Earth and Environmental Science Transactions of the Royal Society of Edinburgh, **101**, 285–299, 2011 (for 2010)

Saltopus, a dinosauriform from the Upper Triassic of Scotland

Michael J. Benton[1] and Alick D. Walker†

[1] School of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, UK

† Alick D. Walker (1925–1999) worked on *Saltopus* through the 1960s, and left substantial notes and sketches, especially documenting the preparation and casting he did in 1961, 1964, 1965 and 1966. These provided information used in the present paper.

ABSTRACT: *Saltopus elginensis*, reported in 1910 from the yellow sandstones of the Lossiemouth Sandstone Formation (Late Triassic) of Morayshire, NE Scotland, has long been controversial. It was described first as a theropod dinosaur, but others disagreed. Reanalysis of the type, and only, specimen using casts from the natural rock moulds, as well as X-rays and CT scans, has revealed new anatomical data not available to previous researchers. *Saltopus* was a small, 800–1000 mm-long biped, whose tail made up more than half its length. It is an avemetatarsalian because it has elongated and tightly bunched metatarsals, the tibia is longer than the femur, the calcaneal tuber is rudimentary or absent, and metatarsal II is equal to or longer than metatarsal IV; a unique assemblage of characters diagnosing this clade. *Saltopus* is a dinosauromorph on the basis of the reduced fingers IV and V, the saddle-shaped dorsal margin of the iliac blade, and the articulation of sacral rib 1 close to the front of the iliac blade. *Saltopus* is a dinosauriform on the basis of the trochanteric shelf and lesser trochanter on the proximal end of the femur, the waisted sacral ribs, and perhaps the rod-like and straight pubis. However, it lacks all apomorphies of Dinosauria, retaining for example the primitive condition of two sacral vertebrae. Cladistic analyses place *Saltopus* within Dinosauromorpha and Dinosauriformes, and between the basal dinosauriform *Pseudolagosuchus* and the derived clade consisting of Silesauridae and Dinosauria, so making it one of a radiation of small pre-dinosaurian bipedal archosaurs in the Triassic found so far in North and South America and in Europe.

KEY WORDS: Archosauria, Avemetatarsalia, Dinosauria, Dinosauromorpha, Elgin reptiles, Lossiemouth Sandstone Formation, Ornithodira

The small Scottish Triassic tetrapod *Saltopus elginensis* Huene, 1910a has been identified as a dinosaur by several authors (e.g. Huene 1910a, 1914; Romer 1966; Steel 1970; Walker 1970; Benton & Walker 1985) and, if this identification were correct, it would count as the oldest dinosaur from the British Isles, and perhaps the oldest, or one of the oldest, from Europe. Others have, however, expressed caution, noting that the single specimen is incomplete and poorly preserved (Norman 1990; Rauhut & Hungerbühler 2000; Langer 2004), and might be identifiable simply as an ornithodiran or a dinosauromorph, a member of the broader clade that includes dinosaurs.

The anatomy and systematic position of *Saltopus* are important in our understanding of the radiation of archosaurs, and particularly the origin of dinosaurs, in the Late Triassic. New work (e.g. Benton 1999; Langer 2004; Langer & Benton 2006; Irmis *et al.* 2007; Brusatte *et al.* 2008, 2010, 2011; Nesbitt *et al.* 2009a, b, 2010; Langer *et al.* 2010) shows that the dinosaur-bird branch of the archosaurs was diversifying during the Middle and Late Triassic, giving rise to two major clades, the dinosaurs and the pterosaurs, but also including many other small, slender, long-limbed animals generally called 'basal dinosauromorphs' or simply 'dinosauromorphs'.

Saltopus is known from a single specimen (NHMUK R3915), preserved as part and counterpart slabs (Figs 1, 2), which shows the middle region of the skeleton of a slender animal, lying belly-down. The surviving parts of the skeleton consist of a 190 mm-long section of the vertebral column, consisting of some ten dorsal vertebrae (perhaps numbers 5–14), the left forelimb, the pelvic region, the hindlimbs sprawled out to the sides, and the proximal part of the tail, consisting of 24 caudal vertebrae.

Since Huene's (1910a) description, several palaeontologists have examined the type specimen in London, but few have been able to make or see casts. This has severely limited their interpretations. However, casts in a variety of media are available and they, together with the original specimens, form the basis of the description in the present paper. The purpose of this paper is to present illustrations and descriptions of the specimen and the casts, to describe the anatomy in as much detail as possible, and to use this information to determine the systematic affinities of the taxon.

Institutional abbreviation: NHMUK, Natural History Museum, London.

1. Materials and methods

NHMUK R3915 (Figs 1, 2), the sole and type specimen of *Saltopus elginensis* Huene, 1910a, was collected by Mr William Taylor of Lhanbryde (1849–1921), and shown to Friedrich von Huene (1875–1969) in October 1909. Taylor was a well known fossil collector in the Elgin area from 1890 to 1920, and he supplied von Huene and other palaeontologists with several specimens of reptiles, including the type specimens of the archosaur *Scleromochlus taylori* Woodward, 1907 and the sphenodontian *Brachyrhinodon taylori* Huene, 1910b, as well as other materials of previously named taxa.

doi:10.1017/S1755691011020081

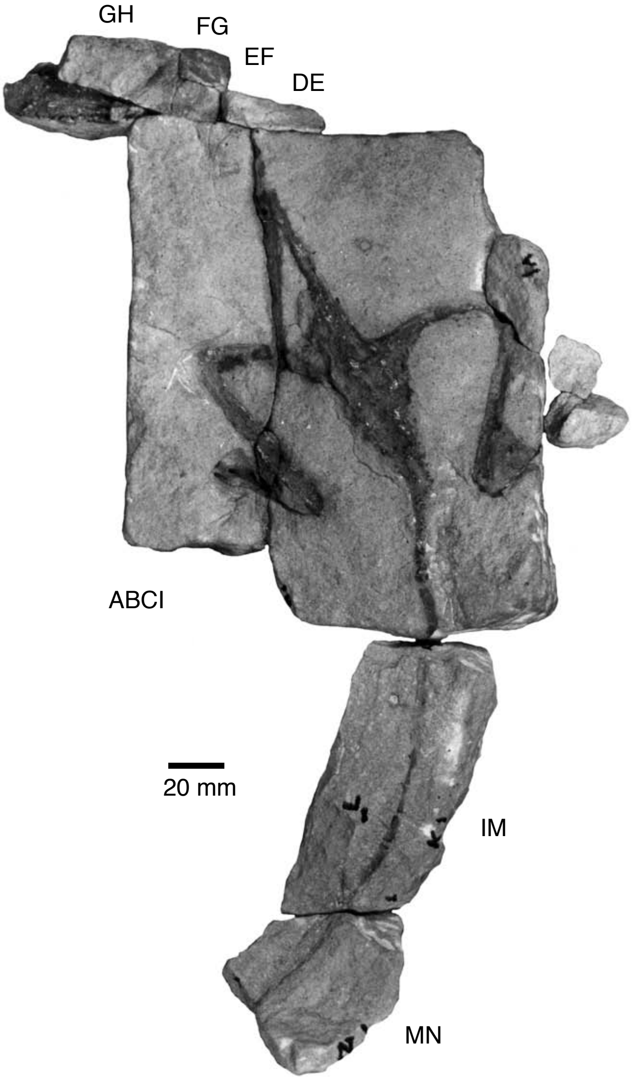

Figure 1 The type specimen of *Saltopus elginensis* Huene, 1910a, from the Lossiemouth Sandstone Formation of Lossiemouth West Quarry (NHMUK R3915), main slab, with the two separate tail slabs, a small piece with the right foot, and blocks at the front with the left forelimb. These additional smaller pieces are named with two-letter codes, and these indicate matching from piece to piece (e.g. FG and GH fit at letter 'G').

Figure 2 The type specimen of *Saltopus elginensis* Huene, 1910a, from the Lossiemouth Sandstone Formation of Lossiemouth West Quarry (NHMUK R3915), counterslab.

Table 1 Classification of the reptiles of the Lossiemouth Sandstone Formation, showing the original description and subsequent major redescriptions.

- Subclass Anapsida Osborn, 1903
    - Family Procolophonidae Cope, 1889
        - *Leptopleuron lacertinum* Owen, 1851; revision Säilä (2010)
- Subclass Diapsida Osborn, 1903
    - Infraclass Lepidosauromorpha Benton, 1983
        - Superorder Lepidosauria Haeckel, 1866
            - Order Sphenodontia Williston, 1925
                - Family Sphenodontidae Cope, 1869
                    - *Brachyrhinodon taylori* Huene, 1910b; revision Fraser and Benton (1989)
    - Infraclass Archosauromorpha Huene, 1946
        - Division Rhynchosauria Osborn, 1903
            - Family Rhynchosauridae Huxley, 1867
                - *Hyperodapedon gordoni* Huxley, 1859; revision Benton (1983)
        - Division Archosauria Cope, 1869
            - Subdivision Crurotarsi Sereno and Arcucci, 1990
                - Family Ornithosuchidae Huene, 1908
                    - *Ornithosuchus longidens* (Huxley, 1877); revision Walker (1964)
                - Family Stagonolepididae Lydekker, 1887
                    - *Stagonolepis robertsoni* Agassiz, 1844; revision Walker (1961)
                - Family Erpetosuchidae Watson, 1917
                    - *Erpetosuchus granti* Newton, 1894; revision Benton and Walker (2002)
            - Subdivision Avemetatarsalia Benton, 1999
                - Family Scleromochlidae Huene, 1914
                    - *Scleromochlus taylori* Woodward, 1907; revision Benton (1999)
                - Infradivision Ornithodira Gauthier, 1986
                    - Family undetermined
                        - *Saltopus elginensis* Huene, 1910a; revision this paper.

The fossil came from Lossiemouth West Quarry (National Grid Reference [NJ 231704]), in the Lossiemouth Sandstone Formation, source of eight taxa of reptiles (Table 1; reviewed by Benton & Spencer 1995; Benton & Walker 1985). Huene (1910a) regarded this rock unit as Ladinian (late Middle Triassic) in age, equivalent to the Lettenkeuper in Germany, but it is now dated as Late Triassic. Dating is on the basis of the tetrapod fauna, which is not an ideal situation. The relative lithostratigraphic age places the Lossiemouth Sandstone Formation somewhere between the underlying Burghead Sandstone Formation (?Early to Late Triassic) and the overlying Rhaetic and Lias (latest Triassic to Early Jurassic). There are no palynomorphs, plants, or invertebrate fossils, nor are there any radiometric dates.

The rich reptilian fauna of the Lossiemouth Sandstone was first compared with faunas from the Keuper of Germany, especially those of the Stubensandstein, and that suggested an early to mid Norian age (Walker 1961; Warrington *et al.* 1980; Benton & Walker 1985). However, wider comparisons suggest that the fauna is more clearly equivalent to faunas from the lower part of the Maleri Formation in India, the upper part of the Santa Maria Formation of Brazil, and from the Ischigualasto Formation of Argentina, with which it shares the rhynchosaur genus *Hyperodapedon*. The Ischigualasto Formation is dated radiometrically as younger than 230·2–231·4 mya, from an ash band at its base (Furin *et al.* 2006), and hence is late Carnian to early Norian in age, according to the revised stratigraphic scheme for the Late Triassic (Muttoni *et al.* 2004;

Mundil *et al.* 2010). The aetosaur *Stagonolepis* may be shared with the Blue Mesa Member of Arizona, which is also dated biostratigraphically as early Norian (Irmis & Mundil 2008).

