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The implications of mandible morphology and dental structure on the feeding ecology and predatory behaviour in Hyaenidae (hyenas) using geometric morphometric analyses

by

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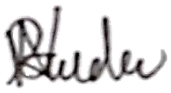
Declaration:

I, Riyanta Naidoo (student number: 1391091), declare that this dissertation is my own, unaided work. It is being submitted in fulfilment for the requirements of the degree of Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other university or similar institution.

Signature:  Date: 13 March 2024

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Abstract

Hyenas are often overlooked as being successful predators due to their scavenging behaviour. However, their morphological adaptations allow them to succeed in bone-cracking behaviour, an act that most carnivores are unable to achieve. Craniodental morphology influences carnivore performance, therefore understanding the functional morphology of carnivore mandibles would allow for the justification of Hyaenidae behaviour. This study investigates the morphological differences between the Hyaenidae mandible and large carnivore mandibles in Africa, as well as the differences in mandible morphology within the Hyaenidae family. This study uses a two-dimensional landmark-based geometric morphometric methodology to analyse morphological features on the carnivore mandibles and dentition to determine the morphological clusters linking the carnivore species, determine how the mandible morphology accommodates biomechanical needs, and to determine the implications that mandible morphology and dentition has on feeding ecology. The results of this study indicated that the sizes (PC1) of the carnivore mandibles were clustered according to their respective families (i.e. Hyaenidae, Canidae, and Felidae), however the shape (PC2) of the mandibles differed according to diet. The mandible morphology of the hypercarnivorous Hyaenidae displayed evident adaptations to osteophagy behaviour, including a thickened corpus, a large masseteric fossa, an anteriorly-displaced coronoid, and robust and blunt-like canines. The *Proteles cristata*, however, displayed mandibular adaptations to a hypocarnivorous diet. Ultimately, it was found that an increased resistance to bending forces and an increased area for muscle attachment on the mandible, directly relates to an increase in the Hyaenidae bite force, improving their feeding and hunting success.

Keywords: Bite force; feeding ecology; geometric morphometrics; mandible morphology; osteophagy.

Introduction

Some of the Earth's most abundant arrays of large carnivorous predators (i.e., those over 20 kilograms) can be found in Africa, ranging from the *Lycaon pictus* (African wild dog) to the *Panthera leo* (lion) (Hayward and Slotow, 2009; Cozzi *et al*. 2012; Vanak *et al*. 2013; Periquet *et al*. 2014; M'soka *et al*. 2016). These animals coexist despite being exposed to similar habitats and terrains, as well as overcoming a higher degree of dietary overlap (Hayward, 2006; Hayward and Kerley, 2008). Carnivore interactions are highly essential to either the enabling or prevention of the coexistence of the different species; however, these interactions are far from understood (Periquet *et al*. 2014). Species interactions range from facilitation to interference and competition, having effects on both the ecosystem functioning as well as shaping the ecological relationships of large carnivores (Hayward and Kerley, 2008; Periquet *et al*. 2014). Large carnivorous predators are some of the highest members of the food chain and are particularly important in shaping the community structure in a given ecosystem as they have a strong influence over the distribution and behaviour of interacting species, therefore the conservation of these species is essential (Vanak *et al*. 2013; Periquet *et al*. 2014). However, these carnivore populations are limited by their food supply due to intra- and interspecific competition from overlapping distributions (Hayward and Kerley, 2008). These carnivores present good opportunities for determining the relationships between form and function due to their ability to persist despite extreme challenges in their environments, such as excessive competition (Tanner *et al*. 2008). The ability to thrive in a specific environment, and the limitations of an individual's performance, are greatly influenced by the carnivore's craniodental morphology (Binder and Van Valkenburgh, 2000; Curtis *et al*. 2018). Morphological similarities of co-occurring species may be a result of adaptations to similar environments, however, these species may also have differences in morphologies in order to reduce competition (Davies *et al*. 2007). The diversity in size, diet and social

behaviour in carnivores can be shown by the shape and size of their skulls and dentitions (Meiri *et al*. 2005).

Bite force

The relationships between predatory behaviour, feeding ecology, and masticatory mechanisms of most large carnivores can be explained by the differences in their bite force (Magalhaes *et al*. 2020). Bite force directly relates to behaviour and diet, therefore it is an important aspect in the understanding of vertebrate ecology and evolution (Magalhaes *et al*. 2020). Community structure and prey size can also be determined by the bite forces of predatory mammals such as carnivores, with bite force being of particular importance due to the significant forces needed from their jaws to be able to capture and consume larger prey (Binder and Van Valkenburgh, 2000; Wroe *et al.* 2005).

Bite force and osteophagy

Osteophagy refers to the consumption of bones, which allows for the utilization of well-decomposed carcass material (Kane *et al*. 2016). Bone-cracking specialists, such as some hyena species, have a higher bite force as they undergo osteophagy (Table 1) (Wroe *et al.* 2005). The evolution of bone-cracking adaptations is only evident in three groups of carnivores, with the only extant members being part of the family: Hyaenidae (Tanner *et al*. 2008; Wang *et al*. 2018). Morphological adaptations on the skull, which bone-cracking specialists are seen to have, include vaulted foreheads, pronounced sagittal crests, powerful jaws and teeth, and an increased attachment area for masticatory muscles as seen in Figure 1 (Ferretti, 2007; Tanner *et al*. 2008; Palmqvist *et al*. 2011; Figueirido *et al*. 2013; Tseng, 2013; Wang *et al*. 2018). A caudally elongated frontal sinus is also a unique feature evident in hyenas, which Tanner *et al*. (2008) hypothesized to increase the resistance to stress and bending forces pertained during osteophagy. Curtis and Van Valkenburgh (2014) further

explained that this elongated frontal sinus seen in hyenas allows for stress to be dissipated evenly across the skull during osteophagy and predatory behaviour.

Table 1: Average bite forces of some of Africa's large carnivores. Bite force at the carnassial is adjusted for the average body mass of each species (BFQ_{carn}) (Wroe *et al*. 2005; Christiansen, 2007; Christiansen and Wroe, 2007).

Species	**Common name**	**Family**	**Body Mass (kg)**	**BFQ_{carn}**
Crocuta crocuta	Spotted hyena	Hyaenidae	63.1	116.15
Parahyaena brunnea	Brown hyena	Hyaenidae	38.9	164.9
Hyaena hyaena	Striped hyena	Hyaenidae	36.3	148.9
Proteles cristata	Aardwolf	Hyaenidae	13.2	77.0
Lycaon pictus	African wild dog	Canidae	22.4	134.9
Panthera pardus	Leopard	Felidae	55.0	105.3
Panthera leo	Lion	Felidae	162.2	108.9
Acinonyx jubatus	Cheetah	Felidae	46.8	95.9

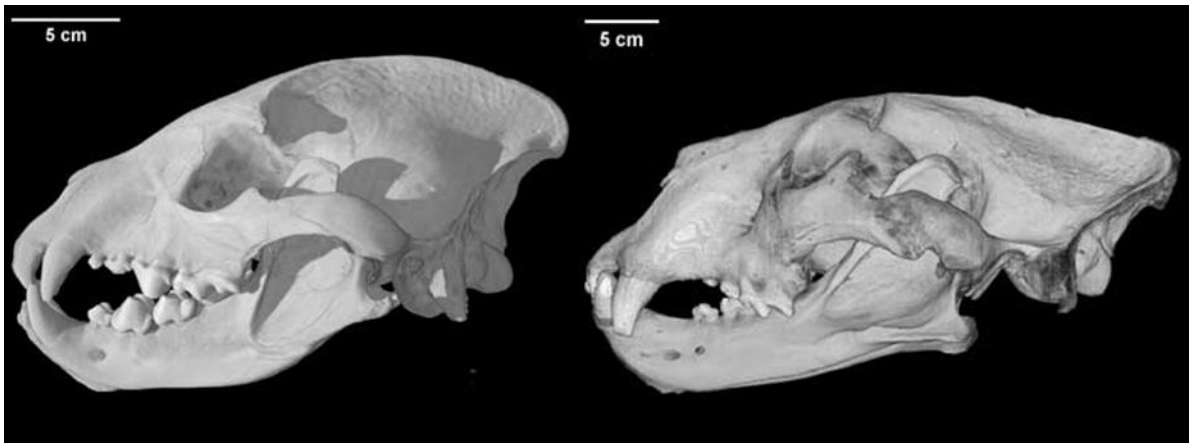

Figure 1: Comparative adaptations of the skulls of bone-cracking (A) and non-bone-cracking specialists (B) (adapted from Owen (2002) and Owen (2006)).

Most carnivores distribute maximal bite forces between adjacent canines during the killing bite at the anterior jaw (Wroe *et al.* 2005). However, carnivores that achieve osteophagy require a more concentrated load on the bone in order for fragmentation to occur (Ferretti, 2007; Tseng and Binder, 2010), resulting in the highest bite forces being achieved by carnassial biting (Table 1) whereby biting is restricted to only one side of the mandible (Wroe *et al.* 2005; Therrien *et al*. 2016). Carnivores that possess bone-cracking qualities have skulls that are well-equipped with cranio-dental characteristics that make the animal capable of feeding on all components of the prey carcass, maximizing consumption and increasing feeding success as no material is wasted (Tanner *et al*. 2008; Schubert *et al*. 2010; Tseng and Binder, 2010; Figueirido *et al*. 2013; Tseng, 2013). Robust dentitions are also required by specialized bone-cracking carnivores, such as *Crocuta crocuta* and *Hyaena hyaena,* in order for maximal bite forces to be applied onto the bones by post-canine teeth (Wroe *et al.* 2005; Ferretti, 2007; Tseng and Binder, 2010; Palmqvist *et al*. 2011; Figueirido *et al*. 2013; Tseng, 2013).

Bite force and feeding ecology

Mammals that form part of the order: Carnivora are some of the most ecologically diverse mammals, with body sizes showing more diversity than any other mammalian order (Christiansen and Wroe, 2007). Bite force can be determined by the nutrition and dietary groupings in carnivores (Kupczik and Stynder, 2012; Hartstone-Rose *et al*. 2019). The variations in cranial and dental components allow for different carnivores to make use of different resources (Meiri *et al.* 2005; Magalhaes *et al*. 2020). Christiansen and Wroe (2007) showed significant differences in the bite forces between various feeding categories when normalized for body size. High bite forces can be seen by mammals that feed on tough fibrous plant material, as well as carnivores that consume larger prey, whereas smaller or more moderate bite forces can be seen by omnivores and carnivores that consume smaller prey (Christiansen and Wroe, 2007). Dietary groupings are defined by the proportion of vertebrate meat in their diets and their corresponding morphological apparatus (Kupczik and Stynder, 2012; Magalhaes *et al*. 2020). A high-meat diet results in the modification of feeding apparatus as well as feeding behaviour (Michaud *et al*, 2020). For example, species with mostly carnivorous diets of more than 70% meat (hypercarnivores) are characterized by broader snouts and an irreversible loss of dental features that allows for larger blade sizes on carnassial teeth used for meat-slicing (Balisi and Van Valkenburgh, 2020). In contrast, species with lower proportions of meat in their diets (hypocarnivores) have narrower snouts and larger grinding areas on their cheek teeth as there is less need for slicing into meat (Magalhaes *et al*. 2020). Due to carnivores relying mostly on biting as a prey-killing mechanism, selective pressures on the cranium and mandible are inflicted to achieve fast and strong bites (Michaud *et al*. 2020). Therefore, some of the most important adaptations to differing feeding ecologies can be represented by differing bite forces throughout the Carnivoran species (Christiansen and Wroe, 2007; Hartstone-Rose *et al*. 2019).

Mandible morphology

Mandibular size and shape can be used to differentiate between carnivore ecological adaptations, including their diet and their membership to small or large predatory guilds (Weijs, 1980; Meloro and O'Higgins, 2011; Prevosti *et al*. 2011; Morales-Garcia *et al*. 2021). Raia (2004), found a strong correlation between carnivore mandible morphology and diet, indicating that mandible morphology can be used to infer feeding habits amongst carnivores.

