A phylogenetic and palaeoecological review of the Pleistocene felid *Panthera gombaszoegensis*.

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ABSTRACT

Panthera gombaszoegensis was a medium – large sized big cat, present in Europe between 1.9Ma and 0.3Ma. It was first identified in 1938 by Kretzoi from the site of Gombasek in Slovakia. The only syntheses of this species were conducted 30 years ago and many more specimens have been discovered since then. This thesis describes specimens from 23 sites which have been studied at first hand and reviews all other published material. Taking the modern *Panthera* species as a baseline, morphometric and morphological variability is assessed and the results of these studies are applied to the fossils. A biogeographic analysis of the larger Pleistocene Carnivora is also conducted. Morphological differences in conjunction with a size increase were noted between older (1.9 – 0.8Ma) and younger (0.8 – 0.3Ma) *Panthera gombaszoegensis* specimens and these may be related to changes in prey size, guild membership and the Pleistocene glaciations. The potential for genetic isolation and extinction of large mammals in Pleistocene refugia is considered and methods of furthering this research are discussed. The subdivision of *P. gombaszoegensis* into two subspecies is rejected and the possibility that *P. gombaszoegensis* is most closely related to the jaguar and tiger is addressed.

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CHAPTER 1 – INTRODUCTION

This thesis offers a detailed examination of the morphology and palaeoecology of *Panthera gombaszoegensis* (Kretzoi, 1938). This cat, often referred to as the European jaguar, is a widely distributed member of the Lower and Middle Pleistocene mammalian fauna of Europe. It was a medium-large sized animal, with a stocky and powerful build. It is this latter feature which has largely led to its identification as a jaguar, together with the fact that the appearance of the true jaguar (*Panthera onca*) in the new world was once thought to be contemporaneous with the arrival of *P. gombaszoegensis* in Europe.

The only systematic studies of this species were undertaken 30 years ago by Hemmer (1971a; 1972a), Hemmer & Schütt (1969) and Jánossy (1969). However, many more specimens have been reassigned in museum collections or discovered at new sites in the intervening period. In addition, in recent years syntheses of the evolution of the Pleistocene larger mammalian fauna (Azzaroli *et al*, 1988) and the Carnivora in particular (Turner, 1995a), have placed the chronology of species appearance and extinction within Europe on a clearer footing. It is now apparent that *Panthera gombaszoegensis* was the sole pantherine cat present in Europe during the Early Pleistocene, a time when the felid component of the carnivore guild was dominated by the sabretoothed genera *Homotherium* and *Megantereon*, and that it continued to thrive once the leopard (*Panthera pardus*) and subsequently the lion (*Panthera leo*) entered the continent towards the end of the Lower Pleistocene. *Panthera gombaszoegensis* survived throughout a period of enormous change in the physical and biotic environment and its eventual extinction occurred at a time of great change in the structure of the European large carnivore guild. It is therefore time for a full reappraisal of this species.

I begin this Chapter with a consideration of theoretical issues related to fossil species identification and designation and go on to establish the chronological and environmental background of *Panthera gombaszoegensis* in Pleistocene Europe. Chapter Two summarises the morphometric methodology and statistical techniques used in this thesis. This is followed by an analysis of morphometric and morphological variability in the extant pantherine cats in Chapter Three. The results of this study are applied to the fossil *P. gombaszoegensis* material in Chapters Four and Five, which also include a morphometric and morphological review of this species. Chapter Five also contains a review of all published *P. gombaszoegensis* material that were not included in this analysis and a discussion of juvenile specimens. Chapter Six is a study of the biogeography and palaeoecology of the Pleistocene hyaenids and felids with a focus on *Panthera gombaszoegensis*. The resulting conclusions are discussed in Chapter Seven. Authorities for all binomens used in this thesis are listed in Appendix 1.

1.1. BACKGROUND TO THE STUDY OF *PANTHERA GOMBASZOEGENSIS*

The pantherine cats have been very successful, as they first appear in the African fossil record at 3.7Ma and have been present ever since (Turner, 1990a). *Panthera gombaszoegensis* is unusual in that it is the only member of this genus to have become extinct. It was first described as a fossil species by Kretzoi in 1938, based on material from Gombaszög (now Gombasek) in Slovakia. Since 1938 it has been reported from 57 sites, now reduced to 51 (see Chapter 5), and the morphology, taxonomy and phylogeny of this cat are not well understood.

Historically, *P. gombaszoegensis* has been most closely compared with the modern jaguar. At various other times it has also been suggested that *Panthera gombaszoegensis* may be ancestral to both the jaguar and leopard, or most closely related to the lion or tiger (*Panthera tigris*), as it appears to have features that are associated with all of these species (Hemmer, 1971a; Bishop, 1982). As one of the aims of this work is to consider the taxonomic position of *Panthera gombaszoegensis*, a discussion of the nature of species is relevant.

1.2. WHAT IS A SPECIES?

The question 'what is a species?' is fundamental to biology, but it lacks a definite answer (Mayr, 1982). Initially regarded as the result of divine creation, the advent of evolutionary theory has led to a proliferation of species concepts which purport to explain what 'a species' is in terms of biological, morphological or molecular characters. A recent review listed 24 separate species concepts, all of which have their adherents and supporters (Hey, 2001). Despite (or perhaps because of) this multitude of ideas, biologists are no closer to agreeing a definition of the term 'species'.

Of the 24 species concepts mentioned above, they can all be reduced to three core ideas – the biological species concept, the morphological species concept and the molecular species concept. Ernst Mayr defined species as 'groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups' (1942:120). This theory is known as the biological species concept or BSC and it largely holds true for most modern sexually reproducing species. Mayr later pointed out that 'an occasional individual in an otherwise perfectly good species may hybridise – isolating mechanisms can only provide the integrity of populations but not of every last single individual' (1982:274). This neatly covers the problem within the genus *Panthera*, where interbreeding does occasionally take place (see section 1.4.3). The application of the BSC to fossils is more problematic as we cannot be sure that they were reproductively distinct. The morphological species concept has existed for years and simply defines a species as something which looks different from something else (Ghiselin, 2001). How different it has to be to be a new species is the sticking point when we come to fossil data. The molecular species concept has come to the fore more recently, with the rise of biomolecular techniques which can assess the relationships both within and between groups at the species level. Again, this depends on the level of difference required to make a new species and molecular types cannot be directly applied to the fossil record.

1.2.1. Palaeontology and species

In one respect the palaeontologist is fortunate as only the bones and teeth of animals tend to survive fossilisation thus restricting them to the morphological species concept. On the other hand this reliance on hard tissues creates unsolvable riddles as we become more aware, through molecular techniques and ethological observations, of the number of creatures that look the same to the human eye but very different to the animals involved. Certain groups have been found to be subdivided although they look the same and are therefore termed cryptic or sibling species (Mayr, 1982). In palaeontology many species either become lumped into a single taxon which reduces our understanding of biodiversity in the fossil record or huge numbers of species are created on the appearance of a single cusp or morphotype which may be well within the range of variation seen within a modern 'species' (see Chapter 3). This splitting of material is equally problematic as animals are named with no regard for where they might fit in – i.e. where are the niches for huge numbers of apparently closely related and morphologically similar creatures? Each time a new fossil species is created, it involves far more than just naming an animal – it automatically begets a living, surviving and reproducing population with all the requirements for ancestral groups, home ranges and ecological niches that that entails. This problem is sometimes resolved by creating a subspecies.

1.2.2. Subspecies

A subspecies has been defined by Brown & Lomolino (1998:635) as 'a taxonomic category used by some systematists to designate a genetically distinct set of populations with a discrete range'. The problem with this definition is that we have no idea whether or not a fossil subspecies was either genetically or geographically distinct. A further difficulty is added by the differing use of subspecies by different authors. A recent publication has named *Panthera gombaszoegensis* as a subspecies of the modern jaguar, making it *Panthera onca gombaszoegensis* (Moullé *et al*, 2000). This use of the trinomial appears to be a form of shorthand for 'most closely related to' or 'ancestral to'. This usage of the subspecific designation as a way of indicating the closeness of a relationship to a species appears to have originated with European taxonomists, notably Hartert and Stresemann in the 1920s and '30s (discussed in Mayr, 1982:291). However, it is not one recognised by modern biologists. Under the current definition of the term subspecies the designation of *P. onca gombaszoegensis* suggests that *gombaszoegensis* is a geographic variant of the modern jaguar, which is not the case. In fact it is a variant in time rather than geographical space, and is therefore a chronospecies.

1.2.3. Chronospecies

The third great problem for the palaeontologist is the introduction of time into the equation. Certain animals must be ancestral to others, but either they both coexist for some time or one overnight becomes another. It is at this point chronospecies loom on the horizon. These are effectively species through time that alter sufficiently for a line to be drawn and a decision to be made as to the point at which one animal becomes another. A good example of this is found in the European Pleistocene where biostratigraphic analyses using rodent teeth underpins much of the chronology. The transition in certain lineages from rooted to non-rooted teeth has been used to separate genera, e.g. *Mimomys* to *Arvicola* (Stuart, 1982). But in other cases, the chronospecies are much less divisible, for example the division of *Panthera gombaszoegensis* into two subspecies by Hemmer (1972a). Mayr suggests that convenient gaps in the fossil record can be used to arbitrarily separate lineages (Mayr, 1982:295). The problem for the palaeontologist working in the relatively short timescale of the European Pleistocene is that such gaps do not exist.

1.2.4. The use of the term species in this thesis.

Considering all of the above problems the term species is used in the following way in this thesis. The morphological species concept is applied to fossil specimens with the proviso that where extant closely related species exist, for example in the modern big cats, what we know of the morphological variation within a modern biological and molecular species has been used to inform decisions made about the variation that can be expected within a fossil species and to assess the validity of these species.

1.3. CHRONOLOGY AND CLIMATE

1.3.1. Terminology

The Quaternary is divided into two separate eras, the Pleistocene and the Holocene, which together make up the last ~1.7Ma of the geological time scale. The Holocene is typically regarded as the last 10,000 years. The Epoch immediately preceding the Pleistocene was the Pliocene, which is generally regarded as beginning at ~5Ma and ending at ~1.7Ma. The Pleistocene has been subdivided into the Lower, Middle and Upper or the Early, Middle and Late depending on whether lithostratigraphic or chronological scales are being used. However, these terms equate with each other; Lower and Early are synonymous and indicate the oldest stage. Only the Lower and Middle Pleistocene are of relevance to this thesis and the boundary between them is commonly accepted to be the Brunhes/Matuyama boundary at ~0.8Ma (Dawson, 1992). These terms and all others explained below are illustrated in Figure 1.1.

A second method of subdividing the last few million years is used (mainly by French and Italian authors) and is based on a concept of large mammal faunal stages. These stages are sequential and begin with the Villafranchian (3.2 – 0.9Ma), followed by the Galerian (0.9-0.4Ma) and then the Aurelian (0.4 –present) (Azzaroli *et al*, 1988). Again, this has been subdivided into the Early, Middle and Late Villafranchian (see Figure 1.1). Only the Late Villafranchian affects this work and this began with the 'wolf' event which roughly correlates with the beginning of the Pleistocene (~1.7Ma) (Azzaroli *et al*, 1988). Other biostratigraphic methods are considered in section 1.3.2.5.

1.3.2. Chronology

Many other schemes or methods are also used to ascertain the age of Pleistocene sites. These can be divided into two main types which produce absolute or relative chronologies. These methods will be discussed below and illustrated with examples that have a direct bearing on the study of *Panthera gombaszoegensis.*

1.3.2.1. Potassium-Argon dating

Potassium-Argon is a radiometric method that counts the ratio of $^{40}K/^{40}Ar$ in a rock. Potassium decays into Argon at a known rate, so the proportion of ^{40}K which has converted to ^{40}Ar can be used to calculate an absolute age for the rock. Argon-Argon dating is more appropriate for sites older than 0.4Ma; this technique is similar to the above, but counts the radioactive decay from ^{40}Ar to ^{39}Ar and has been widely used to date East African hominid sites (Lowe & Walker, 1997). However, the problem with both $^{40}K/^{40}Ar$ and $^{40}Ar/^{39}Ar$ is that they can only be used on volcanic deposits and these are only found in specific areas, e.g. Italy.

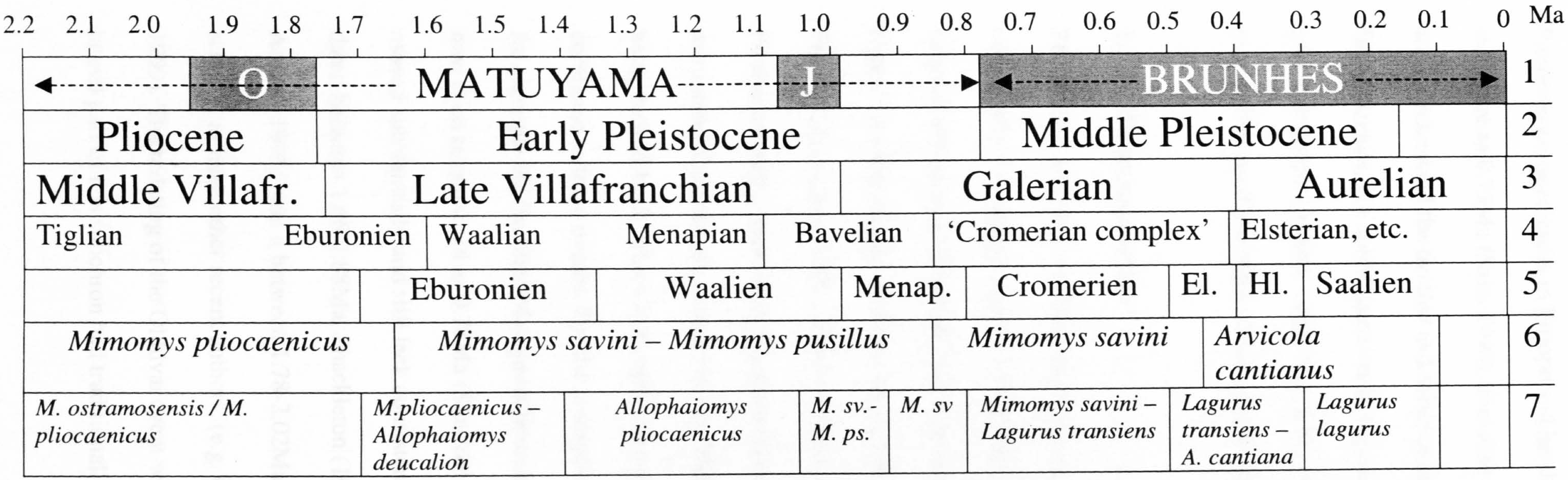


Figure 1.1. Major European chronologies, in millions of years, later Pleistocene (post 0.35Ma) divisions have not been included.

1. Palaeomagnetic timescale, gray areas show normal polarity, O = Olduvai subchron, J = Jaramillo (from Shackleton, 1995).

2. Subdivisons of the Pleistocene (from Dawson, 1992). **3.** Villafranchian subdivisions (from Azzaroli *et al*, 1988).

4. Glacial/interglacial stages based on pollen zones from the Netherlands (from Funnell, 1995). **5.** Glacial stages from Wolsan (1993) Menap. = Menapian, El. =Elsterian and Hl. = Holsteinian. **6.** Europe-wide arvicolid chronology (from Maul *et al*, 1998). **7.** Arvicolid chronology from the Carpathian basin (Kordos, 1994), abbreviations are – *M. sv.* = *Mimomys savini*; *M. ps.* = *Mimomys pusillus*.

The date of the Italian site of Isernia la Pineta is controversial; it contains the earliest *Panthera leo* specimens in Europe and has been dated with the Potassium-Argon technique to 0.73Ma (Sala, 1990). The date of the arrival of lion is very important if we are to understand the decline and subsequent extinction of the archaic Carnivora such as *Homotherium*, but doubts have been expressed about the early date for this site, on both palaeomagnetic (Aitken, 1995) and biostratigraphic grounds (Maul *et al,* 1998). Maul *et al* (1998) used arvicolid remains to redate this site between 0.69 and 0.5Ma.

1.3.2.2. Palaeomagnetism

The Earths' magnetic field has undergone periods of reversal which result in a characteristic magnetic signal in the rocks and sediments that are lain down at these times. Long periods of stability are termed 'chrons' (such as the Brunhes chron in Figure 1.1) and shorter reversals are called 'subchrons' (e.g. the Jaramillo event in Figure 1.1) (Aitken, 1995). These magnetic events were originally dated using the Potassium-Argon technique, but more recently they have been tuned in accordance with astronomical cycles (discussed below). This has resulted in the dates of the reversals being moved back, which has implications for any pre 1990 reports which have been correlated to these events. For the younger events this change has made little difference, for example the Brunhes/Matuyama boundary was originally placed at 0.73Ma and has now been recalibrated as 0.78Ma (Shackleton, 1995). However, the older periods have moved substantially and still lack consistency, e.g. the Olduvai subchron was originally dated between 1.66-1.88Ma, Shackleton (1995) gives a new date of 1.77-1.95Ma while Aitken (1995) puts it between 1.78-2.02Ma. In this thesis I have followed Shackleton's scheme, as have other recent authors, (e.g. Gabunia *et al*, 2000; García & Arsuaga, 1999). The redating of the Olduvai event was particularly important, because the top (or latest) part of this subchron had traditionally been used to signal the start of the

Pleistocene. I am accepting the start of the Pleistocene as the top of the newly dated Olduvai event; it is recognised that this position will not be accepted by all authors, but it marks a definite (and therefore useful) date that may be worked from.

Palaeomagnetism is particularly useful for 'sandwiching' sites between different events and indirectly dating them. For example, the site of Lakhuti 2 in Tadjikistan is placed below the Jaramillo subchron but before the Brunhes/Matuyama boundary, it must therefore have an age of between 0.99 – 0.78Ma (Sotnikova & Vislobokova, 1990).

There are some difficulties with the use of palaeomagnetism. In the first place it requires either volcanic or very fine grained sediments, which are not found at every site. Also, there are long periods of stability between subchrons or chrons when no changes take place, which means that deposits from such time periods can only be roughly dated, e.g. between the Olduvai and Jaramillo subchrons there is a period of stability lasting some 700,000 years (see Figure 1.1).

1.3.2.3. Oxygen isotopes

The oxygen isotope signature contained in the calcium carbonate shells of foraminifera in oceanic sediments have been used to infer periods of climate change through the Pleistocene. The foram tests take up oxygen isotopes from the surrounding water and the quantity of ^{18}O and ^{16}O is dependent upon ocean temperature and world climate (Kump *et al*, 2000). Glaciers take up more of the lighter isotopes (^{16}O) which makes the oceans rich in ^{18}O during glaciations and this is reflected by an increase in the amount of ^{18}O in the shells, which indicates a cold stage (Aitken, 1990).

Figure 1.2 shows the Pleistocene OIS record from Shackleton (1995). The glacial/interglacial sequence can be seen as a series of advances and retreats in a cyclic pattern. The cycles of cold and warm stages have been related to orbital forcing on three separate time scales - 100,000 years, 41,000 years and 26,000 years (Kump *et al*, 2000). Figure 1.2 shows that until 0.9Ma the glacial/interglacial cycles were of low magnitude, which reflects the build up of small icesheets, but after 0.9Ma the oscillations become more pronounced, leading to the fully glaciated conditions of the Middle Pleistocene (Shackleton, 1995). The patterns of cyclicity also changed at approximately 0.7Ma, switching from the 41,000 year cycle to 100,000 years. These differing stages are caused by changes in the Earth's orbit around the Sun and are called Milankovitch cycles.

The 100,000 year cycle is related to the eccentricity of the Earth's orbit about the Sun. This orbit is affected by the gravitational pull of other planets and the changes directly effect the amount of light that reaches the Earth's surface. When the eccentricity is great Northern hemisphere summers occur when the Earth is at its greatest distance from the Sun. The resulting lack of insolation means that the snow build up during winter does not melt, leading to an increase in ice mass. The 41,000 year cycle is caused by variations in obliquity – the tilt of the Earth's axis in relation to the Sun. When obliquity is high the contrast between seasons is greater, leading to colder winters and an increase in ice mass (all above from Kump *et al*, 2000). Therefore the ideal conditions for the build up of ice leading to full scale glaciations are high eccentricity and high obliquity.

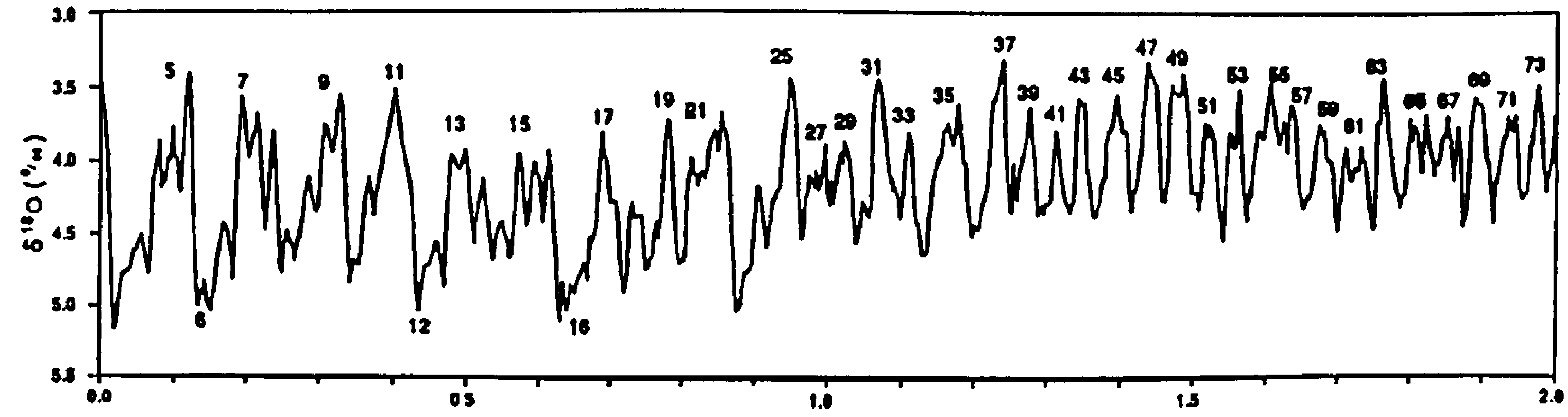


Figure 1.2. Pleistocene oxygen isotope stages from Shackelton (1995). Odd numbers represent periods of warmth and even numbers are cold stages.

1.3.2.4. Glacial/interglacial stages.

Oxygen isotope stages are a good way of getting away from traditional descriptive assessments of glacials and interglacials such as the Alpine Mindel-Riss-Würm classifications, which lack application outside their immediate areas (although this does not stop them being used) (Bowen, 1978). Other classic schemes such as the pollen sequence from the Netherlands (Figure 1.1. column 4) are more useful. One of the biggest problems with this type of classification is the different use of terms by different authors [cf. column 4 (from Funnell, 1995) and Column 5 (Wolsan, 1993)]. The term 'Cromerian' for example, is a distinct problem as it has been applied to many different dates. Most authors place the end of this stage between 0.5 and 0.4Ma, but its beginning is very different - there is a hiatus in the original UK chronology at ~0.65Ma leaving a gap until the Beestonian at ~1.6Ma (Lowe & Walker, 1997). The term 'Cromerian' also covers at least four glacial/interglacial cycles (Lowe & Walker, 1997). The Netherlands chronology (Figure 1.1. column 4) has named the latter part of this section the 'Cromerian Complex' to indicate these discrepancies. Because of these problems I have avoided using descriptive terms like 'Cromerian' in this thesis, preferring to use dates where possible.

The differential use of terms need not necessarily be a problem, so long as a chronology is included in the publication so that dates can be applied. The work of Wolsan (1993) is very important in this respect as he provides dates and faunal lists for 71 central European sites which I have used extensively. In order to use this publication I have taken the relative dates (such as Cromerien) and cross-referenced them in Figure 1 (Wolsan, 1993) to provide absolute date margins for each site. Although this method assumes that the work is internally consistent and is therefore vulnerable to errors, it is in this way that I have cross-correlated the site dates from major syntheses such as

Wolsan (1993); Kahlke (1975) and Koufos (2001), in order to be able to subdivide them for the analyses in Chapters Four, Five and Six.

1.3.2.5. Biostratigraphy

Biostratigraphy is the correlation of sediments using the fossils within them as stratigraphic markers. This method of dating sediments is very widely used in Europe for sites where absolute dating methods are not appropriate. However, there are a variety of problems associated with these techniques. Figure 1.1. shows two rodent chronologies, the first (Column 6) is a Europe wide chronology and the second is a local chronology for the Carpathian basin (Column 7). It can be seen that there are substantial differences between the two schemes, but neither is necessarily wrong. Some differences are undoubtedly due to alternative taxonomic classifications; for example *Mimomys ostramosensis* and *M. pliocaenicus* are probably conspecific, but synonymy cannot be confirmed because of poor type material (Masini & Torre, 1990). Other differences may be explained by localised evolution within the Carpathian basin. Recent evidence from microcharcoal analyses has shown that both cold tolerant (e.g. *Pinus* sp.) and thermophilous (e.g. *Ulmus* sp.) trees were present in Hungary during the last glacial maximum, indicating that this area may have provided a refugia for trees and small mammals in both the last glaciation (Willis *et al*, 2000) and possibly earlier (Stewart & Lister, 2001). This would have distinct implications for the evolution of the microfauna in this area.

The first rodent chronology (Figure 1.1. column 6) is Europe-wide in scale and is therefore much more generalised than the smaller scale, local schemes. Again, this requires care when looking at sites dated by microfaunal remains to see which scheme has been adhered to before making judgements about how old they are and cross-correlating them with other sites. For example, Professor Fejfar places the site of

Koneprusy in the *Mimomys savini* zone (pers. comm). The chronology of Kordos (1994) would place this species between 0.9-0.8Ma, while Maul *et al* (1998) (based on Fejfars' work) put it between 0.85 and 0.45Ma. I have therefore used the most appropriate chronology for the area in which the site is found. The review of the Hungarian sites by Kordos (1994) is the only one available and has therefore been followed, but one should note that it is not directly equivalent to other schemes.

1.4. THE GENUS *PANTHERA*.

1.4.1. Systematics

A pantherine big cat is a member of the Pantherinae, a subfamily of the cat family Felidae, a group of specialist hunters that are almost exclusively carnivorous (Kruuk, 1986). They are adapted to take prey as large or larger than themselves, although they can subsist on smaller animals if necessary (Sunquist & Sunquist, 1989). Cats can retract their claws and can also rotate their radius around the ulna. This allows them to manipulate prey, in a way that dogs and hyaenas cannot (Dayan & Simberloff, 1996). The pantherine cats have an elastic ligament in their hyoids and can all roar, but not purr (Pocock, 1916a). They also have a rounded pupil in contrast to the slit pupil of small cats (Turner & Antón, 1997). The systematics of the big cats down to the genus level is given below and is based on Turner & Antón (1997) and information in Wozencraft (1989) and Wayne *et al* (1989):

Kingdom: *Animalia,*
Phylum: *Chordata,*
Class: *Mammalia,*
Order: *Carnivora,*
Sub-order: *Fissipedia* (or *Feliformia*)
Super Family: *Feloidea* (or *Aeluroidea*),
Family: *Felidae,*
Sub-Family: *Pantherinae,*
Genus: *Panthera.*

1.4.2. Taxonomy

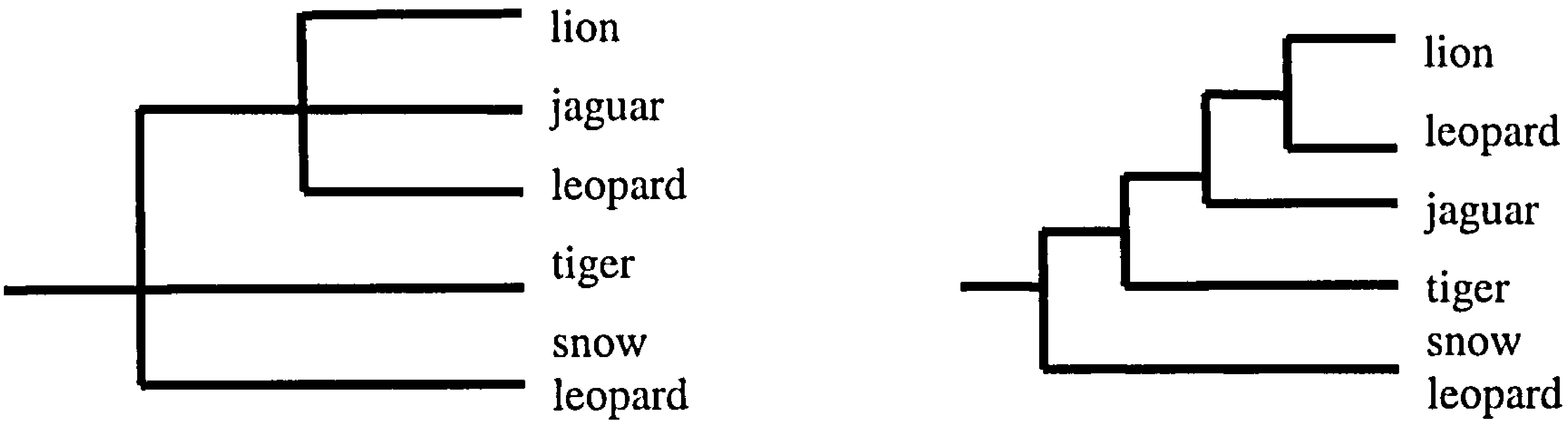
Whether *Felis* Linnaeus, 1758, *Panthera* Oken, 1816 or *Leo* Brehm, 1828 was the most appropriate genus for the big cats was the source of some dispute in the 1960s. Several authors cited *Panthera* Oken, 1816 as the most commonly used name for the genus (e.g. Hemmer, 1967; Mazak, 1968). Van Gelder (1977) advocated the synonomysing of *Panthera* with *Felis*, on the evidence of interbreeding (and therefore lack of reproductive isolation) between the puma (*Felis concolor*) and the leopard (*Panthera pardus*). For the most part the commonly used name has prevailed and big cats are now referred to as *Panthera* by the majority of authors (see Meester *et al* (1986) for a recent taxonomic review of this genus). Despite this, different authors have their own grounds for creating separate genera or species for particular animals, for example Ficcarelli & Torre (1968) placed the lion in a separate genus *Leo*, to distinguish it from other cats, largely based on the position of the postorbital process in relation to the M^1 and a ratio of the C^s to P^4. In contrast, Hemmer (1978) places the tiger in the subgenus *Tigris* and the snow leopard in a separate genus, *Uncia*. Kitchener (1991) summarises the phylogenies of four authors, the most notable of which is Nowak & Paradiso (1983) who place each species of *Panthera* in a subgenus, e.g. *Tigris* for the tiger, *Leo* for the lion, etc. This seems to negate the point of having species level taxa.

The position of the snow leopard (*Panthera uncia*) within the genus *Panthera* is controversial, the review of the taxon by Hemmer (1972b) placed it as a separate genus *Uncia*, a position also suggested by Hast (1989) based on the morphology of the larynx. However, a recent molecular study found only species level distinction between the leopard and the snow leopard and concluded that these two species are congeneric (Yu *et al*, 1996). I have followed Yu *et al* (1996) and Turner & Antón (1997) in referring the snow leopard to the genus *Panthera*.

1.4.3. Phylogeny

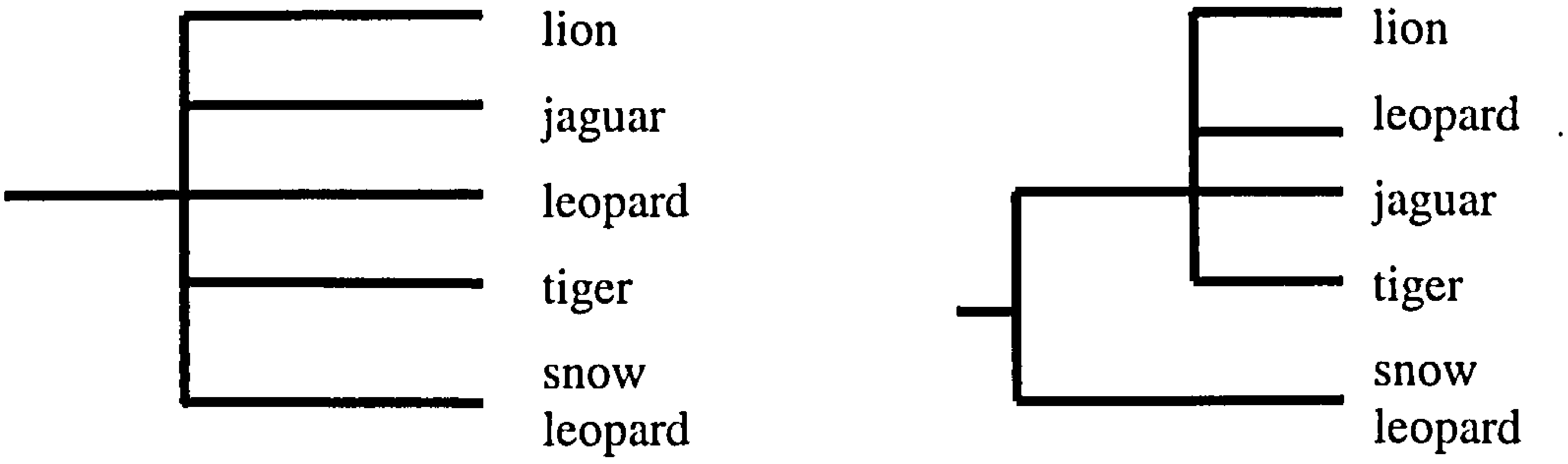
The phylogeny of the larger Felidae has attracted interest for many years, but despite the use of many different methods, it has proved to be problematic. Pocock (1907) suggested that the jaguar and leopard were most closely related on the basis of coat patterns and vocalisations in the two species. Hemmer (1978) used morphological and ethological traits to create a phylogeny in which the lion, jaguar and leopard formed a sister group, while molecular work by O'Brien *et al* (1987) found that the jaguar and leopard were most closely related. In contrast, Janczewski *et al* (1995) found that the lion and leopard were most closely related. A selection of the alternative phylogenies are illustrated in Figure 1.3. It can be seen from these trees that there is a marked difference in opinion between authors as to which cats are most closely related. Some trees have been unable to resolve the differences between any of the pantherine species (e.g. Figure 1.3c from O'Brien *et al* (1996) which leaves all species as a sister group). However, the majority of the phylogenies in Figure 1.3 (and others [not illustrated] such as O'Brien *et al*, 1987) agree that the snow leopard is the most distantly related of the taxa, and several studies also found that the tiger was an early offshoot (e.g. Bininda-Emonds *et al*, 2001; Hemmer, 1978; Janczewski *et al*, 1995). This contrasts with the results of Mattern & McLennan (2000) who found that the jaguar and tiger were most closely related and the snow leopard most distant (Figure 1.3f).

The position of the tiger within the genus is equivocal. Some authors have suggested that it may be most closely related to the clouded leopard (*Neofelis nebulosa*) and have gone so far as to name it *Neofelis tigris* (Leyhausen, 1973 cited in Hemmer, 1978). However, Hemmer (1978) suggested two possible origins for the tiger; the first as a split from the jaguar, lion, leopard stem group and the second as a split from the main *Panthera* lineage which resulted in both the tiger and the snow leopard. The second of these schemes is shown in Figure 1.3a.



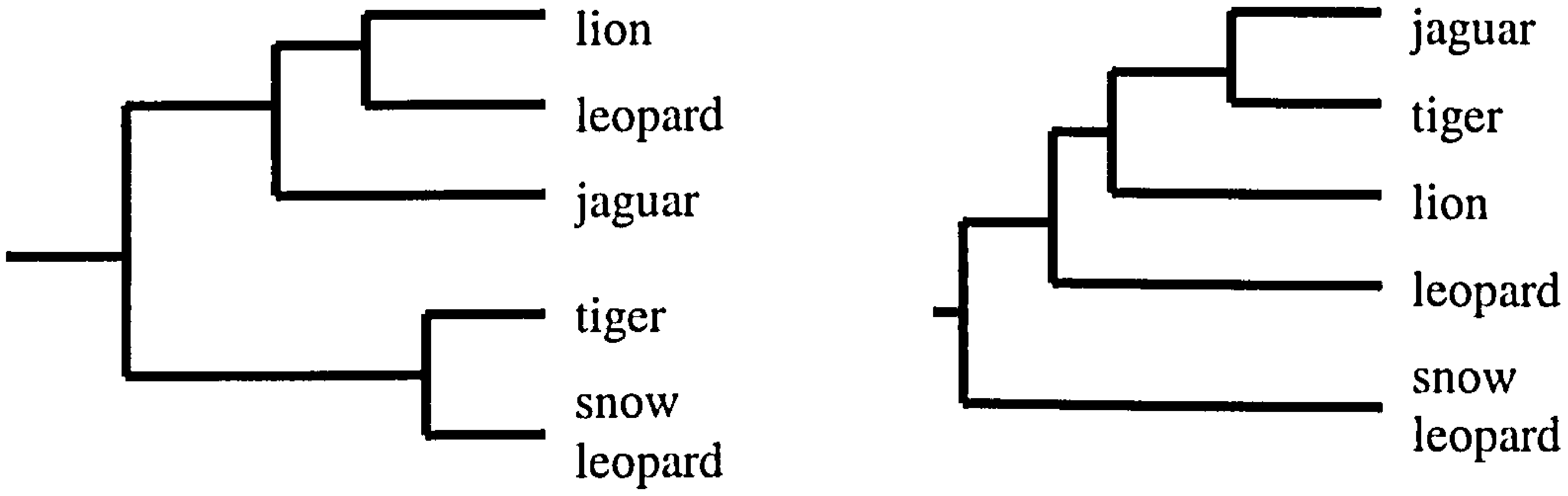
(a) Hemmer (1978) (morphological).

(b) Herrington (1987) (morphological) and Bininda-Emonds *et al* (1999) (super tree)



(c) O'Brien *et al* (1996: Figure 3.1) (molecular)

(d) Johnson & O'Brien (1997) (molecular)



(e) Bininda-Emonds (2001) (lipid analysis of anal sac secretions)

(f) Mattern & McLennan (2000) (total evidence)

Figure 1.3. Some phylogenies of the genus *Panthera* (non *Panthera* species removed). The type of evidence used to construct the trees is given in brackets (Figures a, b and c from Bininda-Emonds *et al*, 2001).

Hemmer (1978) also suggested an Asian origin for the tiger and snow leopard and noted that the tiger was clearly differentiated by 2Ma.

Molecular studies have also been used to try to date the pantherine split. Wayne *et al* (1989) suggested that the origin of the genus *Panthera* was between 2-3Ma, with the snow leopard diverging at 3Ma. Werdelin (1996) dated the pantherine radiation between 3-4Ma using fossil data. Flynn (1996) recommended that fossil and molecular data be used together to understand the relationships within the order Carnivora and suggested a divergence date between 1.5 and 3.5Ma for the lion and leopard.

The danger of using both molecular and fossil evidence together is the potential for circularity to creep into the argument, with fossil data being used to calibrate the evolution times seen in the molecular studies. Some authors have tried to combine the two types of data to form total evidence trees (Figure 1.3f) or supertrees (Figure 1.3b). The total evidence tree of Mattern and McLennan (2000) was constructed using both morphological and molecular data to create a new phylogeny. The supertree method of Bininda-Emonds *et al* (1999) combines previously published phylogenies to create a new 'supertree' based on the results of prior studies.

Further work by Bininda-Emonds (2000) found that both morphological and molecular trees gave statistically valid results and that the type of data used or the year of study (i.e. 1970s to 1990s) did not affect the overall validity of the studies. However, studies by Collard & Wood (2000) sounded a note of caution. These authors found that cladistic and molecular phylogenies produced from studies of two groups of primates were very different, suggesting that the relevance of the traditional morphological and morphometric characters used for such analyses should be reconsidered.

It can be seen from the above discussion that there is currently little consensus on the relationships within the genus *Panthera* and that neither traditional morphological or more recent molecular approaches have been able to resolve the problem.

In terms of the biological species concept, the pantherine cats do not exhibit full reproductive isolation and most extant members of the genus *Panthera* (with the exception of the snow leopard) have successfully interbred, albeit under zoo conditions (see Table 1.1). However, there is evidence of reduced fertility in these hybrids, as the females are fertile and the males are not as in the case of lion x tiger hybrids (Gray, 1972). It is theoretically possible that *P. gombaszoegensis* may have interbred with all these species, thus producing the mosaic of features that have confused so many authors.

Cat	**Lion**	**Jaguar**	**Leopard**	**Tiger**
Lion	✓	✓	✓	✓
Jaguar		✓	✓	✓
Leopard			✓	✓
Tiger				✓

Table 1.1. Interbreeding of modern cat species. Data from Gray (1972) and Hoogesteijn & Mondolfi (1992). A ✓ indicates a successful 1st generation hybrid (the birth of live cubs).

1.4.4. Fossil history of the genus *Panthera*.

There are five extant species of pantherine cat – the lion, leopard, snow leopard, jaguar and tiger. The lion and leopard are regarded as having an African origin, with the leopard making its first appearance at Shungura B (3.5Ma) and the lion at Laetoli (~3.6Ma) (Turner, 1990a). The origins of the snow leopard are more obscure, but some material from the Siwaliks (Pakistan) dated to 1.6Ma has been referred to this species (A.Turner, unpublished data). The earliest tiger specimens are from Java and date to the Lower Pleistocene (Hemmer, 1979). The apparently simultaneous occurrence of the fossil jaguar *P. onca augusta* in North America and *P. gombaszoegensis* in Europe led to suggestions of an Holartic population that migrated south, reaching Europe and America at the same time (Kurtén & Andersen, 1980; Schultz *et al*, 1985). This argument hinged on both species appearing together at 1.6Ma, but it now appears that several New World specimens were wrongly assigned and that the jaguar does not actually occur until 0.8Ma in North America (Seymour, 1993). The first recorded occurrences of *Panthera gombaszoegensis* are at Tegelen, Holland (2.2 – 1.7Ma); Dmanisi, Georgia (1.7Ma) and Slivnitsa, Bulgaria (1.9Ma) (von Koenigswald, 1960; Gabunia *et al*, 2000; Spassov, 1998).

1.4.5. Modern big cats and behaviour.

The palaeoecology of an extinct species can be more easily understood with reference to living relatives. Pleistocene studies are strongly dependant on assumptions of uniformitarianism, but one of the problems is that the current range of an animal does not necessarily reflect its past habits. Van Kolfschoten (1995) uses the example of the Norway lemming, which is now found in subarctic areas but was a common member of temperate woodland assemblages in the Early and Middle Pleistocene. A more relevant example of that of the jaguar which is commonly regarded as being forest dwelling, but did survive in more open areas until recent times (Hoogestejn & Mondolfi, 1996). Although the habits of individual species will vary; there may be a general underlying pattern that can be used to elucidate the behaviour of an extinct animal.

The nature of large carnivores means that they will always be found in low numbers as each tends to range over an area of several tens of kilometres (Schaller, 1967; 1972). Large cats are solitary for the majority of their lives, although there are a few records of animals that hunted in pairs, e.g. two jaguars reported in Hoogesteijn & Mondolfi (1992). Solitary has been defined as an animal that 'never, except when mating, cooperates with conspecfics' (Sandell, 1989:165). This solitary nature may be related to several factors including the availability and ease of locating prey - the lion is the only truly social big cat and it tends to hunt larger game than the solitary leopards that occupy the same areas (Seidensticker, 1976). However, lions are not always found in groups, as Leyhausen (1965) noted that North and West African lions tended to be solitary, whereas East African lions on the plain have large prides. Similarly tigers living in open habitats tend to socialise at kills, whereas those in forested areas usually do not (Sunquist & Sunquist, 1989). It therefore appears that the vegetation type and prey availability affects social structure (Funston *et al*, 1998; Gittleman, 1989; Leyhausen, 1965; Schaller, 1972). Added to this there is the potential for seasonality and for the cats to follow herds of game as they move, as cheetahs do with Thomson's gazelles (Schaller, 1972). There is also evidence that all of the big cats will actively shun confrontation by taking avoiding action where necessary (Durant, 2000; Rabinowitz & Nottingham, 1986). Therefore unless prey was especially abundant, or *P. gombaszoegensis* was a social species like the lion, then it is always going to be found in small numbers. Also one male's home range usually encompasses those of several females or they reside in a fixed area that the females will have to pass through on their way to somewhere else, in order to give the males the most successful breeding opportunities (Sandell, 1989). Implications of range size and tenure during the Pleistocene glaciations will be discussed more fully in Chapter 6.

