A reassessment of the Early Cretaceous reptile ‘Patricosaurus merocratus’ Seeley from the Cambridge Greensand, Cambridgeshire, UK

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The Cambridge Greensand has yielded a diverse fauna of terrestrial and marine vertebrates, including various fish, birds, dinosaurs and marine reptiles. However, this important late Early Cretaceous biome has been severely neglected and the taxonomy and systematics of most of these animals are in need of urgent revision. The small reptile ‘Patricosaurus merocratus’ was named on the basis of a partial femur and sacral vertebra and referred to the Squamata. Re-examination of the type material indicates that ‘Patricosaurus’ represents a chimera composed of indeterminate lepidosaurian and archosaurian elements and that it should be regarded as a nomen dubium. Nevertheless, the syntype femur represents the only material of a terrestrial lepidosaur to be recovered from the Cambridge Greensand. Moreover, this element is currently the largest known terrestrial lepidosaur, living or extinct, to have been recovered from the British Isles.

KEY WORDS: Cambridge Greensand; UK; ‘Patricosaurus’; Lepidosauria; Archosauria; late Albian.

1. Introduction

The Cambridge Greensand is a remainé deposit that crops out in eastern England. In the mid- to late nineteenth century this unit was quarried intensively, as its lower levels contained abundant phosphatic nodules (incorrectly termed ‘coprolites’) that were used widely as agricultural fertiliser and as a source of industrial phosphate (Grove, 1976). During the course of these operations, large quantities of invertebrate and vertebrate fossils were recovered by the quarrymen, who brought them to the attention of local fossil collectors and dealers (Fraser, 1990). The vertebrate material from the Cambridge Greensand represents a diverse fauna that contains a mixed assemblage of marine and terrestrial forms, including chondrichthians, actinopterygians, turtles, sauropotyrgians, ichthyosaurs, crocodilians, dinosaurs, birds and pterosaurs (e.g., Seeley, 1869; Woods, 1891; Buffetaut et al., 1981; Fraser, 1990; Unwin, 2001). However, although this material undoubtedly represents one of the best late Early Cretaceous vertebrate faunas, many of these specimens have not been studied in detail since the late nineteenth century. Exceptions include revisions of the bird (Elzanowski & Galton, 1991), ornithischian dinosaur (Pereda-Suberbiola & Barrett, 1999) and pterosaur (Unwin, 2001) material.

Seeley (1887) described ‘Patricosaurus merocratus’ on the basis of two isolated specimens from the Cambridge Greensand (SMC B58401–2; Figures 1, 4) and considered it to be a large terrestrial lizard. Subsequently, ‘Patricosaurus’ was listed in various taxonomic compilations (Nopcsa, 1908; Kuhn, 1939; Romer, 1956, 1966; Unwin, 2001), but none of these works provided any description or discussion of the material. In most cases the material was referred to as ‘Lacertilia, family incertae sedis’ (Nopcsa, 1908; Kuhn, 1939; Romer, 1956, 1966). Here we redescribe the syntype specimens of ‘Patricosaurus’ and reassess its taxonomic status and systematic position.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; OUMNH, Oxford University Museum of Natural History, University of Oxford, UK; SMC, Sedgwick Museum of Earth Sciences, University of Cambridge, UK; UCLA, Anatomy collections, University College.
2. Geological setting

An extensive literature deals with the geology, stratigraphy and dating of the Cambridge Greensand and the following brief account is based on a variety of sources (see references cited in Pereda-Suberbiola & Barrett, 1999 and Unwin, 2001). The Cambridge Greensand lies immediately below the Lower Chalk and rests unconformably on the Gault Clay. It is very limited in extent, and forms a long, thin band that traverses eastern England, passing through the counties of Bedfordshire and Cambridgeshire. There are few extant exposures because quarrying operations in the nineteenth century effectively removed all surface outcrop (Fraser, 1990). The Cambridge Greensand consists of silty glauconitic marls with a basal lag composed largely of phosphatic nodules. It was deposited in a shallow sea in a region close to land; this observation accounts for the mixture of terrestrial and marine vertebrate faunas. Stratigraphical and biostratigraphical evidence suggests that the Cambridge Greensand was deposited during the early Cenomanian. However, the majority of the macrofossils are derived from the underlying Gault Clay and are considered to be of late Albian age. Indeed, some ‘Cambridge Greensand’ fossils were probably recovered directly from the Gault Clay: the uppermost section of the Gault contains several horizons rich in phosphatic nodules and these are likely to have been mined during the Cambridgeshire ‘coprolite rush’ (Fraser, 1990).