The biomechanical requirements of carnivores are other factors that influence their mandible morphologies (Raia, 2004; Segura *et al*. 2021). Biomechanical requirements include the ability to resist forces such as bending and compression, which occur during mastication (Van Eijden, 2000). A large surface area on the mandible is also required for muscle attachment, which allows for the masticatory movements of the mandible (Figure 2) (Weijs, 1980; Herring, 1993). Mandibular shape differences amongst families are driven by mechanical functioning and loading. The coronoid, condyloid, and angular processes make up the ramus of the mandible (i.e., the area where masticatory muscles attach) (Monteiro and Nogueira, 2010; Meloro *et al*. 2011; Romaniuk, 2018). The relative positions of these processes differ amongst families according to their differences in skull and muscle proportions, as well as their respective areas of attachment (Meloro and O'Higgins, 2011). Carnivores that specialize in the consumption of medium (20 – 100 kg) to large (>100 kg) prey need to withstand high levels of mechanical stress in their mandibles and have an increased resistance to bending loads that come about when biting and chewing (Weijs, 1980; Van Eijden, 2000). The thickness of the mandibular corpus can be seen as an adaptation to withstand these bending loads as a thicker mandibular corpus is an indication that a carnivore feeds on larger prey and harder objects, whereas a thinner mandibular corpus is an indication of the consumption of smaller prey (Van Eijden, 2000; Segura *et al*. 2021). This is evident in

the feeding habits of bone-cracking hyenas, as this behaviour requires the attachment of strong masticatory muscles and mandibles that are highly resistant to bending (Raia, 2004; Meloro and O'Higgins, 2011). The jaw architecture of canids on the other hand offers minimal resistance to bending forces, indicating that canids are less likely to display the same feeding behaviour as hyenas (Raia, 2004). Studies by Weijs (1980), Herring (1993), Raia (2004), and Meloro and O'Higgins (2011) also indicated that the shape of the mandibular corpus is also influenced by the displacement and loading of teeth along the mandible, which is driven by bite mechanics.

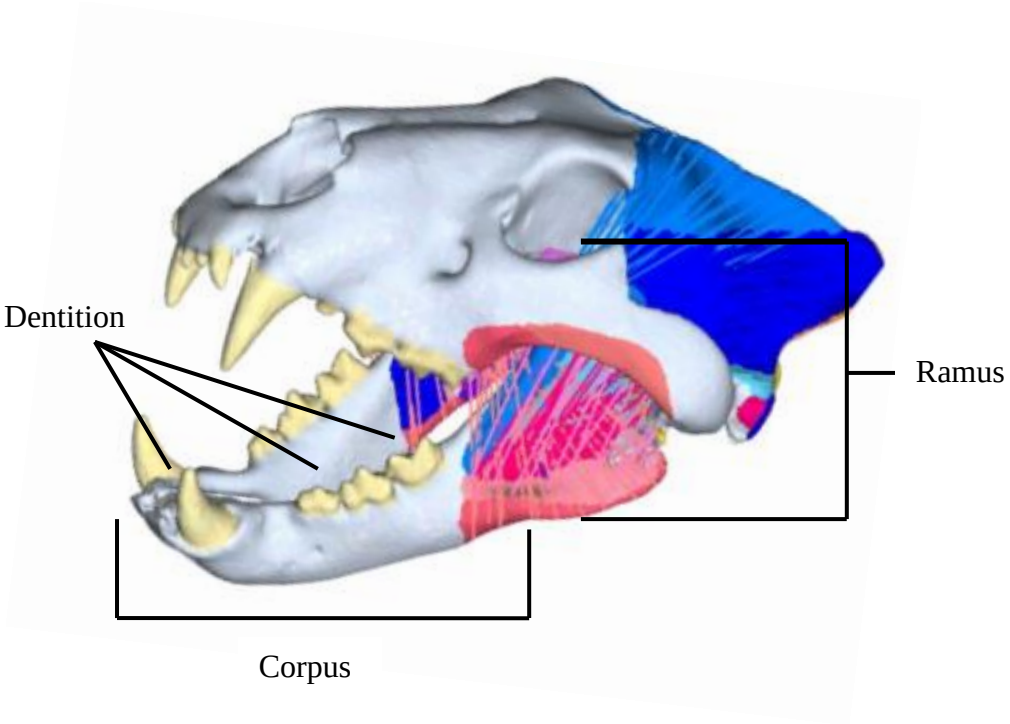

Figure 2: Generalized model of a carnivore skull with the temporalis (blue) and masseter (red) muscle attachment areas (adapted from McHenry *et al*. 2007).

Carnivore dentitions

Terrestrial carnivores generally have a unique pattern of dentitions including long and robust canines that are used for digging into flesh to secure and kill their prey, in addition to carnassials or cheek teeth (premolars and molars) that are primarily involved in the processing of food (Meiri *et al*. 2005; Davies *et al*. 2007; Tarquini *et al*. 2020; Lang *et al*.

2022). Prey sizes and diets are correlated with the shape and size of canines and carnassials (Donadio and Buskirk, 2006; Davies *et al*. 2007). Additionally, Davies *et al*. (2007) indicated that the morphological variations in carnivore dentitions account for approximately 63% of their variations in overlapping distributions. Consequently, carnivore dentition differs between teeth and taxa, in accordance with their diet (Meiri *et al*. 2005).

Carnivores rely on their canines to kill prey by delivering deep bites during hunting (Meiri *et al*. 2005; Hartstone-Rose, 2008; Plavcan and Ruff, 2008; Pollock *et al*. 2021). The size and type of prey that is frequently encountered have an influence over canine shape and size (Meiri *et al*. 2005; Pollock *et al*. 2021). Canine sizes vary within a population, allowing for individuals to specialize in different prey types (Meiri *et al*. 2005; Hartstone-Rose, 2008). Carnivoran canines vary in their sharpness, robustness and curvature. Sharp and slender canines are generally associated with carnivores that kill and feed on smaller prey and softer material such as skin and muscle, whereas more robust and blunt canines are associated with carnivores that consume harder material such as bone (Pollock *et al*. 2021).

Carnassials have various adaptations for dietary differences between carnivores. Blade-like carnassials are used by felids for shearing or slicing meat, blunt-cusped carnassials are used by specific types of hyenas for crushing bones, and canids have a combination of both blade-like and blunt-cusped carnassials (Davies *et al*. 2007). Tarquini *et al*. (2020) also indicated a gradient in carnassial specialization with hypercarnivorous species having more specialized carnassials and hypocarnivorous species having more generalized molars. Therefore, carnassial size and shape may also be used as an indication of the types of resources that are used by different carnivores.

Hyaenidae

Hyenas are some of Africa's most widespread populations of large predators, with current distributions limited to Africa and smaller populations present in the Middle East, evident in Figure 3 (Watts and Holekamp, 2007). The hyena is a common name given to members of the family Hyaenidae, comprising of the *Crocuta crocuta* (spotted hyena), *Hyaena hyaena* (striped hyena), *Parahyaena brunnea* (brown hyena) and the *Proteles cristata* (aardwolf). Hyenas are a family of carnivores that are often overlooked in terms of successful predators due to their scavenging behaviour (Hayward, 2006). However, research has shown that this behaviour can enhance their efficiency as predators due to their added morphological adaptations (Hayward, 2006). Hyenas are carnivores that fall under the Feliformia suborder due to their cat-like resemblance (DeSantis *et al*. 2017). These predators use hunting and killing techniques similar to members of the Canidae family, while having cranio-dental features that mostly resemble members of the Felidae family (Binder and Van Valkenburgh, 2000). The aardwolf lineage, however, originated from small-bodied hyaenids earlier than the emergence of large bone-cracking hyaenids, with the aardwolf being the only hyaenid showing reduced dentitions due to its specialized diet of termites (Tarquini *et al.* 2020; Galiano *et al*. 2022). Due to these contrasts, aardwolves will not be referred to as 'hyenas' for the duration of this study.

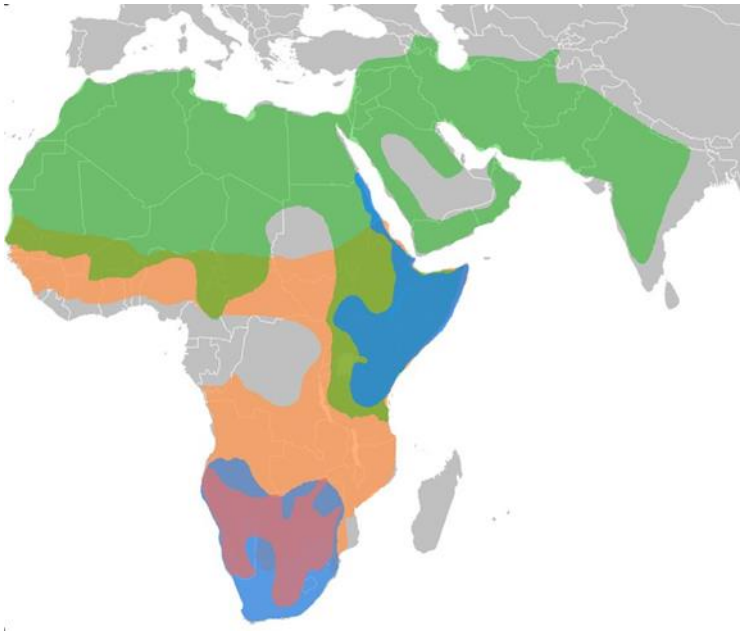

Figure 3: Distribution map of Hyaenidae across Africa and the Middle East. Striped hyena- green; spotted hyena- orange; aardwolf- blue; brown hyena- red (adapted from Westbury *et al*. 2020).

Hyenas have enlarged premolars, robust skulls and teeth that reflect a diet comprising predominantly of flesh and bone (Binder and Van Valkenburgh, 2000; Watts and Holekamp, 2007). Their powerful jaws and increased bite forces are primarily used to inflict damage to prey, as well as for the complete consumption of captured prey. Hyenas are reputable for their osteophagy behaviour, including the crushing and consumption of bones, allowing them to crack open bones to get to the marrow, an act that most carnivores are unable to achieve during feeding behaviour (Egeland *et al*. 2008; Blasco *et al*. 2014; Coil *et al*. 2017). Therefore, hyenas are able to make use of the bones, dry meat and skin, whereas other predators may not be able to consume the full carcass (Binder and Van Valkenburgh, 2000; Periquet *et al*. 2014). Hyenas also have a unique digestive system that is very efficient, with strong stomach acids that allow for the digestion of bones in order to acquire nutrients from the full carcass (Periquet *et al*. 2014).

Hyenas are dominated by social hierarchies within their clans, with each clan being led by the alpha female in the matriarchy (Holekamp and Smale, 1998; Holekamp *et al*. 2012). The alpha female has the highest ranking in the clan, with dominance being passed down to her cubs, and migrant adult males having the lowest rankings (Holekamp *et al*. 2012). A typical hyena feeding time consists of the group finishing a carcass rapidly with individuals having varying access to meat and bone. The highest-ranking individuals have first preference, followed by smaller individuals or cubs, and thereafter lower ranking individuals (Binder and Van Valkenburgh, 2000). The high relative abundance of hyenas, coupled with food scarcity, drives feeding competition within these species (Binder and Van Valkenburgh, 2000). Hyenas mostly prey on mammals that have a body mass ranging between 56-182 kilograms, with their preferred diet consisting of herbivores such as wildebeests, zebras and buffalo (Hayward, 2006). Hyenas and lions have very similar dietary niches with a 58% and 68% actual and preferred prey species overlap, respectively (Hayward, 2006). Lions are the main food competitors of hyenas, while also being the most intense competitors due to the similarities in their timings of predatory behaviour when in sympatry, leading to high levels of kleptoparasitism (i.e., stealing resources) between the two species (Hayward and Kerley, 2008; Trinkel and Kastberger, 2008). Hayward and Kerley (2008) also showed that there are increased levels of aggression between hyenas and lions even when there is no food present, possibly due to the need to show dominance over a coinciding territory.

