

CHAPTER 1

1.1 Background to the Present Study

South Africa is well known for its many, important fossil bearing deposits of Plio-Pleistocene age (Brain, 1981; Pickering, *et. al.*, 2007). Many of these sites contain abundant remains of extinct and extant animals including hominins (see Broom, 1938, 1949; Berger et al., 1993, 1995, 2010; Keyser et al., 2000; Pickering, *et. al.*, 2007).

The Cradle of Humankind (CoH) World Heritage Site is a series of dolomitic karstic caves, which are known to be the single richest source of early hominin fossils and associated faunal and archaeological remains within Southern Africa (Pickering, *et.al.*, 2011). They are located 40 km northwest of Johannesburg and they preserve the fossil remains of at least four early hominin taxa: *Australopithecus africanus*, *Australopithecus sediba*, *Paranthropus robustus*, and early Homo (Pickering, *et.al*, 2011). These hominin remains in the caves are encased in clastic, cave-fill deposits situated in stromatolite-rich, dolomite sequences deposited on a late-Archaeon continental shelf (Eriksson, *et.al*, 2006). The CoH World Heritage area is situated in a region of the Kaapvaal Craton referred to as the Johannesburg Dome (Dirks, *et.al*, 2013). This Dome consists of a near circular, antiformal structure cored by Mesoarchaeon basement gneiss surrounded by outward dipping platform sequences of sedimentary and volcanic rocks of Neo-Archaeon to Paleoproterozoic (3.0-2.1 Ga) age (Dirks, *et.al*, 2012). These include stromatolite-rich dolomite of the late-Archaeon (2.64-2.50 Ga) Malmani Subgroup, occurring to the E, N and W of the “Dome” and host the cave deposits in the CoH. The layered sequences are intruded by the 2060 Ma Bushveld Igneous complex to the N, and unconformably overlain by horizontally-bedded remnants of Permian sediment of the Karoo Supergroup (Dirks, *et.al*, 2012).

The dolomite of the Malmani Subgroup has been sub-divided into five formations known as: the Oaktree, Monte Christo, Lyttelton, Eccles, and Frisco formations (from top to bottom). These divisions are based on stromatolite morphology, chert content and the presence of shale and chert-breccia horizons (Eriksson & Truswell, 1974).

The Oaktree formation is 150-200 m thick and consists of chert-poor dolomite overlying quartzite and conglomerate of the Black Reef formation. Its dolomite is interbedded with thin (< 2 m thick) shale horizons, that are locally carbonaceous, and it contains two thin (< 30 cm) tuff seams near its stratigraphic top (Dirks & Berger, 2012). The most conspicuous tuff layer has been dated at 2585 Ma and is well exposed in Sterkfontein caves forming the roof to the Elephant Chamber and Milner Hall (Martini, *et. al*, 2003).

The overlying Monte Christo formation (600-700 m) is a stromatolitic dolomite, rich in chert, with oolite beds near its base. It is embedded with generally thin (< 50 cm) shale horizons. Its stratigraphic top is a 5 m thick layer sheared chert-breccia in dolomite matrix (Dirks & Berger, 2013). This formation is overlain by the chert-free Lyttelton formation (150-200 m thick), a well bedded, laminated dolomite topped by a 10-15 m wide chert-dolomite breccias horizon in which chert layers are highly deformed, folded and broken into angular blocks within a dolomite matrix (Dirks & Berger, 2012).

The overlying chert-rich Eccles formation is up to 600 m thick with chert breccias near its stratigraphic top interpreted as an erosional feature that separates it from the chert-free dolomite of the Frisco formation, a unit not exposed in the CoH (Eriksson, *et. al*, 2006). The dolomite units are overlain by chert-breccia of the rooihoogte formation, which formed above an irregular karstic paleotopography (Dirks & Berger, 2012).

The Rooihoogte formation has a close spatial association with caves and consists of a layer of clast-supported, chert-breccia in a sandstone matrix (Dirks & Berger, 2012). This layer varies in thickness as a result of syn-sedimentary block faulting of the underlying dolomite (Dirks & Berger, 2013). The Rooihoogte formatin overlies the upper Eccles formation along the NW contact of the Malmani dolomite, and is transgressive onto Monte Christo formation dolomite to the SE, within the CoH (Dirks & Berger, 2012).

In the CoH several parallel ridges of sandstone and chert cropout, and the landscape rises from N to S, drained by the Skeerpoort River to N, and Bloubank River to the S: both tributaries of the Crocodile River (Dirks & Berger, 2012). Both Skeerpoort and Bloubank Rivers host all major fossil-bearing caves within the catchments (Dirks & Berger, 2012).

1.1.1 Lithostratigraphy of CoH

Many fossil-bearing caves occur along stratigraphic contacts within the Malmani Subgroup in the Cradle of Humankind. Bolts Farm, Swartkrans, Sterkfontein, Coopers, Kromdraai, and Minnaars Caves in the valley of Bloubank River, are positioned along the contact of the Oaktree and Monte Christo formations, whilst Malapa and Haasgat are located close to the contact between Lyttelton and Eccles formations (Dirks & Berger, 2012). These caves have formed traps for surface sediment over a period of several million years. These fossil bearing sediments have been classified into different members, units, or facies depending on the site (Brain, 1993; de Ruiter *et.al*, 2009; Dirks *et. al*, 2010). This thesis focuses on the Cooper's Cave.

There are two main sediment types in the South African cave sites, and these are fossil-bearing clastic sediments (often referred to as breccias) and speleotherms, which consist of

chemically precipitated calcium carbonates, usually occurring as stalagmites or flowstones, which are horizontal layers of calcite and rare aragonite, often interbedded with the clastic sediment (Pickering *et. al*, 2011). These cave sites comprise a basal layer of speolotherm; then several units of clastic sediment, separated by flowstone layers or erosional hiatuses (Pickering, *et. al*, 2011). These clastic sediments vary in grain size from massive blocks of dolomite to fine-grained layered mud, with the bulk of the sediment being reddish-brown sands. Most sites in the CoH have undergone major surface erosion, with up to 30 m of material removed to expose the fossil bearing cave deposits at the surface (Dirks *et. al*, 2010). After the caves are opened to surface, the dolomite blocks accumulate directly under or close to shaft-like entrances into underground chambers, forming cones of poorly sorted sediment. Finer grained sediment and more mobile material is washed further into the cave, forming more layered deposits (Pickering, *et. al*, 2010). This type of sorting separates the finer-grained sediments and also separates the more buoyant bone which is often concentrated in the finer, distal portions of the deposits (de Ruiter, *et.al*, 2009).

While there have been significant and important studies on almost every aspect of the mammalian faunas from these sites (e.g. Brain, 1981; Vrba, 1985; Avery *et al.*, 2010; Kuhn *et al.*, 2010; Steininger, 2003), and even considerable attention has been given to the avian faunas (e.g. Pocock, 1971; Stidham, 2007, 2009), little attention has been given to the squamate fauna beyond cursory descriptions of its presence (see Brain, 1981). Non-herpetological fauna have, nevertheless been used successfully to reconstruct a variety of important information about past environments and have additionally been used as critical chronological data (e.g. Brain, 1981; Vrba, 1985; Worthy & Mildenhall, 1989; Mckee, 1995; Vrba, *et. al*, 1996; Reed, 1996 & 1998; Berger *et al.*, 2002; de Ruiter *et al.*, 2008). This is despite the many disadvantages of using mammals and birds for such purposes,

disadvantages that include high adaptability to varied environments and diets, and often wide ranging movement behaviors that cross many different ecological niches (de Ruiter *et al.*, 2008). Herpetological fauna, on the other hand, potentially have numerous advantages in their use for such questions, including typically low vagility (Nelson *et. al.*, 2002, Shine, 2005), more specific food requirements (Shine, 2005; Raven & Johnson, 1999) and other features of their behavior, anatomy and physiology that make them highly appropriate for questions often asked of the mammalian and avian assemblages.

Despite these advantages only a few studies have even mentioned the presence of squamate fauna in the fossil assemblages of these sites (e.g. Brain, 1981). Anecdotally, however, their presence was recognized by various researchers, largely described, in small numbers, within the often abundant micro-mammalian assemblages (de Ruiter *et al.*, 2008). Micro-mammals themselves remain poorly studied within the context of the South African cave systems (Avery, 1992). Perhaps the squamate fauna were excluded from study due to the inherent difficulty in assembling useful comparative collections, or the fact that most modern taxonomic studies of herpefauna are centered on skin or whole body collections in museums (Branch, 1998), and only limited skeletal studies have taken place. This lack of available literature clearly confounds any attempts to study the fossil herpefauna which might be recovered from the South African cave sites. Additionally, southern Africa (and Africa in general) has an abundant herpefauna (Branch, 1998; Maritz & Alexander, 2007; Menegon, *et.al.* 2008), that in and of itself is generally quite poorly studied at a level adequate for comparison with an often fragmentary fossil record.

An additional problem was that prior to this study, it was unknown whether there would be significant, identifiable herpefauna even preserved in the fossil record of the caves in the region. Although there were, as mentioned above, anecdotal accounts of such fauna's

presences, and the candidate had been informed of this, no actual study of the frequency or quality of preservation of such fauna had been made. There was, at the outset of this project, the potential that if herpefauna were found, it would be of such fragmentary nature as to be virtually unidentifiable, or worse, in such low numbers as to be useless for determination of ecology and habitat.

Nevertheless, the potential that such fauna might be present was deemed worthy of exploration given the potential, noted above, for herpefauna to illuminate very specifically habitat and environment. Thus the present study was designed. Initially, the goal was to simply identify the presence or absence of herpefauna within the collections of a broad range of sites in the COH area. The initial idea was to survey the collections of the sites, and then utilize what was found (if anything was found), to survey the quality of material and establish what levels of work would be required to identify this material – specifically with regard to assembling a realistically adequate modern comparative sample for the first time.

Thus, there were several major hurdles to overcome in the initial phase of the study. Firstly, the very presence of adequately preserved herpefauna at the chosen sites had to be established. Then, if found, the quality of preservation, including what areas of anatomy were preserved had to be established. Only once these two issues were settled could the viability of the project be established.

In the initial design of this project, the idea had been to examine the entirety of the major fossil bearing cave site faunal collections. This was designed with the hope that should herpefauna be rare in these collections, an adequate sample could be obtained from all eleven of the major fossil sites. The first site to be examined was Coopers, where the candidates' supervisor had done some work and knew that there were at least a few herpetological specimens in the collection (L.R. Berger, Personal Communication). Specifically, the

excavated area of Coopers D also had, by that time in 2008, an abundant well-provenienced small animal assemblage that it was suspected had a reasonable chance of holding herpetofaunal remains should they be present in such assemblages in any abundance. The quality of the bone coming from Coopers D was also deemed very good, particularly the small animals (Berger, *et.al*, 2003). It was also a small, confined site, with only a few thousand catalogued large mammal specimens (as opposed to sites such as Sterkfontein, Gladysvale, Swartkrans and others that had hundreds of thousands of large mammal specimens in their collections). It was also a recently excavated site, with a number of active researchers working on the geology, provenience and questions of ecology and habitat, with the latter being based largely around traditional examinations of large mammal faunas. For all of these reasons, Coopers was deemed an excellent starting point for the presence/absence of herpefauna phase of the study.

The presence/absence experimental phase turned out to be surprisingly successful but inordinately time consuming, thus requiring alteration of the original plan. Once the initial survey had begun it was realized by the candidate that the sheer number of small animal bones that had to be sorted through, each being examined individually by hand, numbered in the tens of thousands; this, despite the large mammal assemblage being relatively modest. The taphonomic reasons for this will be discussed later in this thesis, but the end result was that it was clear that there would be little possibility of going through the entirety of the COH sites in the time allocated to this study. Furthermore, it became clear very early on that there would be an adequate herpetofaunal sample preserved in such an assemblage. In addition, during this early phase, it was realized that the comparative sample would have to be built from “scratch”, with the anatomical areas preserved being poorly represented in collections, for which those available were not designed for such a study.

Therefore, it was decided to modify the aims of the original study, making them more modest in the process. Coopers D was selected as the sole site for examination in the present study. It was recognized that this would limit the comparative output of the present study and its value, but the very recognition of the presence of abundant herpefauna and establishment of the first comparative database of fossil herpefauna, as well as the process of identification of this important sample would suffice. Thus, over the ensuing next several years, the entirety of the Coopers small animal assemblage numbering in the tens of thousands was examined and all identifiable herpefauna were removed for individual study (numbering 694 specimens; see Appendix, Table 1). These specimens were then individually described, and then compared to the existing collections of herpefauna at such institutions as the Northern Flagship Institute in Pretoria and the University of the Witwatersrand, as well as others (please see the acknowledgements for a complete list of hosting institutions). Identification to higher taxonomic orders, based on the fragmentary material proved the most difficult aspect of this novel project, but eventually significant and important identifications were made. It was also deemed necessary to describe existing herpefaunal collections in a way suitable for comparison with this fossil material and formed a significant part of the body of work.

Thus, the present study was modified from its original aims to test a number of hypotheses related to herpefauna in the karstic fossil-bearing sites in South Africa, to testing the presence of such fauna at a single site and to undertake identification of this fauna. A single cave – the Coopers site - with its very good small animal preservation was used to test this first study of this fauna as the project was recognized as a pathway to building a greater understanding of the presence of this material and its value to various palaeontological questions.

The hypotheses examined in this study therefore are as follows:

- 1) The identified taxa will allow inferences of environments specific to those species.
- 2) The results of this analysis will allow proposals for the way forward for future herpetological studies in similarly aged deposits.

1.1.2 Coopers Cave

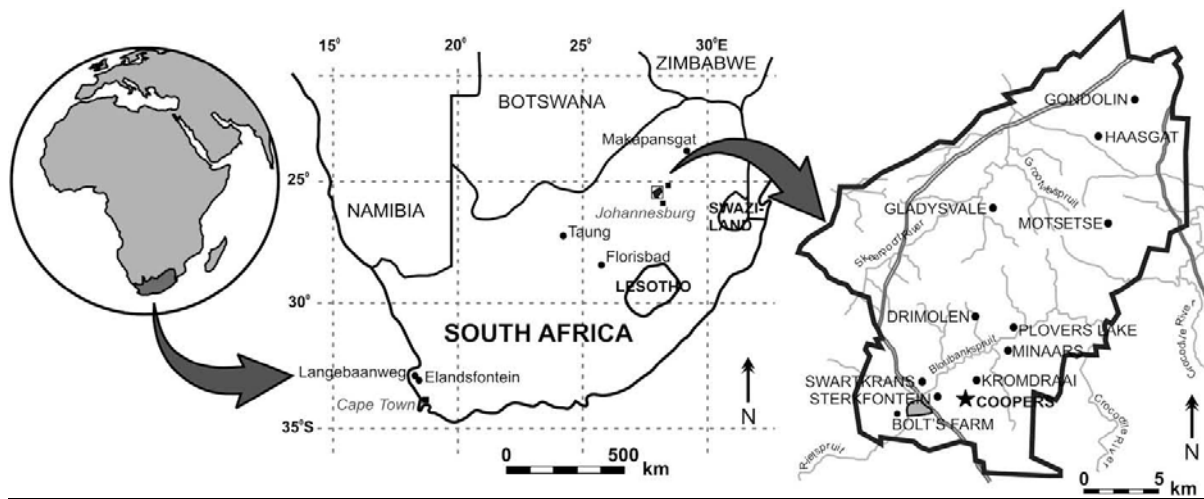


Figure 1: Map showing some of the hominin bearing sites of the Cradle of Humankind (after de Ruiter *et al.*, 2008).

Cooper's Cave is situated about 1 km east of Sterkfontein on the south flank of the Bloubaank Valley and consists of a collection of three spatially distinct infills known as the Cooper's A, B, and D, all of which preserve fossil-bearing sediments (Berger *et al.*, 1995; 2003; Pickering, *et. al*, 2011).