All big cats species are sexually dimorphic, some more so than others (see section 3). Misunderstanding the effects of sexual dimorphism on a population can have serious effects on palaeoecological reconstructions. Kurtén (1975) records an example of subspecific distinctions applied to male and female cave bear skulls because of a sampling bias, which led to erroneous hypotheses of dwarf bears.

For most big cats the only long lasting associations that occur are those between a mother and her cubs, a bond which lasts for at least a year, sometimes two, for most animals [e.g. tigers (Mazak,1981) and jaguars (Mondolfi & Hoogesteijn, 1986)]. This behaviour may be seen in den sites, where the cubs remain during the day whilst the mother is out hunting. However, dens are not used for very long, for the most part only until the cubs are old enough to accompany their mother upon the hunt, when the need for protection is no longer necessary. Den sites of other species such as cave bears have been recognised in the palaeontological record by an abundance of juvenile bones (Andrews & Turner, 1992). It is unfortunate that juvenile bones are those which are least likely to survive and therefore this information may be lost (Guy *et al*, 1997). The importance of juvenile *Panthera gombaszoegensis* specimens is discussed in Chapter 5.

All of the big cats are capable of climbing trees, although the jaguar and leopard are the only two in which the adults are frequently arboreal. They are also adept at moving their prey, either to a place of safety, away from scavengers, such as a tree (in the case of the leopard) or to their dens. Tigers have been recorded as moving 500 kg carcasses, as have many of the other species, while the leopard can carry more than its own body weight up into a tree (Schaller, 1967). Another similarity is the method of hunting and killing, which comprises a stalking phase followed by a rush towards the animal (Kruuk & Turner, 1967). The prey is usually subjected to one of two bites, depending on its size. The neck bite is often used for smaller prey, although the jaguar and tiger will occasionally bite right through the back of the animals skull (Schaller & Vasconcelos, 1978). Otherwise this bite is often used to dislocate the neck vertebrae of the prey (see Leyhausen (1979) for examples with the domestic cat). The throat bite is usually used on larger prey and may be combined with the neck bite (Fox & Chundawat, 1988; Schaller, 1967). The advantage of this hold is that the animal slowly suffocates whilst the cat is compressing the trachea and jugular, a position which allows it to keep away from the feet and horns of the prey (Schaller, 1972).

Large cats can also be found at altitude, a factor which may be important when considering migration in Europe. Jaguars have been recorded at 2000m (Mondolfi & Hoogesteijn, 1986) whilst a leopard was discovered over 5,000 metres up Kilimanjaro (Estes, 1991). The snow leopard habitually lives at high altitude and has been recorded at heights between 1,800m and 6,000m (Kitchener, 1991).

1.5. *PANTHERA GOMBASZOEGENSIS*

The purpose of this thesis is to understand *Panthera gombaszoegensis* and put it in the context of the large Pleistocene Carnivora. *Panthera gombaszoegensis* remains have been identified at 57 sites throughout Europe and Asia. At this stage I have included all sites at which *P. gombaszoegensis* has been reported, whether subsequently re-assigned or not (see Chapter 5). Material from 22 of these sites has been studied at first hand for this thesis and a map showing the location of these sites is shown in Figure 1.4.

The following museums were visited to study either fossil or modern comparative material. Further information on where the specimens are stored and their catalogue numbers are given in Appendices 2 and 3. Modern specimens were studied at: the National Museum of Scotland, Edinburgh; the Zoology Museum, Cambridge; the Manchester Museum; National Museums and Galleries on Merseyside (Liverpool Museum); the Mammalogy Department, British Museum (Natural History), London; the Mammalogy Department, National Museum of Natural History, Budapest, Hungary; the Natural History Museum, Vienna, Austria; the Mammalogy Department, Smithsonian Institution, USA.

Figure 1.4. Map of Europe showing all sites with *P. gombaszoegensis* specimens that have been studied at first hand for this thesis. Numbers represent sites as follows: 1 = West Runton; 2 = Swanscombe; 3 = Westbury-sub-Mendip; 4 = Huéscar; 5 = L'Escale; 6 = Olivola; 7 = Santa Maria, nr. Il Tasso; 8 = Rome (Monte Sacro); 9 = Halykés; 10 = Gerakarou 1; 11 = Slivnitsa; 12 = Kövesvárad; 13 = Gombasek; 14 = Vértesszölös II and Uppony 1; 15 = Somssich Hill; 16 = Stránská Scála; 17 = Koneprusy; 18 = Süssenborn; 19 = Mosbach 2; 20 = Tegelen. The East African site of Garussi Korongo is not shown.

The following museums were visited between October 1998 and November 2000 to study fossil material: the Natuurhistorisch Museum, Maastricht, Holland; the Naturalis Museum, Leiden, Holland; Maison Méditerranéenne des Sciences de l'Homme (MMSH), Aix-en-Provence, France; Museo de Ciencias Naturales (MNCN), Madrid, Spain; the Geology Department of the Universidad de Complutense, Madrid, Spain; the Department of Geology & Physical Geography, Aristotle University of Thessaloniki, Greece; Department of Geology at the University of Athens, Greece; Palaeontological Museum, Department of Earth Sciences, University of Rome "La Sapienza", Italy; Museo di Storia Naturale, Department of Geology and Palaeontology, Florence, Italy; Naturhistorisches Museum, Mainz, Germany; Forshungsinstitut und Naturmuseum Senckenberg, Weimar, Germany; Museum für Naturkunde, Humboldt University, Berlin, Germany; Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; Geological Institute of Hungary, Budapest, Hungary; the Palaeontological Department, National Museum of Natural History, Budapest, Hungary and the Palaeontology department, British Museum (Natural History), London.

The total number of specimens attributed to *Panthera gombaszoegensis* that have been measured and included in the analysis is 201. The numbers of each body part included in the discussion are shown in Figure 1.5. As Figure 1.5 shows, the majority of specimens are cranial or dental remains. This could be for two reasons, the first is that teeth are readily identifiable as felid and then easy to group into the appropriate size class i.e. it's a medium sized felid, therefore it is *Panthera gombaszoegensis*. The second is that teeth fossilise readily and are often found when many other bones have been lost (Kurtén, 1971). In addition this study has concentrated on reviewing the material already identified in the literature rather than seeking out new specimens in museum collections and for the reasons explained above cranial material has dominated the sample.

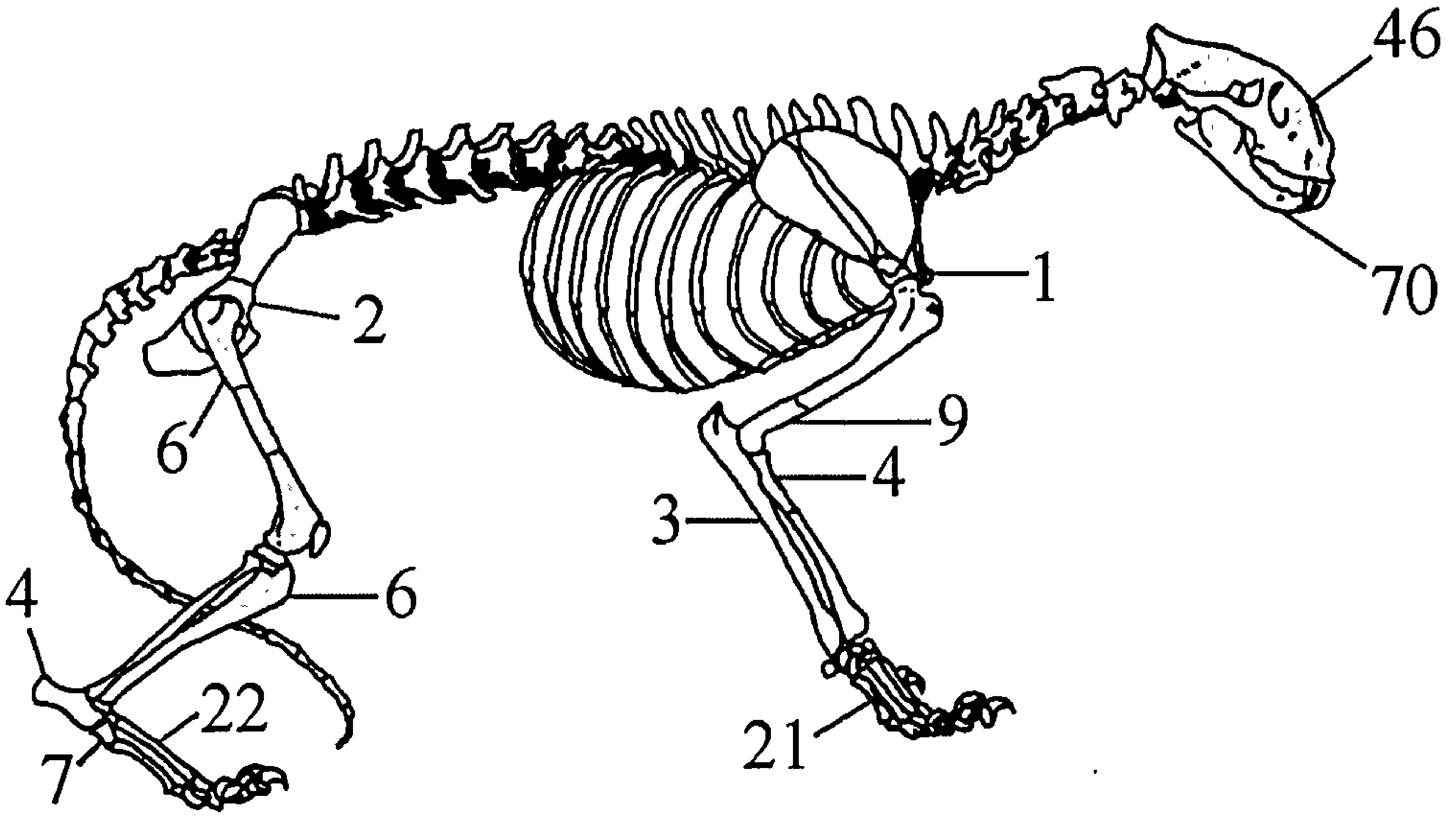


Figure 1.5. Illustration of the total number of *Panthera gombaszoegensis* remains studied at first hand for this thesis. Shaded areas represent bones or parts of bones that have been identified and numbers indicate totals for each bone (modified from Ewer, 1973).

1.6. THE PLEISTOCENE ENVIRONMENT

The Pleistocene was a period of very complex environmental changes. There were major climatic and faunal changes over the ~1.7Ma that *P. gombaszoegensis* existed and these must have had some effect on this species.

1.6.1. Pleistocene vegetation and fauna

The large scale climatic changes would have had a significant impact on the distribution of plants and animals throughout the Pleistocene. Many faunal changes took place, as animals became extinct and new species migrated into Europe from Africa or Asia. An influx of Asian bovids is associated with the 'Meria' cooling and the freshening of the Black Sea at ~1.9Ma, indicating that the Bosphorus would have been closed for a time, allowing animals to make use of a land bridge into Eastern Europe (Spassov, 1997). Between ~1.2Ma and ~0.9Ma there was a change in the herbivorous taxa from slender-legged, cool adapted species to much larger bodied animals which were adapted to moister climates (Alberdi *et al*, 1998).

The vegetation would have been greatly affected by the glacial periods and this in turn affects the composition of the fauna associated with it. Zagwijn (1992) pointed out that forest was the climax vegetation in interglacials whilst tundra or steppe type species would have been common during glacials. It would have been difficult for ambush hunters like the leopard to have operated in such a habitat, although it may have favoured open ground species such as the cheetah (*Acinonyx pardinensis*). Before ~1.0Ma there is no clear pattern of forest succession in the European pollen records, indicating that glacial periods were less intense and that the refugia were close enough for trees to re-colonise quickly (Zagwijn, 1992). However, after this date each interglacial has a characteristic pattern of forest succession as resettlement would have been different in each case, depending on exact climate change that had occurred (Zagwijn, 1992). Chance events such as localised extinctions are also likely to have played a part in the subsequent recolonisations (Birks & Line, 1992). Evidence that refugia did exist quite far north, for example in Hungary (Willis *et al*, 2000), has implications for the speciation of trees or small mammals, although these refugia would have been too small to allow larger mammals to survive. This then leaves only three options for a large European species during a glacial period: either remain where you are and attempt to adapt to a very different environment or prey base; migrate, either to a refugium or out of Europe, or become extinct. However, migration is not simply a procession of animals moving backwards and forwards in time with the icesheets; the large-scale refugia of the Iberian peninsula, Italy and the Balkans would already have been full of animals, each occupying their own territories. Twelve percent of the Middle Pleistocene was spent in full glacial conditions (van Kolfschoten, 1995). In a 0.1Million year cycle that equates to 12,000 years, a period of isolation which has led to the Sumatran tiger being recognised as a subspecies or even a full species in its own right

(Cracraft *et al*, 1998). The problems associated with refugia such as genetic isolation, competition and chance distributions will be discussed further in Chapter 6.

It appears that the change from glacial to interglacial periods occurs much more quickly than that from interglacial to glacial (based on CO_2 levels in ice cores) (Kump *et al*, 2000). This would have distinct implications for the animals and plants, as there would be time to adapt or migrate during the onset of a cold phase, whereas the speed of change from fully glacial to interglacial climate (~4,000 years) would have had a considerable impact.

Geological barriers such as mountain ranges and rivers have traditionally been regarded as hindering the dispersal of animals (e.g. the Pyrenees [Agusti & Moyà-Solà, 1992]). However, it is now being realised that climatological factors such as humidity and temperature are much more important (van der Made, 1992). A recent review of Pleistocene faunas assigned a habitat category to the European carnivores – either open, wooded or forested (Alberdi *et al*, 1998). These categories and assumptions about competition will be tested in Chapter 6.

Although the Pleistocene climate is known at a very detailed level through the oxygen isotope studies, these are very difficult to relate to terrestrial sites. Similarly, much of the work on vegetation has been conducted on the last glacial period, for which much more information is available, and this is then applied to the past. However, there are no analogues for many of the Pleistocene communities.

1.6.2. The Pleistocene guild of large carnivores.

It is important to remember that *Panthera gombaszoegensis* did not exist in a vacuum. There were many other large carnivores present in Europe during the Pleistocene and they would have been competing for similar resources. They included not only felids but also hyaenids and canids.

The first appearance of the lion is at ~0.7Ma at the Italian locality of Isernia la Pineta (Sala, 1990), (See Figure 1.6). The lion is unusual in the cat family, as it is a social animal and hunts cooperatively. It may, therefore, have been able to outcompete some of the larger carnivores that relied on killing individually, as they could have then been driven from their kills by the lion, in much the same way that they scavenge kills from leopards and cheetahs in Africa today (Eaton, 1974; Funston *et al*, 1998; Kruuk & Turner, 1967; Schaller, 1972). There is enormous size variation in fossil lions, but this probably due to sexual dimorphism. It has been noted that there was a size difference of 20% between the upper canines of fossil males and females (Kurtén, 1985).

The first appearance of the leopard is at Vallonnet and *P. gombaszoegensis* is also recorded from this site (Moullé *et al*, 2000). Two forms of the fossil leopard have been noted - the first is a 'robust' type that has been compared to *P. gombaszoegensis*, and the second is a more 'gracile' animal (Spassov & Raichev, 1997). The lion and leopard lingered in the Balkans and only became extinct during the Holocene (Guggisberg, 1975; Nagel, 1999).

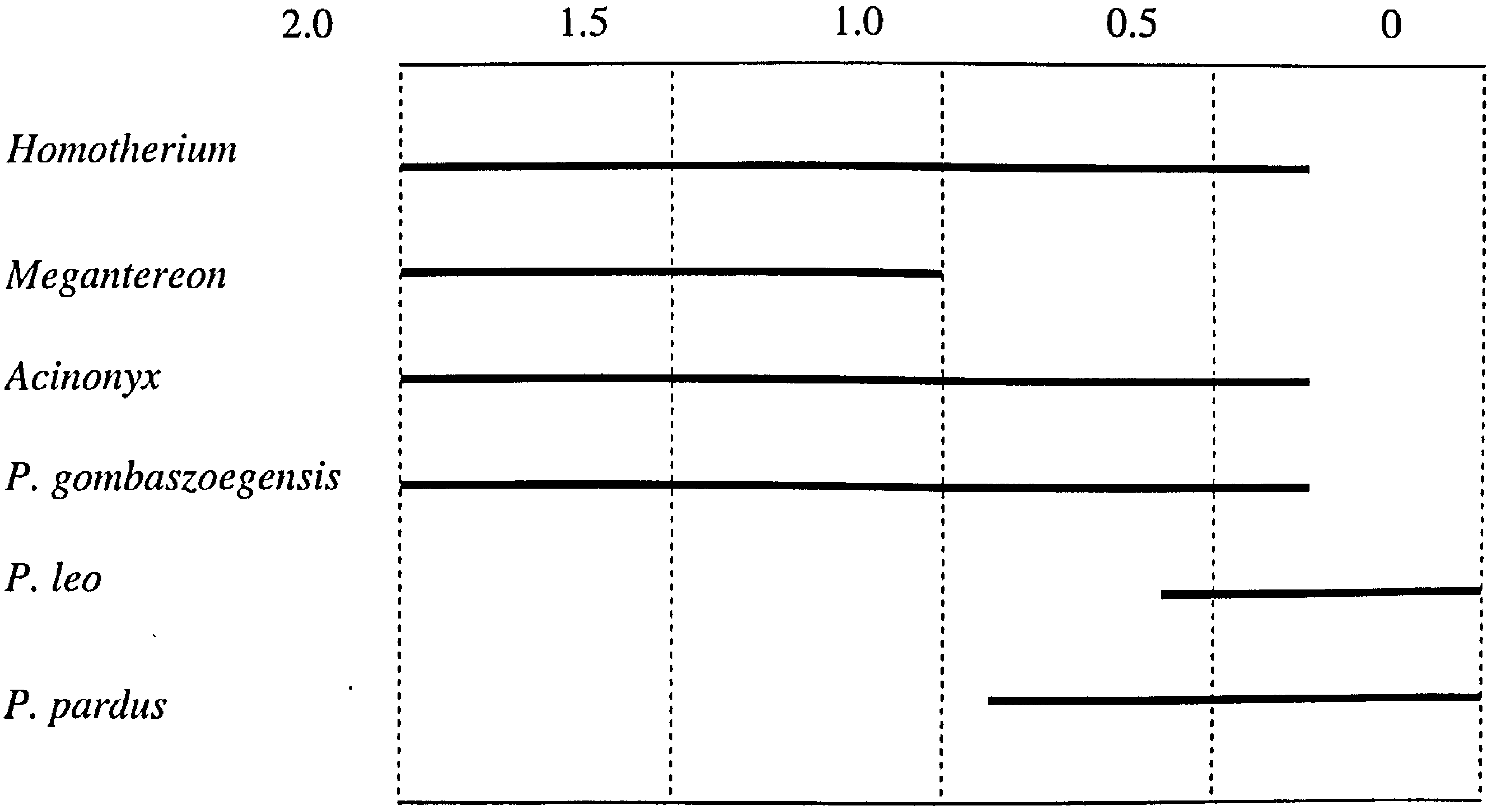


Figure 1.6. First and last occurrences of big cats in Europe from 2 million years ago to present (After Turner, 1995a).

As noted above, the first occurrence of *Panthera gombaszoegensis* in Europe is at the Bulgarian site of Slivnitsa, although this diagnosis was made on postcranial material (Spassov, 1998). The earliest cranial specimens were found at Tegelen, probably in the latest layers (approximately 1.7Ma) (Azzaroli *et al*, 1988) and Dmanisi (1.7Ma) (Gabunia *et al*, 2000). The last recorded occurrences of *P. gombaszoegensis* are at 0.35Ma at Vértesszölös II in Hungary and Swanscombe, UK.

Three other extinct felids – *Megantereon, Homotherium* and *Acinonyx pardinensis* were all present in Europe before the arrival of *Panthera gombaszoegensis.* The taxonomy of the sabretoothed species is confused. Many different species have been proposed for *Megantereon*, although they are probably all conspecific with *Megantereon cultridens* (Turner, 1987). The problems with *Homotherium* are even more acute; at least three generic names are still applied - French authors referring to *Dinobastis* (e.g. Guadelli, 2001); Eastern European authors preferring *Epimachairodus* (e.g. Jánossy, 1969; 1986) and others using *Homotherium* (e.g. Turner, 2000). Again, there are specific subdivisions, but these are also likely to be synonymous with one species – *Homotherium latidens* (Turner & Antón, 1997). I have used the generic names for all following analyses, as for the purposes of this thesis the ecological differences between the cats are more important than the taxonomic ones.

Megantereon was a sabre-toothed cat of approximately the same size as the modern leopard (Turner, 1987). It was a geographically widespread animal with specimens having been found in Europe, Asia, Africa and America (Ficcarelli, 1979). The latest European *Megantereon* specimen was identified at Untermassfeld, dating to 1.0Ma (Kahlke, 2000).

The second sabretoothed cat was *Homotherium*, which was the size of the modern lion and may have had a similar social structure (Turner & Antón, 1997). Recent work has also suggested that it was a pursuit predator, and may have been capable of taking young elephants and hippos (Palmqvist *et al*, 1996). *Homotherium* is found throughout Europe, and the last known occurrences are at a clutch of sites dated to 0.4 – 0.3 Ma [e.g. Mosbach 2 and Hundsheim (Wolsan, 1993)]. However, there is a record of an isolated astragalus from Mealhada, Portugal which is dated between 0.35 and 0.1Ma and has been referred to *Homotherium* (Antunes, 1986). If this identification proves to be correct then this is the last occurrence of this species in Europe.

Acinonyx pardinensis was a close relative of the modern cheetah, but some 50% larger (Turner & Antón, 1997). It was never a common element of the fauna, although found more often in the Pliocene, it is recorded at only nine Pleistocene localities (see Chapter 6). The last occurrence of this species is also at Mosbach 2 (Wolsan, 1993).

The 'giant hyaena' *Pachycrocuta brevirostris* is found at sites throughout Europe, Africa and Asia (Masini & Torre, 1990). It was the largest of the Pleistocene hyaenids and was the only one present in Europe between ~1.6 – 0.9Ma after which the spotted hyaena appeared (Turner & Antón, 1996). It was approximately the size of a modern lion and was probably a social carnivore. The morphology of the limb bones shows that it was not cursorially adapted, so it would have had difficulty running down prey and is therefore likely to have been an aggressive scavenger (Turner & Antón, 1996).

The modern spotted hyaena (*Crocuta crocuta*) arrived in Europe at 0.9Ma and became extinct during the last glaciation (Yalden, 1999). Kurtén (1968) suggested that the arrival of *C. crocuta* led to the eventual demise of *Pachycrocuta brevirostris* as it was outcompeted by a more successful hunter and scavenger. *Crocuta crocuta* is now only found in Africa and hunts in packs, running down prey and tearing it apart (Skinner & Smithers, 1990).

The third species of hyaena that co-existed with *P. gombaszoegensis* was *Pliohyaena perrieri*. It completely disappears from Europe at approximately 1.6 Ma and reappears at 0.7 Ma (Turner, 1995a). It is likely to be most closely related to the modern brown hyaena (*Hyaena brunnea*) (Turner, 1990b). Today the brown hyaena is only found in Southern Africa (Skinner & Smithers, 1990).

The first appearance of the genus *Canis* is in North America at 5.5Ma (Torre *et al*, 1992). *Canis etruscus* was the first true dog to arrive in Europe during the Olivola Faunal Unit (~1.7Ma) (Masini & Torre, 1990). This species was probably ancestral to *Canis mosbachensis* which is regarded as the forerunner to the modern wolf (*Canis lupus*); although a recent publication has cast doubt upon this (Rook & Torre, 1996). Two other canids also arrived slightly later in the Tasso Faunal unit (~1.6Ma) – *Canis arnensis*, a small jackal-like animal and *Canis (Xenocyon) lycaonoides* which was much larger (Masini & Torre, 1990).

The jaguar is the species to which *P. gombaszoegensis* is most often compared. It is currently confined to Central and Southern America, but once ranged as far north as the states of Washington and Oregon in the USA (Daggett & Henning, 1984). The fossil form of the jaguar (*Panthera onca augusta*) is first known from the site of Hamilton Cave in West Virginia and is dated to 0.8Ma (Seymour, 1993). The main differences between the fossil and modern forms are the relatively longer metapodials and radius of the fossil subspecies (Seymour, 1993). There has also been some body size reduction, as the early cat was some 15-20% larger than the modern animal (Kurtén & Anderson, 1980). The extant jaguar is morphologically very similar to the leopard but with a more robust body, a larger and broader head, larger paws and a shorted tail (Mondolfi & Hoogesteijn, 1986).

1.6.3. Prey species

The changes in the carnivore guild reflect changes in their prey species. After the 'End Villafranchian' event of ~0.9Ma new species of previously known genera evolved which were much larger and more heavily built than their ancestors, e.g. *Bison*, *Bos* and *Megaceros* (Azzaroli *et al*, 1988). In general a trend towards larger size was seen in most animals, with the exception of the equids (Azzaroli *et al*, 1988). Cold adapted species such as the reindeer (*Rangifer tarandus*) and woolly rhino (*Coleodonta antiquitatis*) make their first appearances at ~0.6Ma after the change to the 0.1Ma glacial cycle (Turner, 1995a). Changes such as these would have had an impact on the carnivores as they are adapted to take animals of a similar size or smaller than themselves (Sunquist & Sunquist, 1989); unless they group together in which case lions are capable of killing rhinoceroses (Brain *et al*, 1999).

Turner (1995b) provides a checklist of European cervid species over the last 3Ma (shown in Table 1.2). It can be seen from this table that there was an overall shift from small and medium sized species to the medium – large category during the course of the Pleistocene. This change would have had a direct effect on animals who preyed on the small to medium sized species such as the cheetah. More detailed discussions of patterns of faunal turnover can be found in Turner (1995b), Azzaroli *et al* (1988) and Aguirre *et al* (1997). The implications for these changes and those of the carnivore guild on *P. gombaszoegensis* will be discussed further in Chapters Six and Seven.

Time	**small – medium**	**medium**	**medium - large**
2 – 1.5Ma	3	0	2
1.5 – 1.0Ma	2	2	2
1.0 – 0.5Ma	1	1	4
0.5 - present	1	2	3

Table 1.2. Numbers of Pleistocene cervid species in four different time bands and their different body size categories (Modified from Turner, 1995b).

CHAPTER 2 - METHODS

2.1. INTRODUCTION

The system of measurement used in this study is based on that of Kurtén and Turner (pers. comm). Further measurements have been added by myself, where appropriate.

Standard nomenclature and morphological features are discussed in section 2.2. Full explanations of measurements and protocols are given in the following chapter sections: dental measurements in section 2.3.1; cranial measurements in section 2.3.2; mandibular measurements in section 2.3.3 and postcranial measurements in section 2.3.4.

Error analysis was conducted by taking repeated measurements of a leopard skull over a period of days and is further described in section 2.4.

Various statistical methods have been used in this thesis. They are all available in either the Minitab or SPSS computer packages. The uses and limitations of these tests are outlined in section 2.5.

The methods described below have been used throughout this thesis. Other techniques which are relevant to particular sections are explained at the appropriate point in the text.

2.2. NOMENCLATURE AND TOOTH MORPHOLOGY

Certain terms in reference to directions or parts of the body are used throughout this thesis. Where possible these are consistent with recognised standard nomenclature. For example, the directions in the mouth illustrated in Figure 2.1 are consistent with those of Hillson (1986). All drawings of teeth in occlusal view follow this format, with the distal surface to the top of the page.

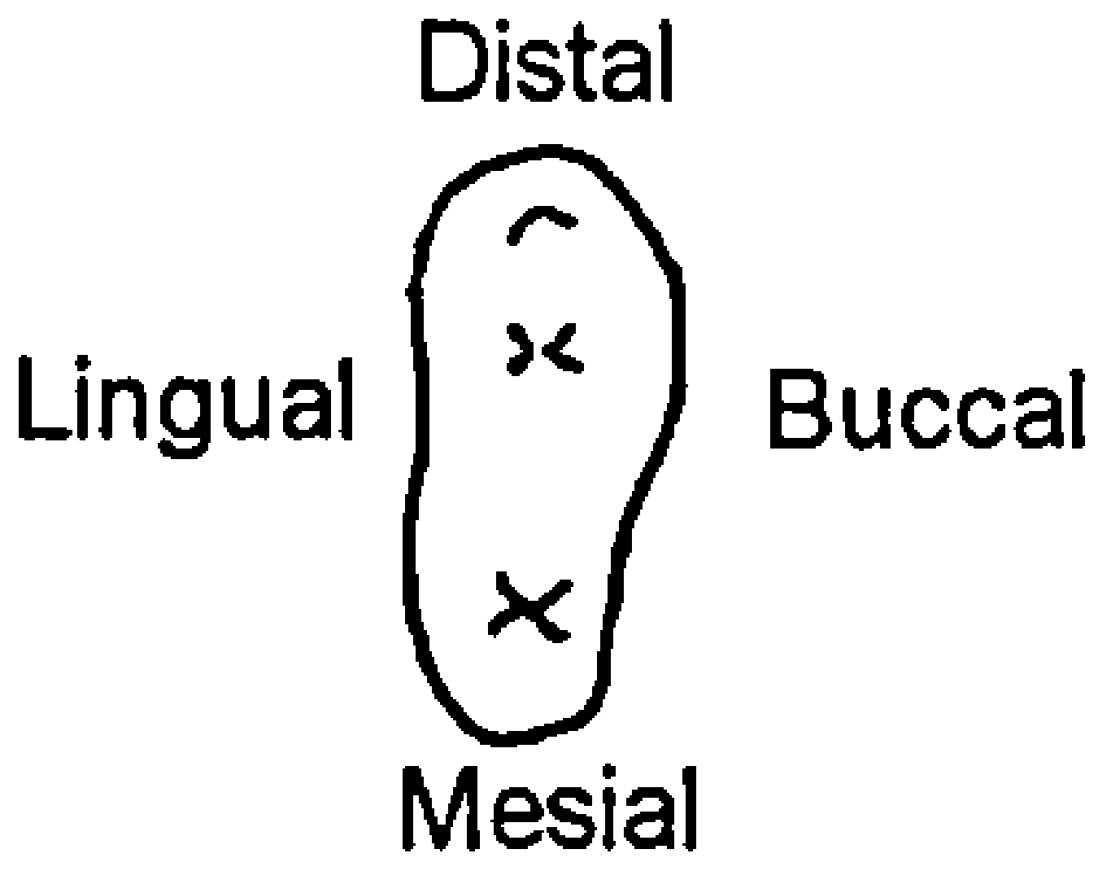


Figure 2.1. Directions within the mouth, illustrated using a lower left premolar in occlusal view (consistent with Hillson, 1986).

Carnassial terminology appears highly variable across different authors (e.g. Hillson, 1986 and Matthew, 1910). The inconsistency is in whether cusps are termed 'cone' or 'style'. For this reason the terminology used in this thesis follows that of Matthew (1910) and Hillson (1986) for the upper carnassial (Figure 2.2) and Hillson (1986) for the lower (Figure 2.3).

The upper carnassial (upper fourth premolar) consists of four main cusps and these are illustrated in Figure 2.2. The ectoparastyle is a variable feature; it is occasionally present as a small cusp on the parastyle of the upper carnassial.

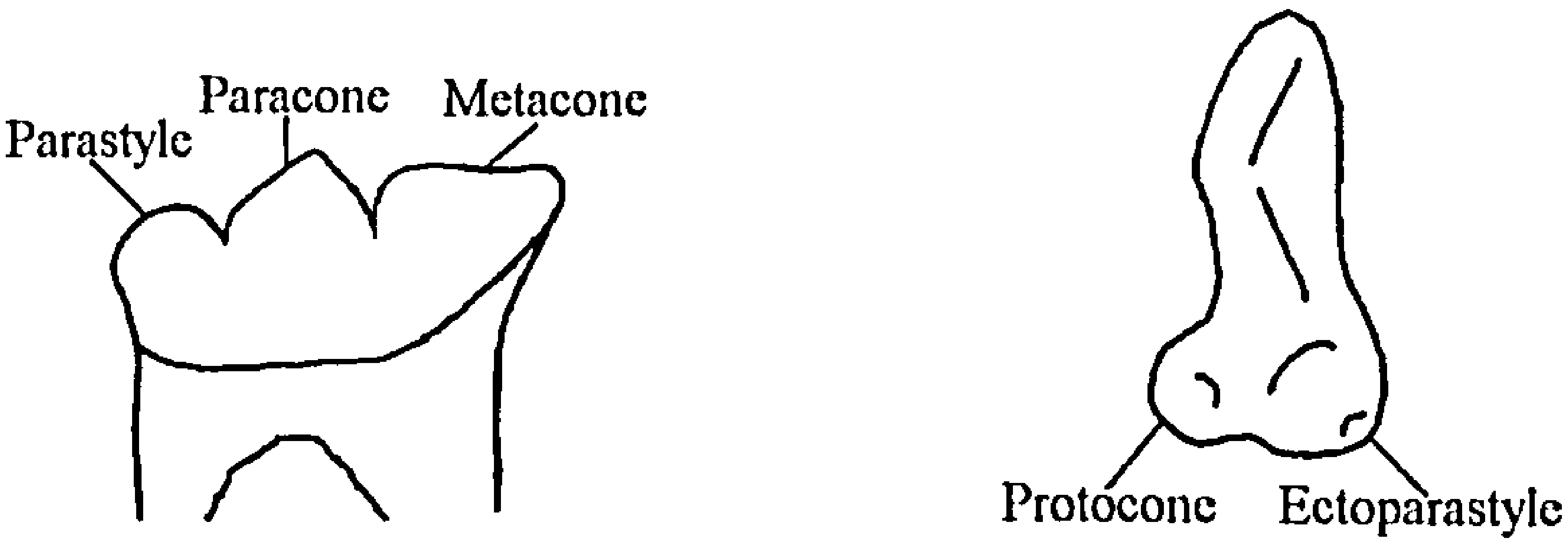


Figure 2.2. Upper carnassial terminology (after Matthew, 1910; Hillson, 1986).

The lower carnassial (lower first molar) consists of two main cusps. Occasionally the breadth of the tooth is enlarged by the presence of a bulge on the lingual surface opposite the point where the protoconid and paraconid meet. This is called a lingual bulge and has been described as the remains of the metaconid (Pocock, 1940). If it is the metaconid then it represents a more primitive feature, but there appears to be some doubt about this, as traditionally the metaconid is regarded as a small cusp above the talonid (cf. Kurtén, 1963a). The talonid is a small subsidiary cusp on the distal surface of the protoconid, just above the cingulum (Figure 2.3). The carnassials in felids have developed purely as slicing teeth and no longer require a crushing adaptation (Hillson, 1986:39). In order to be consistent in this thesis the talonid and metaconid are both regarded as distinct cusps on the posterior of the protoconid. The bulge or 'talonid heel' as it is sometimes called has been referred to here as the cingulum (see Figure 2.3).

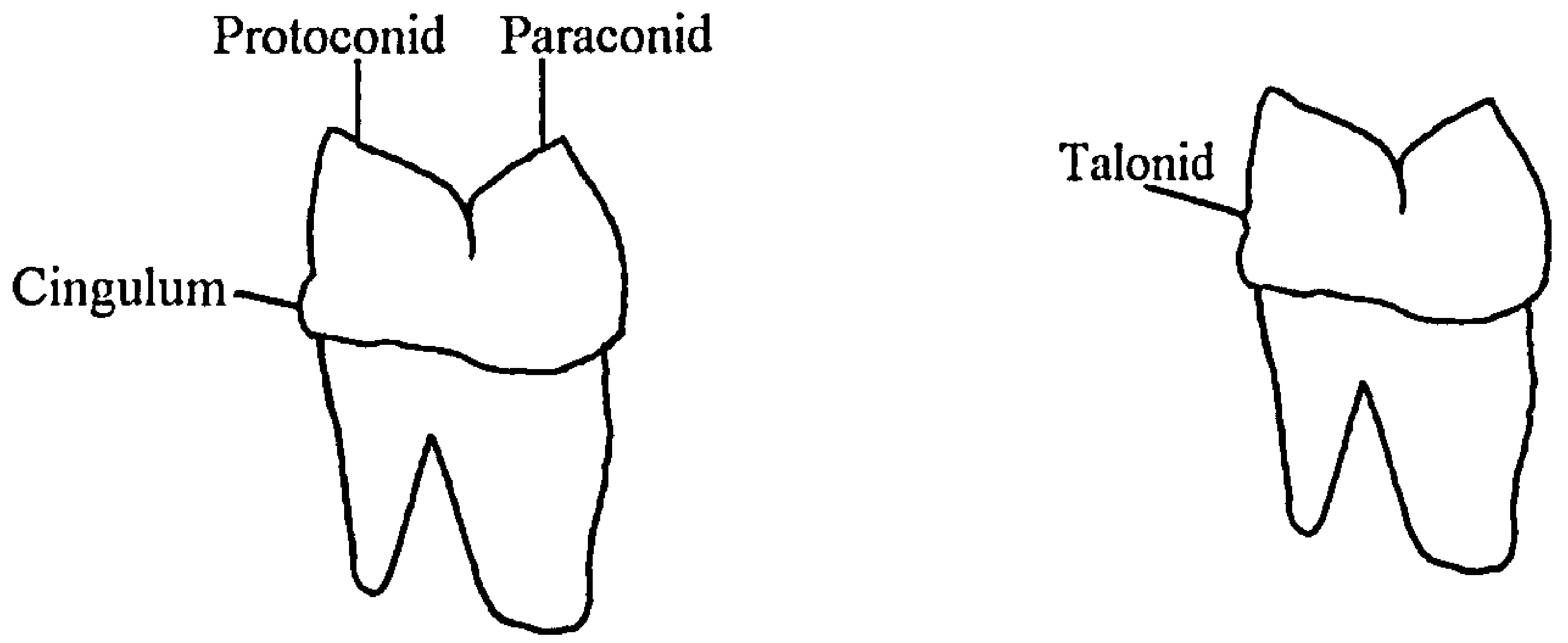


Figure 2.3. Lower carnassial terminology (after Hillson, 1986).

The premolars also appear to lack consistent terminology. The central cusp is most often referred to as the protocone, but there is no standard term for the anterior and posterior cusps. Continental authors (e.g. von Koenigswald, 1960) occasionally refer to them as the paraconid (anterior cusp) and hypoconid (posterior cusp) whilst American authors use the terms anterior and posterior accessory cusps (e.g. Berta, 1987). For the purpose of this thesis they are referred to as the anterior and posterior cusps, as illustrated in Figure 2.4. All premolars (both upper and lower) follow the same pattern of cusps. The only exception is the upper second premolar which is vestigial and lacks defined cusps.

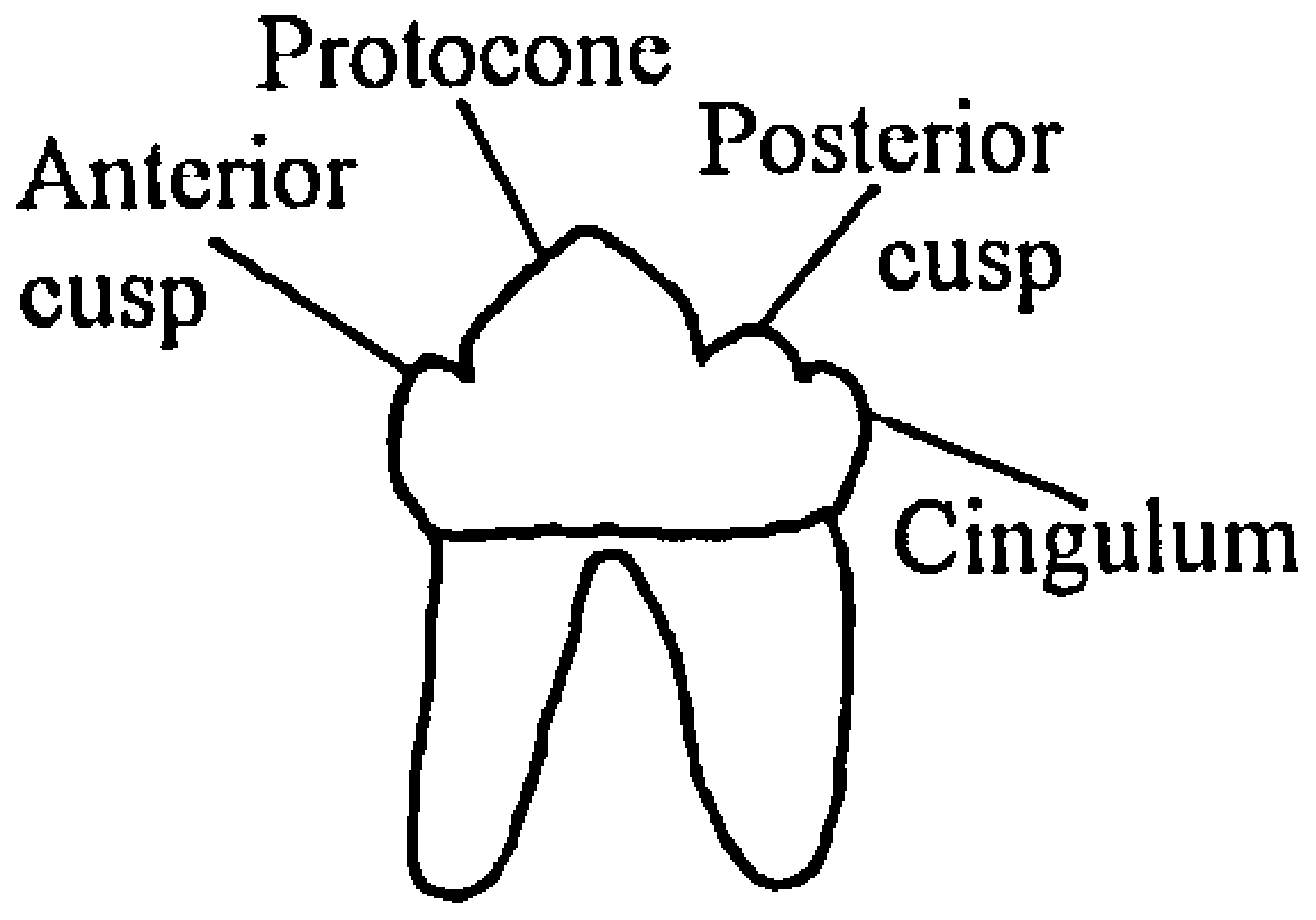


Figure 2.4. Lower left premolar, illustrating premolar nomenclature.

In some specimens the P_4 has a lingual expansion beside the posterior cusp, that moves the posterior cusp towards the buccal surface and is usually accompanied by a very pronounced cingulum. This may be a primitive state and would therefore be a remnant of the crushing capabilities of the tooth.

Postcranial nomenclature is consistent with terms used in the following publications: Walker (1986); Wischnitzer (1988) and Sisson (1914). Osteological plurals follow those of Bass (1995).

2.3. MEASUREMENTS

All measurements were taken with vernier scale calipers to the nearest 0.1mm; the only exceptions were measurements greater than 130mm (such as limb bone lengths) that were taken using a steel tape to the nearest 1mm. Details of all specimens used in this study are given in Appendix 3.

Measurements used in this thesis were taken by myself, with the exception of some fossil and modern measurements of specimens that were unavailable for study, but had previously been measured by Dr A. Turner. These modern specimens are clearly marked in Appendix 3 and fossil measurements are indicated in Chapters Five and Six. Published measurements of specimens that have not been studied at first hand have not been used in any of the analyses because of the potential problems of interobserver error, although they have been discussed where appropriate.