Significance of the study

The majority of the large carnivores in Africa are restricted to conservation areas due to conflicts with human activities, therefore, the survival of these carnivores is increasingly becoming dependent on these areas (Hayward and Kerley, 2008; Periquet *et al*. 2014; Mwampeta *et al*. 2021). Protected areas or game reserves generally contain high densities of

these competing predators in restricted spaces, which increases the likelihood of interspecific competition that may lead to dramatic reductions in the populations of some species (Figure 4) (Hayward and Kerley, 2008; Periquet *et al*. 2014; Mwampeta *et al*. 2021). It is therefore critical to understand the predatory behaviour and interactions between the different carnivorous species with overlapping distribution patterns and diets, in order to introduce or update protected area management programs, as well as to promote conservation of these areas and mammals situated in these areas.

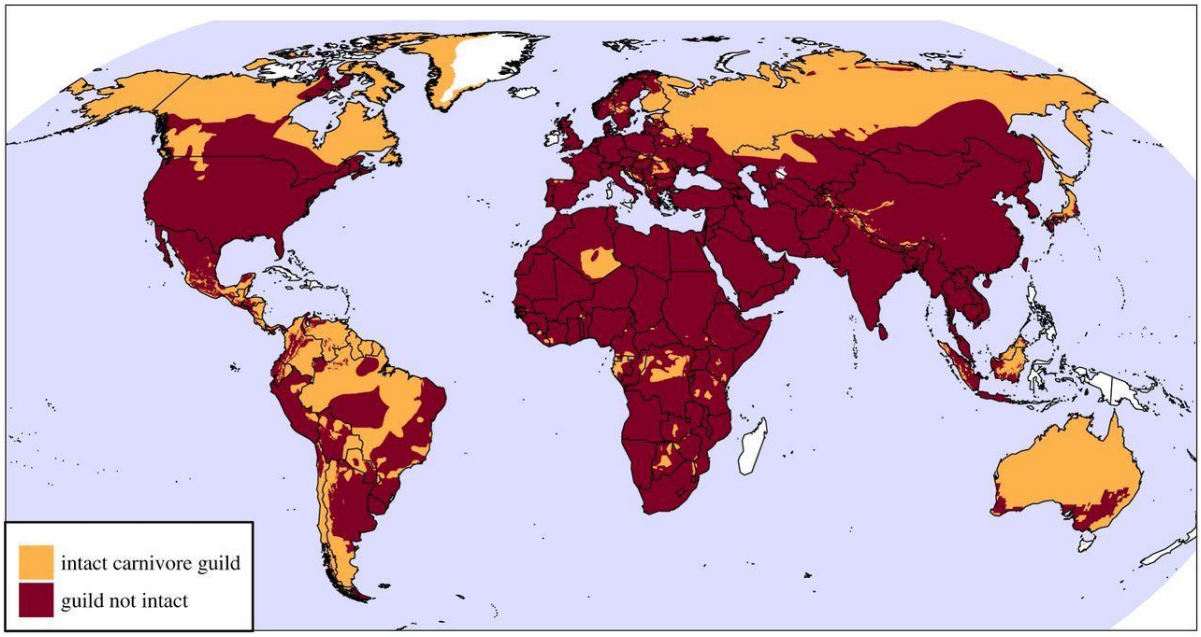

Figure 4: Range contraction map of large carnivore guilds with only 8% of African land covered with intact guilds (adapted from Wolf and Ripple, 2017).

Human-induced mortality is one of the leading causes of death in Africa's large carnivores, even in protected areas (Pangle and Holekamp, 2010; Mwampeta *et al*. 2021). Consequently, the human-wildlife conflict is one of the major threats to the hyena population as they are seen as merely a pest species as they often prey on livestock, resulting in human persecution by means of poisoning, snaring or spearing (Hayward and Kerley, 2008; Pangle

and Holekamp, 2010). Although being considered a pest species, hyenas can also have a positive impact towards public health and economic benefits. Studies suggest that the scavenging behaviour of hyenas can act as a disease control service as they may prevent infections of anthrax and tuberculosis in nearby humans and animals, potentially saving costs for treatment and avoiding further loss of livestock (Sonawane *et al*. 2021). The hyena population is responsible for the annual removal of 4.2% of disposed carcass waste by anthropogenic factors, therefore, hyenas ultimately decrease the spread of disease caused by decaying animal matter (Mwampeta *et al*. 2021; Sonawane *et al*. 2021). Given the significant role that the hyena plays in the ecosystem, it is imperative that their masticatory mechanisms (comprising of the mandibles and dentitions) be studied in order to extend our knowledge of how the variations in form (shape and size) are associated with functional variations, opposed to that of other carnivoran species with overlapping distributions.

The aim of this study was to determine the extent to which the Hyaenidae mandible morphology and dentition differs from that of other selected large carnivorous species in Africa.

The objectives of this study were as follows:

1) To conduct a comparative assessment of the morphology (size and shape) of large carnivore mandibles and dentitions in Africa, as well as to make a comparative assessment of the mandible morphology of species within the Hyaenidae family.
2) Determine whether there are any distinct morphological clusters on the mandibles and dentitions, linking the different carnivorous species.
3) Determine how the carnivore mandible morphology accommodates the biomechanical needs due to muscle attachment and increased bite force.

4) Assess the implications that mandible morphology and dentitions have on carnivore feeding ecology and shifts in diet, as well as its influence over predatory behaviour.

It is hypothesized that the hyena mandible morphology would more closely resemble that of Felidae (i.e. lion, cheetah, and leopard) rather than Canidae (African wild dog), as both Hyaenidae and Felidae fall under the same suborder: Feliformia (Figueirido *et al*. 2011; DeSantis *et al*. 2017). Hyena mandibles are expected to accommodate for more robust and sharpened dentitions such as carnassials (lower molars) used for the grinding of bones, as well as long and slender canines for piercing into flesh and bone (Davies *et al*. 2007; Pollock *et al*. 2021). A larger masseteric fossa is also predicted to provide more surface area for muscular attachment in hyenas, aiding in the increased bite force observed (Attard *et al*. 2011; Prevosti *et al*. 2011). It is expected that the mandibles of the four Hyaenidae species would have similar morphological characteristics due to them being part of the same family, however they would differ in size due to varying body masses (i.e. the spotted hyena is much larger than the aardwolf), as well as the differing diet of the aardwolf (Curtis and Van Valkenburgh, 2014).

Methods

Morphological features of the mandibles and dentitions were analyzed for the selected carnivorous species, namely: (1) *Crocuta crocuta* (spotted hyena); (2) *Parahyaena brunnea* (brown hyena); (3) *Proteles cristata* (aardwolf); (4) *Hyaena hyaena* (striped hyena); (5) *Lycaon pictus* (African wild dog); (6) *Panthera pardus* (leopard); (7) *Panthera leo* (lion); and (8) *Acinonyx jubatus* (cheetah). The species selection included large carnivores from the Felidae, Canidae and Hyaenidae families with overlapping distribution patterns across Africa (Figure 5), as well as an overlap in diet (Hayward, 2006; Hayward and Kerley, 2008; Hayward and Slotow, 2009; Tarquini *et al*. 2020). This study was conducted using two-

dimensional landmark-based geometric morphometric methodology, as explained by Webster and Sheets (2010), whereby a set of landmarks was used to describe the bone morphology. The landmarking was done on ImageJ (version 1.53s) and the analyses were carried out on MorphoJ (version 2.0). This geometric morphometric methodology reduces and simplifies the dimensions of a data set while still retaining important geometric information (Slice, 2007). Landmark-based geometric morphometrics uses Cartesian coordinates to determine shape differences by analysing the variance or covariance of homologous landmarks, while producing graphical representations of these shape differences (Adams *et al*. 2004; Sendaydiego *et al*. 2013). This methodology allowed for the biological form to be quantified and easily interpreted, as well as allowing for more efficient statistical analyses.

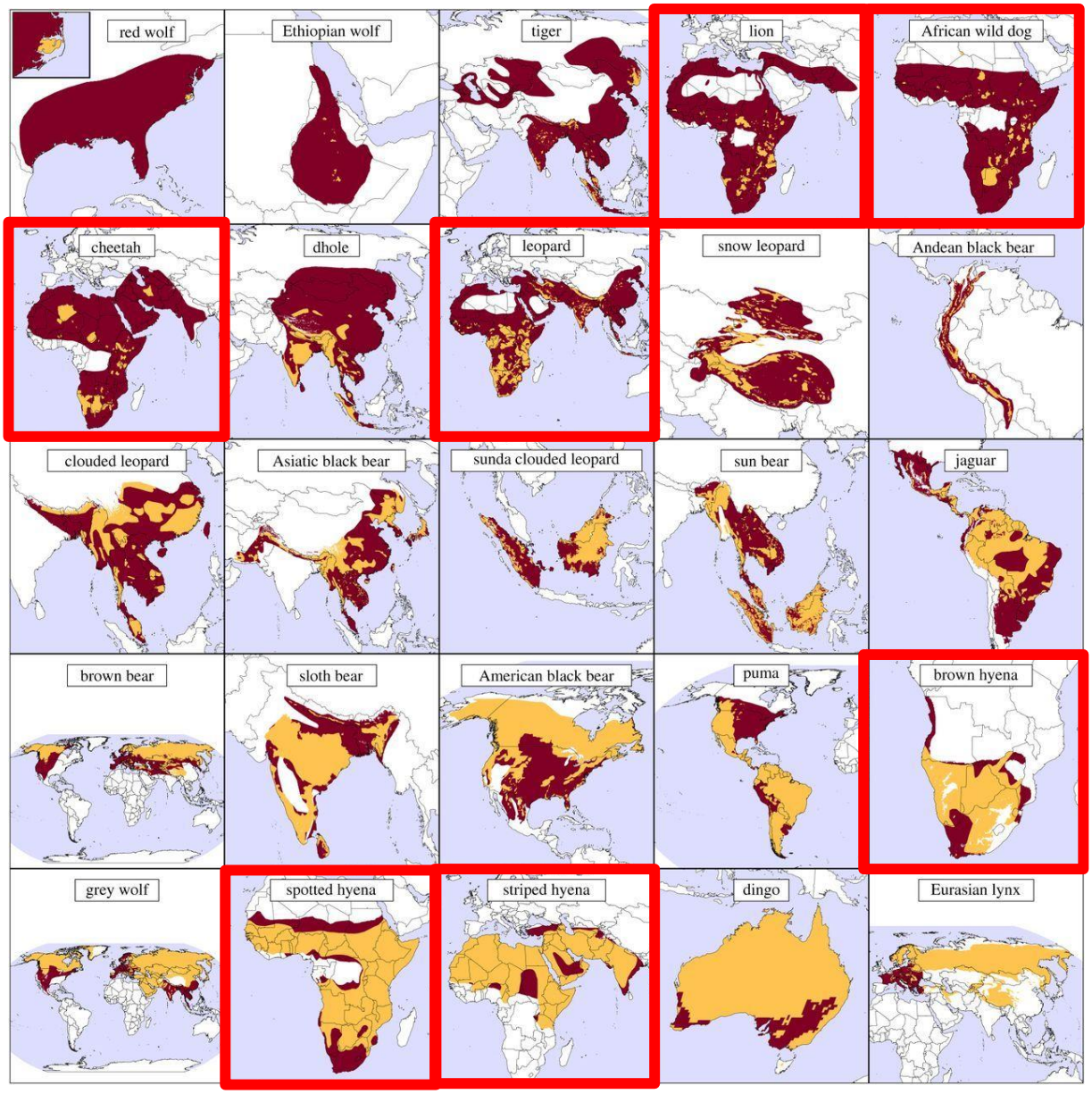

Figure 5: Species distribution maps of large carnivores. Species selected for this study are highlighted in red (excluding the aardwolf) (adapted from Wolf and Ripple, 2017).