The specimen of *Saltopus* (Figs 1, 2) consists of the slab ('ABCI', Fig. 1) and counterslab ('AB', Fig. 2), containing ventral and dorsal portions of the skeleton respectively. Each of these consists of two main pieces, the larger containing the posterior part of the torso, the pelvic region, anterior tail and right hindlimb, and the smaller containing some anterior ribs and vertebrae and much of the left hindlimb. Two additional blocks ('IM', 'MN') fit behind the main counterpart blocks and contain segments of the tail, with caudals 11–20 and 20–25 respectively (Fig. 1). Four small pieces attached to the edge of the counterpart contain parts of the right foot (Fig. 1), and six further small pieces ('DE', 'EF', 'FG', 'GH') attach at the front and contain some anterior dorsal vertebrae and the left forelimb (Fig. 1).

The preservation of the *Saltopus* specimen is modest to poor. The fossil is represented, as is typical of specimens from the Lossiemouth Sandstone Formation, by hollows in the medium-grained yellow sandstone; essentially all bone material has vanished. The moulds of the bones are stained orange in places, remnants of goethite (iron oxide) that accumulated around the bones (Benton & Walker 1985). Unfortunately the two slabs, as well as splitting apart on the plane of the carcass, have also broken into several blocks, some of the breaks extending along parts of the dorsal vertebral column and across the hindlimb bones. The small size of the animal with respect to the grain size of the sandstone, the mineralisation, and the fractures in the rock, obscure some details. Further, the sandstone is unusually poorly cemented, much worse than the sandstone containing some of the other Lossiemouth Sandstone reptiles. This made it especially difficult for ADW to clear debris, iron oxide and degraded bone material from the natural rock moulds before casting. Probably the relatively large grain size and the poor cementation account for the rather excessive amount of goethite growth around bone joints.

Huene (1910a, p. 317) reported the condition of the specimen and his efforts at preparation and study: "However favourable the complete articulated condition of all parts is, the preservation of the bones, particularly in the pelvic region, is poor. Most of the bones are changed into brown iron sand. In the pelvic and dorsal region this metamorphosis has not only affected the bones but also their surroundings in the matrix. Thus one requires time and clear lateral lighting in order to distinguish bones and stone from each other in these parts. A trial preparation was attempted without success since the bones and stone have almost the same constitution in the area referred to". Rauhut & Hungerbühler (2000, p. 81) also noted the poor quality of preservation of *Saltopus*, and such comments are typical for Lossiemouth Sandstone Formation specimens. However, close study of the natural moulds and modern, high fidelity casts have revealed unexpected detail for many taxa (e.g. Walker 1961, 1964; Benton 1983, 1999; Benton & Walker 2002).

ADW made numerous casts of the *Saltopus* specimen between 1961 and 1966, using PVC, Silastomer and other media. S. Mahala Andrews, then a PhD student in Newcastle, made some of the casts. Arthur Rixon, the noted preparator at the Natural History Museum in London, also made injection moulds of the pubis and had X-rays made. These eight X-rays, still in the NHMUK archive, are of the main slab, and they show various views of portions of the skeleton, primarily the pelvic area, currently buried within the rock. Among the casts, there is one cast of the whole skeleton on the counterpart slab, as well as numerous focused casts of particular regions of the vertebral column and limbs. These more localised casts are from part or counterpart slabs, and they represent efforts to retrieve details from deeper within the rock, often after some additional careful removal of mineralised debris from the hollows. The original slabs, and especially the casts, show some slender elements quite clearly, such as neural spines and the dorsal iliac blade, each less than 1 mm in width. Close inspection of the specimen and these casts provides additional information on the anatomy of *Saltopus*, which is the subject of this paper.

Some preliminary computed tomography (CT) scans were also made of the whole specimen, using the Metris X-Tek HMX ST 225 CT System at the NHMUK. Images were produced using Avizo 6.1 (Mercury Computer Systems Ltd., Chelmsford, MA, USA), by systematically assigning material properties to visible structures within each slice of the scan data set. Interpolation and adjustments of contrast allowed recovery of specimen detail in regions that were poorly resolved (because of low scan resolution or concentrations of metal ore). Processing was carried out on a Hewlett Packard PC with 16GB DDR SDRAM.

2. Systematic palaeontology

Division Archosauria Cope, 1869
Subdivision Avemetatarsalia Benton, 1999
Infradivision Dinosauromorpha Benton, 1985
Subinfradivision Dinosauriformes Novas, 1992
Family Uncertain
Genus *Saltopus* Huene, 1910a
Species *Saltopus elginensis* Huene, 1910a

*1910a *Saltopus elginensis* Huene, p. 315, pl. 43.
1914 *Saltopus elginensis* Huene, 1910a; Huene, p. 31.
1985 *Saltopus elginensis* Huene, 1910a; Benton & Walker, pp. 211, 213.
1990 *Saltopus elginensis* Huene, 1910a; Norman, p. 303.
1995 *Saltopus elginensis* Huene, 1910a; Benton *et al.*, p. 177.
1995 *Saltopus elginensis* Huene, 1910a; Benton & Spencer, pp. 65, 68.
1998 *Saltopus elginensis* Huene, 1910a; Lucas, p. 368.
2000 *Saltopus elginensis* Huene, 1910a; Heckert & Lucas, p. 65.
2000 *Saltopus elginensis* Huene, 1910a; Rauhut & Hungerbühler, p. 81.
2004 *Saltopus elginensis* Huene, 1910a; Langer, p. 26.
2007 *Saltopus elginensis* Huene, 1910a; Naish & Martill, p. 496.
2010 *Saltopus elginensis* Huene, 1910a; Langer *et al.*, pp. 56, 59, 68, fig. 1A.

Type material. Sole, and holotype specimen, NHMUK R2915, a partial postcranial skeleton.

Type locality. Lossiemouth West Quarry (National Grid Reference [NJ 231704]), within Lossiemouth town, Morayshire, Scotland. Lossiemouth Sandstone Formation (?early Norian).

Comments on validity of taxon. *Saltopus elginensis* possesses synapomorphies of Archosauria, Avemetatarsalia, Dinosauromorpha, and Dinosauriformes, successive nested clades (see below). Comparison with other basal dinosauromorphs shows that *Saltopus* lacks the fused astragalocalcaneum and functionally didactyl pes of *Lagerpeton* (Sereno & Arcucci 1993), the robust pubis and reduced calcaneum of *Pseudolagosuchus* (Arcucci 1987), and probably the two fused dorsosacral vertebrae, elongate forelimb, very short iliac blade, and reduced calcaneum of *Silesaurus* (Dzik 2003). *Saltopus* shows no unique apomorphies in comparison with these and other taxa, so it could be regarded as a *nomen dubium* until a skull, or some better preserved postcranial remains come to light. However, its character coding (Table 2) is unique, being replicated in no other Triassic archosaur (Brusatte *et al.* 2010), and so the genus and species is valid.

3. Description

3.1. General

The description is based primarily on casts from the counterslab (Fig. 3), with comments added from close observation of casts from the main slab, and from the main slab and counterslab of NHMUK R3915 (Figs 1, 2). The so-called counterslab lay above the slab, so the former shows the dorsal view, and the slab the ventral view of the skeleton. The slabs split apart across the middle of the hindlimb bones, between centrum and neural spine along most of the vertebral column, and through the middle of the iliac blades in the pelvic area. Where appropriate, reference is made to coding of the available characters of *Saltopus* according to the most recent, comprehensive cladistic analysis of basal archosaurs by Brusatte *et al.* (2010).

The head and cervical region are missing, even though Norman (1990, p. 303) referred in error to a low and slender skull like that of *Procompsognathus*.

3.2. Axial skeleton

Estimating the number of presacral vertebrae preserved, and so where the vertebral column begins, is difficult. On the main blocks, two displaced dorsal centra (Fig. 3) are each 7 mm and 7·5 mm long, while two anterior dorsal vertebrae in succession measure 18 mm together, suggesting an overall individual vertebral length of 9 mm. These measurements are confirmed from dorsal and lateral X-rays, which show that two posterior centra are each 8 mm long and spaced about 1 mm apart. The distance from the anterior-most tip of the iliac blades, measured along the line of the presacral vertebral column to the anterior margin of the counterpart slab is 90 mm, so suggesting the presence of ten dorsal vertebrae. Individual dorsal vertebrae vary somewhat in length, from perhaps 8 mm to 10 mm, but it is hard to provide exact measurements. The presacral column continues forward onto two loose fragments (pieces ‘DE’ and ‘EF’), which contain a further two centra. The original number of presacral vertebrae is likely to have been 24 (nine cervicals, 15 dorsals), as in *Herrerasaurus* and primitively for Ornithodira (Novas 1993), and so the anteriormost vertebra in *Saltopus* is probably dorsal 5 (Fig. 3b). Huene (1910a), on the other hand, counted one posteriormost cervical and 14 dorsals, making 15 presacral vertebrae in all, and yet he provided measurements of only ten vertebrae, assuming some were missing or displaced. He seems to have placed the anterior loose pieces against the main counterslab incorrectly, and so created a space for an additional three vertebrae (his missing dorsals 3 to 5). Huene (1910a) stated that the cervical vertebrae were elongate in comparison with the dorsals, and yet there is no evidence for this statement because no cervical vertebra is preserved; even if the anteriormost presacral vertebra is interpreted as a cervical, it is incomplete and the centrum is not preserved.

The dorsal vertebral column begins (Fig. 3b) with the distal tip of the left rib of dorsal 4, followed by a partial centrum and distal half of the left rib of dorsal 5, then the centrum and left rib of dorsal 6, and then poorly preserved centra of dorsals 7–14. An isolated centrum lying to the left of the column, between dorsals 7 and 8, may be a disarticulated anterior dorsal or a cervical: its centrum length (7 mm) matches the neighbouring centra. A further displaced centrum on the left side lies just below and a little behind the position of dorsal 9: it could perhaps be the disarticulated centrum of dorsal 9, and it is 7·5 mm in length. Overall, the dorsal vertebrae appear to lengthen slightly backwards towards the sacrum, but there is no evidence that they become elongate in mid-column, and then shorten again backwards, as suggested by Huene (1910a). The two displaced centra are seen also on the main slab (Fig. 1a) in ventral view. The first displaced centrum is waisted, narrowing from a width of 3·5 mm at the articular end to 2 mm in the middle. The ventral face appears to be smooth, with no sign of a ventral ridge, and the dorsal face, seen on the counterslab (Fig. 1b, 2b), is marked by a shallow central trough that is the base of the spinal cord canal.

It is very hard to make out details of the dorsal vertebrae, other than their positions and the pinching between individual centra in the column. In the casts, dorsals 6 and 7 appear as paired ridges, marking the bases of the neural spines above the centrum. The more posterior dorsals show the top of the neural arch, but little of the neural spine, which is buried in the main slab. In dorsals 9–11, the neural arch measures about 8 mm wide across the transverse processes and 4 mm wide across the postzygapophyses. The two posterior dorsal centra seen in the X-rays are 8 mm long, 6 mm wide across the articular ends, and 4 mm wide in the middle. Of phylogenetically significant characters, the dorsal neural arches appear to be short, certainly less than four times the centrum height (Brusatte *et al.* 2010, character 84), but it cannot be said whether the neural arches of the dorsals bear spine tables or not (Brusatte *et al.* 2010, character 85), whether there are lateral laminae and fossae or not (Brusatte *et al.* 2010, character 86), nor whether there was a supplementary hypantrum/hyposphene articulation (Brusatte *et al.* 2010, character 87).

