Ca7464, right humerus.

**Appendix 3 : Specimens from Clifton in BCM**

Unless stated to the contrary, most of these specimens were referred to *Thecodontosaurus antiquus* by BENTON *et al.* (2000, p. 82, 106) but are basal Sauropodomorpha indet. Gracile and robust morphs were referred to *T. antiquus* and *T. cylindrodon* by HUENE (1908a). Non-*Thecodontosaurus* and non-*Asylosaurus* basal sauropodomorph bones are referred to three groups that are indicated as [A], [B] or [C] at the end of each entry (see Systematic section) ; specimens without identification are Archosauria or even Reptilia indet.

***-/-♦**, proximal large right fibula (RILEY & STUTCHBURY, 1840, pl. 30, figs 7, 7a), one of the first bones brought in by workers to the Bristol Institution (STUTCHBURY, 1836) (Figs 31A, B) [C].
***-/-♦**, manus ungual I (RILEY & STUTCHBURY, 1840, pl. 30, fig. 10) (Fig. 20K) [B].
***-/-♦**, pes ungual II (RILEY & STUTCHBURY, 1840, pl. 30, fig. 12) (Fig. 20O) [C].
**C4528/32**, a proximal right rib in posterior view (HUENE, 1908a, pl. 77, fig. 3), miscited as rib figured by RILEY & STUTCHBURY (1840, pl. 29, fig. 10), a right in anterior view (Fig. 8L), by BENTON *et al.* (2000, p. 104, fig. 10C) (Fig. 8K).
**C4529/2**, left dentary (HUXLEY, 1870, pl. 3, figs 1, 2 ; HUENE, 1908a, figs 207a-c, pl. 74, fig. 2 ; GALTON, 1985b, pl. 9, figs 6, 7 ; BENTON *et al.*, 2000, figs 3B-G, 4 ; GALTON *et al.*, 2007, fig. 1L ; detail of teeth only without specimen number, GALTON, 1984a, fig. 4F, 1985c, fig. 5C, 1986b, fig. 16.4B, 1990, fig. 14.4D ; GALTON & UPCHURCH, 2004, fig. 12.5D), designated by GALTON (1985b) as neotype of *Thecodontosaurus* RILEY & STUTCHBURY, 1836a and *T. antiquus* MORRIS, 1843 (so neotype of *Thecodontosaurus antiquus* RILEY & STUTCHBURY *vide* OWEN, 1842a ; GALTON, 2005a, GALTON *et al.*, 2007) (Figs 4G-T).
**C4530/73**, distal right femur (HUENE, 1908a, pl. 85, figs 4a, b as gracile ; BENTON *et al.*, 2000, p. 82, 105) (Figs 27H-L) [A].
**C4531/77a**, proximal right tibia (HUXLEY, 1870, pl. 3, fig. 8 ; HUENE, 1908a, pl. 88, figs 3a, b ; BENTON *et al.*, 2000, figs 18A-E but A, lateral and D, medial views) (Figs 28D-K) [C].
***C4533/8**, transversely sectioned posterior dorsal vertebra in posterior view (RILEY & STUTCHBURY, 1840, pl. 29, fig. 7 ; as a caudal in BENTON *et al.*, 2000, p. 82, as a dorsal p. 87, as a anterior caudal p. 104) (Figs 10B, C) [A].
***C4534/30**, proximal large chevron (RILEY & STUTCHBURY, 1840 : pl. 29, fig. 9 ; HUENE, 1908b, pl. 6, fig. 3, 1911, fig. 31.3 as phytosaur *Rileya bristolensis* ; BENTON *et al.*, 2000, 90, fig. 10F as *Thecodontosaurus antiquus* but incorrectly identified as BRSMG Ca7510 in caption) (Figs 12R-T) [C].
***Ca4532a-c/17**, mid-caudal vertebra and articulated proximal end of a chevron (**a** ; Figs 11R-Z ; RILEY & STUTCHBURY, 1840, pl. 29, fig. 8 ; HUXLEY, 1870, pl. 3, figs 5, 6 ; HUENE, 1908a, pl. 78, figs 10, 11 ; BENTON *et al.*, 2000, 104, figs 9L, 10D, E ; chevron C4532c/17 and Ca4532c/17 of BENTON *et al.*, 2000, p. 82, 104) ; second slightly more posterior caudal (**b** ; Fig. 12B) and a half caudal (**c**) [A].
**Ca4715a,b**, tooth (**a**, Fig. 4U) [A], **b**, phalanx [C].
***Ca7448/3**, isolated tooth, middle to posterior maxillary or posterior dentary tooth in lingual view, holotype of *Palaeosaurus platyodon* RILEY & STUTCHBURY, 1840 and referred to *Rileyasuchus platyodon* (RILEY & STUTCHBURY, 1840), both *nomina dubia* (RILEY & STUTCHBURY, 1840, pl. 29, fig. 5 ; OWEN, 1841, pl. 62A, fig. 7 ; LYELL, 1841, fig. 296, and in subsequent editions as well as several other books on geology ; PICTET, 1853, pl. 26, fig. 1 ; LYDEKKER, 1888, fig. 30 ; NICHOLSON & LYDEKKER, 1889, fig. 1066 ; ZITTEL, 1890, fig. 625 ; HUENE, 1908a, figs 263a-c ; ANON, 1896, fig. 18D ; SWINTON, 1958, fig. 53] (Figs 32A-G, 33A-D), crurotarsal heterodont Phytosauria indet.
***Ca7449/4♦**, tooth of carnivorous form, holotype of *Palaeosaurus cylindrodon* RILEY & STUTCHBURY, 1840, type species of *Palaeosauriscus* KUHN, 1959 (RILEY & STUTCHBURY, 1840, pl. 29, fig. 4 ; HUXLEY, 1870, pl. 3, fig. 3 ; HUENE, 1908a, figs 266a, b ; GLUT, 1997, fig. p. 673 from HUENE, 1908a, incorrectly cited as after RILEY & STUTCHBURY, 1836) (Figs 32Q-U), Archosauria indet.
***Ca7450/61♦**, partial left ilium (RILEY & STUTCHBURY, 1840, pl. 29, fig. 11 ; HUENE, 1908a, fig. 226) (Figs 21A, 22H) [B].
***Ca7451a,b/81, a :** manual ungual II with **b :** slender left metatarsal III (**a, b** ; Figs 31F-K ; as right in HUENE, 1908a, pl. 90, fig. 1, ?3b and BENTON *et al.*, 2000, p. 96, fig. 18Q, extant p. 82, incorrectly indicated as lost p. 105 (**a** only, Figs 20P-R ; RILEY & STUTCHBURY, 1840, pl. 30, fig. 13 ; **b** only, GALTON & CLUVER, 1976, fig. 8F), **a** [C], **b** [A].
***Ca7452/26♦**, longitudinally sectioned posterior dorsal vertebra (RILEY & STUTCHBURY, 1837, fig. p. 94, 1840, pl. 29, fig. 6 ; HUENE, 1908a, fig. 212) (Fig. 10D) [A].
***Ca7453/66♦**, incomplete right humerus (RILEY & STUTCHBURY, 1840, pl. 30, fig. 5 upside down as ischium ; HUENE, 1908a, pl. 81, fig. 1, gracile humerus ; GALTON *et al.*, 2007, p. 120) (Figs 16E, F) ?*Thecodontosaurus antiquus*.
***Ca7454/87♦**, manual ungual phalanx II (HUENE, 1908a, fig. 235), incorrectly identified by BENTON *et al.* (2000, p. 105) as original for RILEY & STUTCHBURY (1840, pl. 30, fig. 10 ; see Fig. 20K) (Fig. 20L) [B].
***Ca7455/86♦**, pedal ungual phalanx I (RILEY & STUTCHBURY, 1840, pl. 30, fig. 11 ; HUENE, 1908a, pl. 90, fig. 7) (Figs 20M, N) [C].
***Ca7456/67**, left femur (RILEY & STUTCHBURY, 1840, pl. 30, fig. 3 ; HUENE, 1908a, pl. 87, figs 1, 2, robust femur ; BENTON *et al.*, 2000, figs 16A, B), has burn marks, label reads "Air raid - recovered May 1941") (Figs 26A-H) [C].
**Ca7457a-g/63♦,** block (HUENE, 1908a, pl. 84) with 3 ilia : **a** : left (Figs 21E, 22F, G ; SEELEY, 1895, fig. 2) ; **b** : right (Figs 21F, 22C, D, SEELEY, 1895, fig. 3) and **c** : incomplete right (Figs 21G, 22E) ; robust left tibia (**d** ; Fig. 28C) ; **e** : cervical rib (Figs 8H, I ; SEELEY, 1895, fig. 1), **f** : distal caudal vertebra

(SEELEY, 1895, fig. 3c), **g**: ?proximal metatarsal (as proximal fibula, robust, HUENE, 1908a), **a, b** [A], **c** [B], **d-f** [C].

