First fossil *Agama* lizard discovered in the Cradle of Humankind (Bolt's Farm Cave System, South Africa)

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Plio-Pleistocene sites in the Cradle of Humankind World Heritage Site (recognized by UNESCO), including Taung and Makapansgat Limeworks, all in South Africa, have not only yielded a rich collection of macrofauna but also an abundance of microfauna. Even though the extant small lizards are highly diverse with 23 families and 350 species in southern Africa, very few fossil remains have been studied. This is probably due in part to difficulties in accessing comparative osteological collections (the comparative material is usually rarely completely prepared, rendering anatomical study almost impossible). In 2016 an incomplete mandible with acrodont dentition was excavated in Brad Pit A (Bolt's Farm Karst System) by the Hominid Origins and Past Environment Research Unit team. Upon inspection, the fossil resembled agamids, even though it lacked the anterior pleurodont dentition present in Agamids. The fossil specimen can only be identified as Agama sp. due to its fragmentary state, but it represents the first fossil of this genus to be reported from the Cradle of Humankind World Heritage Site.

Keywords: Plio-Pleistocene, Cradle of Humankind World Heritage Site, Agamidae, Chamaeleonidae, Mandible.

INTRODUCTION

Little attention has been given to the squamate fauna at the South African Cradle of Humankind World Heritage Site, beyond cursory mention of its presence in Plio-Pleistocene localities (Brain, 1981; Vilakazi *et al*., 2018). In 2016, during excavations at Brad Pit A (BPA) in the Bolt's Farm Karst System in the Cradle of Humankind World Heritage Site (Gauteng Province, South Africa), a fragment of mandible of a small reptile with acrodont teeth was discovered by the HRU team (Hominid Origins and Past Environment Research Unit). BPA, and the neighbouring locus Brad Pit B (BPB), were discovered in November 2010 during field prospecting by the HRU team on the Klinkert's Property (part of the Bolt's Farm Cave System located in the Sterkfontein Valley (Gommery *et al*., 2012). The site consists of unroofed sections of a palaeo-cave infill, like many Plio-Pleistocene sites in this area of South Africa (Gommery *et al*., 2012, 2016).

Acrodont teeth are present in diverse lower vertebrates (Kardong, 2008) but in southern Africa the low triangular tooth morphology is only known in two families of reptiles, the Agamidae and the Chamaeleonidae (Baig *et al*., 2012; Cooper *et al*., 1970; Kardong, 2008; Meszoely & Gasparik, 2002). The agamids differ from chamaeleons by having pleurodont dentition on the anterior part of the dentary and maxilla (Baig *et al*., 2012; Cooper *et al*., 1970; Fathinia *et al*., 2011).

The relationship between Agamidae and Chamaeleonidae has been actively debated (Conrad, 2008; Frost & Etheridge, 1989). However, only these two comprise the clade of Acrodonta (Cope, 1864). This was confirmed by the most recent molecular research (Pyron *et al*., 2013; Zheng & Wiens, 2016). These two families mainly share acrodont dentition, and the closest relative of Squamata known as Sphenodontida (represented only by one taxon, *Sphenodon punctatus* Gray, 1842, or the tuatara of New Zealand) also has acrodont teeth (which suggests that this type of dentition is plesiomorphic (ancestral)) (Witten, 1993).

These families are very diverse and widespread throughout the Old World, distributed in Africa, temperate and tropical Asia, Australia, some parts of Europe and Madagascar (Estes, 1983; Pianka & Vitt, 2003). In southern Africa, the Agamidae are represented by 12 species in two genera (*Agama* and *Acanthocercus*) and the Chamaeleonidae by 17 species in two genera (*Bradypodion* and *Chamaeleo*) (Alexander & Marais, 2007; Bates, *et*. *al*., 2014; Uetz, 2012).

The aim of this article is to highlight the presence of fossil lizards at a Plio-Pleistocene site, and to list reliable diagnostic features for distinguishing

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mandible fragments from South African Plio-Pleistocene sites. This might contribute to a better understanding of the palaebiodiversity of the Cradle of Humankind during the Plio-Pleistocene, especially of its herpetofauna.