The sacral region is obscure and hard to interpret (Figs 1–4). Huene (1910a, pp. 317–318) was clear that *Saltopus* had four sacrals, Norman (1990, p. 310) reported three, Rauhut & Hungerbühler (2000, p. 81) reduced the number to “probably two”, and Langer (2004, p. 32) was clear that it had two. Huene (1910a, p. 317) reported “six more or less indistinct vertebrae between the long ilia” of which the middle four sent sacral ribs towards the ilia. He reported the lengths of his four sacral vertebrae as 7 mm, 8 mm, 9 mm and 9 mm, making 33 mm in all, and this was matched by long iliac blades on either side, measuring 48 mm in his drawing. On the other hand, Norman (1990, p. 310), Rauhut & Hungerbühler (2000, p. 81), and Langer (2004, p. 33) stressed that the iliac blades were considerably shorter than Huene had assumed, and so their estimates of three or two sacral vertebrae respectively made more sense.

Close study of the part and counterpart slabs, and of various casts (Fig. 4), confirms the presence of two sacral vertebrae, as noted by Rauhut & Hungerbühler (2000, p. 81) and Langer (2004, p. 32). In casts of the pelvic region taken from the counterslab, two neural spines are seen clearly between the iliac blades (Figs 3, 4), the most anterior lying between the anterior tips of the blades, and a third almost comes up to a line between the posterior tips of the blades. Further, likely impressions of the sacral ribs connect to the anterior and posterior parts of the left iliac blade, and this shows fairly clearly the presence of only two broad ribs. The spacing of the neural spines suggests individual vertebral lengths of about 10 mm. The suggestion that *Saltopus* had two sacral vertebrae is supported also by the position and length of

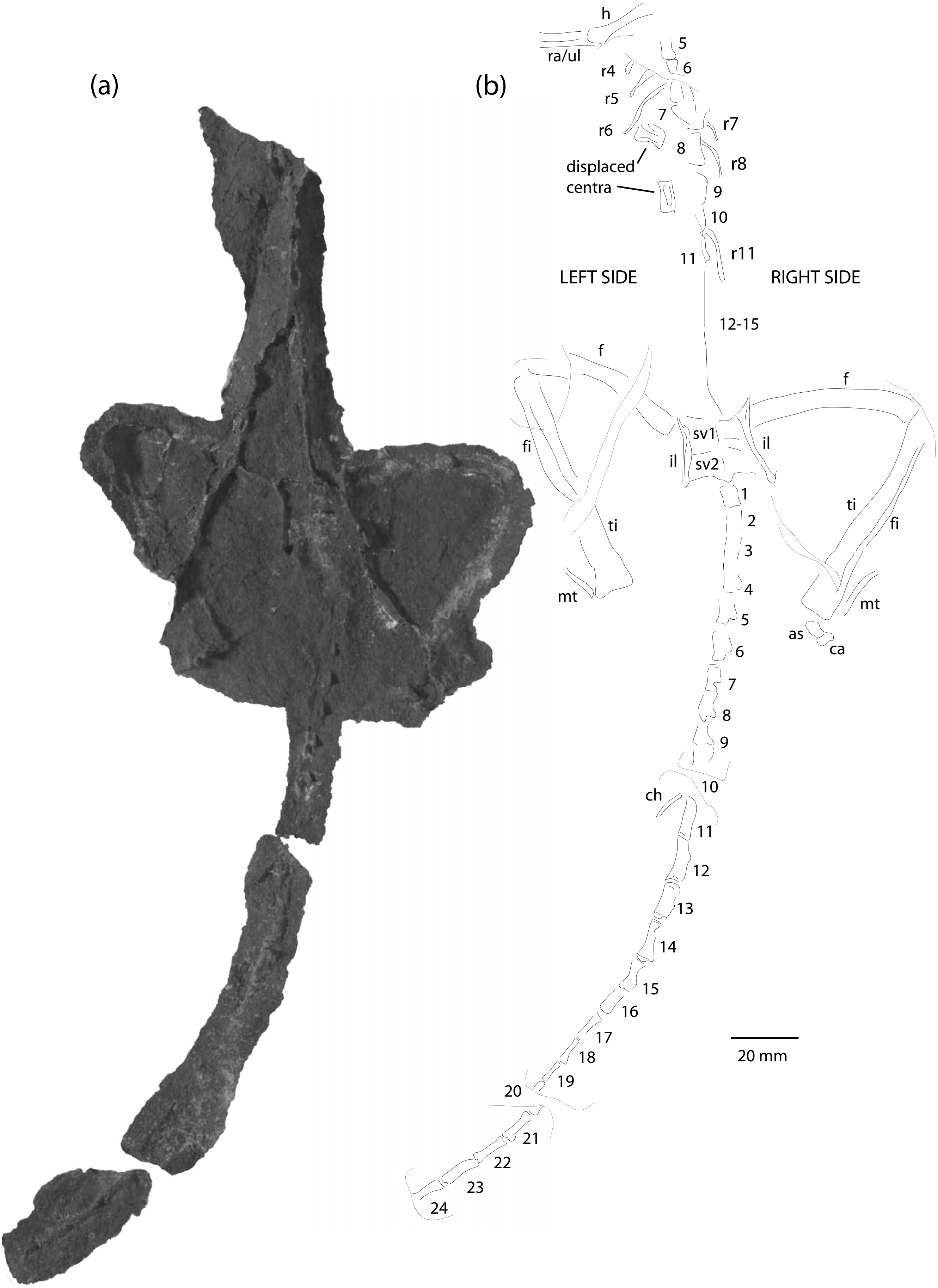

Figure 3 Casts of the counterslab elements of *Saltopus elginensis* Huene, 1910a (NHMUK R3915), showing dorsal view of the trunk, pelvic area, and proximal tail, photograph (a) and interpretive drawing (b). Abbreviations: 1, 2, 3 etc=numbered dorsal or caudal vertebrae, or ribs; as=astragalus; ca=calcaneum; ch=chevron; f=femur; fi=fibula; h=humerus; il=ilium; mt=metatarsal; r=rib; ra=radius; sv=sacral vertebra; ti=tibia; ul=ulna.

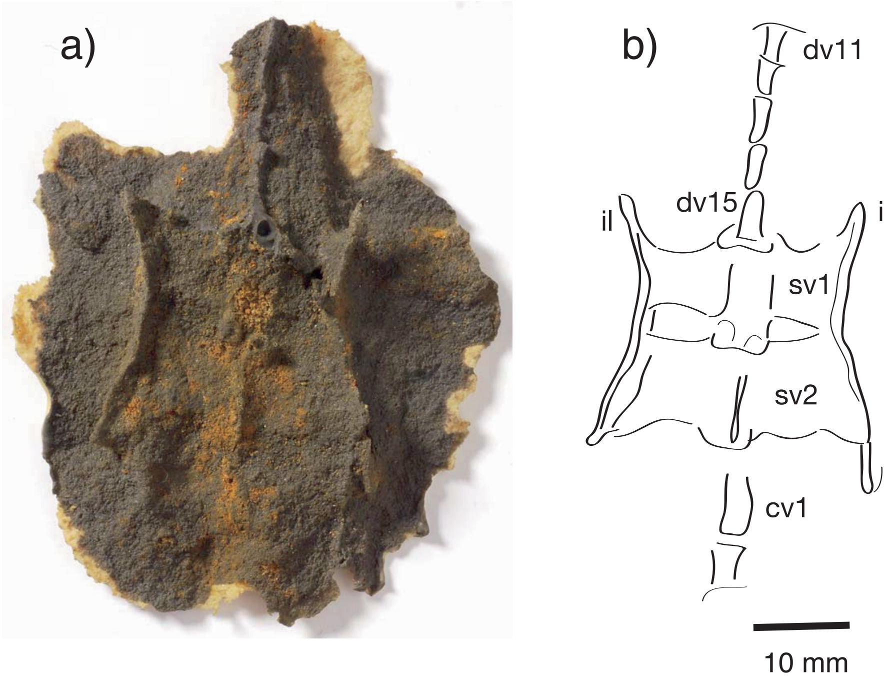

Figure 4 Cast of the sacral and pelvic area of *Saltopus elginensis* Huene, 1910a (NHMUK R3915), viewed from above (taken from the counterslab), shown as a photograph of the cast (a) and an interpretive drawing (b). The orange stains are traces of iron oxide (goethite) lifted from the natural rock moulds in the casting process. The casting medium is PVC, coloured brown. Abbreviations: cv=caudal vertebra; dv=dorsal vertebra; il=iliac blade; sv=sacral vertebra.

the right and left iliac blades, which measure 26 mm and 23 mm respectively across the chord in various casts, and so can accommodate only two sacrals. The neural spine of the first caudal vertebra lies just in line with the posterior margin of the iliac blades, but it is located too far posteriorly to have sent ribs to the ilia. Note that in *Herrerasaurus*, where the pelvic area is much better preserved, there are five vertebrae between the iliac blades (Novas 1993, fig. 3): two posterior dorsals, two sacrals, and the anteriormost caudal, only the two sacrals of which send ribs to contact the iliac blades, as seen also in *Saltopus*.

In terms of phylogenetically informative characters, *Saltopus* lacks the derived condition of three sacral vertebrae (Brusatte *et al.* 2010, character 88), and it cannot be said whether the sacral vertebrae were fused or not (Brusatte *et al.* 2010, character 89), nor can the form of the centrum rims (Brusatte *et al.* 2010, character 90) be seen.

The tail is seen partly in dorsal view anteriorly, and twisted to show the left-hand side further back in the counterslab (Fig. 3). There are 24 caudal vertebrae, of which the anterior ten are 9–10 mm long, based on the spacing of the transverse processes, whereas more posterior centra, in the region of caudals 20–24, measure 11 mm in length and only about 3–4 mm in height. As Huene (1910a, p. 319) noted, "the preserved part of the tail can hardly be half of it, since the length of the vertebrae up to that point is still increasing". The caudal centra are all narrow and elongate, with more or less straight ventral margins, and the transverse processes (identified as neural spines by Huene 1910a, p. 319) are short, 3–4 mm long, and point backwards. The anterior caudal centra in the X-rays are 10 mm long, 3 mm wide across the articular ends, pinching symmetrically to a middle width of 2 mm. The pre- and postzygapophyseal contacts are faintly seen between caudals 7 and 8 and 8 and 9. The neural spines are much less clear; any accessory anterior projection on the neural spine (Brusatte *et al.* 2010, character 91) cannot be determined.

On the counterslab (Figs 1, 2b, 3), three ribs (dorsals 4–6) are visible on the left side, and three on the right (dorsals 7, 8, 11), but detail is lacking. The scapula piece, lying anterior to the counterslab, preserves two ribs (Fig. 5a, b), presumably left ribs of dorsals 2 and 3. Each rib is slightly broadened proximally and tapers, with a substantial curve, distally. The left rib 6 is 17 mm long, around the curve. These anterior ribs may have been two-headed, but the capitulum cannot be seen, possibly lying below the surface of preservation. On the main slab (Fig. 2a), left rib 6 appears to show its distal tip, with a total length of 22 mm. In addition, the proximal end of right rib 11 is seen for some 16 mm of its length (Fig. 2a). In the caudal region the chevrons appear to be short, but details are poor, and they appear to have been displaced from their original attitudes. The chevrons beside caudals 11 (and possibly 12) are about the same length as the associated centra.