Image capturing

A total of 68 museum specimens were used to conduct the present study (*Crocuta crocuta* (spotted hyenas): n=13, *Parahyaena brunnea* (brown hyenas): n=12, *Proteles cristata* (aardwolves): n=7, *Hyaena hyaena* (striped hyenas): n=2, *Lycaon pictus* (African wild dogs): n=5, *Panthera pardus* (leopards): n=10, *Panthera leo* (lions): n=9, and *Acinonyx*

jubatus (cheetahs): n=10), which were obtained from the Ditsong National Museum of Natural History (25.75306°S, 28.18712°E) in Pretoria and from the Iziko South African Museum (33.92870°S, 18.41101°E) in Cape Town. Digital images were captured from the right lateral view of the mandible of each specimen. The setup was kept constant in order to reduce error and minimize any distortion, including the same camera (Canon EOS 600D), distance from the bone (30 centimeters), black background (black tablecloth), and lighting. A ruler was also placed alongside each specimen for scale purposes. Images were edited using the picture editing application, PhotoScissors (version 8.3), in order to remove any noise (i.e. unwanted objects), remove the background, adjust the contrast or brightness, and to ensure the same orientation of all images.

Landmarking

The digital images were landmarked in order to compile a file that could be used to quantify and analyze the differences in the mandible morphologies and dentitions of the different species. The software used for landmarking was ImageJ (version 1.53s). Each of the edited images was imported into ImageJ and landmarked separately. The x and y coordinates of each landmark were recorded into a Microsoft Excel (2010) spreadsheet. A subset of 28 landmarks was positioned on specific features with biological significance on the lateral view of each mandible (Figure 6; Table 2). Landmarks were selected based on previous benchmarked studies (Meloro *et al*. 2008; Figueirido *et al*. 2011; Palmqvist *et al*. 2011; Prevosti *et al*. 2011; Piras *et al*. 2013). Features with biological significance included the dentitions (molars, premolars and canines) used for hunting and processing food, the coronoid, condyloid and angular processes for gape angle and bite force, the masseteric fossa for muscle attachment, and the foramina (Meloro *et al*. 2008; Tanner *et al*. 2010; Prevosti *et al*. 2011; Romaniuk, 2018; Pollock *et al*. 2021). Landmarks were positioned on homologous points in the same order for each image, with each image having the same number of

landmarks. The same scale factor of one centimeter was set for all images and an ID was set for each image in order to maintain consistency. The landmark spreadsheet was saved as a tab-delimited text file.

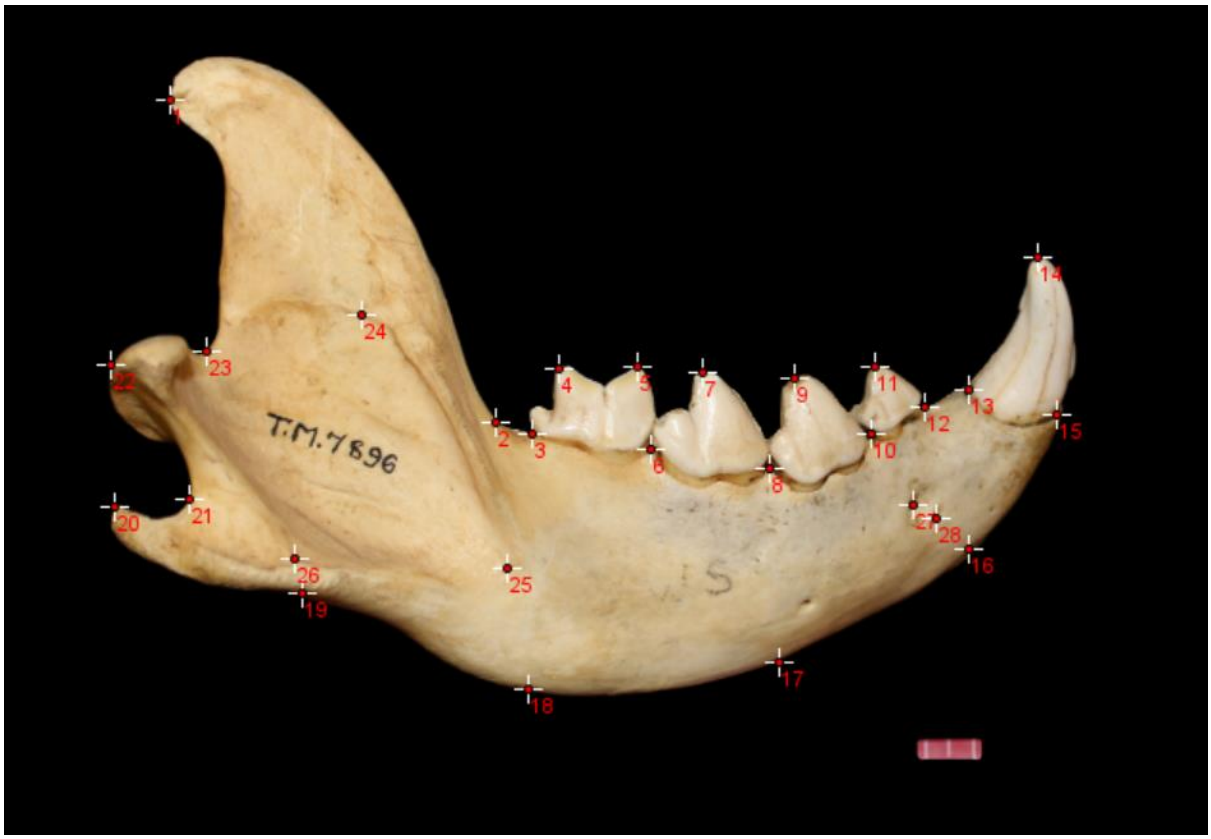

Figure 6: Landmark positions on the lateral view of a carnivore mandible to indicate the dentitions (3-15), corpus mandibular (2, 15-18), and ramus mandibular (1-2, 18-26). Landmarks are expressed as red points.

Table 2: Biological features and their landmark representations on the carnivore mandible.

Landmark	Biological feature	Structure on mandible
3-12	Molars and premolars	Dentition
13-15	Canines	

24-26	Masseteric fossa	Ramus
1	Tip of coronoid process	
22	Tip of condyloid process	
20	Tip of angular process	
27, 28	Foramina	Corpus
13-16	Thickness of mandibular corpus under lower canine	
8-17; 2-18	Thickness of mandibular corpus under molars	

Analyses

The landmark text file was imported into MorphoJ (version 2.0), which is the geometric morphometrics software that was used to carry out the analyses in this study. A Procrustes fit was generated to analyze the distribution of the carnivore mandible morphology, which allowed for the best fit to be determined between the landmarked mandibles. A wireframe was created and classifiers were added from the dataset (i.e., species). The Procrustes coordinates, which were generated by the Procrustes fit, were used to create a covariance matrix for the data. Principal component analysis (PCA) was used in order to reduce and simplify the dimensionality of the dataset, while still maintaining the trends and patterns within the data. The covariance matrix was used to generate PCA plots for the landmarked mandibles in order to reveal any distinct morphological clusters between the different species. A Procrustes ANOVA regression model was then used to test the differences in the mean shape of the mandibles between the different carnivorous species.

Results

Principal component analyses (PCAs) were performed on the carnivore mandibles and principal components were used as an indication of variance within the dataset. The first three principal components accounted for 67.24% of the total shape variance and were therefore inferred as significant in this study (eigenvalues > 10) (Figure A1). The principal components plotted in Figures 7, 9 and 10 shows the relationships between the first three principal components, with distinct clusters linking the different species. PC1 (41.01% of the total variation), PC2 (14.98% of the total variation) and PC3 (11.25% of the total variation) accounts for the majority of the mandible shape variation within the sample, with PC1 (Figure 8) corresponding to the size and PC2 (Figure 9) corresponding to the shape. The Procrustes ANOVA regression further showed a significant difference between the mean shape of the carnivore mandibles ($p < 0.0001$; $F = 17.38$) within the total mandible sample.

PC1 plotted against PC2 illustrates that *Proteles cristata* overlaps with other members of the Hyaenidae family, *Crocuta crocuta*, *Parahyaena brunnae* and *Hyaena hyaena* along PC1 (Figure 7), indicating clear similarities in the mandibular sizes of Hyaenidae. *Proteles cristata* (family: Hyaenidae) is found to have the lowest PC1 score and *Acinonyx jubatus* (family: Felidae) has the highest PC1 score (Figure 7). The Hyaenidae family (i.e., *Crocuta crocuta*, *Parahyaena brunnae* and *Hyaena Hyaena*) overlaps with the only Canidae in the sample (i.e., *Lycaon pictus*) along PC1, indicating that Hyaenidae were closest to Canidae with regards to the mandibular size (Figure 7). *Lycaon pictus* overlaps along PC1 with the *Panthera leo* and *Panthera pardus*, with both species being members of the Felidae family (Figure 7). *Panthera leo* and *Panthera pardus* overlap with each other along PC1 and *Panthera leo* also overlaps with the Felidae *Acinonyx jubatus* along PC1 (Figure 7). *Lycaon pictus* (family: Canidae) lies on the axis that separates species according to their respective

families, with the Hyaenidae family (i.e., *Proteles cristata*, *Crocuta crocuta*, *Parahyaena brunnae*, and *Hyaena hyaena*) comprising of only negative PC1 scores and the Felidae family (i.e., *Panthera leo*, *Panthera pardus*, and *Acinonyx jubatus*) comprising of only positive PC1 scores (Figure 7). *Crocuta crocuta*, *Parahyaena brunnae* and *Hyaena hyaena* (from the same family: Hyaenidae, and showing the same osteophagy behaviour), all show overlaps along PC1 as well as PC2, with PC1 and PC2 scores falling within the same negative quadrant (Figure 7, Figure A2). PC1 shows a clear differentiation between the sizes of the mandibles according to their respective families, with the smallest mandibles in the sample being part of the Hyaenidae family (i.e., *Proteles cristata*) and the largest mandibles being part of the Felidae family (i.e., *Acinonyx jubatus*).

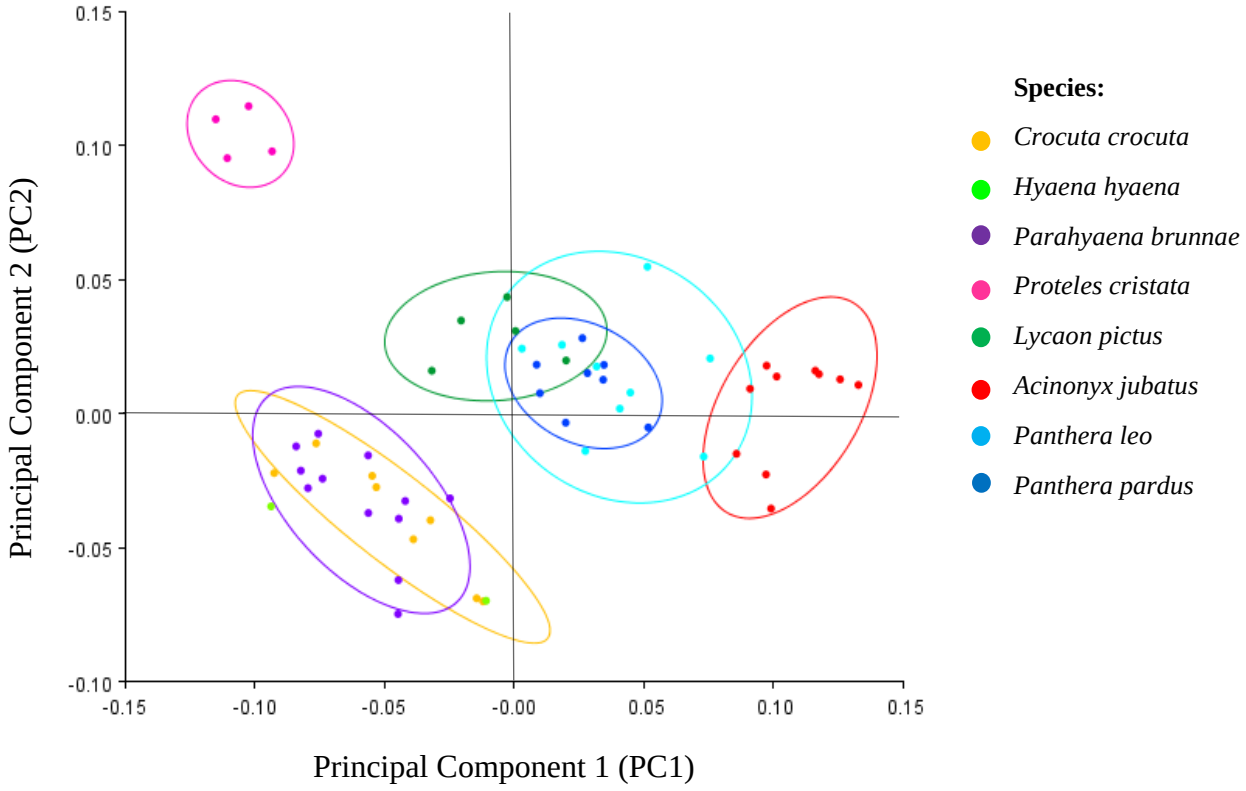

Figure 7: PC1 (x-axis) plotted against PC2 (y-axis). Clusters of species are indicated by confidence ellipses with their respective colouration.