MATERIALS AND METHODS

The fossil specimen was catalogued as BPA 216, where BPA represents the collection prefix for the locus Brad Pit A. It is curated in the Bolt's Farm Cave System (BFCS) collection of the Ditsong National Museum of Natural History (DNMNH) in Pretoria. The specimen was discovered on 12 May 2016 during screening of the decalcified breccia excavated between 2 m and 2.2 m depth (with the reference level Z=0 for the locus) in the southeast corner of the main excavation. This level is very rich in microfaunal remains as well as macrofauna (all these fossils are under study). Preliminary geological observations of the main excavation of this locus indicate the presence of two different types of *in situ* breccia and suggest a complex history of deposition. Preliminary studies of the fauna suggest that both Early Pleistocene and Late Pliocene taxa are represented, including suids (Pickford & Gommery, submitted) and rodents (F. Sénégas pers. comm.).

The comparative specimens for this study came from the Spirit Collection of the Herpetology section at the DNMNH. The comparative sample is limited as the museum depends largely on animal donations from the public (collected from different areas in South Africa and with little contextual information). These specimens were preserved in alcohol. For this study, and to have access to skeletons, a few of the specimens of various genera and species were prepared by one of us (N.V.) using the method recommended by Gans (1952). The Chamaeleonidae are represented by *Chamaeleo dilepis* Leach, 1849 (flap-neck chameleon) ($n = 3$) and the Agamidae by *Agama aculeata* Merrem, 1820 (ground agama) ($n = 3$) and *Acanthocercus atricollis* (Smith, 1819) (southern tree agama) ($n = 3$).

The observations and photography of both extant and fossil specimens were undertaken using a Leica EZ4E stereomicroscope housed at DNMNH.

The anatomical nomenclature used (Fig. 1) for a description of the fossil specimen is adapted from Baig *et al*. (2012), Cernansky (2011), Conrad (2008), Cooper *et al*. (1970), Jordan & Verma (2008), Kosma (2004) and Stilson (2016).

DESCRIPTION AND COMPARISON

BPA 216 is represented by a fragment of a right mandible and comprises part of the dentary with the distal part of the tooth row containing at least five teeth. It is approximately 13 mm long and 6 mm in maximum height.

Teeth

All teeth of BPA 216 are acrodont (teeth ankylosed to the jaw margin and simply fused to the outer surface of the bone or on the margins of the jaw, and not socketed) (Figs 2 & 3) with a triangular shearing portion and compressed laterally. Such teeth are typical of acrodont lizards such as Agamidae and Chamaeleonidae (Baig *et al*., 2012; Cooper *et al*., 1970; Kardong, 2008; Meszoely & Gasparik, 2002). The teeth increase in size progressively posteriorly along the tooth row. The last ones are very robust, with a length of 1.5 mm for the longest tooth at the back of the mandible, and a length of 1.2 mm for the shortest/smallest tooth at the front of the mandible. In the two extant agamids the teeth also increase in size posteriorly along the tooth row (Figs 1 & 4) as observed by Cooper *et al*. (1970) in other agamids. This size increase is related to growth as observed by Moody (1980). The anterior acrodont teeth are ankylosed (permanently connected to the jaw) and do not increase in size. The case is different when looking at *Chamaeleo dilepis* where the teeth seem to vary in size throughout the mandible (Fig. 5). The apices of the teeth are slightly rounded and salient in BPA 216 as in *Agama aculeata* and *Chamaeleo dilepis*, but are very different from the morphology in *Acanthocercus atricollis* where the apex is almost flat. The teeth of BPA 216 are close to each other, the spaces between the teeth being almost nonexistent. In chamaeleons the acrodont teeth are more widely spaced than those of agamids (Delfino, *et al*., 2008).

In labial view, the surface of the teeth of BPA 216 is more flattened than in lingual view, as in all the extant specimens examined, and they have no visible ornamentation.

