New heterodontosaurid specimens from the Lower Jurassic of southern Africa and the early ornithischian dinosaur radiation

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ABSTRACT: Heterodontosaurids are poorly understood early ornithischian dinosaurs with extensive geographic and stratigraphic ranges. The group is best known from the Lower Jurassic upper 'Stormberg Group' (upper Elliot and Clarens formations) of southern Africa, previously represented by at least three distinct species and ten described specimens. This paper describes four additional heterodontosaurid specimens from southern Africa. A partial skull of a large individual of *Heterodontosaurus tucki* (NM QR 1788) is approximately 70% longer than that of the type specimen of *Heterodontosaurus*, and provides new information on allometric changes in mandibular morphology during growth in this taxon. It is the largest known heterodontosaurid cranial specimen, representing an individual approximately 1·75 metres in length, and perhaps 10 kg in body mass. NHMUK R14161 is a partial skull that appears to differ from all other heterodontosaurids on the basis of the proportions of the dentaries, and may represent an unnamed new taxon. Two additional partial skulls (NHMUK RU C68, NHMUK RU69) are referred to cf. *Lycorhinus*. At least four, and possibly five or more, heterodontosaurid species are present in the upper 'Stormberg'. This high diversity may have been achieved by dietary niche partitioning, and suggests an adaptive radiation of small-bodied ornithischians following the end Triassic extinctions.

KEY WORDS: diversity, Elliot Formation, Heterodontosauridae, Ornithischia, South Africa, Stormberg Group, tooth replacement

Ornithischian dinosaurs were the dominant herbivores of the northern hemisphere during the Cretaceous Period, evolving high morphological and taxonomic diversity, complex behavioural and social adaptations, and sophisticated feeding mechanisms (Sereno 1997, 1999; Weishampel *et al*. 2004). However, the evolution of ornithischians during the Late Triassic and much of the Jurassic is poorly understood (e.g. Sereno 1997, 1999; Parker *et al*. 2005; Butler *et al*. 2006, 2007; Irmis *et al*. 2007), primarily because relatively few early ornithischian specimens are known, and because many of those that are known have been incompletely studied. Heterodontosauridae is a clade of small-bodied early ornithischians characterised by an unusual heterodont dentition (Weishampel & Witmer 1990; Norman *et al*. 2004a) that was first described from the Lower Jurassic upper 'Stormberg Group' of southern Africa. The majority of heterodontosaurid specimens are from this region (Broom 1911; Haughton 1924; Crompton & Charig 1962; Thulborn 1970, 1974, 1978; Charig & Crompton 1974; Gow 1975, 1990; Hopson 1975, 1980; Santa Luca *et al*. 1976; Santa Luca 1980; Porro 2007, 2009; Butler *et al*. 2008a; Norman *et al*. in press) although additional specimens are known from the Late Triassic and Middle Jurassic

of Argentina (Báez & Marsicano 2001; Pol *et al*. 2011), the Early and Late Jurassic of western North America (Attridge *et al*. 1985; Sereno 1997; Butler *et al*. 2010), and the earliest Cretaceous of the UK (Norman & Barrett 2002). A heterodontosaurid reported from China was initially described as from the late Early Cretaceous Yixian Formation (Zheng *et al*. 2009); however, the age of the type and only described specimen appears to be uncertain and could be as early as Middle Jurassic (H. You pers. comm. 2010). Heterodontosaurids were thus both stratigraphically long-lived (>60 million years) and geographically widespread, although their fossils are numerically rare and exhibit low species-richness in post-Lower Jurassic faunal assemblages.

Recent work puts Heterodontosauridae at the forefront of debates on early ornithischian evolution. Reanalyses of ornithischian phylogeny have placed heterodontosaurids as either basal members of Marginocephalia (e.g. Xu *et al*. 2006; see also Cooper 1985) or as the most basal clade of Ornithischia (Butler *et al*. 2007, 2008b, 2010); these alternative placements have substantially different implications for the timing and pace of early ornithischian evolution (Butler *et al*. 2007; Butler 2010). Heterodontosaurids included several diminutive species
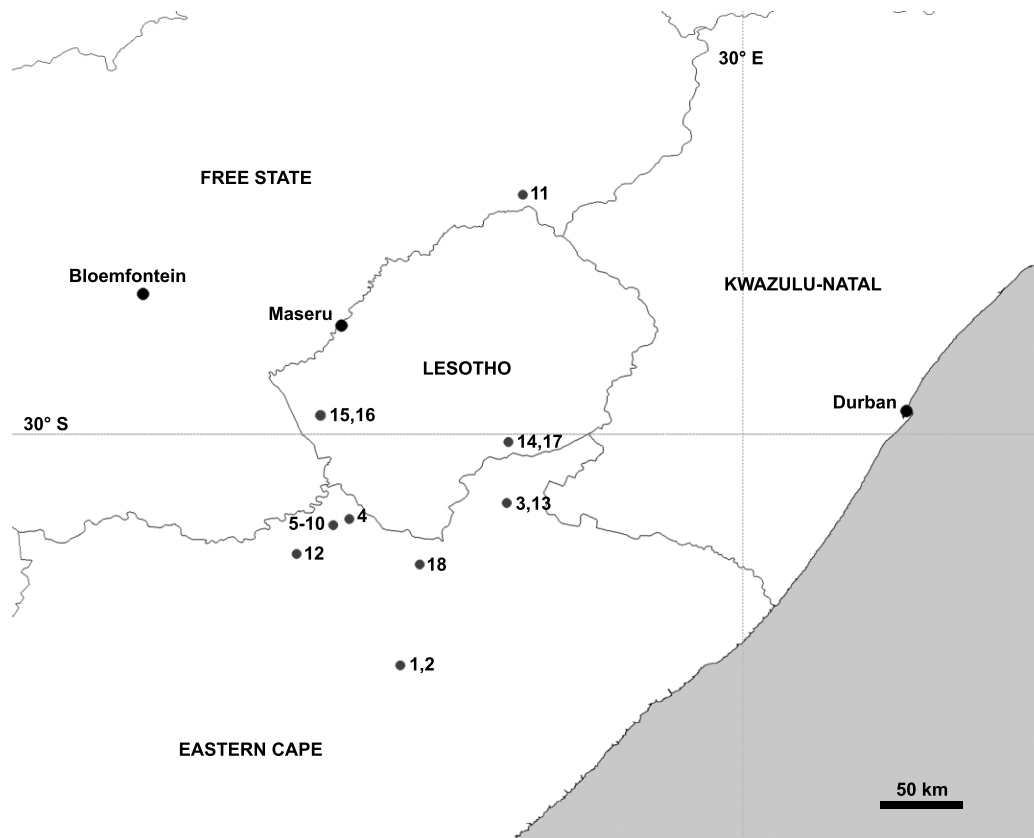
Figure 1 Occurrences of heterodontosaurid specimens in the Lower Jurassic of South Africa and Lesotho. Numbers correspond to numbers for specimens in Table 1.

that appear to be the smallest known adult ornithischians (Butler *et al.* 2010), and at least one heterodontosaurid, *Tianyulong*, possessed filamentous integumentary structures interpreted as possible 'protofeathers' (Witmer 2009; Zheng *et al.* 2009).

The upper Elliot and Clarens formations (upper parts of the informal 'Stormberg Group') have yielded nearly twenty heterodontosaurid specimens since the early twentieth century (Table 1, Fig. 1). These specimens have formed the basis for five genera and species: *Geranosaurus atavus* Broom, 1911, *Lycorhinus angustidens* Haughton, 1924, *Heterodontosaurus tucki* Crompton & Charig, 1962, *Abrictosaurus consors* (Thulborn 1974) and *Lanasaurus scalpridens* Gow, 1975. *Geranosaurus*, *Lycorhinus* and *Lanasaurus* were all based primarily upon fragmentary jaw material, and taxonomic assignments have been made largely upon differences in dental morphology, the ontogenetic and intraspecific significance of which remains uncertain. This has led to a confused taxonomy, in which there has been little agreement upon the number of valid species and the specimens assigned to each taxon. Recent reviews have considered '*Geranosaurus*' a *nomen dubium*, and *Lycorhinus*, *Heterodontosaurus* and *Abrictosaurus* as valid distinct taxa (Weishampel & Witmer 1990; Norman *et al.* 2004a). The status of *Lanasaurus* is uncertain: although it might be referable to *Lycorhinus* (Gow 1990), the material preserved in the holotypes of the two taxa does not overlap. Another specimen, NHMUK RU A100, described by Thulborn (1970), has been controversial, and has been assigned to both *Abrictosaurus* (Hopson 1975) and *Lycorhinus* (Gow 1990). The present authors consider *Heterodontosaurus* and *Abrictosaurus* as valid, and both *Lycorhinus* and *Lanasaurus* as provisionally valid pending discovery of more complete specimens. The taxonomic assignment of NHMUK RU A100 is considered to be uncertain; it may be referable to either *Lycorhinus*

or *Lanasaurus* or, alternatively, *Lycorhinus*, *Lanasaurus* and NHMUK RU A100 may all represent a single taxon (for which the valid name would be *Lycorhinus*). A provisional review of these historical taxa and specimens is presented by Norman *et al.* (in press). In addition to uncertainties over the taxonomy and phylogenetic positions of the southern African heterodontosaurids, palaeobiological discussion has focused on aspects of the jaw mechanics, dental replacement, diet, life history and sexual dimorphism (Thulborn 1970, 1974, 1978; Hopson 1980; Weishampel 1984; Crompton & Attridge 1986; Galton 1986; Barrett 1998; Porro 2007, 2009; Butler *et al.* 2008a; Norman *et al.* in press).

A major factor in prolonging these controversies has been the paucity of published anatomical data for heterodontosaurids. Despite being known for the nearly 50 years, the cranial anatomy of *Heterodontosaurus* has not been described in detail (but see Norman *et al.* in press for a full description), and *Abrictosaurus* and NHMUK RU A100 require further preparation and study. Moreover, nearly half of the known southern African heterodontosaurid specimens have not been described (Table 1). This paper partially redresses this situation by describing four heterodontosaurid specimens that have not previously been discussed in the literature. The aims are to document this important material and provide new insights into the morphology and diversity of southern African heterodontosaurids and, subsequently, to discuss the implications of the southern African heterodontosaurid assemblage for understanding the early evolution of ornithischian dinosaurs across the Triassic/Jurassic boundary.

Institutional abbreviations: BPI, Bernard Price Institute, University of the Witwatersrand, Johannesburg, South Africa; CAMSM, Sedgwick Museum of Earth Sciences, Cambridge, UK; NHMUK, Natural History Museum, London, United Kingdom; LACM, Natural History Museum of Los Angeles

Table 1 Known specimens of southern African heterodontosaurids. Numbering (column #) corresponds to locations marked on Figure 1.