Although only recently being the subject of levels of intensive work for fossils, Cooper's was discovered and first excavated in 1938 (Middleton Shaw, 1939; Berger *et. al.*, 2003). The initial surveys yielded a substantial faunal collection and a tooth described as "human" by

Middleton Shaw (1939). The specimen, an isolated third molar, was further analyzed by Broom and Schepers in the years that followed, and determined to be attributable to *Australopithecus africanus*. A cast of the specimen was again studied in the 1990's, due to the disappearance of the specimen itself. The researchers further corroborated Broom and Schepers' determination and a taxonomic classification of *Australopithecus cf. africanus* was suggested (Berger *et al.*, 1995).

Following the initial excavation in the 1930s, Cooper's B was extensively sampled during the middle part of the 1950s by C.K. Brain. Brain's excavation yielded vastly different fossils from those collected twenty years earlier. This, and the fact that primates were uncommon in the excavated material, led to the longstanding belief that the hominid material attributed to Cooper's may have in fact originated from another site (LR Berger personal communication). With the Cooper's hominid coming from what some considered poor provenience, interest in the site waned until further hominid material was discovered in 1989. The specimen, (COA 1, a right central incisor) was found in the faunal collection of the Transvaal Museum. Its morphological signature suggests that the specimen did indeed come from Cooper's and not one of the neighboring deposits (Berger *et al.*, 1995)

The discovery of this specimen led to the resumption of excavations, and the opening of an entirely new deposit, Cooper's D. Excavation of Cooper's D began in 2001, almost immediately yielding *in situ* hominid remains, confirming Cooper's place amongst the hominid sites of South Africa. Initially, dating of the site was based on the faunal make-up of CD and its similarity to Sterkfontein and Kromdraai, a date of 1.6 to 1.9 Ma has been allocated (Berger *et al.*, 2003). The combined faunal assemblage recovered from Cooper's D East and west is large and well preserved (de Ruiter, *et. al.*, 2009). About 8488 specimens have been identified to skeletal elements and taxonomic family, and a minimum of 200

individual mammals, including primates, carnivores, hyracoids, perrisodactyls, artiodactyls, rodents, and lagomorphs. The majority of ungulate fauna found in Cooper's D are indicative of grassland habitats and these include Alcelaphini, Antilopini, *Equus*, and *Metridiochoerus*. The Cercopithecidae, Giraffidae, Bovini and Tragelaphini are indicative of a rather wooded component, with at least a localized existence of dense riverine underbrush (de Ruiter, *et. al*, 2009).

Table 1: Faunal material recovered from Cooper's D with estimates of minimum numbers of Individuals (MNI) (after de Ruiter, *et. al*, 2009).

Order	Family	Tribe	Genus and species	MNI
Primates	Hominidae		<i>A. robustus</i>	6
	Cercopithecidae		<i>Papio hamadryas robinsoni</i>	12
			<i>Theropithecus oswaldi</i>	8
Carnivore	Felidae		<i>Panthera leo</i>	1
			<i>Panther pardus</i>	4
			<i>Acinonyx jubatus</i>	1
			<i>Felis lybica</i>	3
			<i>Felis caracal</i>	2
			<i>Megantereon whitei</i>	1
			<i>Dinofelis sp.</i>	2

	Hyaenidae		<i>Crocuta crocuta</i>	4
			<i>Parahyaena brunnea</i>	1
			<i>Chasmaporthetes sp.</i>	1
			<i>Proteles cristatus</i>	1
	Canidae		<i>Canis mesomelas</i>	5
			<i>Canis sp.</i>	2
	Viverridae		<i>Herpestes ichneumon</i>	2
			<i>Suricata sp.</i>	3
			<i>Cynictis penicillata</i>	2
	Mustelidae		<i>Poecilogale albinucha</i>	1
Hyracoidea	Procaviidae		<i>Procavia Antigua</i>	5
			<i>Procavia transvaalensis</i>	1
perrisodactyla	Equidae		<i>Equus burchelli</i>	1
			<i>Equus capensis</i>	1
Artiodactyla	Suidae		<i>Metridiochoerus andrewsi</i>	9
			<i>Metridiochoerus modestus</i>	1
	Giraffidae		<i>Sivatherium maurusium</i>	2
	Bovidae	Neotragini	<i>Neotragini sp. Indet.</i>	1
			<i>Raphicerus sp.</i>	2

		Alcelaphini	<i>Megalotragus sp.</i>	5
			<i>Connochaetes sp.</i>	15
			<i>Medium sized alcelaphine</i>	19
			<i>Damaliscus sp.</i>	7
		Antilopini	<i>Antidorcas marsupialis</i>	18
			<i>Antidorcas recki</i>	12
		Hippotragini	<i>Hippotragus sp.</i>	5
		Reduncini	<i>Redunca cf. fulvorufula</i>	2
		Tragelaphini	<i>Tragelaphus strepsiceros</i>	7
			<i>Tragelaphus cf. scriptus</i>	2
		Bovini	<i>Syncerus sp.</i>	2
		Peleini	<i>Pelea sp.</i>	3
Rodentia	Hystricidae		<i>Hystrix africaeaustralis</i>	4
	Pedetidae		<i>Pedetes sp.</i>	2
Lagomorpha	Leporidae		<i>cf. Lepus sp.</i>	12
TOTAL				200

Recent U-Pb testing has further constrained the dates to 1.526 to 1.413 Ma (de Ruiter *et al.*, 2009). The initial excavation of Cooper's, that of CA and CB, resulted in the discovery of hominid fossils as well as a "substantial collection of fossil fauna," (Berger *et al.*, 1995). The more recently excavated deposit, Cooper's D, proved richer in faunal material and the collection has been described as "abundant and diverse" (Berger *et al.*, 2003). The CD collection in 2003 numbered in excess of 9000 large mammal specimens and excavations from 2003 to the present have continued to yield numerous faunal remains. Over 20,000 large animal fossils have been catalogued and provisionally sorted. Identifiable remains, both cranial and postcranial, number in excess of 7000 specimens and some of these have been examined in more recent studies (see Franklin, 2009). The recovered fauna includes numerous primates and hominids as well as animals "not usually common in the Witwatersrand Plio-Pleistocene cave record" (Berger *et al.*, 2003).

Faunally, Cooper's D exhibits an abundance of suids and canids. Cercopithecids, felids, and hyaenids are also well represented. Equids and giraffids are present but rare (Franklin, 2009). As with most sites found within the *Cradle of Humankind*, bovids dominate the large mammal faunal assemblage (Berger *et al.*, 2003).

1.1.3 Geology of the site

The geology of Coopers A has not been extensively studied. Therefore, the geological context of the fossil fauna described here will concentrate on the well studied Coopers D deposits.

Cooper's D East

The cave floor of Section 1 consists of dolomite with the weathered remains of a stalagmite. Above this thick sediment unit, forming a fining upwards sequence of sub-angular dolomite blocks (with or without manganese staining), are some quartz clasts, and abundant fossil bone in a sandy reddish-brown matrix (de Ruiter, *et. al.*, 2009). The sediments are well calcified with pervasive calcite and some microfaunal bone. There is a distinct break in sedimentation at the top of the unit, representing more of an erosive contact than a flowstone marked boundary. The next unit is a coarsening upwards sequence, and like the sediments below, it is massive with no preferred orientation of clasts (de Ruiter, *et. al.*, 2009). This unit consists of up to 40 cm dolomite roof blocks (with clear chert layers) concentrated at the top of the section, cemented in a sandy reddish-brown matrix. Some patches of flowstone cap the sequence, though none of them are suitable for dating.

Section 2 is 1.5 m away from section 1, and preserves notably different looking sediments in a pocket of fossil-bearing material against the northern cave wall (de Ruiter, *et. al.*, 2009). The base of the section is formed by the dolomite cave wall, which is lined with flowstone. This is followed by two layers of dark brown muddy sediment containing 2-5 cm angular blocks of dolomite. This material is most likely not externally derived but is rather a residuum formed as a result of *in situ* dolomite weathering and break down (de Ruiter, *et. al.*, 2009). A 10 cm (thick) flowstone layer with popcorn texture caps this material. The overlying

sediments form an erosive contact and are dark to moderate brown silty sands with weak horizontal layering in an east-west direction (de Ruiter, *et. al.*, 2009). Fossil teeth and bones are common in this section and are horizontally aligned with sediments; there are a few other clasts, apart from isolated dolomite and chert clasts. As the overlying flowstone layer that fills the space between the sediments and the cave roof has no erosive contact, it is possible that the flowstone caps the sediments (de Ruiter, *et. al.*, 2009). Once again there is no suitable material useful for U-Pb dating.

Cooper's D West

These fossil bearing sediments differ from those of Cooper's D East in that they are more spatially restricted and finer grained than the eastern deposits and are extremely fossil rich (de Ruiter, *et. al.*, 2009). Much of the decalcified material has been excavated, leaving calcified material clinging to the dolomite cave walls and a central pinnacle of "breccia", which is notable for the suid fossils it contains.

Section 3 begins with the dolomite cave floor (as with sections 1 and 2), which has the remains of a large stalagmite growing up from it. There is an erosive contact with the overlying sediments, which are reddish-brown, weakly-layered, clast and bone poor, sandy muds with some microfaunal bone. These sediments are well calcified with visible desiccation cracks running from the top surface down, which are lined with calcite cement (de Ruiter, *et. al.*, 2009). Above this is a poorly preserved flowstone, around 1 cm thick with a rippled surface, and which dips to the south at around 40°. On the eastern extent of section 3, above the basal stalagmite, the sediments are massive, poorly sorted, coarse grained with angular to sub-angular 4-10 cm dolomite and chert blocks embedded in a reddish-brown sandy matrix. These two different looking sediments in section 3 are capped by several branching flowstones, all too thin and fragmentary to be suitable for U-Pb dating. However,

the presence of these flowstones allows us to group these sediments together as a single unit. Above this flowstone bounded unit is a second unit consisting of chert rich angular dolomite blocks, 5-15 cm in maximum length, randomly oriented but concentrated towards the eastern side of the section (de Ruiter, *et. al.*, 2009). These sediments are also bone rich, with heavily manganese (Mn) stained fossils concentrated pockets. This entire section, including both lower and upper units, is capped by a small, “pondy” flowstone.

Section 4 is on the southwestern side of the same “breccia” pinnacle as section 3. it is generally similar to section 3, although increasing numbers of small flowstones render section 4 more complex (de Ruiter, *et. al.*, 2009). Once again, resting on the dolomite cave floor is a large basal stalagmite and the overlying sediment, the latter of which contains some rip up clasts, and is coarser grained from west to east across the section. Randomly oriented dolomite clasts fine upwards through a reddish-brown sand matrix. The unit is capped with a popcorn textured flowstone (de Ruiter, *et. al.*, 2009). The western extent of the section preserves a small pocket of sediment, where the lower flowstone is reasonably well developed with a small stalagmite growing up from it. The sediments overlying this flowstone have an erosive contact, and fine upwards. Towards the top of the unit is a large dolomite clast, with no surface weathering and with pronounced chert layers. This is capped by a layered flowstone which splits into several thinner flowstone layers away from the clast, with intercalated reddish-brown sandy sediment; large clasts are lacking, but some fossil bone is present (de Ruiter, *et. al.*, 2009). These units are capped by a slightly thicker flowstone with a popcorn texture and Mn stained top surface which dips in towards the large dolomite block at about 12° and extends around to the west where it can be seen in section 3. In the east this flowstone is discontinuous, and the section is generally poorly calcified. Above this flowstone (in the west) and erosional contact (in the east) is another sediment unit

dominated by dolomite roof blocks with a moderate reddish brown sand matrix and some microfaunal fossil bone (de Ruiter, *et. al.*, 2009). The unit in general coarsens upwards and has an erosional top surface with no flowstone material preserved.

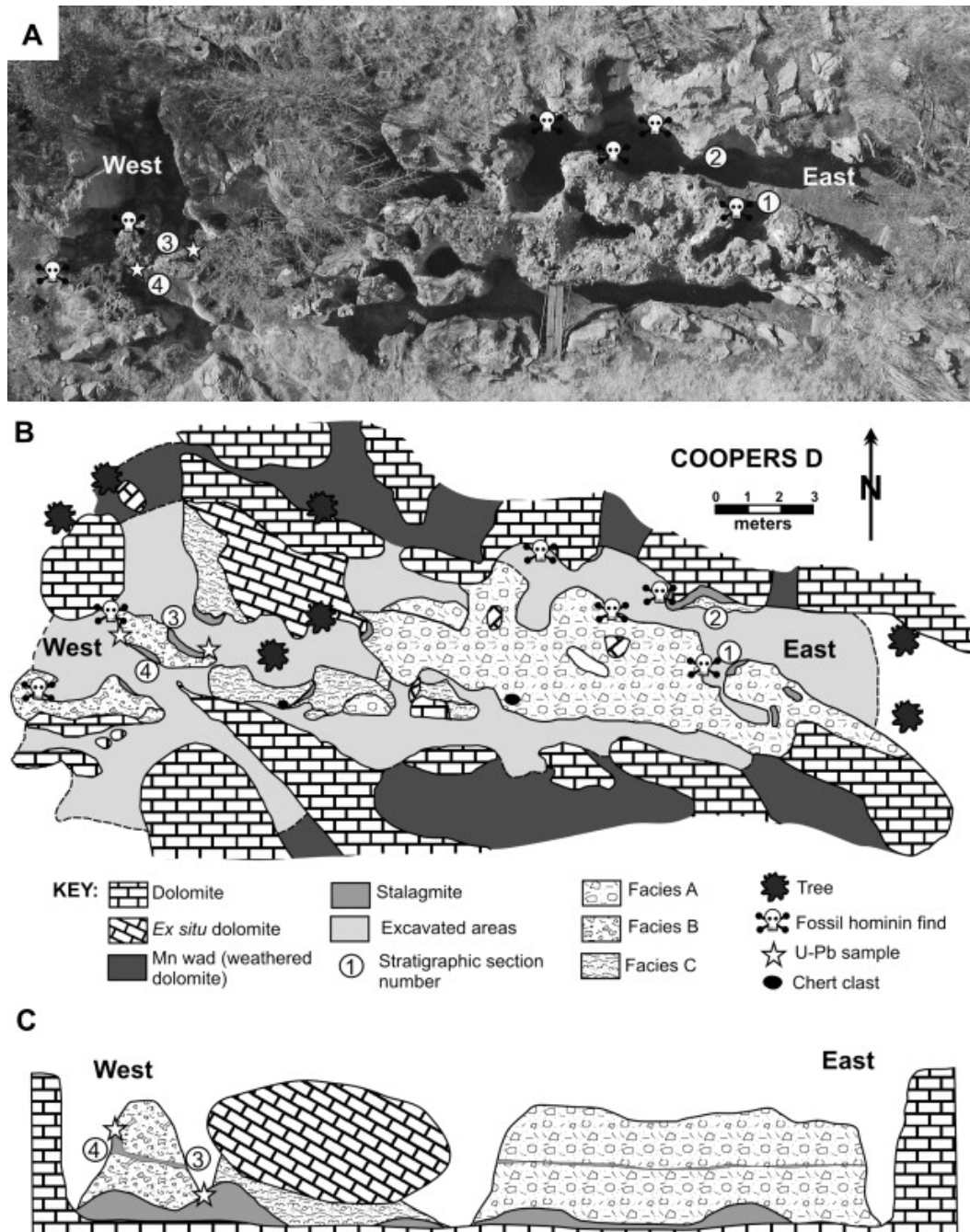


Figure 2: The Cooper's D locality. A, aerial photograph; B, plane-table geological map; C, simplified cross-section, facing north. All to the same scale. Locations of hominin specimens

are indicated in A and B. Hominin specimen CD 17796 is not plotted as it was an *ex situ* fossil discovered from a pile of miner's rubble (after de Ruiter, *et. al*, 2009).