Figure 8 illustrates the morphological displacement of the mandibles along PC1 from the negative to positive end of the axis. Positive PC1 values can be associated with a larger molar region, with premolars being reduced to two instead of the general set of three. A more pronounced ramus can be seen with a slightly enlarged masseteric fossa. The mandibles possessed longer coronoid and condyloid processes, with an angular process progressing downwards. There is also a slight reduction in the size of the mandibular corpus, with the region under the molars decreasing in thickness.

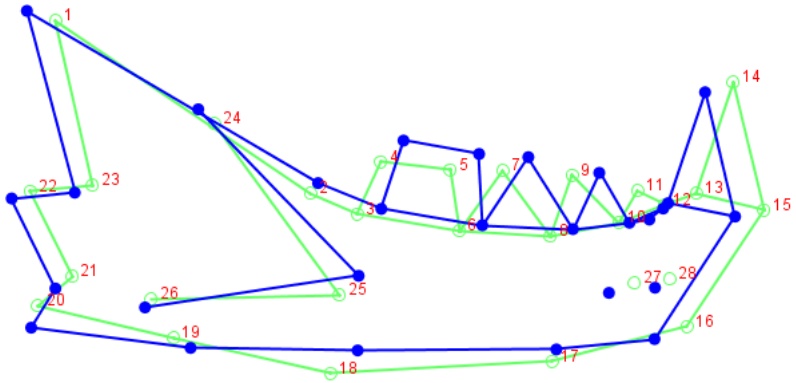

Figure 8: Morphological shape changes of the mandibles shown by the displacement (blue) from the mean shape (green) for the first principal component (PC1).

The hypercarnivorous *Parahyaena brunnea* is seen to have the lowest PC2 score and the hypocarnivorous *Proteles cristata* has the highest PC2 score, with both species being a part of the same family: Hyaenidae (Figure 7), indicating a clear differentiation between the shape of the mandibles within Hyaenidae according to the extent of their carnivorous diets. *Proteles cristata* does not overlap with any other species along PC2 (Figure 7), indicating a notable differentiation between the mandibular shape of the hypocarnivorous *Proteles cristata* and the hypercarnivorous species within the sample. The hypercarnivorous species

within the Hyaenidae family (i.e., *Crocuta crocuta*, *Hyaena hyaena* and *Parahyaena brunnae*) show no overlaps along PC2 with the Canidae family (i.e., *Lycaon pictus*) (Figure 7). *Lycaon pictus* (family: Canidae) overlaps with species within the Felidae family (i.e., *Acinonyx jubatus*, *Panthera leo* and *Panthera pardus*) along PC2 (Figure 7). Species that fall within the Felidae family (i.e., *Acinonyx jubatus*, *Panthera leo* and *Panthera pardus*) all show overlaps with each other along PC2 (Figure 7). *Crocuta crocuta* and *Parahyaena brunnae* (family: Hyaenidae) both show overlaps with all three species within the Felidae family (i.e., *Acinonyx jubatus*, *Panthera leo* and *Panthera pardus*) along PC2 (Figure 7). *Hyaena hyaena* can also be seen to overlap with *Acinonyx jubatus* along PC2 (Figure 7). The overlaps between species of the Hyaenidae family and the Felidae family along PC2 indicate that these hypercarnivorous Hyaenidae are closest in mandibular shape to the Felidae family as opposed to the Canidae family. PC2 therefore shows a clear separation between the shapes of the mandibles according to the carnivore's diet, with the more hypercarnivorous species (i.e., *Crocuta crocuta*, *Hyaena hyaena* and *Parahyaena brunnae*) having the lowest PC2 scores and the hypocarnivorous species (i.e., *Proteles cristata*) having much higher PC2 scores (Figure 7).

Figure 9 illustrates the morphological displacement of the mandibles along PC2 from the negative to positive end of the axis. Positive PC2 values can be associated with a reduction in the sizes of the molar and premolar regions. The premolar closest to the canine is seen to be highly reduced, with an increased gap between the premolars and canine. The ramus includes a smaller coronoid process, with a masseteric fossa that progresses upwards. A straight and more elongated mandibular corpus can also be seen, with the corpus region under the molar and premolars decreasing in thickness.

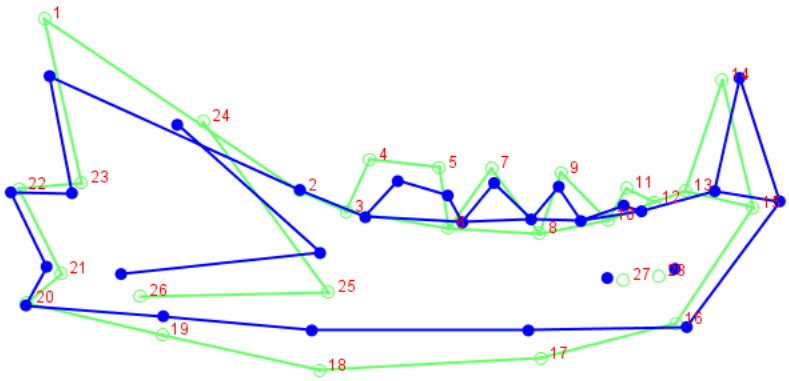

Figure 9: Morphological shape changes of the mandibles shown by the displacement (blue) from the mean shape (green) for the second principal component (PC2).

Figure 10 illustrates the plot of PC2 against PC3. *Lycaon pictus* (family: Canidae) is seen to have the lowest PC3 score and *Panthera pardus* (family: Felidae) has the highest PC3 score (Figure 10). Species within the Hyaenidae family (i.e., *Crocuta crocuta*, *Hyaena hyaena*, *Parahyaena brunnae* and *Proteles cristata*) all show overlaps with each other along PC3, indicating similarities of the mandibles within the Hyaenidae family to an extent (Figure 10). *Panthera pardus* overlaps with *Panthera leo* along PC3 (Figure 10). *Acinonyx jubatus* is the only species within the Felidae family that overlaps with *Lycaon pictus* along PC3 (Figure 10). *Lycaon pictus* (family: Canidae), *Acinonyx jubatus* (family: Felidae) and *Proteles cristata* (family: Hyaenidae) all share the same quadrant despite being species of different families (Figure 10). PC3 shows no clear separation between the mandibles of the different families (Figure 10). The Hyaenidae family does however lie on the axis that separates the species within the Felidae family, with the *Panthera pardus* and *Panthera leo* consisting of only positive PC3 scores and the *Acinonyx jubatus* consisting of only negative PC3 scores (Figure 10, Figure A3).

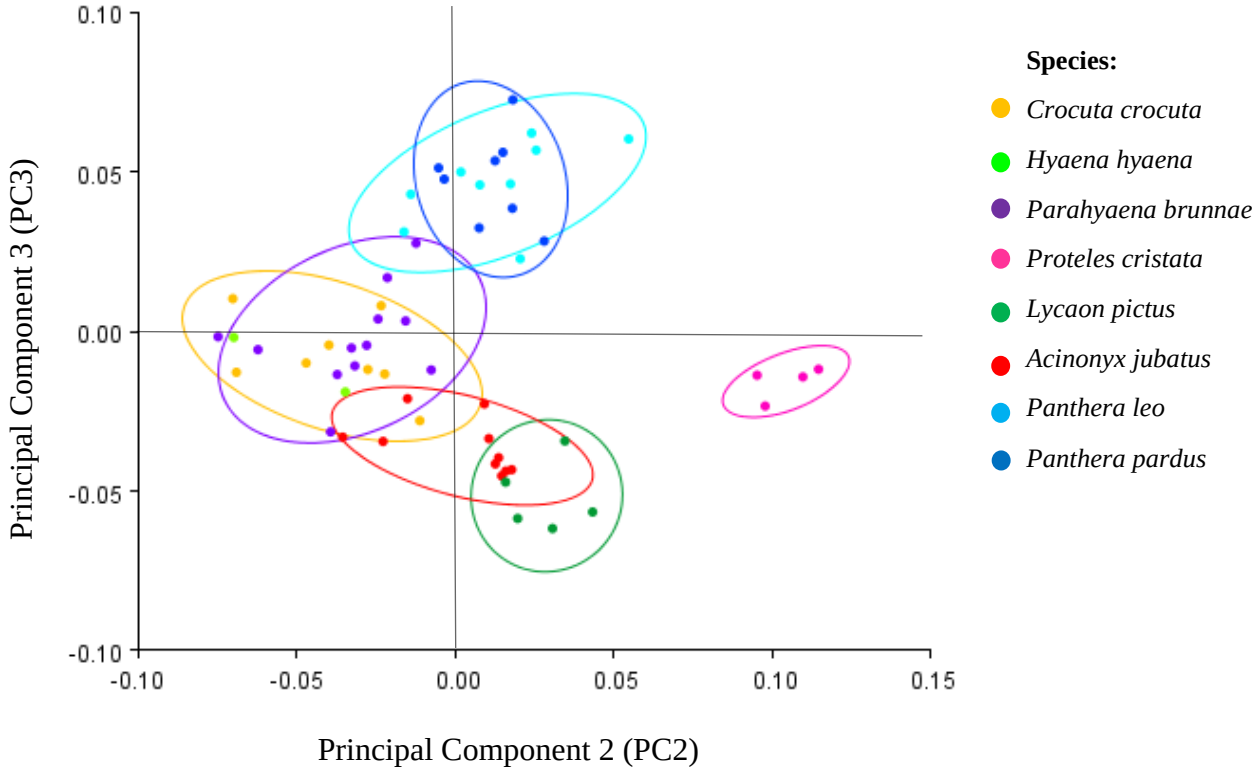

Figure 10: PC2 (x-axis) plotted against PC3 (y-axis). Clusters of species are indicated by confidence ellipses with their respective colouration.

Figure 11 illustrates the morphological displacement of the mandibles along PC3 from the negative to positive end of the axis. Positive PC3 values can be associated with an increasingly more robust mandible. An enlarged molar region can be seen as well as a longer canine, with the premolars being reduced to two as opposed to the general set of three, which is also evident in the morphological displacement of the premolars along PC3. The ramus comprises of a masseteric fossa that slightly progresses upwards. A curved and enlarged mandibular corpus can also be seen, with the corpus region under the premolars increasing in thickness.

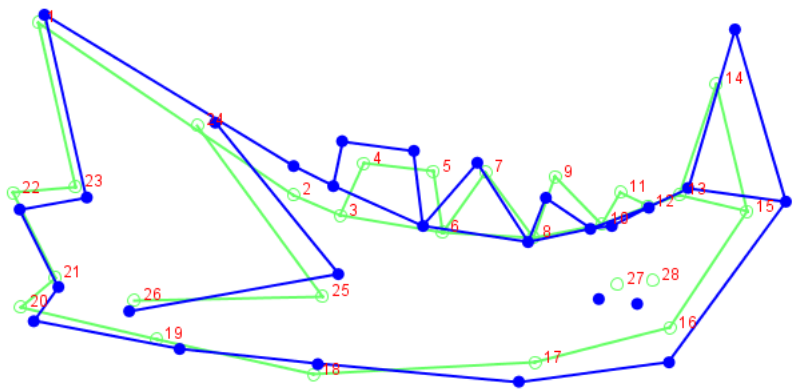

Figure 11: Morphological shape changes of the mandibles shown by the displacement (blue) from the mean shape (green) for the third principal component (PC3).