In lingual view, three different areas can be observed in the teeth of BPA 216 with a longer mesial area separated from a shorter distal area by a strong bulge below the apex of the tooth. The medial shape of the teeth resembles an isosceles triangle. All the extant specimens in this study present the same characteristics.

Dentary

As mentioned above, the fossil dentary is incomplete (broken both anteriorly and posteriorly).

In buccal view of BPA 216, the dentary appears to increase gradually in depth posteriorly. The buccal surface of the dentary presents a uniform aspect without ornamentation and is slightly convex. The interdental groove is visible, and this feature is usually present in both extant agamid species examined (Figs 1A, 4A & 5A).

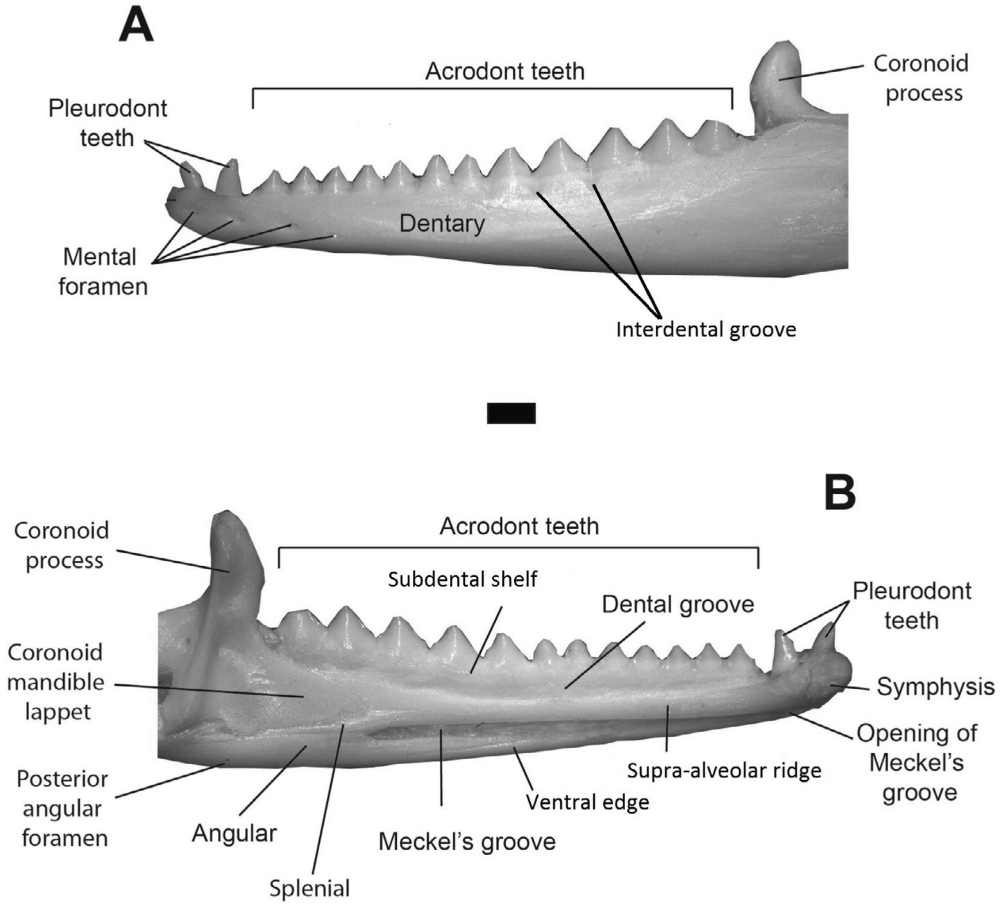

Fig. 1

Annotated diagram of labial (**A**) and lingual (**B**) views of a left mandible of *Agama aculeata* (TM 57940). The anatomical nomenclature is adapted from that of Baig *et al.* (2012), Čerañský (2011), Conrad (2008), Cooper *et al.* (1970), Jordan & Verma (2008), Kosma (2004) and Stilson (2016). (Scale: 1 mm)

The fossil presents no mental foramina, and this could be due to its fragmentary state. The comparative specimens of *Agama aculeata* and *Acanthocercus atricollis* present few of these foramina, only in the anterior region of the mandible, but some are present along the dentary in *Chamaeleo dilepis*. Cooper *et al*. (1970) have also reported foramina for branches of mandibular nerves in anterior parts of lower jaws of *Agama agama*.