3. Systematic palaeontology

Reptilia: Laurenti, 1768
Diapsida: Osborn, 1903
Lepidosauria: Dumerin & Bibron, 1839

Family, genus and species indeterminate
Figures 1A–D, 3E

1887 *Patricosaurus merocratus* Seeley (partim) p. 216, pl. 12, figs 9–10.
1891 *Patricosaurus merocratus* Seeley (partim); Woods, p. 174.
1908 *Patricosaurus merocratus* Seeley (partim); von Nopcsa, p. 44.
1936 *Patricosaurus merocratus* Seeley (partim); Kuhn, p. 53.
1956 *Patricosaurus* Seeley (partim); Romer, p. 565.
1966 *Patricosaurus* Seeley (partim); Romer, p. 367.

Material. SMC B58401 (syntype), the proximal end of a right femur.

Remarks. The syntypes of ‘*Patricosaurus*’ (SMC B58401-2) were discovered at least 20 years apart and were made available for study by independent collectors. It is unlikely that they were recovered from the same locality, given the large number of pits in the Cambridge area and the ephemeral nature of the individual ‘coprolite diggings’. Blandford (cited in Seeley, 1887, p. 219) expressed doubts regarding the referral of SMC B58401 and SMC B58402 to the same taxon and suggested that the name ‘*Patricosaurus*’ be restricted to a single specimen. However, Seeley (1887) was convinced that the femur and sacral vertebra represented the same taxon, though his conclusion was not based on either the presence of shared anatomical features (as the individual elements are, obviously, not comparable) or on the basis of field association (as no such association was recorded). Indeed, the assignment of both specimens to ‘*Patricosaurus*’ is based solely on Seeley’s belief that each of these elements was referable to a lizard: “... out of the many thousands of bones from the Cambridge Greensand ... these are the only fragments of lizards ... and there was little chance of ... two lizards occurring” (Seeley, 1887, p. 220). Although Seeley (ibid., p. 220) suggested that the SMC B58401 could be taken as the name-bearing type (if it was found that the sacral vertebra was not referable to the same taxon), he stated clearly that both the femoral fragment and sacral vertebra should together be regarded as the type series (ibid., p. 218).

Locality. Exact locality unknown. A large number of vertebrate producing ‘coprolite pits’ were concentrated in an area around Cambridge in the late nineteenth century (Grove, 1976), suggesting that the specimen was probably collected in this vicinity (moreover, most of the specimens described by H. G. Seeley, and which are housed in the Sedgwick Museum, were obtained from Cambridge or from the area immediately to the south; N. C. Fraser, pers. comm. 2001). However, it is also possible that the specimen pertains to one of the pits operating in either Bedfordshire or Suffolk. The specimen was collected by Mr A. F. Griffith sometime in the 1880s (Seeley, 1887).

Horizon. Cambridge Greensand, early Cenomanian, Late Cretaceous (e.g., Hart, 1973; Rawson et al., 1978). Remainé fauna reworked from the Gault Clay, late Albian, Early Cretaceous (e.g., Worssam & Taylor, 1969; Morter & Wood, 1983).
Description. SMC B58401 (Figure 1A–D) is apparently from a fully mature animal since the articular surfaces and muscle rugosities are well developed. The specimen bears a dorsoventrally compressed femoral head, with a proximal articular surface that is widest anterodorsally and tapers posteriorly (Figure 1D). The proximal curvature is strong so that the major portion of the articular surface is anterodorsally placed. Seen in dorsal view (Figure 1A), this articular surface delimits a triangular area occupied by a strong scar for the ligament attachments of the M. puboischiofemoralis internus and M. ischirotrochantericus (Romer, 1956). The ventrally placed internal trochanter is also strongly developed (attachment of M. puboischiofemoralis externus; Romer 1956), and has its tip lying at a level slightly distal to that of the femoral head. A relatively narrow groove separates the two regions. Seen in proximal view (Figure 1D), the trochanter has a posterior curvature that helps to define a deep intertrochanteric fossa. The fossa is further emphasised by the development of posterodorsal and posteroventral (trochanteric) ridges (Figure 1C). The trochanteric crests represent the sites of insertion for powerful limb muscles, notably the M. puboischiofemoralis internus (posterodorsal) and the M. puboischiofemoralis externus and M. caudifemoralis (posteroventral) (Perrin, 1895; Romer, 1956; Rewcastle, 1981).