PC1 plotted against PC3 illustrates that *Panthera leo* and *Panthera pardus* both fall within the same positive quadrant (Figure 12, Figure A4). *Lycaon pictus* (family: Canidae) and *Acinonyx jubatus* (family: Felidae) also fall within the same quadrant despite being species of different families (Figure 12), indicating similarities in the mandibular structure between both families. Figure 12 also illustrates that species within the Canidae family (i.e., *Lycaon pictus*) fall in the same negative quadrant as species in the Hyaenidae family (i.e., *Crocuta crocuta*, *Hyaena hyaena*, *Parahyaena brunnae* and *Proteles cristata*), which indicates similarities between the mandibles of the Canidae and Hyaenidae families. It can be seen that *Crocuta crocuta* and *Parahyaena brunnae* (family: Hyaenidae) overlap with each other along PC1, PC2 and PC3 (Figure 7, Figure 10, Figure 12), indicating notable similarities in both the size and shape of their mandibles and dentition. Similarly, *Panthera leo* and *Panthera pardus* (family: Felidae) also overlap with each other along PC1, PC2 and PC3 (Figure 7, Figure 10, Figure 12), also indicating notable similarities in both the size and shape of their mandibles and dentition.

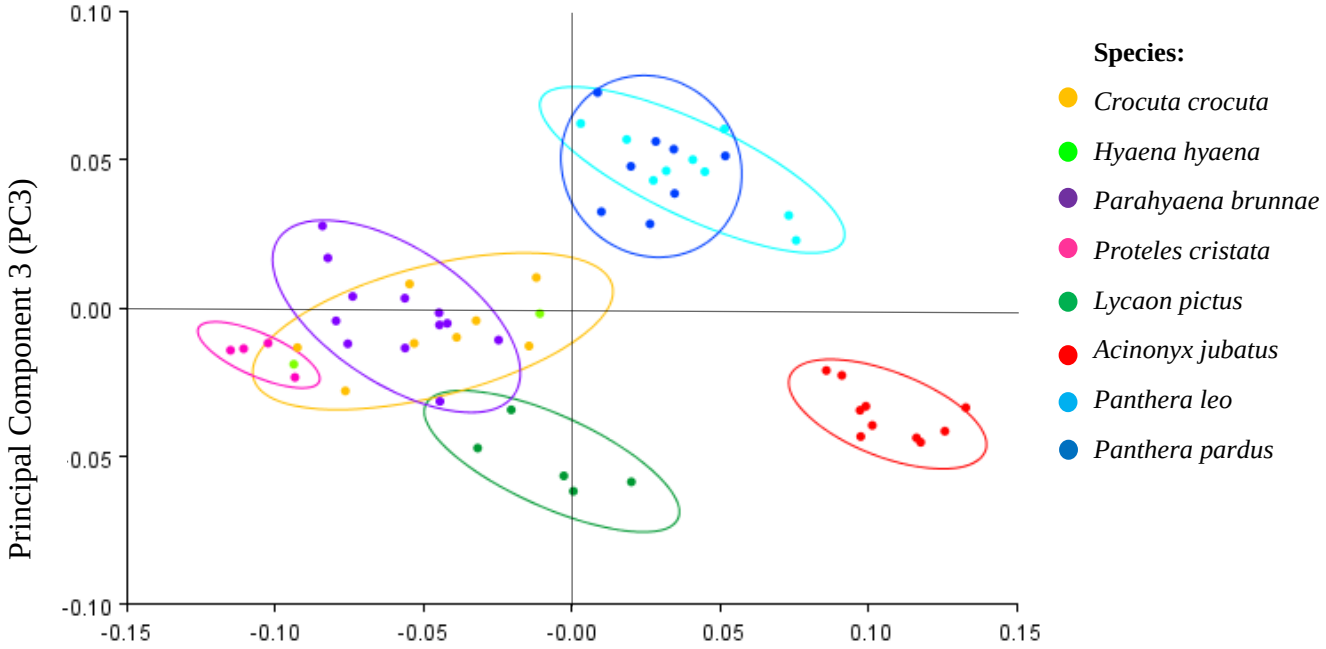

Figure 12: PC1 (x-axis) plotted against PC3 (y-axis). Clusters of species are indicated by confidence ellipses with their respective colouration.

Discussion

Mandible morphology

Principal component analyses were performed on carnivore mandibles, whereby principal components were used to determine the morphological differences between the mandibles of large carnivores in Africa. It was hypothesized that the Hyaenidae mandible would more closely resemble the morphology of the Felidae mandible rather than the Canidae mandible. Hyaenidae were expected to have more robust mandibles, sharpened dentitions, and a larger surface area for muscle attachment in order to accommodate for the

increased bite force observed (Table 1). Species within the Hyaenidae family were also expected to have similar morphological characteristics due to them being part of the same family.

The two major carnivore evolutionary lineages consist of the Feliformia (i.e. Hyaenidae and Felidae) and the Caniformia (i.e. Canidae) (Figueirido *et al*. 2011). The sizes of the carnivore mandibles (PC1) were clustered according to their respective families, with the Hyaenidae having negative PC1 values, the Canidae having PC1 values ranging from -0.03 to 0.03, and the Felidae having positive PC1 values (Figure 7). The mandibular shape (PC2) is differentiated according to diet (Figure 7). Hyaenidae mandibles were found to be closer to Canidae with respect to size (PC1), however the hypercarnivorous Hyaenidae (i.e. *Crocuta crocuta*, *Hyaena hyaena*, and *Parahyaena brunnae*) were found to be closer to Felidae with respect to shape, which is shown by the overlaps of the hypercarnivorous Hyaenidae and the Felidae along PC2 (Figure 7).

The overlaps observed along PC1 and PC2 (Figure 7) for *Crocuta crocuta*, *Hyaena hyaena*, and *Parahyanea brunnae*, indicate that these species share clear similarities in both the mandibular shape and size. All three Hyaenidae species display the same osteophagy behaviour (Biknevicius and Ruff, 1992; Wroe *et al*. 2005; Tanner *et al*. 2008; Hartstone-Rose and Stynder, 2013; Kane *et al*. 2016), while also having the highest bite forces seen within the sample (Table 1). The thickening of the corpus region increases the resistance to bending forces exerted on the mandible during mastication, allowing the Hyaenid mandibles to withstand greater forces brought about by the consumption of larger prey and harder objects such as bone (Figures 7 and 9) (Biknevicius and Ruff, 1992; Figueirido *et al*. 2011; Prevosti *et al*. 2011). The hypercarnivorous Canidae and Felidae specimens also show a degree of corpora thickening although not to the extent of the Hyaenidae, therefore allowing these carnivores to also consume relatively large prey but not harder objects (Figures 7 and 9). The

larger masseteric fossa seen on the ramus of the Hyaenids increases the surface area available for the masseter muscle attachment (Prevosti *et al*. 2011). This increased muscle attachment allows for more force to be exerted by the mandible, resulting in the increased bite force observed in the hypercarnivorous Hyaenidae (Table 1) (Prevosti *et al*. 2011). Biomechanical needs include gape angle and stress resistance due to an increase in mechanical loading on the mandible when biting (Michaud *et al*. 2020). The positioning of the coronoid process on the ramus of carnivore mandibles, as well as the degree of muscle attachment made possible by the masseteric fossa, has an influence on leverage and gape (i.e. the widening of the jaws) when biting, which has an impact on the bite force exerted by the carnivore (Biknevicius and Ruff, 1992; Slater and Van Valkenburgh, 2009; Figueirido *et al*. 2011; Prevosti *et al*. 2011; Michaud *et al*. 2020). Scavengers such as Hyaenidae that feed on large carcasses require smaller gape angles and higher stress resistance to produce large bite forces compared to the Felidae and Canidae mentioned in this study. As mentioned previously, the resistance to bending forces brought about by increased bite forces is made possible due to a thickened corpus region. The anteriorly-displaced coronoid process seen on the hypercarnivorous Hyaenids (Figures 7 and 9), coupled with a larger masseteric fossa for muscle attachment and a thickened corpus, increases the leverage to exert maximal bite forces, thereby increasing mechanical advantage, however, gape would be reduced as a result. Consequently, a more posteriorly-displaced coronoid process, coupled with a smaller massteric fossa and thinner corpus, would decrease mechanical advantage, therefore bite force would decrease and gape would increase. Curtis and Van Valkenburgh (2014) stated that mandible morphology is a trade-off between increased gape to accommodate large prey, and the need for an increased bite force. The consumption of larger prey requires large gape angles and increased bending strength on the mandible to deliver a killing bite, as seen in the predatory behaviour of Felidae (Lautenschlager *et al*. 2020). Longer mandibles are needed to increase gape, which

also increases torsional loads on the mandible when biting (Curtis and Van Valkenburgh, 2014). Bending forces and torsional loads on the mandible is thereby accommodated by an increase in bone volume (i.e., the thickening of the corpus). A killing bite needs to be deep to reach major blood vessels in order for prey to bleed out (Andersson *et al*. 2011), therefore an increase in gape allows the carnivore to have a deeper killing bite, which can be seen in the predatory behaviour of Felidae. Hyenas, however, do not need a deep killing bite due to their pack-hunting behaviour, therefore, rather than having an increased gape, hyenas have an increased bite force that allows for their durophagous diet. It can be deduced that the mandible morphology seen in these Hyaenidae species increases the chances of osteophagy, ultimately improving feeding success.

The variability in carnivore diet and predatory behaviour can be reflected in the size and shape of their dentitions (Meiri *et al*. 2005). Carnivores that are primarily meat-eaters have dentitions that are more adapted for tearing into flesh. This is evident in the dental morphology of Felidae (Figures 7 and 9), which included large cutting carnassials and long and sharp canines used for a killing bite. Solitary hunters (including majority of the Felidae family, with the exception of *Pathera leo*) rely on a deep and powerful bite to take down larger prey with a single bite, whereas carnivores that hunt in packs (i.e., Hyaenidae) deliver a shallow bite as they rely on their numbers to take down prey (Therrien, 2005). Carnivores that consume bone have dentitions that are more specialized to maintain their osteophagy behaviour. This is evident in the dental morphology of Hyaenidae (Figures 7 and 9), which included a reduction in the carnassials as well as robust and blunt-like canines that are worn out due to the osteophagy behaviour seen by scavengers.

The *Lycaon pictus* bite force is closer to that of the hypercarnivorous Hyaenidae (i.e. *Crocuta crocuta*, *Hyaena hyaena*, and *Parahyaena brunnae*) within the sample, in contrast to the bite force of the Felidae (Table 1). Previous studies indicated convergences in the

mandibular shapes of the Hyaenidae and Canidae (Figueirido *et al*. 2011), with both families having developed a coronoid process that provides increased leverage, thereby increasing the bite force. *Lycaon pictus* also hunt in packs, which is similar to the hunting strategies seen in Hyaenidae (Fanshawe and Fitzgibbon, 1993; Courchamp and Macdonald, 2001; Hubel *et al*. 2016), further indicating that Hyaenidae and Canidae would have similar bite forces as well as gape (Biknevicius and Ruff, 1992; Figueirido *et al*. 2011; Prevosti *et al*. 2011). However, PC2 shows no overlaps in the shape of the *Lycaon pictus* mandible with the Hyaenidae mandible, whereas a close relationship can be seen between the mandibular shapes of *Lycaon pictus* and Felidae (Figure 7). The relationship observed is most likely due to *Lycaon pictus* having a similar diet to the Felidae in this sample, as it was previously mentioned by Raia (2004) that there is a strong correlation between mandible morphology and diet.