**Ca7458/97♦**, proximal left scapula in medial view (SEELEY, 1895, fig. 7; HUENE, 1908a, pl. 81, fig. 3, gracile form) (Figs 14G, H) [C].

***Ca7459/46♦**, left ulna (RILEY & STUTCHBURY, 1840, pl. 30, fig. 6 as tibia; SEELEY, 1895, fig. 10; HUENE, 1908a, fig. 223, pl. 82, fig. 3; GLUT, 1997, fig. p. 898) (Figs 17N-Q) [C].

**Ca7460/57♦**, left ilium in medial view (HUXLEY, 1870, pl. 3, fig. 7; HUENE, 1908a, fig. 225, pl. 82, fig. 4; GLUT, 1997, fig. p. 898; BENTON *et al.*, 2000, fig. 15D) (Figs 21C, D, 22J) [B].

***Ca7461/95♦,96♦**, left humerus on slab split into two parts (RILEY & STUTCHBURY, 1840, pl. 30, figs 1, 1a; SEELEY, 1895, p. 153; HUENE, 1902, fig. 75; 1908b, pl. 6, fig. 5, 1911, fig. 31.5; 1920a, fig. 3; 1958, fig. 3A; discussed by BENTON *et al.*, 2000, p. 79 as *Ca7461 but incorrectly listed under *Thecodontosaurus antiquus* on p. 105), holotype of *Rileya bristolensis* HUENE, 1902 [and *R. stutchburi* HUENE, 1920a], type species of *Rileyasuchus* KUHN, 1961a (Figs 37A-F), all *nomina dubia*, Phytosauria indet.

***Ca7462/76♦**, right tibia (RILEY & STUTCHBURY, 1840, pl. 30, fig. 2; HUENE, 1908a, pl. 88, fig. 2) (Figs 28A, B) [C].

***Ca7463/88♦**, slender right metacarpal I (RILEY & STUTCHBURY, 1840, pl. 30, fig. 9; HUENE, 1908a, pl. 90, fig. 4) (Figs 18Q, R) [A].

**Ca7464/118♦**, right humerus (SEELEY, 1896, fig. 8; HUENE, 1908a, pl. 80, fig. 2, robust; GALTON *et al.*, 2007, fig. 1K) (Figs 16A, B) [B].

***Ca7465/1♦**, right dentary, holotype of *Thecodontosaurus* RILEY & STUTCHBURY, 1836a, type species of *T. antiquus* RILEY & STUTCHBURY *vide* OWEN, 1842a and *T. antiquus* MORRIS, 1843 (RILEY & STUTCHBURY, 1840, pl. 29, figs 1, 2; LYELL, 1841, fig. 297 and subsequent editions, also in other geology books; HUENE 1908a, figs 206, 207a-d, pl. 76, fig. 3; GLUT, 2001, fig. p. 543; BENTON *et al.*, 2000, fig. 3A) (Figs 4A-F).

**Ca7466/35**, as distal end of proximal chevron (HUENE, 1908a, pl. 77, fig. 5; ?distal chevron BENTON *et al.*, 2000, p. 82, 104), more probably distal end of dorsal rib (Fig. 12U).

**Ca7467/-**, neural arch of cervical vertebra 5 (HUENE, 1908a, pl. 77, fig. 2; BENTON *et al.*, 2000, figs 7A, B) (Figs 7P-T) [C].

**Ca7468/14♦**, dorsal vertebra 13 or 14 (HUENE, 1908a, fig. 209, pl. 78, fig. 1) (Fig. 9A) [C].

**Ca7469/13♦**, mid-dorsal vertebra (HUENE, 1908a, pl. 78, fig. 2; as 8 or 9) (Fig. 9B) [C].

**Ca7470/9♦**, posterior dorsal vertebra (1908a, pl. 78, figs 4a, b, as 11 or 12) (Figs 9E, F) [C].

**Ca7471/20♦**, posterior dorsal vertebra (HUENE, 1908a, pl. 78, figs 3a, b) (Figs 9C, D) [C].

**Ca7472/16♦**, anterior half centrum of anterior cervical vertebra (HUENE, 1908a, pl. 78, fig. 5) (Fig. 7V).

**Ca7473/16**, proximal caudal centrum (HUENE, 1908a, pl. 78, fig. 6), reidentified by BENTON *et al.* (2000, figs 9E-G) as non-*Thecodontosaurus* and unusual for a dinosaur (Figs 34R-V), Archosauria indet.

**Ca7474/16b,** proximal caudal vertebral centrum of HUENE (1908a, pl. 78, fig. 7) and BENTON *et al.* (2000, figs 9A-D); posterior dorsal centrum (Figs 34M-Q), not basal Sauropodomorpha, ?Ornithischia indet.

**Ca7475/22**, proximal caudal vertebra (HUENE, 1908a, pl. 78, fig. 8; BENTON *et al.*, 2000, p. 82, 105) (Figs 11O-Q) [A].

**Ca7476a/59♦**, distal caudal vertebra (Fig. 12C; HUENE, 1908a, pl. 78, fig. 9) [A] and ilium.

**Ca7476b/59♦**, pedal ungual III (Fig. 20V; HUENE, 1908a, pl. 78, fig. 9) [A] and pubis.

**Ca7477a/37♦**, gracile right humerus (HUENE, 1908a, pl. 81, fig. 2, gracile; SEELEY, 1896, fig. 9; BENTON *et al.*, 2000, fig. 11F; GALTON *et al.*, 2007, fig. 1J) (Figs 16C, D, G), ?*Thecodontosaurus antiquus*.

**Ca7477b/37♦**, proximal right femur (HUENE, 1908, pl. 85, fig. 3, as gracile; BENTON *et al.*, 2000, p. 82, 104) (Fig. 26I) [C].

**Ca7477c/37♦**, proximal end of an anterior dorsal rib (HUENE, 1908a, pl. 78. fig. 12; BENTON *et al.*, 2000, p. 82, 104) (Fig. 8M).

**Ca7478/92♦**, left scapula-coracoid (HUENE, 1908a, pl. 79, fig. 1, as gracile; BENTON *et al.*, 2000, fig. 11C) (Fig. 14C) [C].

**Ca7479/89♦**, left scapula with impression of partial coracoid (HUENE, 1908a, fig. 221, pl. 79, fig. 2, as gracile; BENTON *et al.*, 2000, fig. 11C) (Fig. 14B) [C].

**Ca7480/90♦**, left scapula (HUENE, 1908a, pl. 79, fig. 3, gracile; BENTON *et al.*, 2000, 105) (Fig. 14A) [C].

**Ca7481/91**, left scapula blade (HUENE, 1908a, pl. 80, fig. 1, as robust; BENTON *et al.*, 2000, fig. 11 as right) [also partial femur (BENTON *et al.*, 2000, p. 82)] (Figs 14E, F) [C].