Specimen no.	#	Taxonomic assignment(s)	Material	Notes	References	Locality name	State	Country	Formation
SAM-PK-K1871	1	*Geranosaurus atavus*	Partial skull	Holotype	Broom (1911)	Road cutting near summit of Barkly Pass	Eastern Cape	South Africa	Clarens Formation
SAM-PK-K1857	2	*Geranosaurus atavus*	Hindlimb material	Referred specimen	Broom (1911)	Road cutting near summit of Barkly Pass	Eastern Cape	South Africa	Clarens Formation
SAM-PK-K3606	3	*Lycorhinus angustidens*	Partial left dentary	Holotype	Haughton (1924); Hopson (1975); Gow (1990)	Paballong, Mount Fletcher, Herschel District	Eastern Cape	South Africa	upper Elliot Formation
SAM-PK-K337	4	*Heterodontosaurus tucki*	Skull	Holotype	Crompton & Charig (1962); Norman et al. (in press)	Mountain behind Tyindini trading store, Herschel district	Eastern Cape	South Africa	Clarens Formation
SAM-PK-K1326	5	Heterodontosauridae indet.	Partial maxilla	Undescribed specimen		Voisana, Herschel District	Eastern Cape	South Africa	? upper Elliot Formation
SAM-PK-K1328	6	?*Heterodontosaurid*	Postcranial material	Undescribed specimen		Voisana, Herschel District	Eastern Cape	South Africa	? upper Elliot Formation
SAM-PK-K1332	7	*Heterodontosaurus tucki*	Skull and postcranium	Referred specimen	Santa Luca et al. (1976); Santa Luca (1980); Norman et al. (in press)	Krommespruit, Voisana, Herschel District	Eastern Cape	South Africa	upper Elliot Formation
SAM-PK-K1334	8	*Heterodontosaurus tucki*	Maxilla	Undescribed specimen	Norman et al. (in press)	Site 18a, Voisana, Herschel District	Eastern Cape	South Africa	upper Elliot Formation
SAM-PK-K10487	9	*Heterodontosaurus tucki*	Partial skull, juvenile	Referred specimen	Butler et al. (2008a); Normal et al. (in press)	Voisana, Herschel District	Eastern Cape	South Africa	? upper Elliot Formation
SAM-PK-K10488	10	Heterodontosauridae incertae sedis	Dentaries	Undescribed specimen		Voisana, Herschel District	Eastern Cape	South Africa	? upper Elliot Formation
BP/1/4244	11	*Lanasaurus scalpridens*	Maxilla	Holotype	Gow (1975, 1990)	Buck Camp, Golden Gate Highlands National Park	Free State	South Africa	upper Elliot Formation
BP/1/5253	12	cf. *Lanasaurus scalpridens*	Maxilla	Previously referred to *Lycorhinus*	Gow (1990)	Bamboeskloof Farm, Lady Grey	Eastern Cape	South Africa	? upper 'Stormberg'
NHMUK RU A100	13	cf. *Lycorhinus* & *Lanasaurus*	Partial skull	Previously referred to *Lycorhinus* and *Abrictosaurus*	Thulborn (1970)	Paballong, Mount Fletcher, Herschel District	Eastern Cape	South Africa	upper Elliot Formation
NHMUK RU B54	14	*Abrictosaurus consors*	Skull and postcranium	Holotype	Thulborn (1974); Hopson (1975)	Noosi, east of Whitehill	Qacha's Nek	Lesotho	upper Elliot Formation
NHMUK RU C68	15	cf. *Lycorhinus* sp.	Dentary	Referred specimen	This paper	Maboloka	Mohale's Hoek	Lesotho	Clarens Formation
NHMUK RU C69	16	cf. *Lycorhinus* sp.	Partial skull and femur	Referred specimen	This paper	Maboloka	Mohale's Hoek	Lesotho	Clarens Formation
NHMUK R14161	17	Heterodontosauridae incertae sedis	Partial skull	New taxon?	This paper	Whitehill, Qacha's Nek	Qacha's Nek	Lesotho	? upper 'Stormberg'
NM QR 1788	18	*Heterodontosaurus tucki*	Partial skull	Referred specimen	This paper	Tushielaw, Barkly East	Eastern Cape	South Africa	? upper 'Stormberg'

County, Los Angeles, California, USA; NM, National Museum, Bloemfontein, South Africa; SAM-PK, Iziko South African Museum, Cape Town, South Africa.

1. Materials and methods

Preparation of NHMUK R14161 was carried out by SM-F. Due to the fragmented and fragile nature of the specimen, rotary diamond burrs were used to grind down the overlaying matrix until <0·5 mm remained. This veneer of matrix was then carefully removed using a pneumatic airpen fitted with a 1 mm diameter carbide pin at a very low air pressure (<20 PSI). Cracks, loose pieces and fragile areas were consolidated using a 5–15% solution of Paraloid B72 in acetone. Particularly thin or unsupported areas were strengthened by brushing with molten Carbowax (polyethylene 400); this support was further strengthened by adding layers of fine cotton gauze. The Carbowax was later removed by either heating with a hot needle or by picking away with mounted pins. The remaining wax residue was removed by gently brushing with warm water.

NM QR 1788 was micro-CT scanned at the NHMUK by RLA with a HMX-ST CT 225 system and reconstructed with beam hardening and noise corrections using CT-PRO 2.0 (Metris X-Tek, Tring, UK). The resulting data set had an isotropic voxel size of 48·5 µm. The scan was visualised and segmented by LBP (to extract bones and teeth) using Amira 5.2.2 (Visage Imaging GmbH, Berlin, Germany).

2. Specimen NM QR 1788

2.1. Systematic palaeontology

<div align="center">

Dinosauria Owen, 1842
Ornithischia Seeley, 1887
Heterodontosauridae Kuhn, 1966
Heterodontosaurus Crompton & Charig, 1962
Heterodontosaurus tucki Crompton & Charig, 1962

</div>

2.2. Material

NM QR 1788 is an incomplete articulated skull (Figs 2–3), comprising the incomplete dentaries (with *in situ*, but damaged, dentition), fragments of the postdentary bones, fragments and impressions of the maxillae and maxillary dentition, and a partial palate.

2.3. Locality and horizon

Collected from an undocumented horizon within the 'Stormberg Group' (presumably the upper part of the sequence, of Early Jurassic age) at Tushielaw Farm (30.78°S 27.95°E, coordinates for the farmhouse), near Rhodes, Barkly East District, Eastern Cape Province by P. J. Herselman in 1975. The specimen was previously catalogued as an individual of the basal sauropodomorph dinosaur *Massospondylus*, and was identified as a heterodontosaurid by Dr Adam Yates (BPI, Johannesburg).

2.4. Description

The skull (Figs 2–3) has undergone shear such that the right side of the skull is displaced ventrally and rostrally relative to the left side; moreover, the cranium has been transversely compressed at its rostral end. Most of the elements are damaged and heavily eroded, complicating attempts to identify sutures.

Micro-CT scans of the upper jaw exhibited very poor contrast between bone and matrix; as a result, the rostral cranial elements were not successfully segmented. The left maxilla is represented by a small sliver of bone from its medial surface (Fig. 2c–d); the right maxilla is more complete, represented by fragments of the medial maxillary shelf, alveolar margin and dentition, and rostrally by an impression of the medial maxillary shelf (Fig. 2a–b). Digital moulds of these surfaces were created using Amira to aid visualisation. The maxillary shelves are dorsoventrally expanded rostrally and decrease in height caudally. Six left and six right maxillary teeth are represented by fragments and impressions of the lingual crown surfaces. These fragments/impressions indicate that the crowns are chisel-shaped and packed such that adjacent crowns contacted each other at their apices. Several impressions (right crown fragments 2 and 5, left crown fragment 4) indicate that large apicolingually-facing planar wear facets were present and covered the entire crown apex. Impressions (particularly of left crown fragments 2 and 3) indicate a median ridge on the lingual surface of the maxillary crowns.

The palate is partially preserved and exposed in dorsal view (Fig. 2e–f). The vomers are present as several elongate rostrocaudally extending slivers of bone positioned along the midline between the medial maxillary shelves (Fig. 2f: vom); their caudal ends are not preserved, thus no information on their contacts with other palatal elements is available. Fragments of the palatines are positioned between the preserved caudal ends of the vomers and the maxillary shelves (Fig. 2f: pal). Rostrally, the right palatine contacts the medial surface of the right maxilla; caudally, the palatine fragments contact the lateral edges of the palatal processes of the pterygoids. The pterygoids are partially preserved, including the palatal processes (Fig. 2f: rpt), which are not preserved in any other known specimen of *Heterodontosaurus* (LBP pers. obs.). The palatal processes of the pterygoids are short and triangular, tapering rostrally and diverging laterally from each other to contact the medial edges of the palatines; caudally, the pterygoids contact one another along the midline. There is an elongate ventral process of the right pterygoid (i.e., pterygoid flange) that projects ventrolaterally towards the mandibular fossa of the lower jaw and is arched (laterally convex) along its length. The ectopterygoid is a robust element that extensively overlaps the rostrodorsal aspect of the ventral process of the pterygoid (Fig. 2b, f: ect); it projects rostrally and laterally, contacting the medial surface of the caudal end of the maxilla.

The predentary is missing. Micro-CT scans of the lower jaw exhibit good contrast between fossil material and matrix, revealing the dentaries, splenials, coronoids and prearticulars on both sides (Fig. 3). Fragments of other postdentary bones are present, but cannot be positively identified. Both dentaries (Figs 2a–d, g–h, 3a–b) are incomplete at their rostral ends. The caudal and ventral margins of the dentaries are damaged, and the lateral surfaces (particularly that of the right dentary) have been eroded. The dentary is a robust and transversely thick element. Caudally, it forms the rostral margin of the coronoid eminence. The left dentary bifurcates caudally; the rounded notch between the dorsal and ventral processes forms the rostral margin of the external mandibular fenestra (Fig. 3b). Rostrally, both dentaries exhibit a ventrally-projecting 'flange', resembling that reported in *Psittacosaurus* (Zhou *et al.* 2006; Sereno *et al.* 2007); however, because the ventral margins of the dentaries are heavily damaged, it is possible that this flange is an artefact of preservation. The dentary symphyseal contact is a nearly flat, vertical surface.

