A new specimen of *Dicynodon traquairi* (Newton) (Synapsida: Anomodontia) from the Late Permian (Tartarian) of northern Scotland

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A recently discovered natural mould of a complete, almost undistorted, skull and lower jaw of a dicynodont (*c.* 237 mm overall length), in a block of Upper Permian sandstone (= Dicynodon Assemblage Zone: Hopeman Sandstone Formation) from Clashach Quarry, Hopeman, Morayshire, is described using novel techniques, including Computed Tomography scanning (CT), Magnetic Resonance Imaging (MRI) and rapid-prototype modelling. It is assigned to the taxon *Dicynodon traquairi* (Newton, 1893). When compared with *Dicynodon lacerticeps* Owen, 1845, it is distinguished principally by having the pineal opening sunk deeply between the diverging parietals, subparallel pterygoid rami narrowly separated, with no transverse flanges, and in addition, a deeply grooved lower jaw symphysis. The southern African fauna lived on river flats in a higher (southern) palaeolatitude than the possibly desert-dwelling Scottish species. The Hopeman Sandstone Formation is of the same age as the better-known Cutties Hillock Sandstone Formation, whose fauna is briefly discussed and reviewed.

Keywords: *Dicynodon traquairi,* Late Permian, Hopeman Sandstone Formation, Computed Tomography scanning, Magnetic Resonance Imaging, rapid prototyping.

INTRODUCTION

During the mid- and late 1990s the National Museums of Scotland undertook a major building and upgrade programme of their flagship building in Chambers Street, Edinburgh. Part of the architectural design was a stone-faced façade to the new extensions, which was to be sourced in the Permo-Triassic quarries (including Hopeman) of Morayshire (Anon 2003), in the north of Scotland (Fig. 1a,b) These (especially the Quarry Wood complex of quarries) had yielded a suite of fossils reptiles and trackways of Late Permian age, in the 19th century (Newton 1893; Benton & Spencer 1995), particularly from Cutties Hillock, near Elgin. These fossils occurred as natural moulds in the rock, and yielded at least three dicynodont species and a pareiasaur (Table 1) (Newton 1893; King 1988; Walker 1973, Benton & Spencer 1995). Hopeman Quarry had previously yielded only trackways (Benton & Spencer 1995). Walker (1973) had assumed a Late Permian-Early Triassic age for both Hopeman and the Cutties Hillock sites, based on the supposedly advanced status of the tetrapod faunas of the latter. Currently they are both believed to be Late Permian in age (see below: and King *et al.* (2005) for summary statements).

In 1997, on splitting a large block of sandstone, the workers at Moray Stone Cutters of Clashach Quarry, near Hopeman, Morayshire (National Grid Reference NJ 163702) observed a cavity broaching the broken surface of the block (Fig. 2). The rock at Hopeman is of a lithology and age very similar to the Cutties Hillock locality (Watson & Hickling 1914; Peacock *et al.* 1968; Walker 1973; Benton & Walker 1985) and C.A. Hopkins had instigated a search programme for

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possible fossil material appearing at Hopeman (Hopkins 1999). Realising the importance of the discovery, the two-part sandstone block was sent to the Hunterian Museum, University of Glasgow. The identity of the mould in the rock was resolved by means of CT (computed tomography) and MRI (magnetic resonance imaging) scanning techniques. Preliminary reports have appeared (Clark 1999; Clark *et al.* 2004; Hopkins1999; Hopkins & Clark 2000), and this is now the first detailed account of the identity of the mouldic fossil. We assign the fossil skull to *Dicynodon traquairi* (Newton, 1893), a form hitherto known only from the Quarry Wood, Cutties Hillock, locality (NGR NJ 160630). *D. traquairi* can be distinguished from the type species (*Dicynodon lacerticeps* (Owen, 1845)) (King 1988) by the lack of any remnant of the transverse flange of the pterygoids, its deeply sheltered pineal opening and the deeply grooved dorsal surface to its lower jaw symphysis (Table 2).

The taxa in the Cutties Hillock Sandstone Formation fauna, originally described as members of a new genus, *Gordonia,* by Newton (1893), and revised by King (1988), comprise *Dicynodon traquairi* (Newton, 1893), *Dicynodon juddiana* (Newton, 1893), *Dicynodon huxleyana* (Newton, 1893), *Dicynodon duffiana* (Newton, 1893) and *Geikia elegans* Newton, 1893 (Rowe 1980; Cruickshank & Keyser 1984; Maisch & Gebauer 2005), and are assigned to the Synapsida (Dicynodontia; King 1988). *Elginia miribalis* Newton, 1893, is an anapsid; a pareiasaur (Benton & Spencer 1995). (Table 1).