The sacral ribs are waisted (Brusatte *et al.* 2010, character 93) and the first rib appears to extend to the anterior end of the preacetabular process of the iliac blade (character 94). This latter feature is convergent in Poposauroidea and in the clade of *Lagerpeton*+*Dromomeron* (Brusatte *et al.* 2010). The other three rib characters (characters 91, 92, and 95) cannot be determined, and there is no evidence for osteoderms (Brusatte *et al.* 2010, characters 96, 97).

3.3. Shoulder girdle and forelimb

The scapula and humerus from the left side are preserved, and putative elements from the right side are probably wrongly identified (see below). The forelimb is considerably shorter than the hindlimb (c. 68 mm/156 mm=43·5%; Brusatte *et al.* 2010, character 98), a convergence of Poposauroidea (minus *Yarasuchus*) and Avemetatarsalia (although reversed in *Silesaurus*+*Sacisaurus*+*Eucoeolophysis*+*Lewisuchus*).

The scapula (Fig. 5a, b) is a slender element that curves medio-laterally around the rib cage, and expands to just over twice its minimum anteroposterior breadth (3 mm wide) at the

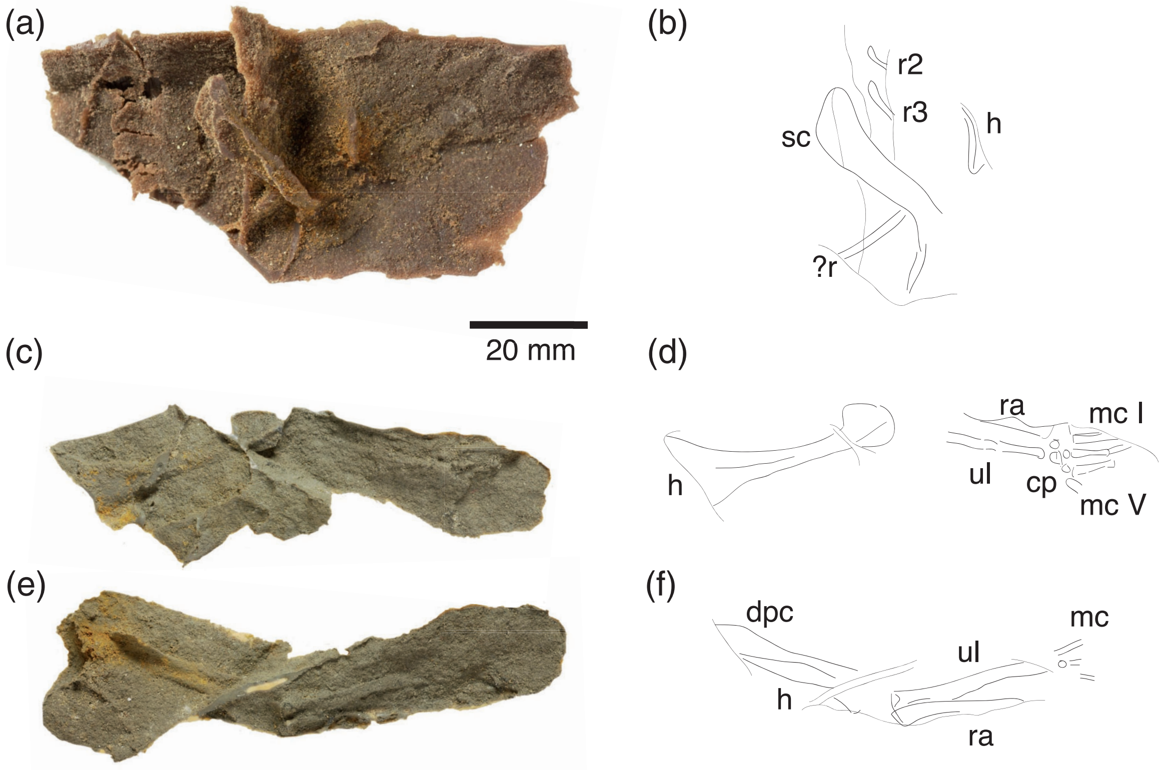

Figure 5 Elements of the left forelimb of *Saltopus elginensis* Huene, 1910a (NHMUK R3915): (a, b) Cast of left scapula, two left ribs, and proximal head of the left humerus; (c, d) cast of dorsal surfaces of the left humerus, radius, ulna, and hand; (e, f) cast of ventral surfaces of the left humerus, radius, ulna, and hand. Abbreviations: cp=carpal; dpc=deltopectoral crest; h=humerus; mc=metacarpal; r=rib; ra=radius; sc=scapula; ul=ulna.

distal end of the blade (6 mm wide), but it does not appear to be strongly expanded distally (Brusatte *et al.* 2010, character 99). The distal part of the blade is angled backwards, forming a 45° angle between the distal and posterior margins. The scapula is 22 mm long, but may have measured 28 mm when complete: proximally, the cast is incomplete, lacking the posterior margin with the glenoid and articulation with the coracoid. The coracoid (characters 100–102), interclavicle (character 103), and clavicle (character 104) are not preserved, presumably lost along the fracture between the small rock fragments that contain the scapular blade and the main blocks of the fossil. The supposed right scapula identified by Huene (1910a, p. 43), lying beside the anteriormost dorsal vertebrae, is too rod-like to be a scapula; it is preserved as a hollow in the rock, and could be part of the proximal head of the left humerus.

The left humerus is 36 mm long, and the thin deltopectoral crest is seen in ventral view (Fig. 5e, f), behind which the shaft narrows. The proximal head of the humerus is exposed close to the left scapula (Fig. 5a, b): it is not very wide, and seems to be quite separate from the deltopectoral crest. Nonetheless, the proximal end is greater than twice the midshaft width (Brusatte *et al.* 2010, character 105), and the deltopectoral crest appears to extend about one-third of the way down the bone, but probably not over 35% of the length of the bone (Brusatte *et al.* 2010, character 107), a synapomorphy of Dinosauria. These measurements are hard to make because the proximal two-thirds of the humerus are in the counterslab, and the distal third is in the main slab (Fig. 5e, f). The humerus expands distally to a width of 7 mm, and it is very thin, represented by a narrow slit in the rock. Perhaps this is a result of crushing of the hollow bone during burial. Huene (1910a, p. 319) described a right humerus also, but this could be a lower portion of the left scapula.

The radius and ulna are seen best in ventral view (Fig. 5e, f). Both elements are 25 mm long. The ulna is straight, and with an expanded proximal end, 3·5 mm wide and narrowing to a 2 mm-wide distal end. There is no olecranon. The radius is less clearly exposed, but the expanded proximal end is tightly pressed to that of the ulna, and it appears to be slightly more slender. The distal ends of these elements are clearer in dorsal view (Fig. 5c, d). Huene (1910a, pl. 43) identified these two elements the other way round.

Carpals and metacarpals are visible in dorsal view (Fig. 5c, d). There appears to be a large centrale and three small distal carpals in the wrist, as well as all five metacarpals. Metacarpals I–IV are subequal in length, gradually increasing in length from I to IV, which is 7 mm long, and V is short and divergent, corresponding to the derived state of Brusatte *et al.* (2010, character 109), where digits IV and V are reduced. Other forelimb characters (Brusatte *et al.* 2010, characters 106, 108) cannot be determined.

3.4. Pelvic girdle and hindlimb

The iliac blades are very clearly seen in dorsal view; they are relatively short, especially in the preacetabular part, as noted by Norman (1990, p. 303) and Rauhut & Hungerbühler (2000, p. 81), and *contra* Huene (1910a, pl. 43). This is shown most clearly by the bone impressions on the counterslab (Fig. 2b), and casts from the counterslab (Figs 3, 4) rather than by the remineralised bone remains on the main slab. As noted earlier, the right and left iliac blades are 26 mm and 23 mm long respectively across the chord in various casts; the discrepancy in length probably represents incomplete clearing of debris from the rock mould on the left-hand side. This supposition is confirmed by the 'incomplete' dorsal margin seen on casts of

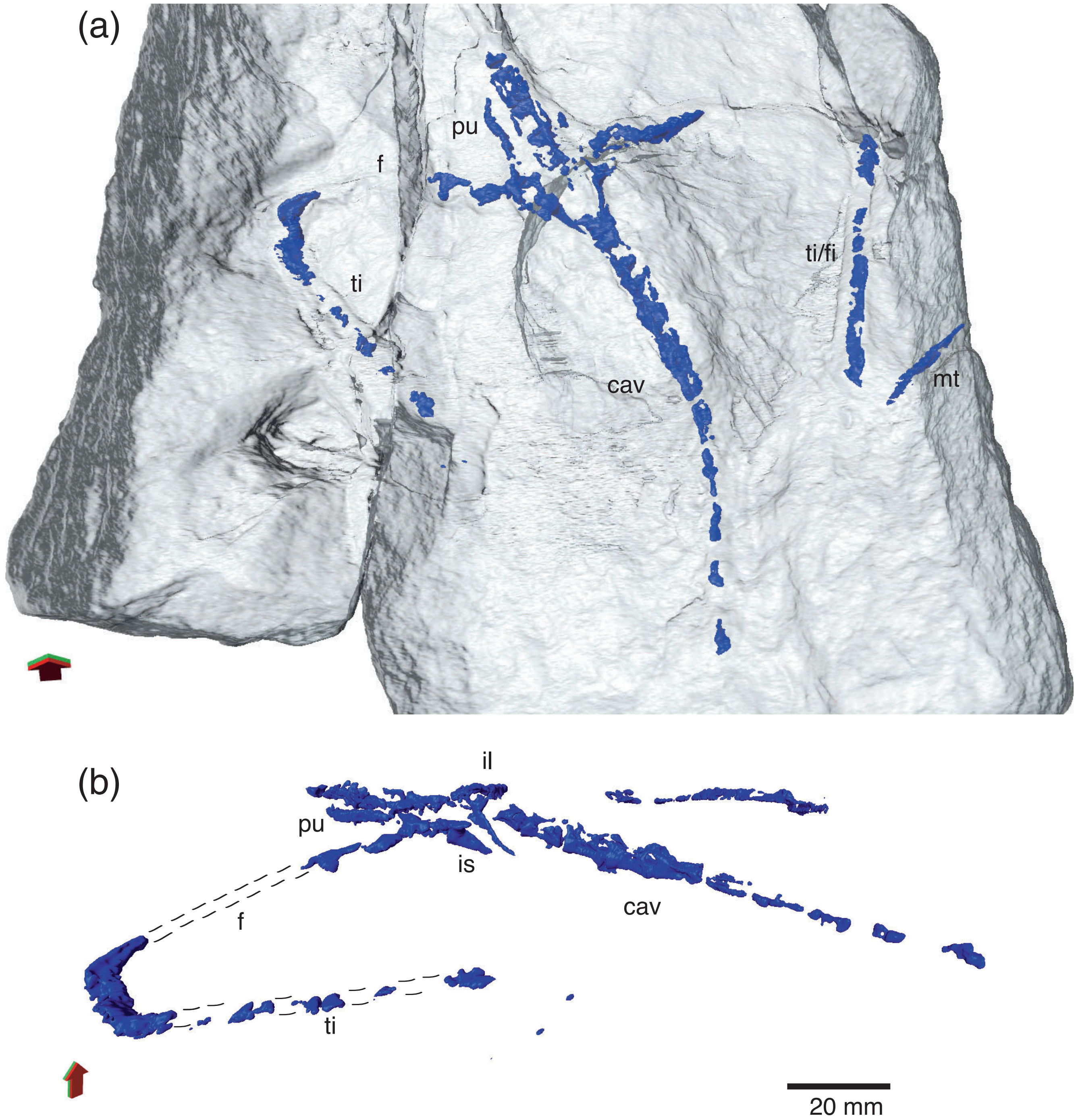

Figure 6 Reconstructed CT scans of *Saltopus elginensis* Huene, 1910a (NHMUK R3915), in dorsal view (a) and three-quarters lateral view (b), showing posterior dorsal, sacral and anterior caudal vertebrae, pelvic elements and the hind limbs. Short dashes are added in (b) to indicate continuity of some elements. Abbreviations: cav=caudal vertebrae; f=femur; fi=fibula; il=ilium; is=ischium; mt=metatarsal; pu=pubis; ti=tibia. Red arrows can be matched to show the relative orientations of both images.

both iliac blades: the blade becomes exceptionally thin dorsally, and attempts to clean debris from the natural rock mould before casting proved immensely difficult.