The similarities seen in the mandibular sizes of all species of Hyaenidae could be in relation to them being in the same family. As *Proteles cristata* mandibles are slightly smaller in size, in comparison to the other Hyaenidae (Figure 7), it is most likely as a result of allometry as the *Proteles cristata* body mass is much smaller in comparison to the other Hyaenidae (Table 1). Mandibular similarities in size may also be an adaptation due to similar environments, which can be seen by the overlaps in distribution patterns in Figure 3. Although having a predominantly insectivorous diet, *Proteles cristata* have also been seen to opportunistically feed on larger prey such as small mammals and birds when needed (De Vries *et al*. 2011), therefore this behavioural plasticity due to undesirable environmental conditions may have resulted in the mandibular similarities seen in Hyaenidae. Although showing similarities in size, the shape (PC2) of the Hyaenidae mandibles differentiated according to their degree of carnivory, with the hypocarnivorous *Proteles cristata* displaying extreme changes in mandibular shape in comparison to the hypercarnivorous Hyaenidae (i.e. *Crocuta crocuta*, *Hyaena hyaena*, and *Parahyaena brunnae*) (Figures 7 and 9). *Proteles*

cristata has a diet comprising of mainly termites (Tarquini *et al.* 2020; Galiano *et al*. 2022), with the mandible being more suited to this hypocarnivorous diet due to the flattened jaw (i.e. ramus and corpus regions) that decreases bite force, and the highly specialized dentitions that allow for the consumption of smaller prey and softer material (Figure 9). Conversely, the hypercarnivorous Hyaenids possess more robust dentitions and a concave jaw that allows for the consumption of larger prey and harder material (Figure 9). Due to the trade-offs between gape and bite force (Biknevicius and Ruff, 1992; Figueirido *et al*. 2011; Prevosti *et al*. 2011), the decreased mechanical advantage of the hypocarnivorous *Proteles cristata* mandible would result in a decreased bite force and increased gape. The hypercarnivorous Hyaenids, however, would have an increased bite force and decreased gape due to the increase in mechanical advantage brought about by the robust dentitions and concave jaws (Figure 9).

The overlaps seen along PC1, PC2 and PC3 (Figures 7, 10 and 12) between the *Panthera leo* and the *Panthera pardus* indicate notable similarities in both the mandibular shape and size, despite having differing hunting strategies (i.e. *Panthera pardus* are solitary hunters while *Panthera leo* generally hunt in groups (Spong *et al*. 2001; Balme *et al*. 2017; Miller *et al*. 2018)). Previous studies suggest that gape and bite force would differ between solitary carnivores and carnivores that hunt in packs (Slater and Van Valkenburgh, 2009; Figueirido *et al*. 2011), therefore the shape of the coronoid process should differ between *Panthera leo* and *Panthera pardus* and these species should have contrasting bite forces and gape. The *Panthera leo* would therefore be expected to have an increased bite force and a decreased gape, in contrast to the *Panthera pardus*, due to the pack-hunting seen in *Panthera leo*, which is similar to the Hyaenidae and Canidae hunting strategies. Conversely, the average bite forces of the *Panthera leo* and the *Panthera pardus* are almost identical (Table 1). The convergence seen in the mandibular shape of the *Panthera leo* and the *Panthera pardus* could be due to both species belonging to the same family (i.e. Felidae), and having

almost identical diets (Hayward, 2006; Hayward and Kerley, 2008; Hayward and Slotow, 2009; Tarquini *et al*. 2020) It can also be noted that the *Panthera leo* is considerably larger in body mass opposed to the *Panthera pardus* (Table 1), while displaying similar mandible morphologies (i.e. similarities in size and shape), suggesting that body mass did not play a significant role in the Felidae mandible morphology in this study.

Limitations

One of the limiting factors in this study was age, as the age groups of most of the specimens were unknown. Due to ontogeny, the morphology of the carnivore mandibles would change over time, from adolescence to adulthood, therefore younger specimens would have differing morphologies as opposed to adult specimens within the same species. The sexes of the mandible specimens were also unknown, therefore sexual dimorphism could have also impacted this study as the males and females of the same species could exhibit differing morphological characteristics as well as differing hunting and feeding behaviours. Increasing the sample sizes of the different families would also be beneficial in obtaining more accurate results as only one species of Canidae was used within this study, which could have impacted the findings observed for the Canidae family. Due to the unknown sex and ages of the specimens in this study, as well as the varying sample sizes between the three families, it is advised that the results should be interpreted with caution when used in future studies. Minimal research has been conducted on mandible symmetry and asymmetry, which may have affected the results of this present study. It is recommended that future studies on mandible symmetry and asymmetry should be conducted to determine its influence on mandible function.

Conclusions

This study aimed to determine the extent to which the Hyaenidae mandible morphology and dentition differs from that of other large carnivores in Africa. This was achieved by conducting a comparative assessment of the size and shape of the carnivore mandibles. It was found that the sizes of the carnivore mandibles were clustered according to their respective families (i.e. Hyaenidae, Canidae, and Felidae), while the shape of the mandibles differed according to diet. The morphology supported that the hypercarnivorous Hyaenidae mandibles were closer to Felidae with regards to shape, however, the Hyaenidae mandibles were found to be closer to Canidae with regards to size. While showing similarities in mandibular size, the degree of carnivory played a major role in differentiating the shape of the Hyaenidae mandibles, with the hypocarnivorous species (i.e. *Proteles cristata*) displaying a morphology that is more suited to a diet of mainly termites. The mandible morphology of the hypercarnivorous Hyaenidae displayed evident adaptations to osteophagy behaviour, with changes in morphology that allows for the increased bite forces seen by these carnivores. Ultimately, it is likely to be found that an increased resistance to bending forces and an increased area for muscle attachment on the mandible would directly relate to an increase in a carnivore's bite force. The analyses of a wider range of carnivore mandibles would allow for a more comprehensive understanding of the relationship between mandible morphology and bite force in carnivores. This study inferred how the mandible morphology accommodates for the carnivore's biomechanical needs such as muscle attachment and bite force, as well as determining the implications that carnivore mandible morphology has on feeding ecology and predatory behaviour.

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Appendix

Table A1: Sample Composition

Species	Family	Specimen Number	Source*
Acinonyx jubatus	Felidae	TM 870	DNMNH
Acinonyx jubatus	Felidae	TM 3254	DNMNH
Acinonyx jubatus	Felidae	TM 12159	DNMNH
Acinonyx jubatus	Felidae	TM 12469	DNMNH
Acinonyx jubatus	Felidae	TM 13275	DNMNH
Acinonyx jubatus	Felidae	TM 25602	DNMNH
Acinonyx jubatus	Felidae	ZM 38630	ISAM
Acinonyx jubatus	Felidae	ZM 38781	ISAM
Acinonyx jubatus	Felidae	ZM 39035	ISAM
Acinonyx jubatus	Felidae	ZM 39048	ISAM
Crocuta crocuta	Hyaenidae	AZ 650	DNMNH
Crocuta crocuta	Hyaenidae	AZ 1954	DNMNH
Crocuta crocuta	Hyaenidae	AZ 1984	DNMNH
Crocuta crocuta	Hyaenidae	AZ 1988	DNMNH
Crocuta crocuta	Hyaenidae	AZ 3040	DNMNH
Crocuta crocuta	Hyaenidae	TM 621	DNMNH
Crocuta crocuta	Hyaenidae	TM 13273	DNMNH
Crocuta crocuta	Hyaenidae	TM 16703	DNMNH
Crocuta crocuta	Hyaenidae	TM 17049	DNMNH
Crocuta crocuta	Hyaenidae	ZM 19469	ISAM
Crocuta crocuta	Hyaenidae	ZM 33341	ISAM
Crocuta crocuta	Hyaenidae	ZM 36871	ISAM
Crocuta crocuta	Hyaenidae	ZM 40361	ISAM
Hyaena hyaena	Hyaenidae	ZM 36335	ISAM
Hyaena hyaena	Hyaenidae	ZM 36848	ISAM
Lycaon pictus	Canidae	TM 177	DNMNH
Lycaon pictus	Canidae	TM 3209	DNMNH

Lycaon pictus	Canidae	TM 5560	DNMNH
Lycaon pictus	Canidae	TM 11500	DNMNH
Lycaon pictus	Canidae	TM 17772	DNMNH
Panthera leo	Felidae	TM 964	DNMNH
Panthera leo	Felidae	TM 38244	DNMNH
Panthera leo	Felidae	TM 38245	DNMNH
Panthera leo	Felidae	TM 38251	DNMNH
Panthera leo	Felidae	TM 38253	DNMNH
Panthera leo	Felidae	ZM 33363	ISAM
Panthera leo	Felidae	ZM 35041	ISAM
Panthera leo	Felidae	ZM 35115	ISAM
Panthera leo	Felidae	ZM 41420	ISAM
Panthera pardus	Felidae	CR 929	DNMNH
Panthera pardus	Felidae	CR 1005	DNMNH
Panthera pardus	Felidae	TM 12161	DNMNH
Panthera pardus	Felidae	TM 12162	DNMNH
Panthera pardus	Felidae	TM 13277	DNMNH
Panthera pardus	Felidae	TM 19199	DNMNH
Panthera pardus	Felidae	ZM 41326	ISAM
Panthera pardus	Felidae	ZM 41400	ISAM
Panthera pardus	Felidae	ZM 41401	ISAM
Panthera pardus	Felidae	ZM 41413	ISAM
Parahyaena brunnae	Hyaenidae	TM 740	DNMNH
Parahyaena brunnae	Hyaenidae	TM 4189	DNMNH
Parahyaena brunnae	Hyaenidae	TM 6186	DNMNH
Parahyaena brunnae	Hyaenidae	TM 6187	DNMNH
Parahyaena brunnae	Hyaenidae	TM 6269	DNMNH
Parahyaena brunnae	Hyaenidae	TM 7896	DNMNH
Parahyaena brunnae	Hyaenidae	TM 14014	DNMNH
Parahyaena brunnae	Hyaenidae	TM 25430	DNMNH
Parahyaena brunnae	Hyaenidae	ZM 33392	ISAM
Parahyaena brunnae	Hyaenidae	ZM 39359	ISAM

Parahyaena brunnae	Hyaenidae	ZM 39696	ISAM
Parahyaena brunnae	Hyaenidae	ZM 40064	ISAM
Proteles cristata	Hyaenidae	AZ 820	DNMNH
Proteles cristata	Hyaenidae	AZ 822	DNMNH
Proteles cristata	Hyaenidae	AZ 2152	DNMNH
Proteles cristata	Hyaenidae	ZM 39572	ISAM
Proteles cristata	Hyaenidae	ZM 39687	ISAM
Proteles cristata	Hyaenidae	ZM 40384	ISAM
Proteles cristata	Hyaenidae	ZM 40439	ISAM

*Key for source: DNMNH – Ditsong National Museum of Natural History; ISAM – Iziko South African Museum.

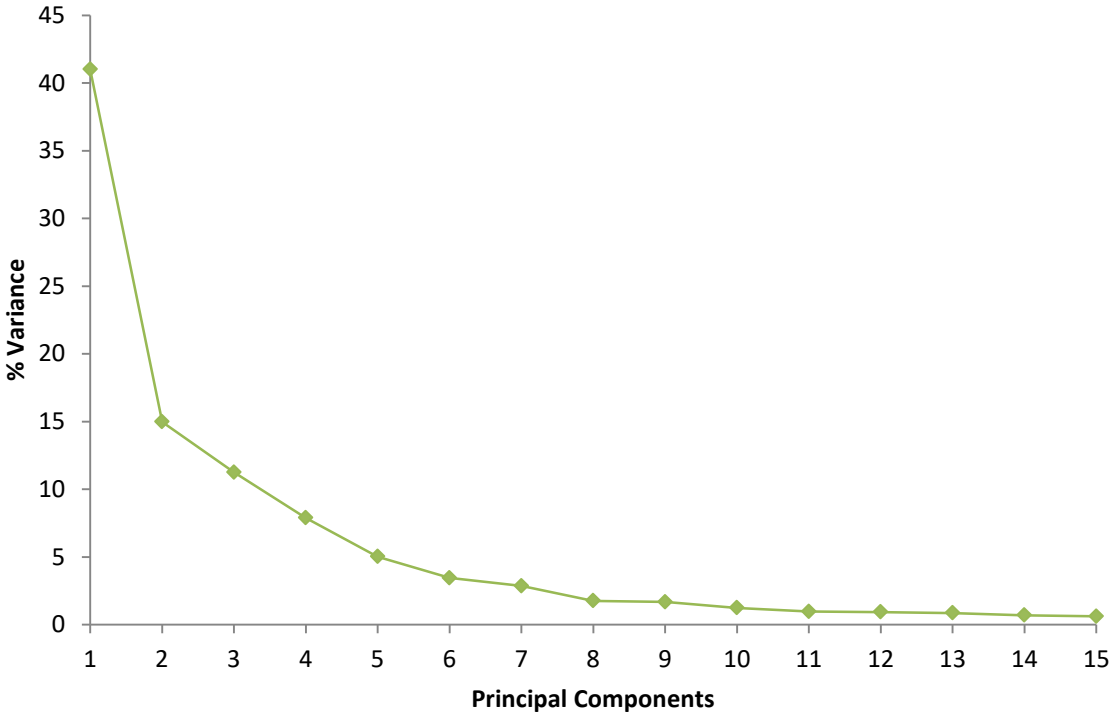

Figure A1: Scree plot representing the percentage variance of the first 15 principal components for the lateral view of the carnivore mandibles.