One further specimen from Morayshire, a dicynodont, collected by Alick Walker in 1953, from York Tower Quarry, Knock of Alves (GR NJ 162629), is in the National
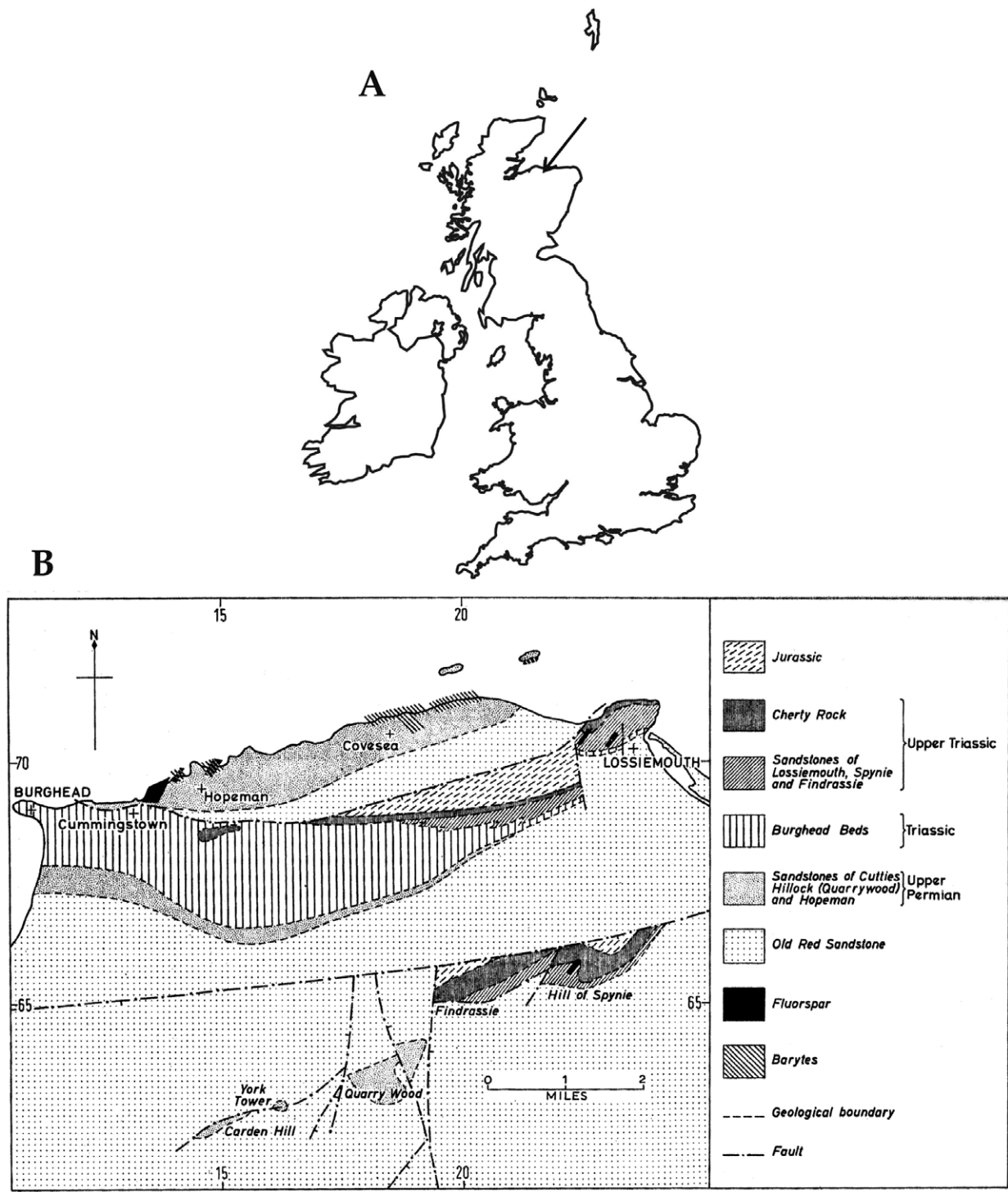
Figure 1. A, Outline map of the British Isles to show location of Hopeman (National Grid Reference NJ 163702). **B**, Geological sketch map of outcrops of the Permo-Triassic rocks in Moray District (Grampian), to show to show positions of Hopeman (Clashach Quarry) and Quarry Wood (Cutties Hillock. Figure 1B modified after Peacock *et al.* (1968).

Museums of Scotland, Edinburgh (NMG G 1984.20.7) (Benton & Spencer 1995).

GEOLOGICAL SETTING

The Hopeman Sandstone Formation has been traditionally assumed to be the broad lateral equivalent of the Upper Permian Cutties Hillock Sandstone Formation (Watson & Hickling 1914; Peacock *et al.* 1968; Benton & Walker 1985), based on the similarity of the trackways found at both localities. Walker (1973) suggested that the Hopeman Sandstone was of earliest Triassic age (= *Lystro-*

saurus Assemblage Zone as then understood), based on the presumed equivalence with an assumed Early Triassic age of the Cutties Hillock Sandstone, which in turn was based on the (incorrect) likelihood that the Cutties Hillock fauna was of a later age than the hitherto accepted Late Permian, because of the derived nature of the reptilian fauna. In turn, Cruickshank & Keyser (1984) drew attention to the fact that *Geikia,* a dicynodont and a component of the Cutties Hillock fauna, was a close relative of the South African Upper Permian (*Dicynodon* Assemblage Zone; Groenewald & Kitching 1995) genus *Pelanomodon,* and not

Table 1. List of specimens from Elgin Permian.

Taxon	Number	Specimens	Remarks
Elginia mirabilis	2	GSE 4783–8	Newton (1893)
		ELGNM 1978.550	Benton & Spencer (1995)
'procolophonid'	1	ELGNM 1978.560	Walker (1973)
		BMNH R4807	Benton & Spencer (1995)
'Gordonia' traquairi	5	GSE 11703	Newton (1893)
		BMNH R4805–6	Benton & Spencer (1995)
		ELGNM 1995.5.1	This paper skull and humerus
		ELGNM 1995.5.2	
		ELGNM 1999. 22	
'G'. huxleyana	2	GSE 11704	Newton (1893)
		BMNH R4799-4802	Benton & Spencer (1995)
'G'. duffiana	1	ELGNM 1978.559	Newton (1893)
			Benton & Spencer (1995)
'G'. juddiana	1	ELGNM 1890.3	Newton (1893)
			Benton & Spencer (1995)
'G'. elginensis	1	GSM 90998–901105	Newton (1893)
			Benton & Spencer (1995)
Specimens indet.	7	BMNH R4794	Benton & Spencer (1995)
		ELGNM 1935.8	
		ELGNM 1978.558	
		ELGNM 1978.886	
		NMS G 1956.8.3	M.A. Taylor & R. Paton,
		NMS G 1966.42.1–3	pers. comm., 2004
		NMS G 1984.20.7	

a lystrosaurid. However, while not being Triassic in age, these two Cutties Hillock reptiles (*Geikia; Elginia*), because of their derived nature, are likely to be of an age later than the *Cistecephalus* Assemblage Zone and with the presence of a member of the genus *Dicynodon,* most probably no later than the *Dicynodon* Assemblage Zone (Groenewald & Kitching 1995). We therefore believe that the Hopeman and the Cutties Hillock Sandstone Formations are the equivalent of the South African (Karoo) *Dicynodon* Assemblage Zone and are of Late Tartarian age (Rubidge 1995).