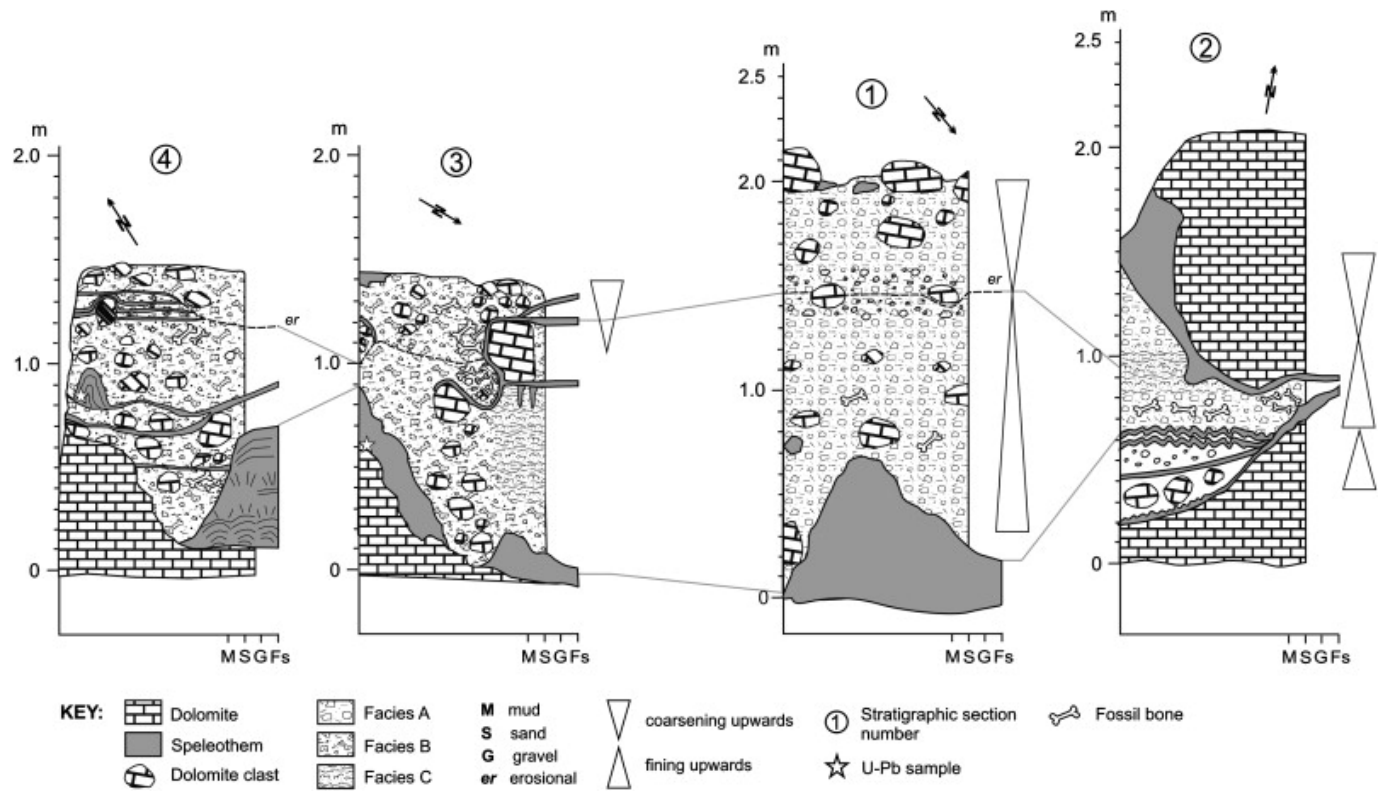


Figure 3: Geological sections of the east and west infills of the Cooper's D locality (after de Ruiter, *et. al*, 2009).

CHAPTER 2

Fossil Materials and Methods

2.1 Lepidosaurs

The Lepidosaurs are the largest group of reptiles containing more than 4800 species of lizards and about 2900 species of snakes in addition to the two species of tuatara (Pough, Janis & Heiser, 2009). Lepidosaurs are predominantly terrestrial tetrapods with some secondarily aquatic species, especially among snakes. This group is characterized by their covering of scales that is relatively impermeable to water. The outer layer of the epidermis is shed at intervals. Tuatara and most lizards have four limbs, however, reduction or complete loss of limbs is widespread among lizards, and all snakes are limbless (Pough, *et.al*, 2009).

Among extant reptiles lepidosaurs are the sister lineage of archosaurs (crocodilians and birds). Within the Lepidosauria, the Sphenodontidae (tuatara) is the sister group of Squamata (lizards and snakes). Within the squamates, lizards can be distinguished from snakes in colloquial terms but not phylogenetically because snakes are derived from lizards (Pough, *et.al*, 2009), hence the word “lizard” denotes a paraphyletic group because it does not include all the descendants of the common ancestor.

2.2 The Radiation of Squamata

Lizards and snakes together form an evolutionary lineage called squamata, a reference to their squamous or scaly skin (Koshland & Kent, 1989). But, using a scaly skin as identification for a lineage is not justifiable because this feature occurs widely in other reptiles like the crocodilians, tuatara, and some other dinosaurs, but one of the features that unites them as a lineage, is the absence of a bony strut bordering the lower temporal opening of the skull (Koshland & Kent, 1989). Some families of squamates have also a few synapomorphies which are firstly the reduced symphyseal inflection of the dentary; and the abrupt shift to closely packed, acutely pointed teeth at the anterior tip of the element (Kennedy, *et. al*, 2010).

There are approximately 8200 species and 58 families of squamates (Vidal & Hedges, 2005). The most derived character of squamates is determinate growth (Pough, *et. al.*, 2009). Growth occurs as cells reproduce in the cartilaginous epiphyseal plates at the ends of long bones, continues while the epiphyseal plates are composed of cartilage, and stops completely when the epiphyses fuse to the shafts of the bones, obliterating the cartilaginous plates (Pough, *et. al.*, 2009). This kind of growth can also be seen in birds and mammals. Determinate growth in squamates is believed to be associated with the insectivorous diet that researchers believe was characteristic of early lepidosaurs (Pough, *et. al.*, 2009).

The fossil record of lizards is largely incomplete through the middle of the Mesozoic, but Late Jurassic deposits in China and Europe include members of most lineages of extant lizards (Pough, *et. al.*, 2009).

2.3 The fossil Material and Methods

Material from Cooper's Cave (Cooper's A and D), stored at the University of the Witwatersrand formed the basis for this study although the majority of material originated from the well excavated Coopers D. There are hundreds of bags with material from the Cooper's Cave and they had to be examined separately, and in the end 694 specimens were identified and not all (as some of them were snake vertebrae) were used for this study. The snake vertebrae were included in the Appendix section just to show how abundant the herpefauna is. Each specimen was examined by hand and analyzed using a stereo light microscope. These fossils were collected by sieve-washing and the meshes comprised 1 mm openings. All other collecting methods were based upon standard best practice, and that is acid preparation (99% glacial acid) which is a specialized technique (L.R. Berger , pers. comm).

When examining the Cooper's material, no amphibian bones were identified. There are lizard maxillae discovered from Cooper's and they were not studied as the scope of the project was already too large due to the need to create the extant comparative collection. It is possible that this additional cranio dental material can be used as an expansion of the existing study at a future date. Only snake vertebrae were found during the course of this work and these were not included in the present study.

Initial photographs of the material from the Cooper's Cave were taken using a Nikon D40 Camera. Selected fossils found and deemed most suitable for identification were then scanned or photographed using a JSM 840 Scanning Electron Microscope. The magnifications used were 10x and 37x (for a more detailed picture). As dentition and anatomical areas specific to the mandible proved the most useful taxonomic separator in the

modern comparative sample, photos were taken focusing mainly on the teeth, and the Meckel's Groove.

2.4 The modern comparative sample

A comparative osteological collection of extant herpefauna was assembled using specimens from the *Spirit Collection* of the Ditsong Museum (previously known as the Transvaal Museum). 80 specimens (two per species) were donated for preparation. These specimens were collected for the museum. They were collected from different areas around South Africa, and there is not much information about the places they collected them from unfortunately. While it was recognized that such a small sample for each species would not address questions of variability in each species, due to the time consuming nature of the preparation of the extant material and the limited availability of specimens that could be skeletonized, the present study was forced to restrict its numbers to this small sample size. These specimens are deemed appropriate as they are the only ones that could be used for this study since the comparative material is almost nonexistent. The method followed for preparation followed that recommended by Gans (1952). The reptiles head was cut off. It was then skinned, and obvious superficial muscles on the skull were also removed. The skull was then soaked in bleach. Soak time depended on the size of the specimen; for larger specimens, a longer time in the bleach was required. For smaller specimens, such as the *Trachylepis* type skink, the specimens were soaked for only two minutes. The bleach reduced muscle mass and weakened ligamentous attachments.

The skull was then rinsed with clear water and left to dry, until hardening of the muscles occurred. Further dissection of the soft tissues then occurred. The skull was placed in bleach again, but very briefly this time (about 30 seconds), then it was rinsed and left to dry. After

the second bleaching, only a small amount of tissue was usually left, and the process was then repeated until only the desired bones were left.

While longer exposure to bleach was attempted to speed up the process, leaving skulls for a long time in bleach either disarticulated or decalcified the bones.

Table 2 - List of modern comparative specimens, by species, prepared for this study.

Family	Species	TM accession numbers
Amphisbaenidae	<i>Chirindia langi</i>	TM 64010 TM 59088
Amphisbaenidae	<i>Monopeltis capensis</i>	TM 22237 TM 43152
Amphisbaenidae	<i>Monopeltis sphenorhynchus</i>	TM 48735 TM 46807
Amphisbaenidae	<i>Dalophia pistillum</i>	TM 54673 TM 33235
Scincidae	<i>Acontias breviceps</i>	TM 53899 TM 61769
Scincidae	<i>Acontias gracilicauda</i>	TM 061195 TM 1886
Scincidae	<i>Acontias plumbeus</i>	TM 85486 TM 85549
Scincidae	<i>Acontias aurantiacus</i>	TM 47686 TM 44066
Scincidae	<i>Scelotes bidigittatus</i>	TM 62404 TM 36449
Scincidae	<i>Scelotes mirus</i>	TM 54107 TM 62507
Scincidae	<i>Mochlus sundevalli</i>	TM 61583 TM 82337
Scincidae	<i>Trachylepis capensis</i>	TM 85306 TM 73396
Scincidae	<i>Trachylepis homalocephala</i>	TM 64275 TM 64285

Scincidae	<i>Trachylepis striata</i>	TM 81088 TM 81084
Scincidae	<i>Trachylepis varia</i>	TM 50302 TM 36692
Scincidae	<i>Afroablepharus wahlbergii</i>	TM 76426 TM 76765
Lacertidae	<i>Ichnotropis squamulosa</i>	TM 82332 TM 83562
Lacertidae	<i>Heliobolus lugubris</i>	TM 28931 TM 14967
Lacertidae	<i>Nucras lalandii</i>	TM 72353 TM 72344
Gekkonidae	<i>Afroedura pondolia</i>	TM 69608 TM 69324
Gekkonidae	<i>Homopholis wahlbergii</i>	TM 66894 TM 13229
Gekkonidae	<i>Chondrodactylus bibroni</i>	TM 73189 TM 73162
Gekkonidae	<i>Pachydactylus capensis</i>	TM 77526 TM 77462
Gekkonidae	<i>Pachydactylus maculatus</i>	TM 72223 TM 72230
Lacertidae	<i>Pedioplanas burchelli</i>	TM 061387 TM 061406
Lacertidae	<i>Pedioplanas lineocellata</i>	TM 81745 TM 81740
Gerrhosauridae	<i>Gerrhosaurus flavigularis</i>	TM 76058 TM 76080
Gerrhosauridae	<i>Gerrhosaurus major</i>	TM 58151 TM 58152
Gerrhosauridae	<i>Gerrhosaurus nigrolineatus</i>	TM 80527 TM 66994
Gerrhosauridae	<i>Tetradactylus africanus</i>	TM 46824 TM 26751
Cordylidae	<i>Chamaesaura aenea</i>	TM 44729 TM 61767
Cordylidae	<i>Chamaesaura anguina</i>	TM 61746 TM 69267

Cordylidae	<i>Cordylus cordylus</i>	TM 36704 TM 56490
Cordylidae	<i>Smaug giganteus</i>	TM 41625 TM 35689
Cordylidae	<i>Cordylus vittifer</i>	TM 78549 TM 78552
Cordylidae	<i>Platysaurus intermedius</i>	TM 72429 TM 72462
Cordylidae	<i>Pseudocordylus melanotus</i>	TM 53906 TM 74276
Agamidae	<i>Agama aculeata</i>	TM 53644 TM 57940
Agamidae	<i>Acanthocercus atricollis</i>	TM 50233 TM 53289
Chamaeleonidae	<i>Chamaeleo dilepis</i>	TM 140 TM 134

Most of the above mentioned species have changed names in the recent years. For example *Afroablepharus* was known as *Panaspis* (Jacobsen & Broadley, 2000); *Ichnotropis* as *Meroles*, and *Pedioplanas* as *Pedioplanis* (Herrmann & Branch, 2013). These have since changed names and the most acceptable taxonomic attributions are used above.

The comparative specimens are now housed as part of the University of the Witwatersrand comparative collections, housed in the PalaeoSciences Centre, Evolutionary Sciences Institute.

2.5 Morphotypes

2.5.1 Meckel's' Groove

The meckel's groove is an antero-posteriorly running groove, situated near the superior aspect of the mandible, and typically beginning in the middle to anterior third of the mandibular body. A morphotype system was devised for comparisons with the fossil material. Divisions into different morphotypes were based on a number of different factors including the shape and form of the Meckel's Groove and tooth form. There is no correlation between the morphotypes, and either habitat or diet of these squamates. The Meckel's Groove was divided by the candidate into three distinct morphotypes;

1. Closed Meckel's Groove;



Figure 4: Picture of a recently processed extant specimen showing a mandible of *G. flavigularis* with no Meckel's groove

2. Meckel's Groove opens all the way;



Figure 5: Picture showing a mandible of *Smaug giganteus* with an open Meckel's groove

3. Meckel's Groove opens half way



Figure 6: Picture showing mandible of *C. vittifer* with a Meckel's groove opened half way

2.5.2 Tooth form

To aid in identification and sorting, the teeth were divided into three different tooth forms, with concentration on the shape, form and general morphology of the tooth tip.

Members of the Amphisbaenian family show a subpleurodont pattern, with the symmetrically rooted teeth arising in a partially closed groove along the lingual face of the bones while a bony ridge forms between the tooth bases (Gans, 1978).

Iguanidae have tricuspid dentition commonly characterized by having a large apical cusp and smaller anterior and posterior cusps (Auge, 2007). Tricuspid teeth are also common in Teiidae, and also in some genera of Lacertidae. The majority of lacertid lizards bear bicuspid teeth (Auge, 2007), but all lacertid lizards show a marked *sulcus dentalis* near the base of the teeth (Auge, 2007). Cordylidae have pleurodont, bicuspid teeth with a *sulcus dentalis* present (Cernansky, 2012).

The difference in age of these fossils was not considered in this study and it may play a major role in these specimens. It is known that there are changes in tooth morphology between older and juvenile lizards due to issues of growth and development, wear and other factors. However, such a study, requiring large control groups of known age individuals was beyond the scope of the present work, though this shortcoming is noted. Another important factor not addressed in the present study could be differences in diet between members of the same species. It is well established that animals eating hard/fibrous food tend to have more highly worn teeth. It is clear that such issues need to be addressed in future studies through controlled experimentation but are beyond the scope of the present study. Other factors that may cause tooth wear and may affect diagnosis are attrition, abrasion, and erosion (Kaidonis, 2008).

Attrition occurs from tooth-to-tooth contact without the presence of food (i.e. tooth grinding), and it is characterized by the facet that is matched by a corresponding facet on a tooth in the opposing arch. When the dentine is exposed, it remains flat with no “cupping” or “scooping” and microwear detail is that of parallel striations typically occurring within the facet border (Kaidonis, 2008).