**Ca7482/80**, robust metacarpal II and two pieces of bone (left III with parts of II and IV, HUENE, 1908a, pl. 81, fig. 4; BENTON *et al.*, 2000, fig. 14H) (Figs 18U-Y) [B].

**Ca7483/82♦**, robust metacarpal III (HUENE, 1908a, pl. 81, fig. 5) (Fig. 18Z) [B].

**Ca7484/56♦**, slender metacarpal IV (HUENE, 1908a, pl. 81, fig. 6) (Fig. 18P) [A].

***Ca7485/46b**, manual phalanx 2, digit II or III (RILEY & STUTCHBURY, 1840, pl. 30, fig. 8; manual HUENE, 1908a, fig. 224, pl. 81, fig. 7; BENTON *et al.*, 2000, figs 14I, J) (Figs 20A-E) [C].

**Ca7486/79**, left ulna, incomplete at ends (HUENE, 1908a, pl. 82, figs 1a-c; BENTON *et al.*, 2000, figs 14A, B), but more probably a slender metatarsal II (Figs 17R-X) [A].

**Ca7487a-c/85♦**, HUENE (1908a, pl. 82, fig. 2): radius (**a**, Fig. 18A) [C], fragmentary left archosaurian (?theropod) dentary (**b**, Fig. 34G) and theropod manual ungual (**c,** Fig. 34H)

**Ca7488/101♦**, proximal right pubis (HUENE, 1908a, fig. 230, pl. 85, fig. 1) (Fig. 24N) [C].

**Ca7489/100♦**, proximal left pubis (HUENE, 1908a, pl. 85, fig. 2) (Figs 24O, P) [C].

**Ca7490/71**, right femur lacking proximal part (HUENE, 1908a, pl. 95, figs 5a, b, as gracile; BENTON *et al.*, 2000, p. 82, figs 16C-H, incorrectly listed as lost, p. 105) (Figs 27A-G) [B].

**Ca7491/68♦**, proximal left femur (HUENE, 1908a, fig. 231, pl. 86, figs 1a-c, as gracile; GLUT, 1997, figs p. 898) (Figs 26J-M) [C].

***Ca7492/69I♦**, left femur lacking proximal end (RILEY & STUTCHBURY, 1840, pl. 30, figs 4, 4a; HUENE, 1908a, fig. 232, pl. 86, fig. 2, as robust; GLUT, 1997, fig. p. 673, from HUENE, 1908a, incorrectly cited as after RILEY & STUTCHBURY, 1836) (Figs 26O-T) [B].

**Ca7493/70♦**, distal left femur (HUENE, 1908a, pl. 86, fig. 3, as gracile) (Fig. 26N) [B].

**Ca7494/69a.II**, distal right femur (HUENE, 1908a, pl. 88, fig. 1, **a** in caption and **II** p. 211, 216, as gracile; BENTON *et al.*, 2000, p. 82, 105) (Figs 27M-O) [C].

**Ca7495/53**, distal right tibia (SEELEY, 1896, fig. 5; HUENE, 1908a, pl. 88, figs 4a, b; BENTON *et al.*, 2000, figs 18F-J) (Figs 30A-J) [A].

**Ca7496/5**, distal dorsal rib (fibula of HUENE, 1908a, pl. 88, fig. 5; BENTON *et al.*, 2000, p. 104) (Figs 8P, Q).

**Ca7497/47**, partial right fibula (HUENE, 1908a, pl. 88, fig. 6 as left; BENTON *et al.*, 2000, fig. 18P) (Figs 31C, D) [C].
**Ca7498/83**, right metatarsal III (as II, HUENE, 1908a, pl. 90, fig. 2, as robust) (Figs 31T, U) [B].
**Ca7499/55**, distal left metatarsal II (as right HUENE, 1908a, fig. 213, pl. 90, figs 3a-c; BENTON *et al.*, 2000, figs 18R, S without number as possible pedal phalanx, listed as distal metatarsal on p. 82, 105) (Figs 31L-R) [C].
**Ca7500/-♦**, ?distal right metatarsal IV with articular surface incompletely exposed or crushed (as right proximal metatarsal I, HUENE, 1908a, pl. 90, figs 6a, b, also a left ilium p. 213) (Figs 31V, W) [C].
**Ca7501/-**, pedal phalanx 2 of digit III or IV (HUENE, 1908a, pl. 90, figs 8a-c) (Figs 29S-X) [C].
**Ca7502/42♦**, poorly preserved tibia (HUENE, 1908a, p. 212; SEELEY, 1895, fig. 6 as left fibula) [C].
***Ca7503a,b/38♦**, dorsal ribs including proximal right in anterior view (**a**, Fig. 8L; RILEY & STUTCHBURY, 1840, pl. 29, fig. 10), proximal metatarsal I (**b**, Fig. 31X; HUENE, 1908a, fig. 234) [C].
**Ca7504/52**, right radius lacking ends (phytosaur *Rileya*, HUENE, 1908b, pl. 6, figs 6a-f, 1911, figs 31.6a-f, 1958, figs 2a-c; *Thecodontosaurus antiquus*, BENTON *et al.*, 2000, p. 79, figs 14C-F, no number given, listed p. 82 but not p.105), ends too robust for radius of a basal sauropodomorph (Figs 18B-H), Archosauria indet.
**Ca7505/102♦**, metapodial (phytosaur *Rileya*, HUENE, 1908b, pl. 6, figs 7a, b, 1911, figs 31.7a, b; *Thecodontosaurus antiquus* BENTON *et al.*, 2000, p. 79, 105), too narrow waisted for basal Sauropodomorpha or Phytosauria (Figs 38J, K), Archosauria indet.
**Ca7506/60♦**, partial right ilium (HUENE, 1908a, fig. 227) (Fig. 22I) [B].
**Ca7507/23**, block with distal caudal in right lateral view (HUENE, 1907-08, fig. 217; BENTON *et al.*, 2000, p. 82, 104), mid-caudal neural arch in left lateral view and top of neural spine of more distal caudal vertebra (Figs 12K, L) [A].
**Ca7508/21♦**, articulated series of four distal caudal centra in ventral view (HUENE, 1908a, fig. 218b) (Fig. 12O).
**Ca7509/20♦**, articulated series of four distal caudal centra in mostly lateral view (HUENE, 1908a, fig. 218a) (Fig. 12N).
**Ca7510/18**, 3 articulated mid-caudal vertebra and an articulated chevron (HUENE, 1908a, fig. 220; BENTON *et al.*, 2000, fig. 9M). BRSMG Ca7510 incorrectly given for BRSMG *C4534/30 in caption by BENTON *et al.* (2000, fig. 10F) (Fig. 12Q) [C].
**Ca7511/-♦**, 3 mid-caudal chevrons (HUENE, 1908a, fig. 219) (Fig. 12P) [C].
**Ca7512/93♦**, proximally incomplete large left humerus (HUENE, 1908a, fig. 222; but ?shown upside down) (Fig. 16K) [C].
**Ca7513/77b♦**, proximal end of right femur (distal ischium HUENE, 1908a, fig. 229; ?ischium BENTON *et al.*, 2000, p. 105) (Figs 36H-J), Herrerasauria indet or basal Theropoda indet.
**Cb2632♦**, wax cast of braincase YPM 2192.
**Cb4151/6**, anterior cervical vertebra, horizontal section through neural arch and zygapophyses (BENTON *et al.*, 2000, p. 82 as indeterminate vertebra) [C].
**Cb4152/7,** indeterminate vertebra (BENTON *et al.*, 2000, p. 82, 105).
**Cb4153/15**, neural arch of posterior dorsal vertebra (BENTON *et al.*, 2000, figs 7E, F as Cb4155) (Figs 9Q-S) [C].
**Cb4154/12**, posterior dorsal vertebra split transversely (BENTON *et al.*, 2000, figs 7N, O), impression of centrum and base of transverse process of second posterior dorsal vertebra (Figs 9M, N) [A].
**Cb4155/11**, neural arch of anterior dorsal vertebra (BENTON *et al.*, 2000, fig. 7D as Cb4153) (Fig. 9P) [C].
**Cb4156/15a**, dorsal vertebra including anterior end (BENTON *et al.*, 2000, p. 82, 104) [C].
**Cb4157**, 37 mm long piece of long bone.
**Cb4158**, fragment of scapula.
**Cb4159**, partial sacral centrum.
**Cb4160**, 43 mm long bone shaft.
**Cb4161**, fragmentary horizontal section cervical vertebra.
**Cb4163a,b/25**, 2 large dorsal vertebrae, sectioned (BENTON *et al.*, 2000, p. 82, 104) [C].
**Cb4164a,b/27**, 2 caudal vertebrae (BENTON *et al.*, 2000, p. 82, 104) [C].
**Cb4165**, diagonally sectioned mid-cervical vertebra, longitudinal section of limb bone (?ulna).
**Cb4166/29**, median section of mid-caudal vertebra.
**Cb4167**, sectioned vertebra (BENTON *et al.*, 2000, p. 82), fibula longitudinal section, dorsal ribs.
**Cb4168a,b/33**, 2 ribs (BENTON *et al.*, 2000, p. 82), ?proximal fibula.
**Cb4169/34**, dorsal rib shaft (Fig. 80; BENTON *et al.*, 2000, fig. 10B).
**Cb4170/36**, dorsal rib shaft (BENTON *et al.*, 2000, p. 82).
**Cb4171/37**, dorsal centrum, mid-section shaft femur (BENTON *et al.*, 2000, p. 82, 105).
**Cb4172/39**, dorsal rib shaft (BENTON *et al.*, 2000, p. 82).
**Cb4173/40**, dorsal rib (BENTON *et al.*, 2000, p. 82).
**Cb4174a-c/41**, transversely sectioned posterior dorsal vertebra (**a**; Fig. 90), dorsal centrum (**b**; Figs 10E, F), robust metacarpal II length 56.6 mm (**c**; Figs 18A', B') shown upside down in BENTON *et al.* (2000, fig. 14G as metacarpal, specimen listed p. 104 as just 2 caudal vertebrae), **a** [C], **b** [C], **c** [B].
**Cb4175/44,** robust femur of HUENE (1908a, p. 205), distal shaft of ?left femur (Figs 25R, S) [C].
**Cb4176/48**, ?sectioned distal femur (BENTON *et al.*, 2000, p. 82) and articulated proximal tibia (?articulated knee), very poor condition.
**Cb4177/49,74**, 2 vertebrae, proximal left femur (BENTON *et al.*, 2000, p. 82, 105) (Fig. 25K) [C].
**Cb4178/50**, mid-caudal centrum (BENTON *et al.*, 2000, p. 82, indeterminate vertebra), slender long bone, ?metatarsal.
**Cb4179/54**, longitudinally sectioned metatarsal IV, (BENTON *et al.*, 2000, p. 82, metacarpal impression) (Fig. 31S) [C].
**Cb4180/58**, anterior dorsal rib (BENTON *et al.*, 2000, p. 82 fragmentary ilium, p. 104 ?partial right ilium) (Fig. 8J).
**Cb4181/62,** postacetabular process and impression of region above acetabulum of left ilium (BENTON *et al.*, 2000, p. 82, 105) [C].
**Cb4182/69**, mid-dorsal vertebra (BENTON *et al.*, 2000, p. 82, figs 7L, M, listed as unidentified on p. 105) (Figs 9U-W) [C].
**Cb4183/72**, right femur lacking ends (HUENE, 1908a, p. 216 as gracile; distal left femur, BENTON *et al.*, 2000, p. 82, 105) (Figs 25H, I) [C].
**Cb4184/75**, proximal left femur (BENTON *et al.*, 2000, p. 82) [C].
**Cb4185**, distal right humerus (partial tibia BENTON *et al.*, 2000, p. 82) (Fig. 15X) [C].
**Cb4186/78**, proximal tibia (BENTON *et al.*, 2000, p. 82, 105), dorsal vertebra [C].
**Cb4187/84**, manual ungual phalanx II (BENTON *et al.*, 2000, fig. 14K as possibly I) (Fig. 20W) [B].
**Cb4188/94**, distal left humerus (proximal tibia, BENTON *et al.*, 2000, p. 82, 105) (Fig. 15W) [C].