The left and right splenials are present (Figs 2g–h, 3c–d), although the left splenial is better preserved. The splenial is transversely compressed and rostrocaudally elongated, and
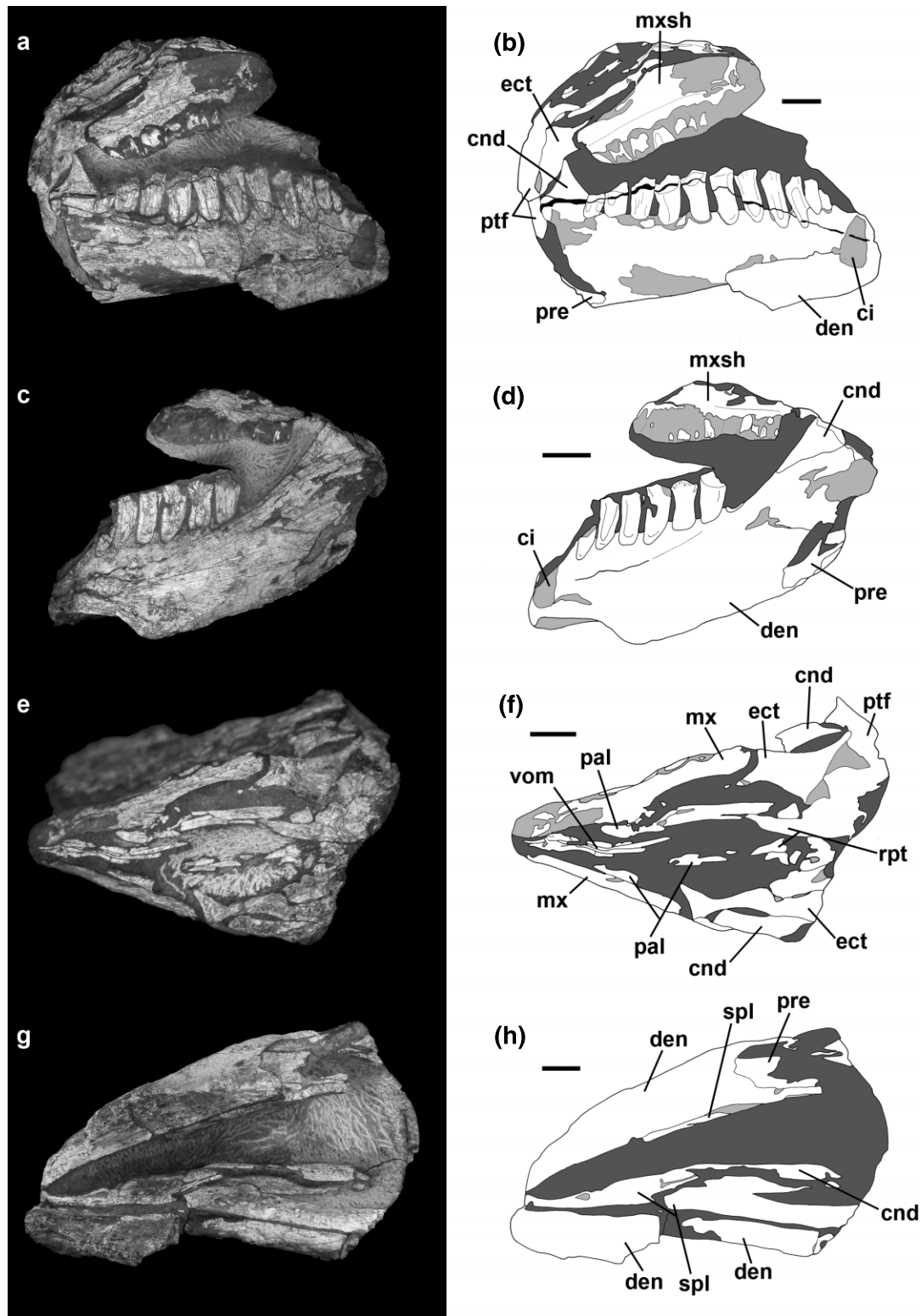
Figure 2 Photographs (a, c, e, g) and line drawings (b, d, f, h) of skull of *Heterodontosaurus tucki* (NM QR 1788): (a–b) right lateral view; (c–d) left lateral view; (e–f) dorsal view; (g–h) ventral view. For line drawings, light grey indicates eroded bone; dark grey indicates matrix. Abbreviations: ci=caniniform tooth impression; cnd=coronoid bone; den=dentary; ect=ectopterygoid; mx=maxilla; mxsh=medial maxillary shelf; pal= palatine; pre=prearticular; ptf=(ventral) pterygoid flange; rpt=rostral (palatal) process of the pterygoid; spl=splenial; vom=vomers. Scale bars=10 mm; photographs are at the same scale as corresponding line-drawing.

medially overlies the Meckelian fossa. Micro-CT scans demonstrate that the splenial medially laps the dentary on the ventromedial surface of the mandible. Rostrally, the ventral edge of the splenial is separated from the ventral mandibular margin.

The coronoid is preserved on both left and right sides (Figs 2, 3c–d), and formed the dorsal margin of the coronoid eminence. Unlike the condition in other basal ornithischians (e.g. Sereno 1991), it is a robust, dorsoventrally-expanded, sheet-like bone that extends rostrally below and medial to the
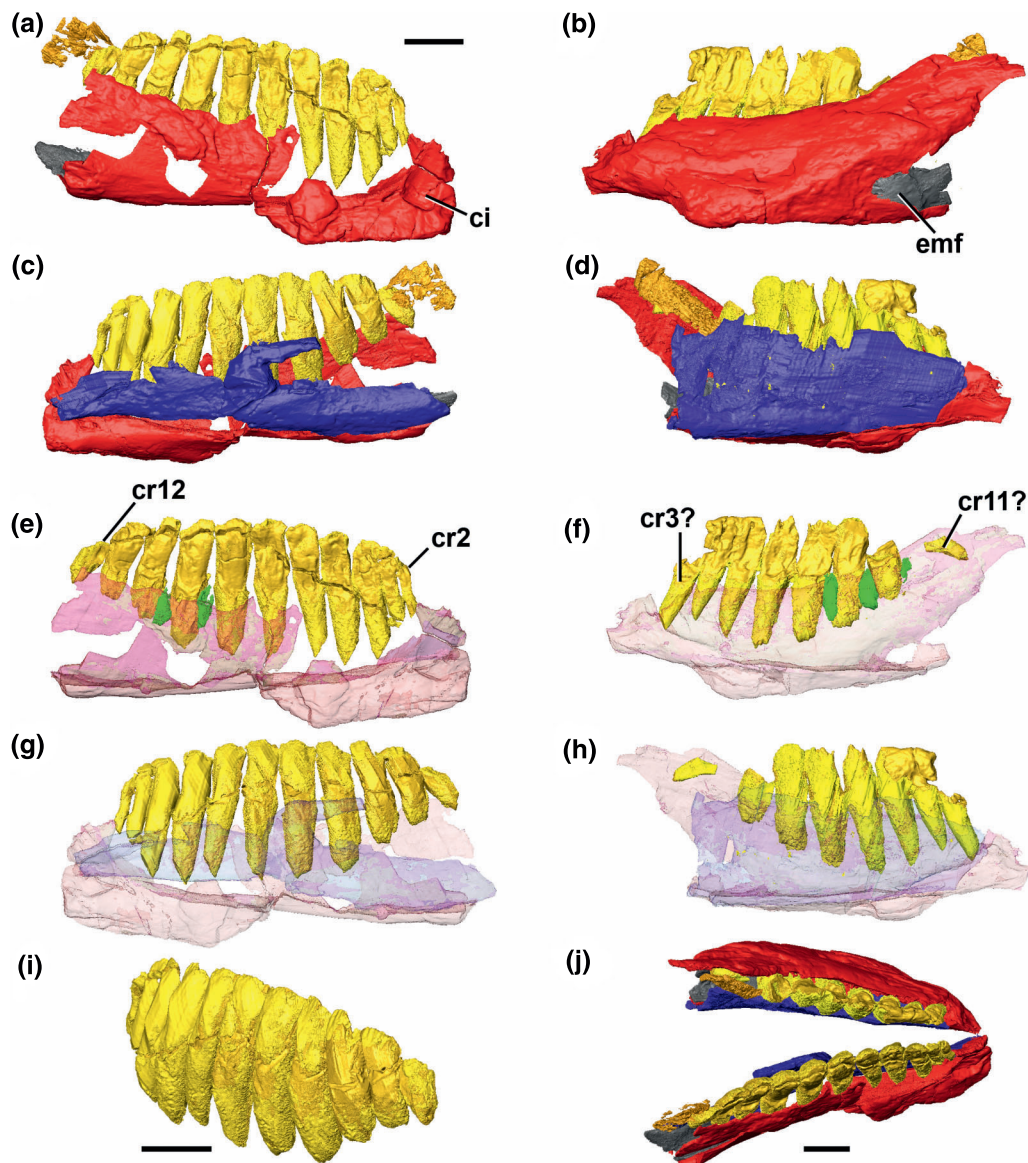
Figure 3 Rostral part of mandible of *Heterodontosaurus tucki* (NM QR 1788) reconstructed from micro-CT data: (a) right rostral mandible, lateral view; (b) left rostral mandible, lateral view; (c) right rostral mandible, medial view; (d) left rostral mandible, medial view; (e) right dentary tooth row, lateral view; (f) left dentary tooth row, lateral view; (g) right dentary tooth row, medial view; (h) left dentary tooth row, medial view; (i) right dentary tooth row (bones removed) in oblique caudomedial view; (j) articulated rostral mandibles, dorsal view. Elements are colour coded as follows: dentary, red; splenial, blue; coronoid, orange; prearticular, grey; functional dentary teeth, yellow; unresorbed tooth roots, green. The bones have been made transparent in several views (e–h) to better visualise dental anatomy. Abbreviations: ci=caniniform tooth impression; cr=crown; emf= external mandibular fenestra. Scale bars=10 mm and scale bar for (a) also applies to (b–h).

tooth row. The coronoid eminence appears to be relatively taller in NM QR 1788 than in other *Heterodontosaurus* specimens (SAM-PK-K337, SAM-PK-K1332).

Both prearticulars are present, although only the left prearticular is visible within the external mandibular fenestra (Figs 2c–d, 3b). The prearticular slots dorsally into a trough formed by the dentary laterally and ventrally, and the splenial medially.