The iliac blade is gently curved in dorsal view (Figs 3, 4), with a gentle slope inwards from the posterior margin anteriorly, and then a sharper expansion at the front; the narrowest point measured across the sacrum and both iliac blades is one-third of the way back from the anteriormost margin. Overall, the iliac blades converge forwards, in dorsal view. Each ilium bears a slender preacetabular and postacetabular process, each terminating in an acute-angled point, but this is somewhat uncertain because of the absence of much of the distal margin of the iliac blade in the casts. The preacetabular process bends over to face somewhat ventrolaterally, rather than simply laterally. The acetabular part of the ilium is not seen, and so it cannot be judged whether the acetabulum was closed or open.

Of the pelvic characters (Brusatte *et al.* 2010, characters 110–130), only eight may be determined, five of the ilium, noted here: the ratio of blade length to depth above the acetabulum appears to be just less than 4·5, but this is based on inference from slab thicknesses and estimates of the position of the acetabulum (character 111); the dorsal margin of the iliac blade is slightly concave downwards, or 'saddle-shaped', as seen in some dinosauromorphs and pterosaurs (character 112); the preacetabular process appears to be shorter than the

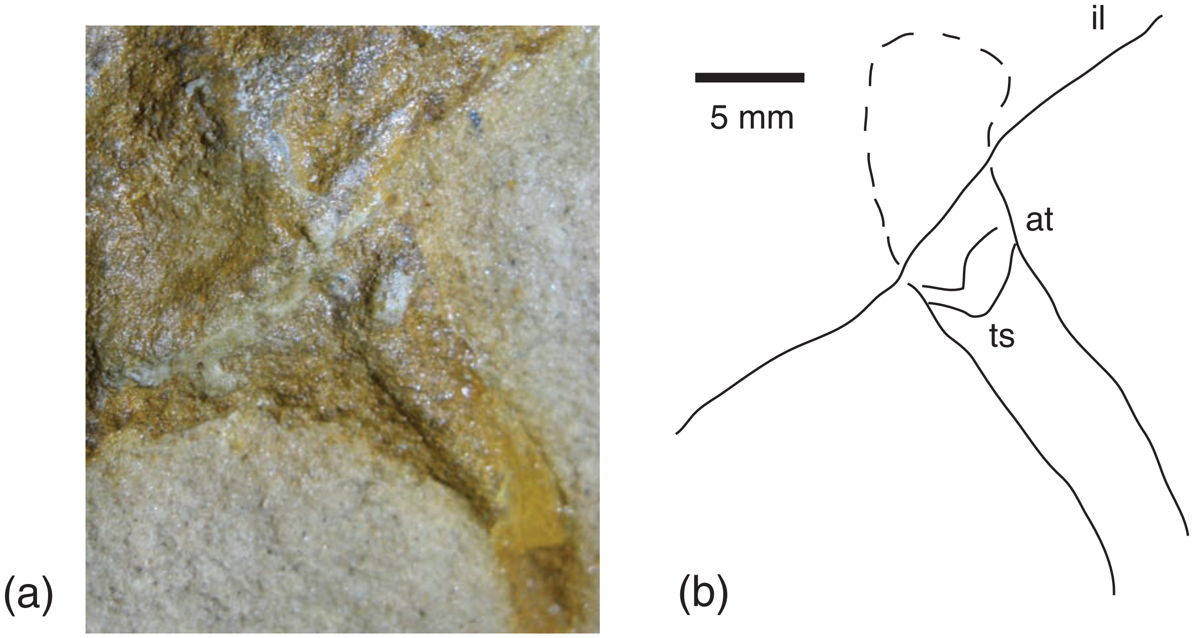

Figure 7 Close up of the proximal end of the right femur of *Saltopus elginensis*, as seen on the main slab (NHMUK R3915), as a photograph (a) and interpretive drawing (b). Abbreviations: at=anterior (= lesser) trochanter; il=iliac blade; ts=trochanteric shelf.

postacetabular (character 116), to be large and deep (character 117), and to terminate posterior to the anterior margin of the pubic peduncle (character 118); and there does not appear to be a lamina of bone connecting preacetabular and postacetabular processes of the iliac blade and rising dorsally above (character 121).

The pubis and ischium were unknown to Huene (1910a), but ADW and Arthur Rixon excavated and cleared these areas in 1965 and 1966, working on the main slab from above and below, and using fine needles to determine the location and length of the pubis and ischium. They also had X-rays made of this area, taken from various angles, and these X-rays informed the pelvic reconstruction in the present paper. Further information comes from recently completed CT scans (Fig. 6). Pubis and ischium are both elongate slender elements. The pubis is narrow and elongate, measuring 33 mm in length to the iliac peduncle, and 3 mm wide in the distal portion. The ischia (Fig. 6b) are seen on the underside of the main slab. They are elongate, with a continuous symphysis and a slight terminal expansion, measuring at least 35 mm and perhaps 40 mm long, some 2 mm wide anteriorly and very slender distally. The obturator process is present, and the ischial margin is concave in front, and extends into an anterior process. The iliac processes of the ischia may be seen clearly in several X-rays, lying precisely in place, behind the femoral heads, and spaced 10 mm apart. They converge towards the midline backwards, meeting 9 mm behind their anterior tips, and the posterior processes of the ischia extend in the midline, precisely below the sacral and caudal vertebral column, as may be seen from the X-rays, and in the scans (Fig. 6b). Of phylogenetically informative characters, the pubis was rod-like and straight (Brusatte *et al.* 2010, character 122), and probably shorter than the ischium (character 123), and the ischium shaft is more robust than the pubis (character 128).

Right and left femora are present (Figs 1–3, 6, 7), both measuring 47 mm in length across the chord of the curve. The total length as seen in the casts is probably short by a few millimetres – the X-rays and scans (Fig. 6) show that the proximal ends of the femora sit in the acetabula, and that they come very close to the midline of the specimen – and was about 55 mm. The left femur shows a gentle sigmoid curve, expanding from a mid-shaft breadth of 5 mm to 6 mm at the distal end. The right femur is more substantially curved than the left, but this appears to reflect some distortion or damage; a small fracture and kink of the bone appears in the X-ray photograph. Close inspection of the main slab, where the right femur disappears beneath the iliac blade, shows some details of the proximal end (Fig. 7). There is an anterior (=lesser) trochanter, but the fourth trochanter and the proximal head are concealed. Langer (2004, p. 37) mentions that "a raised sigmoid insertion for the iliofemoral musculature is seen in *Saltopus*", indicated by a curved ridge on the head of the right femur on the counterslab, just where the femoral head apparently disappears under the iliac blade. This is most probably the trochanteric shelf.

The distal condyles of the femur appear to be well developed. The breakage between slab and counterslab shows clearly that the femora were hollow. Only two of the femoral characters (Brusatte *et al.* 2010, characters 131–147) may be determined: there is an anterior trochanter (character 142) and there is a trochanteric shelf (character 143). The anterior trochanter (142) is convergently acquired in the rauisuchian clade *Ticinosuchus*+*Stagonosuchus*+*Araganasuchus*+*Fasolasuchus* and Dinosauriformes, and the trochanteric shelf (143) is unique to Dinosauriformes.

The tibia, at 66 mm, is longer than the femur (Brusatte *et al.* 2010, character 148; ratio c. 120%), a feature of Avemetatarsalia (reversed in the clade *Silesaurus*+*Sacisaurus*+*Eucoelophysis*+*Lewisuchus*). The tibia and fibula (Figs 1–3, 6) are slender bones, but processes and articular ends cannot be seen sufficiently to identify details of phylogenetic significance (Brusatte *et al.* 2010, characters 149–157), except that the distal end of the tibia appears to be unexpanded and rounded and the distal end of the fibula is only slightly narrower than the proximal (primitive states of characters 154 and 156 respectively).

In the left and right ankle, the astragalus and calcaneum are of roughly equal size, some 3·5–4 mm wide, they are separate (not fused), and the calcaneum has a short tuber (Figs 3, 8a–d). The astragalus has a short dorsolateral process that extends