The Hopeman Sandstone Formation has been variously interpreted as having been deposited under aeolian conditions as part of a substantial transverse dune system (Glennie & Buller 1983; Glennie 2002), or star and crescent dunes (Clemmensen (1987; Anon 2003). There are small areas of fluvial or lacustrine deposits (Peacock *et al.* 1968) and on the foreshore 800 m west of Clashach, an outcrop of thin coarse-grained and pebbly layers, clay clasts and rippled surfaces indicate water-lain horizons (C.A. Hopkins, pers. comm.). Williams (1973) interprets these beds as flash-flood deposits. In the Late Permian, Hopeman was positioned at about 15°N, in the middle of the Pangean supercontinent (King 1992). The South African localities which have yielded the bulk of known dicynodonts, on the other hand, lay at about 60°S palaeolatitude, and this difference, along with differing palaeoenvironments, may well govern their adaptations and, hence, identities (King 1992; Rubidge 1995).

Peacock *et al.* (1968) noted that the first-discovered Elgin reptiles (Newton 1893) occur near the base of the Cutties Hillock Sandstone Formation in a pebbly layer, and that a borehole revealed a layer of pebbles near the base of the Hopeman Formation Sandstone. Discontinuous layers of faceted quartz pebbles are sometimes observed in the base of Clashach Quarry, and stone from the western face also contains occasional scattered pebbles. These pebbles are

similar in appearance to the dreikanters from the Cutties Hillock Sandstone Formation, and suggest a comparable horizon.

Clashach Quarry (Hopeman) is composed of sandstone with large-scale cross bedding with foreset dip angles up to 26°, mainly to the SW. The *Dicynodon* skull was found at the extreme top of the western part of the quarry, in a homogeneous block of sandstone with no evidence of internal bedding structures. The fossil was preserved in the form of a mould, and the sediment–cavity interface was heavily stained with dark brown material. The fossils from the Cutties Hillock Sandstone are preserved in the

Figure 2. Fractured surface of sandstone block, exposing the mouldic fossil of the new skull of *Dicynodon traquairi* (Newton) (ELGNM 1995.5.1). Coin = 24 mm diameter.

same way, and Newton (1893) noted the presence of a black material coating some cavities, which contains iron, manganese and cobalt.

MATERIALS AND METHODS

Materials

ELGNM 1995.5.1. and ELGNM 1995.5.2. A block of red sandstone from the Hopeman Sandstone Formation, containing a natural mould of a complete skull and lower jaw, from high in the succession at Clashach Quarry (Anon 2003), on the west face (National Grid Reference NJ 163702).

GLAHM 114914. A 'rapid prototype' replica of ELGNM 1995.5.1 & .2. (Clark *et al.* 2004; Figs 3–5 herein).

ELGNM 1999.22. A natural mould of a dicynodont right humerus.

GLAHM 114108. A cast of a natural mould of the humerus associated with the skull.

Methods

The techniques and methodology are described in full in Clark *et al.* (2004), but involve three principal techniques: CT scanning for a preliminary analysis, MRI scanning for a higher resolution image and 'rapid prototyping' to produce a 3-D, solid, model of the space in the rock.

SYSTEMATIC PALAEONTOLOGY

Suborder	**Anomodontia** Owen, 1859
Infraorder	**Dicynodontia** Owen, 1859
Superfamily	**Pristerodontoidea** Cluver & King, 1983
Family	**Dicynodontidae** Cluver & King, 1983
Subfamily	**Dicynodontinae** Owen, 1859
Genus	**Dicynodon** Owen, 1845

Species *D. traquairi* Newton, 1893

Locality. Clashach Quarry, Hopeman, Elgin, Morayshire. National Grid Reference NJ 163702

Horizon. Hopeman Sandstone Formation (Upper Level: equivalent of the Tartarian/Dicynodon Assemblage Zone of South Africa (Anon 2003; Rubidge 1995)).

Holotype. 'Newton Specimen Number 1', (GSE 11703). Ascribed to *Gordonia traquairi* Newton, 1893 (Plates 26–28), from Cutties Hillock, Quarry Wood, Elgin, Morayshire. National Grid Reference NJ 160630

Revised diagnosis. A member of the genus *Dicynodon* Owen, 1845 (King 1988), similar in appearance to *Dicynodon lacerticeps* Owen, 1845, with a gracile skull (length-to-width ratio 1.8:1) and the following autapomorphies: anterior palatal rami of the pterygoids horizontal in lateral view, narrowly separated and subparallel, with no evidence of the remains of transverse processes, pineal opening deeply recessed between anteriorly diverging parietals on dorsal surface of skull, and grooved dorsal surface to the lower jaw symphysis.

DESCRIPTION OF SPECIMEN

The skull and lower jaw were anatomically complete before fossilization, but have suffered slight distortion

Table 2. Characters of material described in text.

	Character	Model	CT/MRI
1	Length>100<400	Y	Y
2	Tusks	Y	Y
3	PO covers P	Y	Y
4	SEPT smooth with MX	?	Y
5	SEPT do not meet lacrimal	?	?
6	Low boss over ext. nares	Y	Y
7	Palatal rim sharp, continuous	?	Y
8	Palatal exp. PAL large, flat	?	?
9	PAL short contact with PMX	?	?
10	Very long, narrow	?	Y
11	Ant. border ipt. foss. joins vomerine crest	?	Y
12	Small ECT	?	(Y)
13	ECT displaced laterally	(Y)	Y
14	Labial fossa present	(Y)	Y
15	PT contact with MX short	Y	?
16	BO separated by ridge	Y	Y
17	Fused dentaries with narrow tables	Y	Y
18	Deep dentary sulcus	Y	Y
19	Weak coronoid process	Y	Y
20	Large mandibular fenestra: lateral dentary shelf	Y	Y
21	Occipital surface of OPIS depressed	?	Y

post mortem. Information used in creating the reconstruction (Figs 3–5) has been obtained from the CT-scan, MRI and the rapid-prototyping 3-D model. Each provides a unique view of the specimen, and all sources have to be used to obtain a reliable picture of the outline of the skull and its associated lower jaw. Sutures and other bone boundaries are difficult to define, and in spite of the interpretations of Newton (1893), almost impossible to delimit, except in a very few cases, which includes the parietals and postorbital regions of the skull.