The dentary tooth row is virtually complete on the right side, which preserves a partial impression of the lingual surface of the root of the dentary caniniform and 11 post-caniniform teeth (Fig. 3e, g, i), giving a complete dentary tooth count of 12 in NM QR 1788. The height of the crowns has been accentuated by damage to the lateral surface of the dentary, which in many cases has exposed the roots. Crowns 8–9 on the right side are the best preserved. The left dentary tooth row contains seven badly preserved teeth corresponding to crowns 3–9

(Fig. 3f, h). Additionally, micro-CT scans demonstrate the presence of a small eighth tooth (probably crown 11) lying almost horizontally within the caudal lower jaw, its apex directed rostrally; this displaced tooth is separated from crown 9 by a gap that probably marks the position of the missing crown 10. The first post-caniniform crown (crown 2) is much smaller in size than subsequent crowns, and was clearly separated from the caniniform by a diastema approximately equal in length to the mesiodistal width of a single crown. Caudally, the crowns increase in mesiodistal width and apicobasal height, with the largest crowns (crowns 6–8) located at the midpoint of the tooth row. Individual crowns are widest mesiodistally at their apices and taper gently towards their roots, which extend nearly to the preserved ventral margin of the lower jaw; however, there is no clearly defined mesiodistal expansion ('neck') or transverse expansion ('cingulum') of the crown above the root. Large, planar, dorsolaterally-facing
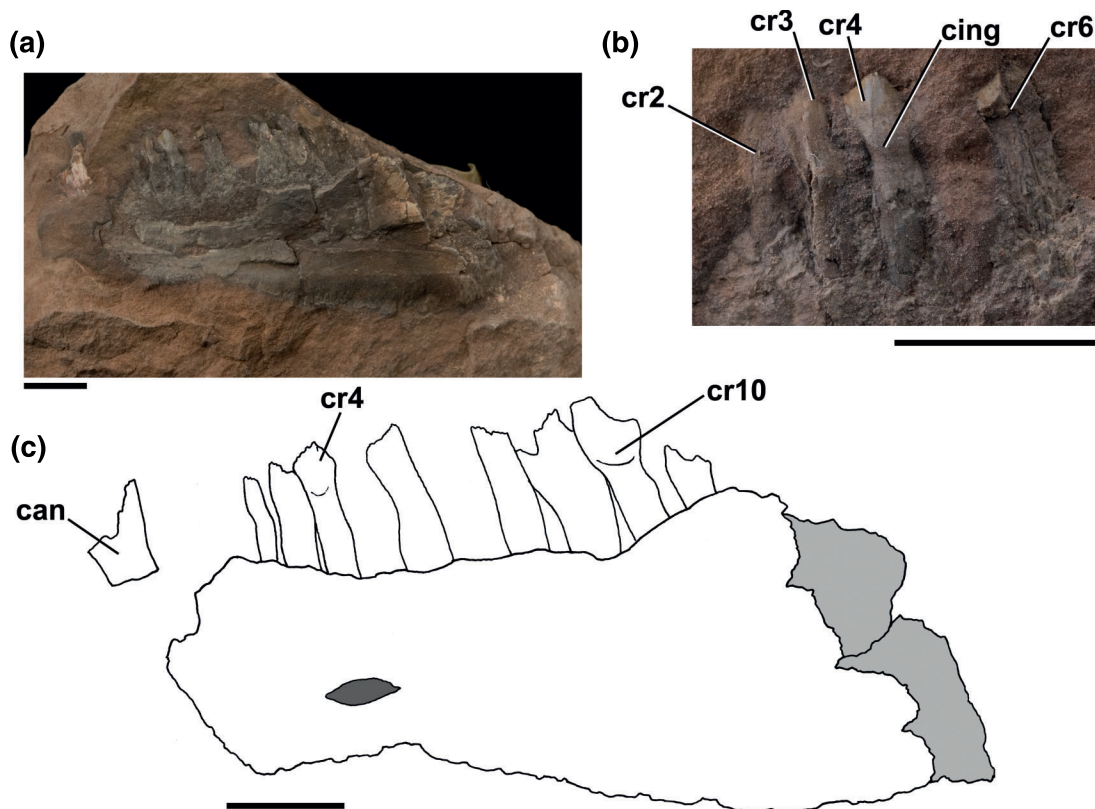
Figure 4 NHMUK RU C68, right dentary of a heterodontosaurid (cf. *Lycorhinus* sp.) from the Clarens Formation (Early Jurassic) of Lesotho: (a) medial view; (b) close-up of crowns 2 to 6; (c) line drawing of medial view. Abbreviations: can=caniniform; cing='cingulum' at base of crown; cr=crown. For line drawings light grey indicates eroded bone; dark grey indicates matrix. Scale bars=10 mm.

wear facets are present on several of the crowns and cover the apical portion of the labial crown surface. A prominent median ridge, mesially offset, is present on the lingual crown surface, as demonstrated on CT scans and suggested by visible tooth wear; there is also a less pronounced distal ridge on the lingual crown surface. Adjacent crowns contact one another apically, but are separated from one another by small gaps basally. The teeth are curved in mesiodistal view, being laterally concave (Fig. 3i); furthermore, the dentary tooth rows are laterally concave in dorsal view (Fig. 3j).

Several of the crowns (9 and 10 the right side and 8 and 9 on the left) have unusual fragments positioned immediately mesial and labial to their crown bases (Fig. 3e–f); a fifth fragment is positioned distal and labial to crown 9 on the left side and was probably associated with the missing tenth crown.

2.5. Taxonomic identity

Heterodontosaurus tucki is characterised by the possession of columnar maxillary and dentary teeth that lack a defined mesiodistal or labiolingual expansion above the root (Charig & Crompton 1974; Hopson 1975; Butler *et al.* 2008a; Norman *et al.* in press). The maxillary and dentary teeth are closely packed, forming a continuous dental battery, with small gaps between the teeth persisting only at the bases; moreover, they are transversely expanded relative to their mesiodistal length and exhibit heavier wear than either *Lycorhinus* or *Abrictosaurus*, with denticles rarely preserved except on the most mesial or distal dentary teeth (Butler *et al.* 2008a). Most of these dental characters are present in NM QR 1788, and this specimen can be confidently referred to *Heterodontosaurus tucki*.

3. Specimens NHMUK RU C68 and NHMUK RU C69

3.1. Systematic palaeontology

Heterodontosauridae Kuhn, 1966
Lycorhinus Haughton, 1924
cf. *Lycorhinus* sp.

3.2. Material

NHMUK RU C68, partial right dentary, including eleven partial crowns (Fig. 4). NHMUK RU C69, articulated but heavily damaged partial skull, with associated vertebra, femur and unidentified bone fragments (Figs 5–6).

3.3. Locality and horizon

Both specimens were found "on the 6,500′ cave sst. plateau lying north of the eastern block of Mabloka Mt. [Frances Mountain]", Lesotho (unpublished field catalogue of K. Kermack and F. Mussett, NHMUK). The specimens were collected by Prof. Kenneth Kermack and Mrs Frances Mussett as part of the 1968 University of London expedition. Although detailed stratigraphic data are not available, the field notes indicate that these specimens were probably collected from the Clarens Formation (='Cave Sandstone'). It is not clear how close to one another the specimens were collected. Although we have been unable to locate 'Mabloka' mountain on maps of southern Lesotho, it seems likely that the locality in question is 'Maboloka' (29.88°S, 27.35°E: Kitching & Raath 1984).
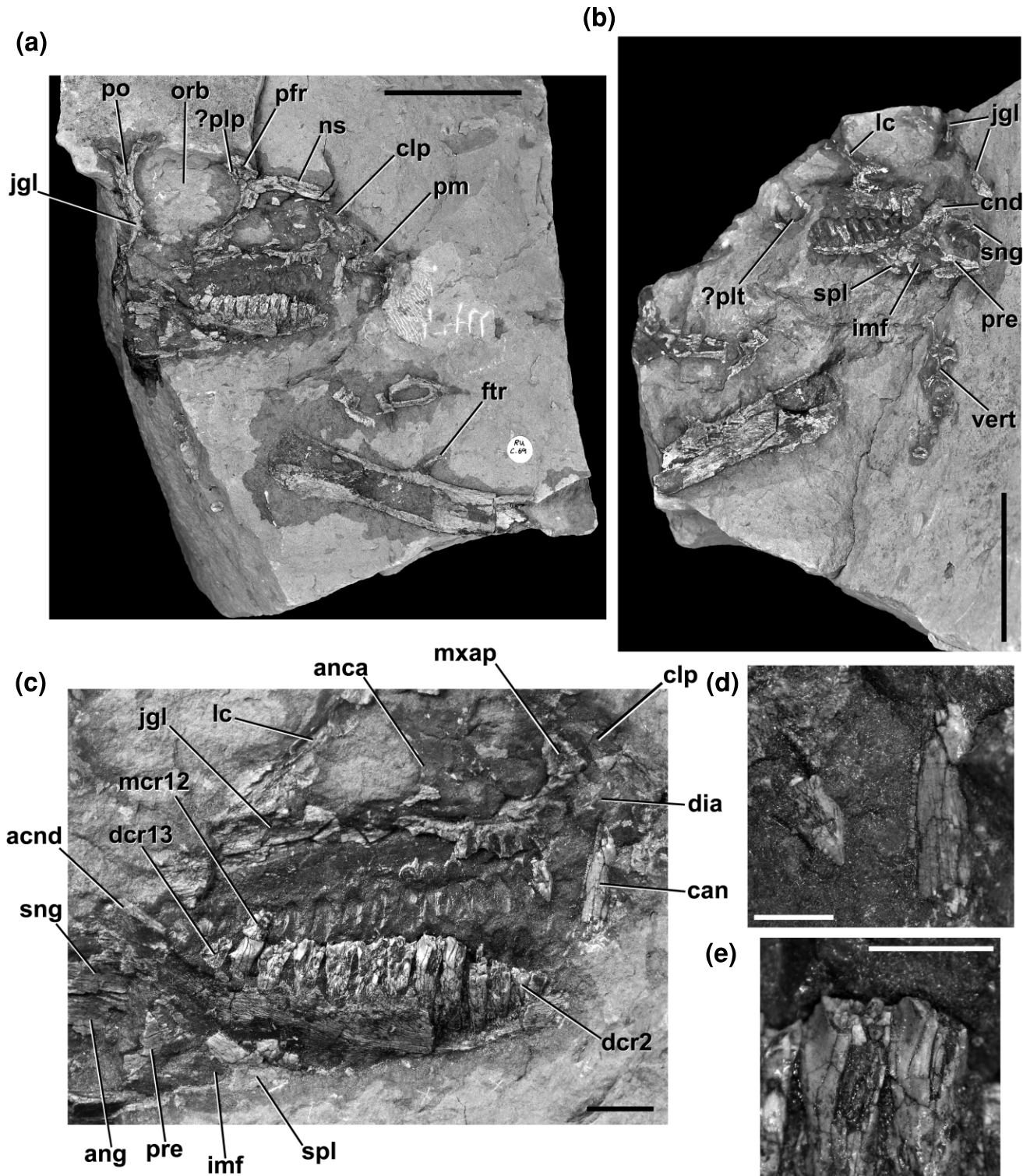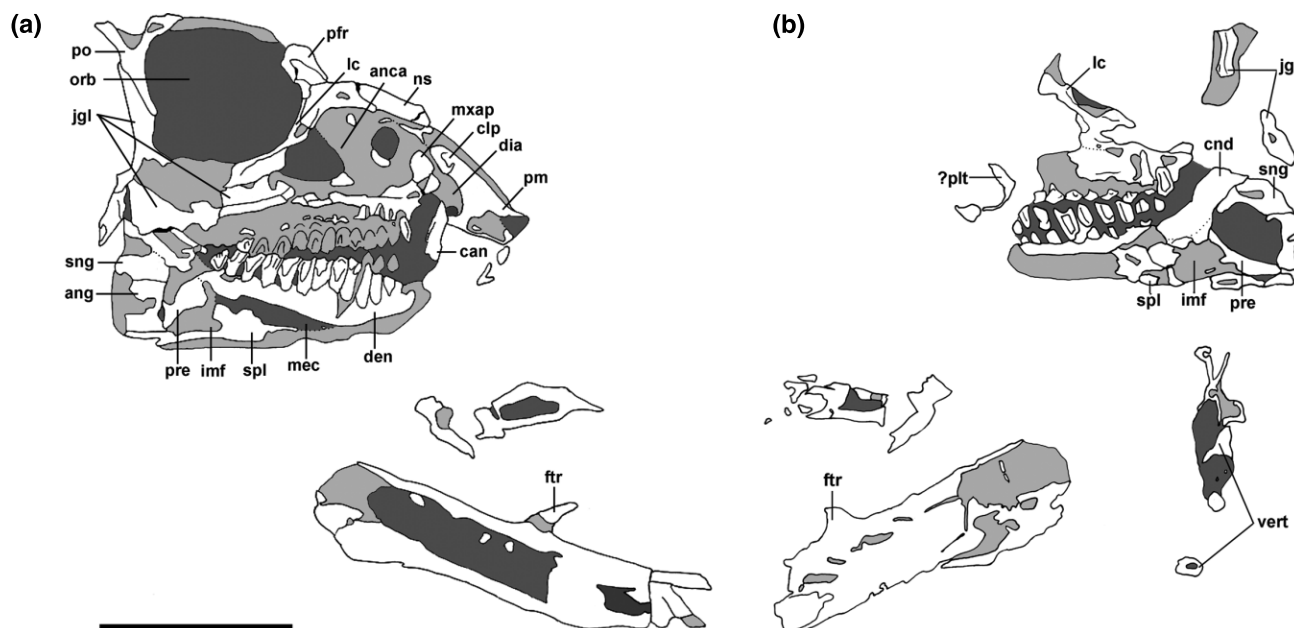
Figure 5 NHMUK RU C69, partial skull of a heterodontosaurid (cf. *Lycorhinus* sp.) from the Clarens Formation (Early Jurassic) of Lesotho: (a) main slab exposing the lateral parts of the bones of the left side of the skull, medial view; (b) counterpart containing the medial parts of the bones of the left side of the skull, lateral view; (c) close-up of the skull in the main slab; (d) left dentary caniniform and left maxillary crown 1, lingual view; (e) left dentary crowns 5 and 6, lingual view. Abbreviations: acnd = apex of coronoid process; anca = antorbital cavity; ang = angular; can = caniniform tooth; clp = caudolateral process of premaxilla; cnd = coronoid bone; dcr = dentary crown; dia = diastema; ftr = fourth trochanter; jgl = jugal; imf = internal mandibular fenestra; lc = lacrimal; mcr = maxillary crown; mxap = ascending process of maxilla; ns = nasal; orb = orbit; pfr = prefrontal; plp = palpebral; plt = palate; pm = premaxilla; po = postorbital; pre = prearticular; sng = surangular; spl = splenial; vert = vertebra. Scale bars = 50 mm (a–b); 10 mm (c); 5 mm (d–e).