**Cb4189/78**, proximal left humerus (proximal tibia BENTON *et al.*, 2000, p. 82, 105) (Fig. 15V) [?B].
**Cb4190/99**, proximal right femur (HUENE, 1908a, p. 216 as gracile ; BENTON *et al.*, 2000, p. 82, 105) (Fig. 25G) [C].
**Cb4191/103**, fragmentary neural arch.
**Cb4192/108**, distal dorsal rib shaft.
**Cb4193/110**, distal dorsal rib shaft.
**Cb4194/115**, dorsal rib (BENTON *et al.*, 2000, p. 82).
**Cb4195,** dorsal rib (BENTON *et al.*, 2000, p. 82).
**Cb4196/116**, dorsal rib shafts (BENTON *et al.*, 2000, fig. 10A as Cb4196, anterior cervical rib fragments, on p. 105 only "116 Cb4195 ?cervical ribs") (Fig. 8G).
**Cb4196a-c/117**, 3 dorsal ribs, best 97 mm long incomplete proximally (BENTON *et al.*, 2000, p. 82).
**Cb4197**, centrum and part of neural arch of posterior dorsal vertebra (BENTON *et al.*, 2000, p. 82) [C].
**Cb4199**, incomplete right astragalus (Fig. 34C), Theropoda indet.
**Cb4200a-c**, 3 dorsal ribs (BENTON *et al.*, 2000, p. 82, 105).
**Cb4201**, scapula blade (partial humerus, BENTON *et al.*, 2000, p. 82) [C].
**Cb4202**, fibula lacking both ends.
**Cb4204**, 2 shafts of long bones.
**Cb4205**, ?end of long bone.
**Cb4206**, dorsal rib shaft fragment (BENTON *et al.*, 2000, p. 82).
**Cb4207**, proximal left femur to base of fourth trochanter (BENTON *et al.*, 2000, p. 82) [C].
**Cb4208**, indeterminate vertebral remains.
**Cb4209**, section of incomplete left humerus (BENTON *et al.*, 2000, p. 82).
**Cb4210**, shaft of forearm bone.
**Cb4212**, dorsal rib shaft (BENTON *et al.*, 2000, p. 82).
**Cb4213**, dorsal rib (BENTON *et al.*, 2000, p. 82).
**Cb4215**, fragmentary section of neural arch of dorsal vertebra.
**Cb4216**, part of scapula blade (BENTON *et al.*, 2000, p. 82).
**Cb4217**, shaft of long bone.
**Cb4218**, proximal humerus, incomplete vertebra (dorsal ribs, BENTON *et al.*, 2000, p. 82).
**Cb4219**, ?proximal tibia (partial humerus, BENTON *et al.*, 2000, p. 82).
**Cb4220**, trace of bone.
**Cb4221**, posterior dorsal vertebra with proximal rib attached (BENTON *et al.*, 2000, p. 82) (Fig. 10A) [A].
**Cb4222**, long bone shaft, longitudinal section.
**Cb4224,** ?any bone.
**Cb4225**, ?any bone.
**Cb4226**, ?forearm bone shaft.
**Cb4227**, proximal dorsal rib (BENTON *et al.*, 2000, p. 82), bone pieces.
**Cb4228**, femoral shaft (BENTON *et al.*, 2000, p. 82).
**Cb4229**, shaft of slender long bone.
**Cb4230**, neural arch of dorsal vertebra.
**Cb4231**, shafts of 2 long bones.
**Cb4232**, bone piece.
**Cb4233**, impression of shaft, ?femur.
**Cb4234**, dorsal rib shaft (BENTON *et al.*, 2000, p. 82).
**Cb4235**, long bone shaft, slender.
**Cb4236**, longitudinal section of shaft of femur.
**Cb4237**, end of long bone, ?radius.
**Cb4238**, long bone shaft.
**Cb4239**, distal large damaged femur, width 66 mm [C].
**Cb4241**, distal femur, damaged [C[.
**Cb4242**, fibula (Fig. 31E) [C].
**Cb4243**, robust right humerus lacking distal end, preserved length 130 mm, 87 mm to base of missing deltopectoral crest (partial femur, BENTON *et al.*, 2000, p. 82) (Figs 15S-U) [B].
**Cb4245**, mid-shaft ?metacarpal.
**Cb4246**, ?distal half metatarsal.
**Cb4247**, long bone shaft fragment.
**Cb4248**, distal small humerus, phalanx.
**Cb4249**, shaft of ?humerus or femur.
**Cb4250**, layer of cortex from shaft of long bone.
**Cb4251**, large proximal femur [C] ; partial left parietal (Fig. 34F), Reptilia indet.
**Cb4252**, shaft impression, ?femur.
**Cb4253**, impression of distal right tibia, distal width 38 mm [C].
**Cb4255**, section dorsal rib shaft (BENTON *et al.*, 2000, p. 82).
**Cb4256**, longitudinal section of dorsal rib (BENTON *et al.*, 2000, p. 82).
**Cb4257**, distal femur with end [C].
**Cb4258**, vertebra.
**Cb4259**, piece of long bone shaft (BENTON *et al.*, 2000, p. 82).
**Cb4260**, distal end of small humerus.
**Cb4261**, femoral shaft.
**Cb4262**, small left scapula, proximal width 37.3 mm [C].
**Cb4263**, end of shaft of long bone.
**Cb4265**, gracile right humerus, incomplete at ends, length 157 mm (BENTON *et al.*, 2000, p. 82 ; GALTON *et al.*, 2007, p. 120 as gracile) (Figs 15Q, R), ?*Thecodontosaurus antiquus*.
**Cb4266**, partial humerus, partial femur (BENTON *et al.*, 2000, p. 82).
**Cb4267**, most of the broad pubic apron of right pubis (as left, BENTON *et al.*, 2000, figs 15E, F) (Figs 24Q, R) [C].
**Cb4268**, anterior half sacral vertebra 1 with ribs (Figs 10R-U) [C].
**Cb4269**, ?proximal humerus (partial femur, BENTON *et al.*, 2000, p. 82).
**Cb4270**, vertebral fragment.
**Cb4271**, small ulna.
**Cb4272**, proximal tibia, width 43 mm, ?left [C].
**Cb4273**, ?, mislaid after returning from a touring exhibit.
**Cb4274**, oblique section of long bone shaft and end, ?femur.
**Cb4275**, ?proximal scapula, half section of fourth trochanter region of large femur.
**Cb4276**, distal caudal vertebra (BENTON *et al.*, 2000, p. 82) (Fig. 12D) [A].
**Cb4278**, scapula blade [C]**.**
**Cb4279**, ?dorsal ribs.
**Cb4280**, caudal centrum in ventral view (unidentified vertebra, BENTON *et al.*, 2000, p. 82).
**Cb4281**, mid-shaft femur (BENTON *et al.*, 2000, p. 82), piece of flat thin bone.
**Cb4282**, dorsal rib piece.
**Cb4283**, vertebra (BENTON *et al.*, 2000, p. 82).
**Cb4284**, partial humerus (BENTON *et al.*, 2000, p. 82) [C].
**Cb4285**, proximal dorsal rib (BENTON *et al.*, 2000, p. 82).
**Cb4286**, distal end of dorsal rib (BENTON *et al.*, 2000, p. 82).
**Cb4287**, ?long bone.
**Cb4289**, distal left femur, crystal damage (BENTON *et al.*, 2000, p. 82).
**Cb4290**, distal left tibia [C].
**Cb4291**, distal small humerus without end [C].
**Cb4292**, fragment of long bone shaft.
**Cb4293**, posterior dorsal vertebra (BENTON *et al.*, 2000, p. 82) (Fig. 9X) [C].