Abrasion occurs by the friction of exogenous material forced over tooth surfaces. Although a multitude of foreign bodies can cause abrasion, the most common yet most overlooked is food (Kaidonis, 2008). The action of food on a tooth surface generally occurs over the whole occlusal surface producing a wear area as opposed to a facet (Kaidonis, 2008).

Erosion can be defined as the chemical dissolution of tooth substance without the presence of plaque (Kaidonis, 2008). If the erosion is active, the dentinal tubules remain open resulting in sensitivity and the depth of scooping increases (Kaidonis, 2008).

Another factor to be considered is erosion by sediments. Sediments play a major role in the deposition of fossils. Bones and teeth may be damaged during the process of deposition, and the amount of damage depends on the grain size. There have to date been no studies of sedimentary erosion on fossil herpetofauna but such studies would be of considerable value in the future.



Figure 7: Teeth of *P. melanotus* with a flattened tip (morphotype 1).



Figure 8: Teeth of *S. giganteus* with rounded tips but thicker in mid section of the tooth (morphotype 2).

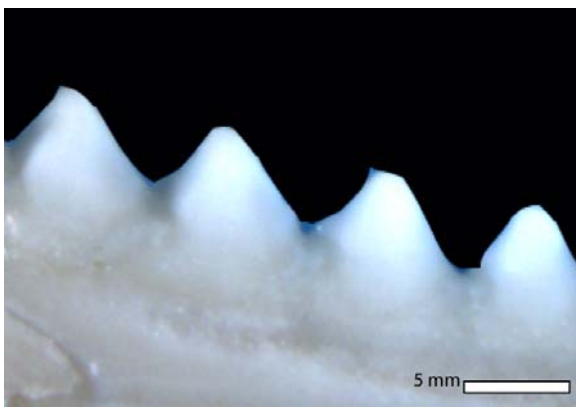


Figure 9: Teeth of *A. aculeata* with a triangular shape (morphotype 3).

CHAPTER 3-SYSTEMATIC STUDY

3.1 Lizards

There are approximately 4500 species of known lizards, and they range in size from geckos less than 3 cm long to the Komodo monitor which is about 3m long at maturity and weighs about 75 kg (Pough, *et. al.*, 2009). Many large lizards are herbivores and many iguanas are arboreal inhabitants of the tropics. Large terrestrial iguanas occur on islands, probably because of the lack of predators has allowed them to spend a large part of their time on the ground (Pough, *et. al.*, 2009).

The evolution of limb reduction has evolved more than 60 times among lizards, and there are one or more families with legless or nearly legless species in every continent. This kind of feature is usually associated with life in dense grass or shrubbery in which a slim, elongate body can maneuver more easily than a short one with functional legs (Pough, *et. al.*, 2009). It is also believed to have evolved because of the squamates' lifestyle (Gans, 1975). A few lizards will be discussed in detail below.

The amphisbaenians (from Greek roots; *amphis*=double, *baen*=walk) are extremely fossorial (*fosso*=a digger) lizards, and their specializations are different from those of other squamates (Pough, *et. al.*, 2009). Most amphisbaenians are legless, but there are about three extant species with well developed forelegs from Mexico (Pough, *et. al.*, 2009).

Most lizards found in Africa fall under the Scincomorpha, and this group comprises scincids, gerrhosaurids, and cordylids (Evans, 2003). Laurasia is very rich with the lizard assemblage of the Mesozoic, whilst Gondwana's assemblage is fragmentary; the pattern is not clear as to where these lizards originated from (Evans, 2003).

The following Lizard species were identified during the course of this study.

3.1.1 Agamidae Forms

Agama aculeata (Ground Agama)

Kingdom Animalia

Phylum Chordata

Class Sauropsida

Order Squamata

Suborder Iguania

Family Agamidae

Subfamily Agaminae

Genus *Agama*

Species *Agama aculeata*

These lizards are medium sized with a SVL of 75-117 mm (males), and females reaching 106 mm in length. The head is triangular with a relatively rounded snout (Branch, 1998). There are often two bars or chevrons between eyes. (Branch, 1998). Females have only the central network, which may be faint or even absent.

Agama aculeata prefer semi-desert to sandveld savannah habitats. They are found throughout most of the subcontinent, absent only from moister coastal regions and true desert. They are also found in S. Angola and Tanzania (Branch, 1998).

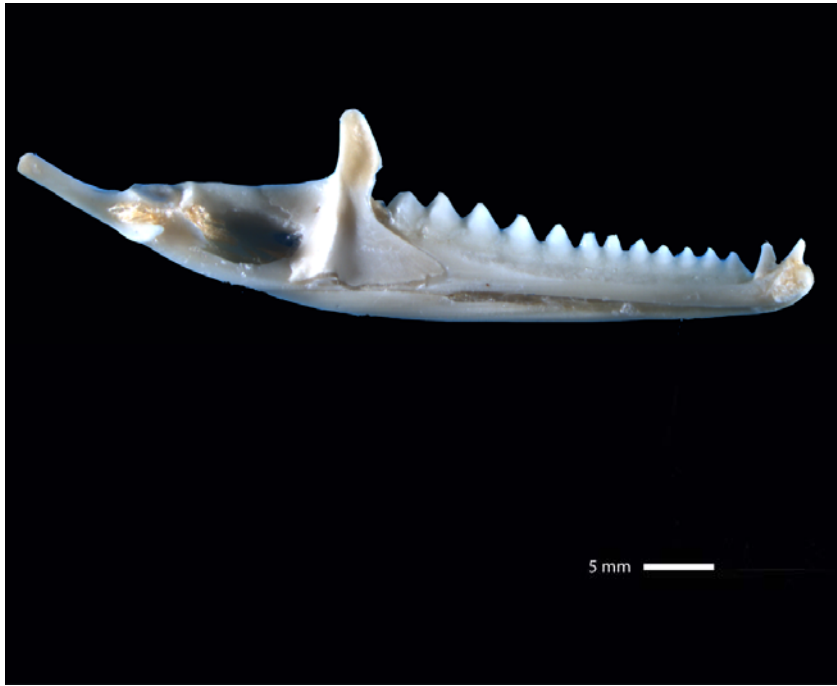


Figure 10:photo showing the left mandible of *A. aculeata*. The Meckel's groove is open and very deep. It goes all the way to the anterior of the mandible (up to the first tooth in the anterior). Teeth vary in size, with the first two teeth (towards the anterior) being sharper and pointing towards the anterior of the mandible. The rest of the teeth have a pyramid shape. They get bigger towards the posterior of the mandible. There is spacing in between since they are unequal and have a triangular shape. The teeth are acrodont.

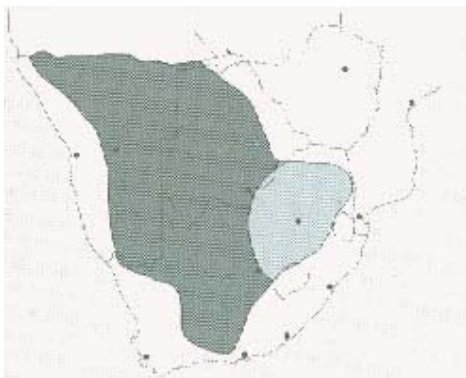


Figure 11: Map showing geographical distribution of *Agama aculeata* in southern Africa (Branch, 1998).

3.1.1.1 Specimens attributed to *Agama aculeata*

Kingdom Animalia

Phylum Chordata

Class Sauropsida

Order Squamata

Suborder Iguania

Family Agamidae

Subfamily Agaminae

Genus *Agama*

One specimen from Coopers was attributed to c.f *Agama aculeata* sp. Specimen 5518 shows several characters that are typical of *A. aculeata*. The front tooth is bigger than the rest of the teeth, and it has a long Meckel's canal. This specimen has teeth with a triangular shape, but with rounded tips forming a peak towards the middle of the tip as seen in extant *A. aculeata*.

Specimen 5518

This right hemi-mandible is 14 mm in length. It preserves most of the dentition but the body has been split. The anterior dentition is closely packed, and shows some slight sharpening of the tips of the teeth. The posterior dentition is morphotype 3, showing a triangular shape with rounded tips. There is some slight spacing to the teeth in the posterior part of the mandible. This specimen may be fairly confidently associated with the genus *Agama*.

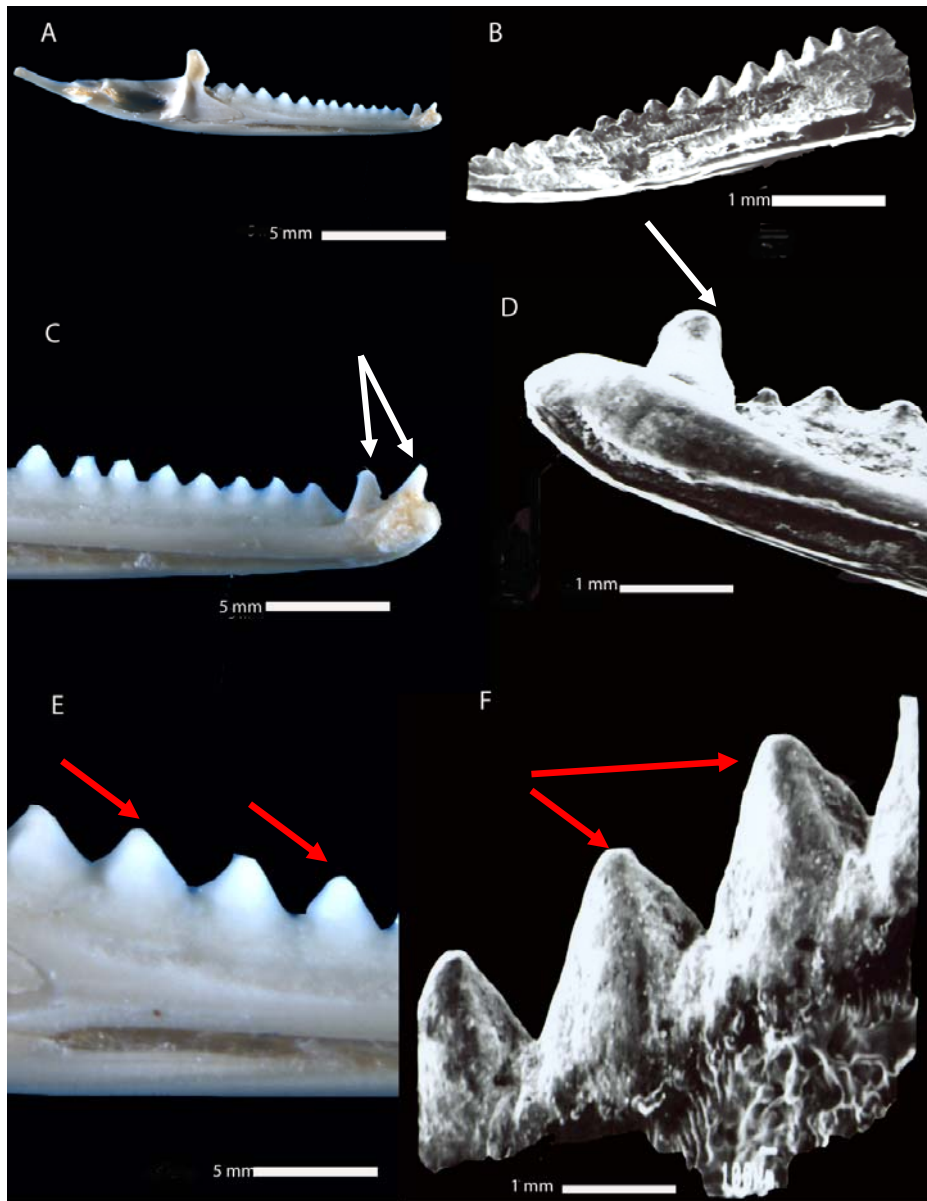


Figure 12: Plate showing fossil material attributed to *A. aculeata*. A- Fresh specimen of *A. aculeata*, B-5518, C-Fresh specimen, D-5518, E-Fresh specimen, and F-5518. With the Fresh specimen, the Meckel's groove is open and very deep. It goes all the way to the anterior of the mandible (up to the first tooth in the anterior). Teeth vary in size, with the first two teeth (towards the anterior) being sharper and pointing towards the anterior of the mandible (illustrated by a white arrow). The rest of the teeth have a pyramid shape (illustrated by a red arrow). They get bigger towards the posterior of the mandible. There is spacing in between since they are unequal and have a triangular shape. The teeth are

acrodont. The same can be said when examining the fossil specimen (5518), the only thing that could not be viewed is the Meckel's groove as the specimen is a bit fragmentary.

Acanthocercus atricollis (Southern Tree Agama)

Kingdom Animalia

Phylum Chordata

Class Reptilia

Order Squamata

Suborder Lacertilia

Family Agamidae

Subfamily Agaminae

Genus *Acanthocercus*

Species *Acanthocercus atricollis*

These are very large lizards, with SVL of up to 167 mm (males) and 137 mm (females). They have broad heads (particularly males). Breeding males have dull blue to bluish back, with bright blue (anteriorly) to straw-yellow (posteriorly) spines (Branch, 1998).

This *Agama* species prefers open savannah particularly with *Brachystegia* and *Acacia* trees (Branch, 1998). They are found in Ethiopia through E. Africa to north eastern parts of the subcontinent, reaching southern limits in coastal KwaZulu-Natal, E. Botswana (Lobatsi) and Ovamboland (Branch, 1998).

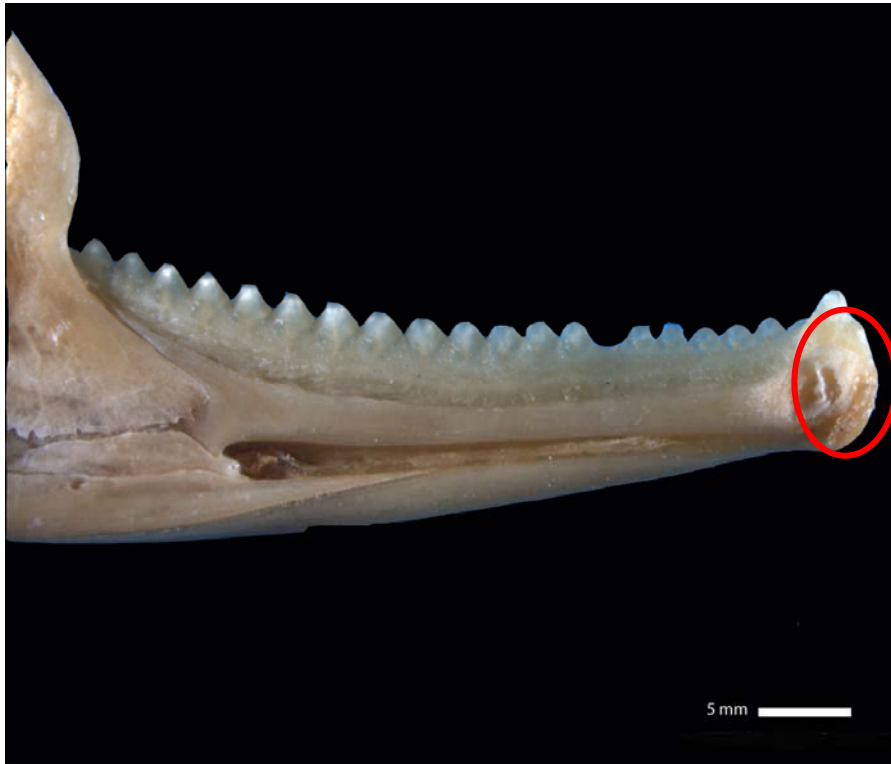


Figure 13: photo showing the left mandible of *A. atricollis*. The Meckel's groove is very deep and goes all the way to the anterior of the mandible. It takes approximately 15 % of the mandible. The first tooth is bigger than all the other tip and has a rounded tip. Tooth morphology is almost similar throughout the mandible in that they also have a triangular shape but with a rounded tip. They are also almost equal in size but the ones towards the anterior of the mandible are the smallest. The mandible is rounded (circled with red) at the front. The teeth are acrodont.