3.4. Description

NHMUK RU C68 comprises a partial right dentary preserved within a block of reddish fine-grained sandstone. The block and attached fossil material have broken into three pieces: the majority of the dentary is preserved in the largest of the three blocks and is exposed in medial view (Fig. 4). Most of the medial surface of the dentary (and presumably the splenial), as well as the lingual parts and/or impressions of the dentary crowns are preserved on the two smaller blocks. The predentary and the anteriormost dentary are either missing or

Figure 6 NHMUK RU C69, partial skull of a heterodontosaurid (cf. *Lycorhinus* sp.): (a) line drawing of main slab exposing the lateral parts of the bones of the left side of the skull, medial view; (b) counterpart containing the medial parts of the bones of the left side of the skull, lateral view. Abbreviations: anca=antorbital cavity; ang=angular; can=caniniform tooth; clp=caudolateral process of premaxilla; cnd=coronoid bone; den=dentary; dia=diastema; ftr=fourth trochanter; jgl=jugal; imf=internal mandibular fenestra; lc=lacrimal; mec=Meckelian canal; mxap=ascending process of maxilla; ns=nasal; orb=orbit; pfr=prefrontal; plt=palate; pm=premaxilla; po=postorbital; pre=prearticular; sng=surangular; spl=splenial; vert=vertebra. For line drawings light grey indicates eroded bone, dark grey indicates matrix. Scale bar=50 mm.

unexposed, the ventral margin of the dentary is incomplete, and the dentary is broken caudally prior to the termination of the tooth row. Observable anatomical details of the dentary are limited because of damage to the specimen, with the exception that the dentary increases in dorsoventral height caudally. A caniniform tooth is present at the mesial end; distal to this tooth there are seven incompletely preserved crowns, two gaps indicating the presence of additional crowns, and one broken root at the distal end. The minimum tooth count for the dentary is 11. The specimen is from a relatively large individual – the length from the mesial margin of the caniniform to the distal margin of crown 11 is 52 mm, and the preserved cheek tooth row is approximately 39 mm in length.

Only the base of the dorsally-projecting caniniform is preserved. Its size cannot be estimated, nor can it be determined whether or not serrations were present on the mesial and distal margins. The caniniform tooth is separated by a diastema from the first post-caniniform crown. This diastema appears to be long compared to *Heterodontosaurus*, but it is possible that another small crown might have been present rostral to the first post-caniniform dentary tooth (crown 2); further mechanical preparation has not been carried out because of the fragility of the specimen in this region. Crowns 3–4 and 10 have relatively well-preserved lingual surfaces; crowns 5 and 7 are missing; crowns 6, 8 and 9 are broken in half through their vertical axes; and crown 11 is represented by a broken root. The chisel-shaped crowns are expanded mesiodistally (forming a 'neck') and labiolingually (forming a 'cingulum') above the root (Fig. 4b). Approximately five denticles are preserved (as impressions on the smaller block) along the mesial margin of crown 3, and appear to be restricted to the apical third of the crown. The mesial and distal margins of the crowns are thickened into low ridges that merge basally with the cingulum. A broad median swelling is present on the lingual surface and merges basally with the cingulum – this swelling is offset slightly mesially and curves gently distally towards its apical margin. On either side of this swelling the crown surface is

gently depressed. There are no preserved secondary ridges on the lingual crown surfaces. The labial surfaces are not exposed, and there is no available information on wear facets. The dentary crowns are imbricated, resulting in an *en echelon* arrangement so that the mesial margin of each crown medially overlaps the distal margin of the preceding crown. The crowns contact one another apically but gaps remain between adjacent crowns basally.

NHMUK RU C69 includes an articulated partial skull and some associated postcranial elements. The left side of the skull is exposed from the premaxilla to the postorbital/jugal bar (Figs 5–6). The skull is preserved as part and counterpart in two red sandstone blocks, and has been split vertically such that one block ('counterpart') contains the medial parts of the left maxilla, lacrimal, jugal, mandible and dentition (Figs 5b, 6b), and the other block ('main slab') contains the lateral parts of these elements as well as additional elements (e.g. postorbital, nasal, premaxilla; Figs 5a, c, 6a). The palate and right side of the skull may also be present in the specimen, but are not currently exposed. The blocks also contain a partial femur and a cross-section through a vertebra, as well as unidentified bone fragments (Figs 5a–b, 6). The preservation of the specimen limits the available anatomical data. The aim at present is to document, figure and briefly describe this specimen; future preparation or CT imaging may provide additional information.

Although parts of a premaxilla, including an elongate tapering caudolateral process (Fig. 5a, c: clp), are present, it is poorly preserved and the oral margin of the element is not exposed. The premaxilla appears to make a point contact with the lacrimal, but this cannot be confirmed with certainty, due to cracks within the encasing sediment in this area. An arched diastema (into which projects the dentary caniniform tooth) separates the premaxilla from the maxilla (Fig. 5c: dia). The approximate outline of an extensive external antorbital fenestra is visible, although its margins are damaged and the medial wall of the antorbital cavity is missing. Only fragments

and impressions of the maxilla are visible, but it has a short, rostrocaudally narrow ascending process that contacts the premaxilla. Fourteen maxillary teeth appear to be preserved; most of these teeth are represented only by impressions (for exceptions, see below). The lacrimal is shaped like an inverted 'L', and forms the dorsal and caudal margins of the external antorbital fenestra (Fig. 5c: lc). It contacts the jugal ventrally. Fragments of the prefrontal, nasal and, possibly, the palpebral are present, but are not anatomically informative in their current state of preparation (Fig. 5a). The rostral process of the jugal is present and visible in medial view, but the details of its contacts with the lacrimal and maxilla are unclear. The elongate tapering dorsal process of the jugal forms the caudoventral margin of the sub-circular orbit, and is overlapped laterally by the descending process of the postorbital. The caudal process of the jugal is dorsoventrally expanded, but only a cross-section of its base is visible. Because the lateral surface of the jugal is not exposed, it is impossible to determine if a jugal boss is present or absent.

Elements of the lower jaw that are exposed include the dentary (in medial view), parts of the splenial and coronoid (mostly preserved in lateral view on the counterslab), and fragments of the surangular, angular and prearticular (Fig. 5a–c). The dentary is poorly exposed, but is relatively deep, rising to form the rostral margin of the coronoid eminence (Fig. 5c: acnd). The sheet-like splenial can be clearly distinguished overlying the caudoventral part of the dentary; its caudal margin is notched for the internal mandibular fenestra (Fig. 5c: imf). The elongate strap-like coronoid extends immediately ventromedial to the tooth row, along the entire length of the preserved tooth row (Fig. 5b: cnd). Caudally it is expanded and lobe-like, forming the apex of the coronoid process. The prearticular forms the caudal margin of the internal mandibular fenestra (Fig. 5c: pre), but other details of its anatomy are unclear. The surangular and angular are poorly preserved, and no particular anatomical details can be discerned.

Only parts of maxillary crowns 1 and 12–14 are preserved, the latter three crowns being heavily damaged. Crown 1 is smaller than more distal crowns, and has a sharply pointed apex (Fig. 5d). Denticles are visible along the distal surface; the mesial surface is not completely exposed. The impressions of the remaining crowns indicate that they were chisel-shaped and contacted each other apically. The dentary contains 13 crowns, including a caniniform tooth rostrally, but all are badly damaged. The length of the 'cheek tooth' row is 46 mm. The caniniform tooth is elongate and tapers to a sharp tip (Fig. 5d). Fine serrations are present along its caudal margin, with approximately three per millimetre. The serrations are square in profile. The caniniform tooth is separated from crown 2 by a diastema, although its exact length cannot be determined because the base of the tooth is not exposed. Crowns 2–13 have elongate roots (partially exposed by breakage of the dentary) that curve labially, such that their lingual surface is apico-basally convex. The crowns are gently expanded labiolingually and mesiodistally above their roots, with a weak basal cingulum (Fig. 5e). The distal margin of the crown forms a distinct ridge that merges with the basal cingulum. Although the lingual crown surfaces are badly damaged, a discrete primary ridge does not seem to be well-developed, although a median eminence is present. The crowns are imbricated and separated from one another by small gaps at their bases.