**Cb4294**, distal humerus, width 62 mm [C].
**Cb4295**, sectioned caudal centrum.
**Cb4296**, dorsal vertebra.
**Cb4297**, rib (BENTON *et al.*, 2000, p. 82), plate of fine-grained banded limestone.
**Cb4298**, proximal rib (Fig. 8N; BENTON *et al.*, 2000, p. 82), distal right radius (Figs 18N, O) [C].
**Cb4299**, shaft of ?forearm bone.
**Cb4300**, dorsal rib (BENTON *et al.*, 2000, p. 82).
**Cb4301/private collection 48**, mid-caudal vertebra [accn. No. 3324, collection of Dr. J. CHANING PEARCE (-1847)], as unidentified vertebrae C4301 and Cb4301, BENTON *et al.*, 2000, p. 82) (Fig. 12A) [A].
**Cb4302**, shaft, ?tibia, label "Collected by RILEY", same history as Cb4301**.**
**Cb4303**, shaft of limb bone in cross section.
**Cb4304**, sliver from side of long bone shaft.
**Cb4305**, thin sheet of bone, ?part of ilium.
**Cb4312**, renumbered as Cb4714.
**Cb4528**, rib (BENTON *et al.*, 2000, p. 82).
**Cb4714** (originally Cb4312 but label lost), vertebrae, ribs (BENTON *et al.*, 2000, p. 82), shaft of long bone; also small jaw of *Clevosaurus* of HALSTEAD & NICOLL (1971, p. 101), reidentified by FRASER (1994, p. 223) as small sphenodontid lepidosaur *Diphydontosaurus avonis* WHITESIDE, 1986 (also BENTON & SPENCER, 1995, p. 88; BENTON *et al.*, 2000, p. 80), left dentary incomplete anteriorly. No reasons published for identification as *Diphydontosaurus* but FRASER (pers. comm.) indicated that it was based on the small number of teeth, their shape and the apparent pleurodont anterior teeth (Fig. 34B).
**Cb4715,** partial articulated skeleton with part of the vertebral column, a femur and a complete hind limb including an intact long slender pes (Fig. 34A), the "lizard" of ANON (1961), TARLO (1962) and HALSTEAD & NICOLL (1971, pl. 23B); reidentified by FRASER (1994, p. 223) as small sphenodontid lepidosaur *Diphydontosaurus avonis* (also BENTON & SPENCER, 1995, p. 88; BENTON *et al.*, 2000, p. 80) but no reasons given in print.
**Cb4726,** posterior cervical vertebra (Fig. 7U) [C].