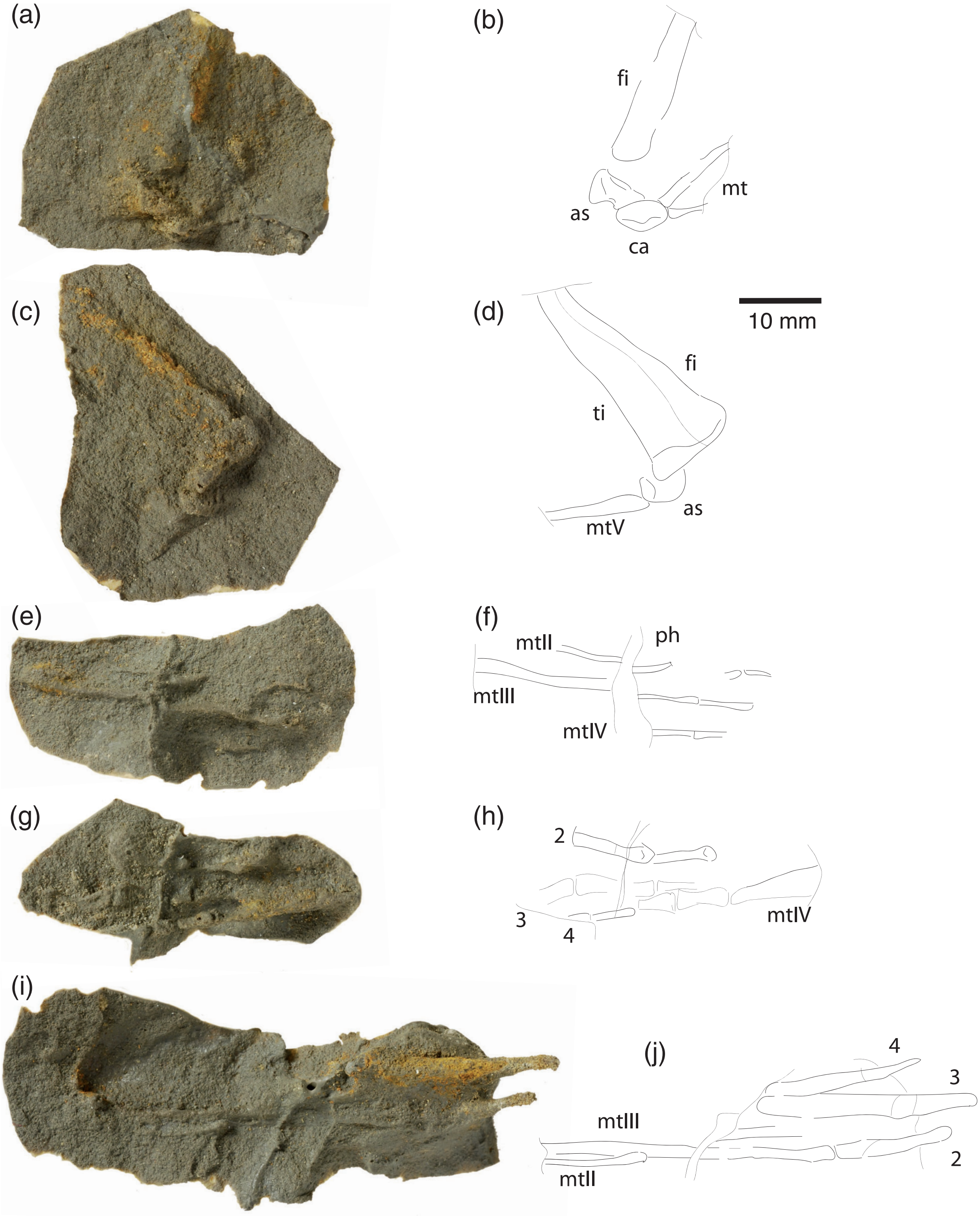

Figure 8 Details of the ankles and feet of *Saltopus elginensis* Huene, 1910a (NHMUK R3915): (a, b) Cast of right ankle region, showing lateral surface of the fibula, astragalus, and calcaneum; (c, d) cast of left ankle region, including ends of tibia and fibula, astragalus, and proximal half of metatarsal V; (e, f) cast of upper surface of right foot, showing ends of the middle three metatarsals at the left, and phalanges to the right; (g, h) cast of lower surface of right foot, showing the distal end of metatarsal IV, and phalanges of digits 2, 3, and 4; (i, j) cast of ventral surface of left foot, showing middle metatarsals and phalanges of digits 2, 3, and 4. In this last specimen, the phalanges have been partly obscured by excavation into the openings using a needle. Abbreviations: 2, 3, 4=digit numbers; as=astragalus; ca=calcaneum; fi=fibula; mt=metatarsal; ph=phalanx; ti=tibia.

over the calcaneum (Fig. 8a, b). There is no sign of reduction in size of the calcaneum, fusion of calcaneum or astragalus to each other or to other elements, or expansion of a dorsal process of the astragalus over the distal end of the tibia; all ornithodiran or dinosaurian features of the ankle. The lower faces of both astragalus and calcaneum (Fig. 8a, b) have a narrow roller-like surface. These appear to indicate the primitive condition for character 158 (astragalus and calcaneum not fused) in Brusatte *et al.* (2010), and the derived condition for character 171 (the calcaneal tuber rudimentary or absent), an apomorphy of Avemetatarsalia. Other ankle characters (Brusatte *et al.* 2010, characters 159–170, 172–177) cannot be determined, and it is not possible to say whether this ankle retains the crurotarsal character of rotation between astragalus and calcaneum, or whether the mesotarsal condition existed, with rotation between metatarsals and proximal ankle elements. In the left foot, there is a large, lateral distal tarsal in contact with the calcaneum and the proximal end of metatarsal V.

In the right foot, metatarsals II to V may be seen, but the first digit is missing. Preservation is poor, so length measurements are all estimates. The three middle metatarsals are very elongated (Figs 3, 8e–h), more than 50% of tibial length (57%). Metatarsals II and IV are subequal in length (c. 35 mm), III is longest (c. 38 mm), and V is shortest (c. 15 mm), all measurements confirmed from both right and left feet (Fig. 7i, j). These estimates are much shorter than the 45–55 mm length Huene (1910a, p. 321) suggested, but he incorporated phalanges into his measurements. The metatarsus is derived, being elongated (Brusatte *et al.* 2010, character 178) and with tightly bunched metatarsals (character 179). These are both synapomorphies of Avemetarsalia, although the bunched metatarsals are seen also in some rauisuchians. Metatarsal II is equal to or longer than metatarsal IV (character 182), a character of Suchia and of Dinosauriformes minus *Marasuchus*. Metatarsal III is 58% of the length of the tibia (38–66 mm; character 183); this character occurs widely across basal archosaurs.

Individual phalanges of digits II–IV may be seen in the right foot (Fig. 8g, h), and these give a probable phalangeal formula of ?-3-4-5-0. Toes II and IV are subequal in length, and III is longest. In the third toe, the phalanges are 12 mm, 8·5 mm and 7 mm long, extending distally, and the fourth phalanx, the ungual, is seen at the anterior end of the block, but is not complete. In the fourth toe, the first phalanx cannot be measured, and the second to fifth (the claw) are approximately 5 mm, 5 mm, 4 mm and 4 mm long, respectively. The pedal unguals appear to be mediolaterally compressed, the primitive state of Brusatte *et al.* (2010, character 187). Other foot characters (Brusatte *et al.* 2010, characters 180, 181, 184–186) cannot be determined.

The pelvis and hindlimb are reconstructed (Fig. 9) based on the length measurements of individual elements, and shapes as seen in the specimens. The pelvic reconstruction is founded on the casts, X-rays and CT scans, the main hindlimb elements on the bones as seen on the slab and counterslab, and details of the foot from the additional material in Figure 8.

4. Phylogenetic position

As noted earlier, *Saltopus* was identified as a dinosaur by several authors (e.g. Huene 1910a, 1914; Romer 1966; Steel 1970; Walker 1970; Benton & Walker 1985) or, perhaps more cautiously, as a dinosauromorph or ornithodiran (Norman 1990; Rauhut & Hungerbühler 2000; Langer 2004). Key to these earlier debates was the number of sacral vertebrae in *Saltopus*. This was particularly significant when ‘more than two sacral vertebrae’ was seen as a core synapomorphy of Dinosauria (e.g. Owen 1842; Gauthier 1986); the issue is less significant now that accepted dinosaurs such as *Herrerasaurus* are known to have retained the primitive total of two sacral vertebrae (Novas 1993), and that the increase from two to three or more sacral vertebrae happened in at least three clades of basal archosaurs: Poposauroidea minus *Yarasuchus* and *Qianosuchus*, *Batrachotomus*+*Prestosuchus* and Dinosauriformes minus *Marasuchus* and *Pseudolagosuchus* (Brusatte *et al.* 2010).

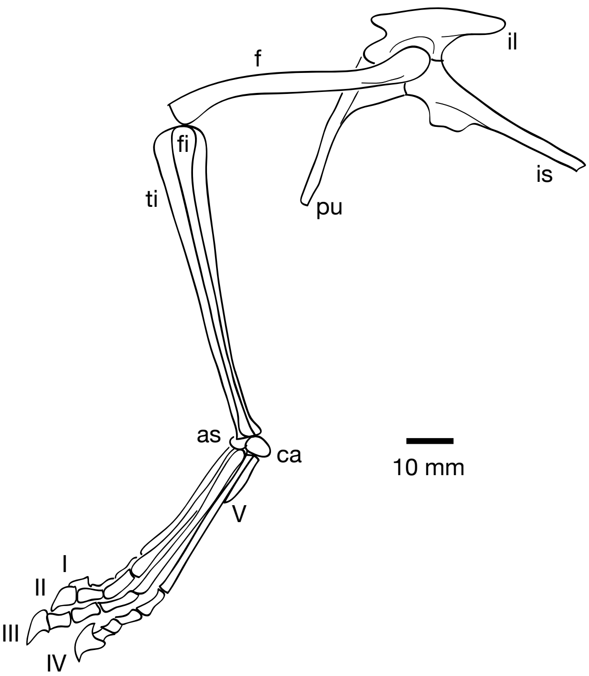

Figure 9 Reconstruction of the left hindlimb and pelvis, in left lateral view, of *Saltopus elginensis*, based on NHMUK R3915. The reconstruction was made in the 1960s, by ADW. Abbreviations: I–V = digit numbers; as = astragalus; ca = calcaneum; f = femur; fi = fibula; il = ilium; is = ischium; pu = pubis; ti = tibia.

Several phylogenetically informative characters have been noted in the text. *Saltopus* could be coded (Table 2) for 30 of the 187 characters in Brusatte *et al.* (2010), a low proportion (16%), but typical for some of the other basal dinosaurs and dinosauromorphs in the sample. Note that the proportion of characters coded is not in itself an impediment against finding the true phylogenetic position of a taxon, providing that at least one of the coded characters provides unambiguous phylogenetic information (Wilkinson & Benton 1996).

Using the Brusatte *et al.* (2010) character list, of the 30 characters that may be coded, *Saltopus* exhibits the derived conditions of 14, namely characters 93, 94, 98, 109, 112, 122 (2), 142, 143, 148, 171, 178, 179, 182, and 183. These codings, although limited, provide strong evidence for the placement of *Saltopus* within successive clades. First, *Saltopus* falls in Archosauria on the basis of one apomorphy (183, metatarsal III more than 40% length of tibia), then in Avemetatarsalia on the basis of three unique characters (148, tibia longer than femur; 171, calcaneum tuber rudimentary or absent; 178, metatarsus elongated) and three seen in the clade as well as in some suchians (98, forelimb less than 60% hindlimb length; 179, metatarsus compact with metatarsals I–IV tightly bunched; 182, metatarsal II equal or longer than metatarsal IV). One further character might be diagnostic of Avemetatarsalia or Dinosauromorpha (112, ilium with concave and saddle-shaped dorsal margin), and another of Dinosauromorpha or Dinosauria (109, manual digits IV and V reduced). Within Dinosauromorpha, *Saltopus* shares one equivocal character with *Lagerpeton* and *Dromomeron* (94, first sacral rib articulates at anterior end of preacetabular crest, but seen also in some rauisuchians). *Saltopus* then nests within Dinosauriformes based on one clear character (143, trochanteric shelf present on femur) and two equivocal characters (93, sacral ribs anteroposteriorly short and waisted in dorsal view; 142, lesser trochanter present on femur, both also in some rauisuchians). One equivocal character places *Saltopus* higher in the cladogram, within Dinosauriformes minus *Marasuchus*