2.3.1. Dental measurements.

All dental measurements in this thesis have been abbreviated and upper and lower teeth are designated by subscript or superscript as appropriate (e.g. an upper fourth premolar is shown as P^4) as described in Table 2.1. Teeth are most commonly found in palaeontological sites, as they are robust and easily recognisable. In addition, even fragmentary specimens can provide morphological or morphometric information, making them very important for this type of study. However, not all fossil teeth will have all of the possible measurements taken, as it depends on their condition. Figures 2.5 – 2.9 illustrate all the possible measurements taken on individual teeth. Tables 2.2 – 2.4 give full descriptions of each abbreviation used. Although the same abbreviations are used for different teeth (B for breadth, for example) this is always qualified in the text by preceding the letter with an indication of the tooth, for example P^4L indicates the length of the upper carnassial, whereas P_3L indicates the length of the lower third premolar.

Tooth	Abbreviation	Upper	Lower
Canine	C	C^s (Superior)	C_i (inferior)
Premolar (all)	P	e.g. P^3	e.g. P_3
Molar	M	M^1	M_1

Table 2.1. Tooth names and abbreviations used throughout this study.

2.3.1.1. Canines

The height of the tooth crown (H) was taken on the buccal (labial) surface from the tip of the crown to the cemento-enamel junction (See Figure 2.5a). It was only taken on complete specimens, of which there were very few because of wear and breakage of the tooth crown. Two measurements were taken on each canine at right angles at the cemento-enamel junction. They were the same for both upper and lower teeth. In the cross section shown in Figure 2.5b L indicates the length of the tooth from the mesial to distal surfaces. The breadth (B) of the tooth was taken at right angles to the length.

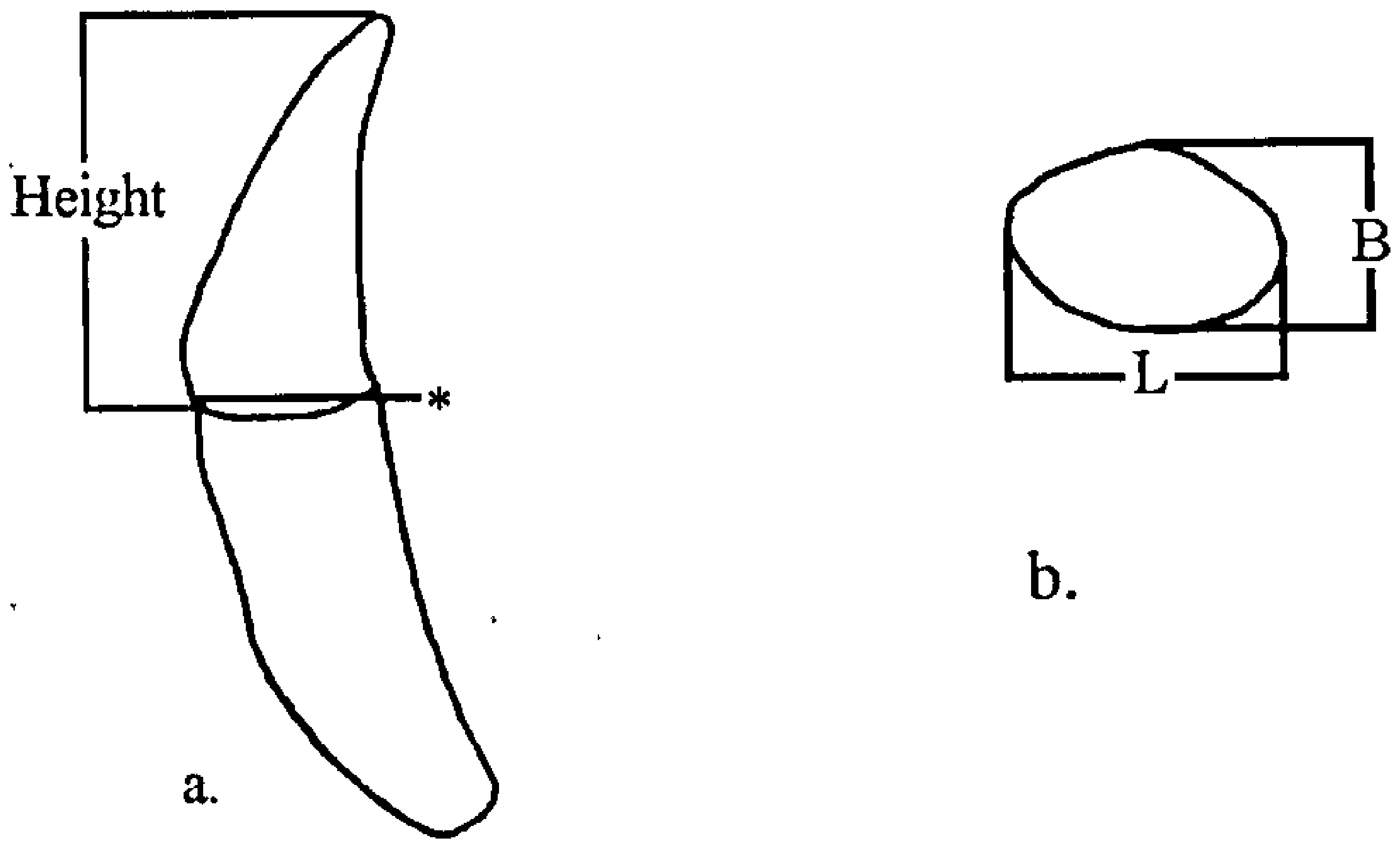


Figure 2.5a. Buccal view of a canine . * denotes the cross-section at the cemento-enamel junction shown in b. Abbreviations explained below.

2.3.1.2. Premolars

The measurements are the same for all premolars, both upper and lower, as they all have very similar morphology. The only exception to this is the P^2 which is vestigial and lacks clearly defined cusps. For this tooth, only the length (L) and breadth (B) were measured. All measurements are depicted in Figure 2.6 and described in Table 2.2. The length of the protocone (Lp) is taken at the base of the protocone notch, as this allows the measurements to be taken on most teeth, even heavily worn specimens.

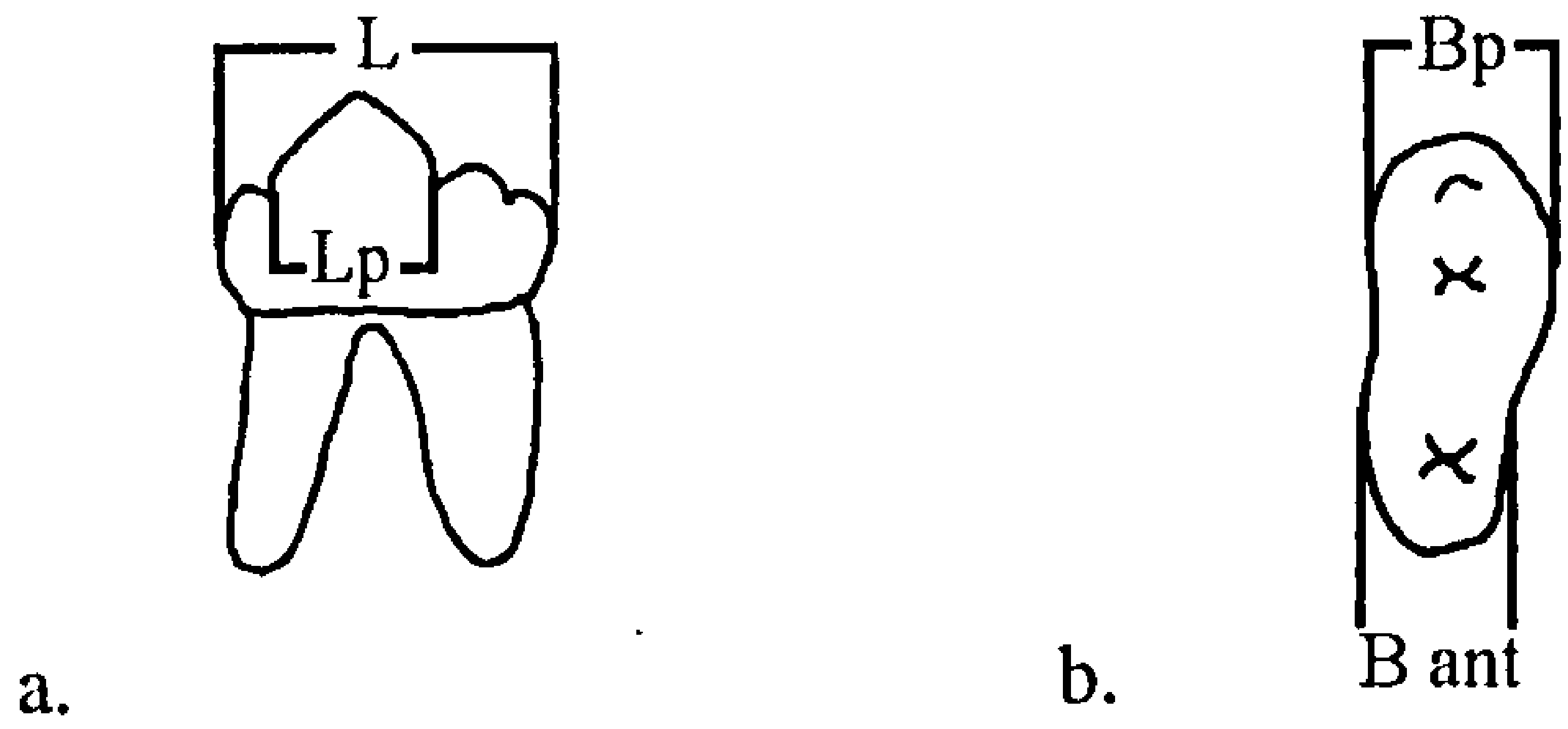


Figure 2.6. Illustration of premolar measurements: a) left premolar in buccal view and b) a right premolar in occlusal view. Abbreviations explained in Table 2.2.

Abbreviation	Description
L	Length of the tooth from mesial to distal surfaces
Lp	Length of the protocone, from the base of the notches separating the protocone from the accessory cusps
B	Greatest posterior breadth of the tooth
B ant	Anterior breadth of the tooth, at or just after, the anterior cusp

Table 2.2. Description of measurements taken on premolars, as illustrated in Figure 2.6.

2.3.1.3. Lower carnassial (M_1).

The lower carnassial is a very distinctive tooth, consisting of two main cusps, the protoconid and the paraconid. The measurements taken on this tooth are illustrated in Figure 2.7. and described in Table 2.3.

Abbreviation	Description
L	Greatest length of the tooth from mesial to distal surfaces
Lproto	Length of the protoconid from the notch at the paraconid to the point where the protoconid meets the cingulum on the distal surface
Lpara	Length of the paraconid from the notch at the protoconid to the mesial surface
B	Breadth of the tooth at the notch between the paraconid and protoconid
Hfiss	Height of the tooth from the bottom for the paraconid/protoconid fissure to the cemento-enamel junction.

Table 2.3. Description of M_1 measurements, as illustrated in Figure 2.7.

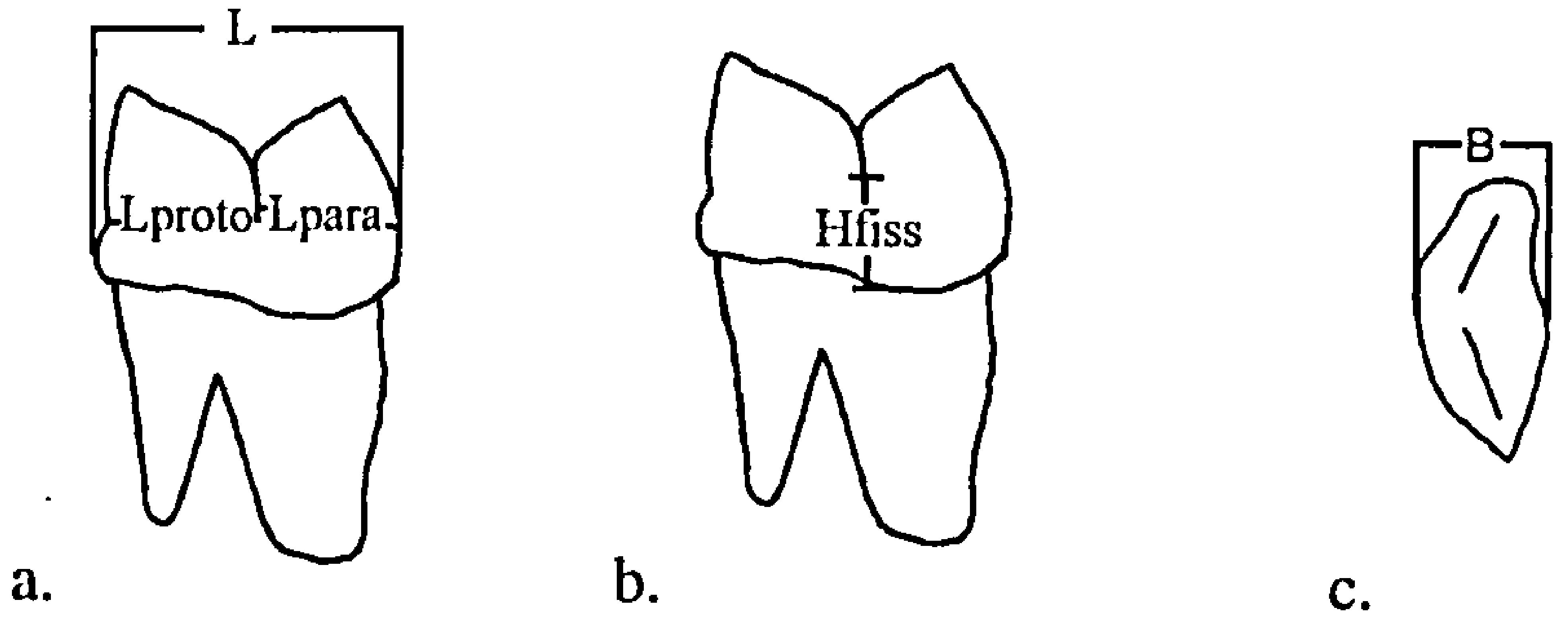


Figure 2.7. Illustration of a right M_1 in: a. & b. Buccal view and c. occlusal view. Abbreviations explained in Table 2.3.

2.3.1.4. Upper carnassial (P^4)

The upper carnassial is also a very distinctive tooth as it is still adapted for both cutting and crushing. Five different measurements were taken on each P^4 and these are illustrated in Figure 2.8. and explained in Table 2.4.

Abbreviation	Description
L	Length from the parastyle to the metacone
Lm	Length of the metacone, taken from the notch at the paracone to the farthest tip of the metacone
Lp	Length of the paracone, from the base of the notch with the parastyle to the notch with the metacone
Bbl	Blade breadth, across the blade, at the notch between the paracone and metacone
Ba	Anterior breadth of the tooth across the parastyle and protocone

Table 2.4. Description of P^4 measurements, as illustrated in Figure 2.8.

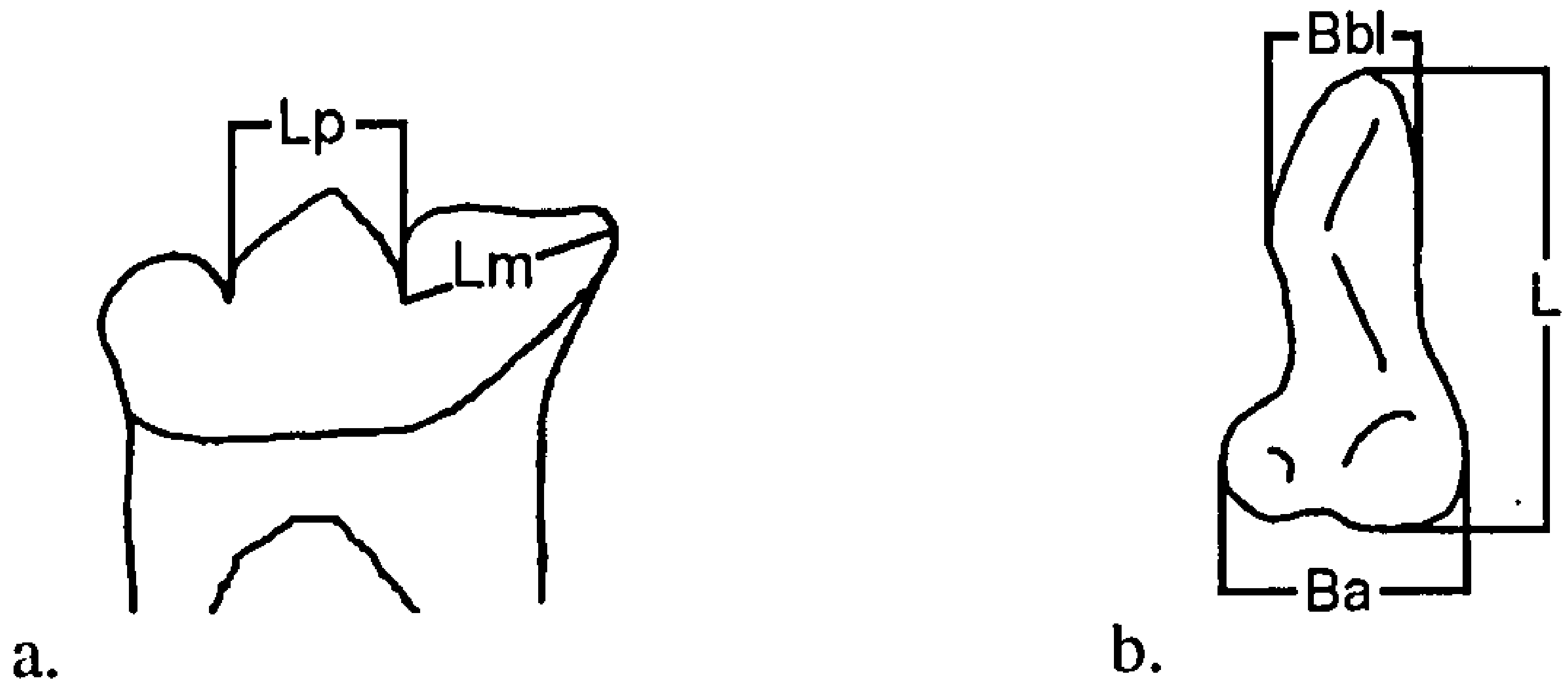


Figure 2.8. Illustration of a right P^4 in: a. Buccal view and b. occlusal view. Abbreviations explained in Table 2.4.

2.3.1.5. Upper molar (M^1)

The upper molar is greatly reduced; it is largely nonfunctional and lacks defined cusps. The long axis of the M^1 is from the buccal to lingual surfaces, rather than the more usual mesial to distal. Only one measurement was taken of the tooth. This is the breadth (B) as shown in Figure 2.9 below.

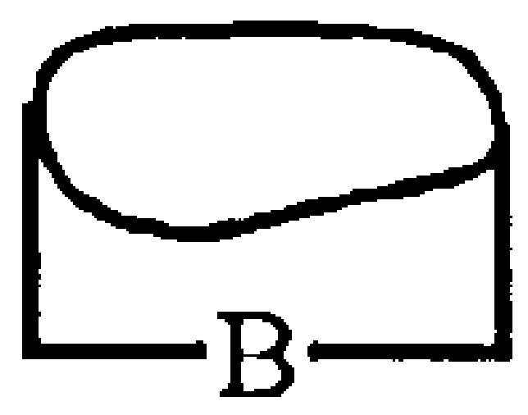


Figure 2.9. Illustration of an M^1 in occlusal view. Abbreviation explained above.

2.3.2. Cranial measurements

The majority of cranial dimensions were measured to the nearest 0.1mm. The exceptions to this were condylobasal length (BL), zygomatic breadth (ZB) and occasionally palate length (PL) in large lion and tiger specimens which were measured to the nearest millimetre. All cranial measurements used are illustrated in Figure 2.10 and the abbreviations are explained in Table 2.5.

Measurement	Definition
BL	Condylobasal length – from the anterior of the foramen magnum to the anterior portion of the premaxilla.
PL	Palatal length – from the posterior of the incisors to the rear of the palate.
RB	Rostral breadth – breadth across C^s from lateral surface to lateral surface.
MB	Muzzle breadth – breadth across the skull from buccal surfaces of P^4 metacones
CB	Condylar breadth – breadth across the occipital condyles, from lateral edges
ZB	Zygomatic breadth – greatest breadth across the zygomatic arches
IO	Interorbital breadth – least width between the orbits
POP	Post orbital process – greatest breadth across postorbital process
POC	Post orbital constriction – least breadth across the braincase

Table 2.5. Abbreviations and description of cranial measurements, shown in Figure 2.10.

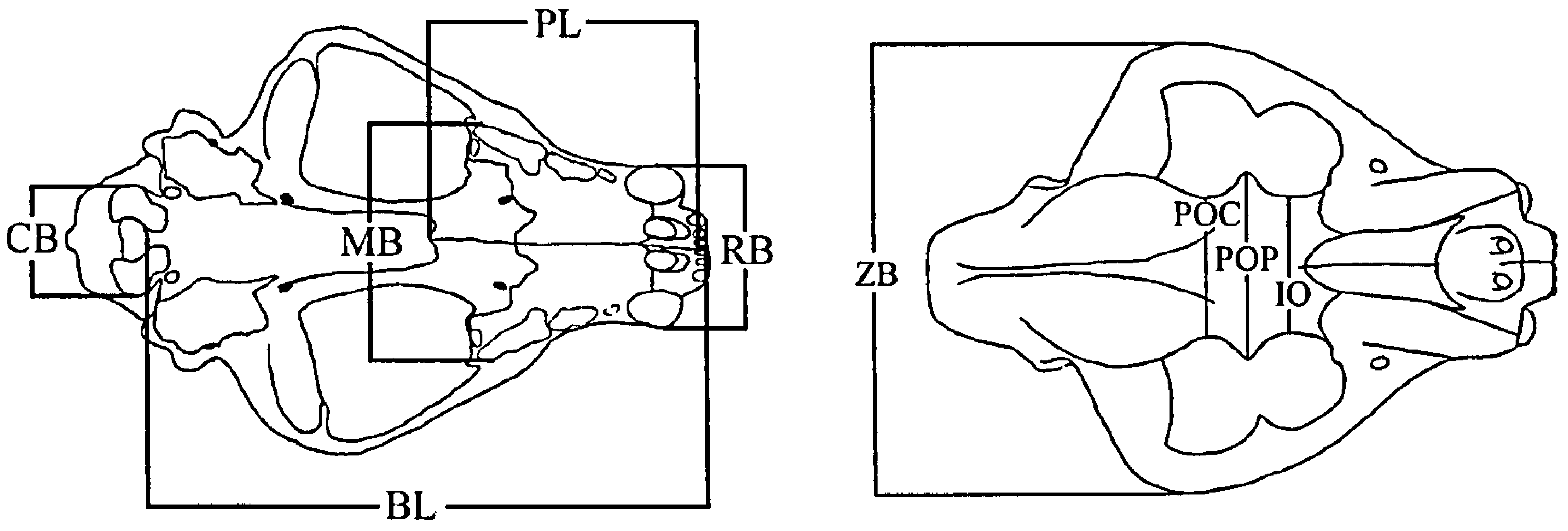


Figure 2.10. Dorsal and ventral views of a tiger cranium, showing measurements used in this thesis. Abbreviations given in Table 2.5.

2.3.3. Mandibular measurements

The mandible is one of the most commonly found *P. gombaszoegensis* fossils; possibly because it is more robust and resistant to breakage than the maxilla in destructive environments, as suggested by Tobias (1991) for African hominid fossils. In addition, all measurements that have been taken are unilateral as opposed to the bilateral measurements of the cranium and are therefore much more likely to be represented in the palaeontological sample, since the mandible usually divides along the unfused suture of the mandibular symphysis. Table 2.6 provides descriptions of the eight mandibular measurements used in this thesis which are illustrated in Figure 2.11.

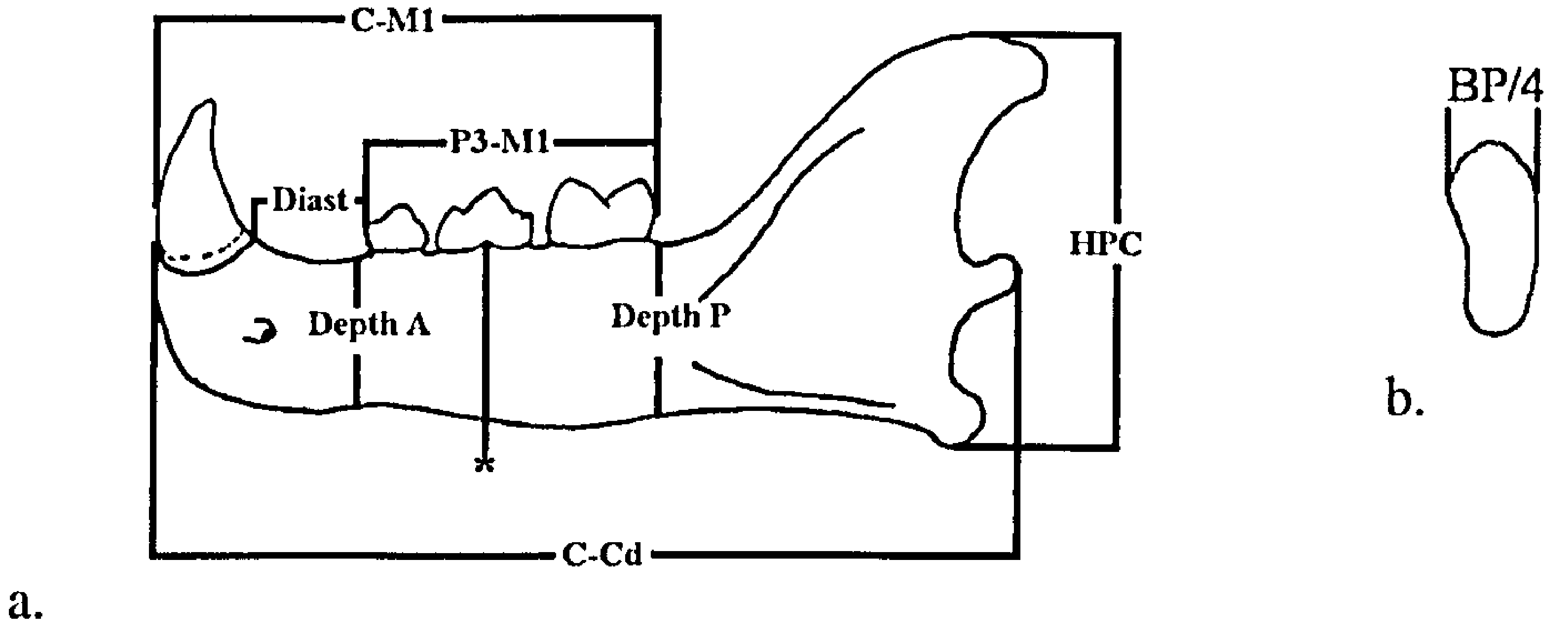


Figure 2.11. a. Lateral view of tiger mandible, b. Cross section of mandible denoted by * on a. All measurements described in Table 2.6.

Measurement	Definition
C-Cd	Total length of mandible from anterior of canine to posterior of condyle
HPC	Height of the coronoid process/ascending ramus
$P_3 - M_1$	Length from mesial surface of P_3 to distal M_1
$C - M_1$	Length from mesial surface of C_i to distal M_1
Diast	Length of Diastema - from posterior of C_i alveolus to anterior of P_3 alveolus
Depth A	Anterior depth of the mandible, anterior to P_3
Depth P	Posterior depth of the mandible, posterior to M_1
$BP/_4$	Greatest breadth of the mandible beneath P_4

Table 2.6. Abbreviations and description of mandibular measurements, shown in Figure 2.11.

2.3.4. Postcranial measurements

Only the most commonly found skeletal elements of *Panthera gombaszoegensis* are illustrated here. These are all elements for which multiple bones are available. Other bones have been recovered and will be discussed in the text where appropriate. However, there are often so few of them that statistical analysis is not possible. The elements and measurements illustrated here have all been analysed in Chapter 5.

2.3.4.1. Humeri

No complete *P. gombaszoegensis* humeri were found. Two measurements were taken on the distal portion of the humerus and these are illustrated in Figure 2.12. The epicondylar width (EPW) is taken as the greatest width across the bone. The trochlear width (TrochW) is taken on the anterior surface at the widest point of the condyle. Minimum shaft width (SWmin)[not illustrated] was also taken at the narrowest point of the shaft, which is usually just above the supracondylar foramen.

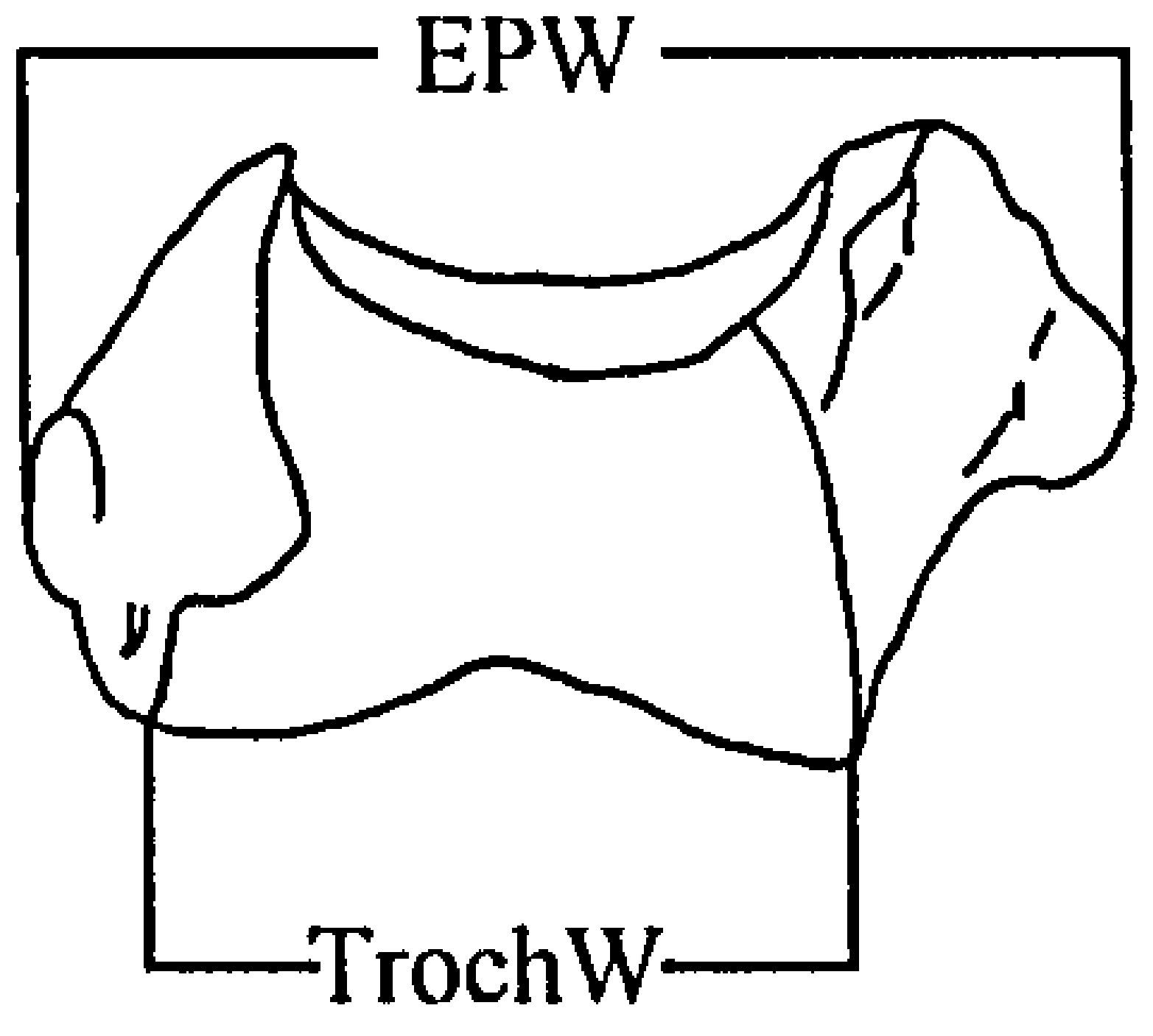


Figure 2.12. Measurements taken on the distal humerus, as described above.

2.3.4.2. Tibiae

Several partial and complete tibiae have been studied. Up to five measurements were taken on each, as shown in Figure 2.13 and described in Table 2.7.

Measurement	**Description**
TL	Total length
PML	Medio-lateral width at the proximal articulation
SW	Least medio-lateral shaft width
DML	Greatest mediolateral width of the distal articulation
DAP	Greatest antero-posterior width of the distal articulation

Table 2.7. Description of tibiae measurements shown in Figure 2.13.

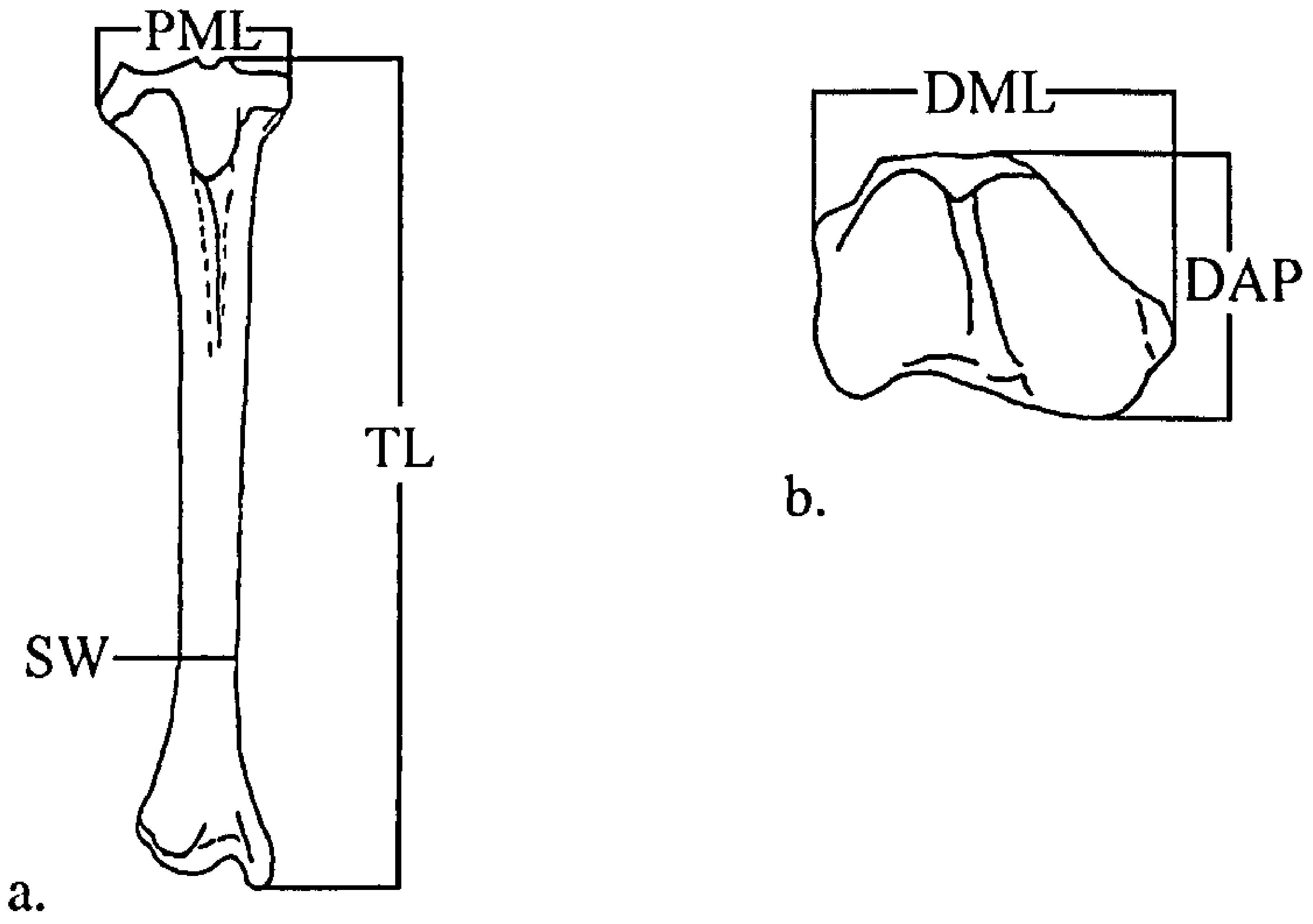


Figure 2.13a & b. Measurements of the tibia, as described in Table 2.7.

2.3.4.3. Calcanea

The calcaneus is another robust bone and four fossil specimens have been studied. The measurements taken are shown in Figure 2.14 below and described in Table 2.8.

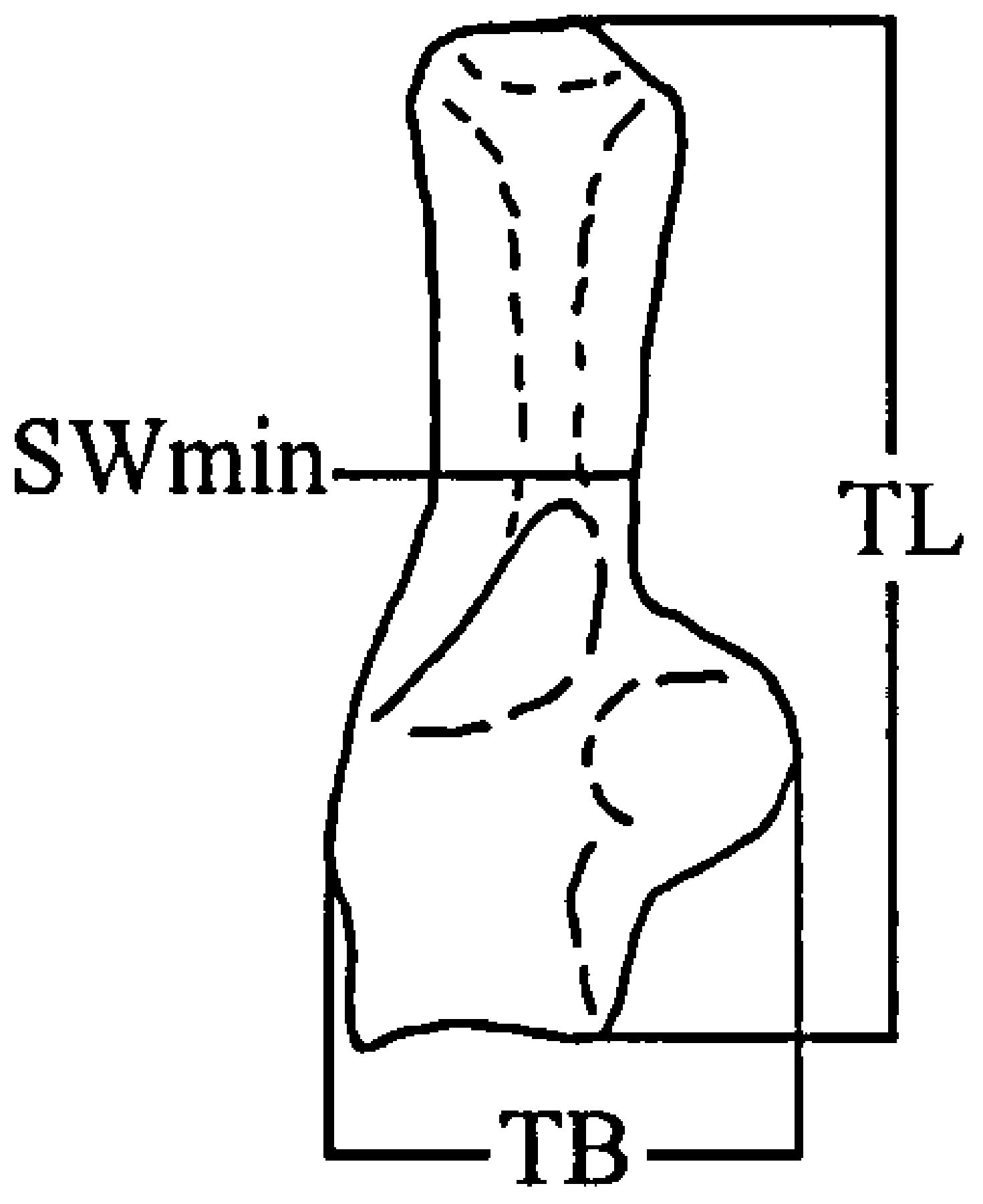


Figure 2.14. Measurements taken on the calcaneus, details in Table 2.8.

Measurement	Description
TL	Total length
TB	Total breadth across the sustentaculum
SWmin	Minimum shaft width

Table 2.8. Explanation of calcaneus measurements shown in Figure 2.14.

2.3.4.4. Astragali

The astragalus is one of the commonest *P. gombaszoegensis* bones, with 10 being recorded from different sites across Europe. Three measurements were taken on each astragalus; these are shown in Figure 2.15 and described in Table 2.9.

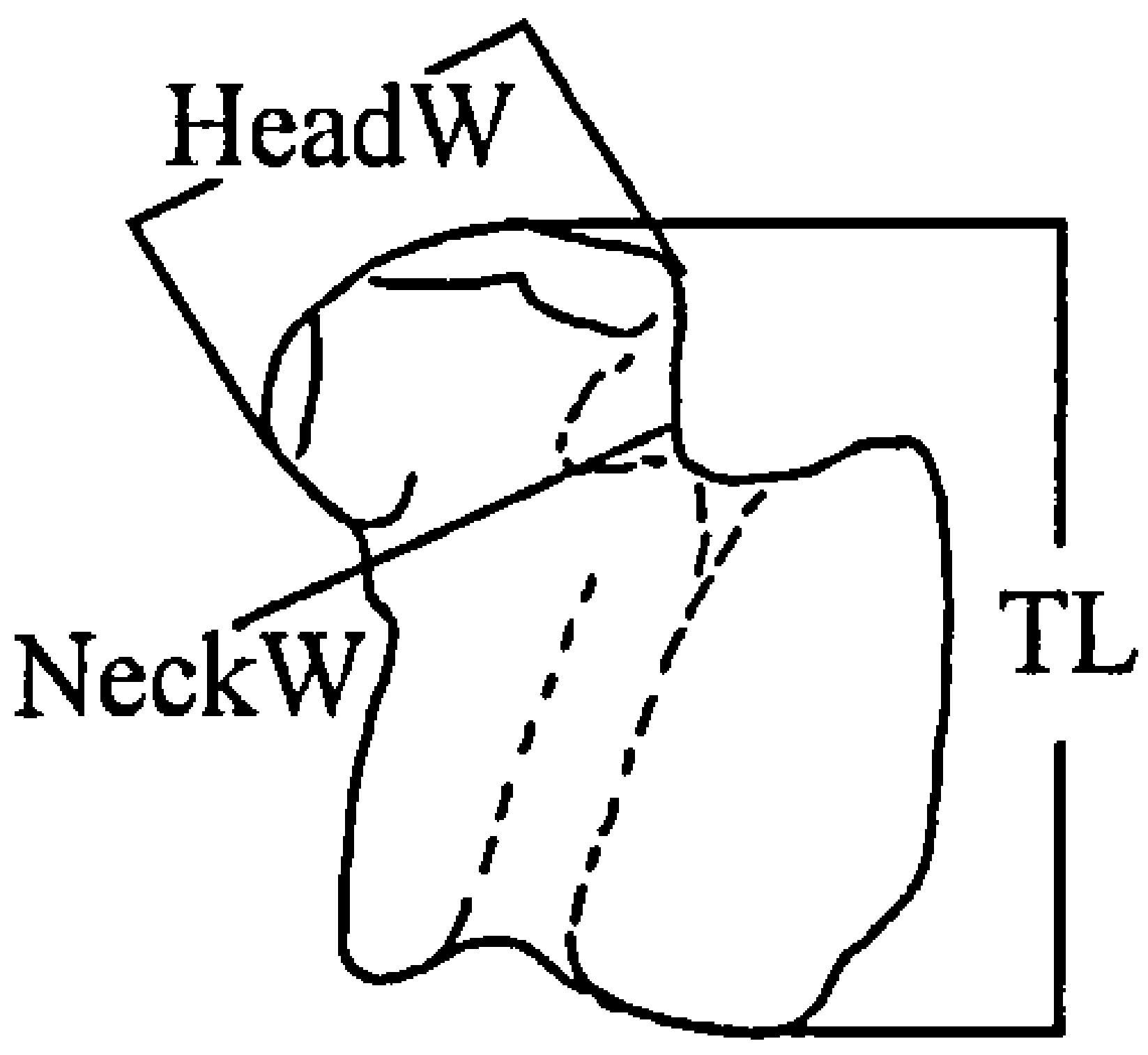


Figure 2.15. Astragalus measurements, described in Table 2.9.