Comparison. The femur is clearly too well ossified to be that of an amphibian, and lacks the characteristic inturned femoral head and distinct neck of mammals.

Figure 1. Syntype of ‘Patricosaurus merocratus’ Seeley (SMC B58401), the proximal end of a right femur in A, dorsal; B, anterior; C, posterior; and D, proximal views. Scale bar represents 10 mm. Abbreviations: i.tr, internal trochanter; i.tr.f, intertrochanteric fossa; l.px.hd, lamination of proximal head (see text); ls, ligament scar; px.hd, proximal head; tr.c, trochanteric crest.
Considering the broad range of reptiles known from the Early Cretaceous, the femur of ‘Patricosaurus’ most closely resembles that of lepidosaurs in the shape and orientation of the femoral head (dorsoventrally flattened, but somewhat upturned from the femoral shaft so that the articular surface has a strong anterodorsal component; Romer, 1956) and the size and position of the internal trochanter (strong and ventrally placed). Chelonian femora have a more hemispherical head and possess paired anterior and posterior trochanters (Romer, 1956). Archosaurs typically show reduction or loss of the internal trochanter (though this is still prominent in some non-avian dinosaurs) and both greater flattening and inturning of the femoral head, culminating in the mammal-like condition seen in dinosaurs (including birds). Marine reptiles of this period (sauropterygians, ichthyosaurs) show reduction of the structures of the proximal region of the femur in association with the loss of a weight bearing function. In contrast, the strong trochanteric crests and processes of the ‘Patricosaurus’ femur suggest a terrestrial animal.

However, it should be emphasised that the lepidosaurian femoral structure is also an essentially one. The femora of primitive diapsids such as Araeoscelis (Reisz et al., 1984) and Youngina (Gow, 1975), for example, are not dissimilar to those of lepidosaurs, and this is also true of basal Triassic sauropterygians (e.g., Rieppel, 1999). A strong internal trochanter is not uniquely lepidosaurian (contra Seeley, 1887). Of taxa recorded, or inferred to be present, in the Cretaceous, the freshwater aquatic choristoderes (e.g., Erickson, 1972; SEE, pers. obs.) have femora similar to those of lepidosaurs, including a strong internal trochanter, despite their aquatic habits. The main differences are in the narrower, more elongate, internal trochanter and an absence of obvious proximal muscle scars or strong muscle ridges.

We therefore agree with Seeley (1887) that SMC B58401 is probably the proximal end of a lepidosaurian (but not necessarily lizard) femur, although uncertainties remain. Lepidosaurs, like mammals, are characterised by secondary centres of ossification in the long bone epiphyses. In immature animals, there is a clearly visible epiphyseal line between the epiphysis and the shaft, but this can be obscured or obliterated in mature adults. No epiphyseal line is visible in ‘Patricosaurus’, either between the head and the shaft or between the tip of the internal trochanter and the shaft. There does, however, appear to be a lamination of the proximal head suggesting that the outermost layer ossified separately from the rest (arrow on Figure 1A), but this layer is too thin to represent a lepidosaurian epiphysis (contra Seeley, 1887) and we may be seeing calcification spreading into part of the articular cartilage. Some mature lizards show a similar morphology (e.g., a specimen of Iguana iguana, AMNH R.97341).