**Appendix 4: Specimens from Clifton in ANSP**
See Systematic section for key to [A-C].

**9854,** sectioned caudal vertebra, proximal right femur (BENTON *et al.*, 2000, p. 82, 106) [C].
**9855,** transverse section of caudal vertebra (unidentified vertebra, BENTON *et al.*, 2000, p. 82, 106) [C].
**9856,** robust right metatarsal III with damaged ends (Figs 29N, O) [B].
**9857,** lateral view of proximal right scapula and adjacent part of coracoid (neural spine of *Thecodontosaurus antiquus*, BENTON *et al.*, 2000, p. 82, 106) (Figs 38A, B), Archosauria indet.
**9858,** right transverse process of dorsal vertebra (unidentified vertebra, BENTON *et al.*, 2000, p. 82, 106) [C].
**9859,** proximal right humerus, part of apron-like anterior ramus of right pubis [C].
**9860,** robust right metatarsal III lacking distal end (?ulna, BENTON *et al.*, 2000, p. 82, 106) (Figs 29K-M) [B].
**9861a,b,** proximal caudal vertebra (**a**; Fig. 11N; dorsal vertebra, BENTON *et al.*, 2000, p. 82, 106) [A], pedal ungual phalanx IV (**b**; Figs 20T, U; BENTON *et al.*, 2000, fig. 18T, pedal) [C].
**9862,** distal left humerus (Figs 38E-G), Archosauria indet.
**9863,** fibula lacking ends (BENTON *et al.*, 2000, p. 82, 106) [C].
**9864,** robust metacarpal II (Fig. 18S) [B].
**9865a,b, a**: transversely sectioned posterior dorsal vertebra (Figs 9Y, Z) [A], **b**: part of apron-like anterior ramus of right pubis (?scapula fragment, BENTON *et al.*, 2000, p. 82, 106) [C].
**9866,** distal right femur to base of fourth trochanter [C].
**9867,** gracile left metatarsal II lacking distal end (partial fibula, BENTON *et al.*, 2000, p. 82, 106) (Figs 29P-R) [A].
**9868, 9872,** fibula lacking ends, split between two blocks (but matrix looks more like that of the Rhaetic bone bed at Aust Cliff, Avon).
**9869,** proximal right fibula (BENTON *et al.*, 2000, p. 82, 106) (Fig. 29H) [C].
**9870a-c, a**: partial right ilium and **b**: distal left ischium (Figs 22A, B, 23; right ilium and proximal femur, BENTON *et al.*, 2000, p. 106, figs 15A, B, but femur listed and described as proximal ischium p. 82, 94); **c**: neural arch of mid-dorsal vertebra (Figs 9A', B') [C].
**9871,** proximal metapodium (partial humerus, BENTON *et al.*, 2000, p. 82, 106) (Figs 38H, I), Reptilia indet.
**9872,** proximal fibula (BENTON *et al.*, 2000, p. 82, 106) [C].
**9873,** distal femur, ?left (BENTON *et al.*, 2000, p. 82, 106) [C].
**9874,** partial femur [C].
**9875,** robust metacarpal II (caudal vertebra, BENTON *et al.*, 2000, p. 82, 106) (Fig. 18T) [B].
**9876,** incomplete blade of right scapula (BENTON *et al.*, 2000, p. 82, 106) [C].
**9877,** tibia or ?humerus (Figs 38C, D), Reptilia indet
**9880,** partial proximal left femur with incomplete fourth trochanter (partial humerus, BENTON *et al.*, 2000, p. 82, 106) [C].

**Appendix 5: Specimens from Clifton in BGS**
See Systematic section for key to [A-C].

**54060**: distal caudal centrum [C].
**54061a,b**: proximal caudal vertebra (**a,** Figs 11D-I; mentioned HUENE, 1908a, p. 201; 1914a, fig. 41, 3 views) [A]; proximal metatarsal II (**b,** Figs 29I, J; HUENE, 1914a, p. 80 as metatarsal) [A]**.**
**54062**: dorsal centrum, presumably one noted by HUENE (1914a, p. 80) [C].
**90792**: left manual ungual phalanx digit I (HUENE, 1914a, fig. 42) (Figs 20X-C') [B].

**Appendix 6: Specimens from Clifton in BMNH**
See Systematic section for key to [A-C].

**49984**, holotype of *Agrosaurus macgillivrayi* SEELEY, 1891, this specimen supposedly came from the Upper Triassic of an unknown locality on the northeast coast of Australia. It was referred to the dinosaur *Thecodontosaurus macgillivrayi* (SEELEY, 1891) by HUENE (1906, p. 147-148), who commented on the similarities of the matrix (a yellowish to grey-yellowish breccia) to that with the bones of *Thecodontosaurus antiquus* from Clifton (as Durdham Down). VICKERS-RICH *et al.* (1999) noted that comparisons of the gross and trace element analysis of the bones and matrix of *Agrosaurus* show that they differ considerably from bones from a possible source bed on the east coast of Cape York Peninsula, Queensland, but closely resemble the bones of *Thecodontosaurus* from Clifton. They

also noted the occurrence in the matrix residue (after acetic acid preparation) with the distal radius of *Agrosaurus* of a 3 mm long posterior piece of a right maxilla (now BMNH R14111) with eight acrodont teeth posteriorly and two pleurodont teeth anteriorly. This combination of tooth implantations in the Triassic only occurs in the sphenodontid *Diphyodontosaurus avonis* WHITESIDE, 1986, a species that also occurs with *Thecodontosaurus* at Clifton (Fig. 34F; FRASER, 1994), the only fossil locality with this association that was known in 1879, the date of acquisition of *Agrosaurus* by the BMNH. The occurrence of *Diphydontosaurus* with *Thecodontosaurus*, together with the close similarities in the chenical components of the bone and matrix, provides very strong evidence that *Agrosaurus* came from Clifton (but listed as Avon, unnamed unit, WEISHAMPEL *et al.*, 2004, p. 522).

Most of the bones of this specimen have been illustrated several times (HUENE, 1906, figs 86-90; VICKERS-RICH *et al.*, 1999, fig. 3; color photos LONG, 1998, p. 80; GLUT, 2001, figs p. 545-547; GALTON, 2000, fig. 15, including radius block with damaged tooth before acid preparation). It consists of the lectotype, a left tibia (Figs 29A-F; SEELEY, 1891, figs 1-5; GALTON & CLUVER, 1976, figs 11H-J; BENTON *et al.*, 2000, figs 17A-D but A, medial and C, lateral views). Associated bones (paralectotypes, **49984a-d**), not necessarily from the same individual or taxon, include a distal caudal vertebra (**a**, Fig. 12F) [A], a distal left radius (**b**, Figs 18I-M) [C], a manual ungual phalanx of digit I (**c**, Fig. 20S; SEELEY, 1891, fig. 6; GALTON, 2000, fig. 15J for longitudinal sectional view) [B], and a proximal right tibia (**d**, Fig. 29G) [C]. There was also the small tooth of a theropod dinosaur (**e♦**, Figs 32V, W; HUENE, 1906, fig. 89; lost during acid preparation) and the posterior piece of a sphenodontid maxilla was renumbered (**R14111**, see below).

**R1108,** cast of neotype BRSMG C4529/2 of *Thecodontosaurus* RILEY & STUTCHBURY, 1836a, type genus of *T. antiquus* RILEY & STUTCHBURY *vide* OWEN, 1842a (=*T. antiquus* MORRIS, 1843); made in BMNH in 1887 (LYDEKKER, 1888, p. 175).

Bones in matrix obtained by exchange from the BCM in 1889 (LYDEKKER, 1890) and no extra specimens were received in 1890 (CHAPMAN, pers. comm; *contra* BENTON *et al.*, 2000).

**R1531**, ?skull roof element (BENTON *et al.*, 2000, p. 105), not located.

**R1532**, transversely sectioned sacral 2 in posterior view with right rib (HUENE, 1908a, fig. 213; BENTON *et al.*, 2000, p. 88 as not located) (Figs 10G, H) [A].

**R1533**, posterior half of sacral 1 and all of sacral 2 (unidentified vertebra BENTON *et al.*, 2000, p. 82, 105) (Fig. 10I) [A].

**R1534,** distal caudal vertebra (LYDEKKER, 1890, p. 248; BENTON *et al.*, 2000, p. 82, 105) [C].

**R1535**, distal caudal vertebra (caudal, LYDEKKER, 1890, p. 247; unidentified vertebra, BENTON *et al.*, 2000, p. 82, 105) [C].

**R1536a,b, R1537a-c, R1538** (all ex BCM 106), shafts of dorsal ribs (BENTON *et al.*, 2000, p. 82, 106).

**R1539**, right ilium, incorrectly referred to *Thecodontosaurus antiquus* (LYDEKKER, 1890, p. 247; BENTON *et al.*, 2000, p. 82, 106, fig. 15C) (Figs 35A-E), Herrerasauria indet or basal Theropoda indet.