Measurement	Description
TL	Total length
Head W	Maximum width across the head
Neck W	Minimum width across the neck

Table 2.9. Astragalus measurements, illustrated in Figure 2.15.

2.3.4.5. Metapodia

The metapodia are all very similar in morphology and the same measurements were taken on all metacarpals and metatarsals. A generalised metapodial is illustrated in Figure 2.16. to show the type of measurements that were taken and these are explained in Table 2.10.

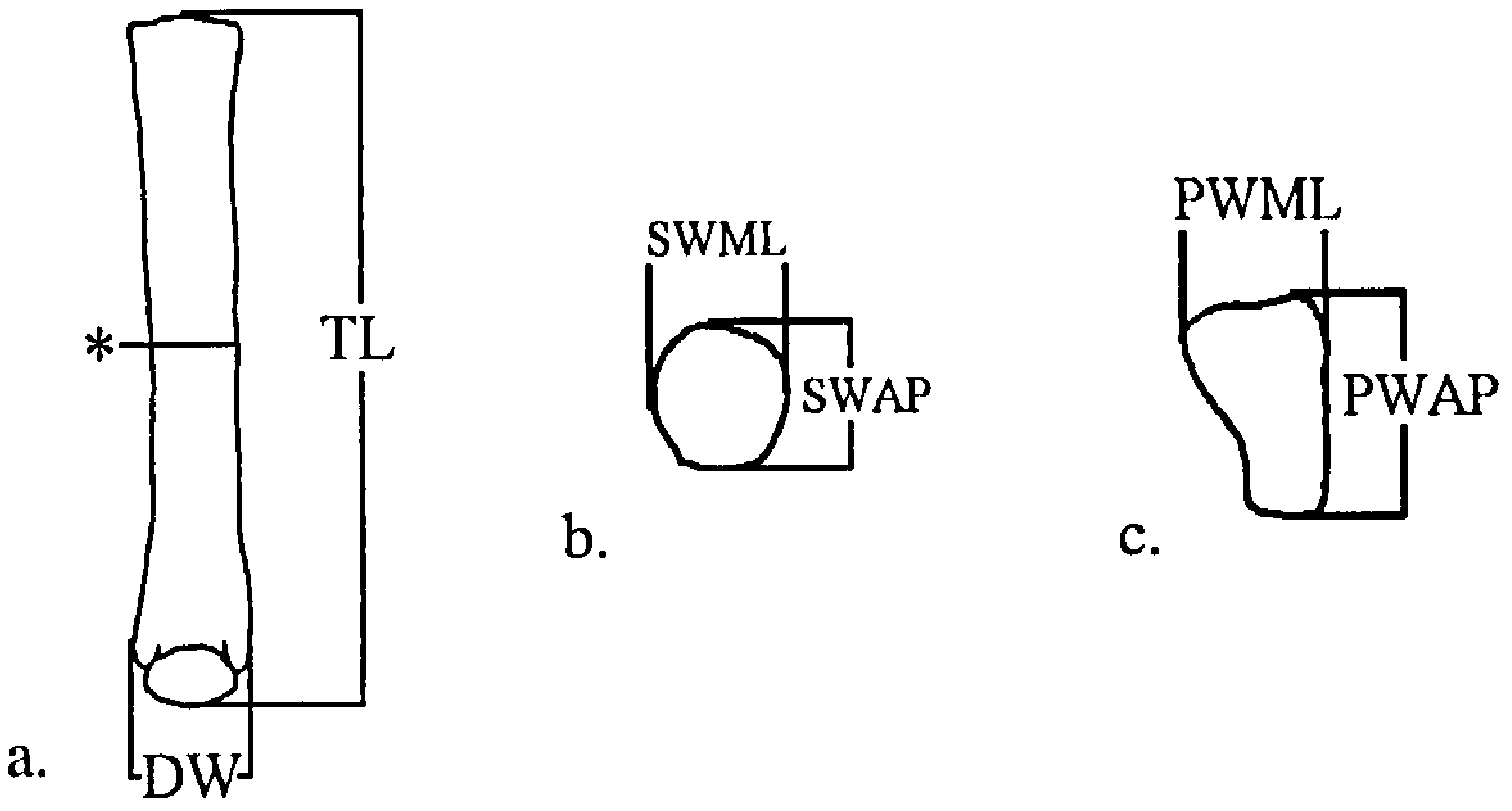


Figure 2.16. Metapodial measurements. 2.16a shows a complete metapodial. 2.16b is a cross section of the metapodial shaft, indicated by an * on 2.16a. 2.16c. illustrates the proximal end of the bone from above. Further explanations are given in Table 2.10.

Measurement	Description
TL	Total length from proximal to distal articulations
DW	Distal width across the epicondyle
SWAP	Antero-posterior shaft width at right angles to SWML
SWML	Medio-lateral shaft width at right angles to SWAP
PWAP	Antero-posterior width of the proximal articulation
PWML	Medio-lateral width of the proximal articulation

Table 2.10. Measurements taken on metacarpals and metatarsals illustrated in Figure 2.16.

2.4. ERROR ANALYSIS

All data collected were entered into Microsoft Excel spreadsheets. They were checked for data entry errors by scatterplotting all datapoints. Where outliers were observed they were checked against the original records to make sure they were accurate. If data had been wrongly entered they were changed. If the originally recorded measurement was obviously incorrect it was deleted. If it was simply an outlier, but within the potential range of the animal, it was retained in the dataset.

2.4.1. Method and results

In order to quantify intra-observer error in the morphometric data an experiment was devised to test the replicability of four of the most commonly taken measurements. These consisted of three dental (M_1L, M_1B and P^4L) and one cranial (BL) measurement, as described in section 2.3.

All four measurements were taken on the left hand side of a leopard skull, once a day for 30 days. The previous results were not visible during this time, to ensure that they did not influence the measurements recorded. The results of this analysis are shown in Table 2.11.

Measurement	n	Mean	Median	s.d.	S.E.	Min.	Max.
P^4L	30	26.16	26.2	±0.085	0.016	26.0	26.3
BL	30	200.00	200	± 0.00	0.00	200	200
M_1L	30	18.74	18.7	±0.050	0.009	18.7	18.8
M_1B	30	9.09	9.1	±0.048	0.0088	9.0	9.2

Table 2.11. Results of error analysis (all in millimetres).

As can be seen in Table 2.11 the results show little variation, with the majority falling within ± 0.1mm of the median. The only exception to this was P^4L with a range of ± 0.2mm; this is a reflection of the judgement that has to be made as to where the metacone actually ends (See Fig. 2.8). However, this is still a small margin of error and is well below the level of variation that would be regarded as significant when analysing fossil material.

2.5. STATISTICAL METHODS

2.5.1. The Mann-Whitney U Test

All datasets were tested for normality using the default Anderson-Darling test in Minitab. Many of the datasets were found to be non-normally distributed and as such, parametric tests such as the students' t test could not be used. Therefore the Mann-Whitney U test was applied for all basic comparisons as it is both non-parametric and can cope with small sample sizes. All datasets were tested with the Mann-Whitney U test, even those which were normally distributed to ensure that all results were directly comparable. The Kruskal Wallis test was used when three or more samples were being compared.

2.5.2. Principal Components Analysis (PCA)

Principal Components Analysis is a form of multivariate statistics which allows comparisons of a large number of measurements for many individuals. It can be used both as an exploratory tool to see which measurements or individuals require further investigation and to find patterns in the data (e.g. between species). A straightforward review of this technique is given in Fowler *et al* (1998).

It works by creating new axes through the data along the lines of the greatest variation within the sample. The axes are produced in descending order, with the first containing the most variation within the sample, the second the next greatest and so on. These results are recorded as factors which can then be scatterplotted for easy visual reference. Where individuals and groups are placed depends upon the differences between them, and the factors can be consulted to see which measurements have had the greatest affects on the results. A factor score of around ± 0.1 indicates that those measurements from which the factors have been derived have contributed little to the overall results. As many axes can be created as there are measurements in the dataset, but in practice only those containing more than 1.0 of the total sample variance are used, as below this point the results could have arisen by chance. The first axis contains the majority of variation within the sample. The extracted factors on the first axis are often high and positive and this is usually interpreted as an indication of size (e.g. Wiig, 1985). The following axes usually reflect differences in shape or morphology within the sample. All of the PCA analyses in this study have been conducted using SPSS.

2.5.3. Chi Squared Test

The chi squared test is a test of association and has such has been used extensively in Chapter Six. Although there are more powerful tests of association available, the chi squared test has been used here because given the nature of palaeontological data it was decided that this was the most appropriate test to reduce the possibility of a Type 2 error (the acceptance of H_1 when it should be rejected). Making a false association between animals in this study would be more damaging than not making an association and the chi squared test, because it is less powerful, is less likely to make this error. For two x two contingency tables Yates' correction was used.

2.5.4. Log Ratio diagrams

Log ratio diagrams were created by G.G. Simpson in 1941 to analyse shape and size changes in palaeontological specimens. It is also known as the 'standard animal technique' because an animal is chosen to represent the species as a whole, to which the other samples are compared (Reitz & Ruff, 1994). In palaeontological material this very useful as it allows direct comparisons of small samples and unlike many of the more powerful techniques it can cope with missing data. The standard animal chosen for the majority of these analyses is the mean of measurements or individual specimens from the type site of Gombasek. The standards used will be made explicit in the text at the appropriate points.

The basic procedure is to convert measurements from the standard animal (in most cases the mean of the Gombasek specimens) to the logarithm of base_{10}. Then all other samples that are to be compared have the means calculated for each site, which are also converted (Log_{10}). The standard logged measurement is then subtracted from the logged site measurements. This procedure results in a list of figures which, when plotted, are standardised about zero (which represents the standard animal). Sites or measurements that fall below zero are smaller than the standard, those above zero are larger. If the sites have the same proportions as the standard then the lines should run parallel to zero, while differences in shape between the samples are indicated by deviations from the parallel.

2.5.5. Tooth ratios

Ratios of measurements such as tooth lengths and breadths have been used for many years to find discrete groupings which correspond with particular species (e.g. Hemmer & Schütt (1969); Spassov & Raichev (1997). These ratios are calculated by taking one tooth measurement and dividing by another to obtain a ratio which is then multiplied by 100 to express the result as a percentage. This is done for all specimens within a sample to create a range. Several ratios have been indicated in the literature as discriminating between *P. gombaszoegensis* and other *Panthera* species. Some of these have been calculated and are shown in Table 2.12.

Cat	n	M_1B/M_1L	n	Hfiss/M_1L	n	Lproto/Lpara
A. pardinensis	10	43.3 – 53.9	1	31.3	1	100
Homotherium	17	36.2 – 43.1				
P. onca augusta	10	47.5 – 54.9	6	26.9 – 32.6	6	97.3 – 114.8
Megantereon	7	44.1 – 51.1				
P. gombaszoegensis	24	44.4 – 51.7	17	24.9 – 30.5	18	95.1 – 120.5
Cheetah	58	39.4 – 47.1	5	24.6 – 31.7	5	97.9 – 111.3
Jaguar	67	46.1 – 55.7	24	24.9 – 33.9	24	90.0 – 118.3
Leopard	106	41.4 – 53.5	28	22.8 – 35.6	28	93.0 – 118.6
Lion	94	41.7 – 55.3	12	26.3 – 33.9	12	99.2 – 122.8
Snow leopard	18	44.5 – 50.5	17	20.9 – 32.3	17	90.0 – 122.8
Tiger	36	45.9 – 54.3	17	28.1 – 38.3	17	89.9 – 114.3

Table 2.12. M_1 ratios expressed as percentages. Blank cells indicate that no data are available for that species.

Spassov & Raichev (1997) suggested that the length of the M_1 divided by the height of the fissure (illustrated in Figure 2.7) might be diagnostic for *P. gombaszoegensis*. This ratio is shown in column two of Table 2.12 and it can be seen that the range of *Panthera gombaszoegensis* specimens overlaps with that of all other species, indicating that this ratio cannot be used to discriminate between species. A similar result was found for the other ratios, with the exception of M_1 breadth divided by M_1 length which shows that *Homotherium* is quite distinct with a much narrower tooth than the other cats, whilst all the other species overlap to some extent. When these ratios were being calculated a distinct sample size effect was noted and this will now be explored further.

2.5.5.1. The effects of sample size on tooth ratios

As shown above different ratios have been constructed to allow comparisons of tooth length, breadth and cusp dimensions between species. However, these do not appear to discriminate as well between species as has previously been claimed. The samples shown above indicate that no species has entirely distinct tooth ratios, but rather many overlap, to a greater or lesser extent. It also becomes apparent when looking at these data that the sample size under investigation appears to affect the discreteness of the result, i.e. that the smaller the sample the less likely two species are to have overlapping ranges. This possibility was tested using a sample of lion M_1s (n=94). Each animal was assigned a number from 1 to 94 and these numbers were used to subsample the dataset. The animals were picked on the basis of these numbers. The data were not randomised as they had not been ordered in the original spreadsheet. The ratio tested was M_1Breadth/M_1Length and the results were expressed as percentages (Table 2.13).

Sample	n	Range	Range (absolute)
Every 20th tooth	4	47.8 – 53.4	5.6
Every 10th tooth	9	47.8 – 53.7	5.9
From 70 - 79	10	41.7 – 53.5	11.8
From 22 - 32	11	45.9 – 52.8	6.9
Every 4th tooth	23	47.8 – 55.3	7.5
From 1 - 45	45	45.9 – 52.8	6.9
From 46 - 94	49	41.7 – 55.3	13.6
From 1 - 94	94	41.7 – 55.3	13.6

Table 2.13. Results of the ratio M_1Breadth/M_1Length expressed as a percentage, calculated from subsamples of 94 lion M_1. All subsamples are taken from numbers assigned to individual specimens.

Table 2.13 indicates the dangers of small samples when using such ratios. There is a general pattern of smaller sample sizes leading to smaller absolute ranges, suggesting that this method may produce misleading and apparently diagnostic results, when very small modern or fossil samples are used to construct the ratios. Of course, the larger the sample, the greater the absolute range and therefore the less likely the method is to produce results which discriminate between species. On the basis of these tests I believe that the use of ratios on small samples sizes as a means of discriminating between species is flawed.

CHAPTER 3 - VARIATION IN MODERN CATS

The variability of modern species has important implications for the study of fossil specimens. The failure to recognise differences between individuals that are due to intraspecific variation such as sexual dimorphism has led to the erroneous establishment of species in the literature (see Turner (1984a) for a discussion of this in relation to fossil lions). Neff (1982) noted that it tends to be the unusual specimens of a species that reach the taxonomists and these then provide the impetus for creating new species and subspecies. A well known example of this is the 'King cheetah', *Acinonyx rex*, which has stripes rather than spots but has been shown to be an aberrant coat pattern of the normal cheetah rather than a separate species (van Aarde & van Dyk, 1986). This study has attempted to understand the intraspecific variation that is present in the genus *Panthera*, in terms of the morphometric and morphological variability that is of direct relevance for the study of fossil pantherines. Six species of large cat have been included in this section: the lion; leopard; tiger; jaguar; snow leopard and cheetah. Where possible postcranial material has been measured to provide a full dataset of modern cats to compare with *Panthera gombaszoegensis* fossils. In the discussion that follows only skulls of extant cats will be referred to as the sample size of postcranial specimens is too low for adequate comparison of intraspecific variation. The complete dataset used is shown in Table 3.1.

Species	Skulls	Postcrania
P. leo	93	7
P. pardus	103	14
P. tigris	37	5
P. onca	67	11
P. uncia	13	12
A. jubatus	53	5

Table 3.1. Total numbers of modern specimens used in this study.

Seven different types of variation will be considered in turn:

3.1 Captive vs. wild cats
3.2 Geographic variation
3.3 Sexual dimorphism
3.4 Age related variation
3.5 Museum collection bias
3.6 Interspecific differences
3.7 Discrete morphological traits

All of these factors will have altered the dataset in some way. This study will explore whether or not these factors have affected the morphometrics of the animals; if so, which dimensions are affected and what implication does this have for the application of modern comparative information to fossil data?

3.1. WILD VS. CAPTIVE CATS

It has been suggested that differences can be observed between the bones of zoo and wild caught cats (Duckler, 1998; Hollister, 1917). These changes and their possible impact on the dataset will be discussed below.

3.1.1. Morphometric change in captive cats

Morphometric differences between wild and captive cats have been recognised in the literature for over 80 years (Hollister, 1917). However, I am unaware of any studies that have done anything more than mention potential changes. Certainly no attempt has been made to quantify the differences between wild and zoo specimens using modern tests of significance. Lions have been the basis for previous studies – Hollister (1917) on East African cats and Smuts *et al* (1978) on Southern African specimens. A summary of variables thought to be affected by captivity is shown in Table 3.2. Only measurements that are directly comparable to my own have been included.

Measurement	Change	Author
Zygomatic Breadth (ZB)	Zoo > wild Zoo > wild	Smuts *et al* (1978) Hollister (1917)
Condylobasal length (BL)	Zoo < wild	Hollister (1917)
Interorbital breadth (IO)	?	Hollister (1917)
Lower canine to condyle length (C-Cd)	Zoo > wild ?	Smuts *et al* (1978) Hollister (1978)
Height of the condylar process (HPC)	Zoo > wild	Smuts *et al* (1978)

? 1917 ?

Table 3.2. Cranial measurements in which captive lions are thought to differ from wild lions. ? indicates measurements tabulated but not discussed in Hollister (1917).

Initially the dataset of male lions from Hollister (1917) was analysed to see if a difference existed between zoo and wild cats in the original study. The dataset of female lions was too small for analysis. The Mann-Whitney U test was used to test for differences between the two groups and the results are given in Table 3.3.

Measurement	Wild (n)	Zoo (n)	Wild median	Zoo median	α
BL	5	5	324.0	309.0	0.2963
ZB	6	5	233.5	261.0	0.0137*
IO	6	5	71.0	75.0	0.2633
C-Cd	6	5	251.0	248.0	0.5219

Table 3.3. Results of Mann-Whitney U test for captive and wild ♂ East African lions (Data from Hollister, 1917). * = $P<0.05$.

It is apparent from the data shown in Table 3.3 that there is a significant difference between the zygomatic breadths of wild and captive lions at the 95% confidence interval. Reference to the medians shows that captive cats have wider zygomatic arches than wild cats.

The measurements listed in Table 3.2 and three tooth measurements have been used for lions and leopards from the comparative dataset to make this study directly comparable to Hollister (1917) and Smuts *et al* (1978). Provenanced samples of other species were too small to allow meaningful comparisons to be made. The modern specimens were divided by sex and provenance and tested using the Mann-Whitney U test, the results of which can be seen in Table 3.4.

The results of these tests agree with the findings of Hollister (1917). Again zygomatic breadth is shown to be greater in zoo cats than wild cats, with the exception of male leopards which showed no significant difference. The larger P^4 in wild male lions is difficult to explain, although the medians of both groups are very similar and it may be that individual variation has played a part in this. The increase in zygomatic breadth when all other dimensions remain the same is perplexing. If all dimensions increased equally then better nutrition amongst captive cats could be the cause, as suggested by Smuts *et al* (1978). This appears plausible for their dataset as three measurements – ZB, HPC and C-Cd were larger in zoo cats than in wild cats from the same geographic area. However, they only looked at specimens up to 36 months of age and it is possible that wild cats could have caught up with the captive cats after this. Schaller (1972) noted that Serengeti lion cubs were smaller than captive cubs of the same age and thought this may be due to periodic starvation in the wild animals. A wild caught but captive raised cub was reported as being nearly twice the size of wild cubs of the same age (Schaller, 1972).

3.1.2. Discussion

Hollister's specimens were all caught in the wild as small cubs and then moved to Washington (Hollister, 1917). The environment in which they were kept would not be regarded as suitable nowadays and it would be easy to dismiss his findings as the result of an unusually harsh regime to which modern animals are not subjected. However the corroboration of not only a modern male lion dataset but also female lions and female leopards suggests that there is some growth factor in captive cats that does not affect their wild counterparts. This work is currently in press (O'Regan, in press a)

Despite the differences observed in captive cats, the majority of variables studied were not affected by captivity. They have been included in all studies as the best sample available as they are often the only fully provenanced specimens with postcrania. Working with some comparative data in which potential biases are recognised is better than working with none.

Measurement	**Species**	**Sex**	**Wild n**	**Zoo n**	**Wild median**	**Zoo median**	α
C^{S}B	*P. pardus*	♂	19	6	10.4	10.85	0.7501
		♀	Sample size too low				
	P .leo	♂	10	9	18.9	18.4	0.5123
		♀	10	9	15.5	16.1	0.3259
P^{4}L	*P. pardus*	♂	20	6	24.7	24.35	0.3454
		♀	13	5	23.5	22.8	1.0000
	P. leo	♂	10	9	38.65	37.4	0.0371*
		♀	11	9	35.6	34.7	0.0870
BL	*P. pardus*	♂	19	6	181.0	180.0	1.0000
		♀	13	5	157.0	171.0	0.1519
	P. leo	♂	11	9	295.0	311.0	0.1022
		♀	11	8	254.0	269.0	0.2643
ZB	*P. pardus*	♂	19	5	135.0	137.0	0.6695
		♀	13	4	119.0	137.5	0.0312*
	P. leo	♂	11	8	223.0	249.5	0.0286*
		♀	11	9	198.0	210	0.0365*
IO	*P. pardus*	♂	19	6	38.4	38.0	0.9493
		♀	13	5	33.2	35.7	0.3243
	P. leo	♂	11	8	66.5	69.3	0.5357
		♀	11	9	61.7	59.7	0.5949
M$_1$L	*P. pardus*	♂	20	6	108.35	18.35	0.6046
		♀	13	5	17.0	17.2	0.9215
	P. leo	♂	11	9	29.3	28.2	0.0575
		♀	11	9	25.9	26.4	0.6754
C-Cd	*P. pardus*	♂	19	6	136.0	136.5	1.0000
		♀	13	5	118.0	132.0	0.0542
	P. leo	♂	10	9	234.0	248.0	0.1777
		♀	11	8	201.0	207.5	0.4328
HPC	*P. pardus*	♂	19	6	65.9	62.15	0.3730
		♀	12	5	54.6	61.9	0.0820
	P. leo	♂	10	9	115.6	116.8	0.9674
		♀	11	8	94.8	97.15	0.9342

Table 3.4. Mann-Whitney U Test results for differences between modern captive and wild lions and leopards. * = $P<0.05$. Abbreviations explained in section 2.3.

3.2. GEOGRAPHIC VARIATION

Many species show variation across their geographic ranges. These differences can be visual [coat colour in leopards, (Kingdon, 1997)]; molecular [karyotypic variation in common shrews (Searle & Thorpe, 1987)] or size related [pumas in North and South America (Gay & Best, 1996)]. Only the latter difference will be seen in the fossil record.

Bergmanns' Rule is often invoked as an explanation of geographic variation within a species. It is an observation that closely related animals from cooler regions will be larger than those in hot areas. In effect this means that the further from the equator an animal lives the larger the body size. This was originally linked to thermoregulation, as large bodied mammals have a smaller surface to volume ratio; which may allow the conservation of heat in cold climates. However, although the observation still stands there is now some dispute over whether it is thermoregulation or another mechanism that is responsible for this pattern (reviewed in Brown & Lomolino, 1998). Bergmanns' Rule is thought to apply to pumas (*Puma concolor*) (Gay & Best, 1996), jaguars (Brock, 1963) and tigers (Mazak, 1981). One of the problems with the rule is that it is merely a generalisation and many factors can serve to confound it. For example, Iriate *et al* (1990) found that puma size is associated not only with latitude, but also available prey size and risk of competition with other large carnivores (in this case the jaguar).

Geographic variation can have quite a large effect on a population - in pumas, specimens can be sexed accurately if their geographic origin is known and the individual is sexed within those population parameters. However, when geographic origin is missing sexing is much less certain (Kurtén, 1973).

Qualitative differences between populations have been identified, but few have been quantified. Observations such as 'Iranian leopards are reputed to be the biggest in the world' (Almeida, 1990:54), and South African cheetahs are 'rangy' [longer legged] in comparison with East African cheetahs (Eaton, 1974:21), have not been tested using modern morphometric methods.

A full understanding of geographic variation in an entire species requires a huge dataset, which is time consuming and expensive to obtain. This is because big cat species have enormous geographic ranges. For example, the lion at its most widespread in the Pleistocene was present on five continents – Africa, Asia, Europe and North and South America (Neff, 1982). In order to fully represent and account for sexual dimorphism, individual variation, etc. many specimens are needed. Unfortunately for the cats, but fortunately for the palaeontologist, hundreds of skulls are stored in museum collections throughout the world, so the data are there to be collected. The largest scale study of feline geographic variation was carried out on the puma with a dataset of 1700 individuals (Gay & Best, 1996). Although such comparisons are beyond the scope of this study, it was deemed important to see if geographic variation could be seen in the data available and to quantify any differences that were found.

3.2.1. Method

Data were collected from the literature on the body mass of big cat subspecies. Weights that had been taken on discrete geographical populations rather than subspecies averages were also included. This provided a baseline for the comparative study of modern cranial measurements to see if geographic variation predicted from body mass could be identified in crania. Body mass was chosen as a variable rather than body length because it is a more reliable measurement, as different ways of measuring length can lead to very different results (discussed in Almeida, 1990), and also because it is a measurement that is often given in the literature.

The modern dataset was divided into geographic zones that were appropriate for each species. Only specimens with known geographic provenance were included. Both sexes were pooled and unsexed individuals included to increase the size of the samples. The cheetah and snow leopard samples were too small for this analysis to be performed.

Six cranial measurements were chosen as being representative of skull size and shape. These were zygomatic breadth (ZB), condylobasal length (BL), M_1 length (M_1L), M_1 breadth (M_1B), lower canine to condyle length (C-Cd) and mandible breadth below P_4 (BP/4). Three types of analysis were used. Firstly measurements of each species were scatterplotted to see if any obvious division of geographic areas was occurring. Secondly, where samples contained at least 5 specimens a Mann-Whitney U test or Kruskal-Wallis test was performed on each variable to see if significant differences were present between regions. Finally for those datasets with large numbers of individuals (lion and leopard) a Principal Components Analysis was carried out, to see if they could be separated geographically by size or shape.

3.2.2. The leopard (*Panthera pardus*)

Twenty eight subspecies of leopard are currently recognised, although the true number is probably much less (Neff, 1982). The leopard is the most cosmopolitan of the pantherine cats. At present it is found throughout Africa and Asia, though it has suffered some range reduction in recent years (Neff, 1982). Fossil leopard material has been found throughout Europe and there is some suggestion that it may have survived into the early Holocene in the Balkans (Spassov & Raichev, 1997). Body mass data for modern leopards are given in Table 3.5.

Region	Sex	n	x̄ Weight (kg)	Min	Max	Author
Tanzania	M	12	62		79	a
Zimbabwe	M	13	60	52	71	b
	F	7	32	28	35	b
Cape	M	27	31	20	45	b
	F	9	21	17	26	b
Iran	M	1			80	a
India	M			52	60	b
	F			39	50	b

missing data?

Table 3.5. Modern leopard body mass by geographic region (data summarised in: (a) Almeida, 1990; (b) Kitchener, 1991)

From these data we could predict that East African leopards would be larger than their Southern African and Asian counterparts and that Iranian (Persian) leopards would be the largest of all. The sample in the modern dataset consists of specimens from six geographic areas (Table 3.6).

Region	n
Persia	3
Asia	6
W. Africa	3
E. Africa	6
S. Africa	42
N. Africa	1
Total	61

Table 3.6. Numbers of modern *P. pardus* skulls, divided by geographic region.

As discussed above, six measurements were chosen as representing overall skull shape and are plotted in Figure 3.1. The specimens show a broad linear relationship between each of the dimensions. When the specimen is large on the x axis, so it tends to be large on the y axis and vice versa, this suggests that size is the major difference between these individuals. Inspection of the data by geographic region shows that there is an overlap between the majority of groups. East African and South African leopards have very similar ranges for each of the dimensions. Asian and Persian cats have similar results although the ranges are slightly reduced; this is probably due to small sample sizes. The most interesting ranges on these graphs are those of the West and North African leopards, which have a similar size distribution to the South African leopards but appear to be larger overall. The West African specimens are from Gabon and were collected in 1909 (Liverpool Museum: 1963.173.113; 1963.173.114 and 1963.173.115). Gabon is on the same latitude as Kenya and Tanzania, suggesting that Bergmanns' Rule is not responsible for the apparent difference in size. The other very large specimen is from Morocco, this cat is considerably larger than any of the Persian specimens from similar latitudes. This difference is worth bearing in mind when considering the discussion of 'robust' vs. 'gracile' leopards in Europe during the late Quaternary (Spassov & Raichev, 1997). A mixing of the Persian group with the North African specimens might lead to a similar conclusion, but a full study of morphological features would need to be undertaken to show this. However, it is possible that a large East African male might change these results and pull the East African range into the range of West and North African specimens. Therefore a larger dataset is required to see if these specimens are within the range of African cats or if West African and North African leopards are bigger than those from elsewhere.

The suggestion that the Persian cats are the largest overall is not proven, although the sample size in this study was very small (n=3). Figure 3.1 shows that the Persian cats have broader zygomatic arches (ZB) for their condylobasal length (BL) than the other cats, but all three were captive cats (Edinburgh Museum: PH1/98; 23.95 and Vienna Museum 2843) and as explained in section 3.1 captivity does appear to affect this area of the skull.

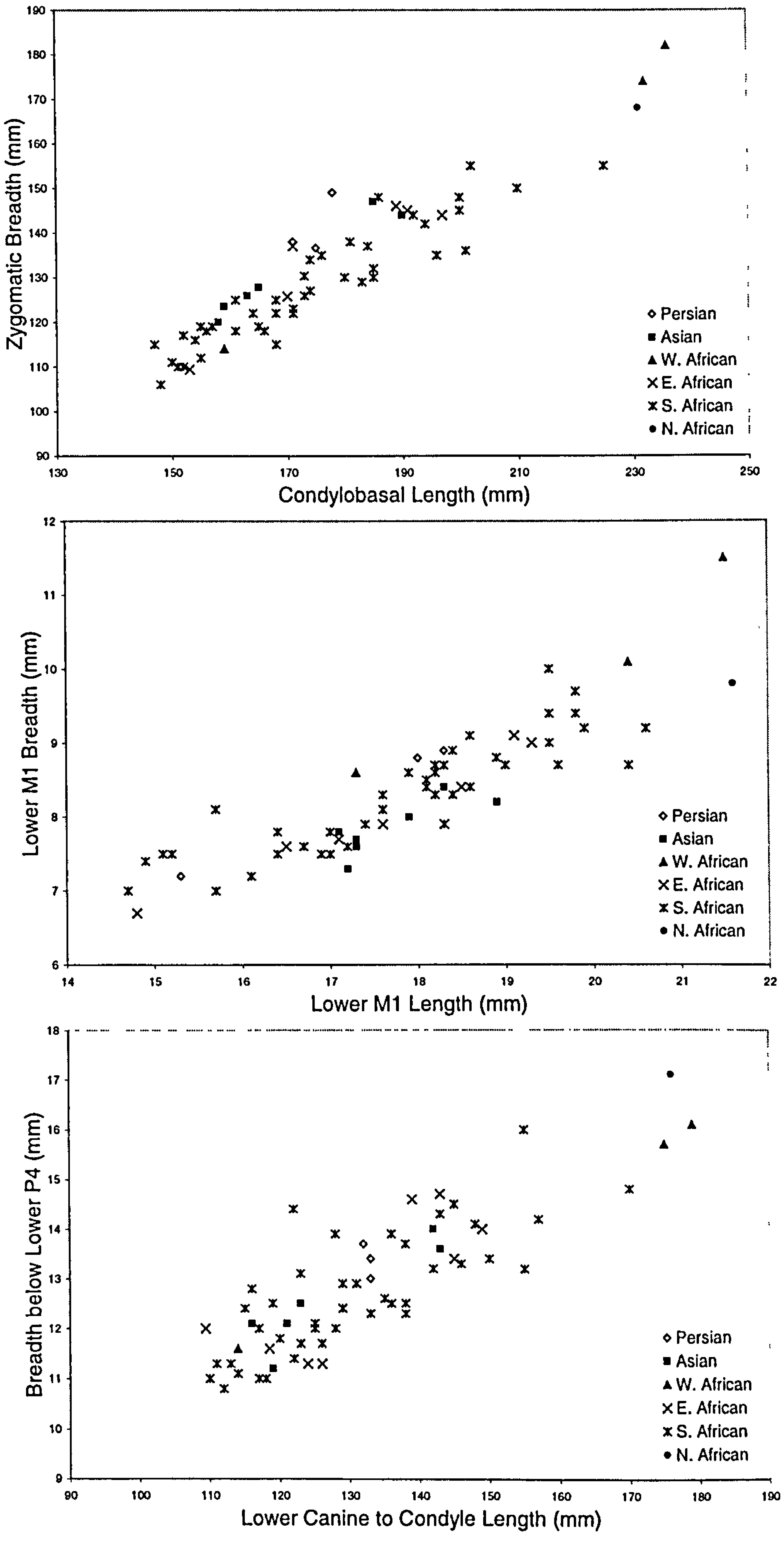


Figure 3.1. Skull measurements of modern leopards plotted by geographic region

The measurements charted in Fig. 3.1 were tested for significance using the Kruskal-Wallis test. Only Asian, East African and South African specimens were included in this analysis. No significant ($P<0.05$) differences were found between different geographic groups for any of the variables.

Principal Components Analysis was conducted on all provenanced cats and all variables. Owing to missing datapoints only 36 specimens remained in the final analysis. Two axes were produced and loadings on the first were all high and positive indicating that this is related to size. This axis accounted for 78.43% of the variance. The second axis had mainly low loadings with the exceptions of the postorbital process (POP) and postorbital constriction (CB). These axes are plotted in Figure 3.2. This again shows that the North and West African cats are larger, as they group together at the right hand side of the plot, it seems likely that these cats are male and that the smaller West African cat is a female. No separation by geographic region is seen on axis 2, indicating that there are no shape differences between the groups.

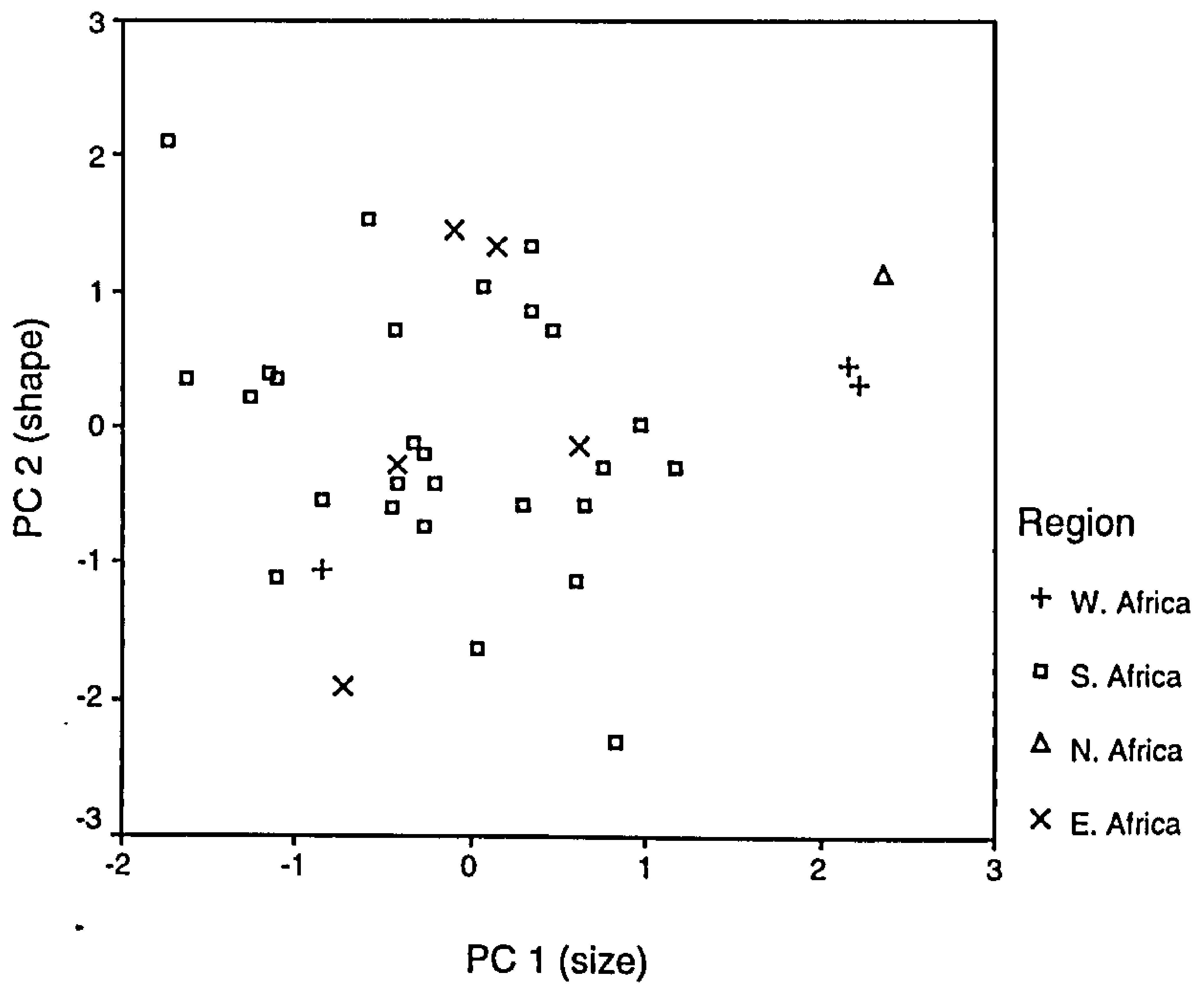


Fig. 3.2. PCA for modern leopard dataset, plotting specimens by region.

PCA is a valuable tool as it shows that the three large North and West African specimens are larger in all dimensions, not just those selected for scatterplotting. It also shows that on the basis of the morphometric dataset no separation can be made between leopards from different geographic regions except in terms of size, although the body mass data appears more variable. Persian leopards did not appear to be larger than cats from other areas and no body mass data are available for North and West African leopards to see if they are larger. Therefore on the basis of this dataset leopard morphology appears to be homogeneous throughout their geographic range and for the purposes of this study specimens from the different geographic regions can be combined.

3.2.3. The lion *(Panthera leo)*.

The lion, has, in the past, been the most widely spread cat of the genus *Panthera*. If the two extinct subspecies (*P. l. atrox* and *P. l. spelaea*), are included then during the Quaternary it was present on all continents except Australia and Antarctica (Neff, 1982). Historically it has been found in India and Eastern Europe, but an extreme range contraction has taken place in the last few centuries leaving a sub-Saharan population and an isolated group in the Gir Forest, India (Neff, 1982). Nine subspecies of lion are recognised, two of which are already extinct – the Barbary lion (*P. l. leo*) and the Cape lion (*P. l. melanochaita*) (Haltenorth & Diller, 1980).

Body mass data for modern lions are given in Table 3.7. This table shows that in general Southern African and Asian lions weigh more and are therefore likely to be larger than their East African counterparts. Sexual dimorphism also appears to be most extreme in the Southern African lion, with the range of female body masses from the Kruger park only just overlapping and the Kalahari females not overlapping at all with the male dataset, despite large sample sizes.

Region	Sex	n	$\bar{x}$ Weight (kg)	Min	Max	Author
Tanzania	M	21	135		180	a
Kenya	M	14	172	150	189	b
	F	5	151	122	182	b
E. Africa	M	25	174.9	145.4	204.7	c
	F	15	119.5	90.0	167.8	c
Zimbabwe	M	26	193.3	172.0	215.9	c
	F	23	133.6	164.0	214.0	c
Kruger park	M	41	187.5	150.0	225.0	c
	F	95	124.2	83.0	152.0	c
Kalahari	M	11	188.4	164.0	214.0	c
	F	8	139.8	127.0	153.0	c
India				180	230	d

Table 3.7. Modern lion body mass by geographic region. Data from (a) Almeida (1990); (b) Schaller (1972); (c) Smuts *et al* (1980); (d) Kitchener (1991).

The sample in the modern dataset consists of specimens from three different geographic regions (Table 3.8).

Region	n
Asia	5
East. Africa	8
South Africa	33
Total	45

Table 3.8. Number of modern *P. leo* skulls divided by geographic region.

The scatterplots in Figure 3.3 again show a linear relationship between the variables, although they are not so defined as those of the leopard (Figure 3.1). There is a distinct mixing of all groups in each graph; the ranges of East African and South African lions are very similar. Asian lions appear slightly smaller in almost all dimensions except M_1 breadth. The Kruskal-Wallis test was used to test for differences between all regions for condylobasal length and zygomatic breadth. The Mann-Whitney U test was used for all other variables to test for differences between East and South African cats. No significant ($P<0.05$) differences were found between any of the geographic groups.

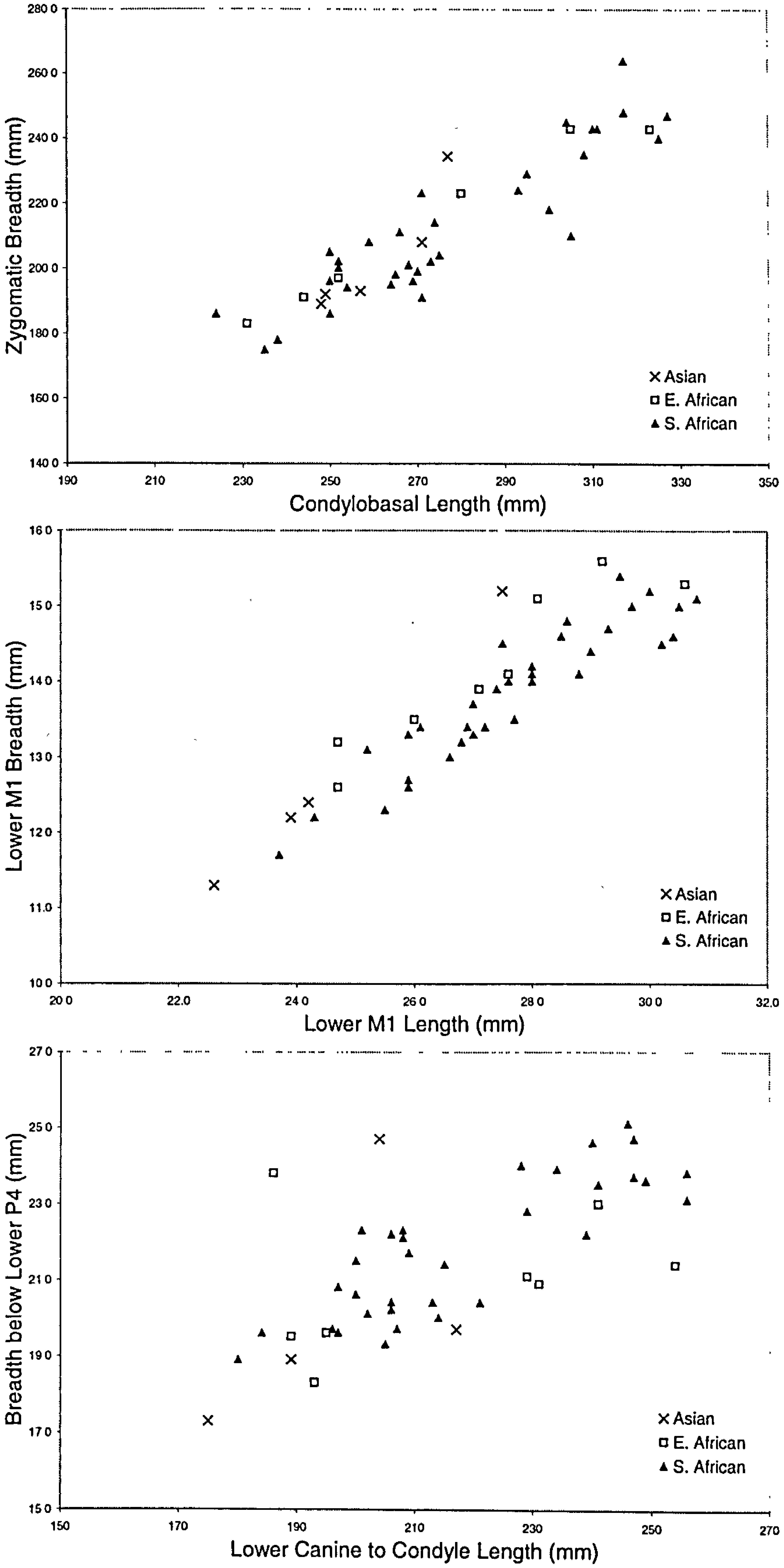


Figure 3.3. Skull measurements of modern lions plotted by geographic region

Principal Components Analysis was run using 29 of the original specimens, the others were excluded because of missing datapoints. Three axes were produced, the first accounted for 68.27% of the variation, the second 13.62% and the third 3.43%. The loadings on the first axis were high and positive, suggesting that it is size related. On the second axis all bone measurements – mandibular and cranial were negative, whereas all teeth measurements were positive, with the exception of C^sB which was negative. There was no separation of specimens by geographic region. Axes 1 and 2 are shown in Figure 3.4. This shows that South African cats are, in general, larger than East African or Asian cats. This hypothesis cannot be confirmed on this sample size, although the body mass data in Table 3.7 appear to support it. Again, no shape differences were apparent on Axis 2, suggesting that there are only size differences between the groups and that for the purposes of this study the lion data can be combined.