The proximal two thirds of the left femur is preserved. The femur is split vertically (lengthwise) revealing a cross-section of the central medullary cavity bounded on either side by cortical bone (Fig. 5a–b). The lateral margin of the proximal end is expanded craniocaudally relative to the shaft; the cranial and greater/dorsolateral trochanters cannot be clearly identified.

The shaft is bowed cranially along its length, and an elongate and very slender ('rod-like') pendant fourth trochanter is present, similar to *Heterodontosaurus* (SAM-PK-K1332).

3.5. Taxonomic identity

The caniniform tooth and the chisel-shaped crowns unambiguously indicate that NHMUK RU C68 and NHMUK RU C69 represent heterodontosaurids. Assessing the affinities of both specimens within Heterodontosauridae is complicated by incompleteness and poor preservation. The dentary crowns of *Lycorhinus* (SAM-PK-3606: lingual crown surfaces described by Haughton 1924), NHMUK RU A100 (Thulborn 1970) and *Heterodontosaurus* (SAM-PK-K1332) have lingual surfaces with mesial and distal ridges and a weak median eminence that is slightly offset mesially. NHMUK RU C68 and NHMUK RU C69 appear to be more similar to *Lycorhinus* and NHM RU A100 in possessing weak but distinct basal cingula, which are absent in *Heterodontosaurus*, and in lacking secondary ridges, which occur on some dentary crowns of *Heterodontosaurus*. The lingual surfaces of the dentary crowns are not exposed in the only known specimen of *Abrictosaurus* (NHMUK RU B54), preventing comparisons. Comparisons to *Lanasaurus* are limited by the absence of the maxilla in NHMUK RU C68 and the scarcity of observable anatomical data for the maxilla of NHMUK RU C69. On the basis of the similarities between NHMUK RU C69 and *Lycorhinus*, this specimen is provisionally referred to cf. *Lycorhinus* sp. If correct, this referral substantially increases the amount of data for *Lycorhinus*, which was previously known only from impressions of the lower jaw and a fragment of the caniniform tooth, and shows that the general form of its skull was similar to that of *Heterodontosaurus*. NHMUK RU C68 most closely resembles *Lycorhinus*, based on the presence of weak basal cingula and absence of secondary ridges on the dentary crowns. However, the curved median ridge and denticles of NHMUK RU C68 are not preserved in NHMUK RU C69, and only impressions of the buccal surfaces of the dentary teeth are preserved in the type of *Lycorhinus*. The absence of the curved median ridge in NHMUK RU C69 and *Lycorhinus* may be preservational, and NHMUK RU C68 is provisionally referred to cf. *Lycorhinus* sp. although it is possible that future discoveries, further preparation of other heterodontosaurid specimens or better characterisation of the taxon *Lycorhinus* may invalidate this referral.

4. Specimen NHMUK R14161

4.1. Systematic palaeontology

Heterodontosauridae Kuhn, 1966
Heterodontosauridae *incertae sedis*

4.2. Material

NHMUK R14161, partial dentaries, maxillae and left lacrimal, with fragmentary dentition and fragments of other cranial bones (Fig. 7).

4.3. Locality and horizon

The only locality data currently available are 'Whitehill', Qacha's Nek District, Lesotho. Whitehill (or White Hill) is a small settlement on the Orange, or Senqu, River (30.05°S, 28.47°E, coordinates from Google Earth), located within a few kilometres of the type locality of *Abrictosaurus consors* (see Thulborn 1974, fig. 1). It is unclear what stratigraphic level the
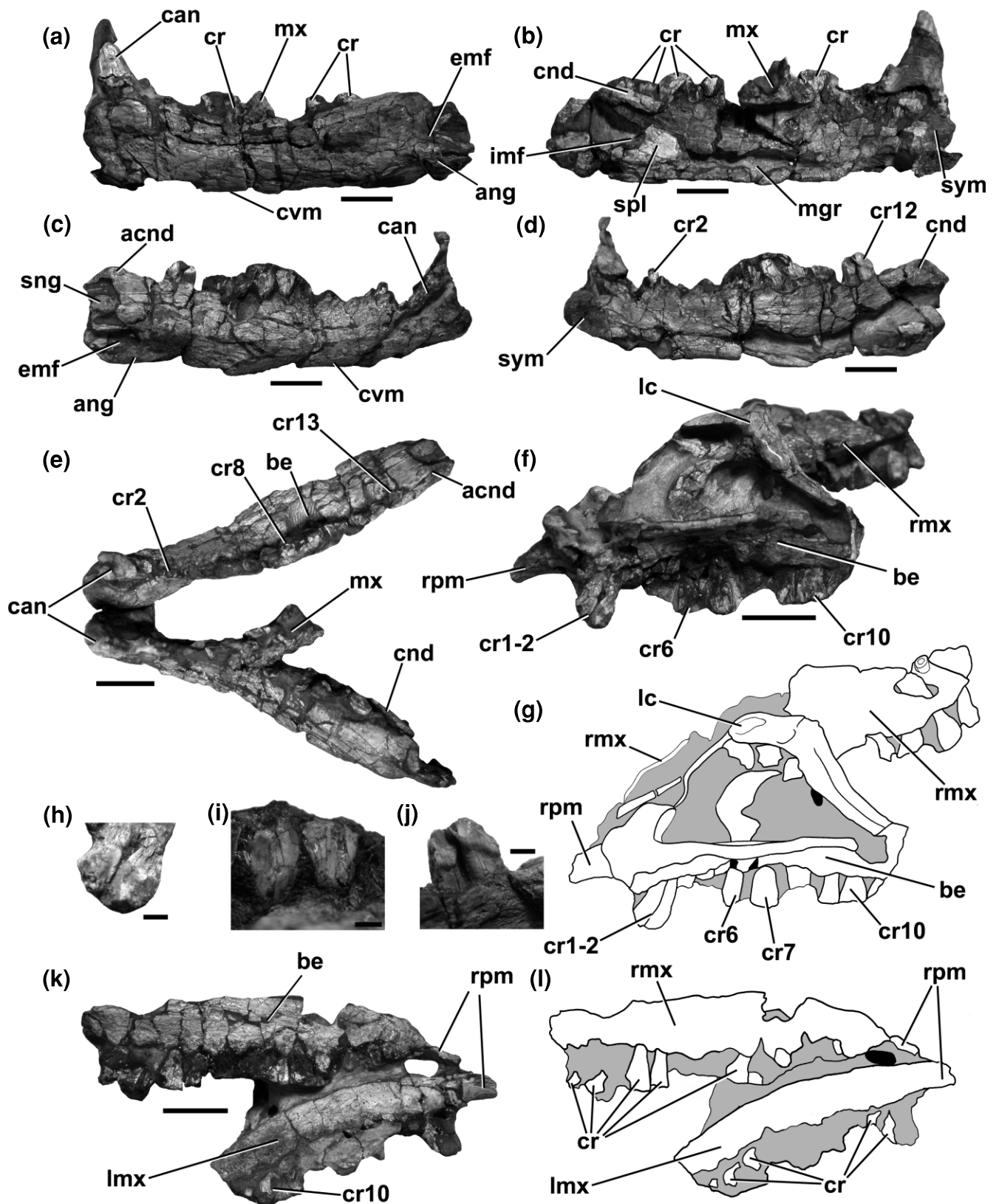
Figure 7   NHMUK R14161, partial skull of a heterodontosaurid (Heterodontosauridae *incertae sedis*) from the ?upper 'Stormberg Group' of Lesotho: (a) left dentary, lateral view; (b) left dentary, medial view; (c) right dentary, lateral view; (d) right dentary, medial view; (e) both dentaries in articulation, dorsal view; (f) left maxilla and lacrimal, lateral view; (g) line drawing of left maxilla an lacrimal, lateral view; (h) left maxillary crowns 1 and 2, labial view; (i) right mid-dentary crowns, labial view; (j) right dentary crowns 11 and 12, lingual view; (k) right maxilla in lateral view, left maxilla in medial view; (l) line drawing of right maxilla in lateral view, left maxilla in medial view. Abbreviations: acnd=apex of coronoid process; ang=angular; be=buccal emargination; can=caniniform; cnd=coronoid bone; cr=crowns; cvm=complete ventral margin of dentary; emf=external mandibular fenestra; imf=internal mandibular fenestra; lc=lacrimal; lmx=left maxilla; mgr=mandibular groove; mx=fragment of the caudal end of the left maxilla; rmx=right maxilla; rpm=rostral process of maxilla; spl=splenial; sng=fragments of the surangular; sym=symphysial surface. For line drawings light grey indicates eroded bone or sediment. Scale bars=10 mm (a–g, k–l); 2 mm (h–j).

specimen is from, although it is most likely to be the Lower Jurassic upper 'Stormberg Group', either the upper Elliot or Clarens Formation (because these stratigraphic levels have apparently yielded all previous specimens of southern African heterodontosaurids). Unpublished correspondence and archival notes in the NHMUK indicate that the specimen was collected during February 1962 by Prof. K. Kermack as part of a 1961–1962 field expedition to South Africa and Lesotho led by Prof. A. W. Crompton (e.g. Crompton & Charig 1962).

4.4. Description

Prior to preparation, the specimen included the dentaries in near articulation. No other cranial elements were visible. However, preparation revealed the additional presence of both maxillae and a left lacrimal, which were all displaced rostrally relative to the articulated mandibles. The specimen is now preserved in three pieces: the left mandible (composed largely of the dentary, with fragments of the splenial, coronoid and angular) and a fragment of the caudal end of the left maxilla (Fig. 7a–b, e); the right mandible (again, comprising most of the dentary with fragments of the coronoid, surangular and angular; (Fig. 7c–e); and the maxillae and left lacrimal (Fig. 7f–g, k–l). The bones are badly cracked and the teeth are unfortunately heavily damaged.

Both maxillae are present, although each is damaged and lacks its caudal and dorsal parts. The tooth rows are inset, forming well-developed buccal emarginations delineated by a ridge dorsally (Fig. 7f–g, k–l: be); the development of the emargination and ridges is similar to that of *Heterodontosaurus* (e.g. SAM-PK-K1332). This ridge forms the ventral margin of the external antorbital fenestra (bounding the antorbital cavity), which is large and subtriangular. Although parts of the medial wall of the antorbital cavity are present, they are incomplete; so it is not possible to determine the size of the internal antorbital fenestra or the presence/absence of an accessory fenestra. Rostral to the tooth row there is a rostral process that presumably formed the medial wall of a recessed diastema between the premaxilla and the maxilla (Fig. 7f–l: rpm). The medial surface of the maxilla, above the tooth row, lacks indications of replacement foramina or a groove for the dental lamina.