There has been no detailed comparative review of lepidosaurian femoral morphology, beyond those dealing with aspects of basic structure and musculature (e.g., Perrin, 1895; Romer, 1956) and locomotor function (e.g., Rewcastle, 1981). A small study was completed for this paper, with the following taxa examined: Hydrosaurus amboinensis (Agamidae: AMNH R.140825); Cyclura cornuta (Iguanidae: AMNH R.57968); Iguana iguana (Iguanidae: AMNH R.97341); Iguana tuberculata (Iguanidae: OUMNH 702, OUMNH 13307); Sceloporus occidentalis (Iguanidae: UCLA unnumbered); Petrosaurus mearnsi (Iguanidae: UCLA unnumbered); Tupinambis teguixin (Teiidae: AMNH R.141941); Heloderma suspectum (Helodermatidae: AMNH R.147173); Varanus sp. (Varanidae: UCLA unnumbered); Varanus salvator (Varanidae: OUMNH 2939); Varanus gouldii (Varanidae: OUMNH 1286; Xantusia henshawi (Xantusiidae: UCLA unnumbered); Elgaria skiltonianus (Anguidae: UCLA unnumbered); Sphenodon sp. (Rhynchocephalia: UCLZ S346); Gephyrosaurus brindensis (Rhynchocephalia: UCLA unnumbered).

The principal features considered in this analysis are shown with reference to a right femur of Varanus in Figure 2.

Generally, the lepidosaurian femoral head appears to be very conservative in its structure. All of the taxa examined shared a common set of features, notably: a slightly dorsoventrally compressed femoral head with a strip-like articular surface wrapped across it; separate well-developed internal trochanter with its own epiphysis; internal trochanter ventrally placed, long axis usually at 90° to that of head; some development of an intertrochanteric fossa; conspicuous dorsal scar marking position of iliofemoral ligament attachment; triangular cross-section (Figure 3A–D). All of these features are also found in the Early Jurassic rhynchocephalian Gephyrosaurus (Evans, 1981), currently the most primitive lepidosaur known. Minor points of variation include:

1. The shape, width and anteroposterior curvature of the femoral head. As seen in dorsal view, the femoral head in ‘Patricosaurus’ is strongly curved, with the expanded anterior region forming a strong angle with the long axis of the shaft (Figure 1A). This is not the case in the majority of the lizards and rhynchocephalians examined (albeit a very small sample). The agamid Hydrosaurus came closest in the degree of curvature, but the femur is much more gracile and the
articulated surface is a different shape. A strong curvature of a somewhat different type is seen in both Xantusia and the anguid Elgaria where the entire head is tilted anteriorly in relation to the shaft (Figure 3B).

2. Degree of separation of the internal trochanter from the femoral head. In 'Patricosaurus', the internal trochanter is placed close to the proximal end of the bone, and the crest joining it to the femoral head is relatively smooth in outline (Figure 1D). The teiid Tupinambis and the iguanid Cyclura are similar to this, although the trochanter in both cases is slightly closer to the femoral head. By contrast, the trochanter is more markedly separated in the other genera examined, sometimes with a strongly notched proximal margin. The separation is strongest in Heloderma and Xantusia (Figure 3B), where the femoral head has a distinct neck.

3. Depth of the intertrochanteric fossa. 'Patricosaurus' has a very deep intertrochanteric fossa, due partly to the rugosity of the flanking muscle crests and also to the more angled position of the internal trochanter in relation to the femoral head (Figure 1C). None of the extant lepidosaurs examined had a fossa of comparable depth, but the deepest were in Tupinambis and Heloderma.

4. Strength and rugosity of the trochanteric crests. 'Patricosaurus' has very strong intertrochanteric fossa, due partly to the rugosity of the flanking muscle crests and also to the more angled position of the internal trochanter in relation to the femoral head (Figure 1C). None of the extant lepidosaurs examined had a fossa of comparable depth, but the deepest were in Tupinambis and Heloderma.

5. Shape and angle of the femoral head and trochanter as seen in terminal view. In 'Patricosaurus', the articulating surface (seen end on) is broad and rounded anteriorly but narrows and then tapers posteriorly. Hydrosaurus, Sceloporus (Figure 3A), Petersaurus, Xantusia (Figure 3B) and Elgaria, in contrast, all have a uniformly band-shaped surface, rounded at both edges. In this feature, the closest similarity to 'Patricosaurus' was found in Cyclura (a large terrestrial iguanid) and in Varanus (Figures 2, 3D).

