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Scleromochlus taylori and the origin of dinosaurs and pterosaurs

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CONTENTS

The phylogenetic position of *Scleromochlus taylori* has been disputed recently, in terms of whether it is a basal sister group of Pterosauria or of Dinosauromorpha. The seven specimens, all from the Lossiemouth Sandstone Formation (late Carnian, Late Triassic) of Lossiemouth, near Elgin, north-east Scotland, suggest that *Scleromochlus* shares no unique features with either Pterosauria or Dinosauromorpha, together the Ornithodira, but is a close outgroup. *Scleromochlus* retains a primitive ankle structure, and it has a slender humerus, femur and fibula. *Scleromochlus* shows the classic bird-like characters of a tibia that is longer than the femur, and a closely appressed group of four elongate metatarsals. A new group name, Avemetatarsalia ('bird feet'), is established here for the clade consisting of *Scleromochlus* and Ornithodira, and their descendants. A reanalysis of crown-group archosaur relationships confirms the split into Crurotarsi (crocodile relatives) and Ornithodira (bird relatives), as well as the clear division of Ornithodira into Pterosauria and Dinosauromorpha. Relationships within Crurotarsi are, however, much less clear: Ornithosuchidae probably reside within that clade, and there might be a clade 'Rauisuchia' consisting of Prestosuchidae and *Postosuchus*, but support for these relationships is weak. *Scleromochlus* was probably a bipedal cursor that could adopt a digitigrade stance. However, it is possible that *Scleromochlus* was also a saltator, capable of leaping long distances.

Keywords: archosaur; dinosaur; origin; pterosaur; phylogeny; Triassic

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Table 1. *Main measurements of* Scleromochlus

(There are seven individuals, which do not vary much in size. The measurements here are based on one of the larger individuals, mainly BMNH R3556 and R3146A.)

measurement	size(mm)	individual
skull length (midline of skull roof)	29	R3556
skull length (tip of jaws to retroarticular process)	30.5	R3556
skull length (tip of snout to occipital condyle)	31	R3146A
presacral column length	55	R3556
glenoid–acetabular length	43	R3556
length of sacrum	10	R3146B
tail length[a]	*ca.* 85	R3557
scapula height	11	R3146A
coracoid length	4	R3556
humerus length	19.5	R3556
radius length	18	R3556
ulna length	18	R3556
metacarpal length	2.5	R3556
ilium, blade length	10	R3556
pubis, maximum length	8.5	R3556
ischium, maximum length	6	R3556
femur length	32	R3556
tibia length	34.5	R3556
fibula length	34.5	R3556
metatarsals I–IV	16.5	R3557
metatarsal V	4.5	R3556
total length of skull and body	*ca.* 181	—

[a] Tail length was restored as 135 mm by Woodward (1907) but the longest tail, in BMNH R3557, measures *ca.* 80 mm.

1. INTRODUCTION

The phylogeny of the basal archosaurs of the Triassic, ancestors of the modern crocodiles and birds, has been much debated recently (Gauthier 1986; Benton & Clark 1988; Benton 1990; Sereno 1991, 1993; Novas 1992, 1993; Parrish 1993; Sereno & Novas 1993; Juul 1994; Sereno & Arcucci 1994*a*,*b*; Bennett 1996; Gower & Wilkinson 1996). One area of dispute has concerned the relationships of the basal members of the Ornithodira, the clade including extinct pterosaurs and dinosaurs, as well as birds. A critical taxon in the debates has been *Scleromochlus taylori*, an unusual small archosaur from the Late Triassic of Scotland, which has been implicated in the origins of the pterosaurs and the dinosaurs (Huene 1914; Padian 1984; Gauthier 1986; Sereno 1991). The anatomy of *Scleromochlus* is known only incompletely, and a re-study of older material, as well as a study of hitherto undescribed specimens and the use of new preparation techniques, should shed light on the phylogenetic dilemma.

The genus and species were named by Woodward (1907) on the basis of four specimens, two collected by William Taylor (BMNH R3556, R3557), and two individuals on a single slab collected earlier by James Grant (BMNH R3146). All of these came from the buff-coloured sandstones of the large quarries that were then worked for building stone in Lossiemouth, near Elgin, Morayshire, north-east Scotland. Huene (1914) provided a fuller description of these four specimens, and of an additional specimen, also collected by William Taylor at Lossiemouth (BMNH R3914). Two further specimens (BMNH R4823/4824 and BMNH R5589) were found after 1914, and have not been described before, although Sereno (1991, fig. 17A) illustrated a humerus from BMNH R4823. In all, there are remains of seven individuals, several of them reasonably complete.

The skeletons of *Scleromochlus* are all small, measuring *ca.* 180 mm from snout to tail tip, and show the animals preserved in a dorso-ventral 'roadkill' orientation, with the forelimbs and hindlimbs extended out to the sides. In all cases, the fossils are natural moulds of the bones, preserved in considerable detail in the fine-grained well-cemented sandstone. The rock moulds are largely hollow and devoid of bone substance, except in some extreme tips of the bones, and it is likely that more soft remnants of bone were originally present before collection (Benton & Walker 1985). Some bones contain crystals of clear or whitish-opaque fluorspar.

It has been necessary to make casts of the natural rock moulds to study the anatomy of the animals: Woodward (1907) used wax squeezes (surface peels), Huene (1914) used modelling clay and plaster to make casts, and the present work is based on brown PVC casts made by Alick Walker in the 1960s (methods described by Benton & Walker (1981)). Casts were also made in the 1980s for the purpose of cladistic studies by Jacques Gauthier, Kevin Padian (Padian 1984) and Paul Sereno (Sereno 1991). As Bennett (1996, p. 265) notes, 'Huene (1914) used low-angle illumination to examine and interpret the molds and peels, but in my experience a considerable amount of imagination is necessary as well'.

Repository abbreviations: BMNH, Natural History Museum, London; RSM, National Museums of Scotland, Edinburgh.

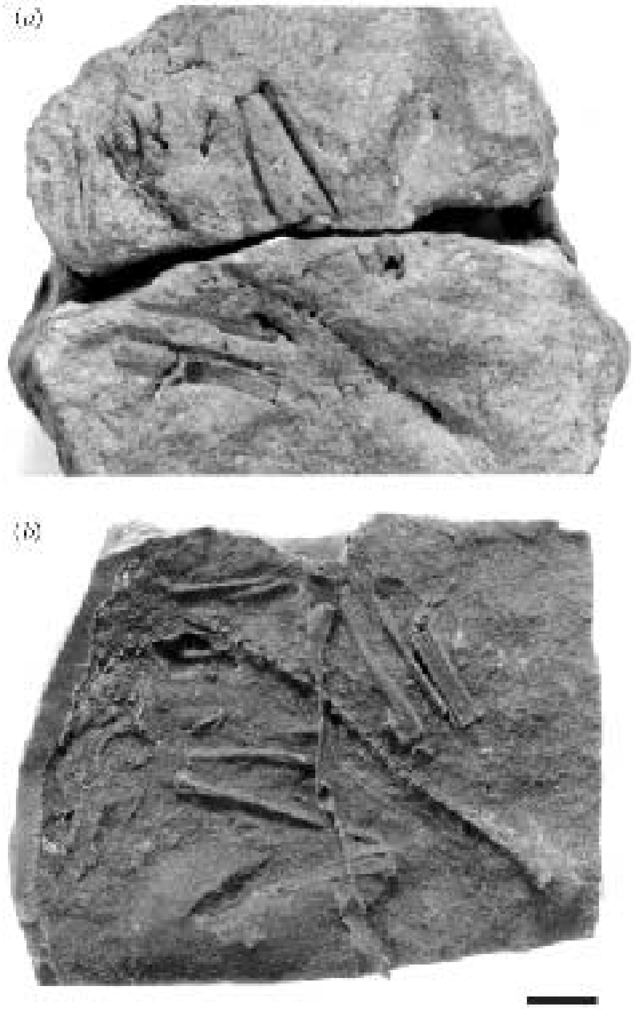

Figure 1. The type specimen of *Scleromochlus taylori* Woodward, BMNH R3556: (*a*) the dorsal slab, preserved as a natural mould in the sandstone; (*b*) cast of this dorsal slab, made in PVC by Dr Alick Walker in the 1960s (RSM collections). Scale bar, 10 mm.

2. SYSTEMATICS

Subclass DIAPSIDA Osborn, 1903
Infraclass NEODIAPSIDA Benton, 1985
Division ARCHOSAUROMORPHA Huene, 1946
Subdivision ARCHOSAURIA Cope, 1869
Infradivision AVEMETATARSALIA Benton, 1999
Family SCLEROMOCHLIDAE Huene, 1914
Scleromochlus taylori Woodward, 1907

1907 *Scleromochlus taylori* Woodward, pp. 140–144, pl. 9.
1908 *Scleromochlus taylori* Woodward; Huene, pp. 390–392, fig. 344.
1913 *Scleromochlus taylori* Woodward; Broom, 629, 631.
1914 *Scleromochlus taylori* Woodward; Huene, pp. 4–14, figs 1–33, pls 1–3.
1961 *Scleromochlus*; Walker, p. 195.
1970 *Scleromochlus*; Walker, p. 361.
1976 *Scleromochlus taylori* Woodward; Krebs, p. 90.
1984 *Scleromochlus taylori* Woodward; Padian, 163–166, figs 1, 3A, B.
1985 *Scleromochlus taylori* Woodward; Benton & Walker, pp. 213, 221, 234, figs 3G, 6E.
1991 *Scleromochlus taylori* Woodward; Sereno, pp. 17, 36–37, figs 16, 17, 18B.
1995 *Scleromochlus taylori* Woodward; Benton & Spencer, pp. 64, 65, 68, fig. 4.14G
1996 *Scleromochlus*; Bennett, pp. 265, 302.
1997 *Scleromochlus*; Bennett, pp. 265–266.
1997 *Scleromochlus*; Padian, pp. 617–618.

Type specimen. BMNH R3556, part and counterpart slab, showing a partial skeleton and damaged skull, purchased by the BMNH from William Taylor in 1907 (figures 1 and 3).

Locality. Lossiemouth East Quarry, Lossiemouth, Morayshire, Scotland (National Grid Reference NJ 236707).

Horizon. Lossiemouth Sandstone Formation, Late Triassic (late Carnian) (Benton & Walker 1985).

Additional material. BMNH R3146 (figure 2), part and counterpart, showing two partial skeletons, each with a skull, but lacking the tail, purchased by the BMNH from William Taylor in 1903 (in the description, the skeleton whose skull lies more anteriorly is designated BMNH R3146A, and the more posterior specimen BMNH R3146B); BMNH R3557 (figure 4), part and counterpart, showing a partial skeleton, lacking the skull, purchased by the BMNH from William Taylor in 1907; BMNH R3914 (figure 5), part and counterpart, showing the anterior part of a skeleton and skull, purchased by the BMNH from William Taylor in 1911; BMNH R4823 and BMNH R4824 (figure 6), part and counterpart of anterior end, showing a partial skeleton, lacking the skull, presented to the BMNH by William Taylor in 1921; BMNH R5589 (figure 7), no counterpart, showing a partial skeleton and skull, purchased by the BMNH from J. W. Denoon in 1929. All these specimens are assumed to have come from the East Quarry, Lossiemouth, but BMNH R5589 is labelled 'West Quarry, Lossiemouth' (i.e. NJ 231704). Five of these specimens are all very much the same size, *ca.* 180 mm in total length, whereas BMNH R3146B and BMNH R4823/4824 are *ca.* 85% as large.

Diagnosis. Small slender-limbed ornithodiran characterized by: low subtriangular skull, twice as broad across orbits as deep, expanded nasal which hides premaxillae and external nares in dorsal view, maxilla with raised anterior margin of antorbital fossa, reduced slit-like upper temporal fenestra, broad quadrangular plate-like parietal, quadrate–quadratojugal bar angled steeply backwards from anteriorly placed glenoid (also posteriorly located braincase and long retroarticular process), and metatarsals I–IV equal in length.

3. DESCRIPTION

(a) ***Skull***

Skulls of six individuals are preserved (two in BMNH R3146, as well as BMNH R3556, R3557, R3914 and R5589). The skull (figure 8) is roughly triangular in dorsal view, with a slightly rounded snout, and it is low and wedge-shaped in lateral view. The external nares are hard to detect. They are not visible in dorsal view, as suggested by Woodward (1907, p. 141) and Sereno (1991, fig. 16), but seem to be placed laterally. Dorsal views of anterior snout regions (figures 9*a* and 10*a*,*c*) suggest that the external nares were elongate slits lying beneath the anterolateral overhang of the nasals and bounded by the

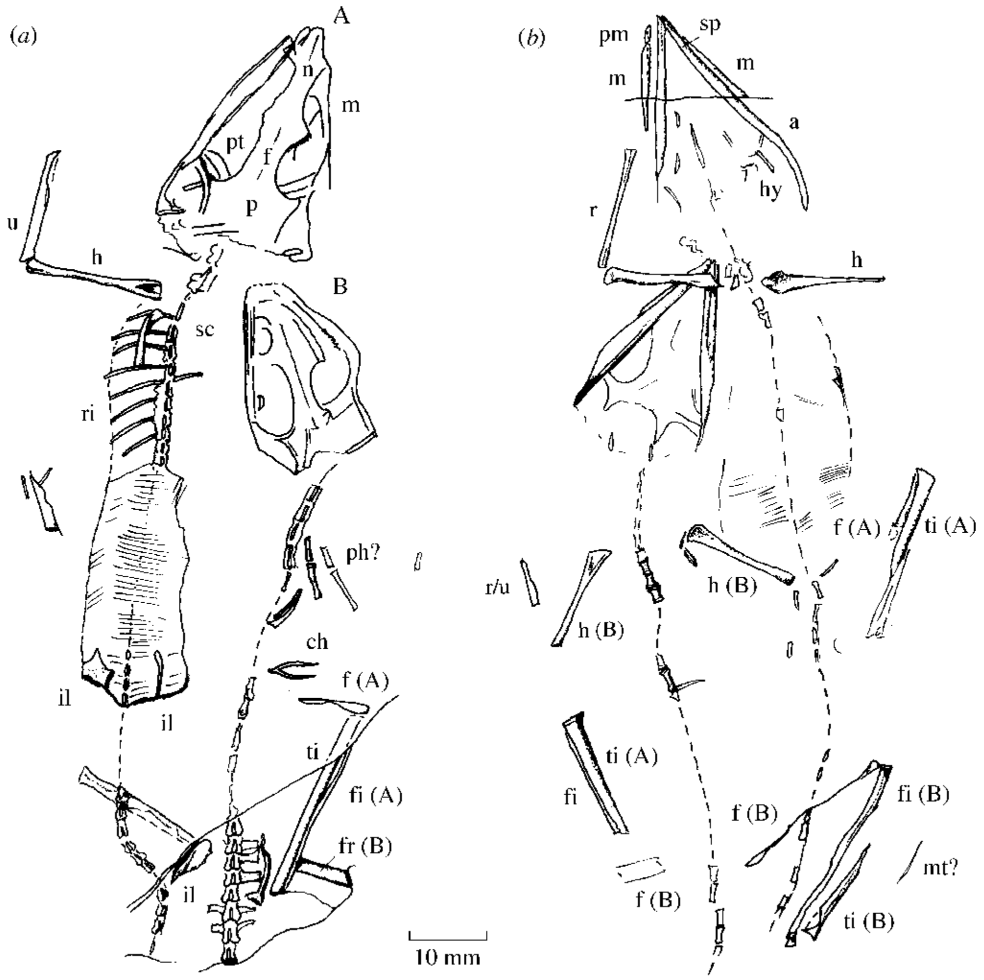

Figure 2. Specimen of *Scleromochlus taylori* Woodward, 1907, BMNH R3146; casts from the dorsal (*a*) and ventral (*b*) slabs. This specimen bears the remains of two individuals, termed A, the more anterior, and B, the more posterior. The snout of R3146B passes below the right rear corner of the R3146A skull, but overlies the right humerus of R3146A. The vertebral column of R3146A crosses the left hindlimb of R3146B. The right hindlimb of R3146A crosses over the vertebral column and right femur of R3146B. Abbreviations are given in Appendix D.

premaxillae. The antorbital fenestra is largely sunk into a fossa, with a longitudinal depression in its lower border (i.e. in the upper surface of the maxilla (figures 8*a*,*c*, 9*a* and 10*a*,*c*)). The orbit is rounded and was probably originally nearly circular. The upper temporal fenestra seems to be a narrow slit between the parietal and the postorbital–squamosal (figures 9*a* and 10*a*). The lower temporal fenestra is hard to discern. In BMNH R3146A (figure 9*a*), the opening seems to slope back behind the jugal–postorbital bar and to terminate near the back of the parietal–squamosal. None of the skull bones show any surface ornament. The premaxilla is elongated and probably bears teeth along its entire length (about six teeth); there are certainly three or more small circular alveoli on the premaxilla in BMNH R3146A (figure 9*b*). The premaxilla is about one-third as long as the maxilla (figures 9*b* and 10*d*,*e*). It forms a short platform in the palate (figure 8*b*), as shown by BMNH R5589 (figure 10*e*), and the lateral portions presumably surround much of the naris, although that is not clearly shown by any specimen. The maxilla has about ten teeth, and approximately the rear third is toothless. Teeth are hard to discern because of their tiny size, but seven clear alveoli can be seen at the anterior end of a maxilla in the ventral casts of BMNH R3146A and R3557 (figures 9*b* and 10*d*). The maxilla sends a narrow process to the nasal in front of the antorbital fossa, and the maxilla forms the extensive interior ventral part of that fossa. Between the antorbital fossa and the orbit, the maxilla contacts the lacrimal–prefrontal and it meets the jugal below the anterior part of the orbit.