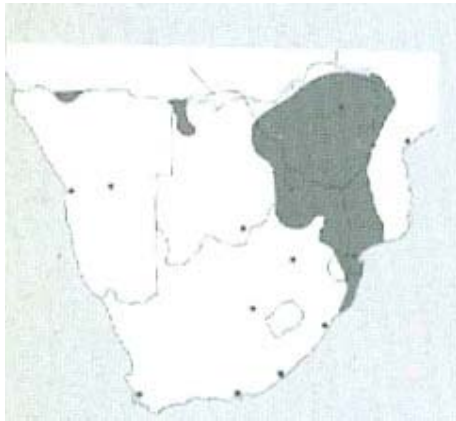


Figure 14: Map showing geographical distribution of *Acanthocercus atricollis* in southern Africa (Branch, 1998).

3.1.1.2 Fossils specimens attributed to *Acanthocercus atricollis*

Kingdom Animalia

Phylum Chordata

Class Reptilia

Order Squamata

Suborder Lacertilia

Family Agamidae

Subfamily Agaminae

Genus *Acanthocercus*

One specimen from Coopers was attributed to cf. *A. atricollis* sp. Specimen 23542 shows several characters that are typical of *A. atricollis*. There is some spacing in between the teeth as they have a triangular shape, the Meckel's canal is not that clear but can be seen. This specimen has teeth with rounded tips as seen in extant *A. atricollis*

Specimen 23542

This right hemi-mandible is 16 mm in length. It preserves most of the dentition but the body has been split. There is some spacing in between the dentition and these teeth have a triangular shape with rounded teeth. The posterior dentition is morphotype 3, flattened with no ridges or grooves. There is some slight spacing to the teeth in the posterior part of the mandible. This specimen may be fairly confidently associated with the genus *Agama*.

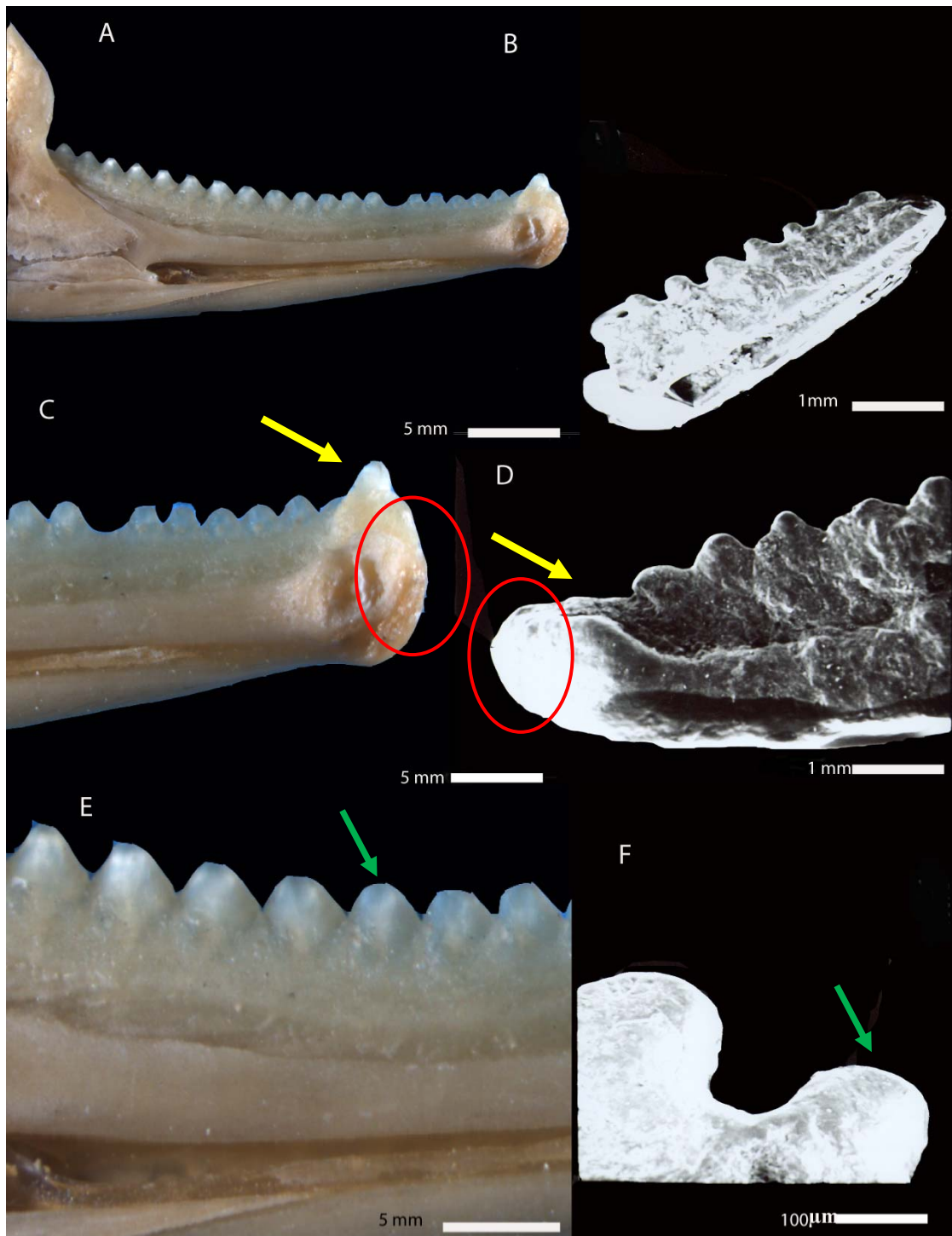


Figure 15: The above plate shows all fossil material attributed to *A. atricollis*. A-Fresh specimen, B-23542, C-Fresh specimen showing the anterior of the mandible, D-specimen 23542 also showing the anterior of the mandible, E-Fresh specimen showing teeth in detail, and F-showing teeth of specimen 23542 in detail. When looking at the fresh specimen, the

first tooth is bigger than all the other tip and has a rounded tip. Tooth morphology is almost similar throughout the mandible in that they also have a triangular shape but with a rounded tip (illustrated by a green arrow). They are also almost equal in size but the ones towards the anterior of the mandible are the smallest. The mandible is rounded (circled with red) at the front. The teeth are acrodont. The same attributes can be said when looking at specimen 23542, except that it lacks the big front tooth (illustrated by a yellow arrow).

3.1.2 Pseudocordylus Forms

Only mandibular remains could be identified in the fossil sample, so morphological comparisons were confined to this anatomical area. Cooper's Cave has an abundance of micro-mammals and they are easily identifiable. Squamate limbs on the other hand, are a bit difficult to identify.

Only fossils thought to be of best quality were taken pictures and included in this study.

Pseudocordylus, or the "Crag Lizards", are small to large girdled lizards from South Africa. Six species of *Pseudocordylus* are known; they are distinguished from *Cordylus* by the presence of granular scales on the back instead of osteoderms. Recent molecular data places *Pseudocordylus* within *Cordylus*. Lang (1991) was one of the first researchers to first present phylogenetic analysis of the Cordyliformes (Gerrhosauridae and Cordylidae) using morphological data. The results showed *Chamaesaura* as the earliest diverging taxon, with *Cordylus* a sister clade comprising *Platysaurus* and *Pseudocordylus*.

Frost et.al's (2001) analysis retrieved a step-like phylogeny, with *Chamaesaura* and two separate lineages of *Pseudocordylus* nested among the 15 species of *Cordylus* sampled. Most authors proposed that *Pseudocordylus* and *Chamaesaura* be incorporated with *Cordylus*, instead of implementing a major taxonomic revision on the basis of an incompletely sampled phylogeny with limited resolution (Stanley, et.al, 2011). Some authors have implemented a combination of the old and new taxonomies, maintaining *Pseudocordylus* in the synonymy of *Cordylus* but treating *Chamaesaura* as a valid genus. These have no phylogenetic basis but rather a matter of preference amongst authors (Stanley, et.al, 2011). They are separated in this study because of the morphological difference, and this could also mean their osteology might differ.

Pseudocordylus melanotus females are approximately 80-120 mm in length (Snout-Vent Length), whilst their male counterparts are 143 mm (SVL). Members of this species have scales on their flanks separated by granular interspaces; and they have a single row of about 4-6 elongate temporal scales (Branch, 1998). The coloration of the species is varied; breeding males are more colorful and have bigger heads. They are strictly diurnal lizards; living among or growing on (saxicolous) rocks (McConnachie, *et. al.*, 2009).

Pseudocordylus occupy rocky outcrops on mountain plateaus and in rolling grassland from the Amatola Mountains to Gauteng and Mpumalanga (Branch, 1998). Individuals can be easily noticed as they attract attention when perching on rocks (McConnachie & Whiting, 2003).

3.1.2.1 Modern Skeletal Sample

Pseudocordylus melanotus

Kingdom Animalia

Phylum Chordata

Class Reptilia

Order Squamata

Family Cordylidae

Genus *Pseudocordylus*

Species *Pseudocordylus melanotus*

Description: Meckel's canal starts in the middle of the dentary. It is deep; adjacent to about 30% of the dentary. It narrows out towards the anterior of the bone. Teeth are

characteristically tightly packed. At the posterior, separation occurs and there is some space in between the teeth. Teeth are in direct contact with each other towards the anterior of the mandible. Teeth towards the posterior have a rather flattened top, whilst towards the anterior; some form a peak at the tip. There is a bony “protrusion” or “beaking” at the anterior of the mandible; next to the first tooth. The coronoid is almost rounded. The foramen is large and found on the opercular.



Figure 16: photo showing the left mandible of *Pseudocordylus melanotus*



Figure 17: Characteristic “beaking” on the anterior mandible of *Pseudocordylus* (indicated by white arrow). Note also the position and form of Meckel’s canal, ending under approximately the 15th tooth. This specimen also shows erupting dentition. The tightly packed anterior teeth are also characteristic of this genus, with wider gaps in the posterior dentition.



Figure 18: Map showing geographical distribution of *Pseudocordylus melanotus* in southern Africa (Brach, 1998).

3.1.2.2 The Fossil Specimens attributed to *Pseudocordylus*

Kingdom Animalia

Phylum Chordata

Class Reptilia

Order Squamata

Family Cordylidae

Genus *Pseudocordylus*

14 specimens from Coopers were attributed to cf. *Pseudocordylus* sp. Specimens 2375, 354, 19882, 24708, 23528, 2608, 24713, and 24714,. All of these specimens show several characters that are typical of this genus. They all share closely packed anterior teeth, a long Meckel's canal and the bony beaking at the most anterior part of the mandible. Some

specimens have teeth with flattened tops towards the posterior, and they form a peak towards the anterior as seen in extant *P. melanotus*.

Specimen 2375

Specimen CD 2375 is a left hemi-mandible. The specimen is 20 mm in length and has lost much of its anterior dentition. Nevertheless, there is sufficient morphology preserved to note several characters that align this specimen with *Pseudocordylus*. In overall shape and form the mandible is lightly built, with a typical “canoe” like shape to the body of the mandible. Although much of the anterior dentition is broken, it is clear that in its original condition, the anterior dentition was closely packed as is evidenced by the roots left in the mandible. The preserved anterior dentition shows some “sharpening” of the tip (see Figure 9), while the posterior dentition is more flattened and without grooves, similar to a morphotype 1 dentition. There is, in addition, slight spacing of the posterior teeth. Most characteristically there is a distinctive beak at the anterior tip of the mandible (Figure 11).

Specimen CD 354

This left hemi-mandible is 22 mm in length. It preserves most of the dentition but the body has been split along its long axis. The specimen has the characteristic beaking of the anterior tip of the mandible common to *Pseudocordylus*. The anterior dentition is closely packed, and shows some slight sharpening of the tips of the teeth. The posterior dentition is morphotype 1, flattened with no ridges or grooves. There is some slight spacing to the teeth in the posterior part of the mandible. This specimen may be fairly confidently associated with the genus *Pseudocordylus*.

Specimen 19882

This left hemi-mandible is 10 mm in length. It preserves most of the dentition but the body has been split along its long axis. The specimen has the characteristic beaking of the anterior tip of the mandible common to *Pseudocordylus*. The anterior dentition is closely packed, and shows some slight sharpening of the tips of the teeth. There is some slight spacing to the teeth in the posterior part of the mandible. This specimen may be fairly confidently associated with the genus *Pseudocordylus*.

Specimen 24708

This left hemi-mandible is 21 mm in length. It preserves most of the dentition but the body has been split along its long axis. The anterior dentition is closely packed, and shows some slight sharpening of the tips of the teeth. The posterior dentition is flattened. There is some slight spacing to the teeth in the posterior part of the mandible. This specimen may be fairly confidently associated with the genus *Pseudocordylus*.

Specimen 23528

This mandible preserves most of the dentition but the body has been split. The specimen has the characteristic beaking of the anterior tip of the mandible common to this genus. The posterior dentition is morphotype 1, flattened with no ridges or grooves. There is some slight spacing to the teeth in the posterior part of the mandible. This specimen may be fairly confidently associated with the genus *Pseudocordylus*.

Specimen 2608

This right hemi-mandible is 23 mm in length. It preserves most of the dentition but the body has been split along its long axis. The specimen has the characteristic beaking of the anterior tip of the mandible common to this genus. The anterior dentition is closely packed, and shows some slight sharpening of the tips of the teeth. The posterior dentition is morphotype 1, flattened with no ridges or grooves. There is some slight spacing to the teeth in the posterior part of the mandible. This specimen may be fairly confidently associated with the genus *Pseudocordylus*.

Specimen 24713

This left hemi-mandible is 18 mm in length. It preserves most of the dentition but the body has been split along its long axis. The anterior dentition is closely packed, and shows some slight sharpening of the tips of the teeth. The posterior dentition is morphotype 1, flattened with no ridges or grooves. There is some slight spacing to the teeth in the posterior part of the mandible. This specimen may be fairly confidently associated with the genus *Pseudocordylus*.

Specimen 24714

This right hemi-mandible is 18 mm in length. It preserves most of the dentition but the body has been split. Beaking cannot be examined since the anterior has been cut off. The anterior dentition is closely packed, and shows some slight sharpening of the tips of the teeth. The posterior dentition is morphotype 1, flattened with no ridges or grooves. There is some slight spacing to the teeth in the posterior part of the mandible. This specimen may be fairly confidently associated with the genus *Pseudocordylus*.