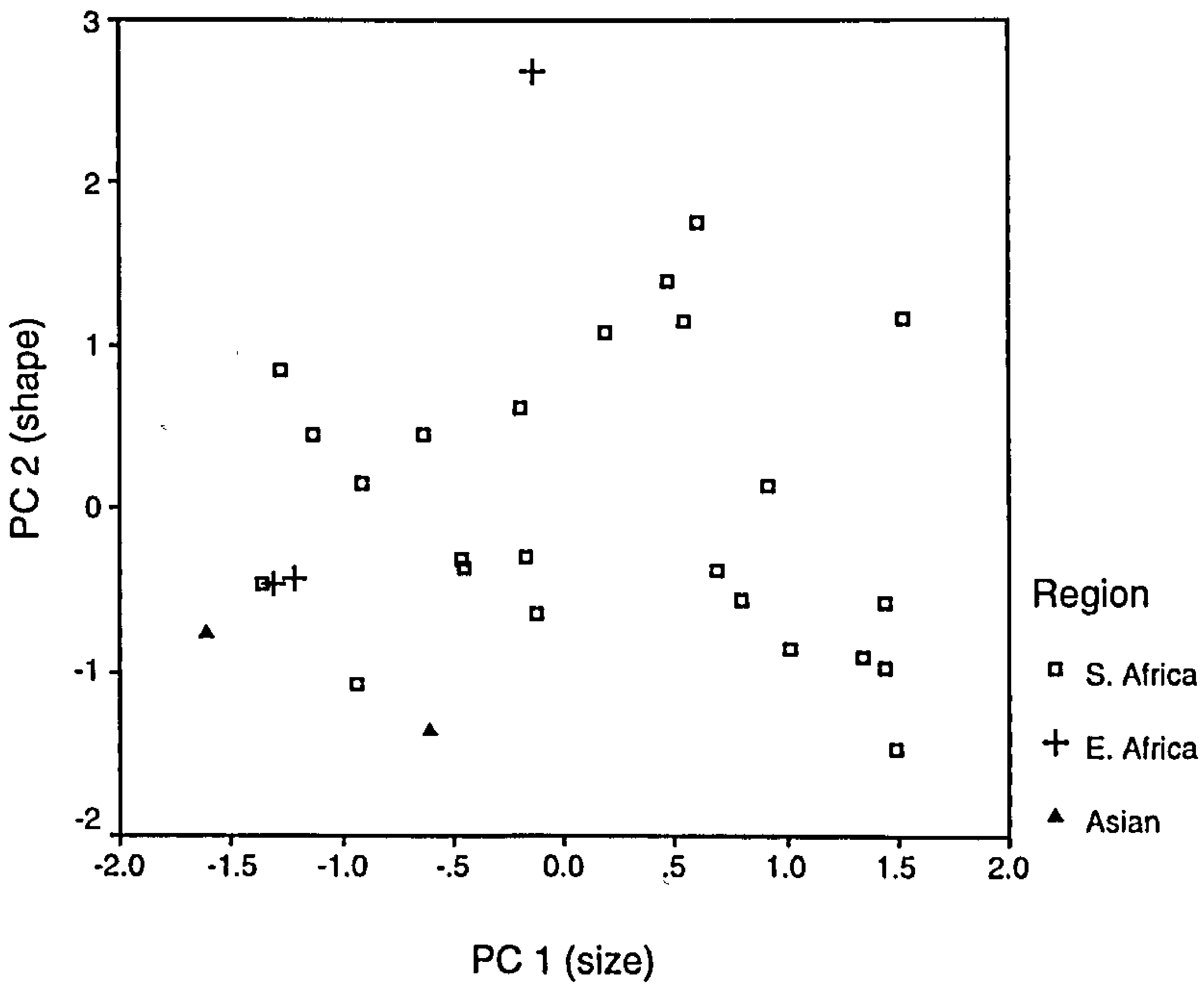


Fig. 3.4. PCA analysis for modern lions, plotted by region.

3.2.4. The jaguar (*Panthera onca*)

In the past the jaguar has been found in North America, but is now restricted to central and Southern America (Neff, 1982). The largest population is in Brazil with small isolated pockets to the North and South (Seymour, 1993). The jaguar was originally divided into eight subspecies on the basis of coat colours and cranial characters (Pocock, 1939). However, more recent work on jaguar taxonomy conducted using multivariate analysis of cranial characters found no evidence for subspecific designations (Larson, 1997).

The jaguar is one of the cats that appears to follow Bergmanns' Rule. Jaguars that live closer to the equator are smaller than those from the northern and southern ends of the range (Larson, 1997). Iriate *et al* (1990) plotted head-body length of both jaguar and puma against latitude, their graph is shown in Figure 3.5. This shows a very good relationship between body size and latitude for both species. The question is whether the modern dataset under investigation can pick up these differences.

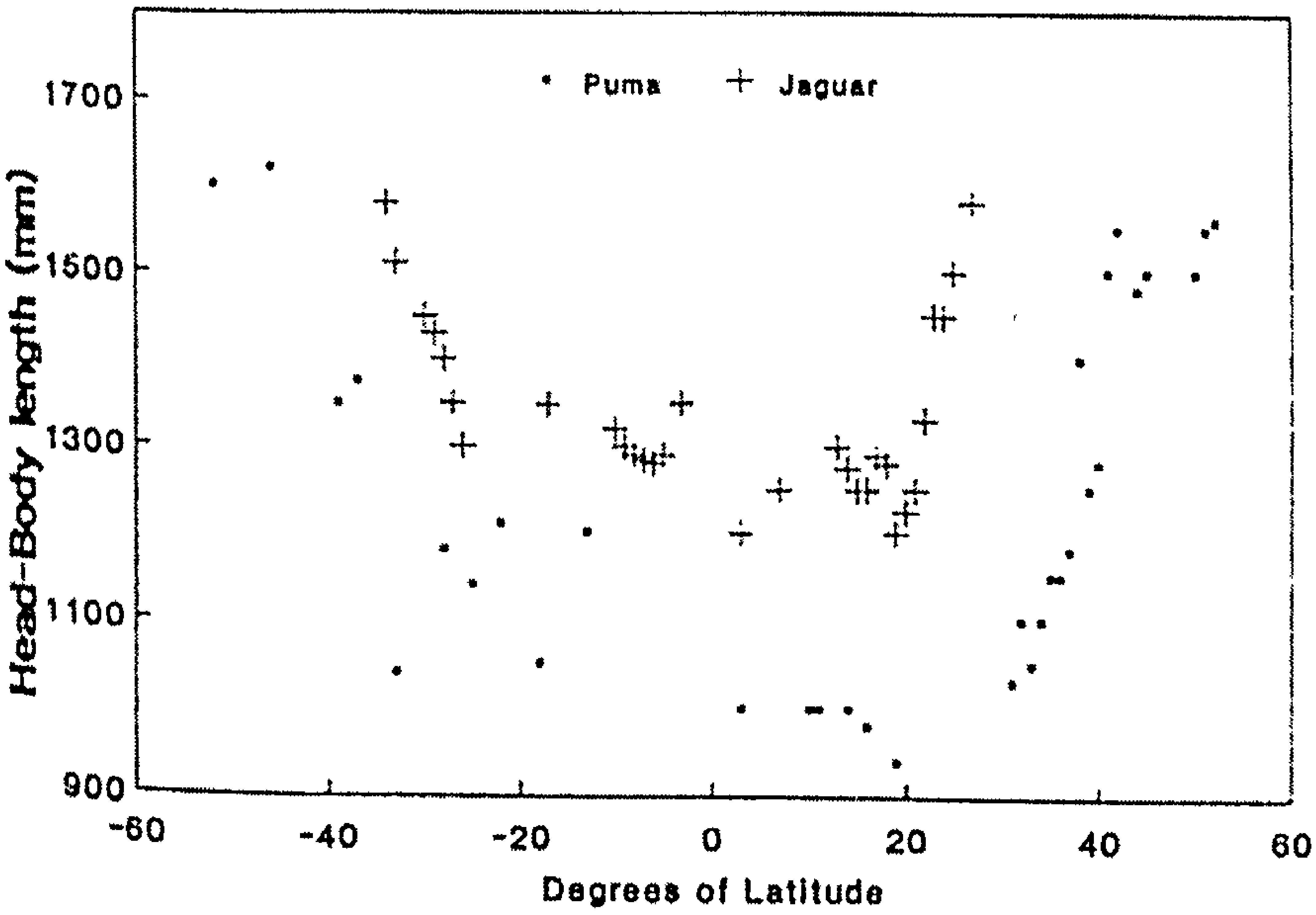


Figure 3.5. The relationship between jaguar and puma head-body length and latitude (from Iriate *et al*, 1990).

Body mass data for modern jaguars are given in Table 3.9. These also appear to show that cats from Central America are smaller than those from Southern America, although the sample size for Central American cats is very small. Sexual dimorphism, at least in terms of body mass, is much less than that of the lion.

Region	**sex**	**n**	**x̄ Weight (kg)**	**Min**	**Max**	**Author**
Venezuela	M	9	95.0			a
	F	3	56.3			a
Brazil	M	6	94.8			a
	F	3	77.7			a
Brazil	M	45	96	66	119	b
	F	21	76.5	62	93	b
Belize	M	6	57.2			a

Table 3.9. Modern jaguar body mass by geographic region. Data from (a) Seymour (1989); (b) Almeida (1990).

The jaguar specimens in the modern dataset have been divided into two groups (Table 3.10).

Region	**n**
Central America	6
South America	16
Total	22

Table 3.10. Number of modern *P. onca* skulls, divided by geographic region.

The graphs in Figure 3.6 show a linear relationship between the variables. They also appear to show a size difference between Central and Southern jaguars. Southern jaguars are larger overall; one specimen in particular is consistently bigger. This is a cat from Northern Argentina, collected in 1901 (BMNH 77.857). It is an important specimen because without it might be concluded that the size range was more or less equal for the cats from each region.

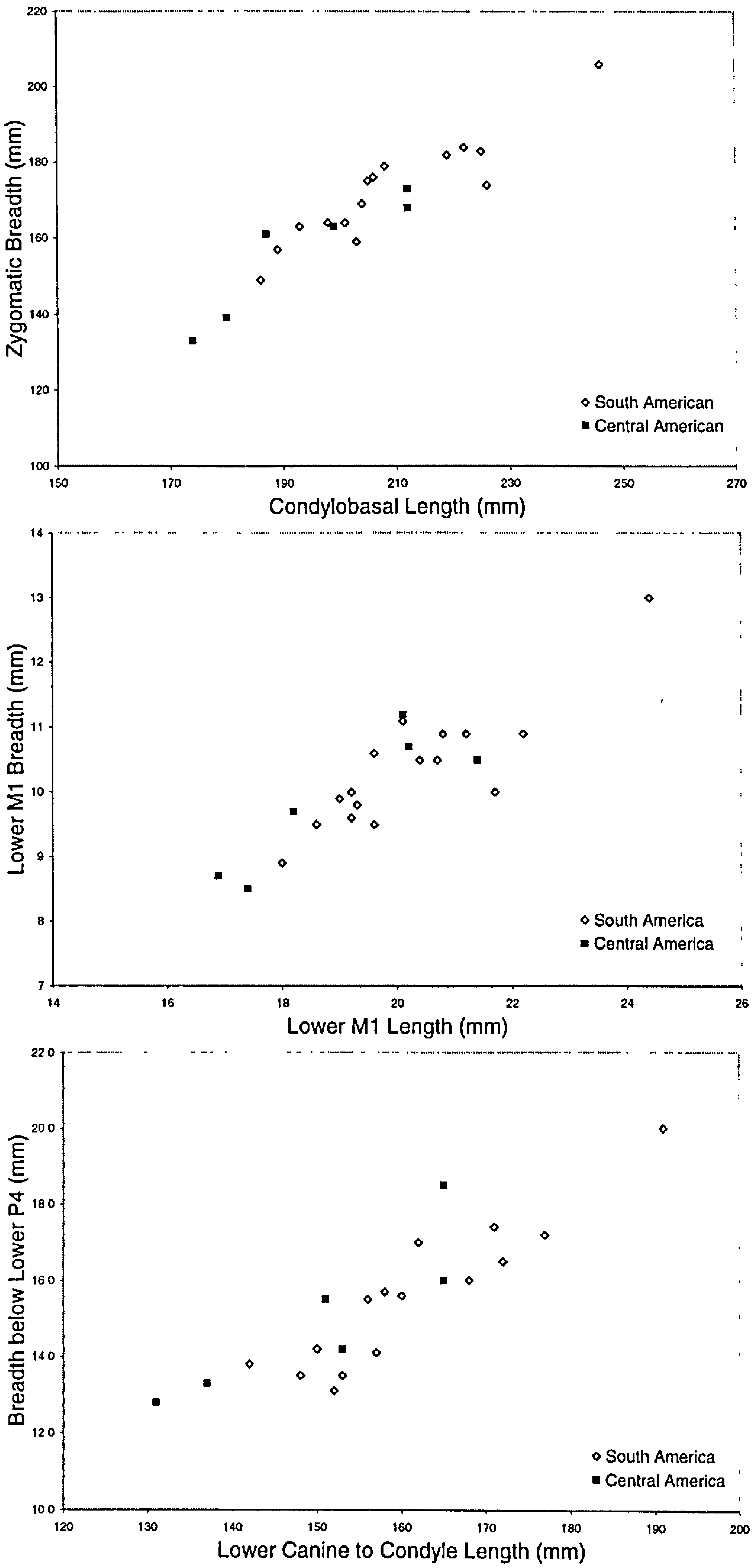


Figure 3.6. Skull measurements of modern jaguars plotted by geographic region

Mann-Whitney U tests were performed on the data to see if differences could be found between the different groups. No significant ($P<0.05$) differences were found for these variables. Therefore although it appears that South American jaguars are slightly larger and this has been corroborated with body weight and head-body length data, it cannot be proven with this dataset.

3.2.5. The tiger (*Panthera tigris*)

The tiger is the largest of the living *Panthera* species, its range extending from Northern Asia down to Bali (Neff, 1982). Like the other pantherine species it has become extinct throughout much of its range in the last few centuries. Historically eight subspecies have been recognised, of which two are already extinct – the Bali tiger (*P. t. balica*) and the Javan tiger (*P. t. sondaica*) (Mazak, 1981). It has been suggested that Bergmanns' Rule also applies to this species (Mazak, 1981). Body mass data for each of the subspecies are given in Table 3.11.

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Subspecies	sex	n	$\bar{x}$ Weight (kg)	Min	Max
P. t. tigris	M			180	258
	F			100	160
P. t. corbetti	M			130	195
	F			100	130
P. t. amoyensis	M			130	175
	F			100	115
P. t. virgata	M			170	240
	F			85	135
P. t. altaica	M			180	306
	F			100	167
P. t. sumatrae	M			100	140
	F			75	110
P. t. sondaica	M			100	141
	F			75	115
P. t. balica	M			90	100
	F			65	80

Table 3.11. Body mass data for modern tiger subspecies (from Mazak, 1981)

Very few provenanced specimens were available for analysis. The majority of these were Indian or Bengal tigers because of the historical links between India and the UK. The modern dataset used in this analysis is shown in Table 3.12.

Region	**n**
India	16
Islands	2
Siberia	1
Total	19

Table 3.12. Number of modern *P. tigris* skulls, divided by geographic region.

No statistical analyses were possible but the data were scatterplotted to see where each region fell (Figure 3.7). Again, the relationships between variables are broadly linear. The island specimens are smaller than the mainland cats. Bergmanns' Rule is thought to apply to this species in general, although there is some reversal of the size cline in central Asia (Herrington, 1987). This apparent reversal is based on a sample of only 45 specimens covering six of the subspecies (Herrington, 1987). It is possible that the full range of variation in each subspecies was not covered in this study, therefore further evidence is needed before the reversal can be proven. Likewise, the suggestion that the Bali tiger was the smallest of the tiger subspecies may be flawed, as this assumption was based on the measurement of all known specimens (n = 7) held in museums. The majority of these crania are female and this may have considerably underestimated the true size range of this cat (Buzas & Farkas, 1997). Tigers are known to exhibit extreme geographic size changes, but this sample is too small to show the extremes and must be regarded as a good 'middle ground' dataset that shows the average size of the cat.

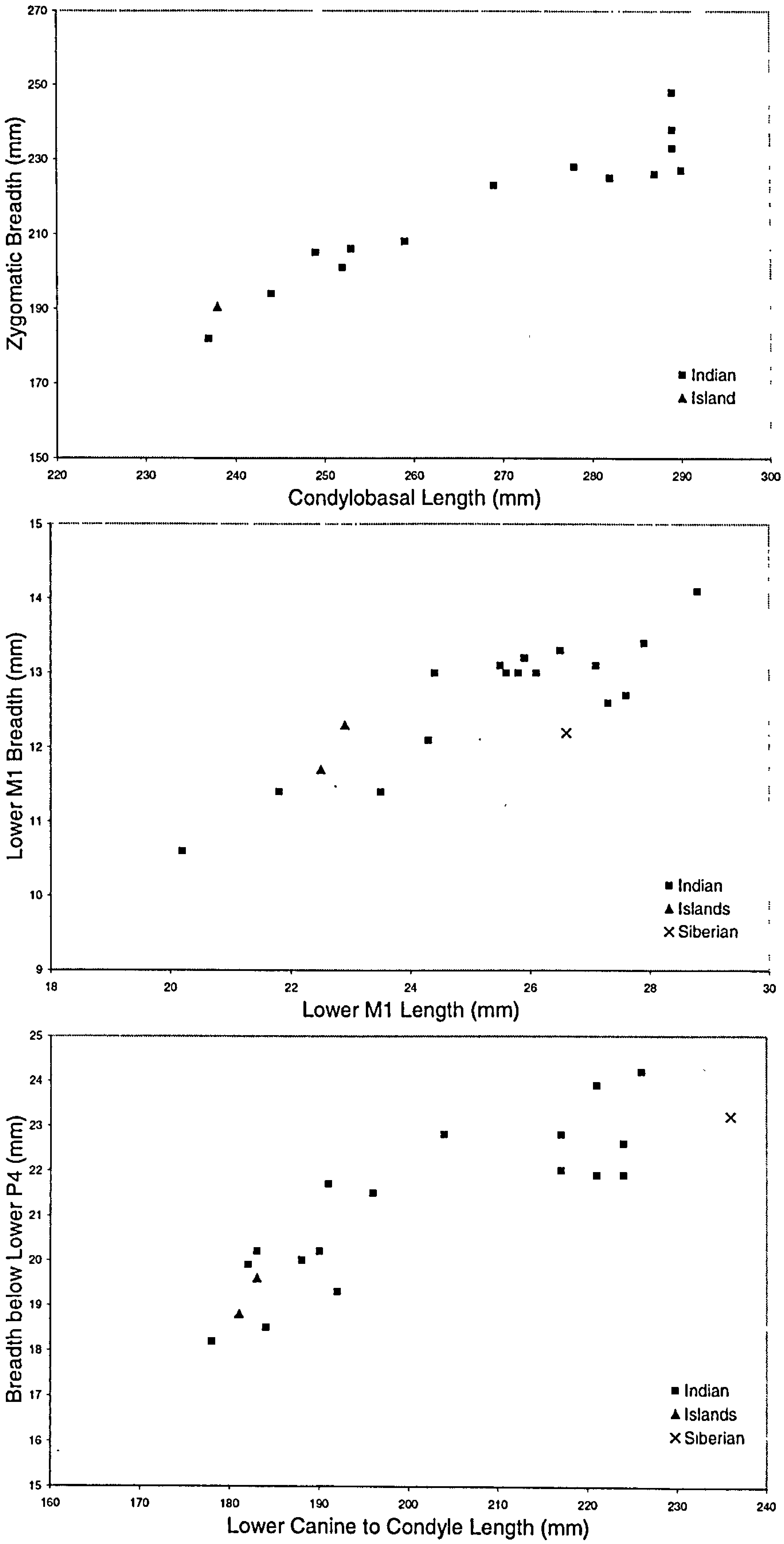


Figure 3.7. Skull measurements of modern tigers plotted by geographic region

3.2.6. Discussion

Although size changes are apparent, geographic variation in big cats has not been proven to be statistically significant for any of the species or variables studied. PCA showed that changes seen in leopard and lion groups were size related and no shape differences were found between cats from different regions. Small sample sizes are the obvious limiting factor in this study. Another geographic study of leopards with a sample of 187 crania could discriminate between animals from large geographic areas (African vs. Asian cats for example), but there was a lower success rate on assigning animals to regions within continents (Miththapala, 1992).

It is likely that larger samples could discriminate between different geographic regions and that the data in this study are under-representing the true range of variation seen in modern cats. However for the purposes of this analysis it provides a good general dataset of large cats, whilst missing possible extreme values at either end of the scale.

3.3. SEXUAL DIMORPHISM

In the animal world sexual dimorphism is common. It simply means a difference between males and females of the same species. This can take many forms; a familiar example is the tail of the male peacock, which is large and colourful in comparison with the brown female. Colour differences are very common amongst bird species but less common in mammals. Size differences also occur; the male is larger than female in the majority of mammal and bird species. However, 'reverse dimorphism', where the female is larger than the male, is found in birds of prey and rabbits as well as some other mammals. Shape differences are also common, with males in some species having ornamentation, such as red deer antlers or exaggerated features such as the enlarged canines of the male baboon (all above reviewed in Andersson, 1994).

Why are these differences important? The majority of differences between the sexes are in soft tissue and will not be seen in the fossil record. However, if criteria could be established by which animals are shown to be dimorphic then this may tell us something of the palaeoecology of the extinct species. The lion is the only social, group living big cat and it is the only big cat that exhibits great sexual dimorphism, not only in terms of size but also in appearance, as the male lion has a large mane. If parameters could be placed upon the range of dimorphism in this species and if there were sufficient fossil specimens it might be possible to ascertain when the lion became social, because the bimodal size range of its bones and teeth would be greater than that seen in the other solitary and less dimorphic cats. This argument also applies to *P. gombaszoegensis*; if the size range of the fossils are greater than that of solitary cats then sociality could perhaps be inferred. This is speculative, however, unless all specimens can be confidently assigned to one species and measurements are found that are sufficiently dimorphic to be used to assign sex reliably.

3.3.1. Method

All the cranial and dental variables listed in Table 3.13 were examined using the Mann-Whitney U test to ascertain which dimensions were significantly different between the sexes. In addition the median percentage dimorphism and maximum percentage dimorphism (between the largest male and smallest female) were calculated on dental measurements for each species. This provides the maximum range of variation in each modern cat and these parameters can then be applied to the fossil specimens. Shape differences between males and females were looked for using PCA and the results were plotted to see if there was any separation between the sexes. The total number of specimens of each species included in the study are shown in Table 3.14. There were too few specimens with both sex and provenance data to allow this investigation to proceed if the dataset had been divided by geographic locality, although it is acknowledged that geographic origin may have had some influence upon the results. There were too few sexed tiger specimens to be included in this analysis.

Upper teeth	**Cranial dimensions**	**Lower teeth**	**Mandibular measurements**
C^sL	BL	C_iL	C-Cd
C^sB	PL	C_iL	HPC
P^2B	RB	P_3L	$P_3 - M_1$
P^3L	MB	P_3B	DepthA
P^3B	ZB	P_4L	DepthP
P^4L	IO	P_4B	$BP/_4$
P^4Ba	POP	M_1L	
P^4Bbl	POC	M_1B	
P^4Lp	CB		
P^4Lm			
M^1B			

Table 3.13. Skull and dental measurements used for calculating sexual dimorphism. Abbreviations are explained in section 2.3.

Cat	**♂ n**	**♀ n**
Leopard	21	10
Lion	25	23
Jaguar	13	8
Snow leopard	8	9
Cheetah	13	8

Table 3.14. Total number of sexed specimens in each sample.

3.3.2. Leopard

All dental measurements showed significant sexual dimorphism with the exception of P^2B, P^4Lm and M^1B. The postorbital constriction was the only cranial measurement that showed no change. PCA was then run on the dataset using all variables except P^2L and M^1B as these are single rooted teeth and are often missing from the sample The analysis produced 3 axes, the first contained 73% of the variation in the sample and the components were high and positive, suggesting that this is a size axis. The variation in the other two axes was 10% and 4% respectively. Axes 1 and 2 were plotted in Figure 3.8.

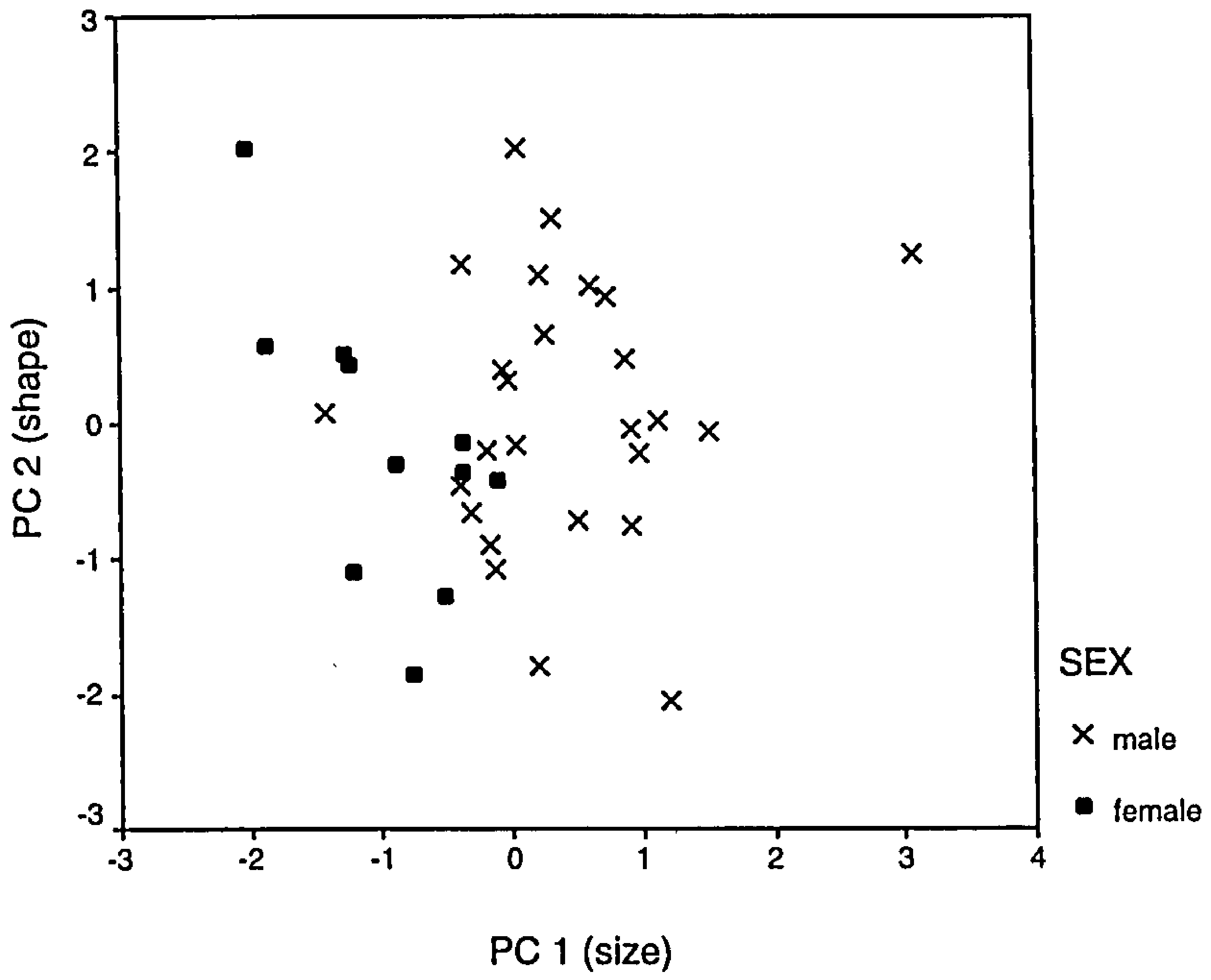


Figure 3.8. PCA results for modern leopard sexual dimorphism

Figure 3.8 shows that some separation was seen on PC 1 (the size axis) confirming that size is the major difference between the two sexes. No separation was achieved when the other axes were plotted and it is assumed that the results of the PCA show individual rather than sex based differences.

3.3.3. Lion

All measurements were significantly sexually dimorphic at the 95% confidence interval for lions. PCA identified three axes in the dataset, the first contained 66.6% percent of the variation, the second 14.7% and the third 4.1%. All measurements on the first axis were high and positive suggesting that this is related to size. An interesting relationship between variables were seen on axis 2, where all dental measurements were negative and all cranial and mandibular measurements were positive. The first two axes are plotted in Figure 3.9.

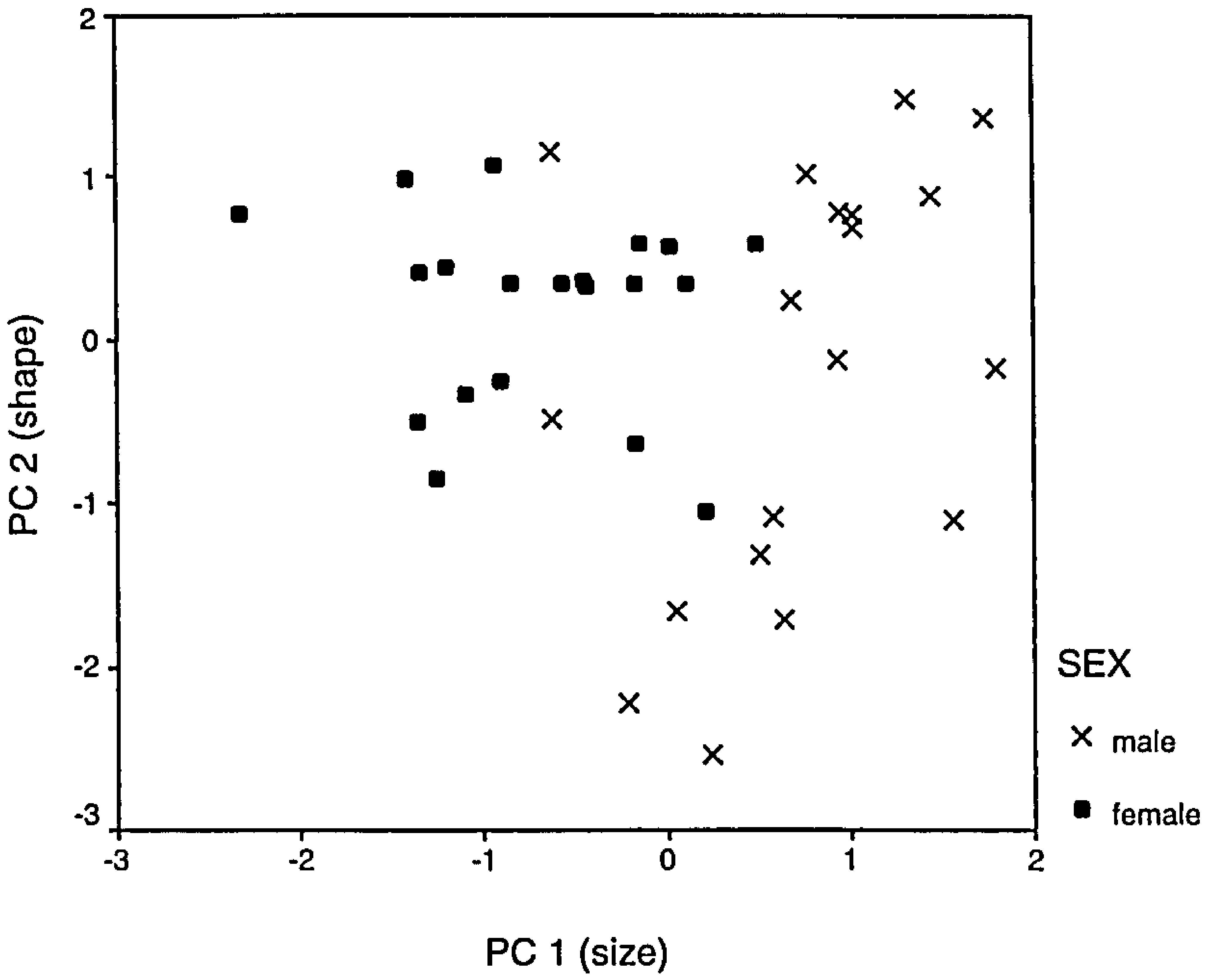


Figure 3.9. PCA results for modern lion sexual dimorphism.

Figure 3.9 shows quite a good separation of males and females on the first axis, but the second axis is largely mixed. Neither the second nor third axis showed any separation between the sexes. Therefore the relationship seen between dental and cranial measurements on axis 2 appears to be unrelated to sexual dimorphism, and is due to another, as yet unknown factor in the dataset.

3.3.4. Jaguar

All jaguar measurements showed significant sexual dimorphism except P^2B, P^3L, M^1B, POP, PC and C_iB. There were too few specimens without missing variables for PCA to be performed.

3.3.5. Snow leopard

Significant sexual dimorphism was found in all snow leopard variables except P^2B, P^3B, P^4Lm, M^1B, MB, PC, P_3B, and B/P_4. Principal Components Analysis was run but only 8 specimens (4 males, 4 females) were eligible, so the results lacked significance. The limited number of specimens did show a distinction between males and females when the PCA axes were plotted, but is likely that there would be an overlap between the sexes if more individuals were included.

3.3.6. Cheetah

The vast majority of cheetah variables showed no significant differences between the sexes. Only C^sL, P^3B, BL, PL, ZB, CB, C_iL, C_iB, P_3B and C-Cd were found to be significant at the 95% confidence interval. PCA was run on the cheetah data and 6 axes were produced, totalling 81.4% of the variation in the sample. Of these the first axis only contained 49.7% of the variation, suggesting that it was not just size that affects a cheetah population. However, when the axes were plotted despite a general trend for male cheetahs to be larger than females there was no separation of the sexes on any of the axes. Figure 3.10 shows axes 1 and 2.

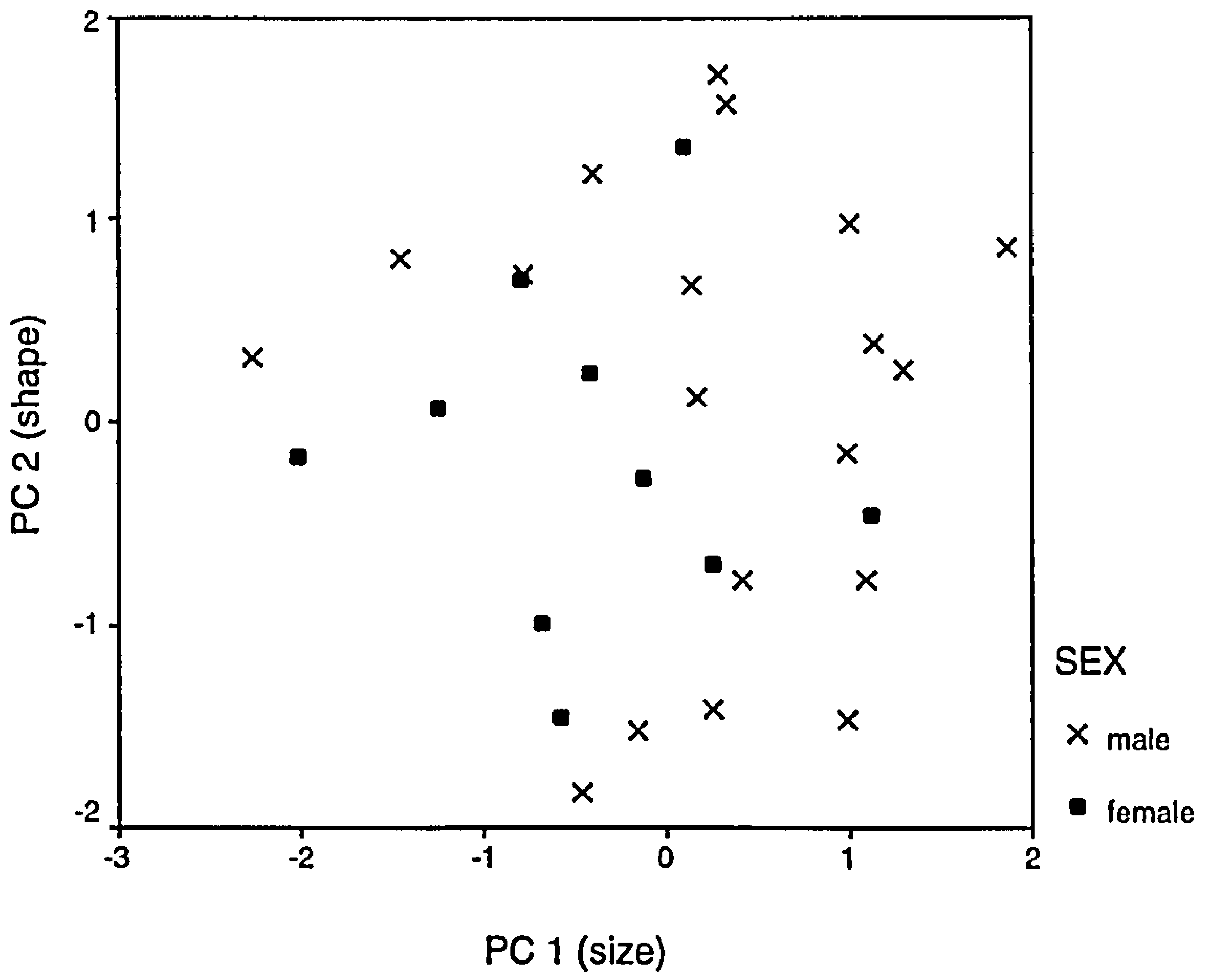


Figure 3.10. PCA results for modern cheetah sexual dimorphism.

3.3.7. Total sexual dimorphism

The total dimorphism for each species was calculated in two ways on all dental measurements: the first is between the medians of the males and females and the second is between the largest male and the smallest female to give a maximum dimorphism. The result of these calculations are shown in Table 3.15.

Measure-ment	**Cheetah**		**Lion**		**Leopard**		**Jaguar**		**Snow leopard**	
	Med	Max	Med	Max	Med	Max	Med	Max	Med	Max
C^sL	105	124	120	168	116	181	115	134	116	140
C^sB	105	123	114	164	112	173	117	136	115	130
P^2B	105	150			101	167	109	150	106	139
P^3L	101	116	108	140	108	161	108	129	111	131
P^3B	105	136	112	156	110	169	119	141	103	124
P^4L	102	112	109	128	107	147	110	128	105	122
P^4Ba	101	117	111	143	109	154	113	130	116	128
P^4Bbl	105	118	109	133	107	151	114	138	113	136
P^4Lp	101	119	106	132	108	154	108	129	109	123
P^4Lm	100	122	108	140	106	160	110	131	105	152
M^1B	104	129			105	152	101	174	109	125
C_iL	104	127	119	159	117	172	110	129	118	134
C_iB	106	129	121	160	115	171	117	151	108	137
P_3L	100	116	110	153	110	166	112	126	113	125
P_3B	102	116	108	151	111	180	119	145	110	128
P_4L	103	111	110	140	107	148	112	126		
P_4B	105	126	110	144	109	153			109	130
M_1L	104	112	109	134	106	152	108	132	113	125
M_1B	101	122	110	131	110	153	110	130	108	127

Table 3.15. Median and maximum sexual dimorphism in modern big cat species (calculated as a percentage). Abbreviations explained in Chapter 2, except: Med = median, Max = maximum.

The results in Table 3.15 show that the cheetah has the lowest levels of dimorphism, with the maximum difference below 30% except for the P^2Ba. The upper and lower canine measurements show the greatest median dimorphism in all species, although the P^3B is jaguars is also very high. The greatest median dimorphism is shown in lion C^sL with a 20% difference between males and females. The level of dimorphism between the median of males and females was less than 20% for all species, but the maximum dimorphism was much greater (up to 80%). Geographical variation has increased this slightly, especially in the leopards, but this makes the outcome more (rather than less) applicable to fossil species, as a mixture of specimens from different areas and times will probably have a similar effect. These results have provided maximum parameters for variation within modern species, unfortunately they are not discrete enough to confidently assign sex or species to the fossil material. However they are of use, as any material which falls outside these extremes is likely to be a different species.

3.3.8. Discussion

One of the interesting results of this review is the discovery that in all species (other than the lion) the P^2B and M^1B do not appear to scale in the same way as all the other measurements. This means that a large cat may have a small M^1 and vice versa. These two teeth are thought to be vestigial and in some specimens they fail to develop altogether, so it interesting to see that they do not seem to be controlled in the same way as the other dental measurements. In addition, although sexual dimorphism is significant for the majority of measurements for the majority of cats, there was no absolute separation of males and females for any of the variables studied, although the upper and lower canines have been shown to be the most dimorphic teeth. Therefore none of the measurements can be used to definitively sex fossil material. However the total range of sexual dimorphism can be used to assign parameters of variation in the fossils beyond which a mixing of species may be suspected.

3.4. AGE RELATED VARIATION

Mammals change size throughout their lives. The changes from birth to sexual maturity are the most obvious and are marked by an increase in the weight and size of the individuals. However, because bone is a living tissue that is constantly being remodelled, subtler changes can also take place. Much of this appears to be related to the deposition of bone in particular areas such as the zygomatic arches and nuchal crest resulting in an overall increase in width as the animals age (Pocock, 1939). When studying fossil specimens it would be helpful to know which measurements are affected by age and which remain constant throughout the life of the cat. For example, is a mandible with a large BP/4 (breadth beneath the P_4) indicative of a large cat or simply an older animal? To answer this question an attempt has been made to quantify the changes that take place in the skulls of big cats as they age.

It is predicted that only cranial variables will alter with age, as the size of an individuals teeth are fixed as soon as the enamel has been deposited. However, teeth can be altered through wear as the animals age so heavily worn specimens were excluded from the analysis as the measurements would not be accurate. The dataset has therefore already selected for teeth that have not altered with age and it is thus expected that cranial changes will have occurred between the two age groups, but dental changes will not.