6. Width vs. depth of the proximal femoral region. In 'Patricosaurus', the anteroposterior (femoral head) and dorsoventral (head to trochanter) axes are almost equal in length (anteroposterior 97% of dorsoventral), while in many of the modern taxa examined, the anteroposterior axis is shorter [e.g., from 78% of dorsoventral depth in Sceloporus, through 86% in Sphenodon, to 90% in the UCLA Varanus (femur length 77 mm)]. However, this is complicated by both intra- and interspecific variation. In Iguana tuberculata, the proportions change with size, such that in an animal with a femoral length of 73 mm (OUMNH 1307), the width of the head is 89% of the dorsoventral depth, while in a larger animal (OUMNH 702: femur length 81 mm), the head is relatively larger (93%). Within Varanus, however, interspecific variation is not simply a matter of size. Thus, for example,
in a large *Varanus salvator* (OUMNH 2939: femur length 124 mm), the head width is 91% of the dorsoventral depth, while in a much smaller *Varanus gouldii* (OUMNH 1286: femur length, 56 mm), width and depth were equal.

Of the taxa examined, the femoral head of *'Patricosaurus'* shows the greatest phenetic resemblance to that of a terrestrial varanid lizard (shape of the articular surface in proximal view; relative size of the internal trochanter and its degree of separation from the femoral head; relative anteroposterior width of the femoral head), although there are differences in the trochanteric angle, the depth of the fossa, the curvature of the femoral head in dorsal view, and the level of development of the muscle ridges (Figures 2, 3D). However, without a comprehensive analysis of lepidosaurian femoral morphology (ontogenetic as well as phyletic) it is impossible to know whether these features have any phylogenetic significance, nor whether femoral characters can be used in diagnosis.

Certainly the femur of *'Patricosaurus'* appears to have come from a mature and fully terrestrial animal. The femur of the aquatic mosasaurs is short and broad, with a small anteroventral trochanter and a straight or angled proximal end (e.g., Russell, 1967, figs 59, 60); that of the less derived aigialosaurs and dolichosaurs is less known (e.g., Carroll & DeBraga, 1992; DeBraga & Carroll, 1993; Caldwell et al., 1995). Carroll & DeBraga (1992) described the aigialosaur femoral head as bulbous, but it appears rather

Figure 3. Comparative anatomy of the proximal end of the femur in Lepidosauria. All femora are from the right-hand side. Left column, dorsal view; central column, anterior view; right column, proximal view. A, Sceloporus occidentalis (UCLA uncatalogued); B, Xantusia henshawi (UCLA uncatalogued); C, Sphenodon sp. (UCLZ S346); D, Varanus sp. (UCLA uncatalogued); and E, *'Patricosaurus merocratus'* (SMC B38401). Not to scale. See text for further details.
to be broadened, with a weakly ossified proximal head and incomplete separation of the trochanter and articular surface.

Rewcastle (1981) discussed femoral structure, musculature and gait. He described two primary movements between the femoral head and the acetabulum of the pelvis. The first is a sliding movement occurring principally during protraction and retraction of the limb in the horizontal plane. The second is a rotatory movement, with the head spinning in the acetabulum during fast locomotion and the limbs carried in a more vertical position. Since both M. caudifemoralis and M. puboischiofemoralis internus are important hip rotators, the strong crests of ‘Patricosaurus’, combined with the anterodorsally expanded articular surface, suggest that the animal may have been capable of fast, effective locomotion (a conclusion also reached by Seeley, 1887, p. 216).

Comparison with modern taxa suggests the original length of the complete femur would have been in the range of 80–100 mm (allowing for differences in femoral proportions in different groups). This would equate to a snout-vent (pygal) length of around 0.8–0.9 m, with a maximum body length of up to 2 m (including the tail). This would represent the largest terrestrial lepidosaur, living or extinct, currently known from the UK.

Comments. The combination of characters present in the femur of ‘Patricosaurus’ is most closely matched by living and extinct terrestrial lepidosaurs, particularly varanids. However, current knowledge of lepidosaurian femoral morphology does not provide a secure basis from which to differentiate a squamate femur from that of a rhynchocephalian, nor to characterise the femora of living lizard groups. Unless, or until, valid characters can be recognised, the femur should not be considered a diagnostic element. SMC B58401 possesses no uniquely autapomorphic features and is here regarded as Lepidosauria indeterminate.