In lingual view, the dental shelf in BPA 216 is reduced but not absent. Estes *et al*. (1988) have noted; however, that the subdental shelf is absent in most chamaeleonids, as well as in agamids (Moody, 1980). The subdental shelf is prominent in *Acanthocercus atricollis*, but absent or reduced in *Agama aculeata*.

There is a well-developed dental groove in BPA 216 (Fig. 3). The specimens of *Chameleon dilepis* did not present a clear dental groove (Fig.5B) as seen in agamids examined in this study (Figs1B & 4B). In *Chameleon dilepis*, this area is very high and looks more like a broad, shallow fossa than a groove.

The supra-alveolar ridge above Meckel's groove (*sulcus Meckeli*) is well-developed in BPA 216 (Fig. 3). Although this ridge can be seen in all comparative material accessible in this study, it seems more prominent in agamids. The height of this ridge also seems to be more constant in *Agama aculeata* and BPA 216 than in *Acanthocercus atricollis* and *Chameleo dilepis* (Figs 1B, 4B & 5B).

The anterior opening of Meckel's groove is lacking, which indicates that BPA 216 is broken posteriorly to this opening. The posterior end of this groove is also lacking, which indicates that the fossil is broken anterior to it. These additional observations suggest that BPA 216 is confidently interpreted to be the posterior third quarter of the dentary.

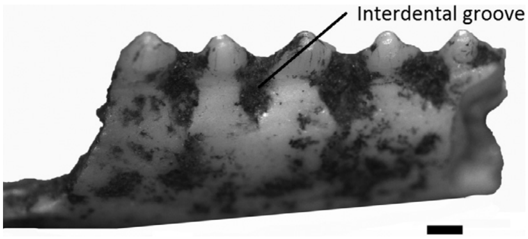

Fig. 2
Labial view of BPA 216. (Scale: 1 mm.)

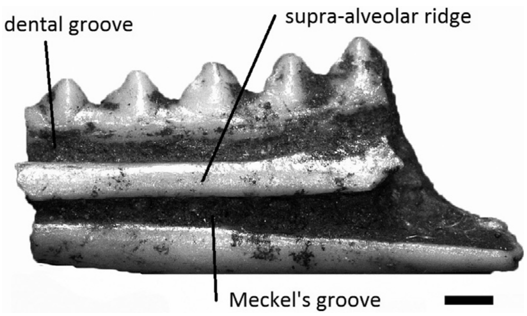

Fig. 3
Lingual view of BPA 216. (Scale: 1 mm.)

Meckel's groove in BPA 216 is deep, as in all the comparative specimens. The height of this groove seems to increase posteriorly in BPA 216, but it is probably due partly to the fact that the specimen is broken posteriorly and partly to the presence of some remnants of sediment, which probably covers the deep angular. The height of this groove seems to be more or less constant in the extant specimens.

Meckel's groove is supported below by a thickened ventral edge along its entire length (Figs 1B, 3, 4B & 5B), but it is more salient and reduced in height posteriorly to form a crest in BPA 2016, as well as in *Agama aculeata* and to a lesser degree in *Acanthocercus atricollis*. In *Chameleo dilepis*, the *crista ventralis* is also thick but stays robust with a rounded aspect. Furthermore, Meckel's groove is longer and continues posteriorly largely.

General aspect

It appears that BPA 2016 corresponds to the posterior third quarter of the dentary. For the same segment of the mandible, the teeth in BPA 216, like those of extant agamids, appear to be bigger than those of *Chameleo dilepis*.