3.4.1. Method

The ageing method used for all cats in this study begins with a sub-adult category (18 – 24 months), so much of the rapid growth associated with juveniles has been completed by this stage. The method used was developed by Smuts *et al* (1978) on modern lions and the age groups will henceforth be referred to as Smuts categories or SCs. These categories divide animals into six broad age ranges on the basis of tooth wear and can be used to age fossil specimens. The categories and their approximate ages are given in Table 3.16.

Smuts category	Description	Relative age (years)
1	Canines just below full eruption	1.5 – 2 ~~years~~
2	Canines fully erupted, teeth seldom worn	2 – 3 ~~years~~
3	First wear on incisor canine and some premolar tips. Distal enamel ridge of canines may be chipped	3 – 4 ~~years~~
4	Canine and incisor wear apparent and high tips of P^3 and P_4. Distal ridges of canines chipped and worn	5 – 6 ~~years~~
5	All teeth show wear. I_1 & I^1 pulp chamber exposed. Distal ridge of canines worn flat	7 – 9 ~~years~~
6	Conspicuous wear and breakage. Incisors worn to stumps with exposed pulp. All cusps of P^3 & P_4 worn	10 – 14+ ~~years~~

Table 3.16. Age categories for modern lions based on tooth wear patterns (from Smuts *et al*, 1978).

It has been assumed for the purpose of this study that wear stages are comparable across all big cat species. Whilst some differences may exist between taxa, the morphology of the dentition is broadly similar, so tooth wear changes are likely to be consistent within species, even if the relative age categories are slightly higher or lower than in other cats. The greatest changes are likely to have occurred between young and old cats so the differences between these two groups were tested using the Mann-Whitney U test. There were fewer animals in the very young and very old categories than for prime individuals. Therefore SC1 and SC2 cats were combined to form a 'young' age group and SC5 and SC6 cats were amalgamated to form an 'old' group. This, in effect, led to the comparison of cats below 3 years of age with those over 7 years of age. These groups may underestimate the actual differences between ages as changes occurring between SC1 and SC2 are likely to be the greatest in terms of the animals reaching their mature size. A diagram depicting the growth of a male tiger cub from birth to 4 years of age is shown in Figure 3.11. This shows that some increase in size takes place between the ages of two and four years, but the majority of growth has been completed by 24 months.

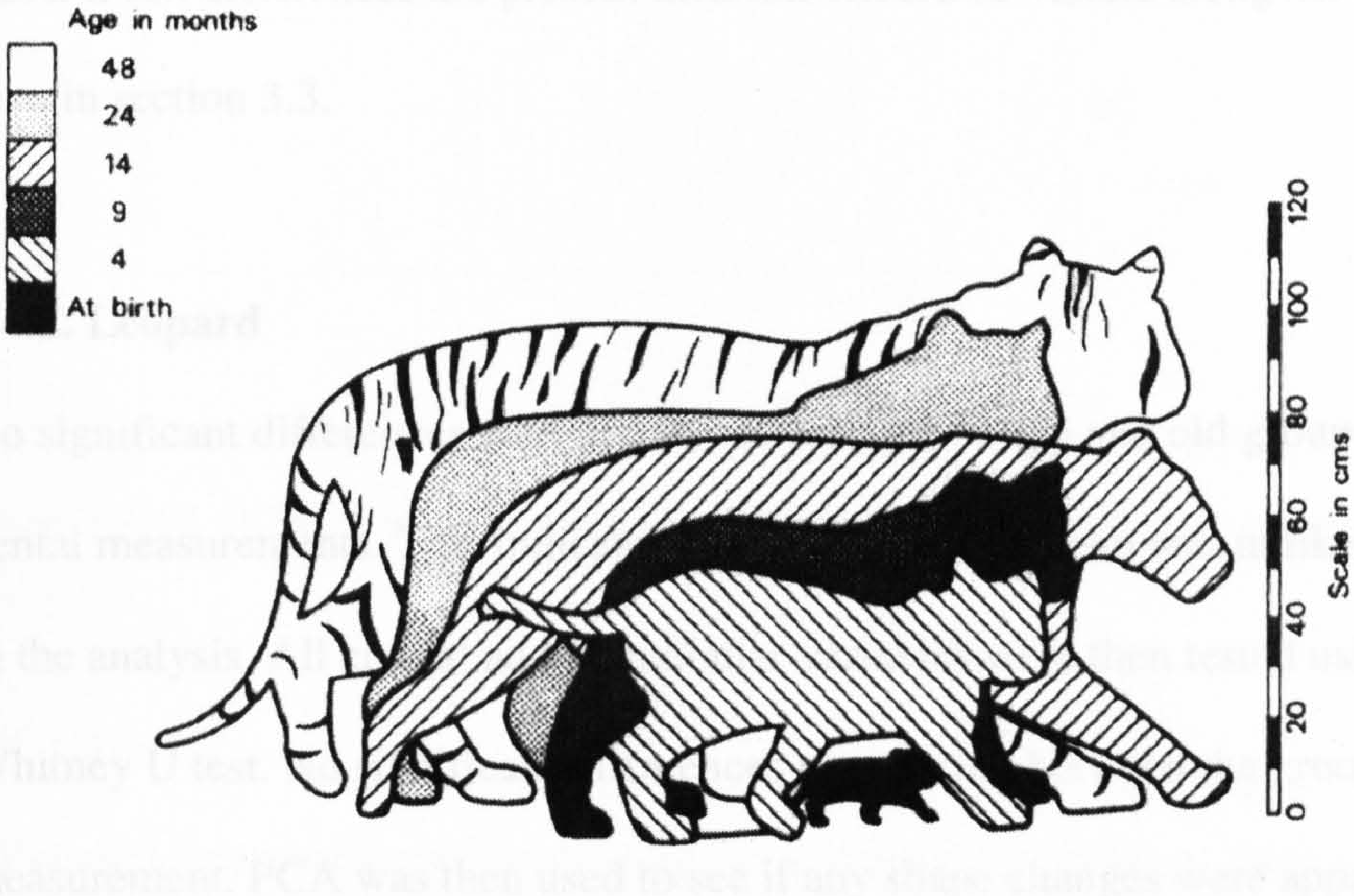


Figure 3.11. Growth of a male tiger cub, from birth to 4 years (from Sankhala, 1978).

Only samples of lions and leopards were large enough to use in this analysis and the sexes were pooled so that unsexed individuals could be included. Both lions and leopards are sexually dimorphic and it also appears that females may mature earlier than males, since body mass data for wild lions appear to show that females reach an asymptote at approximately 4 years of age whereas male body weight does not become asymptotic until they are approximately 7 years old (Smuts, 1982). This pattern of faster maturity in females has been noted in several other carnivore species such as wild cats (Viscioso & Rebollo, 1994) and polar bears (Kingsley, 1979). It is recognised that an imbalance of the sexes in each sample could produce significant differences that were purely due to sexual dimorphism. To test for the effects of sexual dimorphism four tooth measurements were included in the dataset as well as all cranial variables. These were the length and breadth measurements of the upper and lower canines for each species, as these have been shown to be the most sexually dimorphic teeth (Section 3.3). Unlike bones, teeth do not alter with age, so if a significant difference is found between the two age groups then it is likely that sexual dimorphism is a factor and that groups are not evenly mixed. To further test for sexual dimorphism, all specimens were analysed with PCA. If sex differences are present then this should be visible along the x-axis (PC 1) as seen in section 3.3.

3.4.2. Leopard

No significant differences were found between the young and old groups on the basis of dental measurements. This indicated that sexual dimorphism was unlikely to be a factor in the analysis. All cranial and mandibular variables were then tested using the Mann-Whitney U test. No significant differences were found between the groups for any measurement. PCA was then used to see if any shape changes were apparent between the two groups. Two axes were produced, the first was high and positive and represents size, this contained 76.2% of the variation in the sample. The second axis encompassed 9.7% of the variation and appeared be a relationship between a high, positive postorbital constriction (PC) and a negative HPC (height of the coronoid process). These axes are plotted in Figure 3.12.

Figure 3.12 shows a complete mix of specimens, with no partitioning of specimens by age on either axis. Therefore it is concluded that age-related variation does not significantly affect the size of modern leopards in this dataset. It is possible that leopards may mature earlier than SC2 and that a greater sample of SC1 cats may show more significant results.

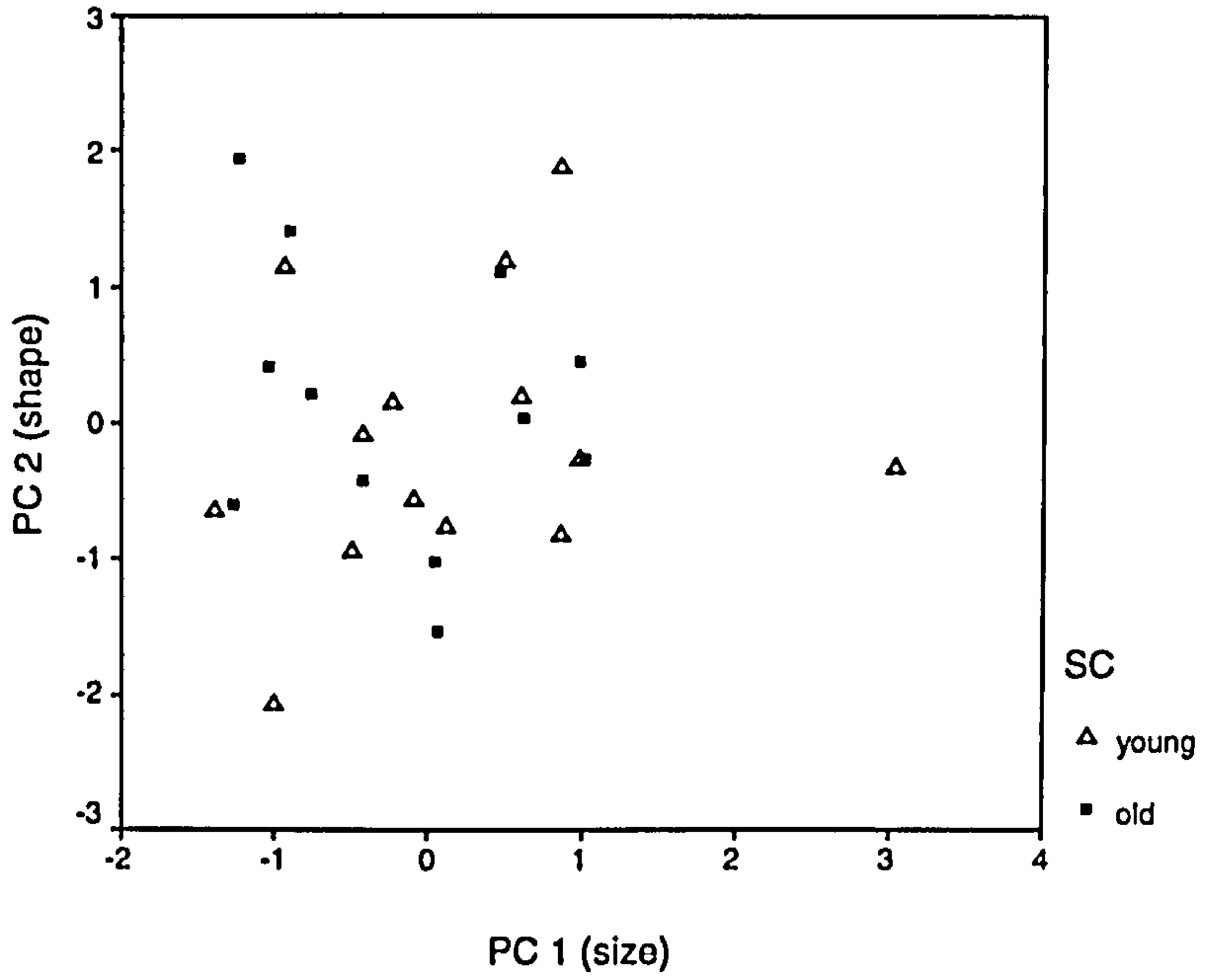


Figure 3.12. PCA of modern leopards, divided into two age categories.

3.4.3. Lion

The canine measurements for modern lions showed a significant difference between young cats and old cats for $C^{S}B$. This measurement is closely associated with sexual dimorphism in the sample. However, the P-value for the Mann-Whitney U test was 0.0465, suggesting that there is only a weakly significant difference between the two. Analysis of the medians showed that the older cats had a higher median than the young individuals (18.4 vs. 16.1 respectively).

PCA was run on all tooth measurements to test the possibility that the differences seen between young and old lions were purely due to the sexual dimorphism in the sample. This produced two axes of variation, containing 75.3% and 7.1% respectively. These are plotted in Figure 3.13. This graph shows that no separation can be made between groups on either the size or shape axis and there are roughly equal numbers of larger (?male) cats in each group, although there are fewer small (?female) old cats. This bias has increased the median for the older age category, which exaggerates size differences between the two groups.

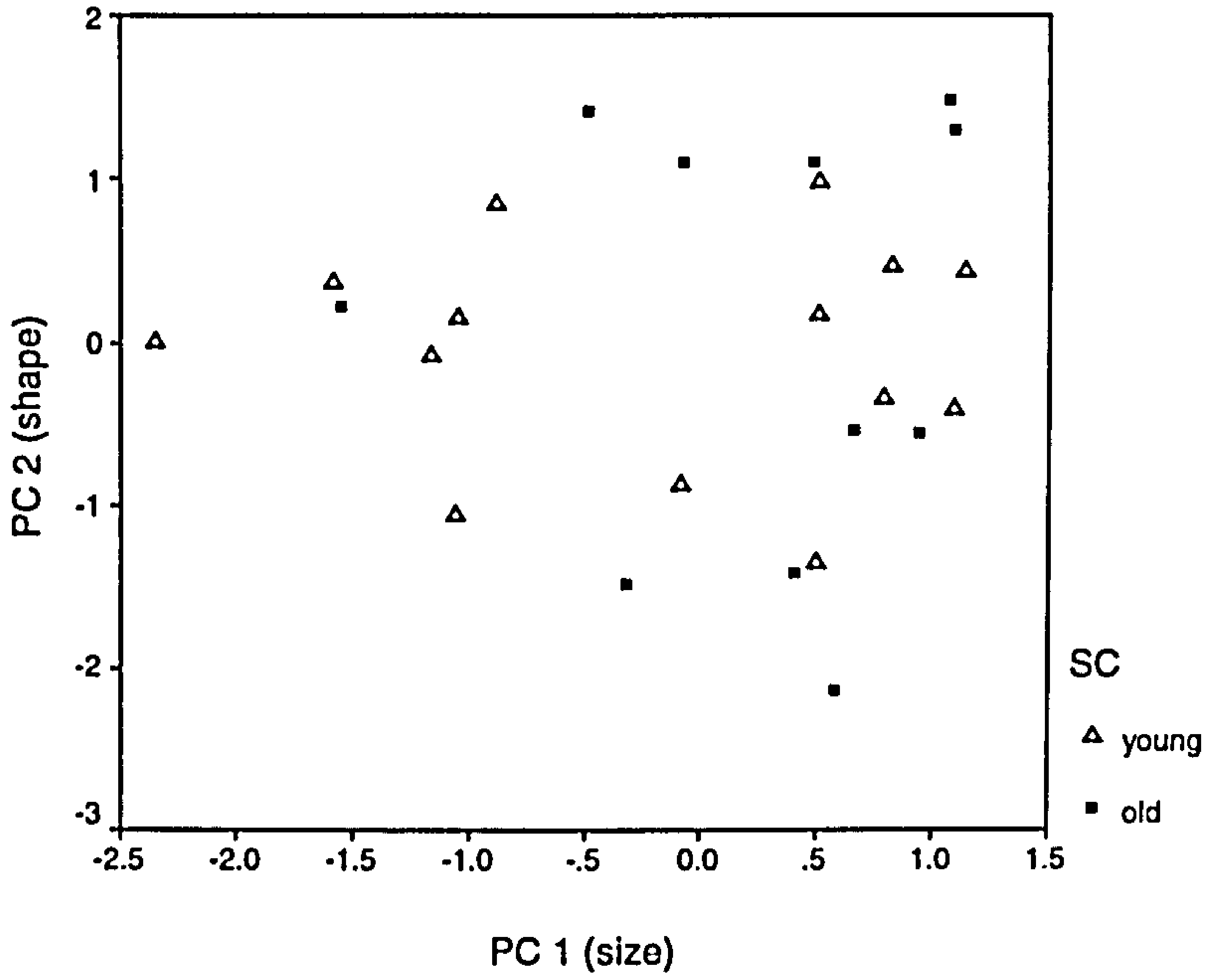


Figure 3.13. PCA results for modern lion dental variables plotted by age categories.

Measurements	Young n	Old n	P.	P <0.05
BL	17	14	0.0001	***
ZB	17	14	0.0000	***
PL	19	14	0.0001	***
RB	19	14	0.0001	***
MB	18	14	0.0003	***
IO	19	14	0.0000	***
POP	18	14	0.0000	***
POC	15	14	0.0078	**
CB	16	12	0.1794	n.s.
C-Cd	17	13	0.0000	***
HPC	17	13	0.0000	***
P_3-M_1	17	13	0.1944	n.s.
Depth A	17	13	0.4140	n.s.
Depth P	16	13	0.0001	***
B/P_4	17	13	0.0011	**

Table 3.17. Mann-Whitney U test results for modern lions divided into two age categories. Abbreviations explained in Tables 2.5 and 2.6. ** = highly significant, *** = very highly significant.

The analysis of cranial measurements was still conducted, but the fact that the dataset was slightly biased against smaller cats in the older age category was borne in mind. Despite this bias, not all cranial and mandibular measurements proved to be significantly different (Table 3.17) and CB, $P_3 - M_1$, and Depth A were found to be similar in both age categories. All other measurements were highly or very highly significantly different.

The non-significant results are the most interesting, as you would expect to find a difference in all measurements, especially with a slightly biased dataset. In fact, studying the medians of each group, the older age category is larger than the younger animals for all variables except anterior depth of the mandible between the lower canine and the P_3 (Depth A). Examination of the medians showed that in this case the young sample had deeper mandibles than the old category. This may appear counter-intuitive until it is put into its context. SC1 is when the canines are just below full eruption and SC2 is when the canine has just erupted. It is likely that remodelling will occur in the area immediately adjacent to the lower canine after the eruption is completed, as it is a large tooth with a substantial root and will have been encrypted in this area of the mandible for some time. This is an important finding as it indicates that reliance on such characteristics as the ratio between anterior and posterior depth of the mandible as a defining feature of particular species may be flawed, if specimens measured are below 4 years of age, [The designation of *Jansofelis vaufreyi* is an example of this (Bonifay, 1971; Hemmer 1972a)]. In a larger study of sexed material this distinction might actually be more pronounced as Figure 3.13 shows that there are more small (?female) cats in the 'young' age category which will have reduced the median for this group, with equally balanced samples the difference between old and young cats might be even greater.

PCA was run again using all cranial and mandibular variables. This analysis produced only one axis, containing 82.3% of the variation. All variables were high and positive so this axis is purely based on size differences within the sample. This suggests that no shape changes take place between these two ages. It is interesting to note that those variables which were shown to be non-significant using the Mann-Whitney U tests are those which have the lowest extraction values on axis 1. PCA was then forced to calculate two axes, the second of which had an eigenvalue of 0.853. Although this is below the usual cut off point of 1.0, it is still quite high. This axis contained 6.1% of the variation within the sample. The calculated component matrix for these analyses is shown in Table 3.18, and the results are plotted in Figure 3.14.

Variable	PC 1	PC 2
BL	0.979	-0.045
PL	0.959	0.112
RB	0.973	0.096
MB	0.933	0.073
ZB	0.947	-0.178
IO	0.920	-0.240
POP	0.934	-0.279
POC	0.763	0.037
C-Cd	0.982	-0.057
HPC	0.970	-0.208
$P_3 - M_1$	0.656	0.657
DEPTHA	0.806	0.405
DEPTHP	0.927	-0.116
$BP/_4$	0.898	0.004

Table 3.18. Component matrix for PCA of modern lions.

Figure 3.14 shows that although there is a small overlap between the smallest old lions and the largest young lions on PC 1, for the most part all cranial dimensions are larger in the older cats. If sexual dimorphism were solely responsible for the significant differences between the two groups, the expected distribution of cats along the x axis would be similar, as seen in Figure 3.13. It is obvious that some partitioning has taken place between the two groups, and that older cats generally have larger crania than their younger conspecifics.

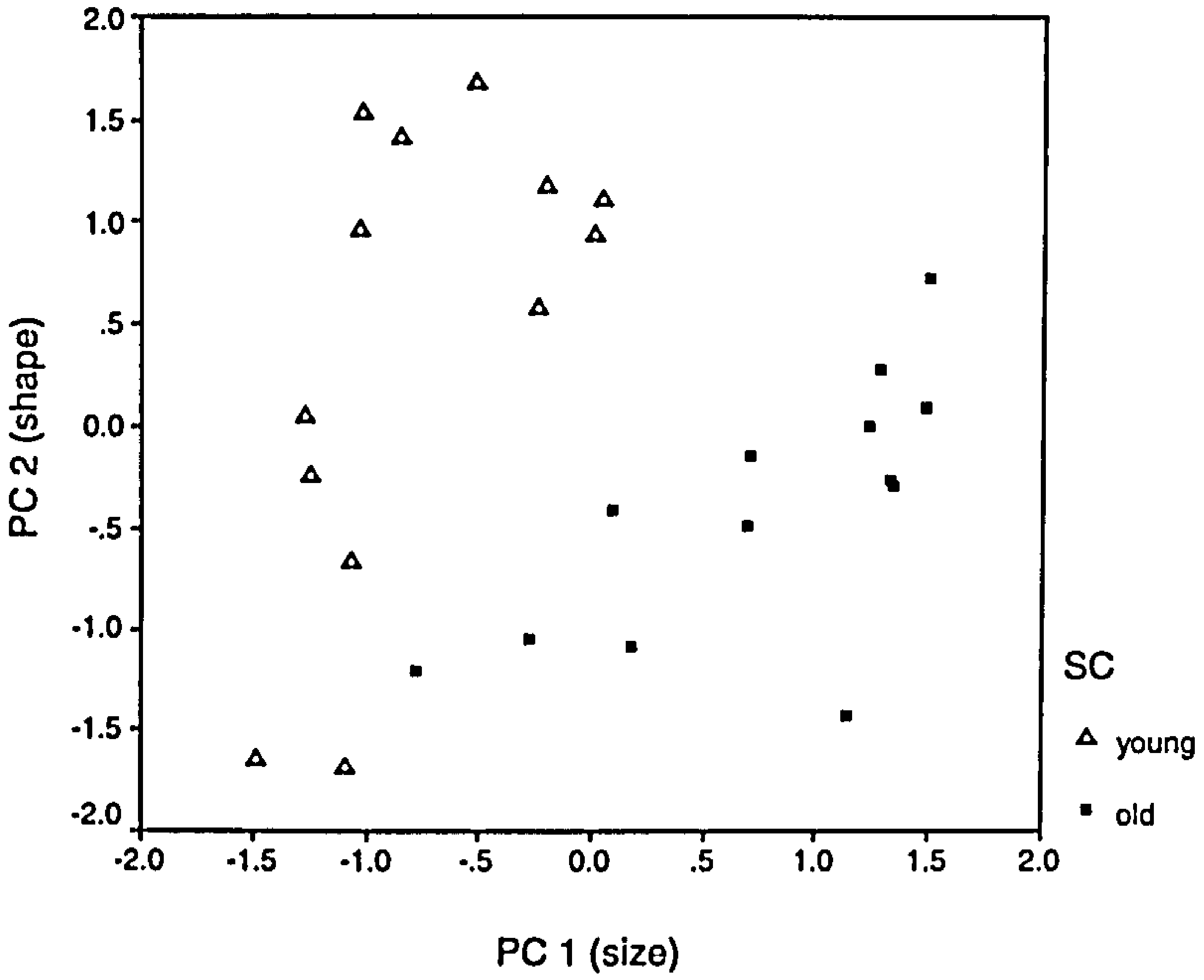


Figure 3.14. PCA results for modern lion cranial and mandibular measurements, divided into age categories.

3.4.4. Discussion

The pooling of the sexes in the above samples may have led to some bias in the dataset, but interesting results have still been obtained. Although mixing the sexes is not ideal when trying to construct testable hypotheses on modern data, it is a much more realistic situation for someone who is testing data obtained from fossil specimens. This analysis has shown that its still possible to recover interpretable results from mixed samples and is therefore a more relevant application to the fossil material than many more refined studies.

A larger sample would be required to test these results further, but it appears that older lions, regardless of sex, are larger than younger animals. In contrast, the leopard, an animal that is solitary and slightly less sexually dimorphic than the lion appears to show no significant increase in size as it ages. It is possible that the leopard matures faster and that the adult size is reached fairly early on in life, whereas the lion is social and there may be some advantage in remaining young and within the pride for as long as possible. It would be interesting to see if this could be proven using morphometrics, but a larger, sexed sample is required before this can be tested.

3.5. MUSEUM COLLECTIONS

All aspects of variation found in the modern samples are affected by museum collection policies (or lack of them). The questions to be answered are what types of bias are ~~be~~ present in the sample and can they be identified?

The majority of museums have collected specimens on an ad-hoc basis. Only very large national institutions such as the British Museum (Natural History) or the United States National Museum (Washington D.C.), had specific collection policies where expeditions were mounted to bring back specimens from particular geographic areas. Most specimens in smaller collections are donated by local people or are collected because a member of staff has a particular research interest in the area. Many of these specimens lack provenance and sex data and are often damaged.

It is important to realise that in the majority of cases animals were not randomly selected. People who are willing to pay to hunt animals are often interested in obtaining the largest specimens possible, which are likely to be males. Reports of big game hunting in the early 20th Century show that prime males of many different species were preferentially selected. In a report of gorilla hunting Merfield (1957) records the disappointment of a client who shot a specimen only to discover it was a young male rather than the intended silverback. A similar story is told of elephant hunting in East

Africa, where only cows and immature elephants were encountered, when the intention was to shoot a large bull (Tilman, 1937). This suggests that even if young animals were shot by accident they were unlikely to be the specimens brought back from the field to display to visitors or to reach museum collections. It seems likely that having shot several animals a hunter would select the 'best' specimens – those with unchipped teeth for example – to transport home rather than taking them all. Cosmetic changes could be made to improve a poor specimen - a tiger skull in Manchester Museum (TN4622) was donated by the local MP and has had three missing canines replaced with bone carved to look like teeth. They are so large that they prevent the jaws from closing, but look very impressive from a distance. M^1s have also been found glued in the place of missing incisors.

Shooting females with young was also frowned upon. In East Africa licences were granted for elephant hunting on the understanding that only mature males would be taken (Tilman, 1937). Stephenson-Hamilton (1954:170) states that female lions with cubs should be shot if they approach the hunter 'however lamentable it may be to have to do so'. It was taboo in some Indian states to shoot tigresses although 'Many a time a hunter has shot a tigress carrying cubs through ignorance of her sex and in the excitement of the moment' (Sankhala, 1978:169).

These sources suggest that specimens that reached museums through the hands of big game hunters are likely to be larger than average, male animals in their prime. This is important as it indicates that the entire dataset may be skewed in favour of these animals, which would then under-represent small or female cats.

3.5.1. Method

In order to test the hypothesis that the biases outlined above have affected the dataset all specimens of each species were plotted by Smuts Categories. All museum collections were pooled for this study. If collections are biased then it is predicted that there will be a marked peak in the number of specimens in SC3 and SC4 (3-6 years) when animals are in their prime. A completely unbiased and truly representative sample of the population should show a decline from SC1 to SC6 as animals die, as there would be far fewer very old cats in the population compared to subadults. As the SC age scale does not start until 18 months, juvenile mortality is not included in this estimate. Figure 3.15 shows a possible distribution of a completely unbiased sample.

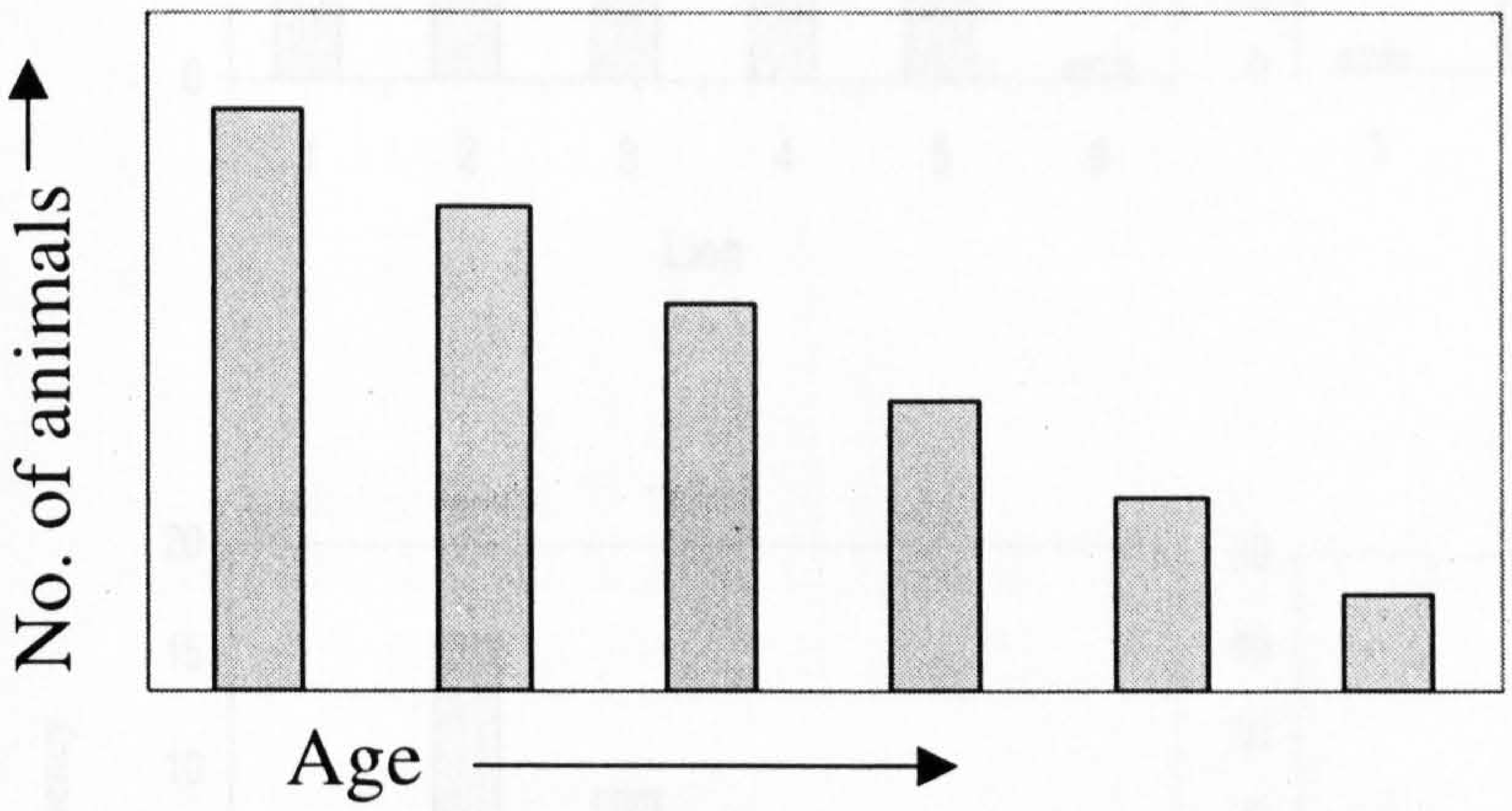


Figure 3.15. Idealised representation of the age structure in a truly unbiased population.

This graph can be compared to those in Figure 3.16, which show the real distribution of age classes within each species sample. As can be seen, those cats for which the largest samples are available show distinct peaks at SC3. This is particularly marked in lions and can probably be explained in terms of mane development as it is at SC3 and SC4 that the mane is at its peak of appearance and individuals become nomadic or pride males, whereas subadult females are difficult to distinguish from adult females from 3 years onwards (Smuts *et al*, 1978). By the time males reach SC6 the mane has become very straggly and is unlikely to interest a hunter (Schaller, 1972). Tigers come closest to the idealised distribution, although there is still a lack of SC1 cats, and this is a fairly small sample (n = 39). The peak in the distribution of lions compared to other cats may be due to the solitary habits of all the other species. Leopards were seen so infrequently in the bush that that Stephenson-Hamilton (1954:190) 'endeavoured to shoot every leopard I happened to see', suggesting that less of a sex bias operated when shooting the more cryptic species.

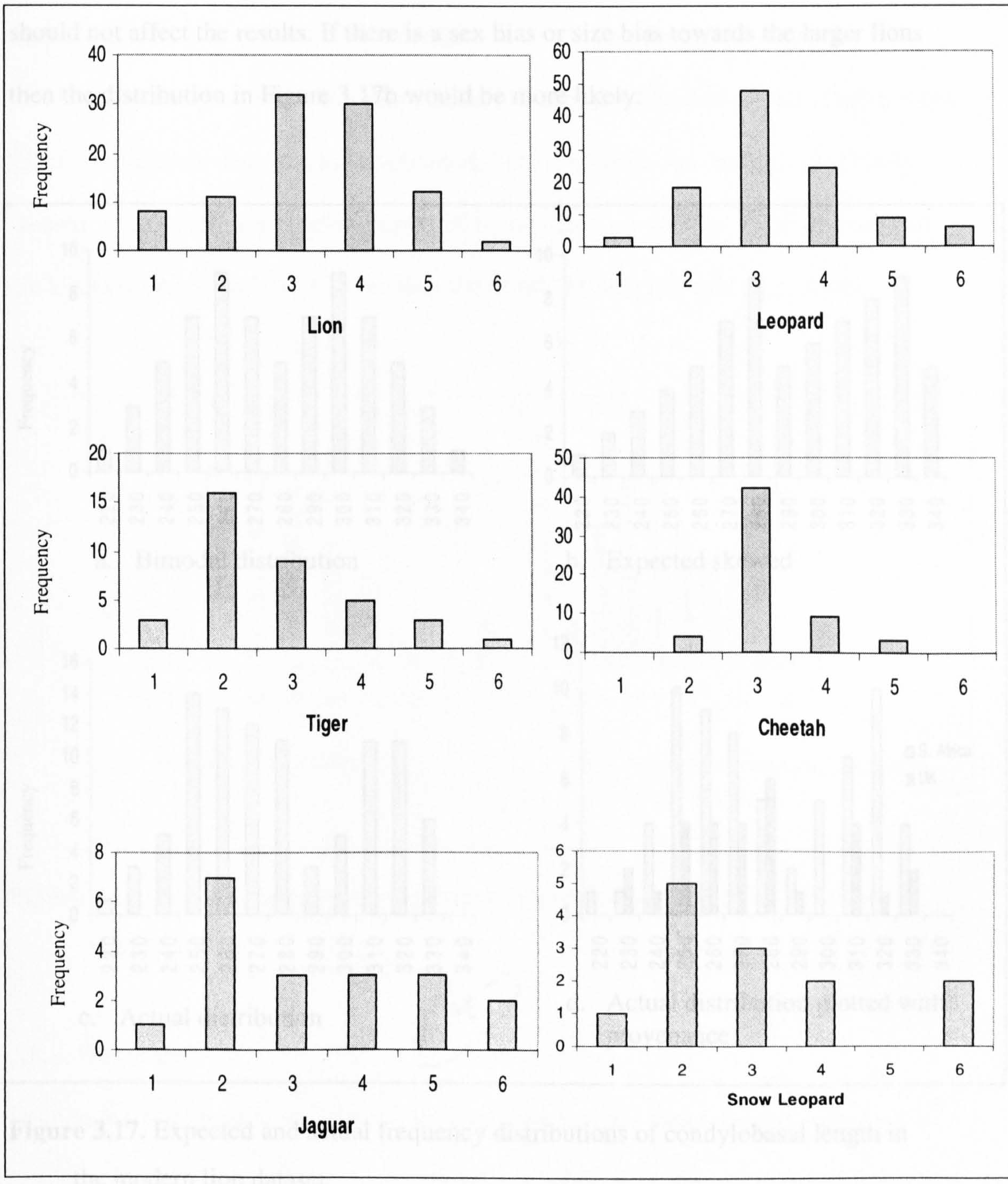
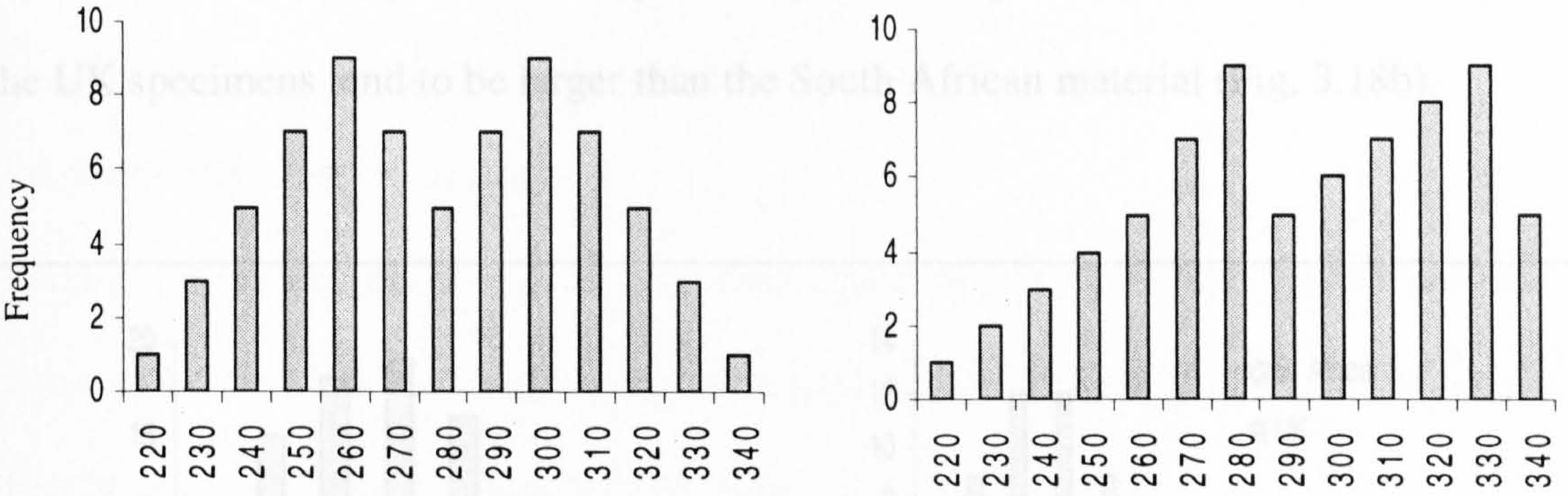


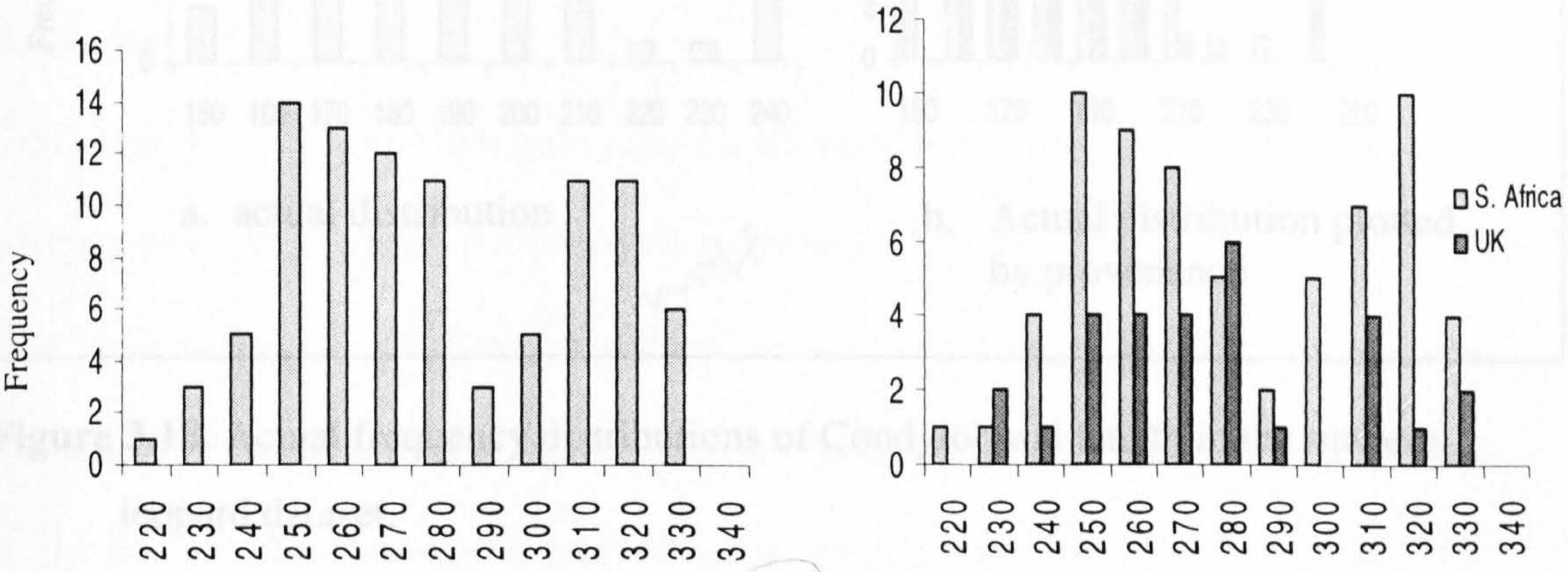
Figure 3.16. Frequency plots of all specimens in the modern dataset, using Smuts Categories as the x-axis.

To test the idea of a sex bias within the sample condylobasal lengths (BL) for all lion specimens were frequency plotted, as this measurement appears to be a good indicator of overall size (Turner & O'Regan, in review). As lions are known to be sexually dimorphic a bimodal distribution such as that seen in Figure 3.17a would be expected. Sex of all specimens is not known, but they must all be either male or female so this should not affect the results. If there is a sex bias or size bias towards the larger lions then the distribution in Figure 3.17b would be more likely.



a. Bimodal distribution

b. Expected skewed



c. Actual distribution

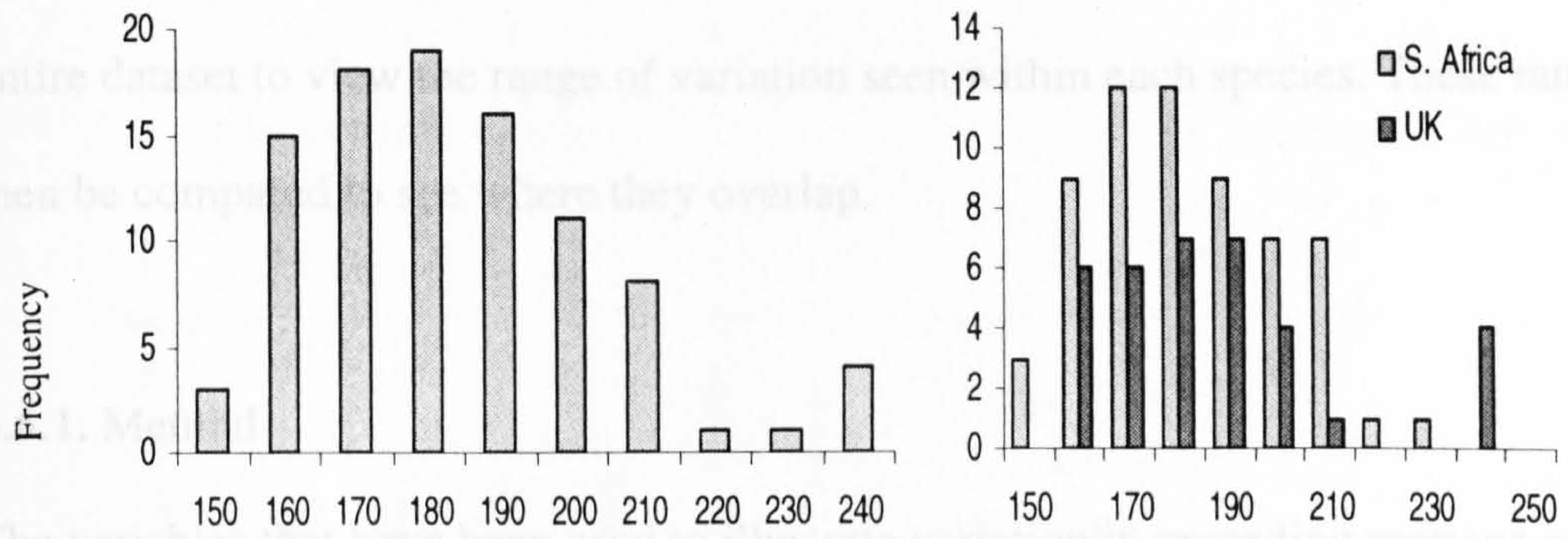
mik?

d. Actual distribution plotted with provenance

Figure 3.17. Expected and actual frequency distributions of condylobasal length in the modern lion dataset.