The prefrontal and lacrimal cannot be distinguished clearly in any specimen. They form the bar between antorbital fossa and orbit below the nasal and meeting the maxilla, as seen in BMNH R3146A (figure 9*a*). The jugal is a slender element, bounding the orbit ventrally and partly posteriorly, as seen in BMNH R3146A and R3556 (figures 9*a* and 10*a*). The rising process that meets the postorbital seems to be broad, whereas the posterior process, which lies below the lower temporal fenestra, is slender and the quadratojugal meets its dorsal posterior tip, as seen in BMNH R3557 (figure 10*c*).

In dorsal view (figures 9*a* and 10*a*,*c*), the nasals form a substantial plate at the front end of the skull, consisting of a diamond-shaped area at the snout tip, narrowing between the antorbital fossae and expanding behind. The suture between nasals and frontals seems to run transversely at the wide point of the skull roof between antorbital fenestrae and orbits. The nasals contact the premaxillae laterally, at the front and back of the external nares, but the premaxillae do not appear on the dorsal face of the skull. Descending flanges beneath the nasals seem to form the dorsal walls within the antorbital fossae. The frontals contract between the orbits and meet the parietals with a transverse contact behind the orbits, but again this cannot be seen clearly in any specimen. The parietals are broad, expanding widely behind the orbits, and probably terminating in a broad, straight posterior

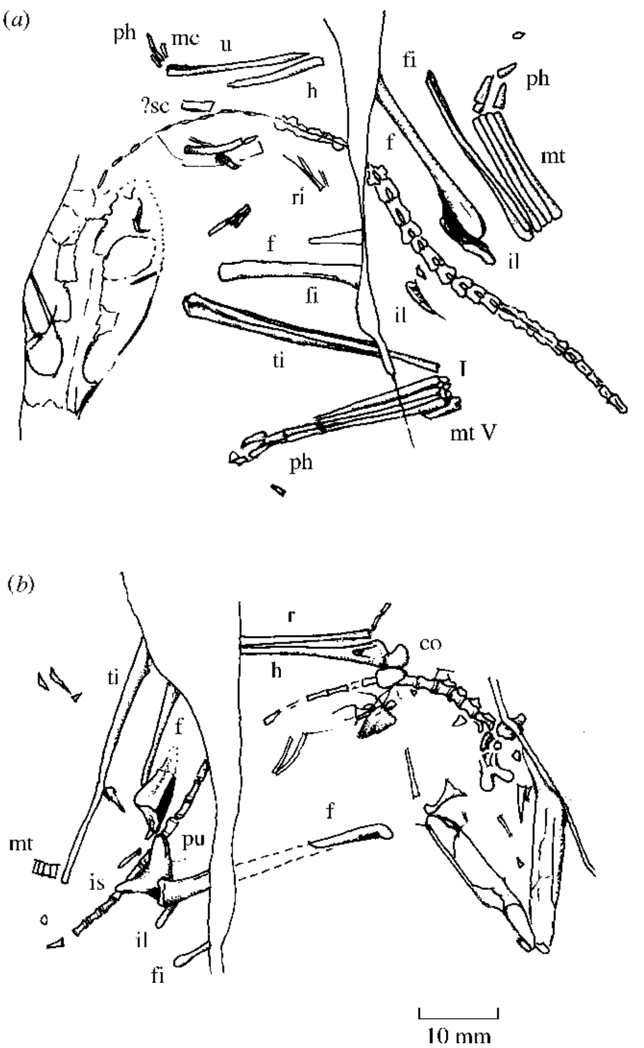

Figure 3. Type specimen of *Scleromochlus taylori* Woodward, 1907, BMNH R3556; casts from the dorsal (*a*) and ventral (*b*) slabs.

margin. A small postfrontal might be present behind the orbit (figure 10*a*), but this is not clear.

The posterior cheek region is the most difficult part of the skull to interpret because of incomplete preservation. The quadratojugal joins the posterior process of the jugal with an elongate suture, as seen on the right side of BMNH R3557 (figure 10*c*) and it sweeps up and slightly backwards from there. The quadrate articulating facet in BMNH R3556 on the left side (figure 10*b*) lies well forward, certainly anterior to the braincase, and roughly in line with the basipterygoid processes. This is confirmed by the position of that articulating surface with respect to the long retroarticular process of the right mandible of the same specimen. The squamosal is a near-vertical blade of bone where it contacts the postorbital, and presumably the parietal, and bounds the upper temporal fenestra, as seen in BMNH R3556 (figure 10*a*). The ventro-lateral branch of the squamosal, which presumably met the quadratojugal, cannot be discerned in any specimen. Nonetheless, the quadratojugal–squamosal bar is reconstructed (figure 8*c*) sloping back from the quadrate articulation to the posterior margin of the parietal, on the basis of the known relative positions of its ventral and dorsal terminations. This differs from previous reconstructions of the skull of *Scleromochlus* (Huene 1914, p. 5, figs 1 and 33; Sereno 1991, fig. 16), which showed a vertical quadratojugal–squamosal bar and a large, square lower temporal fenestra.

Partial palatal views can be seen in BMNH R3146, R3557, R3914 and R5589 (figures 9*b* and 10*b*,*d*,*e*); these allow a tentative reconstruction (figure 8*b*). The anterior part of the palate is not clear in any specimen. BMNH R5589 shows that the premaxillae met in the midline in the palate and seemingly formed a small shelf (figure 10*e*). Behind this, a double vertical structure, presumably the vomers and palatines, extends back in the midline between the choanae; this is indicated vaguely also in BMNH R3146A (figure 9*b*). The palatines sent lateral plate-like processes to meet the posterior portions of the maxillae, as seen in the dorsal view of BMNH R3146A (figure 9*a*) and the ventral view of BMNH R3146B (figure 9*b*). The pterygoids send broad wings to meet the jugals, in conjunction with the ectopterygoids, but this again is only hinted at in the ventral view of BMNH R3146B (pt/ec, figure 9*b*). The posterior part of the pterygoids is more clearly seen in BMNH R3146A, R3146B, R3556 and especially R3557 (figures 9*b* and 10*b*,*d*). The pterygoids separate on either side of a long interpterygoid vacuity and they form deep depressions for the basipterygoid processes of the braincase (bpt, figure 10*d*); the quadrate wings then extend laterally at right angles towards the quadrate articulations. Possible ossified hyoid elements are preserved in several specimens; in BMNH R3557 there is a clear curving rod-like hyoid on the right side, beneath, and lateral to, the basipterygoid region (hy, figure 10*d*). Huene (1914, figs 2 and 3) gave confident figures of two palates of *Scleromochlus*, but both of these are skull roofs.

The braincase is preserved in ventral view in BMNH R3556 and R3557. In BMNH R3556 (bs, bo, ?eo, figure 10*b*), the basisphenoid and basioccipital are slightly disarticulated and a putative right exoccipital is also preserved. The occipital condyle is in contact with the atlas (at, figure 10*b*). In BMNH R3557 (bs, bo, figure 10*d*) the basisphenoid and basioccipital again seem to be disarticulated. In both specimens the braincase is long. The basipterygoid processes (bpt, figure 10*b*,*d*) are long and massive; they enclose a narrow sella turcica. The basisphenoid has a narrow ventral surface that expands towards the contact with the basioccipital. The basioccipital is shorter and the condyle is broad and gently curved.

(b) *Lower jaw*

The lower jaw is best shown by BMNH R3556 (figure 10*b*) for the rear end, and by BMNH R3146A (figure 9*b*) for the front end. The lower jaw is slender and, in lateral view, rather 'slipper-shaped', not straight as shown by Sereno (1991, fig. 16A). The upper margin is concave in front and becomes convex in front of the articular, which is depressed. The lower margin is straight anteriorly and curves down below the articular region, then slightly up again (figure 8*c*). The symphysis is short and strong, and the anterior end of the jaw is wedge-shaped in lateral view. There is a long retroarticular process (rop, figures 9*b* and 10*b*), which bends medially at the posterior end, composed mainly of the angular beneath, and presumably the articular (in part?) above.

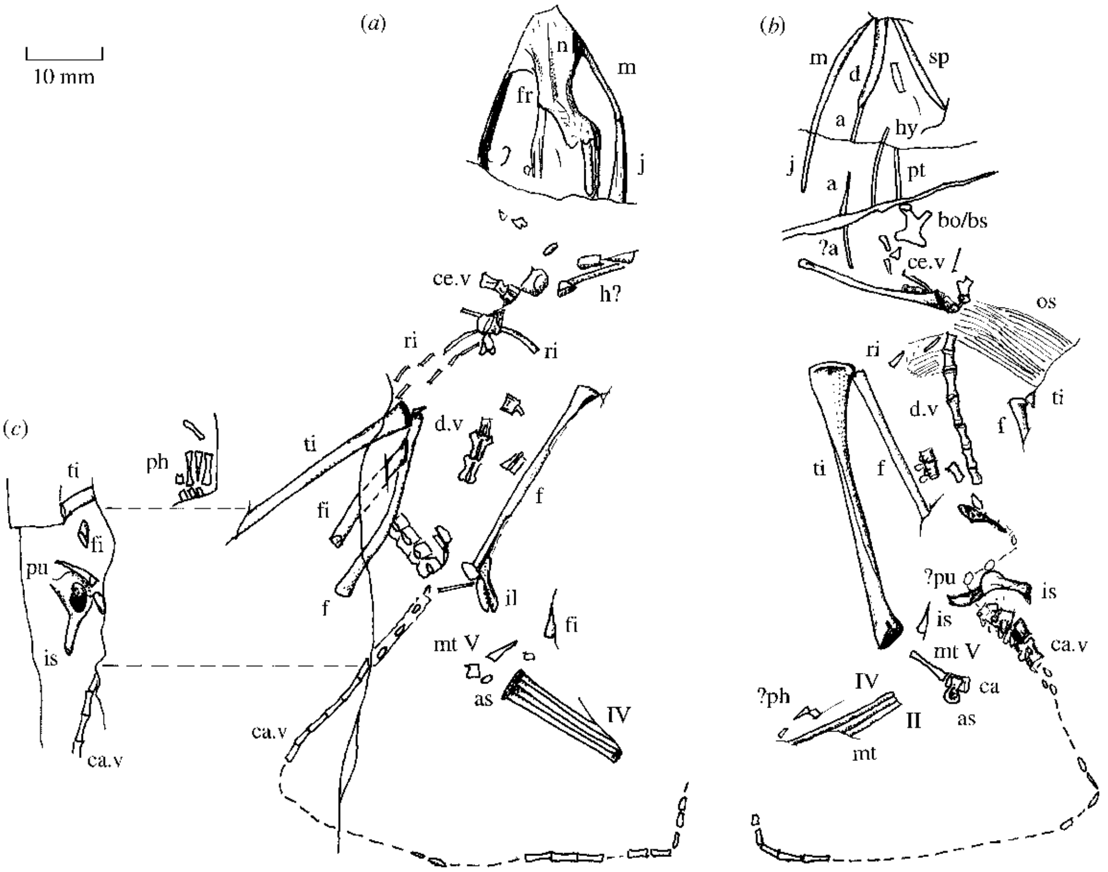

Figure 4. Specimen of *Scleromochlus taylori* Woodward, 1907, BMNH R3557; casts from the dorsal (*a*) and ventral (*b*) slabs. The inset (*c*) shows the pelvic and hindlimb remains seen on the side of the dorsal cast.

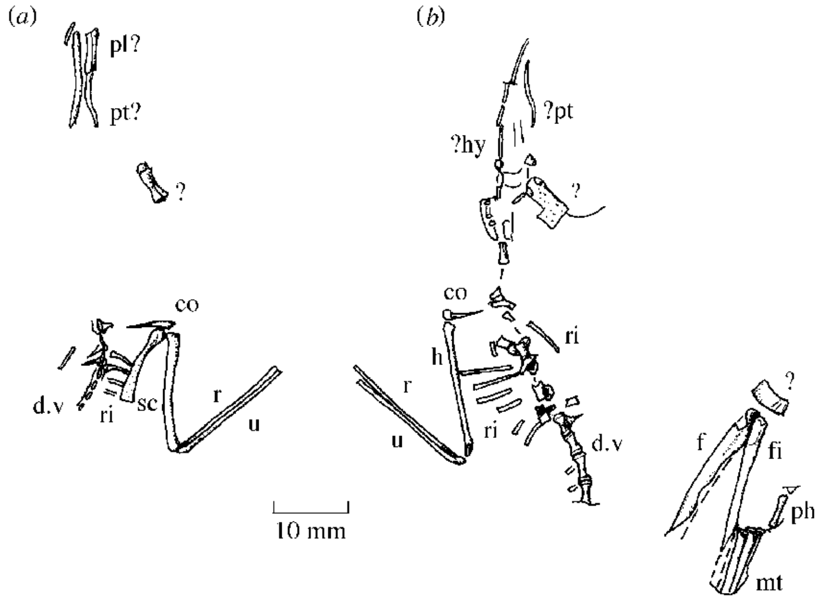

Figure 5. Specimen of *Scleromochlus taylori* Woodward, 1907, BMNH R3914; casts from the dorsal (*a*) and ventral (*b*) slabs.

The surangular is elevated slightly in front of the glenoid. The angular–surangular suture slants down to end below the articular region. BMNH R3557 shows the lower margin of an elongate mandibular fenestra in a posterior position (?mf, figure 10*d*). The dentary seems to bear teeth at the anterior end (BMNH R3146A) but the rear extent of the dentition cannot be determined.

(c) *Dentition*

The dentition is probably isodont and the teeth are small. Details cannot be discerned, however, because the size of the teeth is similar to the grain size of the enclosing sandstone. The skull is reconstructed (figure 8) with six premaxillary teeth, ten maxillary and about 15 dentary, on the basis of information from BMNH R3146 (figure 9*b*) and R3557 (figure 10*d*).