**R1540**, posterior half of right ilium (BENTON *et al.*, 2000, p. 82, 106) (Fig. 21B) [C].

**R1541**, most of right humerus (HUENE 1908b, pl. 6, fig. 4; 1911, fig. 31.4, 1958, fig. 3B), incorrectly cited and listed as *Thecodontosaurus antiquus* (BENTON *et al.*, 2000, p. 82, 90,106); also part of blade of an ?associated scapula (Figs 37G-I), Phytosauria indet.

**R1542**, proximal left humerus lacking head (HUENE, 1908a, pl. 80, fig. 4; BENTON *et al.*, 2000, p. 82, 106) (Figs 15O, P), *Asylosaurus yalensis*.

**R1543**, incomplete right scapula (partial humerus, BENTON *et al.*, 2000, p. 82, 106) [C].

**R1544**, distal left femur (LYDEKKER, 1890, p. 247; BENTON *et al.*, 2000, p. 82, 106) (Figs 25M-Q) [A].

**R1545**, most of outline of anterior edge of small femur plus some of shaft (BENTON *et al.*, 2000, p. 82, 106) (Fig. 25J) [C].

**R1546**, longitudinally sectioned proximal tibia (BENTON *et al.*, 2000, p. 82, 106) [C].

**R1547**, half of radius or ulna (unidentified limb bone, BENTON *et al.*, 2000, p. 82, 106).

**R1548**, proximal right radius/or? incomplete ulna and distal left tibia (unidentified limb bone, BENTON *et al.*, 2000, p. 82, 106).

**R1549**, right metacarpal I (unidentified limb bone, BENTON *et al.*, 2000, p. 82, 106) (Figs 35F-I), Theropoda indet.

**R1550a,b**, proximal left ischium (**a**; Fig. 24L; partial humerus of BENTON *et al.*, 2000, p. 82, 106) [C], distal caudal vertebra (**b**; Fig. 12E), another caudal (2 caudal vertebrae, BENTON *et al.*, 2000, p. 82, 106) [A].

**R1551,** phalanx of pes (LYDEKKER, 1890, p. 247).

**R1552**, partial right pes (phalanges of BENTON *et al.*, 2000, p.106, possibly pedal p. 82) (Fig. 31Y) [A].

**R1553**, phalanx (BENTON *et al.*, 2000, p. 106, possibly pedal p. 82).

**R16119,** tooth of heterodont phytosaur *Palaeosaurus platyodon* (HUENE, 1908a, figs 264a-c, 1908b, pl. 6, figs 1a-c, 1911, figs 31.1a-d) (Figs 32H-N, 33I-L) Phytosauria indet.

**Appendix 7: Specimens from Clifton in YPM**

Specimens were numbered in 1937 with a separate number for each species as assigned by R. S. LULL, irrespective of the accession number, viz., YPM 2192 for *Thecodontosaurus antiquus* with accession numbers [1979] and [2001], YPM 2193 for *T. cylindrodon*, and YPM 2195 for *T. platyodon* (following MARSH, 1892) with YPM 2194 for the unprepared blocks. All the YPM specimens were referred to *Thecodontosaurus antiquus* by BENTON *et al.* (2000, appendix 1). See Systematic section for key to [A-C].

**2192,** part of accession number [2001] (received 05/23/1889), a braincase (MARSH, 1892, pl. 17, figs 1, 2; GALTON, 1973, fig. 1G, 1990, fig. 15.4B; FEDAK & GALTON, 2007, fig. 2B; without specimen number GALTON & CLUVER, 1976, fig. 9F; GALTON & BAKKER, 1985, figs 4J, K; GALTON & UPCHURCH, 2004, fig. 12.5B; FEDAK & GALTON, 2007, fig. 2A; for more detailed figures and descriptions see HUENE (1908a, pl. 76, figs 1a-d, 1914a, figs 35a-c) and BENTON *et al.* (2000, figs 5B-D, 6A-D, endocast figs 6E-G). Series of partial casts as GPIT 2001(?♦)and a wax cast as BRSMG Cb2632♦ (Figs 5A-D) [A].

**2192a**, part of accession number [2001] (received 05/23/1889), consists of a few pieces of bone, the remaining figured and identifiable bones of YPM 2192 are renumbered as YPM 56719 to 56745 (see below) because the Clifton material consists mostly of disassociated bones from a fissure fill.

**2193**, part of accession number [2001] (received 05/23/1889), proximal caudal vertebra (HUENE, 1908a, pl. 77, fig. 4; BENTON *et al.*, 2000, figs 9H-K as mid-caudal YPM 2192 and incorrectly listed as YPM 2195 on p. 106) (Figs 11J-M) [A].

**2194**, accession number [2005] (received 11/13/1890), originally 30 unprepared blocks with pieces of bone visible, now 24 blocks plus two renumbered ones (YPM 56746, 56747; see below).

**2195**, holotype of *Asylosaurus yalensis* GALTON, n. gen. et sp., part of accession number [1979] (received 11/16/1888). The specimen is shown as preserved (Figs 6A-C; HUENE, 1914a, figs 44-47; BENTON *et al.*, 2000, figs 12, 13; GLUT, 2002, fig. p. 544). Two anterior dorsal vertebrae (Figs 8A-C) are partly exposed, the ends of the transverse processes of two others are visible (p, Figs 6B, 8D), and several others are probably covered by the anterior dorsal ribs and matrix (Figs 6B, 8D, E; HUENE, 1914a, fig. 46; BENTON *et al.*, 2000, fig. 12); there are also a few gastralia (l, Fig. 6; Figs 6B, 8D, F). There is also an associated incomplete pectoral girdle, humeri (left poorly preserved) and an almost complete articulated left ulna (with sliver of radius) and manus (b-h, m, n, Figs 6A, B) (Figs 13, 14I-M, 15A-N, 17A-J, 19; HUENE, 1914a, figs 44-47; GALTON & CLUVER, 1976, figs 7D, 11B-G; BENTON *et al.*, 2000, figs 12, 13; GALTON *et al.*, 2007, figs 1H, I). A reconstruction of the left shoulder girdle and forearm was given by MARSH (1892, pl. 16, fig. 5) (Fig. 13A). The partial scapula blade "(right or left?)" of BENTON *et al.* (2000, fig. 11B) is the right scapula (Figs 13B-D, 14I). The left scapula-coracoid fragment (Figs 14K-M) has the specimen number YPM 2192 on it but it was figured by MARSH (1892) and HUENE (1914a) as part of the shoulder girdle (Figs 13A, H) and it also bears the older accession number [1979] (Fig. 14L), the correct one for YPM 2195, rather than [2001] for YPM 2192. The complete left humerus of GALTON & CLUVER (1976, figs 11C, D; also BENTON *et al.*, 2000, figs 13A, B, fig. 13A is not dorsolateral view but posterolateral view, see Fig. 13J) is the right (Figs 13I-K; GALTON *et al.*, 2007, figs 1H, L), so the specimen does not include "an articulated left arm and hand bones" as described by BENTON *et al.* (2000, p. 82, 92, figs 12, 13). In addition to the complete right humerus (Figs 15A-M), there is the proximal half of the left (Fig. 15N), the left ulna is almost complete (Figs 17A-G), and the radius is represented by only a sliver of bone (Figs 17A-C). A reconstruction of the manus (Fig. 13R, reversed as a right) without number was given by GALTON (1973, fig. 1L, 1990, fig. 15.6O) and GALTON & UPCHURCH (2004, fig. 12.8O).