Figure 3.17c shows the actual distribution of lion specimens which is bimodal and skewed towards smaller cats. To see if this was an artefact of provenance the specimens were plotted by museum (Fig. 3.17d). It was hypothesised that specimens from South Africa would show more of a 'normal bimodal' distribution as they were more likely to have been randomly collected than those exported to the UK. However, as can be seen from the graph, both groups show a fairly even distribution of sizes.

Leopard specimens were also plotted to check for evidence of bias (Figure 3.18). These graphs show that leopard condylobasal distribution in the dataset is positively skewed. When these specimens are plotted by museum provenance it can be seen that the UK specimens tend to be larger than the South African material (Fig. 3.18b).



a. actual distribution

b. Actual distribution plotted by provenance

Figure 3.18. Actual frequency distributions of Condylobasal length in the modern leopard dataset.

3.5.2. Discussion

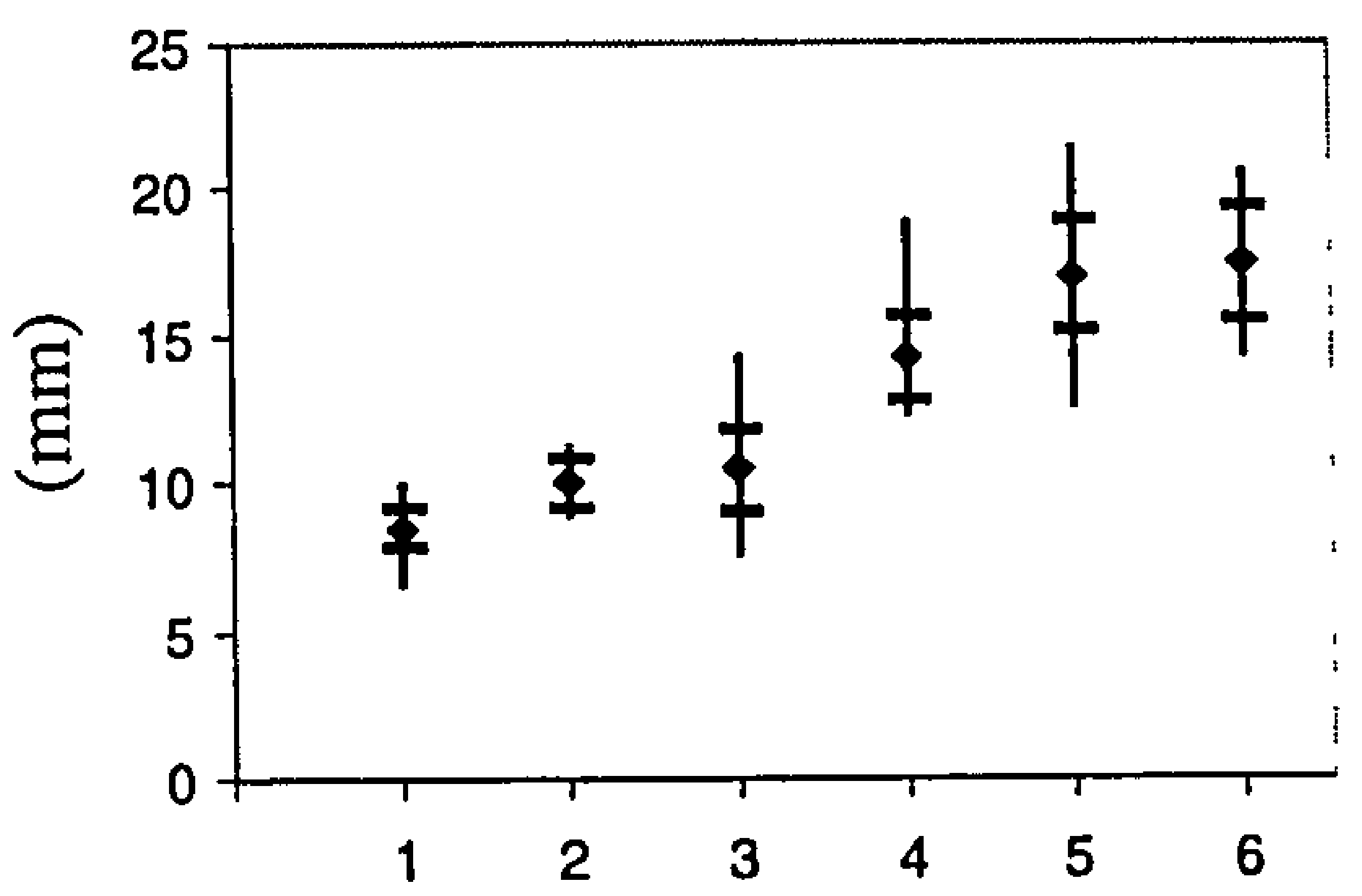
Despite fears of museum collection bias it appears that the data have not been greatly affected. Animals are more likely to appear in collections if they are in their prime (SC3 and SC4) with a bias against older and younger animals. There appears to be a fairly even size distribution in the lion dataset indicating that the full size range of the animals have been sampled, even if the age categories are biased. Likewise the full size range of leopard crania appears to have been sampled, but in this case there does seem to be a bias towards the larger specimens. However, the UK museum leopards are mainly East and West African in origin, so although there appears to be a slight bias within the sample, it is probably as much to do with geographic variation as it is to do with preferential selection of the larger cats. It is therefore concluded that this dataset represents a sample of big cats that has not been significantly biased by the activities of collectors.

3.6. INTRASPECIFIC VARIATION

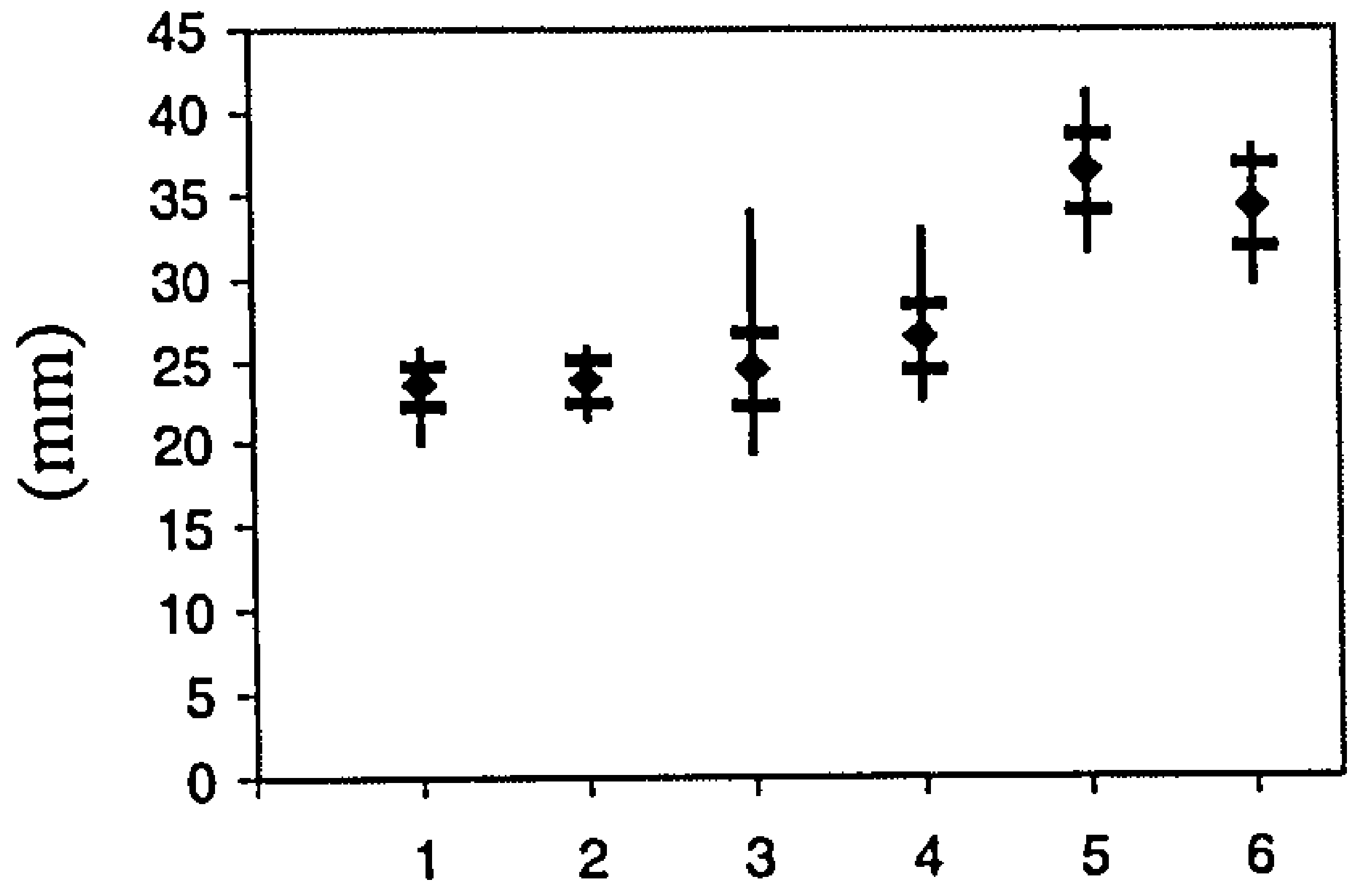
Variation at the species level is an important aspect of this study. This section uses the entire dataset to view the range of variation seen within each species. These ranges can then be compared to see where they overlap.

3.6.1. Method

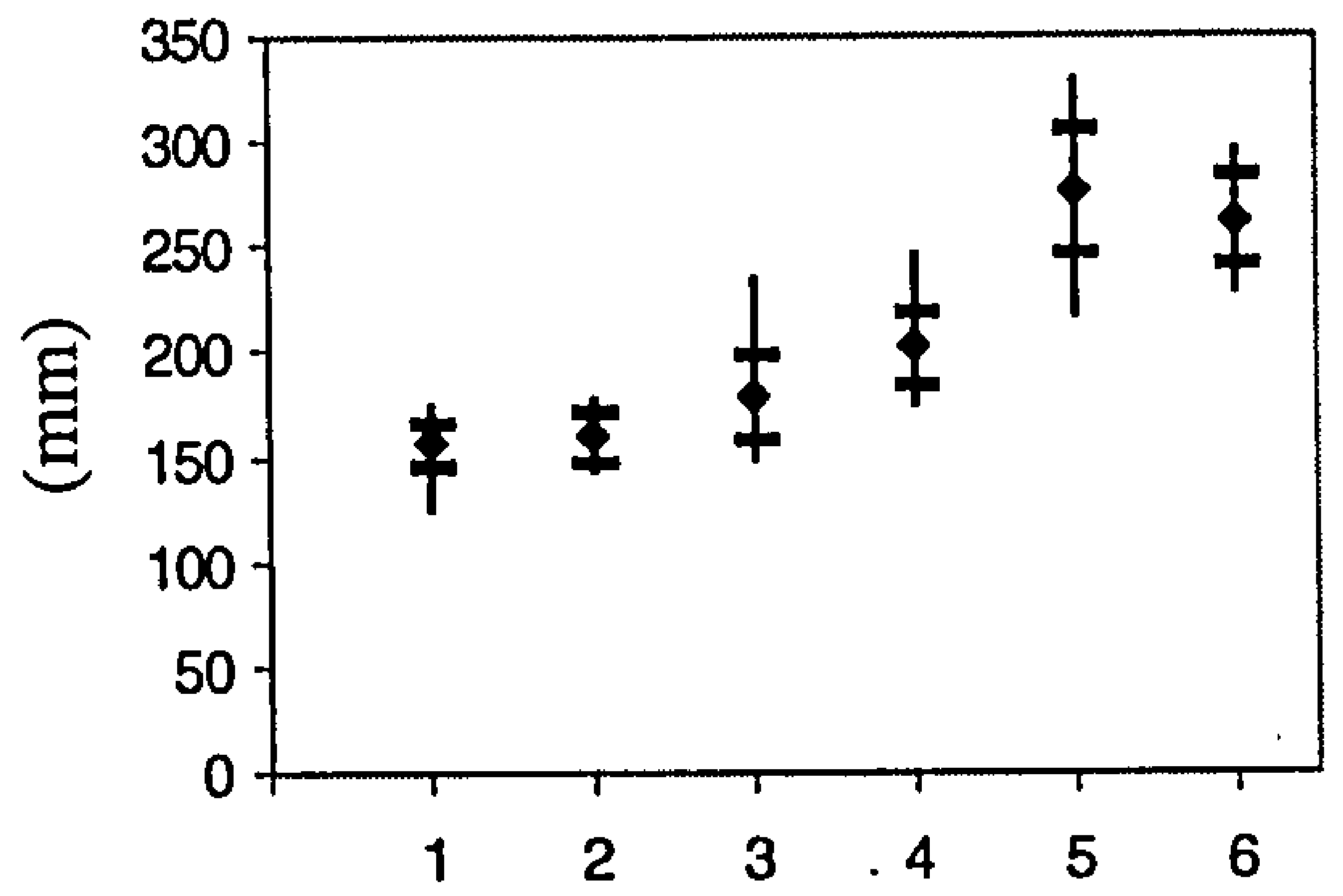
The variables that have been used to illustrate variation in preceding sections of this chapter were boxplotted for all species, these were C^SB, P^4L, BL, ZB, M_1L and C-Cd. The plots in Figure 3.19 show a considerable overlap of ranges for all cats and for all variables. It can be seen that for all variables there is a distinct step up from the leopard to the lion and that the smaller cats are all of a similar size. This observation is consistent with the theory of competitive exclusion that suggests two animals with exactly the same niche cannot co-exist. However, niche differentiation can simply mean that one is diurnal and another nocturnal. Although this is an interesting observation it is difficult to test under natural conditions (Krebs, 2001; Schoener, 1989).



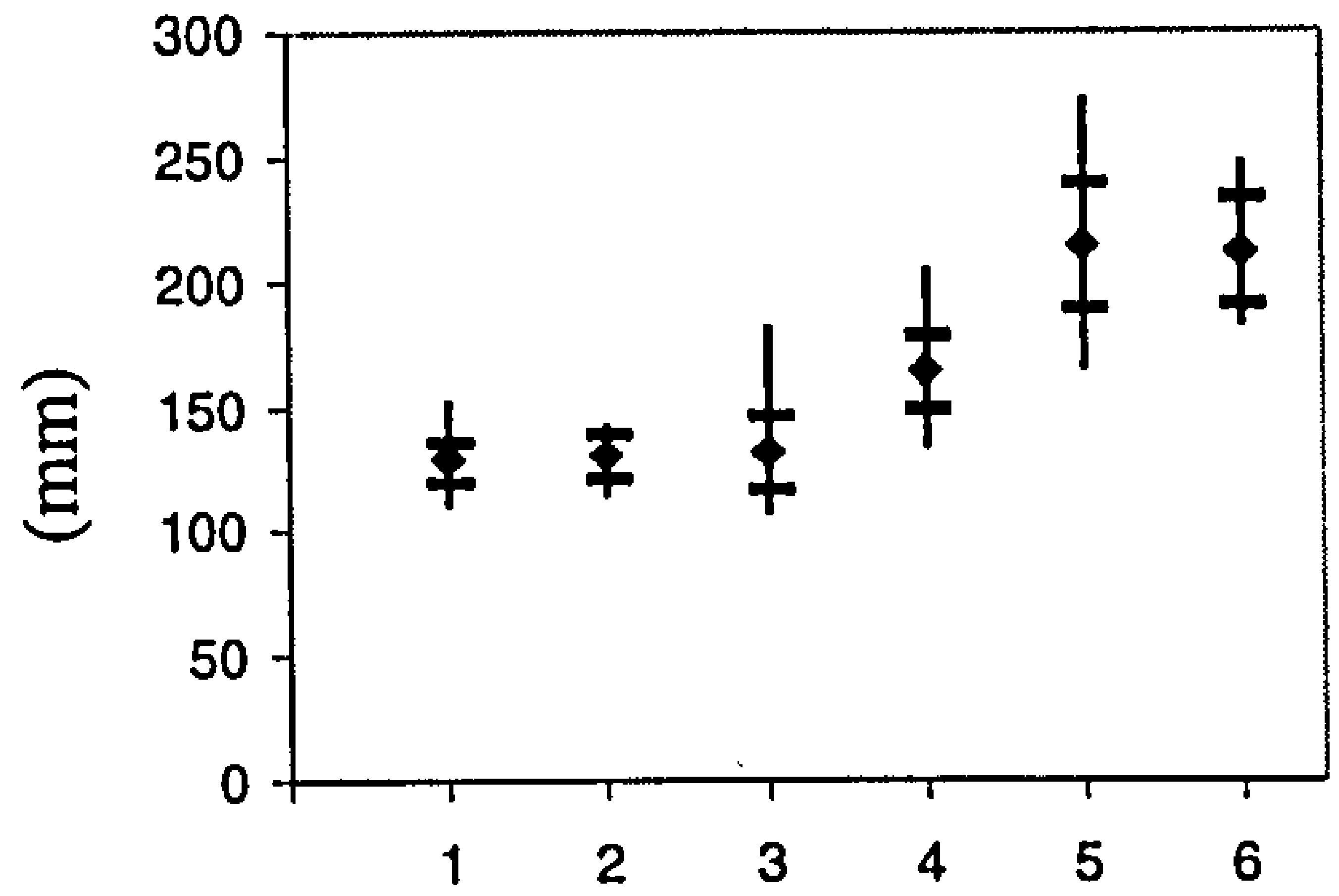
A. Upper Canine Breadth



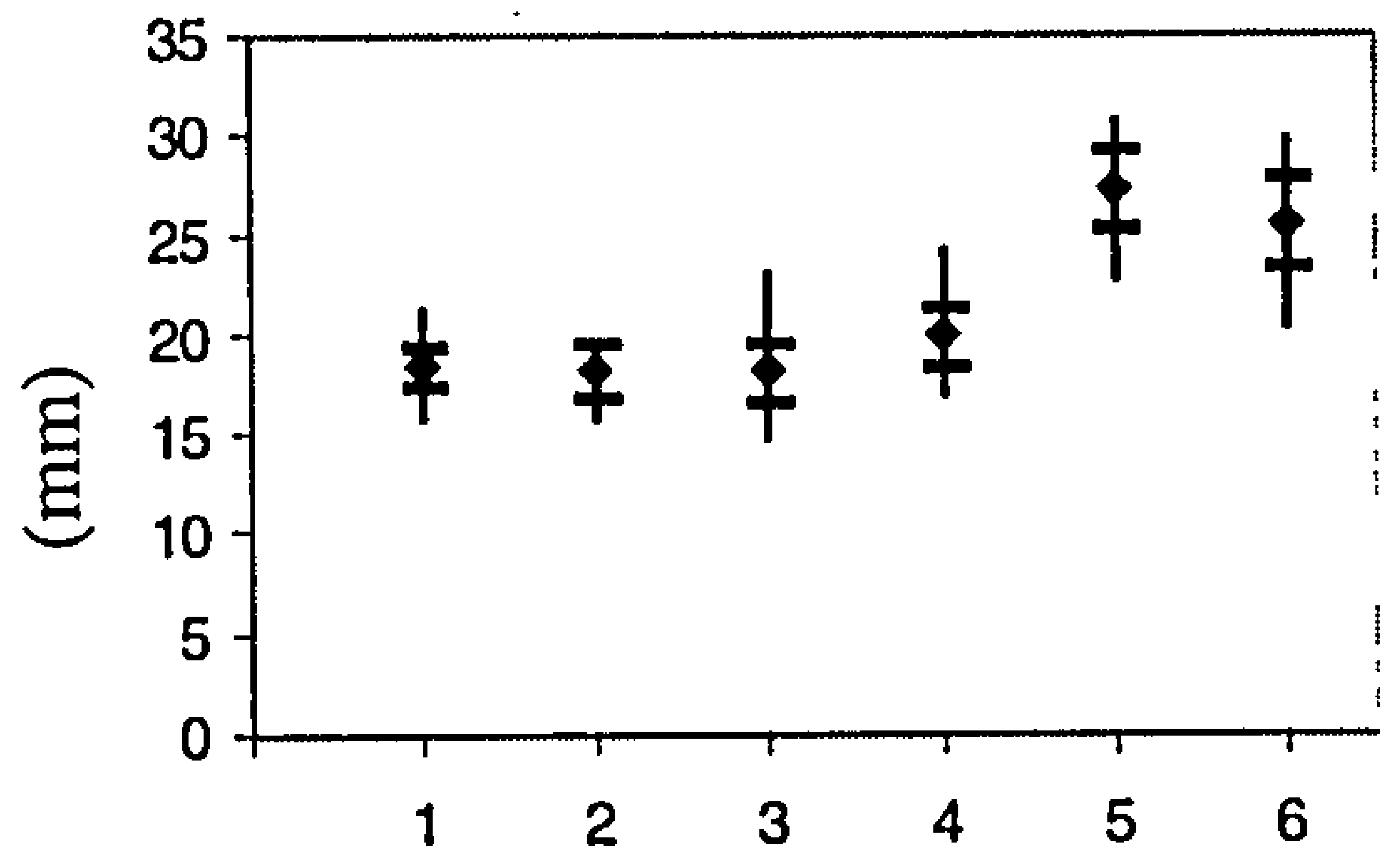
B. Upper P4 Length



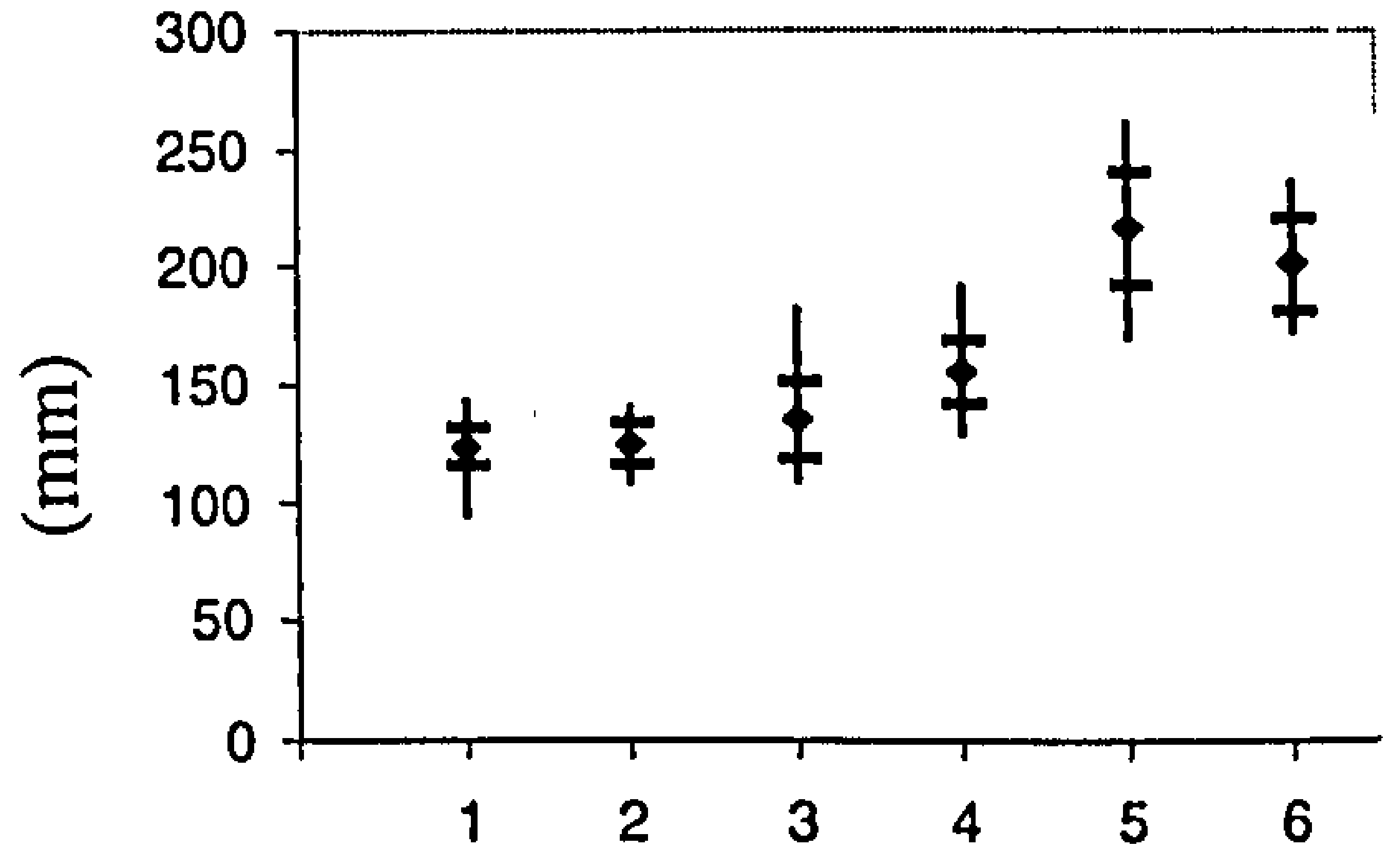
C. Condylobasal Length



D. Zygomatic Breadth



E. Lower M1 Length



F. Canine to Condyle Length

1. Cheetah (n = 57)
2. Snow leopard (n = 14)
3. Leopard (n = 95)
4. Jaguar (n = 49)
5. Lion (n = 87)
6. Tiger (n = 31)

Figure 3.19. Boxplots of craniodental variation in all species of big cats. n = minimum number of specimens in each sample. Diamonds represent the mean, horizontal bars indicate one standard deviation and vertical bars show the total range of the sample.

It is important to realise that the three smaller *Panthera* will never meet under modern circumstances, as they are geographically isolated from each other. The cheetah overlaps in size with all the smaller *Panthera*, but has a very different method of prey capture, so although in direct competition for similar prey sizes, it has a different strategy. It is known that cats adopt avoidance strategies such as scent marking to prevent meetings which may lead to injury, (Seidensticker, 1976). Behavioural differences also occur where larger competitors are absent, for example, the leopard is less nocturnal and spends more of its time on the ground in places where the tiger is not present (Muckenhirn & Eisenberg, 1973). It might be postulated that leopards would also be larger in areas without the lion or tiger, but this requires further investigation. However, Siedensticker (1986) noted that where the tiger and a triumvirate of smaller cats – the clouded leopard, marbled cat (*Pardofelis marmorata*) and Temmincks cat (*Felis temminckii*) are sympatric the leopard does not occur. Siedensticker suggested that this may be due to competition at both ends of the leopards prey size range. Figure 3.20 shows the body masses of each species, with all geographic areas and both sexes included. This shows that although the lion and tiger are larger over all, there is a distinct overlap with the smaller *Panthera*. However, this diagram was produced from the maximum and minimum sizes in the literature and it is unlikely that these extremes are representative of the species as a whole.

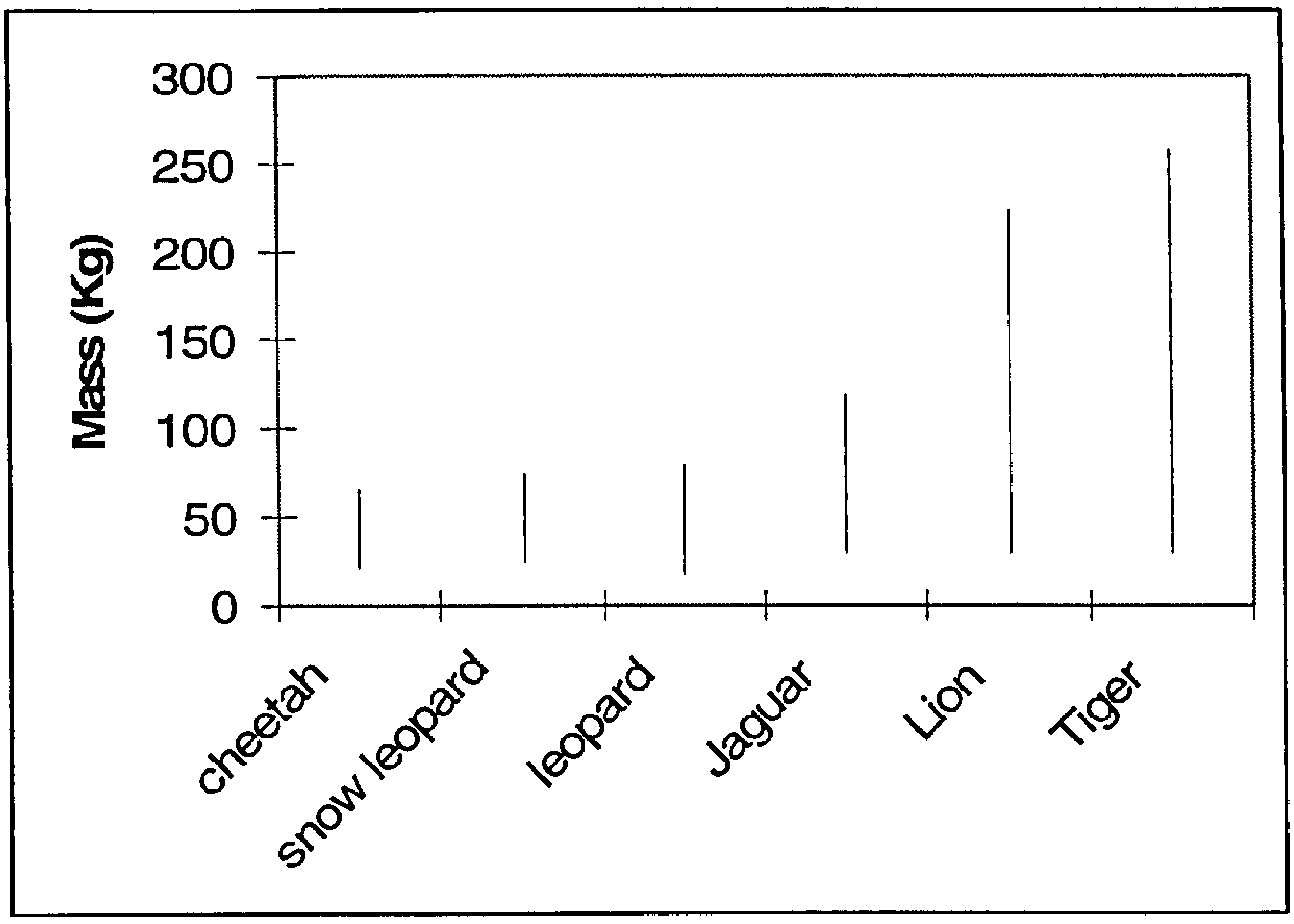


Figure 3.20. Total body mass range for each big cat species (data from sources cited in section 3.2; snow leopard data from Hemmer (1972b).

The problem with applying this information to the fossil record and inferring ecology from these data is that the fossil species were not geographically isolated and any of them could have been sympatric before settling in the range in which they are recognised today. In addition it is known that in many cases animals have changed their bodysize to adapt to prevailing climatic conditions [e.g. spotted hyaenas (Kurtén, 1963b)] and therefore the size of modern organisms is no indication of their past size. However, this study has highlighted one thing; there appears to be partitioning in size between the large cats, with only one large and one smaller *Panthera* being present in any area and this is compatible with the theory of competitive exclusion (Table 3.19). This has implications for the study of the fossil cats. The co-existence of a much larger guild of Pleistocene carnivores may have been possible due to resource partitioning and this can be tested by plotting craniodental measurements of fossil species to see if size ranges overlap (see Chapter 6).

Region	**Large *Panthera***	**Small *Panthera***	**Other**
Eastern Asia	Tiger	Leopard	
Western Asia	Tiger, Lion (h)	Leopard	Cheetah (h)
Himalayas		Snow Leopard	
Africa	Lion	Leopard	Cheetah
America		Jaguar	Puma

Table 3.19. Species of cat by size and region, (h) indicates historical range.

All specimens were entered into PCA to identify which variables best discriminated between species. The dataset was reduced to 151 specimens of all six species of big cat. This analysis found that of 34 cranial and dental variables, only 13 showed differences between *Acinonyx* and *Panthera*, all of which were adaptations in the cheetah to maximise running efficiency. The remaining 23 variables found only size changes between the different species. This indicates both that the evolution of cat crania has been very conservative over the last few million years and that size is the major difference between the members of the genus *Panthera* (O'Regan, in press b). When PCA was run on just the pantherine cats, only one axis was produced (containing 91.6% of the variation) indicating that size is the major difference between the species.

Therefore it appears that the pantherine cats are very variable in body size, able to adapt to conditions by becoming larger or smaller but without substantially changing their shape. This agrees with the findings of Werdelin (1983) who found that the genus *Panthera* could be distinguished from the smaller cats, such as the lynxes and wildcats, but there was little resolution between the species.

3.7. DISCRETE MORPHOLOGICAL TRAITS IN MODERN SPECIES

The preceding section (3.6) illustrated the difficulties of identifying cats to species on purely morphometric criteria. As Merriam & Stock (1932:180) stated in reference to the modern lion and tiger 'while the two living species furnish striking external dissimilarities, a survey of structures revealed in the skull and skeleton and in the dentition has offered as yet no reliable basis or no extensive series of differences on which a satisfactory separation can always be made'. They then went on to summarise the work of Boule (1906) who attempted to find criteria to differentiate between the lion and tiger. To date no morphological studies have been conducted that include all five members of the genus *Panthera.*

Many authors have noted non-metric traits such as the point at which the masseteric fossa ends beneath the M_1, the number of mental foramina (e.g. Hemmer & Schütt, 1969), the length of the mandibular diastema (Nagel, 1999) and the position of the postorbital process (Ficcarelli & Torre, 1968). After studying many specimens of different species, twelve discrete morphological features were chosen as being of potential phylogenetic significance and are discussed further below.

3.7.1. Morphology and method

The twelve morphological features studied in detail can be divided into two groups; six of these refer to the shape of the mandibular corpus and the rest are dental features. They separate into two groups, those that can be defined as presence/absence features and those that refer to overall morphology.

Presence and absence features were as follows:

1. The presence or absence of a lingual bulge on the M_1. The M_1 occasionally has a small lingual cusp or bulge, opposite the point where the paraconid and protoconid meet.
2. The presence or absence of the M_1 talonid. The presence of an M_1 talonid is a primitive feature, as it represents a cusp which has been lost in the majority of the Felidae. The talonid is a small cusp on the distal surface of the protoconid, just above the cingulum and, if present, is usually very small (illustrated in Figure 2.3).

3. The presence or absence of a P_4 'basin'. The scoring of this character requires more of a fine judgement than others, as it is more or less continuous. However, those teeth that definitely have it are immediately obvious, while those that do not are similarly identifiable. In intermediate cases they were usually conservatively counted as not having the feature.
4. The presence or absence of the P^4 ectoparastyle. The ectoparastyle is an immediately obvious feature, as it consists of a small accessory cusp on the mesial surface of the P^4 parastyle (see Figure 2.2).
5. The presence or absence of the P^4 metacone 'bobble'. This feature was highly noticeable on a fossil specimen from Rome (Rome 1191) and was chosen to see if other specimens had it or if the Rome specimen was aberrant. It consists of a large enamel bulge on the distal 'corner' of the P^4. The shape of this tooth appears to be quite variable, but this feature is most distinctive, as seen in Figure 3.21.

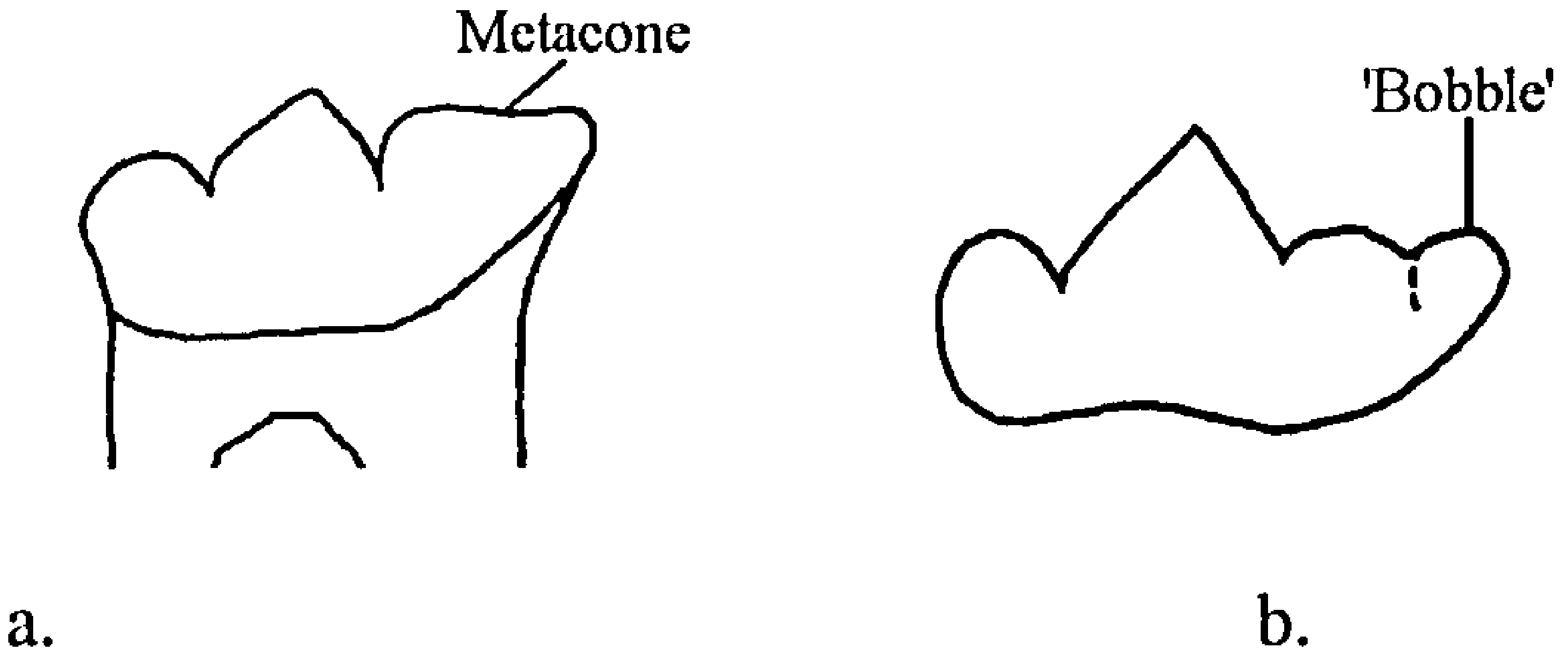


Figure 3.21. a. normal metacone, b. The metacone 'bobble' on Rome specimen 1191.

6. The presence or absence of the symphyseal bulge in the mandible. The symphyseal bulge is an additional area of bone growth beneath the symphysis where the two halves of the rami unite.

Six other features were also defined:

7. Straight or curved lingual border of the mandibular symphysis. This has sometimes been referred to as a diagnostic feature of *Panthera gombaszoegensis* (Spassov &

Raichev, 1997). The lingual border of the ramus is either curved or fairly straight. However, this curvature can be affected by the age of the animal, as this area undergoes remodelling after the eruption of the C_i (see section 3.4). Therefore caution must be used when identifying this feature to check that the animal is mature and that enough of the mandible remains on fossil specimens to be able to identify the shape of the area accurately.

8. The inferior border of the mandibular ramus was identified as an area of interest by Boule (1906). In his study of cave lion remains he discovered that lion rami were curved when placed on a flat surface and those of tiger were straight. This appears to be a valid distinguishing feature for these two cats, but other species of *Panthera* were not considered in his discussion. This feature was used in this study by placing mandibles on a flat surface to see which areas were raised. If the symphysis and angular process touched the surface it was regarded as straight, if they did not both touch the surface it was regarded as curved.
9. The position of the lingual root of the P^3. The posterior lingual root of the P^3 is quite variable in position. In some animals it is placed towards the centre of the tooth, below the protocone, whilst in others it is distally placed.
10. The number of mental foramina. The number of mental foramina were studied as they are often mentioned in site reports. Numbers of foramina vary between individual animals, but it was not known whether there were any differences at the specific level.
11. The position of the anterior end of the masseteric fossa in relation to the M_1. The position of the masseteric fossa is often noted in site reports but it may not be a diagnostic feature. The end of the fossa was indicated by taking a straight line from the most anterior point up towards the M_1 and its position in relation to the M_1 was noted. Three categories were used – before M_1 (fossa ends before reaching the

posterior of the M_1); at M_1 (fossa ends at the posterior edge of the M_1 alveolus) and after M_1 (fossa ends beneath the protoconid of the M_1).

12. The most buccal tooth on the mandible. Again this feature is often mentioned in reports but its diagnostic value is not known. It can be identified on any mandible fragment as long as the alveoli are complete. The most buccal tooth - P_3, P_4, or M_1 - is noted.

To test these features 30 lion, 20 leopard and 30 jaguar skulls in the collections of the National Museum of Natural History, Washington were examined on the same day to ensure comparability of results. These specimens are listed in Table 3.20.

Cat	**Specimen Numbers**
Lion	35990, 161919, 181569, 181570, 181571, 181574, 181580, 181582, 181583, 181592, 182326, 182315, 182332, 184816, 536999, 367397, 216602, 236919, 216601, 216604, 182044, 181930, 182107, 182297, 182293, 182307, 182308, 182309, 182311, 182313.
Leopard	181595, 182329, 184819, 184818, 296142, 163095, 34866, 236921, 236969, 164763, 162145, 162144, 162147, 161911, 162927, 162926, 163094, 163093, 182178, 182323.
Jaguar	251118, 244858, 179170, 249823, 130362, 179171, 249826, 131998, A09704, 256386, A49393, 155603, 12296, 255613, 231961, 247337, 18176, 281420, 61192, 140949, 256385, 256376, 100122, A06480, 362250, 374849, 362249, 395085, 456774, 268871.

Table 3.20. Specimens examined for the morphological study. All specimens in the collection of the National Museum of Natural History, Washington, D.C.

3.7.2. Results and discussion

The results of the morphological analyses were converted to percentages and some are illustrated in Figure 3.22. The results are interesting as they highlight certain features that are prevalent in some species but absent in others. Although none of them can be used to definitively identify a specimen, they can at least be used to eliminate certain species from the list of potential animals.