(d) *Vertebrae and ribs*

No specimen preserves the entire presacral vertebral column. However, eight cervical vertebrae seem to be preserved in natural connection in BMNH R3556 (figure 3), as noted by Huene (1914, p. 6). Huene (1914,

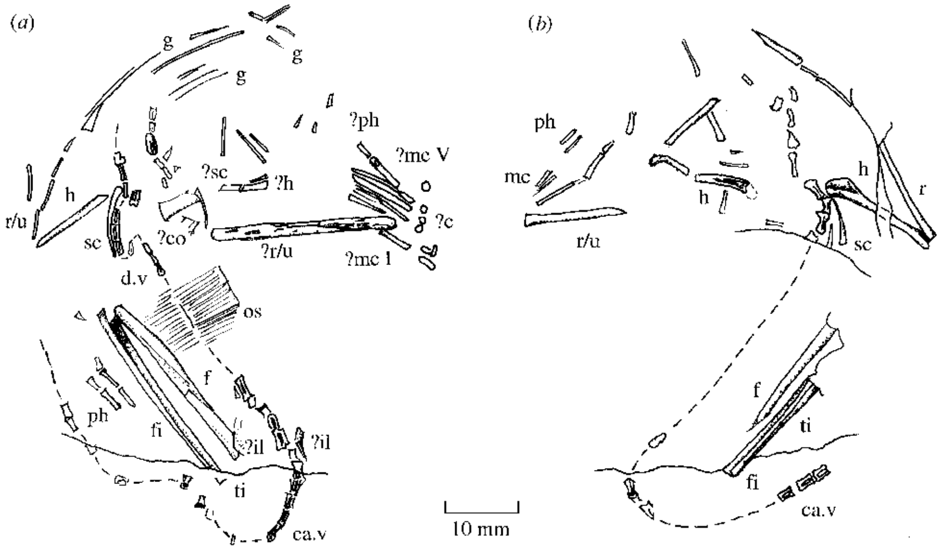

Figure 6. Specimen of *Scleromochlus taylori* Woodward, 1907, BMNH R4323/4; casts from the dorsal (*a*) and ventral (*b*) slabs.

p. 6) also suggested that there were 12 or 13 dorsals, implying an unusually short trunk. However, this is probably an underestimate, based on BMNH R3556 and R3557 (figures 3 and 4), the first of which is curled up and lacks the middle part of the back, and the second of which has a very disarticulated dorsal vertebral column. The two specimens in BMNH R3146 (figure 2) are preserved with their backs straight, and their vertebral columns are not disarticulated, although all vertebrae are not visible; measurements suggest that they had a more normal total of 16 or 17 dorsal vertebrae. There is no sign of intercentra in the presacral column, but these would be too small to be detectable. The atlas and axis are seen incompletely in ventral view in BMNH R3557 (figure 10*d*). The remaining cervical vertebrae are slightly shorter than the dorsals; cervicals range in length from 1.8 to 2.1 mm, whereas dorsals measure 1.9–2.5 mm long (BMNH R3557). The vertebrae are all longer than wide, with typical widths of 1.0–1.3 mm. The centrum is spool-shaped, constricted laterally and ventrally. Articular faces of the centrum are roughly circular and amphicoelous, with deep central depressions. Neural spines of the cervicals are low and long; those of the dorsals are higher and shorter. Transverse processes of some dorsals seem to be long, as shown by an anterior view of a vertebra with attached rib in BMNH R5589 (d.v + ri, figure 7). There seem to be short cervical ribs in BMNH R3557 (ri, figure 4*a*). Ribs are clearer in the dorsal region, those in the anterior trunk region of BMNH R3146A (ri, figure 2*a*) being slender and curving backwards.

It is hard to estimate the number of sacral vertebrae because this region is incompletely preserved in most specimens. The best sacral region, seen in the dorsal view of BMNH R3146B (figure 11), suggests the presence of four sacral vertebrae, each 1.9–2.0 mm long. Four broad ribs are seen on the right side of the vertebral column; these terminate in broad distal ends roughly in line and equivalent in length to the iliac blade, which is slightly displaced away from them. The first putative sacral rib is narrower than the others and it seems to lie in front of the iliac blade, but the latter might have been shifted slightly backwards. This sacral rib does not seem to attach to a vertebra, the latter perhaps having been displaced. The distal end of the second putative sacral rib is broadest; the two ribs behind are slightly narrower. The four putative sacral vertebrae have antero-posteriorly longer neural spines than the vertebrae in front and behind. The first caudals (ca.v 1–4, figure 11) have much more slender neural spines that slope backwards. Woodward (1907, p. 142) and Huene (1914, pp. 6–7) also estimated four sacrals in BMNH R3146B. Huene's (1914, fig. 6) illustration shows four sacral ribs on the right side, but seemingly the wrong four. He missed the first putative sacral rib identified here, and his large fourth rib is shown well behind the ilium and might indeed incorporate the posterior tip of the iliac blade.

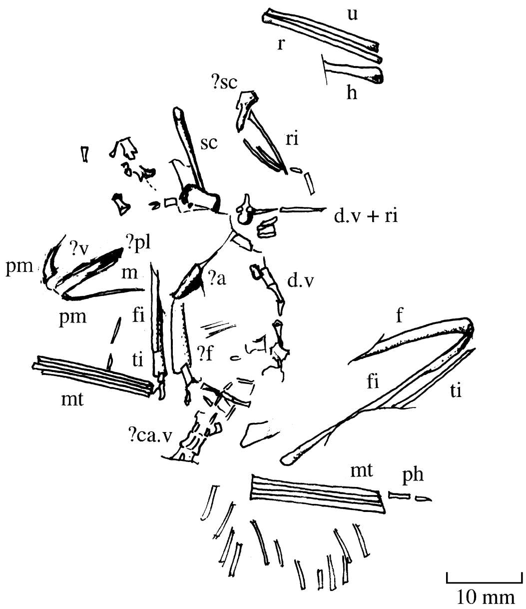

Figure 7. Specimen of *Scleromochlus taylori* Woodward, 1907, BMNH R5589; cast from the dorsal slab. There is no counterpart of this specimen.

The tail is long and consists of *ca.* 35 vertebrae. In BMNH R3557, which preserves the longest tail, nine proximal caudals are present, followed by a gap for a further 12, and then a final nine, making 30 in all. The

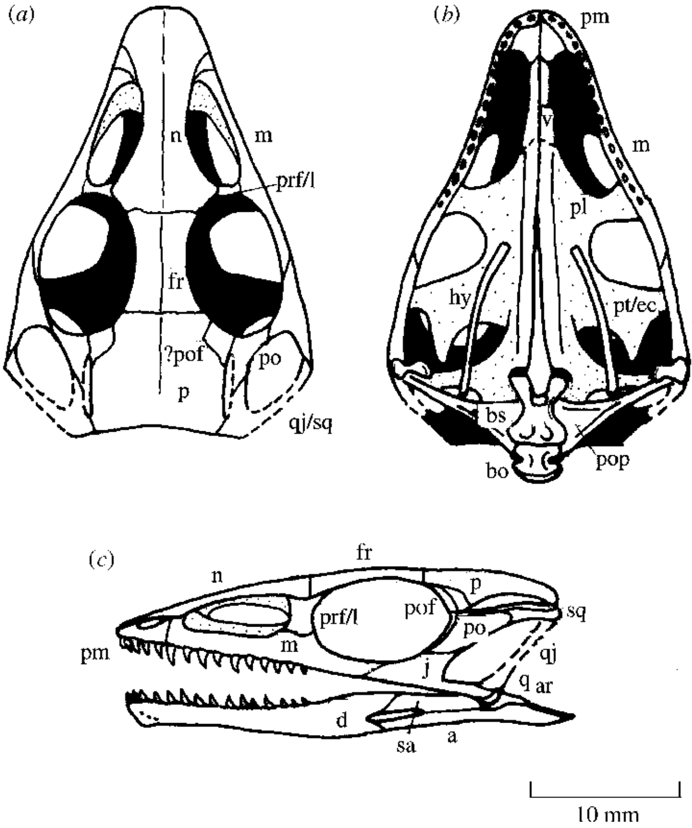

Figure 8. Reconstruction of the skull of *Scleromochlus taylori* Woodward, 1907, in dorsal (*a*), ventral (*b*) and lateral (*c*) views. The reconstruction is based mainly on BMNH R3556, with additional information from BMNH R3146A and R3146B, R3557 and R5589.

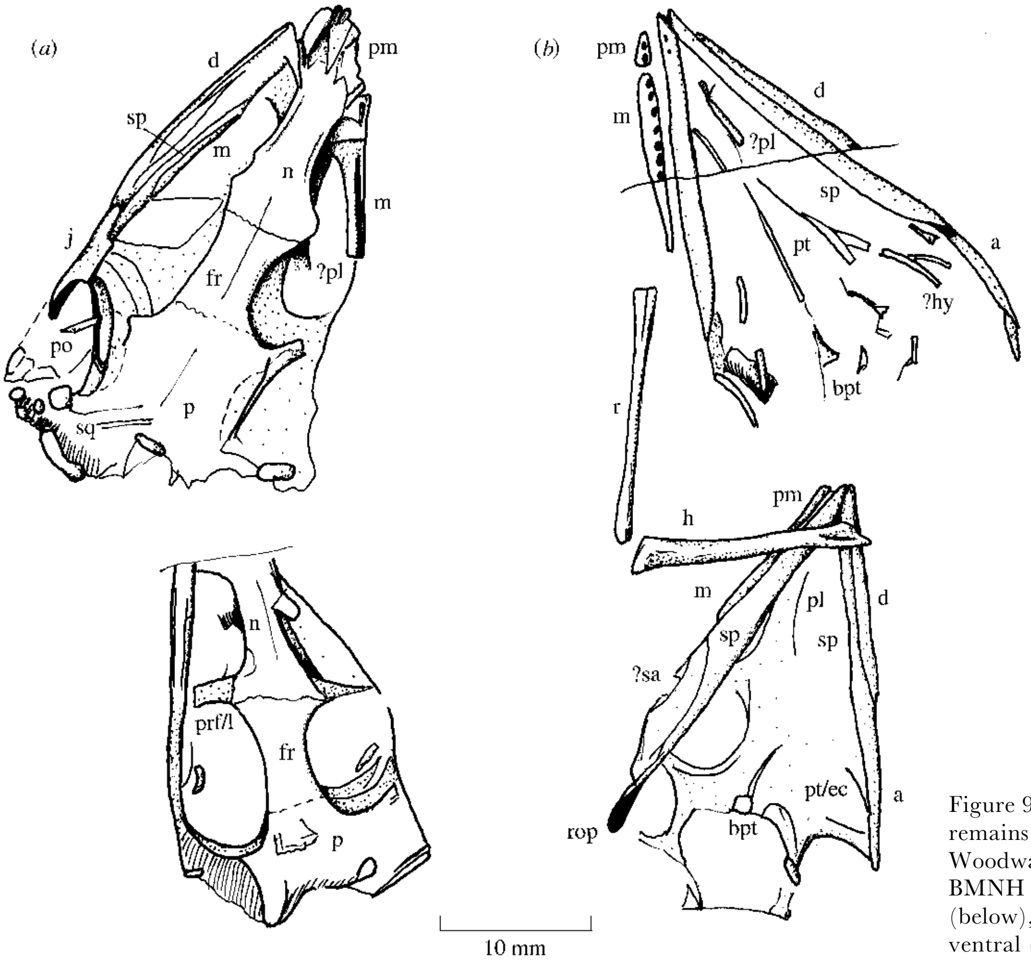

Figure 9. Details of the skull remains of *Scleromochlus taylori* Woodward, 1907: the two skulls of BMNH R3146A (top) and R3146B (below), seen in dorsal (*a*) and ventral (*b*) views.

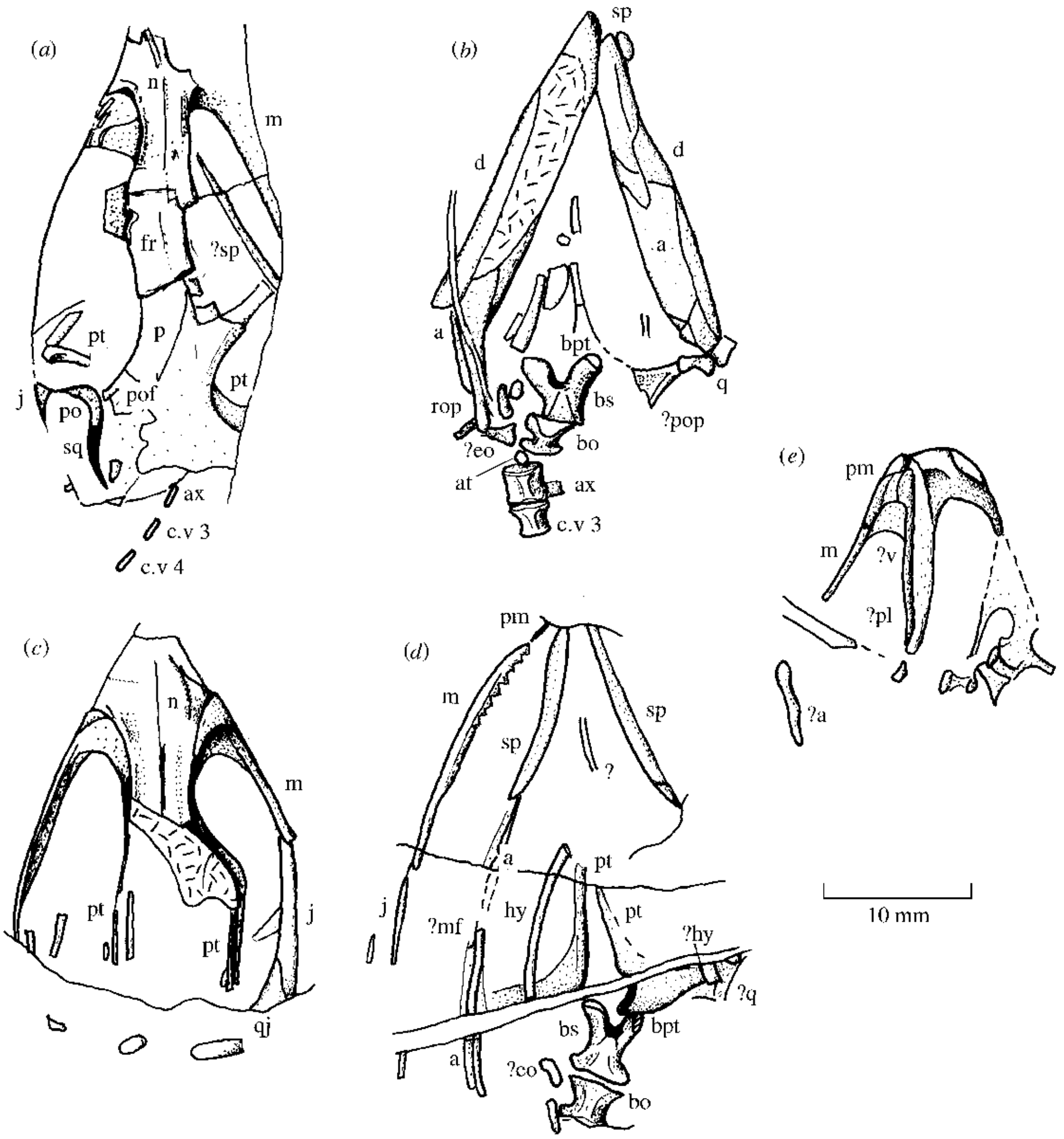

Figure 10. Details of the skull remains of *Scleromochlus taylori* Woodward, 1907: BMNH R3556 in dorsal (*a*) and ventral (*b*) views, BMNH R3557 in dorsal (*c*) and ventral (*d*) views, and BMNH R5589, snout tip and anterior palate in dorsal view (*e*).

tail is not complete and there were probably a few more tiny distal caudals. Woodward (1907, p. 141) estimated 52 caudal vertebrae, Huene (1914, fig. 33) about 60, and Sereno (1991, fig. 18B) only 25. The anterior caudals bear narrow neural spines that slope backwards, and long transverse processes (figure 11). A disarticulated chevron bone in BMNH R3146 (ch, figure 2*a*) is a broad V-shaped element, presumably originally attached to an anterior caudal. Woodward (1907, pl. 9, fig. 3*b*) showed three chevrons in close association in BMNH R3557, but these cannot be found in the specimen. More posterior caudals lose the transverse processes, and the most posterior caudals lose most of the neural arch. The caudal vertebrae increase in length from 2.1 mm (first caudal, BMNH R3556) to 2.7 mm (middle caudal, BMNH R3557) and 3.0 mm (distal caudal, BMNH R3557).

Gastralia are present in BMNH R4823 (g, figure 6*a*). There are several long slender curved subparallel elements at the anterior end of the dorsal slab; these are probably anterior elements of a gastral system that has been displaced 30 mm in front of the shoulder girdle. These putative gastralia are quite different in appearance from the osteoderms, which are present in the same and in other specimens (see below).