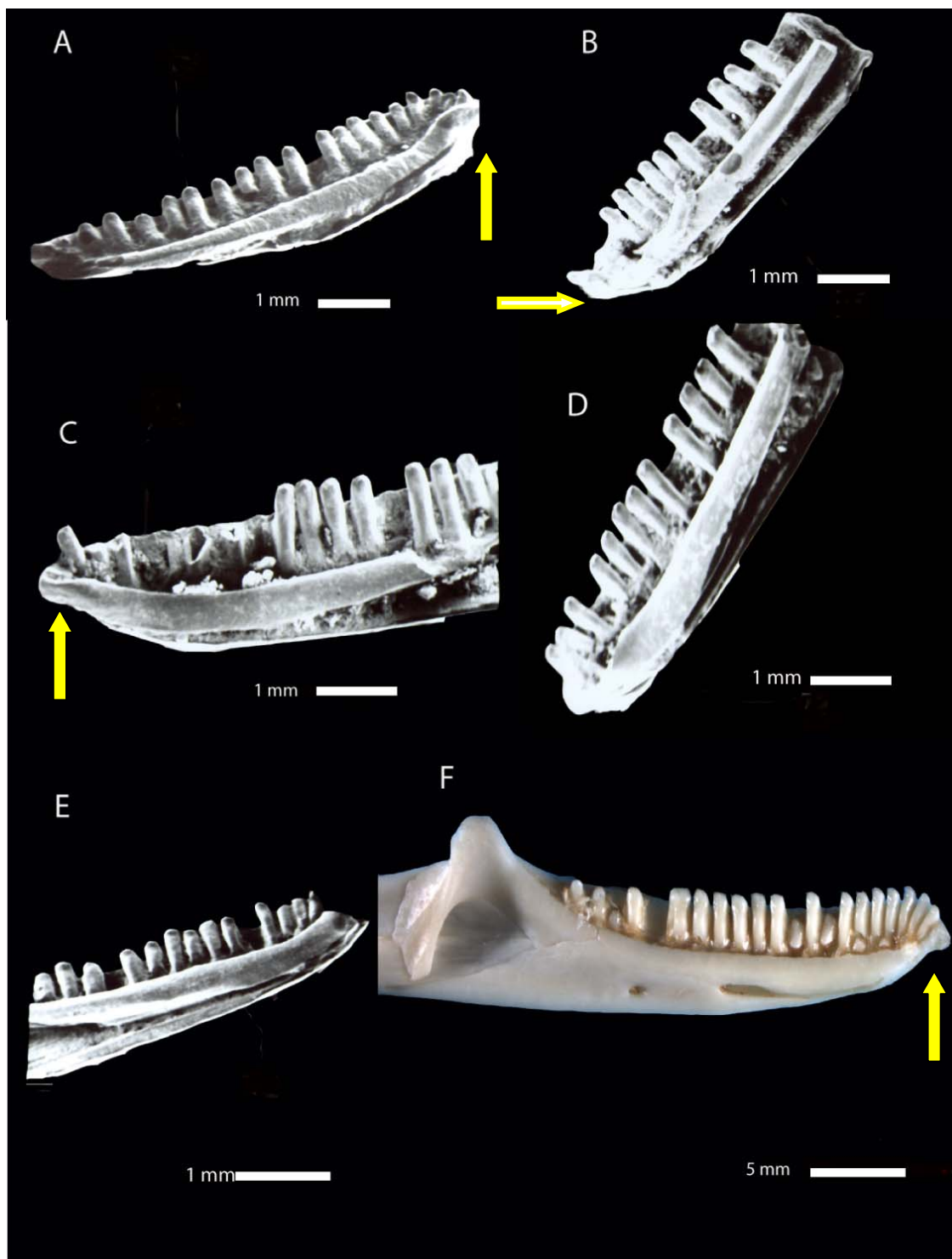


Figure 19: the above picture plate shows all fossil material attributed to *P. melanotus*. A-CD 354, B-2608, C-CD 2375, D-24708, E-24713, and F-Fresh specimen. In all of the above

specimens some form of beaking is seen (illustrated by a yellow arrow). The tightly packed anterior teeth are also characteristic of this genus, with wider gaps in the posterior dentition. Note also the position and form of Meckel's canal, ending under approximately the 15th tooth on specimen F and this specimen also shows erupting dentition.

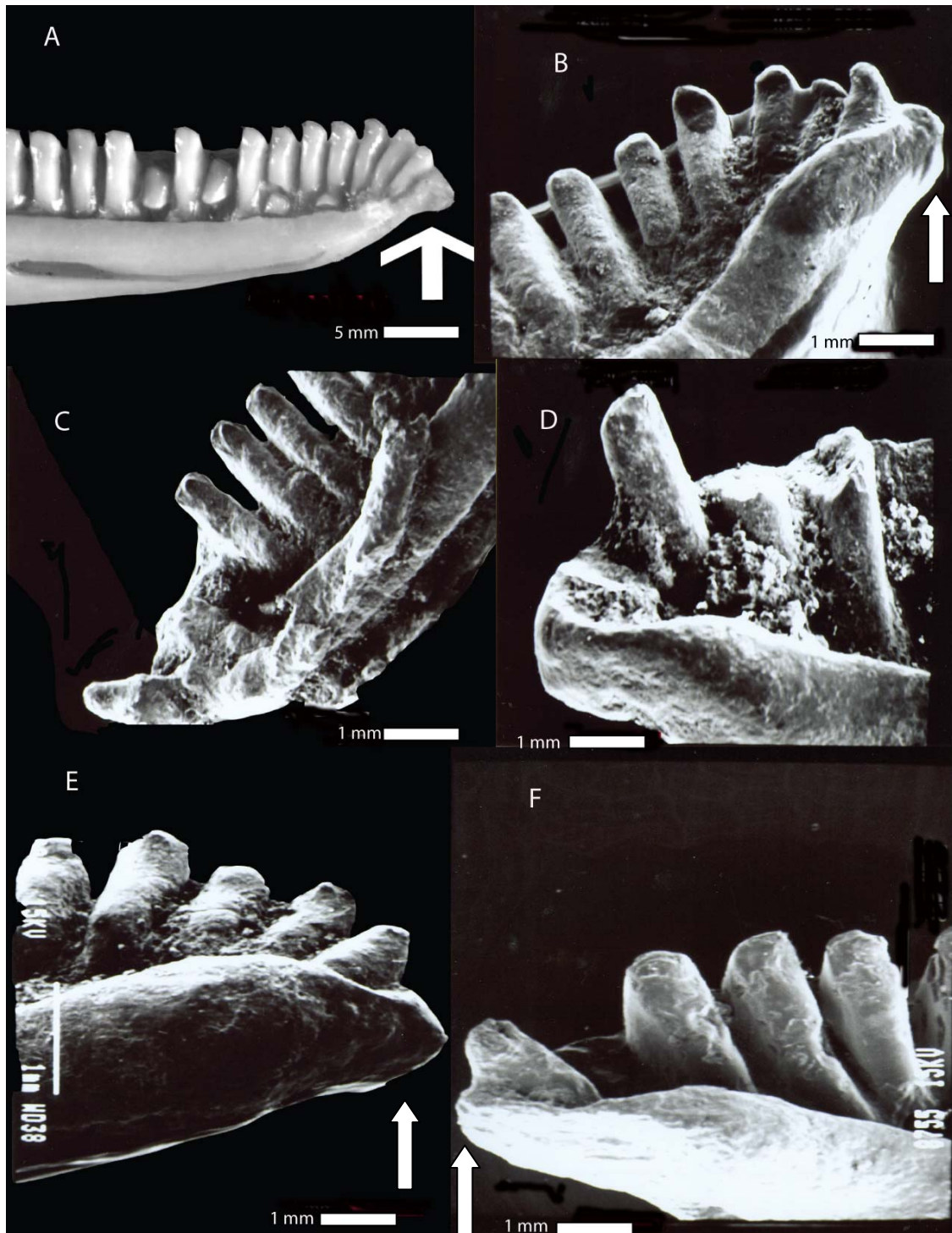


Figure 20: The above picture plate shows beaking in close range (illustrated by a white arrow). This is seen as the most important characteristic of this genus. A-Fresh specimen, B-CD 354, C-2608, D-2375, E-19882, and F-24078. All the above specimens show beaking,

and in some specimens like B, D, and E beaking is very extensive as seen on the Fresh specimen (A).

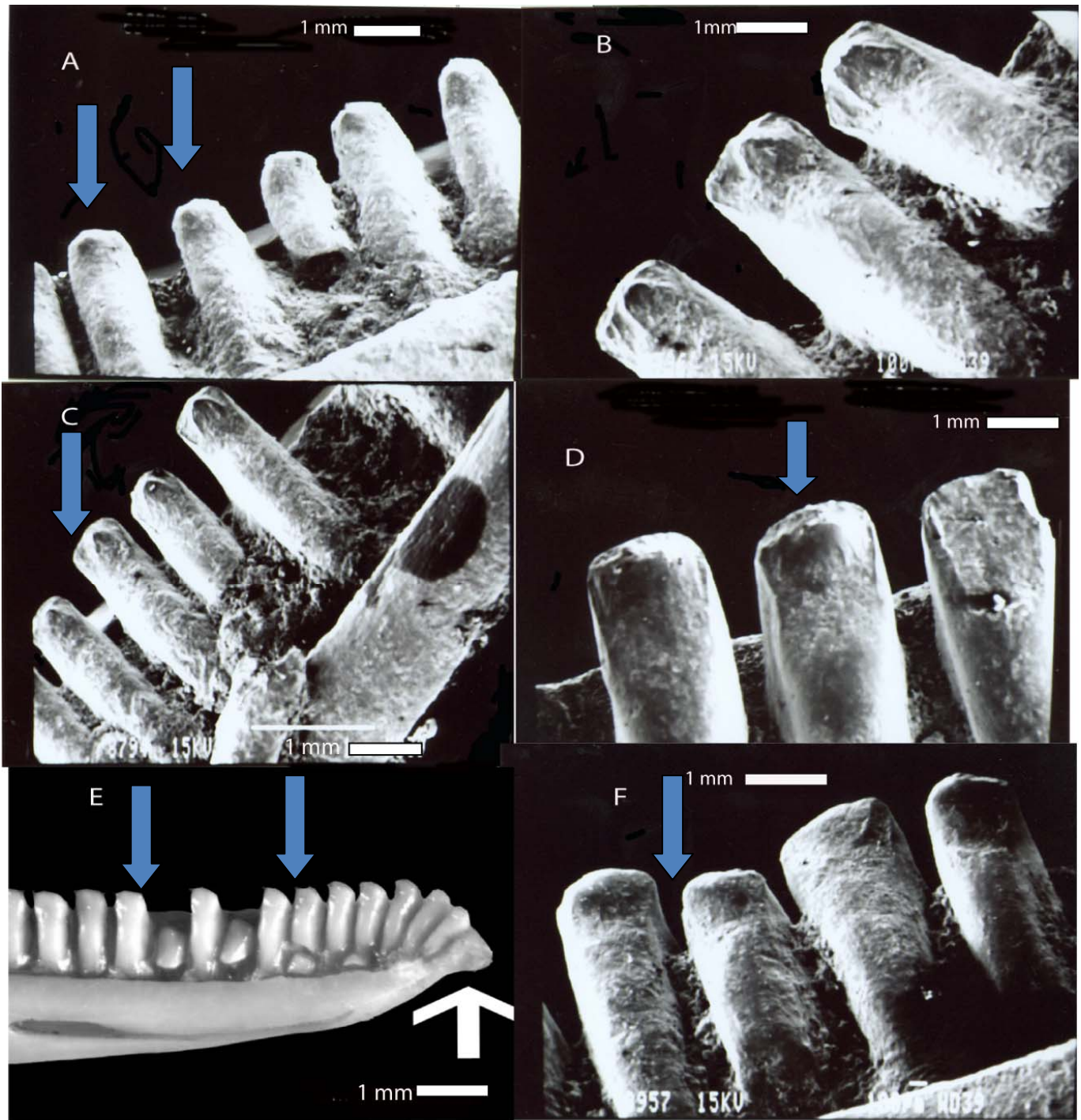


Figure 21: the above picture plate shows teeth of specimens attributed to *P. melanotus* in detail. A-CD 354, B-24713, C-24714, D-CD 2375, E-Fresh Specimen, and F-23528. All the above mentioned specimens show tightly packed anterior teeth and spacing begins to occur as one moves posteriorly in the dental row. Most if not all tips are flattened, another

characteristic of *Pseudocordylus* species. The anterior teeth show some sharpened tips whilst the posterior show flattened tips (illustrated by a blue arrow).

3.1.3 Cordylus Forms

Cordylus or “girdled lizards” are considered to be the most characteristic lizards of southern Africa (Branch, 1998). They are known to be very vigilant predators in that they can wait for their prey for long hours before capturing them. This family is found only on the African continent (unlike other families). Cordylids have a stocky body with well developed limbs. They have a triangular head (flattened on top), covered with large shields fused to the skull (Branch, 1998). Their fossil history is fragmentary and the only known fossils that were referred to as Cordyliformes (and this was the group that contained both Cordylidae and Gerrhosauridae) are known from the Early Eocene to the Early Miocene of Europe (Branch, 1998).

Most of the genera are restricted to Africa, whilst others are found only in southern Africa (Branch, 1998).

Cordylus cordylus (Cape Girdled Lizard)

Kingdom Animalia

Phylum Chordata

Class Reptilia

Order Squamata

Family Cordylidae

Genus *Cordylus*

Species *Cordylus cordylus*

These lizards have a flattened body and a triangular flattened head; males have wider heads than females (Branch, 1998). Their Snout-Vent-Length (SVL) is between 65-98 mm. These lizards are rupicolous. They are very diverse in that some are found in coastal cliffs, rock plateaus in fynbos and montane grassland, and shale bands in mesic thicket (Branch, 1998).

They are found in the coastal regions of the Cape, from Saldanha Bay to East London, but absent from George to Witelsbos (Branch, 1998).

Inland, they can be seen through the Cape fold Mountains and montane grassland of NE Cape and SE Free State, to inland E. Cape.

There are certain fossils that resemble this species, and this seems odd as it is found in the Cape. This could be because of limited number of comparative material, or it is telling a story about the palaeo-environment and origin of the species.



Figure 22: photo showing left mandible of *Cordylus cordylus*. Recently processed extant specimen of *C. cordylus* shows one foramen and an open Meckel's groove. The groove is

deep (about 15%) and seems to open all the way to the anterior of the mandible. There is some form of beaking (illustrated in red). Teeth are almost (if not) equal in size and they have rounded tips (but sharpened in the middle). There seems to be some constriction in the mid section of the tooth.

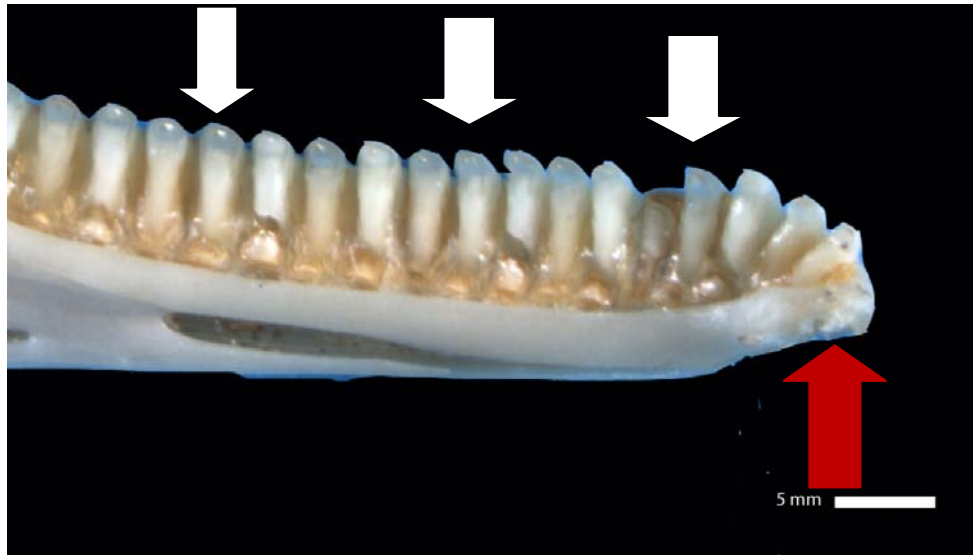


Figure 23: The difference between *C. cordylus* and *P. melanotus* is that teeth of *C. cordylus* are rounded at the tip; with almost a pointy tip in the middle. And the “beaking” is not as vigorous as in *P. melanotus* (red arrow).



Figure 24: Map showing geographical distribution of *Cordylus cordylus* in southern Africa (Branch, 1998).

3.1.3.1 Fossil specimens attributed to *Cordylus cordylus*

Kingdom Animalia

Phylum Chordata

Class Reptilia

Order Squamata

Family Cordylidae

Genus *Cordylus*

One specimen from Coopers was attributed to cf. *Cordylus cordylus* sp. Specimen 24706 shows several characters that are typical of this genus. It has closely packed anterior teeth, a long Meckel's canal. This specimen has teeth with rounded tips, forming a peak towards the middle of the tip as seen in extant *C. cordylus*.