The skull is 237 mm long, and 131 mm wide, with a length–width ratio of 1.8:1. The overall appearance of the skull is that of a gracile structure, with delicate postorbitals and zygomatic arches. The lower jaw is significantly shorter than the palatal dimension (155 mm), so that the anterior of the palate is overshot, leaving the tusks standing free and prominent, even when the jaw is in its protracted position (Cox 1998). There are indications of a 'notch' on the midline of the premaxillae, similar to that figured by Newton (1893), and the anterior dorsal surface of the dentary symphysis is deeply grooved, with the possible presence of a midline notch on the anterior face of the symphysis (Figs 3f & 5e).

Low midnasal and supraorbital ridges are present. The parietals are drawn up to a prominent crest, but diverge anteriorly, with the oval pineal sunk between their anterior arms. Little else than this can be seen in dorsal view, though Newton (1893, Plate 28) shows a number of sutures quite clearly, with some having unusual boundaries when compared with conventional material. In dorsal view, the posterior wings of the squamosals obscure their ventral rami and the quadrates, but in this case it may be an artefact of preservation, with the specimen suffering slight asymmetrical dorso-ventral compression (compare Cluver & Hotton 1981; Cluver & King 1983, figs 8 & 23 with Fig. 5a–e herein).

In lateral view the dorsal surface is gently curved (Figs 3c 4c & 5c) and paralleled by the zygomatic arch, which in
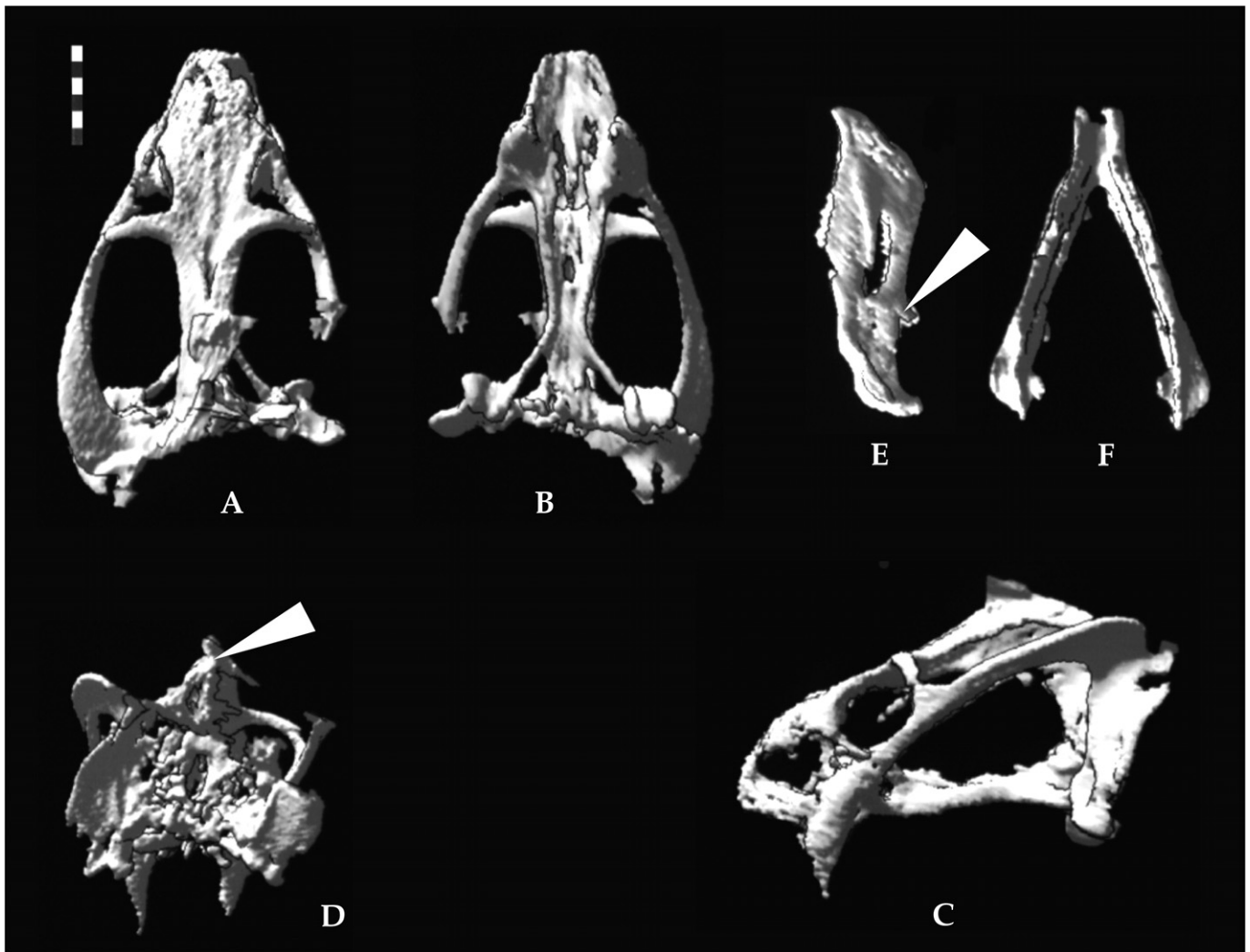
Figure 3. CT scan images of skull of *Dicynodon traquairi* (Newton) (ELGNM 1995.5.1). **A**, Dorsal view. **B**, Palate showing the relatively complete premaxillary surface of the palate. **C**, Right hand side of skull (reversed), note displaced left postorbital and apparent lack of bone in region of external nares. **D**, Occiput, note poor resolution of detail and displaced right postorbital. **E**, Right ramus of the lower jaw, note poor resolution of detail of the reflected lamina (arrowed) of angular. **F**, Dorsal view of lower jaw, note deep groove in the surface of the symphysis (arrowed), and possible notch at the anterior limit of the symphysis. Scale bar = 60 mm.

turn descends more steeply at the level of the orbit, to run into the caniniform process. There is a single pair of tusks. The palatal bars of the pterygoids are straight and on the same level as the rim of the premaxilla. The descending rami of the squamosals lie at almost 90° to the line of the pterygoid bars.