(e) *Shoulder girdle and forelimb*

The scapula is slender, as shown in BMNH R3914 (sc, figure 12*a*). In lateral view, in BMNH R4823/4 (sc, figure 6*a*), the scapula curves from a broad proximal end to a narrow blade. The coracoid is short and oval in shape, a little longer than wide, as seen clearly in BMNH R3556 (co, figures 3*b*, 12*b*). Huene (1914, fig. 11) suggested that *Scleromochlus* had an 'elongated coracoid', a view repeated by Padian (1984), but Huene's 'coracoid' in BMNH R3146 is the right humerus of the anterior individual. In BMNH R3556 his 'coracoid' is a rib; in BMNH R3914 the coracoid that he interprets as exhibiting only its proximal end (Huene 1914, fig. 12) is actually seen in dorsal view and shows its full length (compare figure 12*a*). The dermal

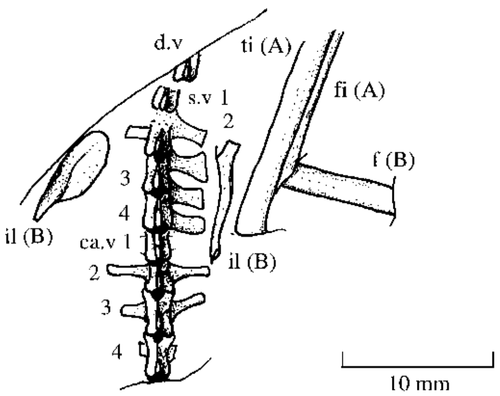

Figure 11. Sacral region of *Scleromochlus taylori* Woodward, 1907: BMNH R3146B, in dorsal view, showing four putative sacral vertebrae and sacral ribs on the right side.

elements of the girdle (clavicles and interclavicle) are unknown but the grain size of the matrix makes the recognition of such slender elements very difficult.

Several humeri are preserved, but the best is the left humerus in BMNH R4823/4 (figure 12*d*). The humerus is long and slender, with the proximal articular head backwardly inclined and a short but well-developed deltopectoral crest. The shaft is circular in cross-section; the distal end expands mediolaterally and shows a deep division on the ventral face. The radius and ulna (figure 12) are slender and about the same length as the humerus. Neither element has particularly expanded articular ends. The carpus is short; six or seven small putative carpal elements are preserved in BMNH R4823/4 (?c, figure 6*a*), but details are not clear. The hand is short. The right hand of BMNH R3556 (figure 12*b*,*c*) shows apparently one short metacarpal (I) and three subequal metacarpals (II–IV) on the dorsal slab, and one of these metacarpals, bent away from the humerus, as well as a phalanx in line on the ventral slab. The probable right hand in BMNH R4823/4 (figure 6*a*) shows five metacarpals, all subequal in length.

(f) *Pelvic girdle and hindlimb*

The pelvis is small, with a low iliac blade, short pubis and ischium, and a closed acetabulum. The pelvis is preserved in BMNH R3146A, R3146B (ilia only), R3556 and R3557. The iliac blade is low, it has a horizontal dorsal margin and it shows elongate anterior and posterior processes, but the anterior is marginally longer (figures 11 and 13*b*). The anterior and posterior processes are moderately pointed. The ilium has a strong supra-acetabular ridge (figure 13*a*). The internal view of the left ilium of BMNH R3146B (figure 11) shows a broad groove along the posterior process and a ridge running forwards above the supra-acetabular region, marking off the dorsal field for attachment of the distal ends of the sacral ribs. The pubis extends anteroventrally as a narrow process; in BMNH R3556 (figure 13*b*) this expands slightly into a mediolateral sheet distally. The pubis forms a heavy acetabular margin, and it seems to extend into a substantial medial process below the acetabulum in BMNH R3557 (figure 13*a*). Note that the right pubis in BMNH R3556 (figure 13*b*) is distorted and massive-looking in the cast, because the corresponding hole in the specimen has been over-deepened. The ischium is slightly shorter than the pubis and it extends posteroventrally (figure 13*a*,*b*). Sereno (1991, p. 31) coded the ischium as longer than the pubis, an error noted by Bennett (1996, p. 281). The distal termination is gently pointed and there is no evidence for the small knob shown by Huene (1914, fig. 19).

The acetabulum is closed, as shown in BMNH R3556, R3557 and R3146B (figures 11 and 13*a*,*b*). The bar of matrix on BMNH R3556 that Woodward (1907, p. 142) thought might be an acetabular perforation is actually the infilling of the embayment behind the acetabulum, below the posterior projection of the blade. The proximal femoral heads are generally in place within the acetabulum, as seen in BMNH R3146B, R3556, right side of R3557, R4823/4 (figures 2*a*, 3*b*, 4*a*, 6*a*, 11 and 13*b*), or displaced slightly upwards, as seen on the left side in BMNH R3557 (figures 4*a*,*c* and 13*a*).

The femur is a slender slightly arched element without any prominent trochanters. The proximal end is expanded anteroposteriorly and there is a low ridge round it, possibly a reduced fourth trochanter, as seen in BMNH R3556 (figure 13*c*), but there is no sign of the boot-like medial expansion of the proximal end noted by Sereno (1991, p. 37, fig. 17B) in BMNH R3557 (figure 13*d*). The distal end of the femur seems narrow in anterior view (figure 13*c*), but it is expanded mediolaterally into two condyles for contact with the tibia and fibula. The tibia and fibula are a little longer than the femur. The tibia is a heavy straight bone, with expanded articular ends. The proximal end shows a curved articular condyle in medial view in BMNH R3556 (figure 13*c*) and it is expanded mediolaterally in BMNH R3557 (figure 13*d*). The shaft is slightly bowed and twisted, as shown by a slender ridge down the anterior face (figure 13*d*). The distal end of the tibia is expanded mediolaterally in BMNH R3557 (figure 13*d*) but there is no evidence of a fused astragalus at this point, nor of a dinosaurian ascending flange, as suggested by Sereno (1991, p. 37, fig. 17B). The fibula is a slender flattened element that extends from knee to ankle in close association with the medial face of the tibia. The articular ends are slightly expanded. The shaft is circular in cross-section at the proximal end (figure 13*c*,*e*) and it expands into a short anterior plate-like portion before reverting to a more typical slender shaft for the remaining five-sevenths of its length.

The ankle is incompletely known. The ventral cast of BMNH R3557 shows the right tarsus (figure 13*d*) but although it seems clear that these two elements are the proximal tarsals, it is not so obvious which is the astragalus and which the calcaneum. The interpretation followed here is that the element to the fore is the astragalus and its dorsolateral square process partly overlaps the calcaneum, on the basis of a comparison with figures of the tarsus of *Marasuchus* (Sereno 1991, fig. 9). The uppermost face of the astragalus, as preserved, is presumably the proximal face, bearing a broad concave depression for the distal end of the tibia. The calcaneum is elongated, showing the fibular face uppermost, and with a 'heel' that extends medially behind the astragalus. This 'heel' has a transverse trough with a raised posterior rim. If these identifications are correct, the calcaneum is similar in size to the astragalus, and the ankle structure might show something between the primitive archosaurian condition

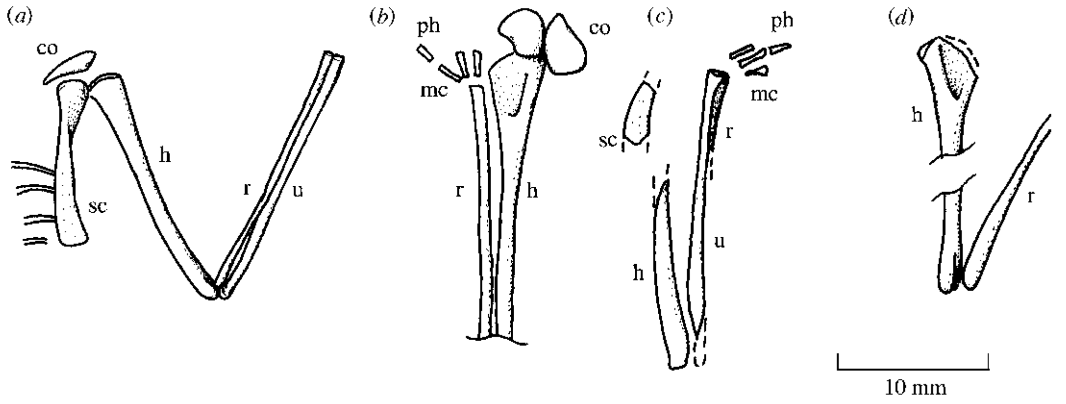

Figure 12. Forelimb remains of *Scleromochlus taylori* Woodward, 1907: (*a*) right shoulder girdle and forelimb, BMNH R3914 in dorsal view; (*b*, *c*) partial right shoulder girdle and forelimb, BMNH R3556, in ventral and dorsal views; (*d*) partial left forelimb, BMNH R4823/4, in ventral view.

and the derived ankle condition of dinosauromorphs (Sereno 1991). The putative astragalus is similar to that of ornithodirans, being flattened and with its greatest width in dorsoventral rather than anteroposterior view, but the putative calcaneum is similar in size and shows no sign of reduction. The alternative view, presented by Woodward (1907, pl. 9, fig. 4) and Huene (1914, fig. 29), is that the top element is the calcaneum. Sereno (1991) suggested that it is most like a left crurotarsal calcaneum in lateral view, but because the limb is manifestly from the right this particular identification must be wrong.

The identity of the elements in BMNH R3557 interpreted here as astragalus and calcaneum has been controversial. Padian (1984, fig. 3A) re-identified the element to the fore as a lateral distal tarsal, a view followed by Sereno (1991, fig. 17B), who interpreted the astragalus as distal tarsal 4 and the calcaneum beneath as distal tarsal 3. However, these two bones cannot be distal tarsals 3 and 4 because they are too large, both being much wider than any of the metatarsals. Indeed, the dorsal cast of BMNH R3556 shows the left foot in some detail: four small ovoid distal tarsals are preserved in position at the proximal ends of the metatarsals (figure 13*c*). Huene (1914, fig. 28) identified another element, in BMNH R3557, as the astragalus, but it is the inner surface of the blade of the right ilium.

Distal tarsals 1–3 in BMNH R3556 (figure 13*c*) are cuboid elements of approximately similar size, but distal tarsal 4 seems to be a small bone squeezed between the proximal head of metatarsal V and metatarsal IV. Metatarsals I–IV (figure 13*c*,*d*) are closely appressed and subequal in length, a little less than half the length of the tibia, and they diverge slightly at the distal end in some cases at least. These metatarsals are somewhat flattened dorsoventrally and their articular ends are slightly expanded. Huene (1914, p. 11) argued that metatarsals I–IV were not closely bound together but he was clearly wrong because these metatarsals retain a close association in all specimens in which they are seen (figures 3–5 and 7). Metatarsal V is short, seemingly pointed, and it probably lacked phalanges, as seen in BMNH R3556 (figure 13*c*). An elongate element lying close to the calcaneum in BMNH R3557 (figure 13*d*) is metatarsal V rotated out of place, as suggested by Huene (1914, fig. 32) and Sereno (1991, fig. 17B).

The phalanges of the foot are not preserved in complete articulation in any specimen. Whereas metatarsals I–IV form a coherent unit that is not broken up, the phalanges generally seem to be missing or displaced. Phalanges are present on both feet in BMNH R3556 (figures 3*a* and 13*c*). Those of the right foot have been displaced, whereas digits III and IV of the left foot seem to have nearly their full complement. They each bear a proximal phalanx preserved in line with the metatarsals, rather long and as broad as those elements. Distally there are a further four phalanges on digit IV, the most distal being the ungual phalanx. A probable ungual is present in line with digit III, leaving a gap for two phalanges. Digit III is *ca.* 29 mm long, composed of the metatarsal (17.5 mm), the proximal phalanx (4+ mm), two distal phalanges (each *ca.* 2.5 mm) and the ungual (2.3 mm). An isolated piece of BMNH R3557 preserves further phalanges (figure 4*a*), and more phalanges are seen in an isolated piece associated with BMNH R3914. The phalangeal formula of the foot, from BMNH R3556, is ?-?-4-5-0.

The limb bones are hollow. Limb bone ratios were measured in as many specimens are possible; these include: radius–humerus, 92%; humerus–femur, 60%, 61%, 63%; tibia–femur, 104%, 107%, 108%, 117%; metatarsal–tibia, 47%, 46%, 45%, 45%; radius–femur, 54%, 56%, 59%.

(g) ***Probable scutes***

BMNH R3146 shows, in strong oblique cross-lighting, a number of narrow transverse bands, each less than 1 mm across, which Woodward (1907, p. 143) and Huene (1914, p. 11) interpreted as 'abdominal ribs'. However, on the dorsal cast (figure 2*a*) they are definitely draped over the neural spines, which form a faint ridge beneath them. These are probably very thin scutes or horny scales. Similar bands are seen in the anterior part of the trunk of BMNH R3557 (figure 4*b*) and BMNH R4823/4 (figure 6*a*); these seem to confirm that the structures are dorsal and lie above the vertebral column.

4. RECONSTRUCTION OF THE SKELETON

The skeleton of *Scleromochlus* is reconstructed here in side view (figure 14), with overall proportions based on BMNH R3556, the type specimen. The skull is taken from figure 8*c*. The vertebral column is based on information from all specimens: several vertebrae are seen in lateral view, providing the models for different regions of the column, and the vertebral counts are based on information from several specimens (see above). The

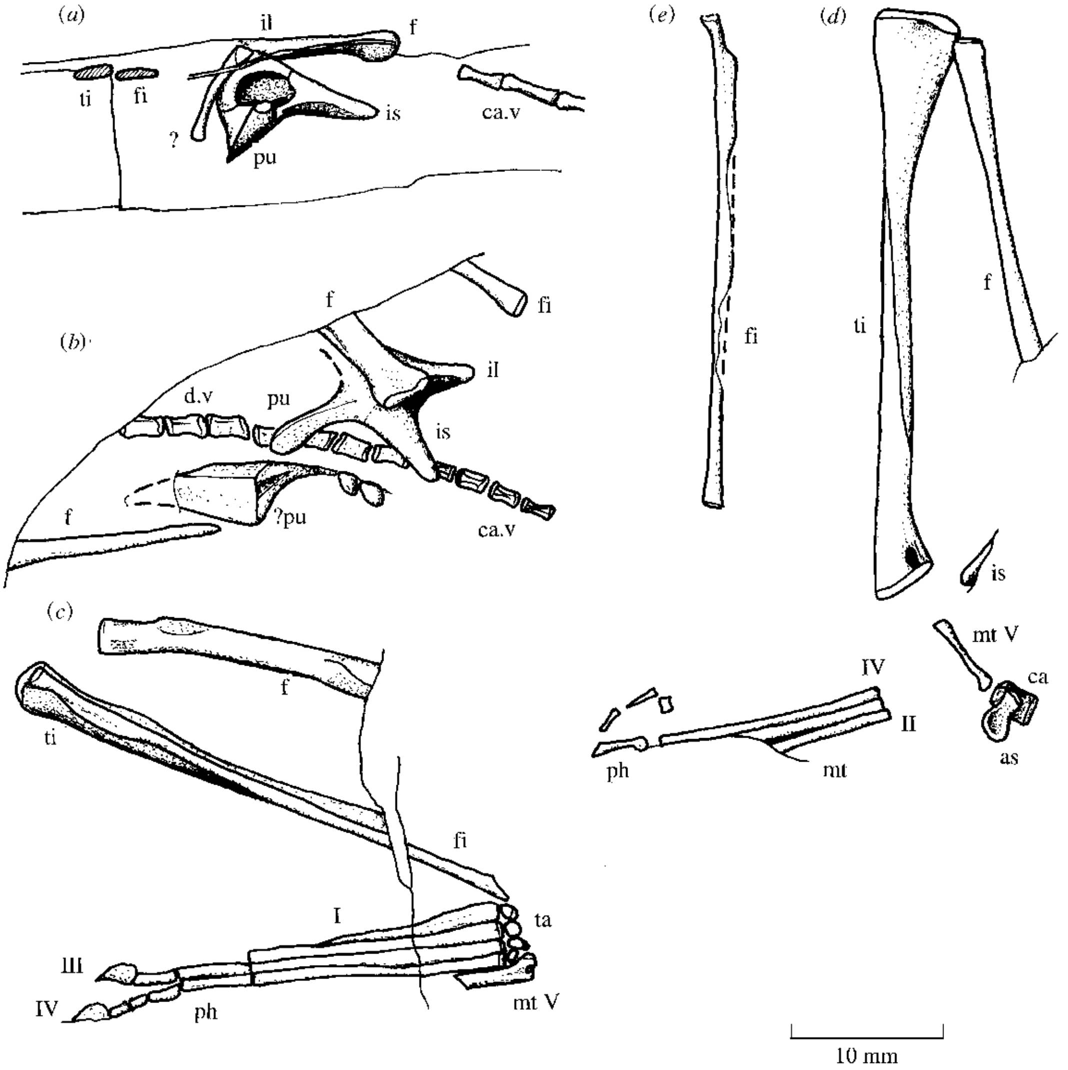

Figure 13. Hindlimb remains of *Scleromochlus taylori* Woodward, 1907: (*a*) left pelvic region, BMNH R3557, in lateral view; (*b*) right and left pelvic region, BMNH R3556, in ventral view; (*c*) left hindlimb, BMNH R3556, in dorsal view; (*d*) right hindlimb, BMNH R3557, in ventral view; (*e*) right fibula, BMNH R5589, in dorsal view.

pectoral girdle and forelimb are based on BMNH R3914. The pelvis and hindlimb are based mainly on BMNH R3556 and R3557. Uncertainties exist in the lateral view of the skull, especially the posterior portion, in the exact vertebral counts and in the hand.