The main block includes some other bones (a, i-k, Fig. 6A, C, D), most of which may be from the holotype individual but, as this is not certain, they and a few loose bones have been assigned letters. These include cervical vertebra 5 (**a**, Figs 7B-F; GALTON & CLUVER, 1976, fig. 11A; BENTON *et al.*, 2000, fig. 7C), and two proximal caudal vertebrae (**b, c**, Figs 11A-C; HUENE, 1914a, fig. 40; as YPM 2192 in BENTON *et al.*, 2000, p. 106). Two distal femora, a right (**f**, Figs 25A-C) and a left (**g**, Figs 25D- F; as distal gracile right femur, HUENE, 1908a, p. 211, 216, pl. 90, fig. 1; BENTON *et al.*, 2000, p. 106 as right, YPM 2192), can still be attached to the main block (Figs 6A,C) and, although both are plesiomorphic in lacking an anterior intercondylar groove, one is slightly larger than the other (right ~20-25% larger) so they are from two individuals. The original position of the distal medial part of the right ulna (**d**, Figs 17H-J; [1879] Fig. 17J is incorrect for YPM 2192, see above) and of the distal right tibia (**h**, Fig. 6D) is not known but, because the latter has a natural mold of the side of a rib and red paint marks, it probably came from the lower side of the block (Fig. 6B). The distal right ischium (**e**, Figs 24F-J) was still on the end of the block in 1901 (Fig. 24H, YPM photo, BCM Archives, Geology file No. 51). The very small jaw fragment (**i♦**, Fig. 34I; HUENE, 1914a, p. 87, fig. 36) is Archosauria indet and it was lost sometime after 1911 during preparation.

**56719-56745** – part of accession number [2001] (received 05/23/1889), originally part of YPM 2192:

**56719**, Based on a photograph sent by the YPM in 1901, HUENE (1902, fig. 76) referred two caudal vertebrae shown on side of a block to phytosaur *Rileya platyodon* (also HUENE, 1908b, pl. 6, fig. 2b, 1911, fig. 31.2b; cited as such by FRASER, 1988, p. 136). However, the upper one was reidentified as a dorsal vertebra (Fig. 9T) of *Thecodontosaurus* by HUENE (1914a, fig. 55), who noted that it was on same block as hand (Figs 6F, G) but this does not refer to YPM 2195; this dorsal not listed but figured by BENTON *et al.* (2000, p. 106, fig. 7G) [C]. This block also contains broken dorsal ribs and gastralia (Fig. 6E; HUENE, 1914a, fig. 54), parts of several disarticulated and incomplete metacarpals (Figs 6F, G, all [C]), and a problematic ?cranial bone (Fig. 34E). The other caudal vertebra of HUENE (1902, fig. 76), a proximal femur (HUENE, 1914a) (Figs 36A-G), is now YPM 56744 (see below).

**56720**, cervical vertebrae 5 and 6 (HUENE, 1908a, pl. 77, fig. 1, 1914a, figs 37a, b, not 36 as listed in BENTON *et al.*, 2000, p. 106) (Figs 7G-O) [A].

**56721,** 3 dorsal ribs, 1 as HUENE (1908a, pl. 77, fig. 6; BENTON *et al.*, 2000, p. 106), now free of matrix and in pieces.

**56722,** mid-dorsal vertebra (HUENE, 1908a, pl. 77, figs 7a, b, 1914a, figs 38a, b; not fig. 37 as listed by BENTON *et al.*, 2000, p. 106, figs 7H-K) (Figs 9G-L) [C].

**56723**, right pedal phalanx 1 of digit I (of manus or pes HUENE, 1908a, p. 207, pl. 80, fig. 3; three phalanges of BENTON *et al.*, 2000, p. 106) (Figs 30Y-B') [C].

**56724**, left humerus shown in matrix (HUENE, 1908a, pl. 83, fig. 1, robust), now free of matrix (HUENE, 1914a, fig. 48, inverted; as right; BENTON *et al.*, 2000, figs 11D, E in posterolateral and anteromedial views, not posterior and anterior views, listed as left p. 106) (Figs 16H-J) [B].

**56725**, distal right ischium shown in matrix (HUENE, 1908a, pl. 83, fig. 2), now free of matrix, described by BENTON *et al*, (2000, p. 94) (Fig. 24K), ?*Asylosaurus yalensis*.

**56726**, distal left ischium shown in matrix (HUENE, 1908a, pl. 83, fig. 3), now free of matrix, described by BENTON *et al*, (2000, p. 94) (Figs 24A-E), ?*Asylosaurus yalensis.*

**56727**, distal left femur mentioned by HUENE (1908a, p. 211) as a small gracile femur (based on YPM photo now in BCM Archives, Geology file No. 51) (Fig. 25L) [C].

**56728**, poorly preserved distal part of left femur to base of fourth trochanter, mentioned by HUENE (1908a. p. 211) as large robust femur (based on YPM photo now in BRSMG Archives, Geology File No. 51) [C].

**56729**, right proximal tibia free of matrix (HUENE, 1908a, pl. 89, fig. 3 as left in matrix, originally twice length with damaged shaft, incomplete distally; left in BENTON *et al.*, 2000, p. 106) (Figs 28L, M) [C].

**56730**, left proximal tibia with more distal 15 mm ground down to give histological section (HUENE, 1908a, pl. 89, fig. 5 as left, 1914a, fig. 50 as right; left in BENTON *et al.*, 2000, p. 106) (Figs 28N, O) [C].

**56731**, distal left tibia with astragalus (HUENE, 1908a, pl. 89, figs 2a, b; 1914a, fig. 51; BENTON *et al.*, 2000, figs 18K-O) (Figs 30K-P) [A]. HUENE (1914a, figs 52, 53) also figured the calcaneum (actually the ventral part of the distal condyles of a phalanx of the pes, Figs 30Q-W) and the proximal end of "metatarsal I" (Fig. 30X, lost), a fragment of bone.

**56732**, proximal half metatarsal, badly crushed transversely

(HUENE, 1908a, pl. 89, fig. 4 as distal right tibia in matrix ; distal right tibia BENTON *et al.*, 2000, p. 82, 106).

**56733**, sacral vertebrae 1 and 2 (HUENE, 1914a, figs 39a, b ; GALTON, 1999, figs 4F-H ; BENTON *et al.*, 2000, p. 87, fig. 8, no number in caption) (Figs 10J-P) [A].

**56734♦**, very distal caudal vertebra (HUENE, 1914a, fig. 43 ; as YPM 2193 in BENTON *et al.*, 2000, p. 106 but more probably part of ex YPM 2192) (Fig. 12M) [?C].

**56735**, proximal left ulna (HUENE, 1914a, fig. 49, 3 views as right ; right in BENTON *et al.*, 2000, p. 106) (Figs 17K-M) [C].

**56736,** distal caudal vertebra (BENTON *et al.*, 2000, figs 9N-Q but N is right lateral view, not left, as YPM 2193) (Figs 12G-J) [C].

**56737**, distal caudal vertebra (more anterior than Fig. 11T) [C].

**56738**, posterior end of distal caudal vertebra [C].

**56739**, distal left ischium, ?*Asylosaurus yalensis*.

**56740**, proximal two thirds of poorly preserved right tibia [C].

**56741**, distal half of poorly preserved left tibia with small piece of astragalus [C].

**56742**, crushed distal metatarsal.

**56743**, proximal end of pedal phalanx 1, very small middle cross-section.

**56744**, described by HUENE (1902, fig. 76) as the lower of two caudal vertebra shown on side of block (originally part of YPM 2192, now YPM 56719, see above), and referred to phytosaur *Rileya platyodon* (also HUENE, 1908b, pl. 6, fig. 2a, 1911, fig. 31.2a), reidentified as *Thecodontosaurus* with upper caudal vertebra as a dorsal (Fig. 9T, YPM 56719) and lower one as a proximal right femur by HUENE (1914a, figs 56a-e) (Figs 36B',C', E'-G') who was miscited as reidentifying it as a dorsal vertebra of *Thecodontosaurus* by BENTON *et al.* (2000, p. 79, but not listed on p. 106) (Figs 36A-F), Herrerasauria indet or basal Theropoda indet.

**56745,** right manual phalanx 1 of digit I (Figs 20F-J), *Asylosaurus yalensis.*

**56746**, accession number [2005] (received 11/13/1890, originally part of YPM 2194, as was 56747), sacral vertebrae 1 and 2 (Fig. 10Q) [A].

**56747**, left ischium lacking distal end (Fig. 24L) [C].

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