Specimen 24706

This left hemi-mandible is 15 mm in length. It preserves most of the dentition. The anterior dentition is closely packed, and shows some slight sharpening of the tips of the teeth. The posterior dentition is morphotype 2, rounded with no ridges or grooves. There is some slight spacing to the teeth in the posterior part of the mandible. This specimen may be fairly confidently associated with the species *C. cordylus*.

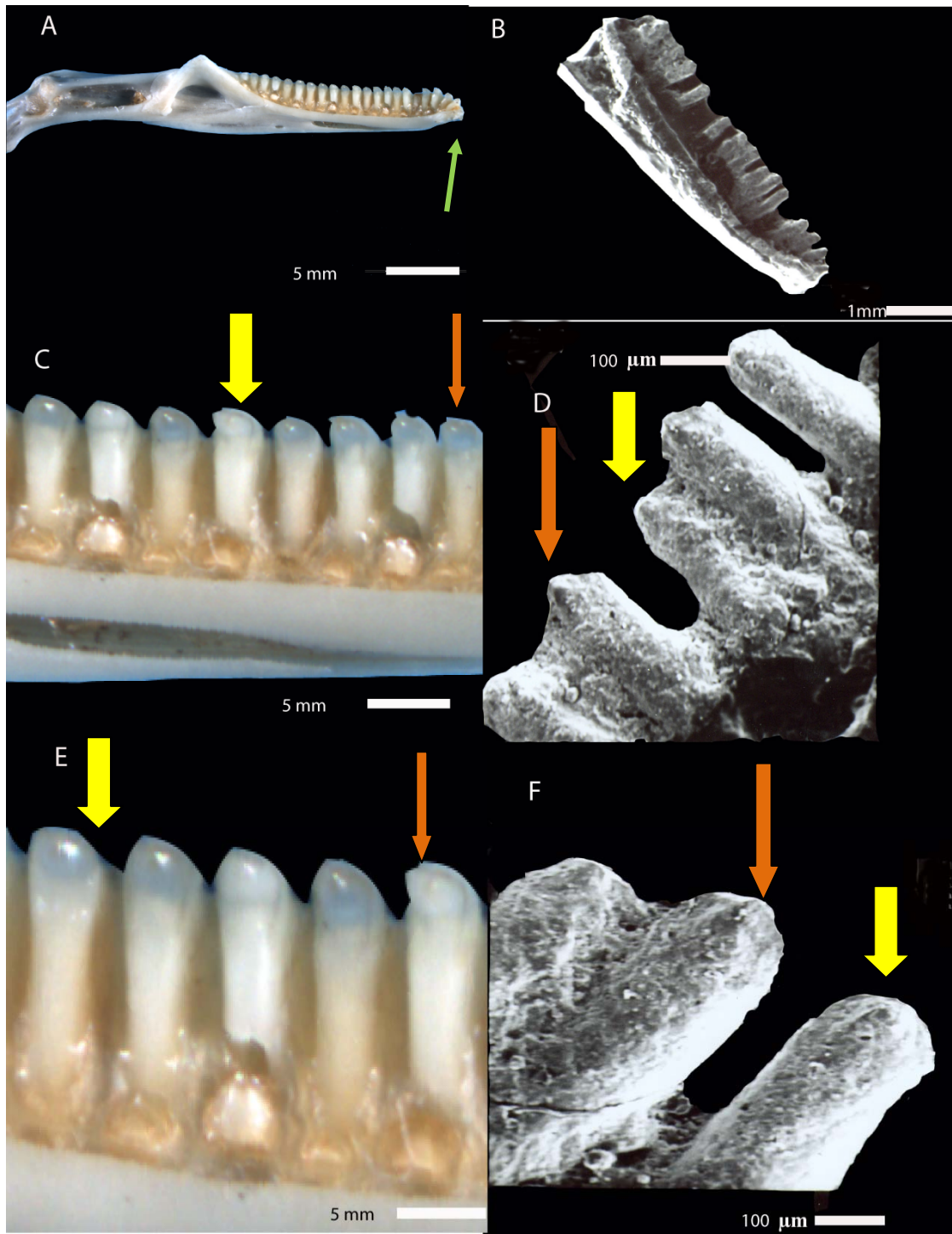


Figure 25: The above picture plate shows all fossil specimens attributed to *Cordylus cordylus*. A-Fresh specimen, B-specimen 24706, C-Fresh specimen showing the mid-section, D-midsection of specimen 24706, E-teeth of Fresh specimen, and F-teeth of specimen 24706.

When looking at the fresh specimen of *C. cordylus* there is one foramen and an open Meckel's groove. The groove is deep (about 15%) and seems to open all the way to the

anterior of the mandible. There is some form of beaking (illustrated in green). Teeth are almost (if not) equal in size and they have rounded tips (but sharpened in the middle; illustrated in yellow and orange). There seems to be some constriction in the mid section of the tooth. The difference between *C. cordylus* and *P. melanotus* is that teeth of *C. cordylus* are rounded at the tip; with almost a pointy tip in the middle. And the “beaking” is not as vigorous as in *P. melanotus* (green arrow). The same is seen in the fossil specimen except beaking, and the teeth have varied tips (as illustrated in yellow and orange).

Cordylus vittifer (Transvaal Girdled Lizard)

Kingdom Animalia

Phylum Chordata

Class Reptilia

Order Squamata

Family Cordylidae

Genus *Cordylus*

Species *Cordylus vittifer*

These lizards are quite small with a flattened body and a triangular head with rough shields (Branch, 1998). The SVL is 70-95 mm. There is an isolated population in Free State; and this population is different in that it has a prominent dark lateral band and glandular scales on the thighs (in females) (Branch, 1998).

C. vittifer is closely related to *C. machadoi* (Machadoe's girdled lizard) found in northwestern Namibia (Broadley, *et.al*, 2002). The pale vertebral stripe found in *C. vittifer* is not present though.

C. vittifer prefer rocky outcrops in grassland. They are found in Gauteng and adjacent Mpumalanga, N. Free State, SE Botswana, Swaziland, KZN, and Mozambique (Branch, 1998).



Figure 26: photo showing left mandible of *C. vittifer*. *Cordylus vittifer* also has some form of “beaking” but different from that of *P. melanotus* in that it is not as easily recognized as in the latter. Teeth are equal in size (length) and they have varied tips; some are rounded whilst others have flattened tips. There is slight spacing in between teeth, and there are some erupting teeth. The tips of the teeth point towards the posterior of the mandible. The Meckel’s groove is open but is not that visible; it takes about 5 % of the mandible. It is not open all the way. There are two foramina; with one bigger than the other and forming part of the Meckel’s groove (illustrated in orange).

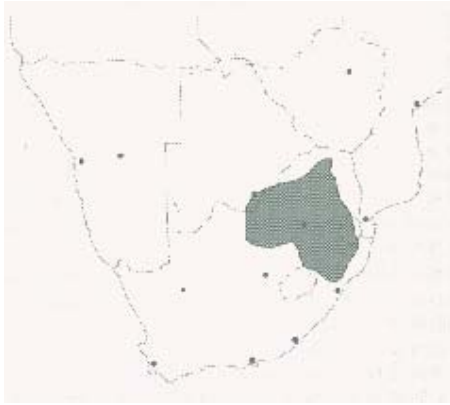


Figure 27: Map showing geographical distribution of *Cordylus vittifer* in southern Africa (Branch, 1998).

3.1.3.2 Fossil specimens attributed to *C. vittifer*

Kingdom Animalia

Phylum Chordata

Class Reptilia

Order Squamata

Family Cordylidae

Genus *Cordylus*

One specimen from Coopers was attributed to cf. *C. vittifer* sp. Specimen 24711 shows several characters that are typical of this genus. It has closely packed anterior teeth and they are almost equal in size, the Meckel's canal cannot be viewed as this specimen is a bit fragmentary. There is some variation when it comes to the tips of this specimen; typical of *C. vittifer* but most of them have a flattened tip.

Specimen 24711

This left hemi-mandible is 16 mm in length. It preserves most of the dentition but the body has been split. The dentition is closely packed throughout the mandible, and shows some slight sharpening of the tips of the teeth, whilst most of them are rounded. The posterior dentition is morphotype 1, flattened with no ridges or grooves. There is some slight spacing to the teeth in the posterior part of the mandible. This specimen may be fairly confidently associated with the genus *Cordylus*.

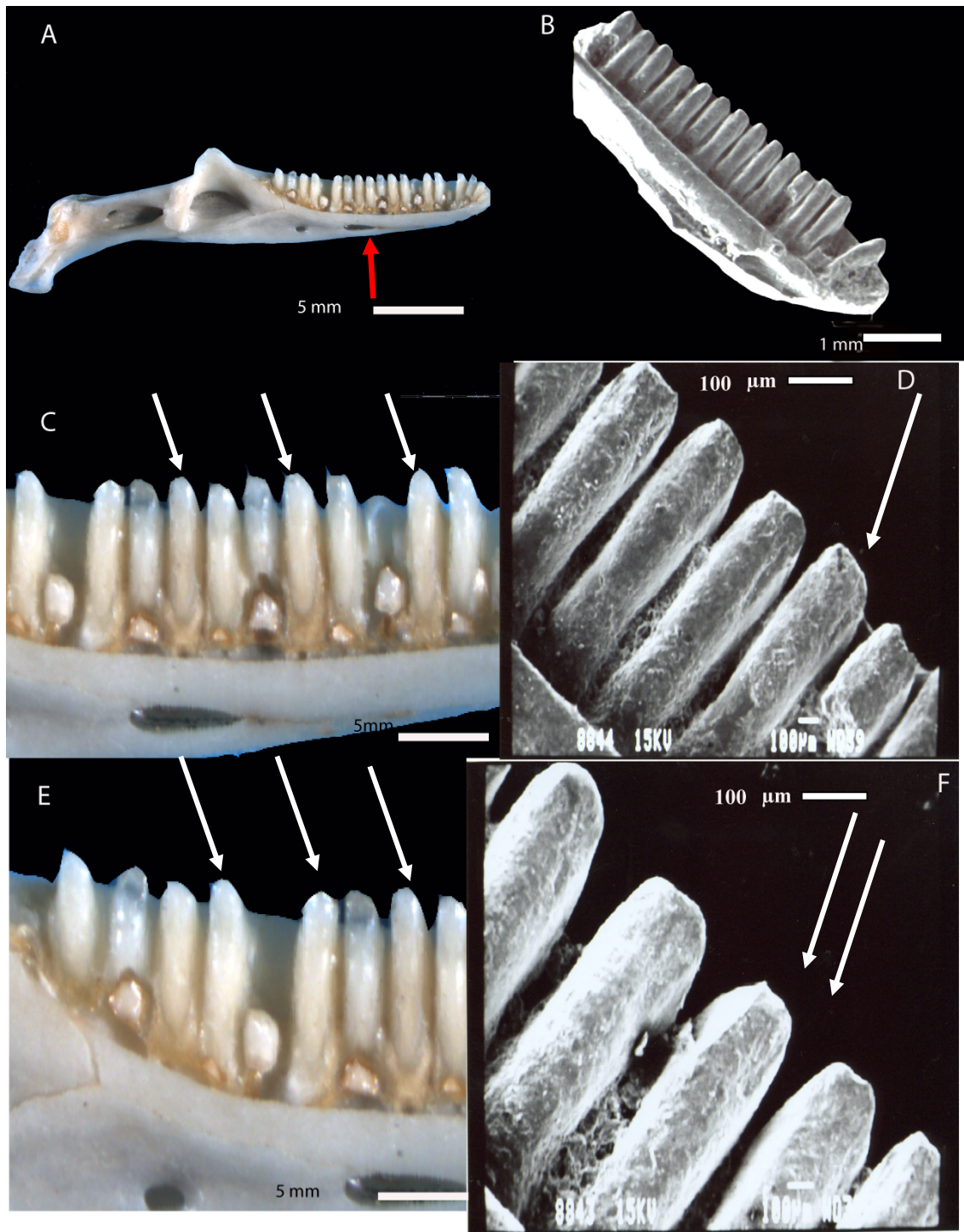


Figure 28: The above picture plate shows all fossil specimens attributed to *C. vittifer*. A- Fresh specimen of *C. vittifer*, B-Fossil specimen 24711, C-midsection of the Fresh specimen, D-midsection of 24711, E-Teeth of the Fresh specimen, and F-teeth of specimen 24711. When looking at the fresh specimen, teeth are equal in size (length) and they have varied tips; some are rounded whilst others have flattened tips. There is slight spacing in between teeth,

and there are some erupting teeth. The tips of the teeth point towards the posterior of the mandible. The Meckel's groove is open but is not that visible; it takes about 5 % of the mandible. It is not open all the way. There are two foramina; with one bigger than the other and forming part of the Meckel's groove (illustrated in red). The same can be said when looking at the teeth of specimen 24711, they are tightly packed and most of them point towards the posterior of the mandible (illustrated in white). They are also almost equal in size. Nothing can be said about the foramina and the Meckel's groove as this specimen is a bit fragmented.

Trachylepis capensis (Cape Skink or Cape three-lined Skink)

Kingdom Animalia

Phylum Chordata

Class Reptilia

Order Squamata

Family Scincidae

Genus *Trachylepis*

Species *Trachylepis capensis*

These lizards have a length of 80-135 mm maximum. They are large fat (often obese) skinks with a large window in each lower eyelid (Branch, 1998). The body is light brown to olive grayish-brown, with three pale stripes. Between these stripes and extending onto the flanks are a series of dark brown to black spots or short bars.

Trachylepis capensis live in varied habitats; they prefer arid karroid veld, moist coastal bush, and montane grassland. They can be found throughout most of the country, and they also occur in Botswana and Namibia, and a few isolated populations have been found in Zimbabwe (Inyanga Mountains) and in Liuwa Plain in Zambia (Branch, 1998).



Figure 29: photo showing left mandible of *T. capensis*. The above mandible has no Meckel's groove. The teeth are almost equal in size, and they are tightly packed but there is slight spacing towards the posterior of the mandible. There are two foramina next to the 14th tooth; and they are unequal in that the bigger one looks like a groove rather (illustrated in white). Teeth are almost equal in size, and most (if not all) of them have flattened tops. The flatness is different from that of *P. melanotus* in that most of the *P. melanotus* teeth are flattened but almost rounded (at the tip). There is some eruption (towards the posterior of the mandible; illustrated in blue).

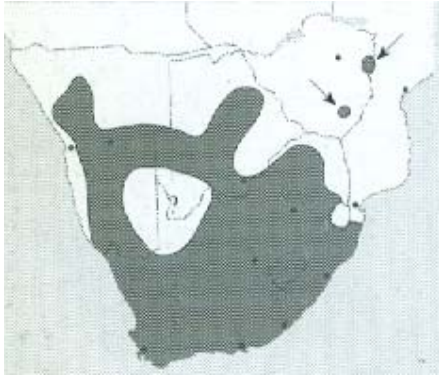


Figure 30: Map showing geographical distribution of *Trachylepis capensis* in southern Africa (Branch, 1998).

3.1.3.3 Fossils specimens attributed to *Trachylepis*

Kingdom Animalia

Phylum Chordata

Class Reptilia

Order Squamata

Family Scincidae

Genus *Trachylepis*

Three specimens from Coopers were attributed to c.f *Trachylepis* sp. Specimens 24710, 24712 and 16379 show several characters that are typical of this genus. They have closely packed teeth throughout the mandible, no Meckel's canal. These specimens have teeth that are equal in size, flattened tips with a sharpened edge pointing towards the posterior of the mandible.

Specimen 24710

This left hemi-mandible is 17 mm in length. It preserves most of the dentition but the body has been split. The anterior dentition is closely packed, and shows some slight sharpening of the tips of the teeth on the edge towards the posterior of the mandible. The posterior dentition is morphotype 1, flattened with no ridges or grooves. There is some slight spacing to the teeth in the posterior part of the mandible. This specimen may be fairly confidently associated with the genus *Trachylepis*.