The new reconstruction is broadly similar to Sereno's (1991, fig. 18B), but the proportions of his version are incorrect. *Scleromochlus* has a relatively shorter trunk and smaller forelimbs and hindlimbs than in Sereno's reconstruction. In addition, the new skull reconstruction differs from Sereno's (1991, fig. 16) version in the entirely lateral position of the nares, the reduced sloping lower temporal fenestra region and the slipper-shaped lower jaw with a long retroarticular process. The numbers of vertebrae in Sereno's version are also increased to eight cervicals (from seven), four sacrals (from three) and 35 caudals (from 25).

The skeleton of *Scleromochlus* was reconstructed earlier by Woodward (1907, p. 141) in dorsal view, and this is a reasonably faithful rendition of the four specimens that he had available, as preserved in the rock. He shows four sacral vertebrae and a very long tail. Huene (1914, fig. 33) also gave a reconstruction, in side view, that has been reproduced several times, but it is not very accurate. He exaggerated the size of the skull, and his restoration of the skull is incorrect. The presacral vertebral column is too short in relation to the skull, but the skull is not exceptionally large when compared to the humerus or femur. Huene shows the presacral column length as 42 mm, whereas this should measure 55 mm, and he makes the shoulder girdle and pelvis too close together (glenoid–acetabulum distance is 30 mm in the drawing but it is actually 43 mm). He makes the tail far too long, the humerus is a little too long and the radius and ulna are much too long. The hindlimb is rendered more accurately.

It is not clear whether *Scleromochlus* was plantigrade or digitigrade in posture. Woodward (1907) and Huene (1914, p. 12) showed clearly plantigrade reconstructions, a view followed by Walker (1961, p. 195; 1970, p. 361), who suggested that a broad plantigrade foot might have acted as a kind of 'snowshoe' for *Scleromochlus* as it waded through moving dune sands. Padian (1984) and Sereno (1991), in contrast, suggested that it was digitigrade.

Digitigrade mammals can be distinguished from plantigrade forms by a number of features (Carrano 1997): a longer calcaneal heel, metatarsals relatively longer and less widely spread, a more symmetrical astragalar pulley, a larger angle to the head of the astragalus, and deeper astragalar and femoral condyles. Details of the astragalus and calcaneum cannot be determined in *Scleromochlus* but the metatarsals are apparently united in a single functional unit and they form a narrow

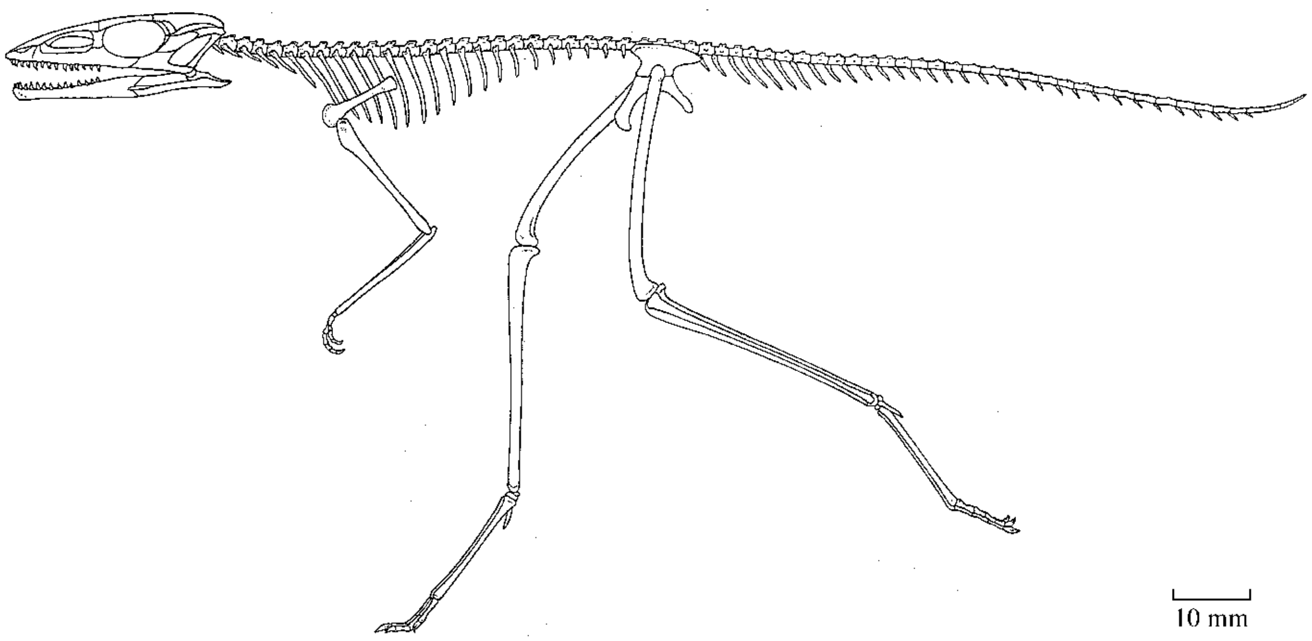

Figure 14. Restoration of the skeleton of *Scleromochlus taylori* Woodward, 1907, seen in lateral view. The restoration is based mainly on the type specimen, BMNH R3556, for proportions of the skull, vertebral column and limbs. The skull is restored from several specimens (see figure 8). Drawing by John Sibbick.

bunch, which are features of digitigrade mammals. In addition, the tibia is longer than the femur, and the foot as a whole is nearly as long as the tibia, features of digitigrade dinosaurs and mammals. Tentative evidence for plantigrady is that the fourth digit is longest and the foot is not symmetrical about the midline (figure 13*c*). However, in the absence of details of the ankle, it is hard to decide conclusively whether *Scleromochlus* was exclusively digitigrade or plantigrade in posture. Perhaps it adopted both poses. It is reconstructed here in a cursorial digitigrade posture (figures 14 and 15), but settling back on its entire foot, in a plantigrade posture, while resting (figure 15).

5. MODE OF LIFE

Three modes of locomotion have been proposed for *Scleromochlus*: arboreal, cursorial and saltatorial. Evidence for the first is not convincing; one of the last two is more likely. It is not possible to make a final decision because the body size and limb proportions of *Scleromochlus* are exactly those of modern saltatory mammals, whereas the limb proportions could also point to cursoriality, a view supported by the apparently digitigrade posture.

Huene (1914, pp. 13–14) envisaged *Scleromochlus* as a tree-climbing animal, grasping branches with the hand and the prehensile fifth toe, and feeding on insects. He interpreted the foot as plantigrade and the hindlimb as adapted for leaping: 'I hold the animal for a tree-jumper, but which could also make long daring jumps from one branch or trunk to another.' He extended this idea further: '. . . *Scleromochlus* was a parachuting animal, which had skin duplications on the forelimbs, perhaps also in other places.' Huene was led to this interpretation by the length of the forelimbs and the structure of the coracoid, which he mistakenly believed was long. He imagined that, during flight, *Scleromochlus* held the forelimbs outstretched, with the hindlimbs trailing straight behind. He compared the structure of the foot with that of bats, which use the foot not only for hanging but also for climbing. He noted that the foot of a bat is shorter than that of *Scleromochlus*, that the metatarsals are shorter and the phalanges longer, but that the metatarsals of equal length is a shared feature. Huene found even more resemblance between the feet and hindlimbs of *Scleromochlus* and those of pterosaurs: the bunch of four equally long metatatarsals, the reduced fifth metatarsal, and the proportions of the femur to the lower leg and to the metatarsus.

It seems unlikely, however, that *Scleromochlus* was arboreal. It shares some of the basic attributes of climbing mammals today (Hildebrand 1974, pp. 553–562), such as long limbs and slender bones, but these are seen also in cursors. Some specific attributes of climbers are not seen in *Scleromochlus*: lack of shortening of the proximal limb segment, a back that is long, strong and flexible, spherical proximal femur and humerus articular heads, and grasping feet that are not elongated. In particular, neither the hand (so far as it is known) nor the foot of *Scleromochlus* was in any way modified for grasping. In the foot the separate metatarsals were closely connected, or fused, to form a single functional unit. The fingers were long but there is no sign that the penultimate phalanx was longer than the more proximal phalanx, a typical feature of climbers (Hildebrand 1974, p. 555), nor is there any sign of one or more opposable digits. It is hard to see how such a foot could have operated in climbing, whether in pushing the animal up a tree trunk, or in perching on a branch. The only possibility might have been for the foot to act like a bat's in hanging the animal upside down beneath a branch. The hand is apparently small, further evidence against climbing.

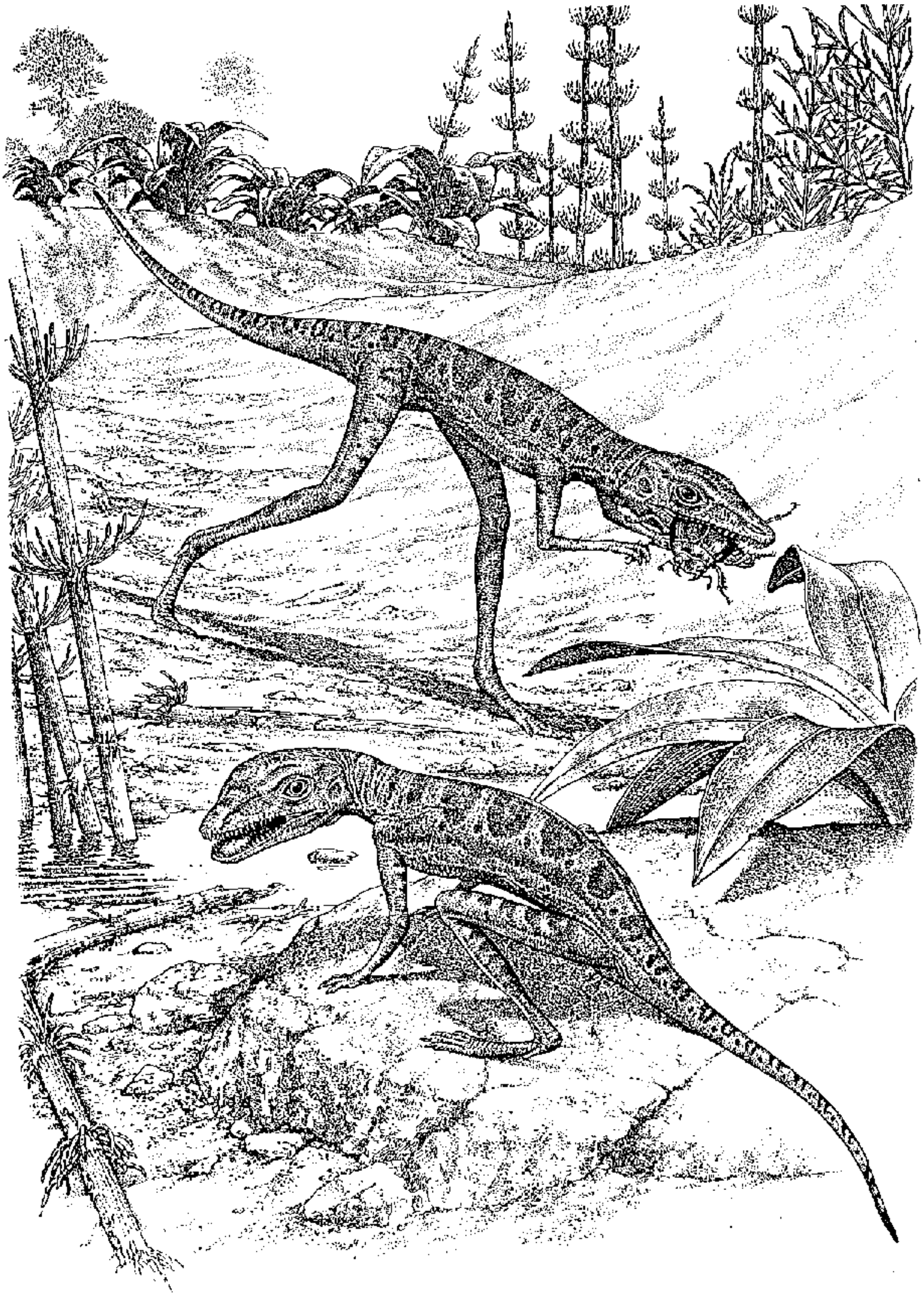

Figure 15. Life reconstruction of *Scleromochlus taylori* Woodward, 1907. Two individuals, shown in the sandy dune-like setting of the Lossiemouth Sandstone Formation. The plants and insect are based on specimens from other comparable Late Carnian units elsewhere in the world. The insectivorous diet and postures of *Scleromochlus* are postulated here. Drawing by John Sibbick.

Padian (1984) suggested that *Scleromochlus* was a cursorial animal and that its mode of locomotion was functionally ancestral to pterosaurs, which, according to him, evolved flight from the ground up. The implications for the origin of pterosaur flight are controversial (Bennett 1997) and will not be explored further. Cursorial animals show a number of adaptations for speed, including 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 (Hildebrand 1974, pp. 492–511). All of these characters are seen in the hindlimb of *Scleromochlus*, although it might have been able to adopt a digitigrade or plantigrade posture (see above). There is no evidence that *Scleromochlus* used its forelimb a great deal in locomotion, because 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. Equally, there is little indication in *Scleromochlus* for the involvement of the scapula in extending the forelimb stride length, nor for up-and-down flexion of the spine, seen in modern quadrupedal runners. However, most cursors today, and in the past, are medium-sized to large animals, their overall body size being part of their adaptation for speed over flat ground. *Scleromochlus* was much smaller, only 170 mm long, the size of a blackbird, so it might have been more than just a cursor.

The third proposal, that *Scleromochlus* was a saltator, also seems possible. This suggestion was first made in discussion of Woodward's (1907, p. 144) paper, by C. W. Andrews, who suggested that *Scleromochlus* was a sand hopper, on the basis of a comparison of the hindlimb and foot with those of the jerboa. Walker (1961, p. 195; 1970, p. 361) supported this life model. Saltators, jumping animals, show all the features of bipedal cursors, as well as (Hildebrand 1974, pp. 512–515; Emerson 1985) further lengthening of the hindlimb, further lengthening of the distal segments of the hindlimb, an elongate tail for balance while jumping, and shortening of the anterior trunk region to concentrate more weight over the hindlimbs. In these characters, and in its overall body size, *Scleromochlus* apparently has much in common with small mammalian saltators, many of which have converged on a common set of adaptations, seen in both marsupials and placentals. These mammals generally have plantigrade posture, but perhaps *Scleromochlus* was facultatively plantigrade for jumping, while being digitigrade for running (see above; figures 14 and 15). *Scleromochlus* had a medium-length tail, whereas in modern saltators the tail is often much longer than the rest of the body. Other close relatives of *Scleromochlus*, such as *Marasuchus* ('*Lagosuchus*') and *Lagerpeton*, share similar evidence of saltatory habits (Sereno & Arcucci 1994*a*), in particular a relatively small pelvic girdle in proportion to femur length, and *Marasuchus* at least has a very long tail.