Ventrally, the most important observation is that the anterior rami of the pterygoids are narrowly separated, and do not have any remnants of their transverse flanges (compare Cluver & King 1983, figs 5 & 25 with Fig. 5a,b herein). The interpterygoid vacuity is oval and relatively short but difficult to measure accurately because of lack of precision in the imaging processes. The quadrate rami of the pterygoids diverge widely towards the quadrates. Otherwise the basicranium is very similar to that of *Dicynodon lacerticeps* (Owen), allowing for artefacts of preservation and the different illustrations obtained from these contrasting techniques.

In occipital view there are several areas that are unclear in both MRI and CT scans, and in the model (Figs 3d & 4d), and which has led us to believe that a reconstruction of the occiput would not be informative. Overall it shows no

unique characters. The interparietals and the dorsolateral edges of the supraoccipital have marked turned-out rims (Figs 3d & 4d). The quadrate articular surfaces lie slightly below the level of the basioccipital tubera, but both stapes appear to have been lost prior to fossilisation. There are ridges on the surface of the squamosal immediately above the medial condyles of the quadrates for the mandibular depressor muscles (*cf*. Cox 1957, 'tympanic processs').

With the exception of the deeply grooved dorsal surface of the symphysis, the lower jaw is similar to that of *Dicynodon lacerticeps* in most respects, with the lateral shelves on the dentaries lying just above the mandibular fenestrae. The tips of the conjoined dentaries are upturned, with an apparent median notch, which may have matched that proposed for the premaxillae (Fig. 3f) (Newton 1893, plate 28, figs 1 & 2). The reflected laminae of the angulars are apparently broken away (Fig. 3e), but seem to have been close to the main bodies of the jaw rami and did not approach closely to the lateral articular surfaces. The posterior of the dentaries occlude with the palatines and this does not allow the tip of the jaw to fully occlude the anterior surface of the palate (Cox 1998), so

Figure 4. MRI-sourced model of skull *Dicynodon traquairi* (Newton) (ELGNM 1995.5.1). Note the ridged artefact, particularly on the surface of the squamosal, and compare the detail preserved on the dorsal and lateral surfaces of the snout, with those from the CT scan images. **A**, Dorsal view. **B**, Palate, note possible premaxillary notch. **C**, Lateral view. **D**, Occiput. Scale bar = 50 mm.

a substantial thickness of horny bone coverings on the palatal surface is proposed. The presence of dentary sulci (Figs 3e & 5d) give further resemblance to *Dicynodon*.

A single right humerus is preserved in association to the skull as a 2-D, compressed, flattened, shape. Little information can be obtained from it, but the capitellum is larger than the trochlea, and the ventral part of the bone seems to have reasonably complete proportions. However, the proximal portion was damaged post mortem. The delto-pectoral crest is largely broken away and only partially preserves the proximal articulation. Overall length of the humerus, as preserved, is 105 mm, and the distal width is 64 mm.

DISCUSSION

Comparisons of techniques

Of each of the techniques used to illustrate this specimen (Figs 3–5), the CAT-scan images are in many ways the most complete. At the same time they are the least precise. MRI-imaging depends on the use of liquids to penetrate all areas of the fossil, some of which may be so narrow

that, unless of great fluidity, the fluids cannot penetrate the finest passages, leaving such areas devoid of any response (Fig. 4a,b). Here the thin-boned areas of the snout, and more particularly the mid-line of the snout roof, have not allowed penetration of the imaging fluid. The 3-D model obtained through the 'rapid prototyping' process shows best the very small degree of distortion suffered by the specimen (Figs 3d & 4d), but cannot improve on the detail preserved. Overall the skull has been obliquely distorted, with the right side being slightly depressed relative to the left. This distortion has caused the postorbitals to be 'lifted' and these are the most clearly outlined bones in the entire skull and lower jaw. Although the best resolution is obtained from the MRI scan, although with even a 2 mm 'slice' interval and a 1 mm overlap, the surface of the imaged bone shows abundant ridging artefacts (Fig. 4a). The completeness of the bone imaged by MRI techniques is also dependent on obtaining optimum 'thresholding' (Clark *et al.* 2004). The optimum thresholding for larger spaces is different to that for narrow spaces, hence a compromise has to be made to produce the best overall image.
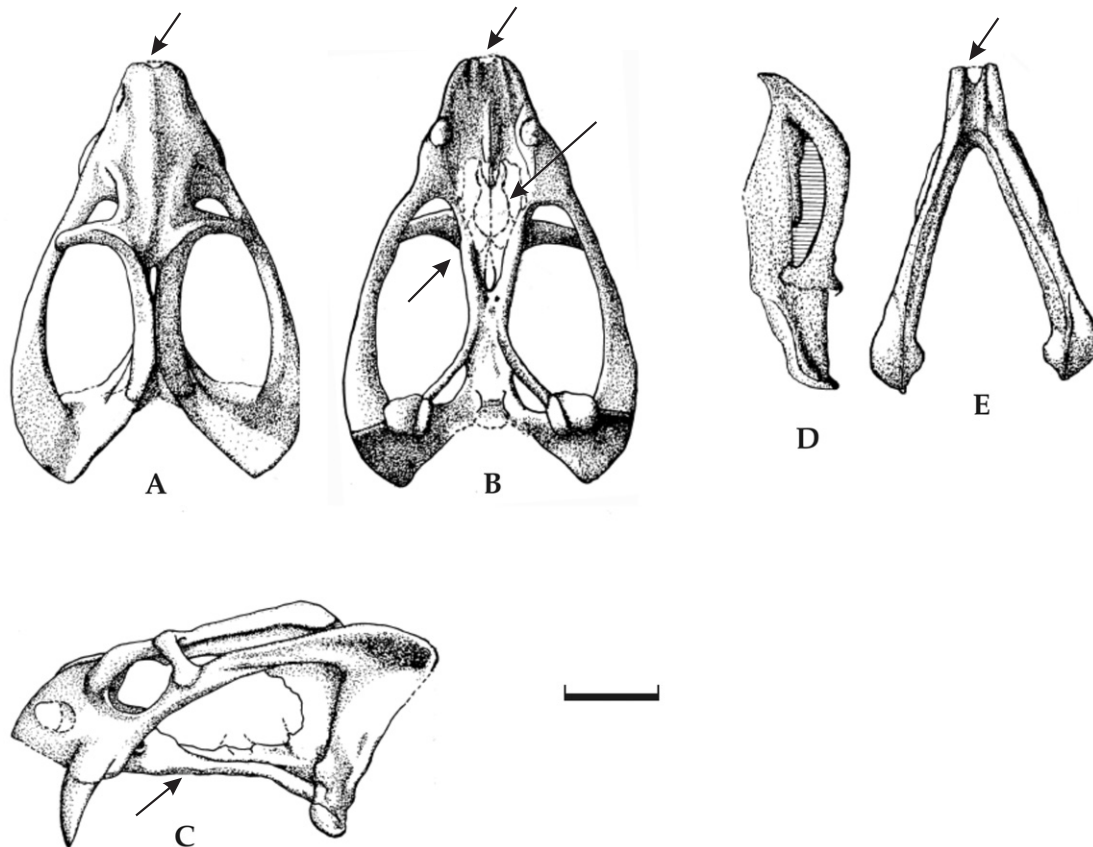
Figure 5. Skull of *Dicynodon traquairi* (Newton) in reconstruction based on information obtained from ELGNM 1995.5.1. **A**, Dorsal view, note possible notch in anterior of premaxillaries (arrowed). **B**, Palate, note possible premaxillary notch, proportions of reconstructed palatines and lack of pterygoid flanges (arrowed). **C**, Left lateral view, note lack of transverse flanges on the pterygoid (arrowed). **D**, Lateral view of lower jaw. **E**, Dorsal view of lower jaw, note deep groove on dorsal surface of symphysis and possible notch on anterior of symphysis (arrowed). Scale bar = 50 mm.