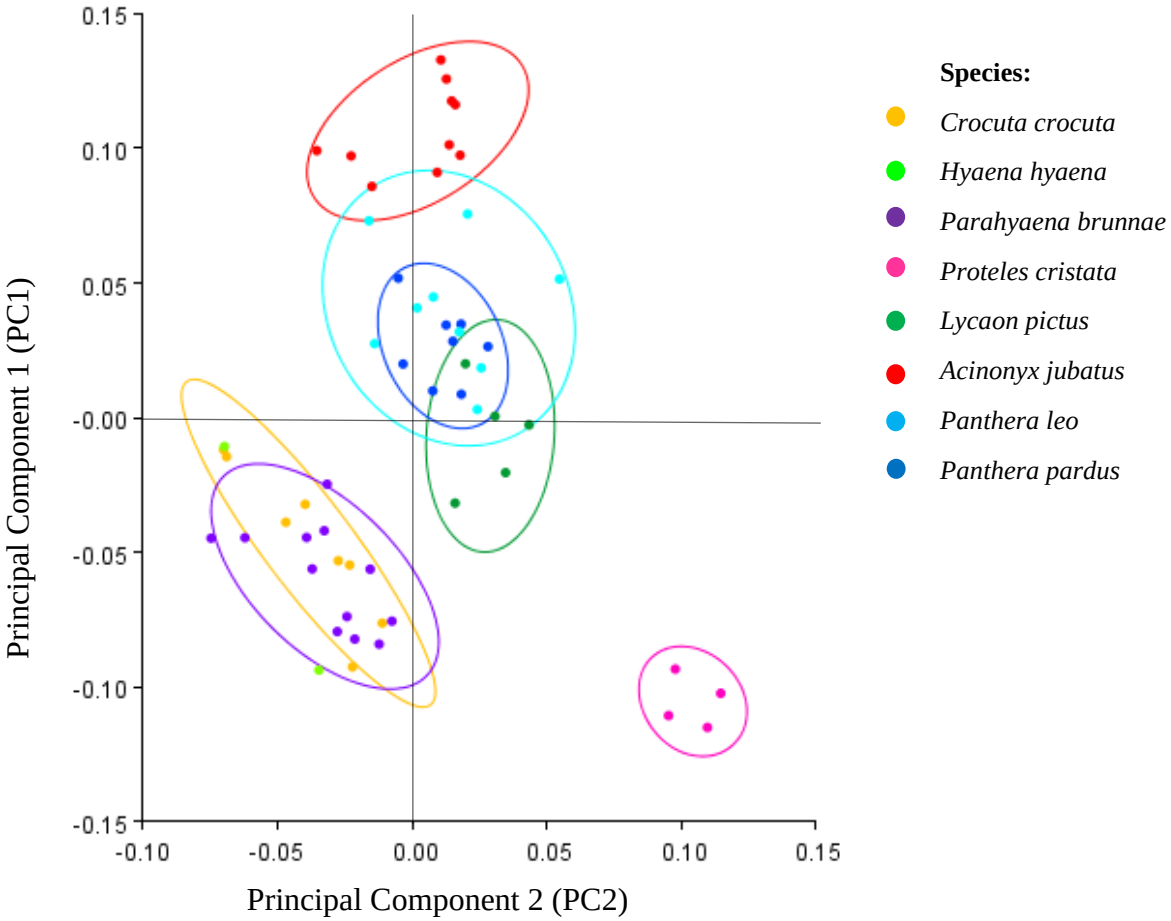

Figure A2: PC2 (x-axis) plotted against PC1 (y-axis). Clusters of species are indicated by confidence ellipses with their respective colouration.

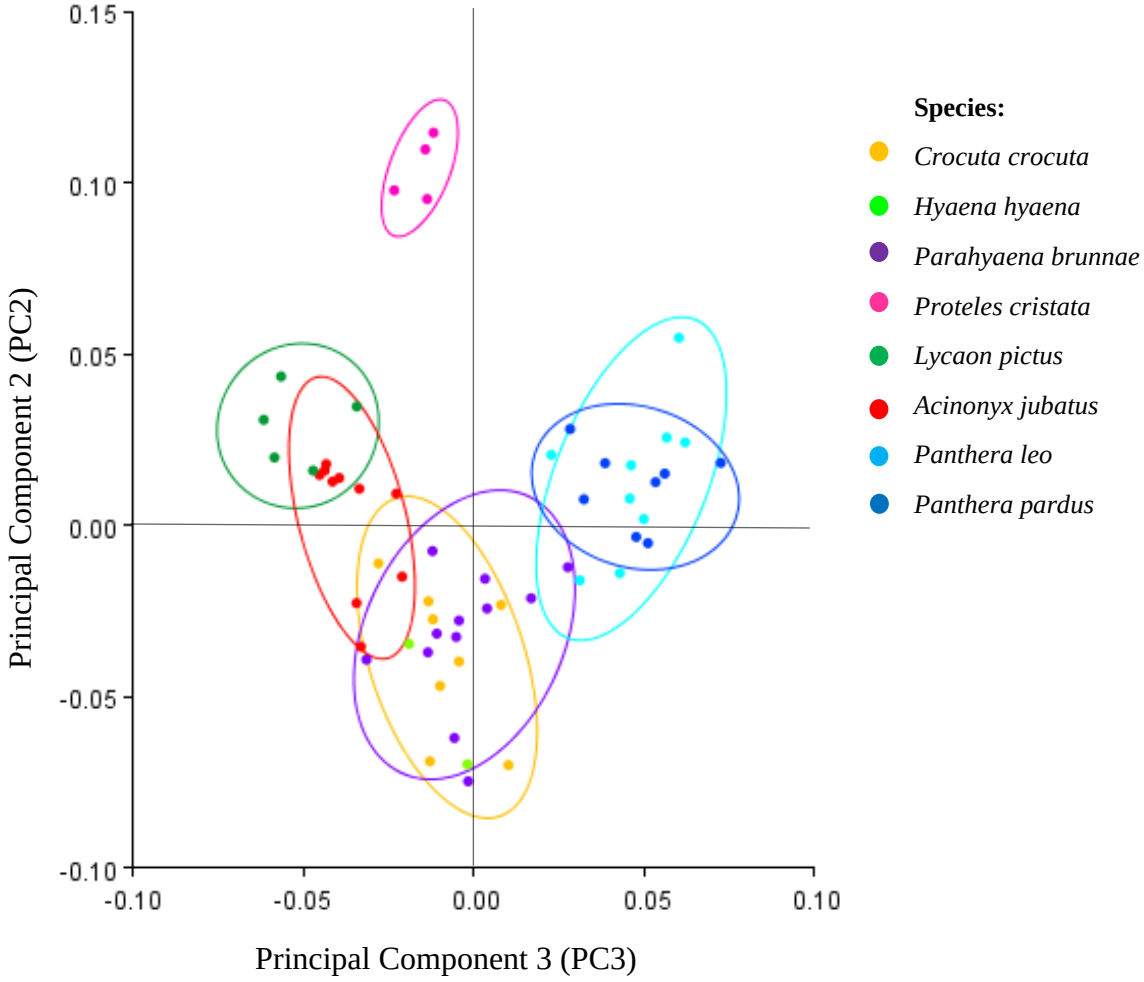

Figure A3: PC3 (x-axis) plotted against PC2 (y-axis). Clusters of species are indicated by confidence ellipses with their respective colouration.

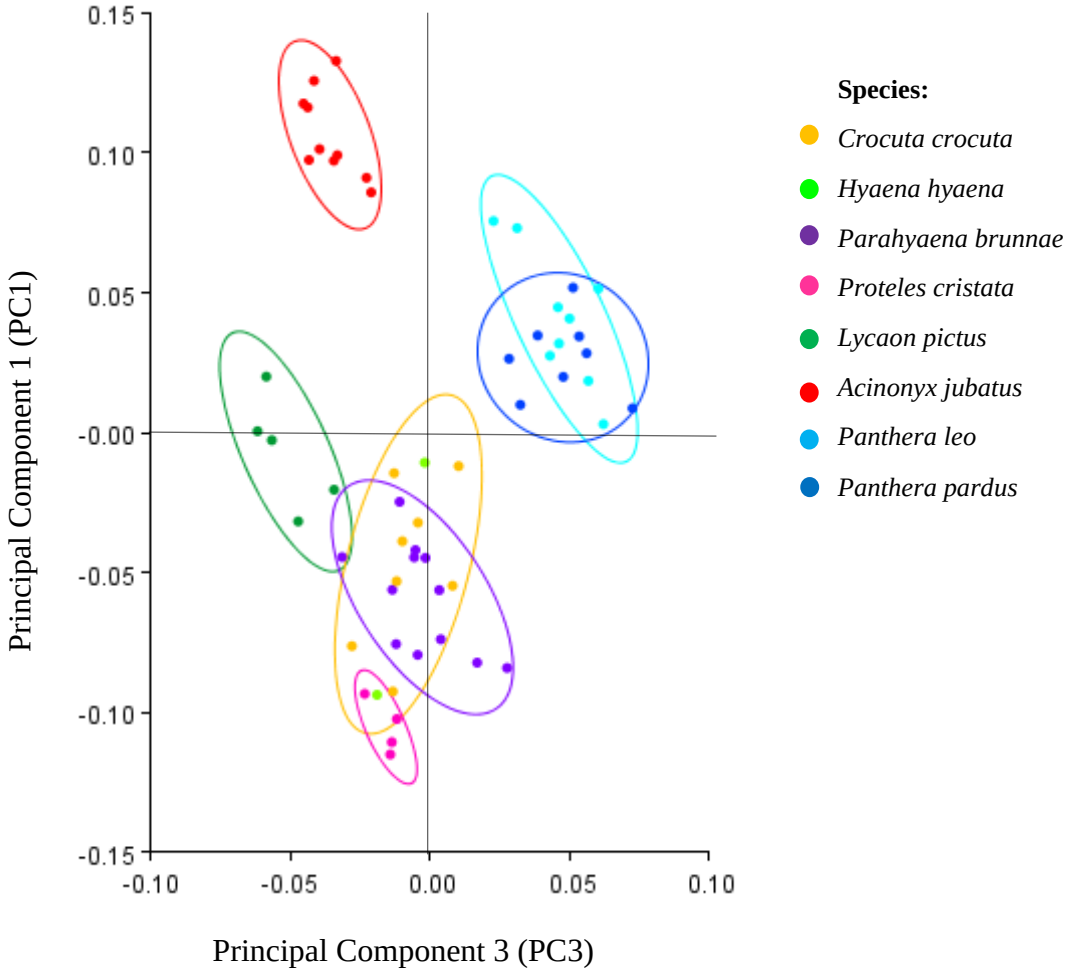

Figure A4: PC3 (x-axis) plotted against PC1 (y-axis). Clusters of species are indicated by confidence ellipses with their respective colouration.