The lacrimal forms the dorsal and caudal margins of the external antorbital fenestra (Fig. 7f–g: lc). The medial lamina of the lacrimal is not preserved, and the presence or absence of a groove on its lateral surface and the position of the lacrimal foramen cannot be confirmed. There appears to be a distinct slot in the rostral process of the lacrimal, lodged within which is a splinter of either the ascending process of the maxilla or the caudolateral process of the premaxilla.

Parts of 11 crowns are present in the preserved portion of the left maxilla, and 12 crowns are preserved in the right maxilla (both maxillae have empty alveoli, indicating a minimum tooth count of 13). The tooth rows seem to be slightly curved inward (laterally concave) along their length. All of the maxillary crowns are badly damaged and details are limited. The crowns are expanded slightly labiolingually above the root, and each has a weak basal 'cingulum'. The first two crowns (preserved on the left side) are rather spatulate in shape (Fig. 7h), with coarse denticles restricted to the apical third of the crown and present on mesial and distal margins. More distal crowns are chisel-shaped and denticles are not well-preserved. The maxillary teeth appear to have broad median eminences (rather than a distinct ridge) on the lingual and labial surfaces. This eminence is flanked by mesial and distal ridges (clearly developed on the lingual surface) that merge with the weak basal 'cingulum'. Poor preservation makes it impossible to identify wear facets or accurately assess the

degree of packing of adjacent crowns, although spaces are clearly present between the crowns at their bases.

The dentary is elongate and dorsoventrally shallow in lateral view (Fig. 7a, c), although it is slightly expanded dorsoventrally at its rostral end (beneath the caniniform tooth). Caudally, the dentary rises at a shallow angle to form the rostral margin of a low coronoid eminence that does not extend higher than the apices of the dentary crowns (Fig. 7c: acnd). The ventral margin of the dentary is nearly straight in lateral view. The dorsoventral height of the dentary beneath the apex of the coronoid eminence is <150% of its height at the midlength of the tooth row; by contrast this value is >200% in *Abrictosaurus* (NHMUK RU B54) and *Heterodontosaurus* (SAM-PK-K1332).

The lateral surface of the dentary is strongly convex dorsoventrally and the tooth row is strongly inset, forming a deep buccal emargination (Fig. 7e: be). The depth of this emargination increases caudally, and is greatest lateral to the last few dentary crowns. At its rostral end, beneath the caniniform tooth, the ventral margin of the dentary is in-turned and thickened to form a symphysial surface that is similar to the 'spout-shaped' symphysis seen in other ornithischians (Fig. 7e). The predentary is not preserved and no facets for the predentary are evident on the rostral ends of the dentaries, although this area is poorly preserved. In dorsal view, the dentary tooth row is curved inward (laterally concave) along its length; when the dentaries are held in articulation they diverge caudally from one another at an angle of 55–60° (Fig. 7e).

Medially, the Meckelian groove is present along the ventral part of the dentary. The apparent depth of this groove appears to have been exaggerated by breakage of the bone surface. There is no evidence of replacement foramina or a groove for the dental lamina medial to the tooth row. A fragment of the left splenial and fragments of both left and right coronoids are attached to the caudal ends of the dentaries (Fig. 7b, d). The fragment of the left splenial is positioned adjacent to the adductor fossa and is emarginated by the smoothly curved margin of the internal mandibular fenestra (Fig. 7b: imf). The coronoid forms the medial surface of the apex of the coronoid process (it does not extend dorsal to the dentary), and extends rostrally beneath the tooth row as a strap-like element (Fig. 7b, d: cnd). Because only short fragments of the coronoid are preserved, it is not possible to assess the length of this element.

An elliptical external mandibular fenestra is present, most clearly visible on the right side (Fig. 7a, c: emf). The dentary forms its rostral margin. The ventral margin of the fenestra is formed by the angular, fragments of which are preserved; it is unclear whether the dorsal margin of the fenestra is formed by the angular (as in *Heterodontosaurus*: SAM-PK-K1332) or by the surangular (as in most other ornithischians).

A large, poorly preserved and procumbent caniniform tooth is present at the rostral end of both dentaries. Poor preservation makes it impossible to assess the presence or absence of serrations on the caniniform tooth. Caudal to the caniniform tooth there appear to be 12 teeth (crowns 2–13, some of which are missing and represented only by roots or alveoli), based on the complete tooth row of the right dentary. This right 'cheek tooth' row is 46 mm in length. All crowns are poorly preserved, yielding few observable details. Crown 2 is separated by a short diastema (the approximate width of a single crown) from the caniniform tooth and is smaller than subsequent crowns. The cheek crowns are chisel-shaped (Fig. 7i) and weak cingula are present, at least on the lingual surfaces (Fig. 7j). Because of poor preservation, it is not possible to identity wear facets. The tip of a possible unerupted replacement crown is situated basolingually to right crown 8, and the last crown present on the left side also appears to be unerupted.

4.5. Taxonomic identity

NHMUK R14161 cannot be clearly assigned to any existing heterodontosaurid taxon. It is distinguished from *Heterodontosaurus* and *Abrictosaurus* by a low coronoid eminence and the presence of basal 'cingula' on the maxillary and dentary crowns. It is further distinguished from *Heterodontosaurus* by the absence of strongly developed primary, mesial and distal ridges on the labial surfaces of the maxillary crowns; the strongly divergent mandibles also suggest that the skull of NHMUK R14161 was wider than that of *Heterodontosaurus*. NHMUK R14161 is further distinguished from *Abrictosaurus* (NHMUK RU B54) by the inwardly curved maxillary and dentary tooth rows (although the apparent absence of this feature in NHMUK RU B54 might reflect taphonomic compression of the skull), the well-developed buccal emargination on the maxilla, and the presence of a dentary caniniform. Comparisons to *Lycorhinus* are difficult (because of the highly fragmentary nature of the *Lycorhinus* holotype specimen, SAM-PK 3606); the dentary caniniform teeth of both specimens are identical in size, but the dentary of *Lycorhinus* is deeper than that of NHMUK R14161. Furthermore, the maximum depth of the dentary beneath the tooth row is 40% of the length of the 'cheek teeth' row in SAM-PK 3606 and approximately 30% in NHMUK R14161, although it should be noted that the tooth row might be incomplete in SAM-PK 3606. Overall, it appears that the dentary of NMHUK R14161 was more slender than that of the *Lycorhinus* type, despite the specimens being of similar size, and despite the missing ventral margin of the dentary and the coronoid eminence of SAM-PK 3606. As the dentary appears to become deeper and more robust during ontogeny in *Heterodontosaurus* (see Discussion, section 5), it is not expected that two similarly-sized *Lycorhinus* individuals would exhibit such different mandibular proportions. NHMUK R14161 appears to differ from *Lanasaurus* (and from the enigmatic specimen NHMUK RU A100) in lacking sharply-developed distal ridges on the labial surface of the maxillary crowns (a possible autapomorphy of *Lanasaurus*: Norman *et al.* in press), although it is emphasised that the poor preservation of the maxillary dentition of NHMUK R14161 makes it impossible for this difference to be confirmed with certainty.

Because NHMUK R14161 cannot be clearly referred to any existing heterodontosaurid taxon, it may represent a new species that is characterised primarily by its shallow dentary and coronoid eminence. The dentition shows some similarities (particularly the presence of basal 'cingula') to *Lanasaurus* and *Lycorhinus*, but comparisons to these taxa are particularly difficult. NHMUK R14161 and NHMUK RU C69 (described above as cf. *Lycorhinus* sp.) clearly differ substantially in the depth of the coracoid eminence, indicating that at least two species must be present within the known *Lycorhinus*/*Lanasaurus*-like material. Given the fragmentary nature of NHMUK R14161, the difficulties of comparisons to *Lanasaurus* and *Lycorhinus* and the already murky taxonomy of the 'Stormberg' heterodontosaurids, the present authors refrain from erecting a new species name for this specimen, pending the discovery of more complete material and further preparation of key specimens (notably NHMUK RU A100).

5. Discussion

5.1. Maximum body size and cranial ontogeny in *Heterodontosaurus*

The right dentary 'cheek' tooth row (i.e. crowns 2–12) of NM QR 1788 measures 56·8 mm in length. By comparison, the dentary 'cheek' tooth row of SAM-PK-K1332, the largest specimen previously referred to *Heterodontosaurus*, measures 32·5 mm. Based upon a basal skull length (premaxilla–quadrate) of 95 mm for SAM-PK-K1332, a basal skull length of 166 mm is estimated for NM QR 1788. SAM-PK-K1332 has an approximate body length of 1 metre (Santa Luca 1980). An isometric scaling relationship would give a total body length of 1·75 metres for NM QR 1788, making this the largest heterodontosaurid specimen yet described. Henderson (*in* Butler *et al.* 2010: electronic supplementary material) estimated a body mass of 2·59 kg for *Heterodontosaurus tucki*, based upon a body length of 1·12 metres, while Seebacher (2001) estimated a mass of 1·8 kg based upon a body length of 1 metre. Scaling these estimates to a body length of 1·75 metres suggests a body mass for NM QR 1788 of just under 10 kg, four to five times heavier than previously known specimens of *Heterodontosaurus tucki*. Furthermore, NM QR 1788 is over three times longer than the smallest known individual of *Heterodontosaurus tucki* (SAM-PK-K10487; Butler *et al.* 2008a; Fig. 8). Extensive skeletal fusion (Santa Luca 1980), including complete closure of all neurocentral sutures, suggests that SAM-PK-K1332 is an adult specimen (although see Irmis 2007). The much larger body size of NM QR 1788 might demonstrate that substantial growth occurred after individuals reached maturity (and following closure of neurocentral sutures). However, it might also reflect sexual dimorphism, temporal, geographic or intraspecific variation, or indicate that two closely related species of *Heterodontosaurus* of different sizes inhabited the environments of the upper 'Stormberg'. At the moment, it is not possible to distinguish between these alternatives.

SAM-PK-K1332 has a complete dentary tooth count of 11 (including the caniniform) while the larger NM QR 1788 possesses 12 dentary teeth. Seven dentary teeth are preserved in the juvenile specimen SAM-PK-K10487 (Butler *et al.* 2008a). Addition of teeth during ontogeny is common among extant reptiles, and usually occurs by the eruption of new teeth at the distal end of the tooth row (Cooper & Poole 1973; Kline & Cullum 1984). Although tooth count increases with age, dental morphology is nearly identical in all described specimens of *Heterodontosaurus tucki*.

NM QR 1788 provides information on allometric changes during growth in *Heterodontosaurus tucki*. The dorsoventral height of the right dentary below crown 6 is 34% of the length of the tooth row in SAM-PK-K1332; by comparison, the height of the dentary below the crown 6 is 44% of the length of the tooth row in NM QR 1788. Thus, the preserved mandible of NMQR 1788 is proportionately deeper than that of SAM-PK-K1332. The coronoid eminence appears taller and more pronounced in NM QR 1788 than in either the holotype (SAM-PK-K337) or SAM-PK-K1332; unfortunately, both the coronoid eminence and the dentary below it are incomplete in the new specimen, making quantitative comparisons difficult.