Although the general quality of the CT-scan images is not so good as those obtained from MRI, because the former technique does not rely on penetration of fluid into restricted spaces, an overall more complete surface is seen in the CT-scan images of the snout dorsal surfaces, and the palate (Figs 3a,b & 4a,b). However, definition of the outlines of the skull and lower jaw is not so complete as in the MRI scan. The model, being a direct reproduction of the scanned spaces in the rock, is a 3-D representation of the MRI images, and suffers from the strengths and weaknesses of both the imaging processes and the conversion to the prototyping technique (Clark *et al.* 2004). On the other hand, it is the easiest to handle.

Therefore following on from both scanning techniques, taxonomically important information can be obtained from these and the model (Table 2). The model can be more easily examined, with lighting from different directions, for instance, to show surface detail. From this (using all sources), it is possible to outline the likely limits of the postorbitals, and make possible interpretations of the anterior palatal bones; palatines, ectopterygoids and their relationships with the pterygoid rami. The model is least informative in the occipital region, where 'noise' seems to have obscured much of the detail round the basioccipital tubera, and all but eliminated evidence for presence an intertuberal ridge (Figs 3d & 4d) and the basioccipital condyle. In the region of the external nares, the model shows very little detail of the snout surface (Fig. 4c), although some indication is shown of the possibility of

the septomaxillae not being as deeply recessed as in *Dicynodon lacerticeps* (Cluver & King 1983). Examination of the CT-scan and MRI images shows that the narial area is not sunk, and the surface of the snout was smooth (Figs 3c & 4c).

Details of the lower jaw are shown more clearly in the MRI images, compared with both the model and CT-scan images, but in none of the resulting images can any sutures be seen. The reflected laminae of the angulars (Fig. 3e) appear to be broken off and obscured by their closeness to the body of the lower jaw, but do not seem to approach the lateral condyle of the articular at all closely. Their apparent damage may also be the result of being too thin to be resolved by either CT or MRI scanning, in a similar manner to the loss of detail on the snout and palate in the MRI images.

The reconstructions in Fig. 5a–e are a composite of the information obtained from all three techniques. King (1988) lists 21 characters used to define the genus *Dicynodon* (Table 2). From the model, 12 of these characters are seen clearly. Nine are doubtful, or not seen clearly. In combination, from the CT- and MRI-scans, 17 characters agree with King's definition. It is concluded that the specimen in the block of rock is a member of the genus *Dicynodon,* as currently defined. However, closer examination shows that the Hopeman specimen is more gracile than typical members of the genus, and especially of the type species, *D. lacerticeps* (King 1988; Cluver & Hotton 1981; Cluver & King 1983). Other differences are; the deeply recessed

pineal opening, the deeply grooved dentary symphysis, and the subparallel and narrowly separated pterygoid rami, leading to reduced contacts between the palatines and the premaxillae. In all of these characters, the Hopeman Sandstone specimen agrees with Newton's original descriptions and figures of *Dicynodon traquairi* (Newton, 1893, plates 26–28).

Scottish Permian amniotes

Dicynodon traquairi (Newton 1893) differs in several notable respects from the types species (*D. lacerticeps*) as recorded here; namely it is more gracile than *D. lacerticeps.* Characters which may be of significance, but which cannot be reliably decided, are the notches postulated for the premaxillae and dentaries (Figs 3f, 4b & 5a,b). The lower jaw cannot occlude the palate in *D. traquairi,* as is also proposed by Cox (1998) for several other dicynodont genera, and this has a bearing on their feeding function and requires that there must have been substantial pads of horn on the palate in order to make an effective bite, which in turn might affect the expression of the notches in palate and snout.

Speculating that the notches on the premaxillae and anterior dentaries were present in life, then the implication is that this species might have possessed a protrusable, prehensile, tongue as proposed by Cruickshank (1978) for the Triassic dicynodont *Dolichuranus*; either to more easily ingest vegetable matter, or to act as a means of apprehending small arthropods. The latter are suggested as a component of the fauna, if only to explain the invertebrate burrows reported previously as 'rainprints' (Brickenden 1859; C.A. Hopkins, pers. comm.).