Specimen 24712

This right hemi-mandible is 16 mm in length. It preserves most of the dentition but the body has been split. The anterior dentition is closely packed, and shows some slight sharpening of the tips of the teeth. The posterior dentition is morphotype 1, flattened with no ridges or grooves. There seems to be no Meckel's canal, meaning it could be another *Trachylepis* species. There is some slight spacing to the teeth in the posterior part of the mandible. This specimen may be fairly confidently associated with the genus *Trachylepis*.

Specimen 16379

This left hemi-mandible is 14 mm in length. It preserves some of the dentition. The anterior dentition is closely packed, and shows some slight sharpening of the tips of the teeth at the edge pointing towards the posterior of the mandible (even though the specimen is not properly cleaned). There is some slight spacing to the teeth in the posterior part of the mandible. This specimen may be fairly confidently associated with the genus *Trachylepis*.

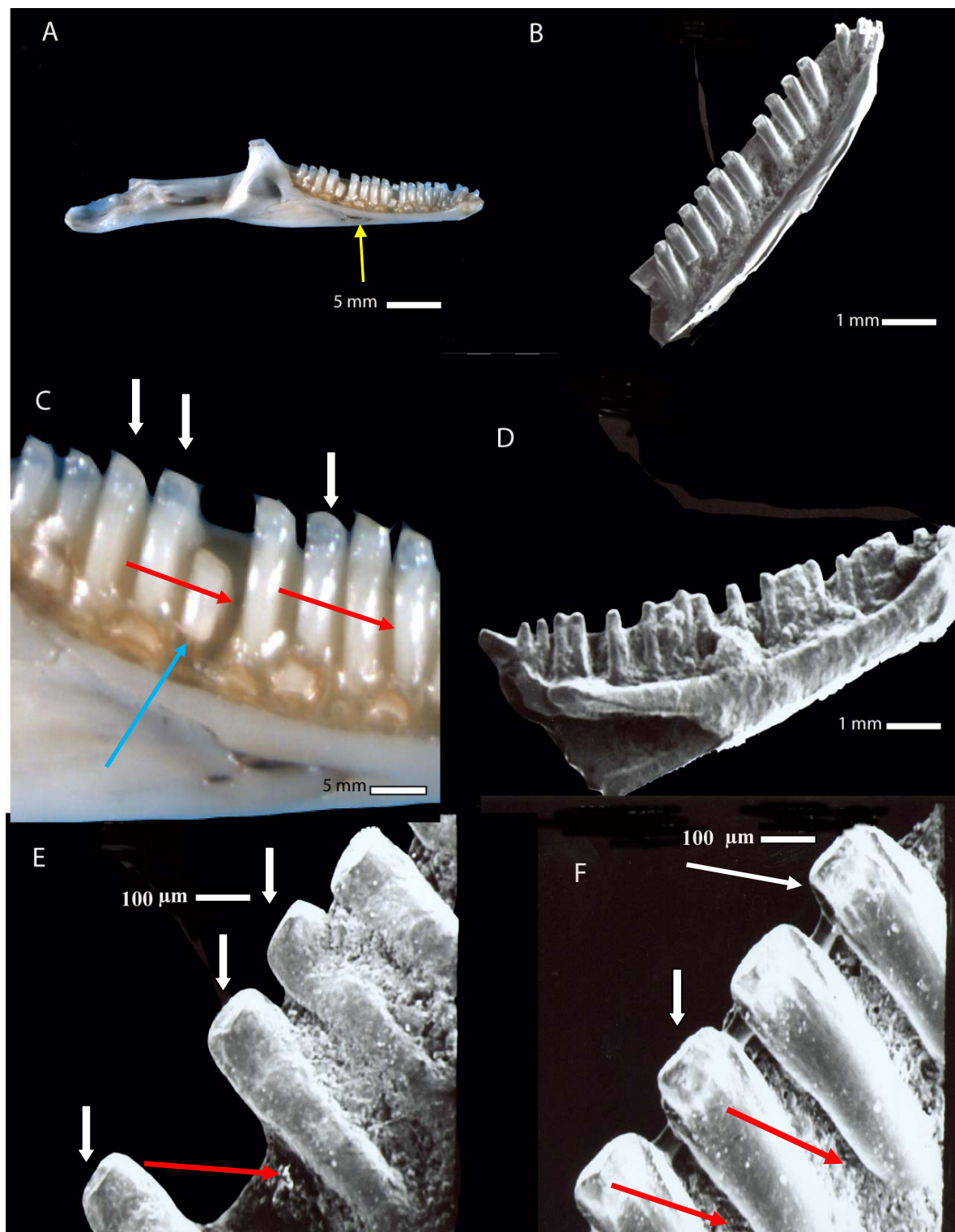


Figure 31: The above picture plate shows fossil material attributed to *Trachylepis capensis*. A-Fresh specimen of *T. capensis*, B-specimen 24710, C-Teeth of a Fresh specimen towards the posterior, D-specimen 16379, E-Teeth of specimen 24712, and F-Teeth of specimen

24710. When looking at the fresh specimen, the mandible has no Meckel's groove. The teeth are almost equal in size, and they are tightly packed but there is slight spacing towards the posterior of the mandible. There are two foramina next to the 14th tooth; and they are unequal in that the bigger one looks like a groove rather (illustrated in yellow). Teeth are almost equal in size, and most (if not all) of them have flattened tops. The flatness is different from that of *P. melanotus* in that most of the *P. melanotus* teeth are flattened but almost rounded (at the tip). There is some eruption (towards the posterior of the mandible; illustrated in blue). When looking at the fossil specimens, the same can be said about the teeth in that they are almost equal in size (see Fig 29B), and they have flattened tops. The flatness differs from one specimen to the other in that in Fig 29E the flatness shows roundness on some teeth and Fig 29F shows flatness only. There are some tooth morphology changes (illustrated in red); teeth show some constriction from the root to midsection of the tooth.

CHAPTER 4

4.1 Discussion and Conclusions

This study has demonstrated that herpefauna exists, in reasonable levels of abundance and with adequate preservation within the fossil record of the dolomitic region now known as the Cradle of Humankind. Using the site of Coopers as a proxy for other fossil bearing sites, herpefauna, particularly lizards, though other reptiles exist, are found in significant numbers and significant frequency to potentially be used as a compliment to classical methods of establishing past ecologies and environments such as large and small mammals. The present research has demonstrated for the first time the presence of a relative abundance of herpefauna at numbers far greater than any previous study has recognized. In the present survey of the Coopers assemblage over 600 individual specimens (of which approximately 60% was identifiable) were pulled from the fossil fauna, the majority being very small forms found among micro-mammals. While the percentage of total specimens searched was not calculated in this study it is clear that the presence of these forms is not insignificant. This bodes well it is highly likely that these high concentrations of herpefauna will be found at other sites in the Cradle as well based on the description of its fauna to date. In fact, based upon present studies of the Coopers site, and the “newer” sites such as Malapa (Berger *et al.*, 2010; Dirks *et al.*, 2010), and investigations of their microfaunal components (e.g. Val *et al.*, 2011), it is clear that Coopers is not an exception and one may additionally hypothesize that other sites will broadly follow its faunal composition.

The present study, however, did not examine a critical area of research necessary for establishing the true value of this herpetofaunal assemblage in that it did not examine the taphonomy of the herpefaunal fossils. The way in which these fossils came to originally be preserved alongside the mammals at Coopers bearing on what environment their presence in

the assemblage is predicated. Based upon the Families of reptiles described in this thesis, it is not unlikely that many of these animals were living in, or in close proximity to the entrance of the cave and found themselves within the assemblage through natural death or predation by animals either living in the cave or hunting in the cave. However, the possibility that some significant percentage of the herpefaunal assemblage is being brought to the cave by birds of prey cannot be overruled and is in fact likely. Birds of prey of all kinds are well known to include herpefauna in their diets (Steyn, 1982; Maclean, 1985; Berger, *et. al.*, 1995). Included among these birds of prey are not only owls but many types of falcons and other small raptors that might use the entrance of caves or trees within the entrance of caves (Brain, 1981) to roost in, use as feeding points or to hunt from. It is important to note, and is an important outcome of the present study, that most of the forms of reptile discovered and described here are diurnal forms, thus while owls may in fact have contributed to this assemblage, the mere fact that these animals are found among the remains of micro-mammals – which we traditionally associate with owl collecting (see Brain, 1981; Levinson, 1982; Kusmer, 1990; and Stahl, 1996) – does not mean that these animals were collected by the same agent. Their presence among this assemblage potentially has more to do with the way in which the excavations were conducted in that the specimens were recovered during fine sieving operations and not directly *in-situ*. Thus, the vast majority of the herpefauna do not have singular provenience as they were too small to be noted by excavators during excavation in most cases and are only recorded to a small area of a few centimetres. While this level of accuracy has been previously seen as acceptable, the results of this study (namely the recognition that there are diurnal herpefaunal forms mixed with nocturnal small mammal forms) indicate that there is a need to examine the relationship between these individual micro-animals. This recognition may lead to the identification of previously unrecognized forms of collectors such as other birds of prey or even small mammals or other reptiles.

Unfortunately, as with many areas of taphonomy, the understanding of the behaviour of animals around caves in this and other regions of fossil bearing interest is woefully inadequate. It is quite clear from this study that there need to be extensive and detailed studies of such environments, studies that do not only concentrate on the traditionally “super” - collectors such as hyenas, porcupines, humans and owls - but that also examine less frequent (or less frequently recognized) utilizers of the cave environment that may contribute to an assemblage, and thus be potential contributors to an ancient assemblage. Furthermore, it points to the need to examine how animals, including small animals such as lizards, snakes and rodents utilize these environments, both the subterranean environment as well as the entrance environment. Without such studies, the results of such a study as the present one, and in fact any study of the micro-level fauna in particular relies on a significant degree of speculation when utilizing these animals to predict past environments, as one does not know “which” past environment one is actually examining – the immediate, or the distant – and if the distant the potential maximum of that distance.

Having said this, these problems challenge many of the fields of taphonomy including the study of large mammals, which suffer from the same issues of lack of primary research into behaviours of animals in *these* environments of interest, rather they largely base behaviour on studies conducted in dissimilar environments and *assume* that the behaviour of an animal, or group of animals will be similar in a karstic environment. So, as with many other studies, the present study simply highlights the need for greater research into animal behaviour in the karstic environments of southern Africa, as well as highlighting the need for more detailed taphonomic studies of modern animals and death assemblages within cave systems. The present study also highlights the need for greater precision during excavation of even micro-fossils in order to understand the relationship of even the smallest part of the assemblage.

Present work on scanning blocks using X-ray technologies, including the use of micro-focus X-ray shows promise for answering this author's call for such levels of taphonomic and spatial analysis. At least one study (Smilg, 2013) has demonstrated that standard X-ray technology can be used to find and identify fossils, including relatively small specimens, still encased in hard matrix and such methods and technologies may in fact hold promise for identifying the presence of, and the spatial positioning of, remains as small as the majority described in this thesis. Further advances in the use of micro-focus CT has shown that our field has reached a stage where such technology can even be used to identify animals of the size of small herpefauna while still wholly encased in rock (Val *et al.*, 2011). Thus the advance of technology shows great promise for removing, in the near future, many of the problems with the present herpefaunal assemblage alluded to above where provenience and spatial information is highly important.

Beyond establishing simply whether herpefaunal remains were present in the South African Quaternary fossil bearing assemblages, the present study also wished to examine whether these fauna, if present, were preserved in sufficient abundance and of sufficient quality to be of use as ecological and environmental indicators. What was not anticipated at the beginning of this project was the inadequacy of present zoological methods of collecting, storing and identifying living herpetological forms to answering questions of taxonomy in a fossil assemblage comprised of isolated bony elements. Modern Zoological collections of herpefauna typically comprise either skinned specimens or whole preserved specimens. Few if any are prepared to a level that allows examination of the whole of the skeleton or even part. The notable exception to this are some of the larger herpefauna such as monitor lizards, large snakes, crocodiles and turtles and tortoises, but even in these cases the numbers tend to be so low for such specimens on an individual basis that their use in establishing even

whether the individual displayed or skeletonised is “normal” for the population is nearly impossible, and thus studies of variation are by definition impossible. Thus, the present study was handicapped by having to spend hundreds of hours preparing specimens for examination and comparison with the fossil assemblage. This work, which is the basis for a larger, important collection of comparative herpefaunal skeletal material, and is important, proved in the time it took to finish it. An outcome of this recognition is to highlight to museum curators and others responsible for assembling such collections that this is an important area of future potential research, and thus the construction of adequately catalogued and well curated large collections of skeletonised herpefauna is desirable.

In addition to the need for larger samples, it was quickly recognized that by the nature of the available herpefauna collections for this study – both existing and prepared by this study, the research was handicapped by having to select its comparative sample from regionally available forms. Thus, in the identifications made in the present study, extreme caution must be taken in that they do not take into account variation beyond the regional, and certainly do not take into account variation that may be found in tropical and more distant populations of the hypothesized species identified. In addition, this study, by its nature a pilot study in a novel area of research, could not take into account morphologies of species not available for examination in the present study. As has been noted, herpefauna in their living morphologies (and behaviours) are poorly studied at best and thus this proves a severe handicap to studies such as the present one, which is in the “infant” stages of establishing a science of the study of quaternary aged fossils of herpefauna. It is, in this candidates opinion, important to note that prior to the present study, there was no singular documentation of the presence or abundance of herpefauna in the southern African record and thus the shortcomings noted above should be viewed in the temporal context in which the present study was undertaken.

As recognition of the existence of this important component of the fossil faunal assemblage grows, and recognition of its potential value occurs, then museums and principle investigators and other interested parties should begin to redress these shortcomings making future work both simpler and of greater value.

The potential of herpefauna to elaborate on past environments is clear for the many reasons noted in the introduction to this thesis. The present study was handicapped in its ability to utilise the material at hand to interpret past environments as it simply did not have the comparative material available to move beyond the family or generic level in most cases with any degree of confidence. Given the small comparative sample sizes available due to preparation time and simply material available an attempt at higher taxonomic identification would have been imprudent. Nevertheless, the present study did demonstrate beyond a doubt that such work is possible. There are clear morphological variations in particular the dentitions and those dentitions are in relative abundance. This means that these specimens will be of taxonomic value at levels useful for ascertaining ecological and adaptive niches. It is a subjective result of this study that many of these specimens could have been identified to a higher taxonomic value (perhaps the species level), but due to the sample sizes and lack of other comparative material this was not seen as prudent and in fact may be misleading. The important result to note is that variation in dental and mandibular form is present among the species studied in the present work and that this indicates the potential for future studies based on larger and better comparative samples. Finally, while not specifically examined in this study for obvious reasons of lack of comparative material, the post-cranial material of herpefauna is abundant and well preserved. As has been found in the study of related forms such as dinosaurs and birds, as comparative samples increase, these areas of anatomy may prove of significant value to future workers.

It was noted in the introduction to this thesis the many reasons why herpefauna were seen as potentially of significant value in their use as informants to ancient ecologies and environments. To reiterate, they tend to be more specialized in their niche behaviour, they are often highly adapted to specific environments as species, but even at higher taxonomic orders. They are certainly more temperature sensitive and thus may be used potentially as proxies for past temperature regimes and even, under the right context, as markers of temperature change through time. By and large, studies of living forms indicate that they tend to have more limited home ranges due to body size and thermoregulatory constraints than do mammals. Thus, herpefauna will be superb indicators of past environments as we overcome the many issues that have been highlighted by this work. Future studies based on larger comparative sets that are better provenienced from larger and more varied geographical regions will vastly improve the quality of output. The important points that the present research has made are that herpefauna do exist in abundance within the fossil bearing deposits of the region and preserved adequately for comparative studies to be made that should allow taxonomic identification based on skeletal remains. The many shortcomings that this work highlighted should not be seen as reason not to pursue the study of herpefauna, but to improve present comparative collections and collecting methods around the fossils themselves.

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