6. *SCLEROMOCHLUS* AND THE ORIGIN OF DINOSAURS AND PTEROSAURS

(a) *Background*

Scleromochlus was initially placed in the 'Dinosauria' (Woodward 1907), but Broom (1913) and Huene (1914) reassigned it to the Pseudosuchia. It is currently generally classified in a family on its own, the Scleromochlidae (Walker 1970, p. 361; Benton 1993, p. 698). There are currently two broad views on the phylogenetic relationships of *Scleromochlus*, that it falls either on the crocodilian line of archosaurs (Crurotarsi) or on the dinosaur–bird line (Ornithodira). The crurotarsan intepretation was given by Walker (1970, p. 361), who noted skull specializations that ally it to the aetosaurs (see also Krebs 1976, p. 90; Benton & Walker 1985, p. 213). Padian (1984, 1997), in contrast, suggested that *Scleromochlus* was an ornithodiran, in particular a basal outgroup of pterosaurs, on the basis of characters of its limbs and its overall proportions (see also Gauthier 1986). Sereno (1991, pp. 17, 38–41) accepted the ornithodiran affinities of *Scleromochlus* and also placed this genus as sister group to Pterosauria, but he was doubtful and argued that it could equally be closer to Dinosauria, or basal to both. Novas (1996) followed this point of view. Padian (1997) named the postulated clade containing *Scleromochlus* and Pterosauria the Pterosauromorpha.

The characters proposed to link *Scleromochlus* with either pterosaurs or dinosaurs are not wholly convincing. Sereno (1991, pp. 36–37) listed the following as potential synapomorphies of *Scleromochlus* and Pterosauria:

'(33) Skull more than 50 percent presacral column length';
'(34) Length of scapula is less than 75 percent of humeral length';
'(35) Fourth trochanter absent';
'(36) Metatarsal 1 length is at least 85 percent of metatarsal 3 length'.

The first three of these could relate simply to the small size of the animals. Character (33) is true also for phytosaurs and many crocodylomorphs (although because of snout elongation). Character (34) is probably spurious because it compares what is genuinely a relatively short scapula in *Scleromochlus* with the relatively elongated forelimbs of pterosaurs (Bennett 1996, p. 279). Character 36 is present also in some basal crocodylomorphs, so it can evidently arise convergently. The postulated synapomorphies of *Scleromochlus* and Dinosauromorpha are (Sereno 1991, p. 37):

'The length of the forelimb is less than 50 percent of hind-limb length, the femoral head projects medially perpendicular to the shaft axis rather than anteromedially; the distal tibia is transversely expanded with a subrectangular end, the astragalus appears to be characterized by a broad ascending flange as in dinosaurs, and metatarsal 5 is reduced and appears to lack the strong lateral deflection of the digit.'

Of these five characters, *Scleromochlus* lacks the second (projecting femoral head) and fourth (ascending flange of astragalus). The first (forelimb much shorter than hindlimb) is true of all ornithodirans except pterosaurs, which are excluded by having evolved elongate forelimbs, and their ancestral non-flying condition cannot be established. The third (distally expanded tibia with subrectangular end) and fifth (metatarsal 5 reduced) are poorly defined and apply to many archosaurs.

These divergent opinions can now be reassessed, on the basis of the new anatomical information about *Scleromochlus* presented here and on the new understanding of archosaur phylogeny that has developed in the past 20 years. Since 1975, more than 30 phylogenetic analyses of archosaurs have been published, and these broadly agree (Gower & Wilkinson 1996) in the arrangement of the basal forms, *Proterosuchus*, *Erythrosuchus*, *Euparkeria* and Proterochampsidae as successive outgroups to a crown-group Archosauria (Avesuchia nov., see §6(d)). Avesuchia is divided into a clade that includes crocodiles, Crurotarsi, and a clade that includes birds, Ornithodira. Crurotarsi includes Parasuchia (phytosaurs), Aetosauria (stagonolepidids), 'rauisuchians' and crocodylomorphs. Ornithodira includes dinosaurs, pterosaurs and some basal forms. Ornithosuchidae might fall on either branch but they are probably crurotarsans. Bennett (1996) found that pterosaurs occupied a basal position among Archosauria, but he achieved this result only after hindlimb characters had been deleted from consideration. This result is not further explored here, because Bennett's procedure for the deletion of characters was questionable; each rejected character should have been retested on specimens for homology or non-homology and a precise anatomical conclusion given.

Since 1975, many potentially phylogenetically informative characters have been used in attempting to discover the phylogeny of archosaurs: nearly 300 such characters, according to the review by Juul (1994). Many of these characters turn out to be redundant, poorly defined or uninformative, and have been discarded from more recent analyses such as those by Sereno (1991), Juul (1994) and Bennett (1996).

(b) *Characters*

In the present analysis, inevitably, most of the characters used were proposed by earlier authors and they have been redefined more recently by Sereno (1991), Parrish (1993), Juul (1994), Bennett (1996) and Novas (1996). I follow the conclusions of these recent writers to a certain extent, but not fully. Both Sereno (1991) and Juul (1994) deleted many characters from their lists, some because they were poorly explained or difficult to code; some of these are re-instated here with revised definitions. In Sereno's (1991, p. 51) list of 36 characters, numbers 4–6, 21 and 26 are not used because of ambiguities and difficulties in coding (Parrish 1993; Juul 1994). His characters 15–20 are also excluded because they are synapomorphies of Ornithosuchidae. In Juul's (1994, pp. 33–34) list of 74 characters, characters 4, 13, 15, 16, 23–32 and 34–74 are used here. His characters 1–3, 5–12 and 17–22 refer to basal archosaurs not included in the present analysis, and characters 14 and 33 are partly redundant with others. Other partly repetitive characters in Juul's list are combined as multistate characters here. Additional characters were selected from analyses by Novas (1992, 1993, 1996), Parrish (1993), Sereno (1993), Sereno & Novas (1993) and Sereno & Arcucci (1994*a*,*b*).

Characters used in the present analysis are listed according to anatomical region, from head to toe (Appendix A), rather than according to their placement as synapomorphies in the cladistic hierarchy. This anatomical sequence makes it easier to find specific characters and it implies no expected phylogenetic solution. Character codings (Appendix B) were checked from specimens and literature, especially where recent revisions, such as Long & Murry (1995) on *Postosuchus*, have modified the earlier conclusions. For the larger clades (for example Crocodylomorpha, Theropoda, Sauropodomorpha and Ornithischia) the ancestral condition of a character was coded as far as possible.

The derived archosaur ankle types are atomized into a number of focused characters, following Sereno (1991), namely crurotarsal (characters 57–61 and 63), crocodile-normal (character 51) and advanced mesotarsal (characters 52–56). This approach has the advantage of allowing variation in each of the ankle types to be represented accurately: for example, not every animal with an advanced mesotarsal ankle has all of characters 52–56. The disadvantage of this approach is that the number of ankle attributes is multiplied and these might overwhelm the other characters in a cladistic analysis. However, this apparently does not happen: Dyke (1998) has found that published cladograms of archosaurs do not change when ankle characters are omitted.

(c) *Phylogenetic results*

The data matrix (Appendix B) was analysed with PAUP 3.1.1 (Swofford 1993) with the branch-and-bound search option: a single most-parsimonious tree (figure 16*a*) was obtained (16 taxa, 73 characters, characters weighted equally, unordered, tree length 139, consistency index (CI) 0.619, homoplasy index (HI) 0.381, rescaled consistency index (RC) 0.498). This tree was assessed by bootstrapping (1000 replicates) for the robustness of nodes, and the crurotarsan clade collapsed at this point (figure 16*b*), because most nodes were supported only in fewer than 50% of bootstrap replicates. The Phytosauridae might be the outgroup to other crurotarsans, but that is indicated in only 52% of cases. All other nodes survived in 50% or more of bootstrap replicates, but only Avesuchia (91%), Avemetatarsalia (97%), Dinosauromorpha (97%), Dinosauria (100%) and Saurischia (98%) achieved values greater than 90%. The other clades, Ornithodira (59%), Dinosauriformes (83%) and Theropoda (including *Herrerasaurus*) (60%) are not well supported. The position of *Scleromochlus* as outgroup to Ornithodira is at least clear.

The present analysis was performed to establish the phylogenetic position of *Scleromochlus* and not to provide a full-scale revision of archosaurian phylogeny. However, in view of a number of controversies in recent analyses, the main phylogenetic conclusions are summarized here.

1. *Euparkeria* and Proterochampsidae are confirmed as outgroups of crown-group Archosauria (Avesuchia), the conclusion of most previous authors, except Gauthier (1986), who included *Euparkeria* in Ornithodira. The order of these two taxa was not assessed here; Benton & Clark (1988) and Bennett (1996) found that Proterochampsidae was the more basal outgroup, whereas Sereno (1991) and Juul (1994) found that *Euparkeria* was more basal.
2. Avesuchia is a relatively strong clade, supported in 94% of bootstrap replicates. The clade has three postulated synapomorphies: absence of palatal teeth, calcaneal tuber orientated more than 45° posterolaterally, and continuous articular surfaces for fibula and distal tarsal IV on the calcaneum, as discovered by Sereno (1991) and Juul (1994).
3. The Crurotarsi is slightly less well supported, surviving in 88% of bootstrap replicates. The clade has eight postulated synapomorphies: cervical ribs short and stout, scapulocoracoid notch at anterior junction of

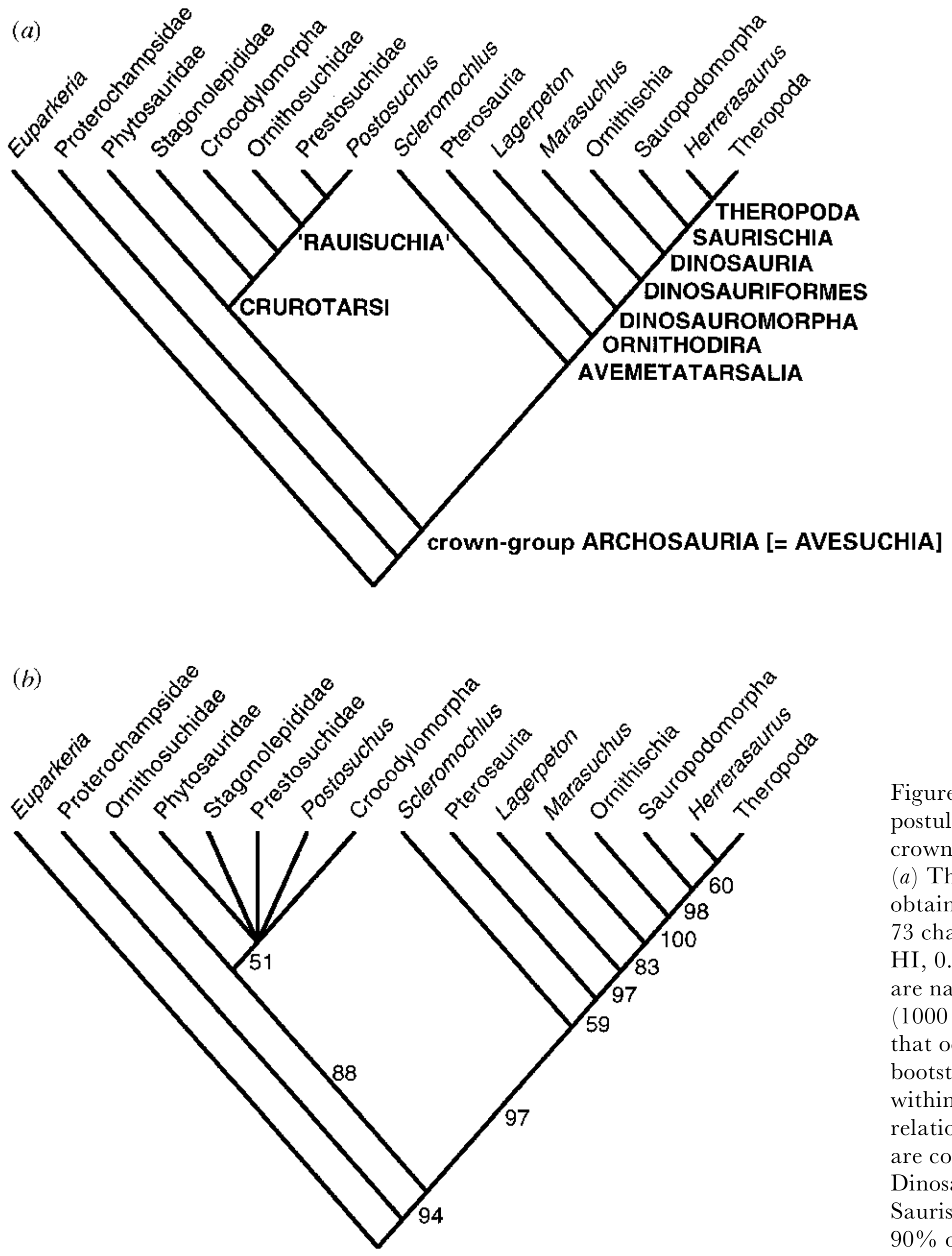

Figure 16. Cladogram showing postulated relationships of the crown-group archosaurs (Avesuchia). (*a*) The single most-parsimonious tree obtained from an analysis of 16 taxa and 73 characters (tree length, 139; CI, 0.619; HI, 0.381; RC, 0.498); the major clades are named. (*b*) Results of bootstrapping (1000 replicates) and retention of nodes that occur in more than 50% of the bootstrap replicates; relationships of taxa within Crurotarsi cannot be resolved; relationships of taxa within Ornithodira are confirmed, but only Ornithodira, Dinosauromorpha, Dinosauria and Saurischia are supported in more than 90% of bootstrap replicates.

scapula and coracoid, ventral astragalocalcaneal articular facet large, astragalar tibial facet flexed, calcaneal tuber shaft broader than tall, calcaneal tuber distal end rounded, and hemicylindrical calcaneal condyle and osteoderm sculpture.

Relationships within Crurotarsi, however, are not well established. The single most parsimonious tree (figure 16*a*) shows Phytosauridae as the basal crurotarsan group, then Stagonolepididae, Crocodylomorpha, Ornithosuchidae and 'Rauisuchia' (Prestosuchidae + *Postosuchus*) as crown group. However, only one of these nodes survives in more than 50% of bootstrap replicates; the suggestion that Phytosauridae is outgroup to the other crurotarsans (52% (figure 16*b*)) and the pattern of relationships indicated here cannot be defended. This phylogeny confirms that Ornithosuchidae are crurotarsans, as postulated by Sereno (1991) and followed by Juul (1994) and Gower & Wilkinson (1996), rather than ornithodirans, as initially proposed by Gauthier (1986) and Benton & Clark (1988). Perhaps also the Phytosauridae are the basal crurotarsans, a result found by previous authors, but bootstrapping supports this only weakly (figure 16*a*,*b*). The present analysis (figure 16*a*) seems to suggest that previously identified clades within Crurotarsi are invalid, namely Crocodylotarsi (i.e. Phytosauridae + Suchia), Suchia (i.e. Stagonolepididae + 'Rauisuchia' + Crocodylomorpha), and Pseudosuchia (i.e. Stagonolepididae + 'Rauisuchia'), but these conclusions are insupportable on present character evidence. It should be noted that the crurotarsan portions of previous cladograms are equally poorly supported, although these earlier authors did not provide bootstrap or other metrics. For example, in Sereno's (1991, fig. 26A) cladogram, his clade Ornithosuchidae + Suchia is supported in only 71% of 1000 bootstrap replicates. In Juul's (1994, fig. 1) cladogram, his whole clade Crurotarsi is supported in only 71% of bootstrap replicates; within Crurotarsi, only the clade *Gracilisuchus* + *Postosuchus* + Crocodylomorpha is distinguished by a bootstrap measure greater than 50% (51%). All his other clades within Crurotarsi collapse. Parrish (1993) provided a detailed cladogram of Crurotarsi, but bootstrap testing and Bremer support values (Gower & Wilkinson 1996) show similar weaknesses. The problems still evident were noted by Benton & Clark (1988), that some taxa, such as *Postosuchus*, show a strange mix of crocodylomorph and 'rauisuchian' characters, and others, such as Ornithosuchidae and some basal crocodylomorphs, share hindlimb features with ornithodirans. These archosaurs require much further analytical anatomical study.