The other Permian dicynodonts described by Newton (1893) were all subsumed into *D. traquairi* by King (1988) in the latest overall review of the Anomodontia. However, closer examination of Newton's (1893) figures and an opportunity to see casts in the British Geological Survey office in Keyworth, Nottingham, U.K., demonstrated that these synonymies may not all be valid.

For example *D. huxleyana* (GSE 11704) has a flat frontal with a larger pineal than *D. traquairi.* The tusk of the latter seems smaller, but this may be due to the smaller overall size of *D. huxleyana*: 110 mm as opposed to 234 mm for this specimen of *D. traquairi.* These differences therefore may be possibly ontogenetic, or due to sexual dimorphism (*cf Aulacephalodon* Tollman *et al.* 1980: *Diictodon* Sullivan & Reisz 2003).

Dicynodon duffiana (ELGNM 1978.659) has a relatively large pineal, widely separated postorbitals, with substantial exposure of the parietals. It has no mid-nasal ridge and is about 112 mm overall length. It is unlikely that these differences with *D. traquairi* are ontogenetic, and is here regarded as being a separate taxon, until further work can be reported on this taxon. The specimen questionably referred to *D. traquairi* (ELGNM 1978.550) is tuskless and shows ontogenetic differences from *D. traquairi s.s.* It is only 93 mm overall length, and is likely to be referable to one or other of the tuskless families of Dicynodontia (King 1988), but because of its small size, maybe a juvenile. The second *D. huxleyana* (ELGNM 1978.549) is very poorly

preserved, but is the same size as the type, and hence possessing a general similarity to it, is likely to be conspecific with it. *D. juddiana* (ELGNM 1890.3) is distorted, has a length of 118 mm and is considered to be another specimen of *D. traquairi.*

Geikia elegans Newton, 1893 is a pelanomodontid (Cruickshank & Keyser 1984) and *Elginia mirabilis* Newton, 1893 a pareiasaur. However, it is timely that these taxa should be revised and the whole fauna reassessed to put it accurately in context with the faunas in Eurasia, China and South Africa.

Sidor *et al.* (2004) suggested that the lack of dicynodonts in a newly recorded Late Permian fauna from the Moradi Formation of northern Niger is due to the desert environment. However, if dicynodont faunas are found in what is now Scotland, and in a desert, then other factors must be found to support their absence in Niger. Notable endemism is seen in both the Scottish fauna and in the other, relatively low latitude faunas of Russia, China and South Africa (Sidor *et al.* 2005), and this may well explain the observed differences.

SUMMARY AND CONCLUSIONS

A recently recovered mouldic specimen of a skull, lower jaw and humerus of one of the species known from Cutties Hillock, near Elgin, Morayshire, *Dicynodon traquairi* (Newton, 1893), is described, using novel techniques. This new specimen is the first from Clashach Quarry, Hopeman, to the north of Elgin. Overall this species of *Dicynodon* is very similar to *D. lacerticeps* (Owen, 1845).

The species *Dicynodon traquairi* is distinct from *D. lacerticeps* (Owen, 1845), in having narrowly separated pterygoids, with no indication of transverse flanges, a pineal sunk deeply between the postorbitals, and a deep groove on the dorsal surface of the lower jaw symphysis. Notches may have been present on the midline of the premaxillae and dentaries.

Of the four described species of *Dicynodon 'traquairi'* from Cutties Hillock, specimens assigned to *D. duffiana* and doubtfully assigned *D. traquairi,* are considered distinct. *D. huxleyi* is possibly a juvenile of *D. traquairi* and *D. juddiana* a distorted adult *D. traquairi. Geikia elginensis* is a pelanomodontid and *Elginia mirabilis* a pareiasaur.

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INSTITUTIONAL ABBREVIATIONS

ELGNM Elgin Museum, High Street, Elgin, Morayshire, IV30 1EQ Scotland, U.K.

GLAHM Hunterian Museum, University of Glasgow, University Avenue, Glasgow G12 8QQ, Scotland, U.K.

GSE British Geological Survey, Murchison House, West Mains Road, Edinburgh EH9 3LA, U.K.

GSM British Geological Survey, Kingsley Dunham Centre, Keyworth, NG12 5GG, U.K.

NMS National Museums of Scotland, Chambers Street, Edinburgh EH1 1JF, U.K.

REFERENCES

ANON. 2003. GCG field trip to the Hopeman Sandstone Formation. 20th May 2003. London, Geological Curators Group.

BENTON, M.J. & SPENCER, P.S. 1995. *Fossil Reptiles of Great Britain.* Geological Conservation Review Series. London, Chapman & Hall.

BENTON, M.J. & WALKER, A.D. 1985. Palaeoecology, taphonomy and dating of Permo-Triassic reptiles from Elgin, north-east Scotland. *Palaeontology* **28**, 207–234.

BRICKENDEN, L.B. 1852. Notice of the discovery of reptilian foot-tracks and remains in the Old Red Sandstone or Devonian strata of Moray. *Quarterly Journal of the Geological Society of London* **8**, 97–100.

CLARK, N.D.L. 1999. The Elgin Marvels (part 2). *Journal of the Open University Geological Society* **20**(2), 16–18.

CLARK, N.D.L. 2001. The Elgin Marvel; a scientific investigation of a fossil that isn't there! **In**: Bennet, S. (ed.), *New Fossil Evidence; Moray and the North East*, 30–33. Elgin, Elgin Museum.

CLARK, N.D.L., ADAMS, C., LAWTON, T., CRUICKSHANK, A.R.I. & WOOD, K. 2004. The Elgin Marvel: using magnetic resonance imaging to look at a mouldic fossil from the Permian of Elgin, Scotland, U.K. *Magnetic Resonance Imaging* **22**, 269–273.