Archosauria: Cope, 1869

Family, genus and species indeterminate

Figure 4A–C

1887 Patricosaurus merocratus Seeley (partim), p. 216, pl. 12, figs 11, 12.
1891 Patricosaurus merocratus Seeley (partim); Woods, p. 174.
1908 Patricosaurus merocratus Seeley (partim); von Nopcsa, p. 44.
1936 Patricosaurus merocratus Seeley (partim); Kuhn, p. 53.
1956 Patricosaurus Seeley (partim); Romer, p. 365.
1967 Patricosaurus Seeley (partim); Romer, p. 367.

Material. SMC B58402 (syntype), a sacral vertebra (see remarks on the syntypes, above).

Locality. Exact locality unknown, though it is likely that the specimen was collected from one of the many ‘coprolite pits’ near Cambridge (see above). The specimen was obtained by the Rev. H. G. Day prior to 1859 (Seeley, 1887).

Horizon. As above.

Description. The specimen is abraded and lacks the distal extremities of the sacral ribs, the neural spine and most of the prezygapophyseal and postzygapophyseal articular surfaces. Preparation of the specimen has led to further damage, particularly in the region of the neural canal. The centrum is relatively short and broad and its maximum length is approximately equal to its maximum transverse width (in the region of the parapophyses). In anterior view (Figure 4A), the articular surface of the centrum is subcrescentic in outline and is strongly concave. In contrast, the posterior articular surface is subelliptical in outline and flat to mildly convex (Figure 4B). Consequently,
the centrum is gently procoelous. The anterior articular surface is wider transversely, and slightly higher dorsoventrally, than the posterior articular surface; consequently, the centrum tapers posteriorly. Small notochordal pits are present on both anterior and posterior articular surfaces. The articular surfaces are slightly abraded, but the presence of finished bone suggests that this centrum was not fused to any other sacral vertebrae in life. Dorsally, the centrum bears a gentle longitudinal excavation that forms the ventral border of the neural canal. In ventral view, a broad, rounded, longitudinal keel extends along the entire length of the centrum (Figure 4C). The parapophyses are large and robust and are situated on the anterolateral corners of the centrum: they extend posteriorly for approximately 75% of the length of the centrum. The centrum is relatively small with respect to the proximal ends of the sacral ribs: the dorsoventral thickness of the sacral rib (measured where it fuses to the centrum) is approximately twice the dorsoventral height of the anterior articular surface.

The neural arch is almost completely fused to the centrum, although a small, unfused contact is still visible at the anteroventral margin of the right arch pedicle (Figure 4A). In anterior view, the neural canal is circular in outline, whereas in posterior view it is subquadangular. However, neither of these features can be considered to be the ‘natural’ shape of the neural canal as these regions have been heavily prepared. The neural arch pedicles are stoutly constructed and extend dorsally at 90° to the long axis of the centrum. The bases of the pedicles occupy the anterior 75% of the centrum and lie directly above the parapophyses. The neural platform is very flat and bears a very shallow concavity on either side of the base of the neural spine. The broken base of the neural spine indicates that it extended along the full length of the neural arch. The neural platform tapers laterally to give rise to the transverse processes. The pre- and postzygapophyses extend beyond the anterior and posterior margins of the neural platform, respectively, but are generally too badly damaged to yield any other information. The right postzygapophysis is largely complete, however; the articular surface is subtriangular in outline and faces posterodorsally. There is no indication of any hyposophene/hypantrum articulations. Pneumatic fossae are absent.

The sacral ribs are robust, are partially fused to most of the anterolateral portion of the centrum and completely cover the neural arch in lateral view, fusing dorsally with the transverse processes. A thin layer of matrix between the proximal ends of the ribs, the centrum and the neural arches indicates that fusion was not complete, however, suggesting that the sacral pertains either to a juvenile or to an habitually aquatic form. The sacral ribs are subtrapezoidal in parasagittal section and taper distally. The posterior surfaces of the sacral ribs are gently concave, whereas the dorsal, ventral and anterior surfaces are gently convex.