4. The clade consisting of *Scleromochlus* + Ornithodira, named here Avemetatarsalia (see below) is well supported (97% of bootstrap replicates); unlike Crurotarsi, relationships within the clade seem to be clear (figure 16*a*,*b*). There are seven postulated synapomorphies: forelimb–hindlimb ratio less than 0.55, pubis longer than ischium, tibia–femur ratio more than 1.0, distal tarsal 4 subequal in transverse width to distal tarsal 3, compact metatarsus with metatarsals I–IV tightly appressed, metatarsals II–IV more than 50% tibial length, and absence of dorsal body osteoderms. The elongate hindlimb with elongate tibia and foot, and the appressed elongate metatarsus, are striking characters of *Scleromochlus* and other ornithodirans. The node above *Scleromochlus*, Ornithodira, is less well supported (59% of bootstrap replicates) and is associated with five postulated synapomorphies: presacral centrum 8 longer than presacral centrum 18, deltopectoral crest on humerus subrectangular, fibula tapering and calcaneum reduced in size, astragalar posterior groove, and calcaneal tuber rudimentary or absent. *Scleromochlus* lacks the classic 'ornithodiran humerus' with an elongate deltopectoral crest and it has an unreduced fibula.
5. Dinosauromorpha seems to be an unequivocal clade, supported in 97% of bootstrap replicates. The clade has at least seven synapomorphies (Appendix C): the subrectangular and distinctly offset femoral head, astragalar ascending flange on anterior face of tibia, astragalar anteromedial corner acute, calcaneal distal articular face less than 35% of that of astragalus, articular facet for metatarsal V less than half of lateral surface of distal tarsal 4, midshaft diameters of metatarsals I and V less than II–IV, and metatarsal V bearing no 'hooked' proximal end and articular face for distal tarsal 4 is subparallel to shaft axis. There are many equivocal synapomorphies at this node and the next two (Appendix C) due to incomplete coding of *Lagerpeton* and *Marasuchus* and uncertainty about the location in the cladogram where a number of dinosauromorph features were acquired. Dinosauriformes (i.e. Dinosauromorpha minus *Lagerpeton*) is poorly supported (in only 83% of bootstrap replicates) but *Marasuchus* and Dinosauria show parallelogram-shaped cervical centra, an acetabular antitrochanter, an articular surface on the femur that extends under the proximal head, and a weakly developed lesser (anterior) trochanter on the femur, features that are absent from *Lagerpeton*.
6. Dinosauria is another unequivocal clade, present in 100% of bootstrap replications. It is characterized by many features, including an exposed quadrate head in lateral aspect, an ectopterygoid that lies dorsal to the pterygoid, an elongate deltopectoral crest on the humerus, a brevis shelf on the ventral surface of the postacetabular part of ilium, an extensively perforated acetabulum, a tibia with a posterolateral flange, and an ascending astragalar flange on the anterior face of the tibia. There are probably further synapomorphies at this point, but incomplete coding of *Marasuchus* makes the placement of many of these equivocal (Appendix C). Within Dinosauria, the Saurischia is distinguished in 98% of bootstrap replicates. Saurischian dinosaurs are characterized by features of the jugal, which overlaps the lacrimal and has a forked posterior process, the thumb is robust, the bases of metacarpals III and IV lie on the palmar surfaces of manual digits III and IV respectively, and the calcaneal proximal articular face is concave. Another possible synapomorphy is the subnarial fenestra between the premaxilla and maxilla, but this is seen also in 'Rauisuchia'. Theropoda, including *Herrerasaurus*, is characterized unequivocally only by the well-developed intramandibular joint. According to earlier cladograms, *Herrerasaurus* was an outgroup of all other Dinosauria (see, for example, Gauthier 1986; Benton 1990; Novas 1992), whereas Sereno & Novas (1992, 1993) have argued strenuously that it is a true basal theropod. Here, *Herrerasaurus* is allied with other theropods (Neotheropoda), but only weakly (60% of bootstrap replicates) because of the large number of reversals and equivocal characters that it possesses (e.g. short cervical vertebrae, two (plus one?) sacral vertebrae, reduced thumb, no brevis shelf on the ilium, lesser trochanter on femur weakly developed, and unreduced fibula).

(d) *Avesuchia, new taxon*

The term 'crown-group Archosauria' is awkward, and I replace it here with the new taxon term Avesuchia (= 'bird-crocodile'), a node-based taxon consisting of Avemetatarsalia and Crurotarsi and all their descendants. Some workers (e.g. Gauthier 1986) recommend applying well-known group names, like Archosauria, Crocodylia, or Aves to the minimal crown group subtended by living members only. However, an archosaur is an archosaur, a crocodile a crocodile, and a bird a bird. The new notion has few advantages, and has already caused untold confusion (see critiques by Patterson 1993; Lee 1996; Sereno 1998). The major clade of archosaurs consisting of the crocodile and bird lines has no name, and that omission is hereby rectified.

(e) *Avemetatarsalia, new taxon*

The clade consisting of all avesuchians closer to Dinosauria than to Crocodylia, is termed here the Avemetatarsalia (= 'bird feet'), a new stem-based term to include archosaurs on the 'bird line', namely Ornithodira plus more basal forms. The name refers to the most striking feature of *Scleromochlus* and the Ornithodira, namely the elongate metatarsals, more than 50% of the length of the tibia. The elongate metatarsals I–IV are closely appressed in *Scleromochlus* and in most Ornithodira; in birds they form a characteristic fused element, the tarsometatarsus.

(f) Scleromochlus *and the Scleromochlidae*

The present phylogenetic analysis places *Scleromochlus* outside Pterosauria, Dinosauromorpha and Ornithodira, as the most basal known member of the bird line. However, because *Scleromochlus* has been identified previously as a basal pterosaur or a basal dinosauromorph, it is important to compare it in further detail with basal members of each clade. *Scleromochlus* shares none of the numerous apomorphies of Pterosauria (Bennett 1996; Unwin 1996), nor does it share any codable apomorphies of *Lagerpeton* or *Marasuchus* (Sereno & Arcucci 1994*a*,*b*).

Potential autapomorphies of *Scleromochlus*, in comparison with other archosaurs, are as follows.

1. Low subtriangular skull, twice as broad across the orbits as deep (Sereno 1991, p. 17). Other avemetatarsalians have high narrow skulls.
2. Expanded nasal that hides the premaxillae and external nares in dorsal view; the external nares are narrow elongate slits located entirely laterally on the snout. Ornithodirans retain the plesiomorphic condition of a narrow nasal between the external nares.
3. Maxilla with raised anterior margin of antorbital fossa (Sereno 1991, p. 17). The antorbital fossa extends well in front of the fenestra, and much of the inner wall seems to be formed from the maxilla, which bears a ridge round the ventral and anterior sides of the fossa. Other archosaurs do not have such a sharp ridge demarcating the external part of the maxilla from the part of the maxilla that forms the anterior part of the antorbital fossa.
4. Reduced slit-like upper temporal fenestra. Other archosaurs retain a roughly circular fenestra, although this opening is occluded in many crocodylomorphs, presumably independently.
5. Broad quadrangular plate-like parietal. Other archosaurs have a narrow parietal, similar in width to the frontal.
6. Quadrate–quadratojugal bar is angled steeply backwards from the glenoid placed anteriorly. Allied apomorphies are the braincase located partly behind the quadrate condyles and the elongate retroarticular process on the lower jaw. In most archosaurs the quadrate glenoid is set well back, the braincase lies entirely in front of the jaw joint and the retroarticular process is short. Pterosaurs share the backward-sloping quadrate–quadratojugal bar and the braincase located partly behind the glenoids, but the retroarticular process on the lower jaw is short.
7. Metatarsals I–IV are equal in length. Other ornithodirans show varying degrees of shortening of metatarsal I (dinosauromorphs) or IV (pterosaurs).

Scleromochlus is currently the sole member of the family Scleromochlidae. However, two small gliding reptiles from the late Triassic Madygen Svita of Kirgizia, *Sharovipteryx* and *Longisquama*, share some superficial similarities with *Scleromochlus*; the first has been specifically allied with Scleromochlidae (Sharov 1971).

Sharovipteryx (named *Podopteryx*, name preoccupied; Cowen 1981) is known from a single specimen preserved in ventral view (Sharov 1971). The skull seems to be diapsid. Like *Scleromochlus*, *Sharovipteryx* has four sacral vertebrae, the pelvis is small and the tibia is longer than the femur. From the original description it also seems that the hindlimb is more than twice the length of the forelimb. However, the elements identified as those of the forelimb by Sharov (1971) seem to be the shafts of anterior dorsal ribs (Unwin *et al.* 1999). In addition, *Sharovipteryx* lacks an antorbital fenestra and the hindlimb elements lack any archosaurian or ornithodiran synapomorphy. The foot is hard to interpret but there seem to be five long fingers, of which digit V is the longest. The metatarsals are short and they are not appressed. Unwin *et al.* (1999) suggest that *Sharovipteryx* is in fact a prolacertiform, because of its elongate cervical vertebrae with low neural spines, and possibly an incomplete lower temporal bar.

Longisquama (Sharov 1970), found in the same horizons as *Sharovipteryx*, is an archosaur (diapsid temporal region, antorbital fenestra, mandibular fenestra). Only the anterior part of the skeleton is known, together with numerous elongate dorsal structures that might have assisted in gliding. *Longisquama* cannot be assigned more precisely within Archosauria (Unwin *et al.* 1999): most of the diagnostic characters of Crurotarsi and Ornithodira refer to the hindlimbs, and these are unknown in *Longisquama*.

7. CONCLUSIONS

1. Seven specimens of *Scleromochlus taylori* Woodward, 1907 have been identified from the Lossiemouth Sandstone Formation (late Carnian, Late Triassic) of Lossiemouth, near Elgin, Morayshire, north-east Scotland.
2. *Scleromochlus* has an unusual skull, with expanded nasals that conceal the premaxillae and external nares in dorsal view, a deep antorbital fossa with its anterior margin formed by two faces of the maxilla separated by a ridge, narrow slit-like upper temporal fenestrae, a broad quadrangular parietal and an anteriorly located jaw articulation with a steeply backwards sloping quadrate–quadratojugal bar, a posteriorly located braincase and a long retroarticular process on the lower jaw.
3. *Scleromochlus* has four sacral vertebrae.
4. The hindlimb is more than twice as long as the forelimb, and the tibia is considerably longer than the femur. The metatarsus consists of four elongate metatarsals (I–IV) that are equal in length, more than half the length of the tibia and bound in a tight bunch, and a shortened hooked metatarsal V that apparently bore no phalanges.
5. The ankle seems to be primitive in comparison with that of ornithodirans, with similar-sized astragalus and calcaneum, and a non-tapering fibula.
6. A cladistic analysis suggests that *Scleromochlus* is the most basal member of the bird line, neither a sister group of Pterosauria nor of Dinosauromorpha.
7. Cladistic analysis of the main groups of crown-group Archosauria (Avesuchia nov.) supports a split into Crurotarsi and Avemetatarsalia nov., the latter consisting of *Scleromochlus* plus Ornithodira, which is composed of Pterosauria and Dinosauromorpha. *Lagerpeton* and *Marasuchus* are successive outgroups of Dinosauria. Ornithosuchids are probably crurotarsans but relationships within Crurotarsi are very unstable and no firm relationships within the clade can be established.

8. *Scleromochlus* was a biped; it might have been an active small cursorial animal (elongate hindlimbs, elongate distal hindlimb elements, ?digitigrade stance), although it shows features of saltatory forms also (highly elongate hindlimbs and distal portions of the hindlimbs, shortened trunk region, elongate tail).

I acknowledge my greatest debt of gratitude to Alick Walker for making the casts of *Scleromochlus* that were used in this study and for his continuing help and good advice on the Elgin reptiles. I thank Sandra Chapman for the loan of the BMNH specimens, and Simon Powell for the photographs. Many thanks are due also to John Sibbick for the superb reconstruction drawings. I thank David Gower, Kevin Padian and David Unwin for reading the typescript and for many helpful comments. This work was funded partly by NERC grants GR9/1569 and GR3/11124.

APPENDIX A

Characters used in the analysis of relationships of crown-group Archosauria (Avesuchia), and the placement of *Scleromochlus*. Characters were chosen from the 300 or so published characters. The original citation of each character is given, as well as the source of any major redefinition of the character. Most characters are binary (0, 1), but several are multistate (0, 1–4). In the latter cases, no order of transformation is assumed.

(a) *Skull and lower jaw*

1. Skull length: less (0) or more (1) than 50% of length of the presacral vertebral column [Sereno 1991, character 33].
2. Subnarial fenestra or foramen between premaxilla and maxilla: absent (0), present (1) [Benton & Clark 1988; Juul 1994, character 37].
3. Jugal–lacrimal articular relation: lacrimal overlaps jugal (0), jugal overlaps lacrimal (1) [Sereno & Novas 1993, character 16].
4. Jugal posterior process, shape: tapering (0), forked (1) [Sereno & Novas 1993, character 17].
5. Postfrontal: present (0), absent (1) [Gauthier 1986; Benton & Clark 1988; Juul 1994, character 16; Bennett 1996].
6. Postorbital–jugal bar behind orbit: curved or straight (0), ‘stepped’ (1) [Benton & Clark 1988; Juul 1994, character 38].
7. Lower temporal fenestra shape: non-triangular (0), triangular and reduced in size (1) [Benton & Clark 1988; Juul 1994, character 31].
8. Squamosal overhanging quadrate and quadratojugal laterally: absent (0), present, and contacting the lower temporal fenestra dorsally (1), present, but excluded from the rim of the lower temporal fenestra by postorbital and quadratojugal (2) [Benton & Clark 1988; Juul 1994, character 74].
9. Quadrate head in lateral aspect: hidden by squamosal (0), exposed (1) [Sereno & Novas 1992; Juul 1994, character 64].
10. Pterygoid–ectopterygoid articular relation: ectopterygoid ventral (0), ectopterygoid dorsal (1) [Sereno & Novas 1993, character 12].
11. Size of post-temporal opening: fenestra (0), foramen (1) [Sereno & Novas 1993, character 14].
12. Parasphenoid rostrum: rodlike (0), a dorsoventrally expanded wedge (1) [Parrish 1993; Juul 1994, character 70].
13. Palatal teeth (pterygoid, palatine, vomer): present (0), absent (1) [Benton & Clark 1988; Sereno 1991, character 1; Juul 1994, character 23].
14. Intra-mandibular joint: absent or poorly developed (0), well developed (1) [Sereno & Novas 1993; Juul 1994, character 73].

(b) *Vertebrae and ribs*

15. Centrum shape in presacrals 6–9 (or 10): subrectangular (0), parallelogram-shaped (1) [Gauthier 1986; Sereno 1991, character AA].
16. Length of presacral centrum 8 divided by length of presacral centrum 18: less (0) or more (1) than 1.0 [Gauthier 1986; Juul 1994, character 65].
17. Cervical ribs: slender (0), short and stout (1) [Gauthier 1986; Benton & Clark 1988; Juul 1994, character 26].
18. Hyposphene–hypantrum accessory intervertebral articulations in trunk vertebrae: absent (0), present (1) [Gauthier 1986; Juul 1994, character 66].
19. Number of sacral vertebrae: two (0), two plus an incipient third (1), three or more (2) [Gauthier 1986; Juul 1994, character 46].
20. Accessory neural spine on mid-caudal vertebrae: absent (0), present (1) [Benton & Clark 1988; Sereno 1991, character 23; Juul 1994, character 34].

(c) *Forelimb*

21. Clavicle: present (0), rudimentary or absent (1) [Gauthier 1986; Sereno 1991, character 24].
22. Interclavicle: present (0), absent (1) [Gauthier 1986; Juul 1994, character 44].
23. Scapulocoracoid notch at anterior junction of scapula and coracoid: absent (0), present (1) [Parrish 1993, character 14].
24. Forelimb–hindlimb length ratio: more than 0.55 (0), less than 0.55 (1) [Gauthier 1986; Sereno 1991, character BB; Juul 1994, character 45].
25. Deltopectoral crest on humerus: rounded (0), subrectangular (1) [Sereno 1991, character 25; Juul 1994, character 51].
26. Deltopectoral crest elongate and with apex situated at a point corresponding to less (0) or more (1) than 38% down the length of the humerus [Benton 1990; Juul 1994, character 59].
27. Manual digit I (pollex–thumb): metacarpal I and ungual phalanx similar in size to those of manual digits II–V (0), metacarpal I robust and half or less the length of metacarpal II, first phalanx longer than metacarpal I or any other phalanx in the hand, ungual phalanx I much larger than other unguals (1) [Gauthier 1986; Benton 1990].
28. Manual digits I–III: comparatively short with relatively blunt unguals on at least digits II and III (0), long penultimate phalanx with trenchant unguals on digits I–III (1) [Gauthier 1986; Juul 1994, character 69].
29. Metacarpal III and IV bases: lie more or less in the same plane as the inner metacarpals (0), lie on palmar surfaces of manual digits III and IV respectively (1) [Gauthier 1986; Juul 1994, character 67].
30. Manual digit IV: five (0), four (1), fewer than four (2) phalanges [Gauthier 1986; Benton & Clark 1988; Sereno 1993, character 10].