CLEMMENSEN, L. B. 1987. Complex star dunes and associated bedforms, Hopeman Sandstone Formation (Permo–Triassic), Moray Firth Basin, Scotland. **In**: Frostrick, L. & Reid, I. (eds), *Desert Sediments, Ancient and Modern,* 35–231. Geological Society of London, Special Publications **35**.

CLUVER, M.A. & HOTTON, N. 1981. The genera *Dicynodon* and *Diictodon,* and their bearing on the classification of the Dicynodontia (Reptilia, Therapsida). *Annals of the South African Museum* **83**, 99–146.

CLUVER, M.A. & KING, G.M.1983. A reassessment of the relationships of Permian Dicynodontia (Reptilia, Therapsida), and a new classification of Dicynodonts. *Annals of the South African Museum* **91**, 195–273.

COX, C.B. 1959. On the anatomy of a new dicynodon genus with evidence of the position of the tympanum. *Proceedings of the Zoological Society of London* **132**, 321–367.

COX, C.B. 1998. The jaw function and adaptive radiation of the mammal-like reptiles of the Karoo basin of South Africa. *Zoological Journal of the Linnean Society* **122**, 349–384.

CRUICKSHANK, A.R.I. 1978. Feeding adaptations in Triassic dicynodonts. *Palaeontologia africana* **21**, 121–132.

CRUICKSHANK, A.R.I. & KEYSER, A.W. 1984. Remarks on the genus *Geikia* Newton, 1893, and its relationships with other dicynodonts: (Reptilia: Therapsida). *Transactions of the Geological Society of South Africa* **87**, 35–39.

GLENNIE, J.W. 2002. Permian and Triassic. **In**: Trewin, N.H (ed.), *The Geology of Scotland* (4th edn), 301–321. London, The Geological Society.

GLENNIE, K.W. & BULLER, A.T. 1983. The Permian Weissliegend of NW Europe: the partial deformation of aeolian sand dunes caused by the Zechstein transgression. *Sedimentary Geology* **35**. 43–81.

GROENEWALD, G.H. & KITCHING, J.W. 1995. Biostratigraphy of the *Lystrosaurus* Assemblage Zone. **In**: Rubidge, B.S. (ed.), *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*, 35–39. South African Committee for Stratigraphy, Biostratigraphic Series 1. Pretoria, Council for Geoscience.

HOPKINS, C.A. & CLARK, N.D.L. 2000. The Clashach skull. *Moray Field Club* **28**, 35–37.

KING, G.M. 1988. Anomodontia. *Handbuch der Paleoherpetology,* Teil 17, C. Stuttgart, Gustav Fischer.

KING, G.M. 1992. The palaeobiogeography of Permian dicynodonts *Terra Nova* **4**, 33–341.

KING, M.J., SARGEANT, W.A.S., THOMPSON, D.B. & TRESISE, G. 2005. A revised systematic ichnotaxonomy and review of the vertebrate footprint ichnofamily Chirotheriidae from the British Triassic. *Ichnos* **12**, 241–299.

MAISCH, M.W. & GEBAUER, E.V.I. 2005. Reappraisal of *Geikia locusticeps* (Therapsida: Dicynodontia) from the Upper Permian of Tanzania. *Palaeontology* **48**, 309–324.

NEWTON, E.T. 1893. On some new reptiles from the Elgin Sandstones. *Philosophical Transactions of the Royal Society of London B* **184**, 431–503

OWEN, R.1845. Description of certain fossil crania discovered by A.G. Bain, Esq., in the sandstone rocks at the south-eastern extremity of Africa, referable to different species of an extinct genus of Reptilia (*Dicynodon*), and indicative of a new tribe or suborder of Sauria. *Transactions of the Geological Society of London* **7**, 59–84.

OWEN, R.1859. On the orders and of fossil and recent Reptilia and their distribution in time. *Report to the British Association for the Advancement of Science* **1859**, 153–166.

PEACOCK, J.D., BERRIDGE, N.G., HARRIS, A.L. & MAY, F. 1968. **In**: *The Geology of the Elgin District,* 54–76. Edinburgh, Her Majesty's Stationery Office.

ROWE, T. 1980. The morphology, affinities and age of the dicynodont reptile *Geikia elginensis,* **In**: Jacobs, L.L. (ed.), *Aspects of Vertebrate History,* 269–194. Flagstaff, Museum of Northern Arizona Press.

RUBIDGE, B. S (ed.) 1995. *Biostratigraphy of the Beaufort Group (Karoo Supergroup).* South African Committee for Stratigraphy, Biostratigraphic Series 1. Pretoria, Council for Geoscience.

SIDOR, C., DAMIANI, R., LARSSON, H.C.E., O'KEEFE, F.R. SMITH, R.M.H. & STEYER, J-S. 2004. Late Permian tetrapod biogeography; new insights from West Africa. *Journal of Vertebrate Paleontology* **24**, 938–958.

SIDOR, C.A., O'KEEFE, R., DAMIANI, R., STEYER, J-S., SMITH, R.M.H., LARSSON, H.C.E., SERENO, P.C., IDE, Q. & MAGA, A. 2005. Permian tetrapods from the Sahara show climate-controlled endemism in Pangaea. *Nature* **434**, 886–889.

SULLIVAN, C. & REISZ, R. 2004. The cranial anatomy and taxonomy of the Permian dicynodont *Diictodon. Annals of the Carnegie Museum* **74**, 45–75.

TOLLMAN, S.M., GRINE, F.E. & HAHN, B.D. 1980. Ontogeny and sexual dimorphism in *Aulacephalodon* (Reptilia, Anomodontia). *Annals of the South African Museum* **81**, 159–186.

WALKER, A.D.1973. The age of the Cuttie's Hillock Sandstone (Permo-Triassic) of the Elgin area. *Scottish Journal of Geology* **9**, 177–183.

WATSON, D.M.S. & HICKLING, G. 1914. On the Triassic and Permian rocks of Moray. *The Geological Magazine* **6**, 399–402.

WILLIAMS, D.1973. *The sedimentology and petrology of the New Red Sandstone of the Elgin basin, North east Scotland.* Unpublished Ph.D. thesis, University of Hull.