The dentition of *Heterodontosaurus* indicates that it ate primarily plants, although some degree of omnivory may have occurred (Barrett 1998, 2000; Butler *et al.* 2008a; Porro 2009); furthermore, emarginated tooth rows (implying the presence of fleshy cheeks) and heavy tooth wear suggest *Heterodontosaurus* processed its food by chewing (Thulborn 1978; Hopson 1980; Crompton & Attridge 1986; Galton 1986; Barrett 1998; Porro 2007, 2009). Larger individuals would be capable of generating greater absolute muscle force, and allometric changes in mandibular morphology, such as increased relative height of the coronoid eminence, may have further increased mechanical advantage and bite force in older and larger animals. The greater relative depth of the mandible in larger specimens of *Heterodontosaurus* may reflect the need to counter increased
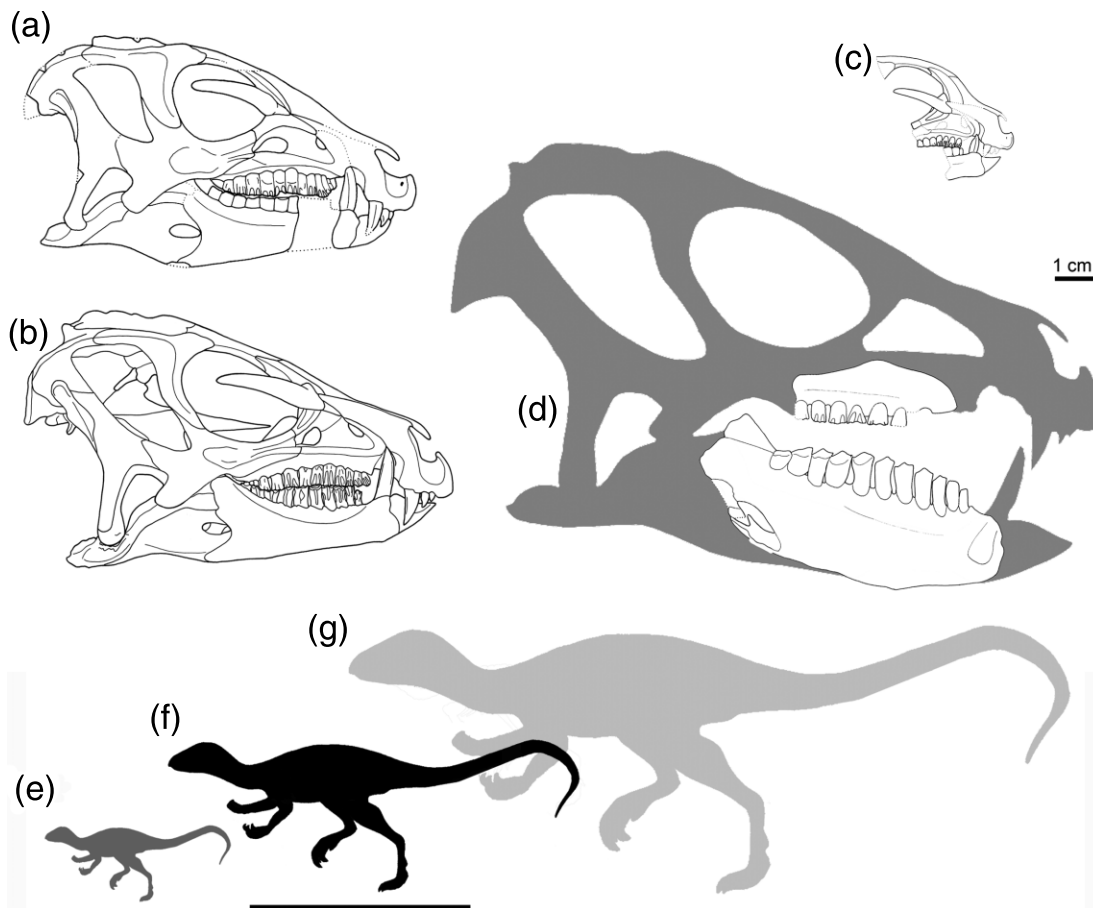
Figure 8 Skull and body reconstructions for known specimens of *Heterodontosaurus*, illustrating size variation and cranial ontogeny in the genus: (a) skull reconstruction of SAM-PK-K337 (holotype); (b) skull reconstruction of SAM-PK-K1332 (Santa Luca *et al.* 1976; Santa Luca 1980); (c) skull reconstruction of SAM-PK-K10487 (juvenile: Butler *et al.* 2008a); (d) skull reconstruction of NM QR 1788 (this paper); (e) silhouette of SAM-PK-K10487, extrapolated from SAM-PK-K1332; (f) silhouette of SAM-PK-K1332, based upon nearly complete, articulated skeleton; (g) silhouette of NM QR 1788, extrapolated from SAM-PK-K1332. Scale bars = 10 mm (a–d); 50 cm (e–g).

shear and bending within the lower jaw due to these higher bite forces (Hylander 1984).

5.2. Tooth replacement in heterodontosaurids

NM QR 1788 exhibits unusual fragments labial and mesial to several of the dentary teeth (Fig. 3e–f). Micro-CT scans reveal these fragments to be conical and tapering ventrally, resembling shallow tooth roots that lack crowns. Replacement teeth in reptiles, including the heterodontosaurid *Fruitadens* (Butler *et al.* 2010), are typically found lingual and distal to corresponding functional teeth (Cooper 1966; Edmund 1969). The replacement tooth moves upwards, laterally and rostrally: as replacement proceeds, the root of the functional tooth is resorbed and the old worn crown is finally lost (Edmund 1969). The shape and position of the fragments suggests these are the unresorbed roots of shed tooth crowns. Tooth replacement in *Heterodontosaurus* appears to have been sporadic and slow compared to other herbivorous dinosaurs, including other heterodontosaurids (Butler *et al.* 2008a; Norman *et al.* in press); thus, it is possible that complete resorption of tooth roots was correspondingly slow. Nonetheless, such unresorbed root fragments have not been observed in CT scans of other ornithischian dinosaurs, or in extant reptiles (LBP pers. obs.).

Replacement teeth appear to be visible in NHMUK R14161, and have also been documented recently in *Fruitadens* (Butler *et al.* 2010) and several other heterodontosaurid specimens (Norman *et al.* in press; LBP and RJB unpublished data). Continuing examination of heterodontosaurid speci-

mens thus demonstrates that replacement teeth are known in most members of the clade (*contra* Thulborn 1974, 1978).

5.3. Diversity of the southern African heterodontosaurids, and implications for the early ornithischian dinosaur radiation

Although heterodontosaurids were widely distributed both geographically and temporally, current knowledge of their fossil record suggests that they were most abundant and diverse in the Early Jurassic of southern Africa. At least four (*Heterodontosaurus*, *Abrictosaurus*, *Lycorhinus* and at least one other species in the *Lycorhinus*/*Lanasaurus*-like material, see above), and possibly five or more (depending on the taxonomic status of *Lanasaurus*, NHM RU A100, and the undescribed SAM-PK-K10488), heterodontosaurids inhabited the Elliot and Clarens Formations. Current stratigraphic data are insufficient to determine how many of these taxa were contemporaneous. With the exception of *Heterodontosaurus* and the partially prepared *Abrictosaurus*, these taxa are known primarily from cranial material, and all are currently primarily distinguished by differences in cranial and dental morphology, tooth wear and tooth replacement rate. Steep wear facets suggest that *Abrictosaurus* and *Lanasaurus* used orthal shearing, while the shallower wear facets of *Lycorhinus* and *Heterodontosaurus* suggest these animals used more complex jaw movements to process food (Hopson 1980; Weishampel 1984; Crompton & Attridge 1986; Barrett 1998; Porro 2009).

In addition to heterodontosaurids, there are at least two small-bodied 'fabrosaurid' (basal genasaurian) ornithischians that come from the upper Elliot and Clarens Formations (Galton 1978; Butler 2005) and are known from more than 40 specimens (RJB unpublished data). Knoll *et al.* (2010) suggested that the upper Elliot Formation was deposited over a short time interval, and used this supposition as partial support for their argument that only a single 'fabrosaurid' taxon (*Lesothosaurus*) is present in this unit. However, the length of time over which the Elliot Formation was deposited is completely unknown due to poor stratigraphic control, and the high diversity of heterodontosaurids demonstrates that there is no *a priori* reason to assume that the diversity of other early small-bodied ornithischians was low. Compared to heterodontosaurids, these 'fabrosaurids' exhibit more gracile skulls and lightly-worn, leaf-shaped teeth that were more rapidly replaced, and probably utilised orthal puncture-crushing or shearing to process food (Thulborn 1971; Sereno 1991; Barrett 1998; Norman *et al.* 2004b).

In contrast to most other Lower and Middle Jurassic localities, the number of small ornithischian species found within the Elliot and Clarens formations is high (at least six, and possibly greater), suggesting a short-lived adaptive radiation of small-bodied basal ornithischians. The variability in cranial and dental morphology, tooth replacement rates and inferred jaw mechanisms may have been important in niche partitioning among the 'Stormberg' ornithischians; for example, *Heterodontosaurus* may have fed upon tough, fibrous vegetation, while *Abrictosaurus* and 'fabrosaurids' selected more nutritious, less abrasive plants or engaged more frequently in omnivory.

There is a striking difference between the ornithischian fauna of the lower Elliot Formation (presumed to be Upper Triassic in age), which has yielded only a single specimen (Butler *et al.* 2007), and the relatively abundant (more than 60 specimens known) and diverse (at least six species) fauna of the Lower Jurassic upper Elliot and Clarens formations. This difference between Late Triassic and Early Jurassic ornithischian faunas is also documented elsewhere globally (for example, ornithischians are apparently absent in Late Triassic North America, but represented by abundant material in the Lower Jurassic Kayenta Formation of Arizona; Tykoski 2005; Irmis *et al.* 2007) and has been taken as evidence for a global radiation of ornithischians following the end-Triassic extinction events (e.g. Butler *et al.* 2007). Traditionally the entire 'Stormberg' sequence was considered Late Triassic in age, but the upper Elliot and Clarens were re-dated as Lower Jurassic based upon biostratigraphic arguments (see Olsen & Galton 1984). The position of these units within the Lower Jurassic remains poorly constrained. Recently, Smith *et al.* (2009) have suggested, on the basis of new ichnological data, that the entire upper Elliot Formation could be Late Triassic in age. These differing interpretations of the position of the Triassic/Jurassic boundary impact dramatically upon our understanding of the early ornithischian radiation; a fundamental requirement for establishing the reality and timing of this inferred radiation is better constrained dating for the 'Stormberg Group'.

6. Acknowledgements

7. References

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