(d) ***Hindlimb***

31. Supra-acetabular crest on ilium: absent (0), present (1) [Gauthier 1986; Juul 1994, character 39].
32. Brevis shelf on ventral surface of postacetabular part of ilium: absent (0), present (1) [Gauthier 1986; Juul 1994, character 47].
33. Acetabulum: laterally orientated (0), ventrally deflected (1), open ventrally (2) [Benton & Clark 1988; Juul 1994, character 36].
34. Acetabulum: imperforate (0), semi-perforated (1), extensively perforated (2) [Gauthier 1986; Juul 1994, character 60].
35. Acetabular antitrochanter on ilium and ischium: absent (0), present (1) [Sereno & Arcucci 1994*a*, character 12].
36. Pubis length: shorter than ischium (0), longer than ischium (1) [Benton & Clark 1988; Juul 1994, character 32].
37. Pubis length: less (0) or more (1) than three times width of acetabulum [Sereno 1991, character 13; Juul 1994, character 35].
38. Pubic acetabular margin, posterior portion: continuous with anterior portion (0), recessed (1) [Sereno 1991, character 14].
39. Pubic foot: absent (0), present (1) [Gauthier 1986; Juul 1994, character 68].
40. Tibia–femur ratio: less than 1.0 (0), more than 1.0 (1) [Gauthier 1986; Sereno 1991, character 27; Juul 1994, character 48].
41. Femoral proximal head: rounded and not distinctly offset (0), subrectangular and distinctly offset (1) [Gauthier 1986; Juul 1994, character 61].
42. Femoral head articular surface: limited extent (0), extends under head (1) [Sereno & Arcucci 1994*a*, character 14].
43. Fossa trochanterica on femoral head: absent (0), present (1) [Novas 1996, character 7].
44. Femoral fourth trochanter: absent (0), moundlike (1), sharp (aliform) ridge (2) [Gauthier 1986; Benton & Clark 1988; Sereno 1991, character 35 (in part); Juul 1994, character 4; Bennett 1996, character 81].
45. Femoral lesser (anterior) trochanter: absent (0), weakly developed (1), a spike or crest (2) [Gauthier 1986; Novas 1992; Juul 1994, character 42].
46. Cnemial crest on tibia prominent: absent (0), present (1) [Benton & Clark 1988; Juul 1994, character 43].
47. Tibial distal end: unexpanded, or only slightly expanded, and rounded (0), transversely expanded, with a subrectangular end (1) [Gauthier 1986; Sereno 1991, p. 37].
48. Tibia with posterolateral flange, with receiving depression on dorsal aspect of astragalus: absent (0), present (1) [Novas 1992; Juul 1994, character 62].
49. Fibula and calcaneum shape: unreduced (0), fibula tapering and calcaneum reduced in size (1) [Gauthier 1986; Juul 1994, character 49].
50. Ventral astragalocalcaneal articular facet size: small (0), large (1) [Sereno 1991, character 11].
51. Astragalar tibial facet: concave (0), flexed/convex (1) [Sereno 1991, character 7; Juul 1994, character 28—wrongly given as 'fibular facet'].
52. Astragalar ascending flange, on anterior face of tibia: absent (0), present (1) [Gauthier 1986; Novas 1992].
53. Astragalar posterior groove: present (0), absent (1). [Sereno 1991, character 28].
54. Astragalar anteromedial corner shape: obtuse (0), acute (1) [Sereno 1991, character CC; Juul 1994, character 55].
55. Calcaneal proximal articular face: convex or flat (0), concave (1) [Novas 1992; Juul 1994, character 63].
56. Calcaneal distal articular face: transverse width more (0) or less (1) than 35% of that of the astragalus [Sereno 1991, character DD; Juul 1994, character 56].
57. Calcaneal tuber: prominent (0), rudimentary or absent (1) [Gauthier 1986; Sereno 1991, character 29; Juul 1994, character 52].
58. Calcaneal tuber orientation: lateral (0), deflected more than 45° posterolaterally (1) [Sereno 1991, character 2; Juul 1994, character 24].
59. Calcaneal tuber shaft proportions: taller than broad (0), broader than tall (1) [Sereno 1991, character 9; Juul 1994, character 29].
60. Calcaneal tuber distal end: anteroposteriorly compressed (0), rounded (1) [Sereno 1991, character 10; Juul 1994, character 30].
61. Calcaneal tuber distal end, with dorsoventrally aligned median depression: absent (0), present (1) [Parrish 1993, character 21; Juul 1994, character 72].
62. Articular surfaces for fibula and distal tarsal IV on calcaneum: separated by a non-articular surface (0), continuous (1) [Sereno 1991, character 3; Juul 1994, character 25].
63. Hemicylindrical calcaneal condyle: absent (0), present (1) [Sereno 1991, character 8; Juul 1994, character 27].
64. Distal tarsal 4: transverse width broader (0) or subequal (1) to distal tarsal 3 [Sereno 1991, character 30; Juul 1994, character 53].
65. Distal tarsal 4, size of articular facet for metatarsal V: more (0) or less (1) than half of lateral surface of distal tarsal 4 [Sereno 1991, character EE].
66. Metatarsus configuration: metatarsals diverging from ankle (0), compact metatarsus, with metatarsals I–IV tightly bunched [Benton & Clark 1988; Sereno 1991, character 31; Juul 1994, character 50].
67. Metatarsal midshaft diameters: I and V subequal or greater than II–IV (0), I and V less than II–IV (1) [Sereno 1991, character GG; Juul 1994, character 58].
68. Metatarsal I length, relative to length of metatarsal III: 50–75% (0), 85% or more (1) [Sereno 1991, character 36].
69. Metatarsals II–IV: shorter (0) or longer (1) than 50% of tibial length [Sereno 1991, character 32; Juul 1994, character 54].
70. Metatarsal V, 'hooked' proximal end: present (0), absent, and articular face for distal tarsal 4 subparallel to shaft axis (1) [Sereno 1991, character FF; Juul 1994, character 57].
71. Phalanges on pedal digit V: four (0), three (1), two (2), one (3), none (4) [Gauthier 1986; Benton & Clark 1988; Juul 1994, characters 40, 41 and 71].

(e) ***Dermal structures***

72. Dorsal body osteoderms: absent (0), present as a single median row (1), a paramedian pair per cervicodorsal vertebra (2) , more than one paramedian pair per cervicodorsal vertebra (3) [Gauthier 1986; Benton & Clark 1988; Sereno 1991, character 12 (in part); Juul 1994, character 15].
73. Osteoderm sculpture: absent (0), present (1) [Parrish 1993, character 16].

APPENDIX B

Matrix of character codings used in the analysis of relationships of crown-group Archosauria (Avesuchia), and the placement of *Scleromochlus*. Characters are listed in the table, and they were coded for 16 archosaurian taxa. A hypothetical ancestor is not used, but two taxa, *Euparkeria* and Proterochampsidae, are included as postulated outgroups of Avesuchia. Some of the taxa have alternative names which are approximately equivalent, and have been used synonymously in previously published cladistic analyses: Phytosauridae (= Parasuchia), Stagonolepididae (=Aetosauria), Prestosuchidae (= Rauisuchidae, in part), *Marasuchus* (=*Lagosuchus*), 'Theropoda' (= Theropoda, excluding *Herrerasaurus*, or Ceratosauria + Tetanurae). Character codings: 0, postulated plesiomorphic condition of character; 1–4, postulated derived conditions of character; ?, character state uncertain; X, character uncodable because of transformation.

		10		20		30		40		50		60		70	
Euparkeria	00000	00000	00000	00000	00000	0000?	00000	00000	00010	00000	00000	00000	00000	00000	120
Proterochampsidae	00001	00000	10000	00000	?0000	0000?	00000	00000	00010	00000	00000	00000	00000	00000	410
Phytosauridae	10000	00000	00100	01000	00100	00001	00000	00000	00010	00001	10000	00111	01100	00000	021
Ornithosuchidae	00000	00000	00100	00020	00000	0000?	10010	11100	00022	1100X	10000	00111	01100	00000	120
Stagonolepididae	00000	01000	00100	01?00	00100	00002	00100	10100	00000	01001	10000	00111	11100	00000	021
Prestosuchidae	01000	10000	00100	01?01	00100	00000	10100	0?100	00010	00001	10000	00111	11100	00000	130
Postosuchus	01000	11200	11100	01100	11100	00000	10210	11110	00010	00001	10000	00111	11100	02000	4?0
Crocodylomorpha	00001	00100	11100	01001	00100	00000	00010	1110?	00010	00001	10000	00111	11100	00100	221
Scleromochlus	1??00	000??	???00	00?20	??010	0????	10000	10?01	00?00	0100?	00???	00100	0??1?	10110	400
Pterosauria	10000	00000	00100	10020	11001	00101	00000	00001	00000	0001X	00100	01X00	0X010	10110	200
Lagerpeton	0????	?????	?????	???0?	?????	?????	?0000	00001	10020	0001X	00110	11???	?1011	11011	400
Marasuchus	0????	?????	????1	10000	???11	0????	10011	10001	01121	0001X	00110	11100	01011	11011	400
Herrerasaurus	01111	00011	10111	10110	11011	10112	10021	11011	11121	1110X	01111	11100	01011	11011	300
'Theropoda'	01111	00011	10111	10120	11011	11112	11021	11011	11122	1111X	01111	11100	01011	11011	400
Sauropodomorpha	01111	00011	10101	10120	11011	11012	11021	11001	11122	1110X	01111	11100	01011	11011	300
Ornithischia	00001	00011	10101	10020	11011	10002	11021	11001	11122	1111X	01110	11100	01011	11011	400

APPENDIX C

Characters diagnosing the clades in the cladogram shown in figure 16. The apomorphic condition (1) is normally not indicated, but for multistate characters (numbers 8, 18, 30, 34, 44, 45, 67, 71 and 72), the condition (1–4) is shown. Character state reversals are indicated by a minus sign. Equivocal character placements are indicated with an asterisk (*) at each possible node. The clade diagnoses include only the unequivocal characters.

Euparkeria + Proterochampsidae + crown-group
Archosauria: 44(1)
Femoral fourth trochanter moundlike.
Avesuchia: 13, 30(1)*, 58, 62
Absence of palatal teeth, calcaneal tuber orientated more than 45° posterolaterally, articular surfaces for fibula and distal tarsal IV on calcaneum continuous.

Crurotarsi: 17, 23, 50, 51, 59, 60, 63, 72(2)*, 73
Cervical ribs short and stout, scapulocoracoid notch at anterior junction of scapula and coracoid, ventral astragalocalcaneal articular facet large, astragalar tibial facet flexed, calcaneal tuber shaft broader than tall, calcaneal tuber distal end rounded, hemicylindrical calcaneal condyle, osteoderm sculpture.

Stagonolepididae + Crocodylomorpha + Ornithosuchidae + 'Rauisuchia': 36*, 38, 61
Pubic acetabular margin posterior portion recessed; calcaneal tuber distal end with dorsoventrally aligned median depression.

Crocodylomorpha + Ornithosuchidae + 'Rauisuchia': −30(1)*, 34(1)*, 37*, 71(1)*

Ornithosuchidae + Rauisuchia': 31*, −73
Loss of osteoderm sculpture.

'Rauisuchia': 2*, 6, 7, ?18*, ?72(3)*
Postorbital–jugal bar behind orbit is 'stepped', lower temporal fenestra triangular and reduced in size.

Avemetatarsalia: 1*, 19(2)*, 24, 31*, 36, 40, 64, 66, 68*, 69, 71(2)*, 72(0)
Forelimb–hindlimb ratio less than 0.55, pubis longer than ischium, tibia–femur ratio more than 1.0, distal tarsal 4 subequal in transverse width to distal tarsal 3, compact metatarsus with metatarsals I–IV tightly bunched, metatarsals II–IV more than 50% tibial length, dorsal body osteoderms absent.

Ornithodira: 16, 21*, 22*, 25, 49, 53, 57
Presacral centrum 8 longer than presacral centrum 18, deltopectoral crest on humerus subrectangular, fibula tapering and calcaneum reduced in size, astragalar posterior groove, calcaneal tuber rudimentary or absent.

Dinosauromorpha: −1*, 5*, 41, 44(2)*, 52, 54, 56, 65, 67, −68*, 70, 71(3)*
Femoral proximal head subrectangular and distinctly offset, astragalar ascending flange on anterior face of tibia, astragalar anteromedial corner acute, calcaneal distal articular face less than 35% of that of astragalus, articular facet for metatarsal V less than half of lateral surface of distal tarsal 4, midshaft diameters of metatarsals I and V less than II–IV, metatarsal V has no 'hooked' proximal end and articular face for distal tarsal 4 is subparallel to shaft axis.

Dinosauriformes: 15, 34(1)*, 35, 42, 43, 45(1)
Centrum shape of cervical centra parallelogram-shaped, acetabular antitrochanter on ilium and ischium, femoral head articular surface extends under head. Fossa trochanterica on femoral head, femoral lesser (anterior) trochanter weakly developed.

Dinosauria: 9, 10, 11*, 26, 30(2)*, 32, 34(2), 37*, 45(2)*, 46*, 47*, 48, 52

Quadrate head exposed in lateral aspect, ectopterygoid lies dorsal to pterygoid, deltopectoral crest elongate and with apex situated at a point corresponding to more than 38% down the length of the humerus, brevis shelf on ventral surface of postacetabular part of ilium, acetabulum extensively perforated, tibia with posterolateral flange and receiving depression on dorsal aspect of astragalus, astragalar ascending flange on anterior face of tibia.

Saurischia: 2*, 3, 4, 18*, 27, 29, 55

Jugal overlaps lacrimal, posterior process of jugal forked, robust saurischian thumb (metacarpal I robust and half or less the length of metacarpal II, first phalanx longer than metacarpal I or any other phalanx in the hand, ungual phalanx I much larger than other unguals), metacarpal III and IV bases lie on palmar surfaces of manual digits III and IV respectively, calcaneal proximal articular face concave.

Theropoda: 14, 28*, 39*

Intra-mandibular joint well developed.

Euparkeria: 71(1)*, 72(2)*
Proterochampsidae: 5*, 11*, 71(4)*, 72(1)*
Phytosauridae: 1*
Ornithosuchidae: −17, 19(2)*, −23, 44(2)*, 45(2)*, 46*, 47*, −61
Stagonolepididae: 7*, 30(2)*, 33(1)*, −44*, 47*
Prestosuchidae: 20*, 33(1)*, −34, −36, 72(3)*
Postosuchus: 7*, 8(2), 11*, 12*, 18*, 21*, 22*, 33(2), 39*, 67(2), 71(4)*
Crocodylomorpha: 5*, 8(1), 11*, 12*, 20*, 68*, 71(2)*
Scleromochlus: 36*, −44*, 47*, 71(4)*
Pterosauria: −24, 28*, −31, −44*
Lagerpeton: −1*, −19*, 71(4)*
Marasuchus: −1*, −19*, −41, 71(4)*
Herrerasaurus: −16, 19(1), −27, −32, 45(1)*, −49*
Neotheropoda: 71(4)*
Sauropodomorpha: −49*
Ornithischia: 71(4)*

APPENDIX D. ABBREVIATIONS USED IN THE FIGURES

a	angular
ar	articular
as	astragalus
at	atlas
ax	axis
bo	basioccipital
bs	basisphenoid
c	carpal(s)
ca	calcaneum
ca.v	caudal vertebra(e)
ce.v	cervical vertebra(e)
ch	chevron
co	coracoid
d	dentary
d.v	dorsal vertebra
ec	ectopterygoid
eo	exoccipital
f	femur
fr	frontal
g	gastralia
h	humerus
hy	hyoid
il	ilium
is	ischium
j	jugal
l	lacrimal
m	maxilla
mc	metacarpal(s)
mf	mandibular foramen
mt	metatarsal(s)
n	nasal
os	osteoderms
p	parietal
ph	phalanx/phalanges
pl	palatine
pm	premaxilla
po	postorbital
pof	postfrontal
pop	paroccipital process
prf	prefrontal
pt	pterygoid
pu	pubis
q	quadrate
qj	quadratojugal
r	radius
ri	rib
rop	retroarticular process
s.v	sacral vertebra
sa	surangular
sc	scapula
sp	splenial
sq	squamosal
ta	distal tarsal(s)
ti	tibia
u	ulna
v	vomer

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