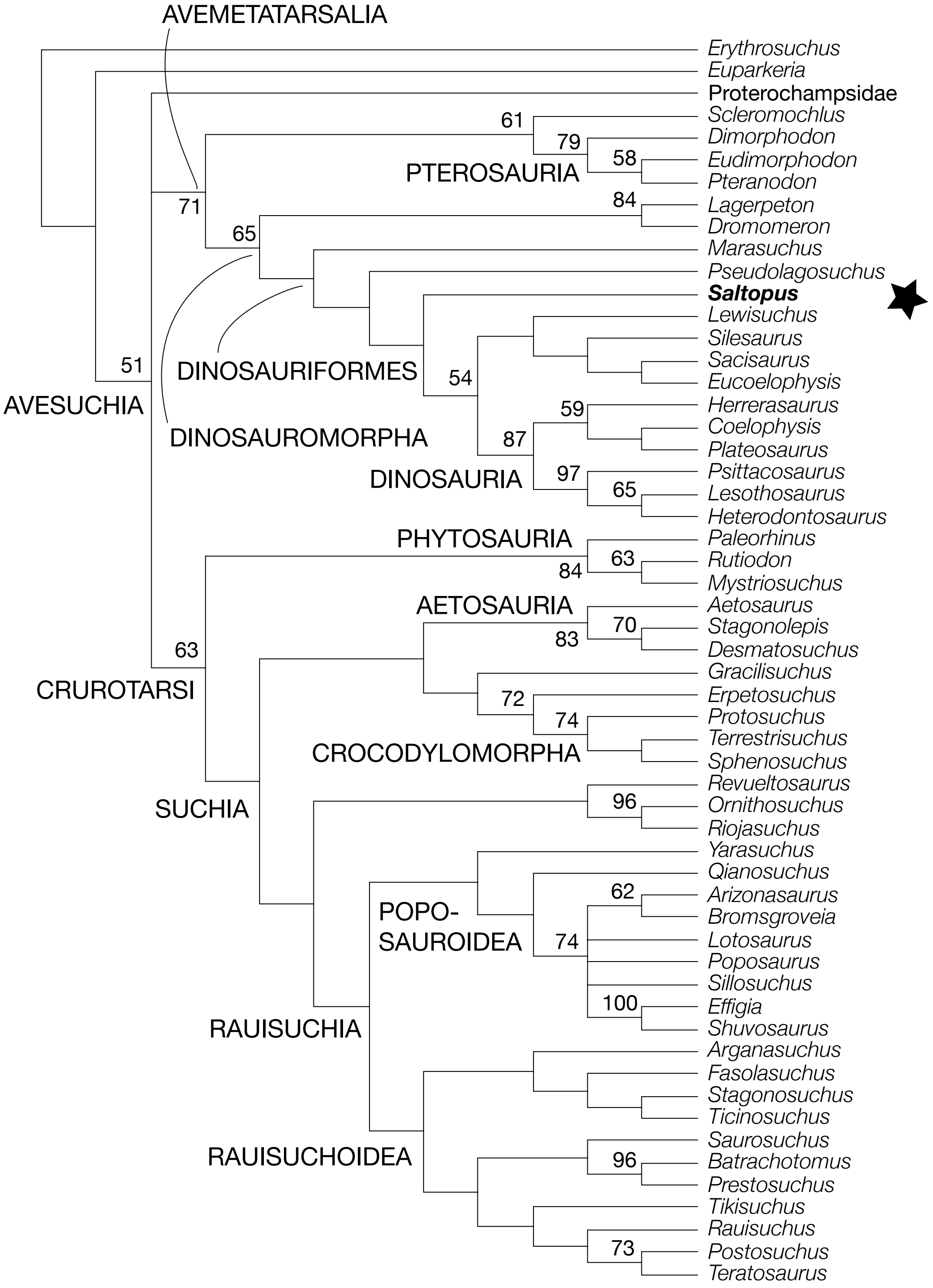

Figure 10 Cladogram showing relationships of *Saltopus* to other archosaurs, based on characters in Brusatte *et al.* (2010). Codings for *Saltopus* are listed in Table 2. Strict consensus of 15 MPTs (length 746 steps, CI 0·30, RI 0·68, RC 0·20). Bootstrap values over 50% are indicated at appropriate nodes; nodes without such numbers yielded <50% support. Major clades are named according to conventional understandings (based on Brusatte *et al.* 2010).

Table 2 Phylogenetic coding of *Saltopus*, using the two data sets.

Brusatte *et al.* (2010), characters 1–187:									
?????	?????	?????	?????	?????	?????	?????	?????	?????	?????
?????	?????	?????	?????	?????	?????	???0?	??0??	??11?	??10?
????0	?0?1?	01???	000??	020??	??0??	?????	?????	?11??	??1??
???0?	0?0??	?????	?????	1????	??11?	?11??	?0		
Irmis *et al.* (2007), characters 1–127:									
?????	?????	?????	?????	?????	?????	?????	???00	????1	?0?01
??0?1	???0?	1????	??1??	?????	??1??	?????	????1	???0?	???0?
???0?	?1???	?????	?11?1	???1?	??				

and *Pseudolagosuchus*, or even within Dinosauria (122, state 2, pubis rod-like and straight, also seen in some rauisuchians).

For the cladistic analysis *Saltopus* was included, with the codings as described above, in the Brusatte *et al.* (2010) data matrix. A heuristic search returned 15 most parsimonious trees (MPTs) of length 746 steps, with consistency index (CI) of 0·30, retention index (RI) of 0·68, and rescaled consistency index (RC) of 0·20. Interestingly, the inclusion of *Saltopus* improved the tree statistics over those reported by Brusatte *et al.* (2010) for the same data matrix, excluding *Saltopus* (they found 70 MPTs of length 747 steps; CI, 0·31, RI, 0·68). The strict consensus (Fig. 10) shows essentially the same tree as reported by Brusatte *et al.* (2010, fig. 5), but with lack of resolution of the position of Proterochampsidae, and full resolution of the *Sacisaurus*+*Eucolophysis*+*Silesaurus* clade, left as an unresolved tritomy in their analysis. *Saltopus* is placed unequivocally within Avemetatarsalia, Dinosauromorpha and Dinosauriformes, and it sits between *Pseudolagosuchus* and the unnamed clade that combines Silesauridae and Dinosauria (Nesbitt *et al.* 2010), but with only 45% bootstrap support. However, note the lack of acceptable bootstrap support for many other nodes among basal dinosauromorphs, except within Dinosauria.

As a cross-check, *Saltopus* was also assessed against the phylogenetic analysis in Irmis *et al.* (2007): a heuristic search, using the character list and settings from Irmis *et al.* (2007: see Table 2 for character scorings), found the same tree as reported by those authors, with the addition of a clade composed of *Saltopus* and *Marasuchus* with a 58% bootstrap value (1000 replications). This is too low a value to say that *Saltopus* is a close sister group of *Marasuchus*, and key taxa such as *Pseudolagosuchus*, *Lewisuchus*, and *Sacisaurus* are not included in the Irmis *et al.* (2007) data matrix. Further, of the eight autapomorphies of *Marasuchus* (Sereno and Arcucci 1994, p. 57), only two can be determined in *Saltopus* (mid-caudal centra twice the length of anterior caudal centra; broad scapular blade), and the Scottish taxon lacks these features.

The occurrence of a third basal dinosauromorph in Europe, besides *Silesaurus* from Poland and *Agnosphitys* from England, extends evidence for the early expansion of the clade and, with the recently reported basal silesaurid *Asilisaurus* from the Anisian of Tanzania (Nesbitt *et al.* 2010), might cast doubt on the general assumption of an American, and perhaps South American, origin of Dinosauromorpha. Importantly, forms that are more basal than Silesauridae, namely *Lagerpeton*, *Marasuchus*, *Pseudolagosuchus*, and *Lewisuchus* come from the Ladinian of Argentina, suggesting very tentatively a South American origin, and then expansion of Silesauridae to Africa, North America and Europe. In addition, several basal dinosaurs, such as *Herrerasaurus*, *Eoraptor*, *Saturnalia*, *Pisanosaurus* and *Guaibasaurus*, come from the Ischigualastian of Argentina and Brazil, formerly dated as late Carnian, but now regarded as late Carnian to early Norian (Furin *et al.* 2006; Langer *et al.* 2010). Whether any of the North American basal dinosauromorphs, such as the lagerpetid *Dromomeron*, the silesaurid *Eucoelophysis* and the theropods *Coelophysis* and *Tawa*, are older than early or mid Norian now seems unlikely. Joining the dots in making palaeogeographic assumptions is dangerous, however, but the numbers of specimens and taxa currently speak for a South American origin of Dinosauromorpha and Dinosauriformes, and possibly also of Dinosauria (Langer *et al.* 2010).

5. *Saltopus* in the Elgin fauna

Saltopus was a slender biped, perhaps 800–1000 mm in length (preserved dorsal portion 125 mm, sacrum 30 mm, preserved length of tail 270 mm), assuming the preserved portion of the tail is half the whole, and the proportions of the neck and head were similar to other basal dinosauromorphs (length of head and neck equals length of dorsal and sacral columns). Although Huene (1910a) noted the relative length of the forelimbs, and the even greater length of the hindlimbs, he envisaged *Saltopus* as a frog-like hopper, similar to his interpretation of *Scleromochlus* (Huene 1914; Benton 1999). Huene (1910a) noted that the "thin and flexible tail could be no hindrance to hopping despite its length", and he named the animal accordingly *Saltopus* (from the Latin *salto*, to jump).

Few since have accepted Huene's interpretation, and most have made the reasonable assumption that *Saltopus* was a bipedal runner, using its long tail for balance, the standard mode of locomotion in all basal avemetatarsalians. Cursorial animals show a number of adaptations for speed, including (Hildebrand 1974, pp. 492–511): relatively elongate legs; relatively elongate distal limb segments (tibia as long as, or longer than, femur); foot skeleton as long as, or longer than, middle limb segment (especially by elongation of the metatarsals); digitigrade posture of the foot; and reduction of one or more lateral toes. Most of these characters are seen in the hindlimb of *Saltopus*. There is no evidence that *Saltopus* used its forelimb a great deal in locomotion, since the arm overall is much shorter than the leg, there is little elongation of distal segments (radius as long as, or longer than, humerus), and the metacarpus is not elongate.

It might be reasonable to assume that *Saltopus* was an agile hunter that perhaps fed on insects and small vertebrates, similar to assumptions about the much smaller, 180 mm-long *Scleromochlus* (Benton 1999), even though the skull and teeth in *Saltopus* are unknown. *Saltopus* is a rare member of the Lossiemouth Sandstone Formation community (Benton & Walker 1985), represented by one partial skeleton. It may have preyed on the smaller, and commoner, Elgin reptiles, such as the basal avemetatarsalian *Scleromochlus* (length 180 mm; 7 individuals), the procolophonid *Leptopleuron* (length 110–250 mm; c. 30 individuals), and the sphenodontid *Brachyrhinodon* (length 150 mm; ?11 individuals). The other members of the fauna, such as the aetosaur *Stagonolepis* (length 2·1–2·7 m; >30 individuals), the rhynchosaur *Hyperodapedon* (length 1·0–1·5 m; 35 individuals), the crurotarsans *Ornithosuchus* (length 1·0–3·7 m; 12 individuals) and *Erpetosuchus* (length 0·6 m; 1 individual), were all probably too large to have been preyed on by *Saltopus*, and indeed *Ornithosuchus* may well have preyed on it. It is perhaps a curiosity of the Lossiemouth Sandstone Formation fauna that four of the eight taxa were carnivores, but two of these are represented by single specimens, and the herbivores *Hyperodapedon* and *Stagonolepis* were relatively abundant. Further, other elements of the fauna, such as fishes and arthropods, are not preserved, but must have been available as food for the smaller flesh-eaters.

6. Acknowledgements

I thank the organisers of the symposium on the origin of dinosaurs, held during the 69th Annual Meeting of the Society of Vertebrate Palaeontology in Bristol, for the invitation to participate. This is the final paper in a series started by Alick Walker in 1961, redescribing all the fossil reptiles of the Lossiemouth Sandstone Formation, a series he sadly did not live to complete. We thank Alan Charig and Arthur Rixon at the NHMUK for their help in the 1960s, and their modern counterparts, Paul Barrett and Richie Abel, for assistance with CT scanning. Tom Fletcher made the 3D reconstructions in Figure 6. Simon Powell at the University of Bristol helped immeasurably in making, and improving, the very difficult photographs in Figures 1–5, 8, and Chris Addison at the Elgin Museum supplied the specimen photograph in Figure 7. Further, we thank Max Langer and Oliver Rauhut for very helpful comments that have much improved the MS.

7. References

Agassiz, L. 1844. *Monographie des poissons fossiles du Vieux Grés Rouge ou Systéme Dévonien* (*Old Red Sandstone*) *des Iles Britanniques et de Russie*. Neuchâtel: Jent et Gassman. 171 pp.

Arcucci, A. B. 1987. Un nuevo Lagosuchidae (Thecodontia-Pseudosuchia) de la Fauna de los Chañares (Edad Reptil Chañarense, Triásico medio), La Rioja, Argentina. *Ameghiniana* **24**, 89–94.