DISCUSSION AND CONCLUSION

The above descriptions and comparisons between the fossil from BPA and extant specimens suggest that the fossil could be an agamid, even though it lacks anterior pleurodont teeth, which are only

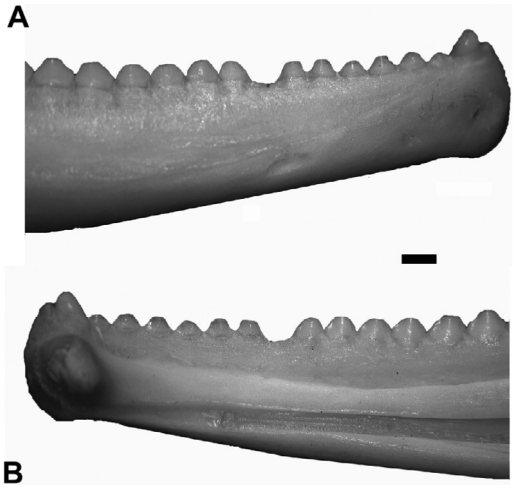

Fig. 4
Part of a right mandible of *Agama atricollis* (TMS 50233). **A:** labial view; **B:** lingual view (showing a deep Meckel's groove and the tightly packed teeth). (Scale: 1 mm.).

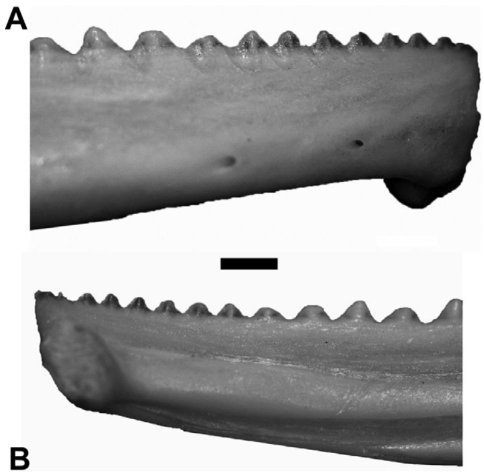

Fig. 5
Anterior portion of left mandible of *Chamaeleo dilepis* (TM 134). **A:** labial view **B:** lingual view. (Scale: 1 mm.).

found in agamids and not in chamaeleons. Even though all specimens seem to possess a deep Meckel's groove, the ventral edge seems to differ in agamids and the fossil (which possesses a more salient crest). The interdental groove occurs in agamids used in this study, and in the fossil. The chamaeleon specimen examined does not appear to have a visible dental groove, but instead a broad shallow fossa. The teeth in the fossil are grouped, and they increase in size from anterior to posterior along the tooth row, as in extant agamids. In chamaeleons the teeth are more widely spaced and their size varies along the tooth row, i.e. they do not increase (or decrease) in size along the tooth row as seen in the fossil and agamids. The relative size of the teeth appears to be smaller in chamaeleons than in agamids. We therefore conclude that BPA 216 represents a fragment of a mandible of an agamid lizard. The shearing shape of the tooth apices as well as the morphology of the medial surface of the dentary of BPA 216 are most similar to those of the mandible of *Agama aculeata*. BPA 216 could represent a fragment of mandible of the genus *Agama*; however, no species-level details can be established.

Systematics

Class Reptilia Laurenti, 1768
Order Squamata Oppel, 1811
Suborder Lacertilia Owen, 1842
Infraorder Iguania Cope, 1864
Family Agamidae Spix, 1825
Genus *Agama* Daudin, 1802
Agama sp.

The Agamids are small to large animals, mainly terrestrial, with some species dependant on rocky to arboreal habitats, but they are known almost everywhere in southern Africa (Alexander & Marais, 2007; de Villiers & Bates, 2014). Agamids are widely distributed around southern Africa, with some specimens of *A. aculeata* present in Gauteng (including the Cradle of Humankind World Heritage Site). The Bolt's Farm specimen is the first record of the presence of this group in a Plio-Pleistocene site of the Cradle of Humankind despite more than 80 years of research. Of course this study had limitations, with access to comparative material being the main drawback, but it demonstrates that a small fragmentary specimen can contribute to information regarding palaeobiodiversity.

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