Comparison. The finished bone on the articular surfaces of the centrum and postzygapophysis of SMC B58402 demonstrates that it was not fused to any other sacral vertebrate. However, this character provides only a weak phylogenetic signal as the degree of sacral fusion varies among amniotes and is often dependent on the age of the individual (Romer, 1956). However, the clearly differentiated zygapophyses and articular surfaces of the centrum probably indicate that SMC B58402 was not part of a synsacrum, such as that present in pterosaurs or birds. Moreover, pterosaurs, birds and many saurischian dinosaurs (sauropods and non-avian theropods) have sacral vertebrae that are perforated by large pneumatic fossae (e.g., Britt, 1997), whereas these features are absent from SMC B58402.

The centrum of SMC B58402 is quite distinct from the amphicoelous, disk-like centra of ichthyosaurs. Furthermore, the sacral region of ichthyosaurs is not strongly differentiated from the rest of the axial skeleton and the sacral ribs do not fuse to the centra (e.g., Romer, 1956). Mosasaur sacrals differ from SMC B58402 in the possession of small foramina on the lateral surfaces of the centra and in the positioning of the sacral rib articulation (e.g., Brown, 1981). In plesiosaurs the contact between the sacral rib tuberculum and the neural arch is much smaller than the capitulum-centrum contact, whereas in SMC B58402 the tuberculum has an extensive contact with the neural arch that is at least as large as the capitulum-centrum articulation.

Turtle sacrals have transversely broad, dorsoventrally low neural spines that differ from the transversely narrow neural spines of SMC B58402. Moreover, the sacral ribs attach to the neural arch, directly above the neural central suture, and do not contact the lateral surface of the centrum (Romer, 1956). Lepidosaurus have either amphicoelous, notochordal vertebrae (rhynchocephalians, basal squamates and most gekkotans) or show marked procoely (all crown group squamates except amphicoelous gekkotans). Since the sacral vertebra referred to ‘Patricosaurus’ is only very gently procoelous, it unlikely to be lepidosaurian. It also differs markedly
from choristoderan vertebrae, where the centra are more cylindrical in shape (rather than dorsoventrally flattened).

Although the combination of character states present in SMC B54802 excludes it from referral to any of the aforementioned taxa, these features are consistent with its referral to either a crocodilian or a small ornithopod dinosaur, such as a hyspsilophodontid (PMB, pers. obs.). However, on the basis of the available evidence, it is not possible to determine to which of these two groups SMC B54802 should be referred.

Comments. SMC B54802 possesses no autapomorphic features: each of the character states mentioned above has a more general distribution within Archosauria. Consequently, we regard SMC B54802 as Archosauria indeterminate.

4. Conclusions

No anatomical or stratigraphical/geographical evidence supports the referral of SMC B54801 and SMC B54802 to the same taxon. Comparison of the femoral fragment and sacral vertebra with a wide variety of amniote taxa indicates that they are referable to the Lepidosauria and Archosauria, respectively. The syntype series of ‘Patricosaurus’ is, therefore, a chimera. Neither syntype possesses any autapomorphic features that support the validity of this taxon and ‘Patricosaurus merocratus’ should be regarded as a nomen dubium.

SMC B54801 provides the only known evidence for the presence of a large terrestrial lepidosaur in the Cambridge Greensand fauna (Seeley, 1887): indeed it represents the largest known terrestrial lepidosaur, living or extinct, to be recovered from the British Isles. Consequently, the identification of this isolated element is of considerable regional importance.

Crocodilians and small ornithischian dinosaurs are known from the Cambridge Greensand on the basis of isolated vertebrae (Seeley, 1874, 1879; Pereda-Suberbiola & Barrett, 1999), though their records are relatively poor. Although the referral of SMC B54802 to one of these clades slightly increases the amount of known material (in the case of crocodilians only four vertebrae have been described; Seeley, 1874) the lack of diagnostic features severely limits the utility of this material. Continued revision of the Cambridge Greensand vertebrate material (Elzanowski & Galton, 1991; Pereda-Suberbiola & Barrett, 1999; Unwin, 2001) is offering valuable new information on the composition and biogeographic relationships of late Early Cretaceous terrestrial faunas, a time interval that is poorly represented globally. A better understanding of this neglected, but important, fauna, will eventually provide one of the best windows onto this interesting period in Earth history.

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