Benton, M. J. 1983. The rhynchosaur *Hyperodapedon gordoni* from the late Triassic of Elgin: functional morphology and relationships. *Philosophical Transactions of the Royal Society B* **302**, 605–718.

Benton, M. J. 1985. Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society* **84**, 97–164.

Benton, M. J. 1999. *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. *Philosophical Transactions of the Royal Society B* **354**, 1423–46.

Benton, M. J., Martill, D. M. & Taylor, M. A. 1995. The first Lower Jurassic dinosaur from Scotland: limb bone of a ceratosaur theropod from Skye. *Scottish Journal of Geology* **31**, 177–82.

Benton, M. J. & Spencer, P. S. 1995. *Fossil Reptiles of Great Britain*. London: Chapman & Hall.

Benton, M. J. & Walker, A. D. 1985. Palaeoecology, taphonomy, and dating of Permo-Triassic reptiles from Elgin, north-east Scotland. *Palaeontology* **28**, 207–34.

Benton, M. J. & Walker, A. D. 2002. *Erpetosuchus*, a crocodile-like basal archosaur from the Late Triassic of Elgin, Scotland. *Zoological Journal of the Linnean Society* **136**, 25–47.

Brusatte, S. L., Benton, M. J., Ruta, M. & Lloyd, G. T. 2008. Superiority, competition and opportunism in the evolutionary radiation of dinosaurs. *Science* **321**, 1485–88.

Brusatte, S. L., Benton, M. J., Desojo, J. B. & Langer, M. C. 2010. The higher-level phylogeny of Archosauria (Tetrapoda: Diapsida). *Journal of Systematic Palaeontology* **8**, 3–47.

Brusatte, S. L., Benton, M. J., Lloyd, G. T., Ruta, M. & Wang, S. C. 2011. Macroevolutionary patterns in the evolutionary radiation of archosaurs (Tetrapoda: Diapsida. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **101** (for 2010), 367–82.

Cope, E. D. 1869. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. *Transactions of the American Philosophical Society, New Series* **14**, 1–252.

Cope, E. D. 1889. Synopsis of the families of the Vertebrata. *American Naturalist* **23**, 849–77.

Dzik, J. 2003. A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. *Journal of Vertebrate Paleontology* **23**, 556–74.

Fraser, N. C. & Benton, M. J. 1989. The Triassic reptiles *Brachyrhinodon* and *Polysphenodon* and the relationships of the sphenodontids. *Zoological Journal of the Linnean Society* **96**, 413–45.

Furin, S., Preto, N., Rigo, M., Roghi, G., Gianolla, P., Crowley, J. L. & Bowring, S. A. 2006. High-precision U–Pb zircon age from the Triassic of Italy: Implications for the Triassic time scale and the Carnian origin of calcareous nannoplankton and dinosaurs. *Geology* **34**, 1009–12.

Gauthier, J. A. 1986. Saurischian monophyly and the origin of birds. *Memoirs of the Californian Academy of Sciences* **8**, 1–55.

Haeckel, E. 1866. *Generelle Morphologie der Organismen. Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformirte Descendenz-Theorie*. Berlin: Georg Reimer.

Heckert, A. B. & Lucas, S. G. 2000. Global correlation of the Triassic theropod record. *Gaia* **15**, 63–74.

Hildebrand, M. 1974. *Analysis of Vertebrate Structure*. New York: Wiley.

Huene, F. von 1908. Die Dinosaurier der europäischen Triasformation mit Berücksichtigung der aussereuropäischen Vorkommnisse. *Geologische und Paläontologische Abhandlungen, Neue Folgung, Supplement-Band* **1**, 1–419.

Huene, F. von 1910a. Ein primitiver Dinosaurier aus der mittleren Trias von Elgin. *Geologische und Paläontologische Abhandlungen, Neue Folgung* **8**, 315–22.

Huene, F. von 1910b. Über einen echten Rhynchocephalen aus der Trias von Elgin, *Brachyrhinodon taylori*. *Neues Jahrbuch für Geologie, Mineralogie, und Paläontologie* **1910**, 29–62.

Huene, F. von 1914. Beiträge zur Geschichte der Archosaurier. *Geologische und Paläontologische Abhandlungen, Neue Folgung* **13**, 1–53.

Huene, F. von. 1946. Die grossen Stämme der Tetrapoden in den geologischen Zeiten. *Biologische Zentralblatt* **65**, 268–75.

Huxley, T. H. 1859. Description of *Hyperodapedon gordoni*. *Quarterly Journal of the Geological Society, London* **15**, 435.

Huxley, T. H. 1867. On a new specimen of *Telerpeton elginense*. *Quarterly Journal of the Geological Society, London* **23**, 77–84.

Huxley, T. H. 1877. The crocodilian remains found in the Elgin sandstones, with remarks on the ichnites of Cummingstone. *Memoirs of the Geological Survey of the United Kingdom* **3**, 1–58.

Irmis, R. B. & Mundil, R. 2008. New age constraints from the Chinle Formation revise global comparisons of Late Triassic vertebrate assemblages. *Journal of Vertebrate Paleontology* **28**, 95A.

Irmis, R. B., Nesbitt, S. J., Padian, K., Smith, N. D., Turner, A. H., Woody, D. & Downs, A. 2007. A Late Triassic dinosauromorph assemblage from New Mexico and the rise of dinosaurs. *Science* **317**, 358–61.

Langer, M. C. 2004. Basal Saurischia. *In* Weishampel, D. B., Dodson, P. & Osmólska, H. (eds) *The Dinosauria* (2nd edn), 25–46. Berkeley: University of California Press.

Langer, M. C. & Benton, M. J. 2006. Early dinosaurs: a phylogenetic study. *Journal of Systematic Palaeontology* **4**, 309–58.

Langer, M. C., Ezcurra, M. D., Bittencourt, J. S. & Novas, F. E. 2010. The origin and early evolution of dinosaurs. *Biological Reviews* **85**, 55–110.

Lucas, S. G. 1998. Global Triassic tetrapod biostratigraphy and biochronology. *Palaeogeography, Palaeoclimatology, Palaeoecology* **143**, 347–84.

Lydekker, R. 1887. The fossil Vertebrata of India. *Records of the Geological Survey of India* **20**, 51–80.

Mundil, R., Pálfy, J., Renne, P. R. & Brack, P. 2010. The Triassic timescale: new constraints and a review of geochronological data. *Geological Society, London, Special Publications* **334**, 41–60.

Muttoni, G., Kent, D. V., Olsen, P. E., Di Stefano, P., Lowrie, W., Bernasconi, S. M. & Hernández, F. M. 2004. Tethyan magnetostratigraphy from Pizzo Mondello (Sicily) and correlation to the Late Triassic Newark astrochronological polarity time scale. *Bulletin of the Geological Society of America* **116**, 1043–58.

Naish, D. & Martill, D. M. 2007. Dinosaurs of Great Britain and the role of the Geological Society of London in their discovery: Saurischia. *Journal of the Geological Society, London* **164**, 493–510.

Nesbitt, S. J., Irmis, R. B., Parker, W. G., Smith, N. D., Turner, A. H. & Rowe, T. 2009a. Hindlimb osteology and distribution of basal dinosauromorphs from the Late Triassic of North America. *Journal of Vertebrate Paleontology* **29**, 498–516.

Nesbitt, S. J., Smith, N. D., Irmis, R. B., Turner, A. H., Downs, A. & Norell, M. A. 2009b. A complete skeleton of a Late Triassic saurischian and the early evolution of dinosaurs. *Science* **326**, 1530–33.

Nesbitt, S. J., Sidor, C. A., Irmis, R. B., Angielczyk, K. D., Smith, R. H. M. & Tsuji, L. A. 2010. Ecologically distinct dinosaurian sister group shows early diversification of Ornithodira. *Nature* **464**, 95–98.

Newton, E. T. 1894. Reptiles from the Elgin Sandstone. Description of two new genera. *Philosophical Transactions of the Royal Society* **184**, 573–603.

Norman, D. B. 1990. Problematic Theropoda: 'coelurosaurs'. *In* Weishampel, D. B., Dodson, P. & Osmólska, H. (eds) *The Dinosauria*, 280–305. Berkeley: University of California Press.

Novas, F. E. 1992. Phylogenetic relationships of the basal dinosaurs, the Herrerasauridae. *Palaeontology* **35**, 51–62.

Novas, F. E. 1993. New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. *Journal of Vertebrate Paleontology* **13**, 400–23.

Osborn, H. F. 1903. The reptilian subclasses Diapsida and Synapsida and the early history of the Diaptosauria. *Memoirs of the American Museum of Natural History* **1**, 449–508.

Owen, R. 1842. Report on British fossil reptiles. *Report of the British Association for the Advancement of Science* **11**, 60–204.

Owen, R. 1851. Vertebrate air-breathing life in the Old Red Sandstone. *Literary Gazette* **1851**, 900.

Rauhut, O. W. M. & Hungerbühler, A. 2000. A review of European Triassic theropods. *Gaia* **15**, 75–88.

Romer, A. S. 1966. *Vertebrate Paleontology*. Chicago, Illinois: University of Chicago Press.

Säilä, L. K. 2010. Osteology of *Leptopleuron lacertinum* Owen, a prolophonoid parareptile from the Upper Triassic of Scotland, with remarks on ontogeny, ecology and affinities. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **101**, 1–25.

Sereno, P. C. & Arcucci, A. B. 1990. The monophyly of crurotarsal archosaurs and the origin of bird and crocodile ankle. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **180**, 21–52.

Sereno, P. C. & Arcucci, A. B. 1993. Dinosaurian precursors from the Middle Triassic of Argentina: *Lagerpeton chanarensis*. *Journal of Vertebrate Paleontology* **13**, 385–99.

Sereno, P. C. & Arcucci, A. B. 1994. Dinosaurian precursors from the Middle Triassic of Argentina: *Marasuchus lilloensis*, gen. nov. *Journal of Vertebrate Paleontology* **14**, 53–73.

Steel, R. 1970. Saurischia. *Handbuch der Paläoherpetologie* **14**, 1–87.

Walker, A. D. 1961 Triassic reptiles from the Elgin area: *Stagonolepis*, *Dasygnathus* and their allies. *Philosophical Transactions of the Royal Society B* **244**, 361–79.

Walker, A. D. 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. *Philosophical Transactions of the Royal Society B* **248**, 53–134.

Walker, A. D. 1970. A revision of the Jurassic reptile *Hallopus* victor (Marsh). *Philosophical Transactions of the Royal Society B* **257**, 323–72.

Warrington, G., Audley-Charles, M. G., Elliott, R. E., Evans, W. B., Ivimey-Cook, H. C., Kent, P. E., Robinson, P. L., Shotton, F. W. & Taylor, F. M. 1980. A correlation of Triassic rocks in the British Isles. *Geological Society, London, Special Report* No. **13**.

Watson, D. M. S. 1917. A sketch-classification of the pre-Jurassic tetrapod vertebrates. *Proceedings of the Zoological Society, London* **1917**, 167–86.

Wilkinson, M. & Benton, M. J. 1996. Sphenodontid phylogeny and the problems of multiple trees. *Philosophical Transactions of the Royal Society B* **351**, 1–16.

Williston, S. W. 1925. *The osteology of reptiles*. Cambridge, Masachussetts: Harvard University Press.

Woodward, A. S. 1907. On a new dinosaurian reptile (*Scleromochlus taylori*, gen. et sp. nov.) from the Trias of Lossiemouth, Elgin. *Quarterly Journal of the Geological Society, London* **63**, 140–44.

MS received 26 December 2009. Accepted for publication 23 October 2010.