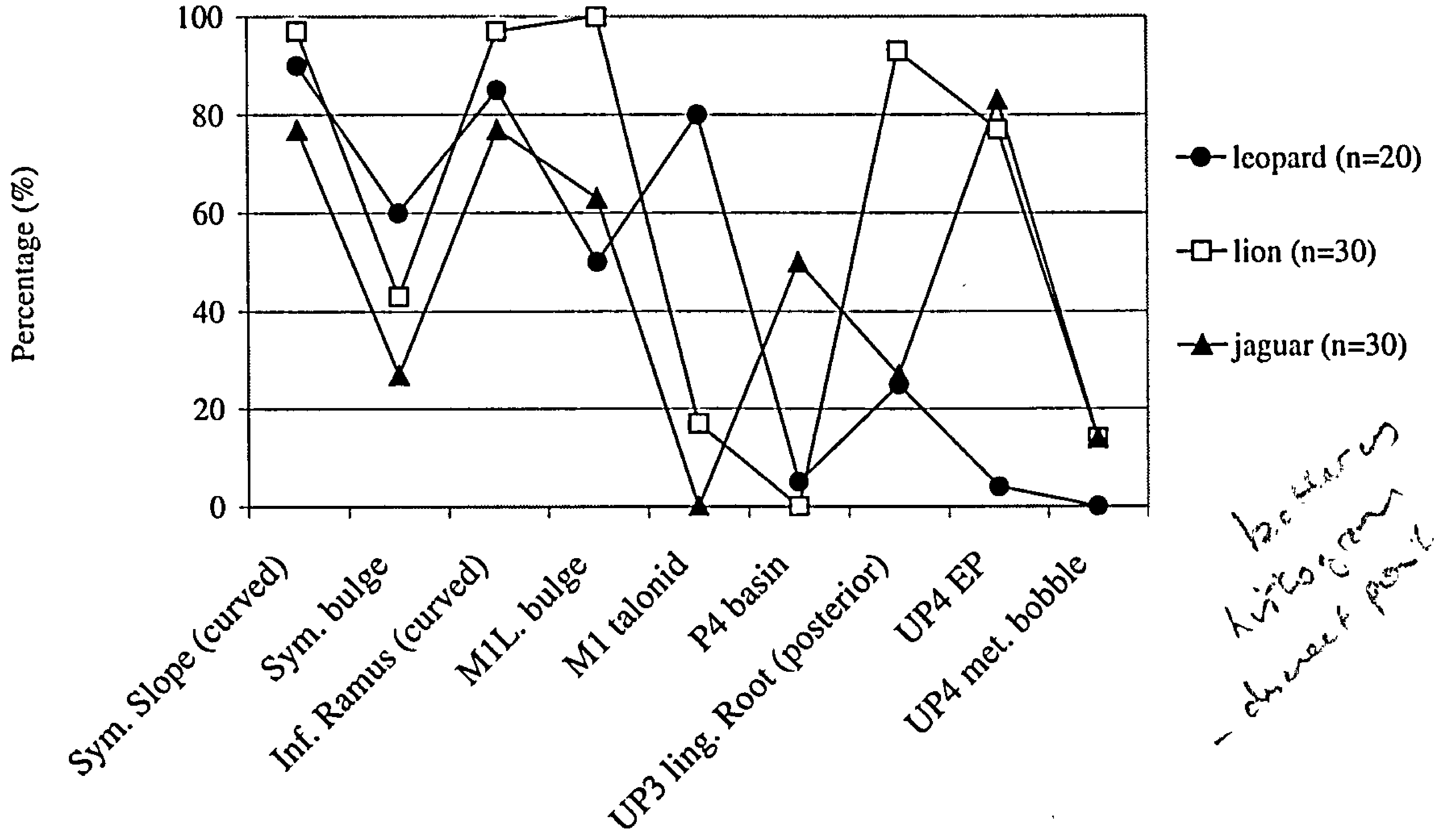


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Figure 3.22. Graph showing the percentage occurrence of particular morphological features in a sample of modern big cats. Shape categories are indicated in brackets, for all others the percentages illustrated refer to the presence of features.

It appears that the shape of the symphyseal slope and the inferior border of the ramus are variable across all three species, but they each follow the other in terms of prevalence, perhaps indicating the constraints of biomechanics upon these areas.

The position of the masseteric fossa was similar across all species. None of the animals studied had a fossa that ended beneath the M_1, the other two possibilities, at the M_1 and before the M_1 both occurred, but before the M_1 was the most common position (lion = 70%; leopard 65% and jaguar 83%). The number of mental foramina was highly variable across species, ranging from two to five in the 20 leopard specimens examined (these results are given below in Table 3.21). The mental foramina carry the mandibular branch of the trigeminal nerve to the teeth and skin of the lower jaw (Walker, 1986). No cat had a single foramen, indicating that all species require at least two mental foramina for this nerve, but it is not known whether additional foramina provide an advantage to the individual. It appears from these samples that jaguars have less variation in the numbers of mental foramina in comparison with the lion and leopard. However, it is worth bearing in mind that the above data were collected on the left hand side only and that this trait is not always bilaterally symmetrical (e.g. BMNH jaguar specimen 1926.12.4.29 has three mental foramina on the right and four on the left hand side of the ramus).

Cat	n	one	two	three	four	five
Lion	30	0	40	43	17	0
Leopard	20	0	50	25	20	5
Jaguar	30	0	27	73	0	0

Table 3.21. Number of mental foramina found in individuals of three modern species of *Panthera*. Results expressed as a percentage of the total sample for each cat.

The most buccal tooth was also noted and again, all species were very similar. In the vast majority of cats of all species the P_4 was the most buccally placed tooth (90% of lions and jaguars and 100% of leopards). Three lions and one jaguar had both the P_3 and P_4 as the most buccal teeth; whilst in one jaguar the P_3 was most buccal. In no case was the M_1 most buccal, a finding that makes sense from a functional viewpoint as the M_1 is the inside blade of the carnassial pair.

3.7.2.1. Lion.

Certain features appear to be diagnostic of lion (*Panthera leo*). The combination of an M_1 lingual bulge (100%) and the lack of a P_4 'basin' (0%) when used in conjunction with morphometric measurements should be good criteria for distinguishing this cat. In addition it had the highest prevalence of a posteriorly placed lingual root (93%) and curved inferior border of the ramus (97%), although similar results were found for both the jaguar and leopard for the latter feature. However, it does indicate that Boules' diagnostic criteria of mandibular shape largely holds true, although it is not infallible (lion specimen No. 181569 was straight).

3.7.2.2. Jaguar

In many ways the jaguar (*Panthera onca*) is most closely allied to the lion with a similar occurrence of the P^4 ectoparastyle (83% versus 77% for lion). However, the jaguar has the highest presence of the P_4 'basin' with half of all specimens exhibiting this feature. In contrast, no jaguar specimen (0%) had an M_1 talonid. The jaguar and leopard were most similar in terms of the presence an M_1 lingual bulge (63% and 50% respectively) and the posterior position of the P^3 lingual root (only 27% and 25%).

3.7.2.3. Leopard

The leopard (*Panthera pardus*) has an interesting mosaic of features. An M_1 talonid was present in 80% of all leopards examined , yet few other cats had this feature. Only one individual (No. 162147) had a P_4 'basin' and only one specimen (No. 182329) had a P^4 ectoparastyle. The leopard also has the lowest numbers of individuals with a lingual bulge (50%).

3.7.3. Species conclusions

3.7.3.1. Lion

Nearly all specimens have a straight inferior border of the ramus. All M_1s have a lingual bulge, but are unlikely to have a talonid and the combination of this with the total absence of a P_4 basin and the overall size of the teeth should provide enough criteria to identify an unknown mandible. In terms of the cranium, a lion is likely to have the lingual root of the P^3 to the rear of the tooth and have a large ectoparastyle on the P^4, and these together with the overall size of the cat should prove sufficient for identification to species.

3.7.3.2. Jaguar

Jaguar remains are more difficult to identify absolutely (especially as they are of a similar size to the leopard) although some features do stand out. If a specimen has an M_1 talonid then it is not a jaguar. If it does not have talonid, but has an M_1 lingual bulge and a P_4 'basin', then it is likely to be a jaguar. The combination of these three features should be enough to exclude the leopard. In terms of the upper teeth things are less clear, although a more centrally placed P^3 lingual root, combined with a P^4 ectoparastyle would indicate jaguar, but not confirm it.

3.7.3.3. Leopard

An M_1 with a talonid in conjunction with a P_4 without a 'basin' is highly indicative of leopard, although not all specimens have these features. Likewise a P^3 with a centrally placed lingual root and no ectoparastyle on the P^4 would make the identification of leopard likely, although this would require further study and measurements to confirm this.

3.7.3.4. Other features.

Other, less quantifiable features have also been noted. In general, lion teeth tend to be very rounded and squat in their cusp morphology. Jaguars also tend to be quite robust, but retain some sharpness of definition. Leopard teeth appear gracile in comparison, with sharply defined cusps and an overall slender appearance.

3.7.4. Sexual dimorphism

The possibility that some or all of these features might be sexually dimorphic was considered. Only the sample of lion skulls had enough sexed specimens to perform this analysis (sexed specimens n=25). Although samples of most features, when divided into groups, were too small to formally test for dimorphism, a chi-squared test was performed on the presence or absence of the symphyseal bulge in male and female lions. The results was non-significant. Therefore the sex of an animal does not significantly influence the presence of a symphyseal bulge. Further research on well provenanced modern specimens may indicate whether any of the other cranial and dental features are sexually dimorphic.

3.7.5. Summary

The metacone 'bobble' was seen at a low level amongst all species (14% for lion and jaguar and 0% for leopard), suggesting that it is present in most populations and is therefore not a useful diagnostic criterion. Overall, features of the mandibular corpus do not appear to be useful diagnostic indicators but dental traits are more informative. Some of these features used in combination and with morphometric data should be sufficient to identify many individuals within each species. However, the morphology is highly variable and care should be taken when assessing the specimens.

3.8. CONCLUSION

None of the morphometric factors discussed above stand alone. Each one will have had a subtle effect on the other types of variation. Figure 3.23 shows the complexities of working with modern species, particularly when considering relatively small samples.

For example, collection strategies will have affected all of the factors because all data have been collected on specimens in museums.

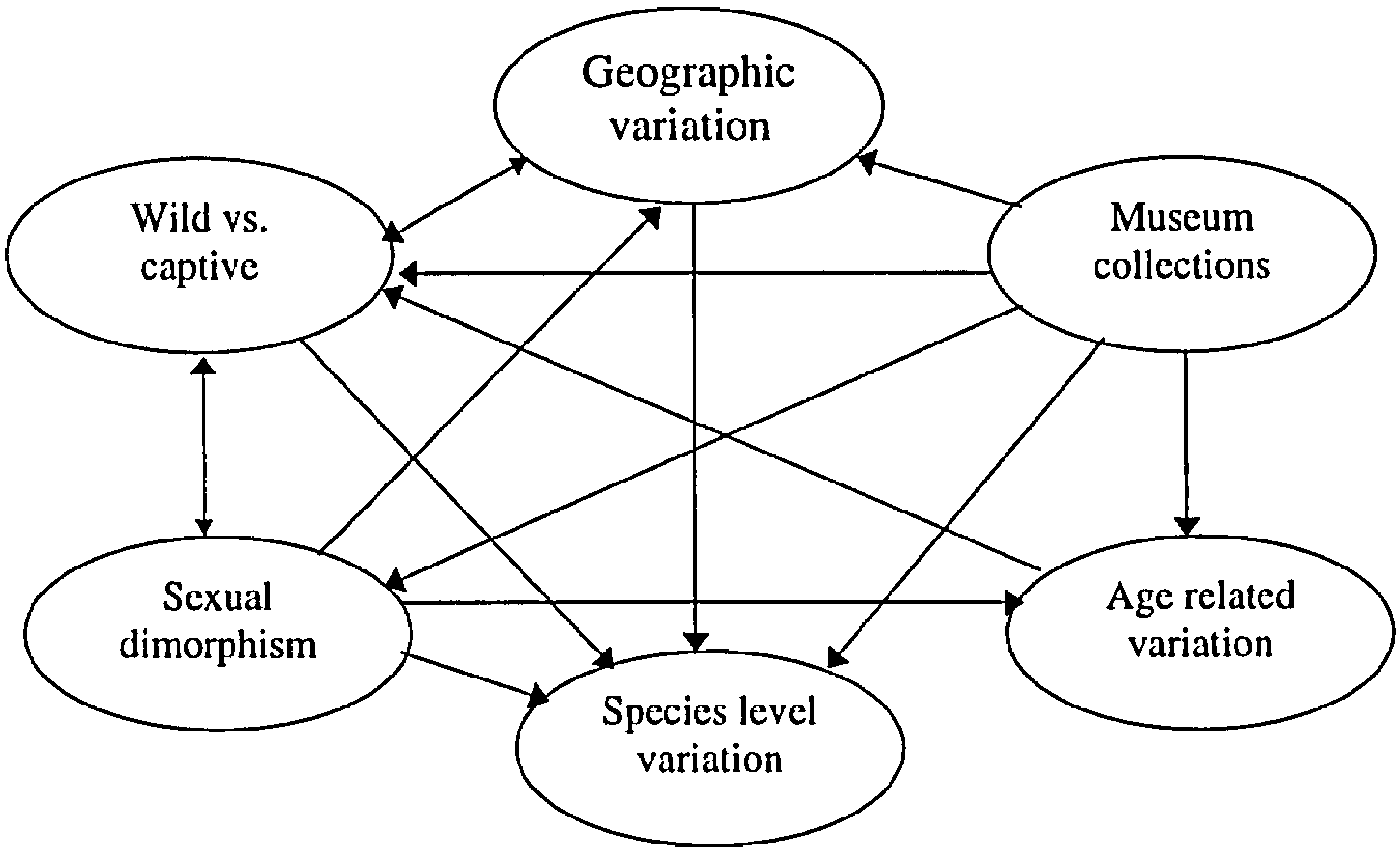

Figure 3.23. Schematic diagram showing probable interplay between factors affecting the modern dataset.

As the diagram above shows, one factor can have been influenced by as many as four other factors, making the task of identifying the effects of particular types of variation very difficult. However, this chapter has highlighted several areas that require further study or areas for caution in the interpretation of results.

These can be summarised into seven conclusions:

i) Captivity influences the growth of the cranium in both lions and leopard, although how or why this occurs has not been resolved.

ii) Cats are known to be influenced by geographic variation, in terms of body mass and cranial size, but no geographic differences could be determined from the current dataset.

iii) Sexual dimorphism is significant in most species for most variables, with the exception of the cheetah. These are all size related changes, with males being larger than females in all species. No shape changes were detected.

iv) Age related changes were found in lions but not in leopards. This may be because leopards mature earlier, but this cannot be tested on these data. Older lions were larger than young lions for all variables, with the exception of the anterior depth of the mandible, in which young cats were larger. This is probably related to remodelling during and after the eruption of the lower canine.

v) Museum collections are biased towards cats in their prime (3-6 years) and against young or very old animals. There does not appear to be a significant bias towards larger animals or males, despite hunting being responsible for many of the specimens.

vi) Differences between species are mainly size related. Cheetah skulls are shaped very differently from those of the other big cats, but within the genus *Panthera* size appears to account for most of the variation between species. In addition, there is a distinct difference in the size of craniodental measurements between the smaller and larger *Panthera*, although body mass data overlap considerably. This observation is consistent with theories of competitive exclusion.

vii) Non-metric mandibular features have little diagnostic value, but certain dental morphologies do appear to be of use. Morphological variation cannot identify species outright, but a combination of dental features and morphometric data can be used to discriminate between animals.

In conclusion, the parameters of modern variability can be applied to the fossil material. It is not possible to determine the sex of specimens accurately but differences between the sexes have been explored. If *P. gombaszoegensis* falls outside the maximum range of modern *Panthera* species, then a mixing of species may be suspected. The age related changes in the mandibles have also highlighted measurements to be treated with caution in younger specimens. Competitive exclusion may be inferred if Pleistocene species have distinct size ranges.

CHAPTER 4 - *PANTHERA GOMBASZOEGENSIS* : SKULL AND DENTAL MORPHOLOGY

Panthera gombaszoegensis is a cat with a chequered history. It has been referred to by many different names – the Tuscany lion, (Kurtén, 1968); the European jaguar, (Hemmer, 1971a) and the leopard (Stuart, 1982). In addition many different specific names have been created over the last 100 years. Hemmer (1971a; 1972a) attempted a revision of this material and synonymised several of the current taxa. However, many authors have rejected this revision for different reasons and these are discussed below.

4.1. TAXONOMIC REVIEW

The first publication of specimens that are now referred to the species *Panthera gombaszoegensis* was by del Campana (1915; 1916). These cranial and postcranial specimens were all found in the Val d'Arno and he referred them all to *Leopardus arvernensis* Croizet & Jobert, 1828.

The most important publication was by Kretzoi (1938) in his monograph of the site of Gombaszög (now Gombasek), in Slovakia. He referred the medium sized felid material to *Leo gombaszoegensis* on the basis of its smaller size in comparison with the lion, *Panthera leo*, and its dental morphology. However, the specimens available to Kretzoi for his study were all isolated teeth. The holotype of *Leo gombaszoegensis* is a P^4 with another seven isolated (and in some cases fragmentary) teeth as the paratypes. The holotype is currently missing and the paratypes have no official status in terms of nomenclature (DeBlase & Martin, 1981). This makes comparisons with other material difficult and is the source of the some of the problems surrounding the definition of the species.

Schaub (1949) showed that the type specimen of *Leopardus arvernensis* Croizet et Jobert was not the same species as the Italian material published by del Campana (1915, 1916) and that the referral of the Olivola material to this taxon was therefore invalid. Schaub proposed the name *Felis toscana* for the Italian specimens as they had all been found in Tuscany and designated a mandible from Il Tasso (IGF 851) as the type specimen of this new species (Schaub, 1949:499).

The question then arose as to whether *Felis toscana* and *P. gombaszoegensis* were synonymous. Hemmer (1971a) believed that they were and that *Panthera gombaszoegensis* had time priority. However, prior to this *Felis toscana* had become a popular taxon, being used in many different publications (e.g. Ficcarelli & Torre, 1968; Lehmann, 1953, 1957). One argument put forward for the retention of *Felis toscana* is that the original description of *P. gombaszoegensis* was based on such poor material that it is not possible to compare the specimens adequately (Ambrosetti *et al,* 1979). However, under Article 23 of the International Code of Zoological Nomenclature (Anon, 1985), the oldest named taxon has time priority. Whilst the holotype and paratypes are based on poor material, it is still possible to make comparisons between these specimens and fossils from other sites. The type specimen, although currently missing, is figured in Kretzoi's 1938 publication (Kretzoi, 1938:Plate 1) and he named many paratypes, all of which are extant. If the holotype remains lost it may be possible to elect another specimen as the neotype (new type specimen) as permitted under exceptional circumstances (including loss of the holotype) in Article 75 of the ICZN (Anon, 1985). In the light of the above discussion and despite the reservations of some authors, *Panthera gombaszoegensis* retains time priority, with adequate material available for study; it is therefore the valid name for this species.

Additional species have also been created, which were referred to *Panthera gombaszoegensis* by Hemmer (1971a). One of these species was named *Felis (Panthera) schreuderi* by von Koenigswald (1960) based on several isolated teeth recovered from the Russel-Tiglia-Egypte Quarry in Tegelen, Holland.

Bonifay (1971) named *Jansofelis vaufreyi* on the basis of material from L'Escale, France. This species has been extensively discussed by Hemmer (1972a) who felt it was synonymous with *P. gombaszoegensis*. I agree with Hemmer that the description of a new genus and species on a collection of juvenile postcrania with a few immature mandibles is a doubtful procedure. However, this synonymy was regarded as unproven by Ambrosetti *et al* (1979).

Another specimen that is commonly assigned to *P. gombaszoegensis* was described by Portis (1907) who referred a complete cranium from Rome to *Felis arvernensis* Croizet & Jobert. This was referred to *P. gombaszoegensis* by Hemmer & Schütt (1969) but was redescribed as *Panthera pardus* by Kotsakis & Palombo (1979). Despite this re-description, some authors are still retaining this specimen as *P. gombaszoegensis* (e.g. Athanassiou, 1996).

Hemmer (1972a) named two subspecies of *P. gombaszoegensis*, based on the material from the sites of Olivola and L'Escale. The Olivola material was named as *Panthera gombaszoegensis toscana* to differentiate it from the L'Escale material (*Panthera gombaszoegensis gombaszoegensis*). The subspecific diagnosis of *Panthera gombaszoegensis toscana* was made on the basis of a more robust build, shorter muzzle and narrower mandibular premolars in the Olivola specimens. Olivola is some 1.0Ma older than L'Escale and these are effectively chronosubspecies, the validity of which will be examined in the following review. In recent publications *P. gombaszoegensis* has been made a subspecies of the jaguar, *Panthera onca*, and is referred to *Panthera onca gombaszoegensis* (Kahlke, 2000; Moullé *et al,* 2000). Although the close affinity of *P. gombaszoegensis* with *P. onca* has often been discussed it has yet to be adequately proven; the advisability of making *Panthera gombaszoegensis* a subspecies of the modern jaguar will be investigated in the following sections.

Kurtén (1968) suggested that *Panthera gombaszoegensis* might be synonymous with *Panthera palaeosinensis*, whilst Ficcarelli & Torre (1968) felt that *Panthera palaeosinensis* was more similar to the tiger. This view was reiterated by Mazak (1981) who also felt that *P. palaeosinensis* was ancestral to the tiger.

Other enigmatic European specimens have also been included in this study. The specimen from Stránská Scála 1 (No.1938) is a mandible fragment with P_3 and C_i. It has been assigned to several different species, including the snow leopard (Thenius, 1969) and the leopard (Hemmer, 1971b) and doubts still remain over its affinities to either. It has been included in this analysis to investigate its relationships further. A mandible from Rabenstein (specimen 1894 I504) that has been assigned to the 'robust' lineage of leopards (Hemmer, 1971b; Spassov & Raichev, 1997) has been included to test the affinities and validity of the separation of Pleistocene leopard specimens into two groups.

The above discussion illustrates the confusion about the taxonomy of the medium sized pantherine fossils in Europe. Many different species have been created, not all of which have been adequately refuted and regional names are still persisting despite Hemmer's 1971 and 1972 papers. Therefore these taxa are in need of revision and all of the key specimens mentioned above have been studied and are included in the following analysis. The rest of this section will be devoted to placing these specimens within their context, to compare them to the original type material and attempt to reach a robust taxonomic conclusion.

4.1.1. Gombasek

Kretzoi's original diagnosis of *Panthera gombaszoegensis* (1938: 101) is extremely short and describes a cat that is similar to the lion, but smaller and with some primitive traits. The specific differences given to diagnose *P. gombaszoegensis* were as follows:

P^4 small, weak paracone; strong protocone.

P_3 strong cusps, paraconid is obvious.

P_4 strong distal cingulum.

C small and weak in comparison with lion.

This diagnosis is based on an isolated P^4 as Holotype, seven other isolated teeth as paratypes and four other specimens consisting of two juvenile mandibles, a C_i fragment and an upper incisor.

A re-analysis of the Gombasek material, including unpublished specimens in the Geological Institute of Hungary and using all teeth (not just isolated specimens) gives the following morphological details:

P^4 (n = 3) large, robust parastyle; low, backward-sloping paracone; protocone variable in size; one specimen (β 767) has a small ectoparastyle; curved metacone; straight anterior edge.

P^3 (n = 2) low but defined cingulum; low, pointed protocone; variable definition of anterior cusp.

C^s (n = 2) very robust.

M_1 (n = 7) protoconid strong and large in comparison with paraconid; talonid absent; small cingulum; two teeth have very small lingual bulges; of the five paraconids present three have a tiny cusp on the mesial surface – an ectoparaconid (two of which are paratypes, β915 and M9).

P_4 (n = 3) strong cingulum; protocone very large, dominates tooth; two teeth have a slight lingual 'basin'.

P_3 (n = 2) pronounced anterior cusp; defined cingulum.

C_i (n = 6) short crown; strongly curved.

The above specimens represent *Panthera gombaszoegensis* and as such will form the basis of all comparisons with material from other sites. The morphology exhibited in the Gombasek material is variable, but does appear to have some definable features. The presence of the ectoparaconid on the lower M_1 deserves further attention, as does the crown height of the lower canines. In addition, one unpublished specimen (GIH no number) is a left mandible with complete C_i, P_4, M_1 and P_3 alveolus; this is the only specimen where teeth are in situ and as such it will be used as a standard for the type site material in comparisons with other assemblages.

4.2. MORPHOLOGICAL ANALYSIS

The morphology of specimens from each site studied will be reviewed below, in approximate date order, beginning with the oldest (See Appendix 2 for full dates of each site). In each case the morphology discussed is of the site sample as a whole. Teeth in specimens with both a left and right side present (e.g. a complete cranium) were scored together, so that each individual contributes as n=1 in all morphological analyses. For example, in the P^4 morphological study below, Olivola specimens are described as n=5, but eight specimens are listed in Table 4.1. This is because three of the specimens have been paired in the morphological analysis. Measurements taken on alveoli are also included in the tables, but do not feature in the morphological analyses. The morphology of other modern and fossil species in comparison with *P. gombaszoegensis* are discussed in section 4.7.

In the following log ratio diagrams, Gombasek specimens have been used as standard, where other standards have been used these are made explicit in the text. Where more than one specimen is known from a site, a mean has been calculated from all the specimens. Only complete specimens have been included in the sample used to calculate the means. If only one specimen is available from a particular site, the raw data are used; in these cases partial teeth are also included, in order to represent that site in the analysis. In some cases where sites may have a mixture of material the samples have been plotted separately, e.g. Ficcarelli & Torre (1968) interpreted the smaller specimens from Olivola as female and these have been separated from the main Olivola sample in the following graphs. For the purpose of this thesis the material from the Vald'Arno sites are grouped with those of Olivola. The exception to this is the Santa Maria nr Il Tasso mandible which has been kept separate because it is the type specimen of *Felis toscana* (Schaub, 1949).

Two log ratio diagrams have been produced for each tooth using the following groups - an 'early' sample (1.9 – 0.8 Ma) and a 'young' sample (0.8 – 0.3Ma). These group dates were chosen because many of the sites are not accurately dated but have been termed 'Cromerian' (~0.75 – 0.5Ma). In addition many sites are dated more accurately by the Brunhes/Matuymama boundary (~0.78Ma) which makes a convenient cut off point (see Section 1.3.2. and Appendix 2).

4.2.1. P^4

Gerakarou 1. P^4 (n=1) tiny ectoparastyle; backward-sloping paracone; quite pronounced protocone; curved metacone with stepped profile; anterior edge straight (right side) dipped (left side).

Tegelen. P^4 (n=1) distinct protocone; rounded metacone with stepped profile.

Olivola. P^4 (n=5) ectoparastyle present, varying from small to very large; low protocone, varying from weak to strong; backward-sloping paracone; one specimen (IGF 10032) has distinctive enamel 'bobble' on tip of paracone; curved metacone with no step; anterior edge dips towards protocone.

Huéscar. P^4 (n=1) weak protocone; small ectoparastyle; metacone curved; straight anterior edge.

Gombasek. P^4 (n = 3) large, robust parastyle; low, backward-sloping paracone; protocone variable in size; one specimen (β 767) has a small ectoparastyle; curved metacone; straight anterior edge.

L'Escale. P^4 (n=2) very pronounced protocone; ectoparastyle present; curved metacone; straight anterior edge.

Westbury-sub-Mendip. P^4 (n=3) ectoparastyle present, variable size. Low protocone, back sloping paracone; stepped profile on metacone; straight anterior edge (M33681), slightly dipped (M33683).

Rome. P^4 (n=1) very narrow, low indistinct protocone, tiny ectoparastyle, very rounded metacone 'bobble'; protocone posterior to anterior edge.

Vértesszölös II. P^4 (n=1) metacone bobble; large ectoparastyle.

The morphology of the P^4 is highly variable in the fossil material. The size of the protocone appears to be indicative of *Panthera gombaszoegensis*; the type specimen β991 (illustrated in Kretzoi, 1938) shows a robust tooth with a low but distinct protocone. All specimens of *P. gombaszoegensis* had ectoparastyle features, ranging from a simple line on the tooth up to a fully developed cusp. In order to make this analysis comparable with the modern cat data any deviation from a smooth surface on the parastyle was defined as an ectoparastyle, as no attempt was made to differentiate degrees of development of this feature in the modern material (see section 3.7). Using these criteria it is apparent that all *P. gombaszoegensis* specimens studied had some sort of ectoparastyle feature. The position of the protocone in relation to the paracone is also of interest; in the Rome specimen (1191) the protocone is offset, giving a large dip in the anterior border of the tooth. In most other specimens (including the Holotype) the anterior border is straight. However, this is a variable feature, as the anterior edge of the Gerakarou 1 P^4 is straight on the right hand side and dipped on the left, but only in the Rome specimen is the protocone distinctly posterior.

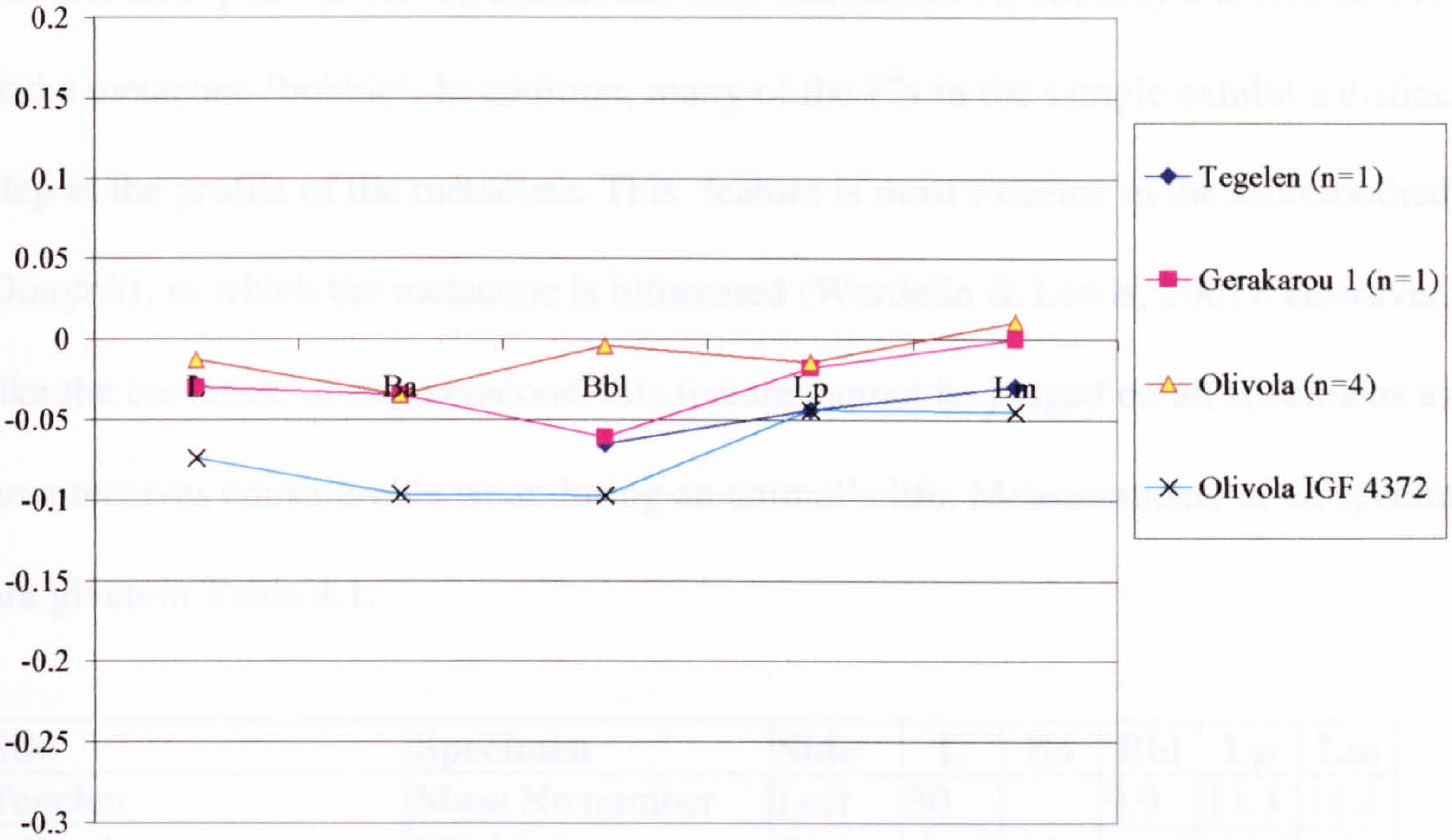

Figure 4.1a. Log ratio diagram of all Early (2.0 – 0.8Ma) *P. gombaszoegensis* P^4 with Gombasek specimen (ß 767) as standard.

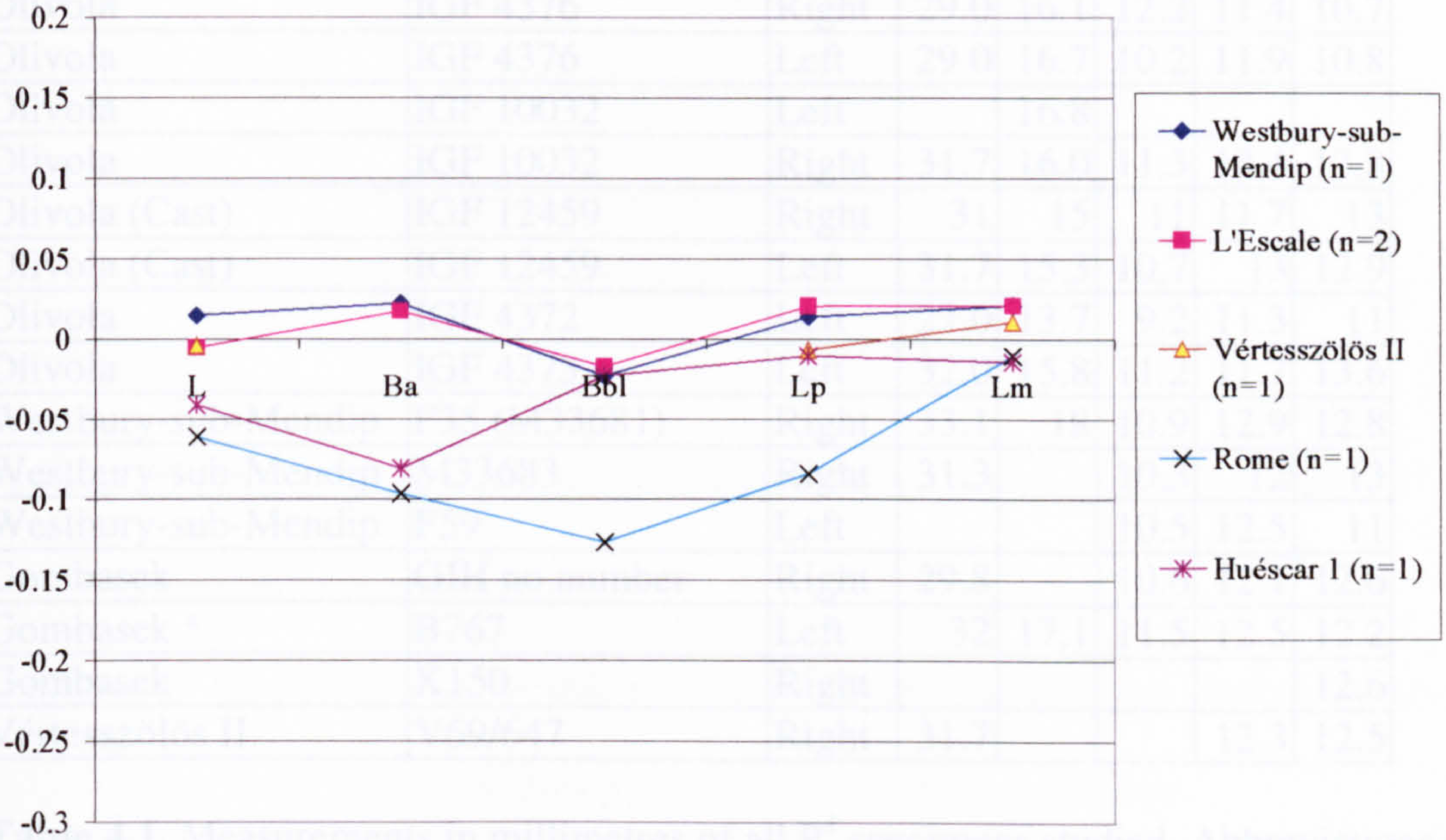

Figure 4.1b. Log ratio diagram of all Late (0.8 – 0.3Ma) *P. gombaszoegensis* P^4 with Gombasek specimen (ß 767) as standard.

Figure 4.1. Log ratio diagrams of the P^4, using Gombasek specimen (ß 767) as standard.

Several teeth possess curved metacones (e.g. Gerakarou 1), but only one (Rome 1191) had a metacone 'bobble'. In addition, many of the P^4s in the sample exhibit a distinct step in the profile of the metacone. This feature is most extreme in the sabretoothed *Dinofelis*, in which the metacone is bifurcated (Werdelin & Lewis, 2001). However, like the curvature of the metacone, this feature cannot be judged on all specimens as this area receives considerable wear during an animal's life. Measurements of all specimens are given in Table 4.1.

Site	**Specimen**	**Side**	**L**	**Ba**	**Bbl**	**Lp**	**Lm**
Tegelen	Maas No number	Left	30		9.9	11.3	11.4
L'Escale	CD 1142	Right	31.7	18.9	11.5	13.4	12.8
L'Escale	C-D 795	Right	31.5	16.7	10.6	12.8	12.8
L'Escale †	C-D 764		32.4		11.6	13.5	12.8
Rome	1191	Left	27.8	13.7	8.6	10.3	11.9
Huéscar	HU-1-86 D49	Right	29.1	14.2	10.9	12.2	11.8
Gerakarou 1	GER 165	Right	29.9	15.8	10.0	12.0	12.2
Gerakarou 1	GER 165	Left	29.4	16.2	9.8	12.2	12.0
Olivola	IGF 4376	Right	29.0	16.1	12.2	11.4	10.7
Olivola	IGF 4376	Left	29.0	16.7	10.2	11.9	10.8
Olivola	IGF 10032	Left		16.8			
Olivola	IGF 10032	Right	31.7	16.0	11.3	12.4	12.8
Olivola (Cast)	IGF 12459	Right	31	15	11	11.7	13
Olivola (Cast)	IGF 12459	Left	31.7	15.3	10.7	13	12.9
Olivola	IGF 4372	Left	27.0	13.7	9.2	11.3	11
Olivola	IGF 4373	Left	32.0	15.8	11.2	11.7	13.6
Westbury-sub-Mendip	F35 (M33681)	Right	33.1	18	10.9	12.9	12.8
Westbury-sub-Mendip	M33683	Right	31.3		10.3	12	13
Westbury-sub-Mendip	F59	Left			10.5	12.5	11
Gombasek	GIH no number	Right	29.8		10.6	12.1	12.6
Gombasek *	B767	Left	32	17.1	11.5	12.5	12.2
Gombasek	K150	Right					12.6
Vértesszölös II	V69/647	Right	31.7			12.3	12.5

Table 4.1. Measurements in millimetres of all P^4 specimens studied. Abbreviations as in Table 2.4. * denotes the specimen used as standard in the log ratio diagrams. † indicates specimens measured by A. Turner; these are not included in the morphological analyses

The specimens are divided into groups for the log ratio diagrams in Figure 4.1. These groups consist of early specimens (pre 0.8 Ma) and late specimens (post 0.8Ma).

Numbers of specimens are given in brackets. Figure 4.1a shows that the majority of early specimens are similar to the Gombasek specimen in proportions, but that they are all smaller than the standard. The smaller Olivola specimen (IGF 4372) is quite narrow in comparison with the standard and other teeth, but it is not too dissimilar to the Gerakarou 1 cat. The second graph (Fig. 4.1b) highlights the similarity in size and proportion of all the later sites to the Gombasek specimen. The only exceptions to this are the specimen from Rome (1191) which has a much narrower tooth and smaller paracone for its size and Huéscar (Hu186D49) which is very similar with a narrow anterior breadth. All teeth, with the exception of Rome 1191, have very similar paracone and metacone proportions.

4.2.2. P^3

Gerakarou 1. P^3 (n=1) no anterior cusp; large posterior cusp; slight cingulum.

Olivola. P^3 (n=6) large, well defined anterior cusp; large, strong, backwards-sloping protocone; small cingulum; small posterior cusps with the exception of those on IGF 4376 and IGF 10032 which are much larger. IGF 1225V is an anterior fragment, no measurements possible.

Gombasek. P^3 (n = 2) low but defined cingulum; low, pointed protocone; variable definition of anterior cusp.

L'Escale. P^3 (n=4) large, backwards-sloping protocone; anterior and posterior cusps large; small cingulum, except CD1142 cingulum pronounced.

Westbury-sub-Mendip. P^3 (n=1) small anterior cusp, distinct in lingual view.

Uppony 1. P^3 (n=2) low, well defined anterior cusp; strong cingulum, very rounded.

Vértesszölös II. P^3 (n=1) large anterior cusp.

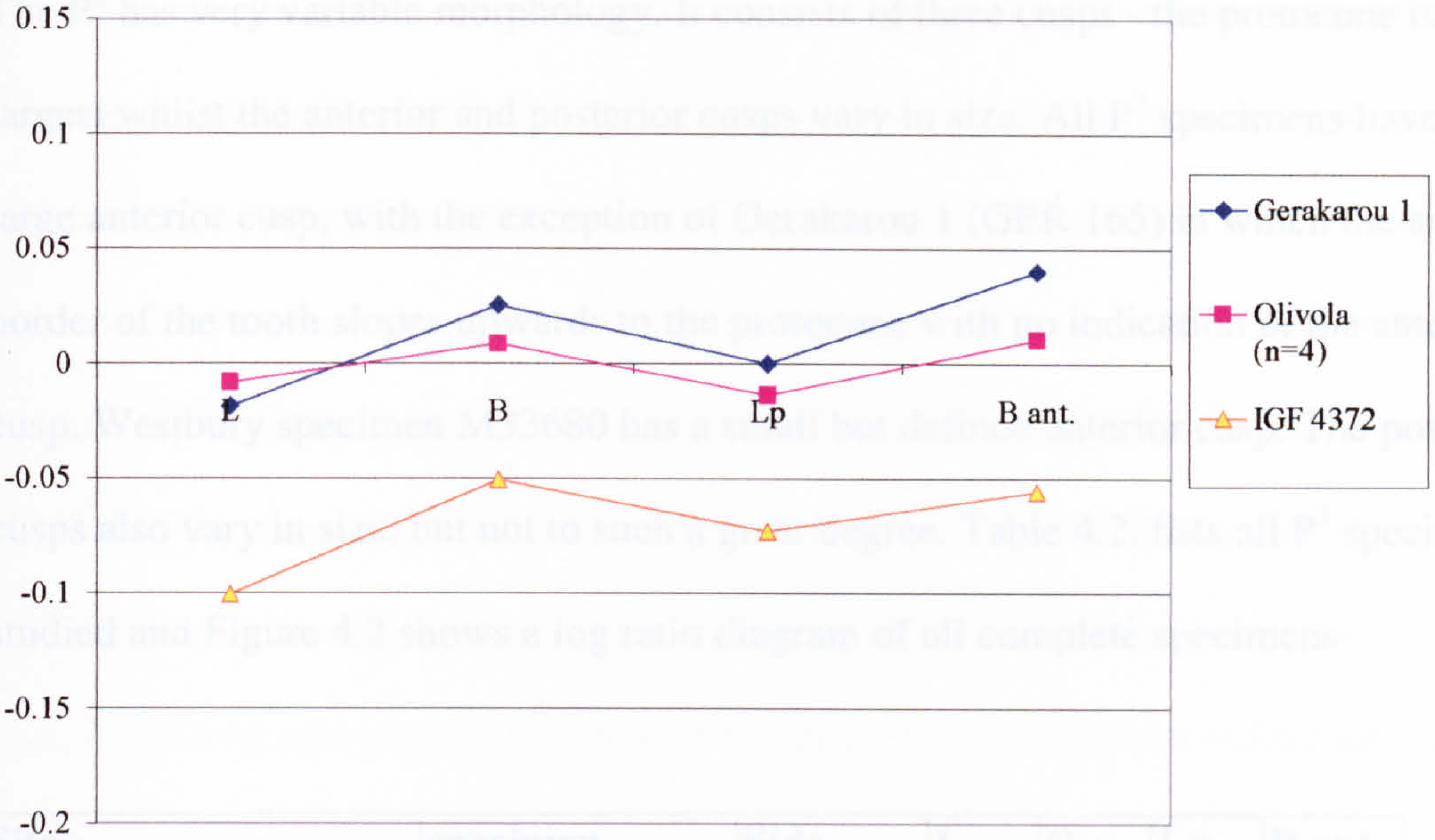

Figure 4.2a. Log ratio diagram of all Early (2.0 – 0.8Ma) *P. gombaszoegensis* P^3 with Gombasek specimen (GIH no number) as standard.

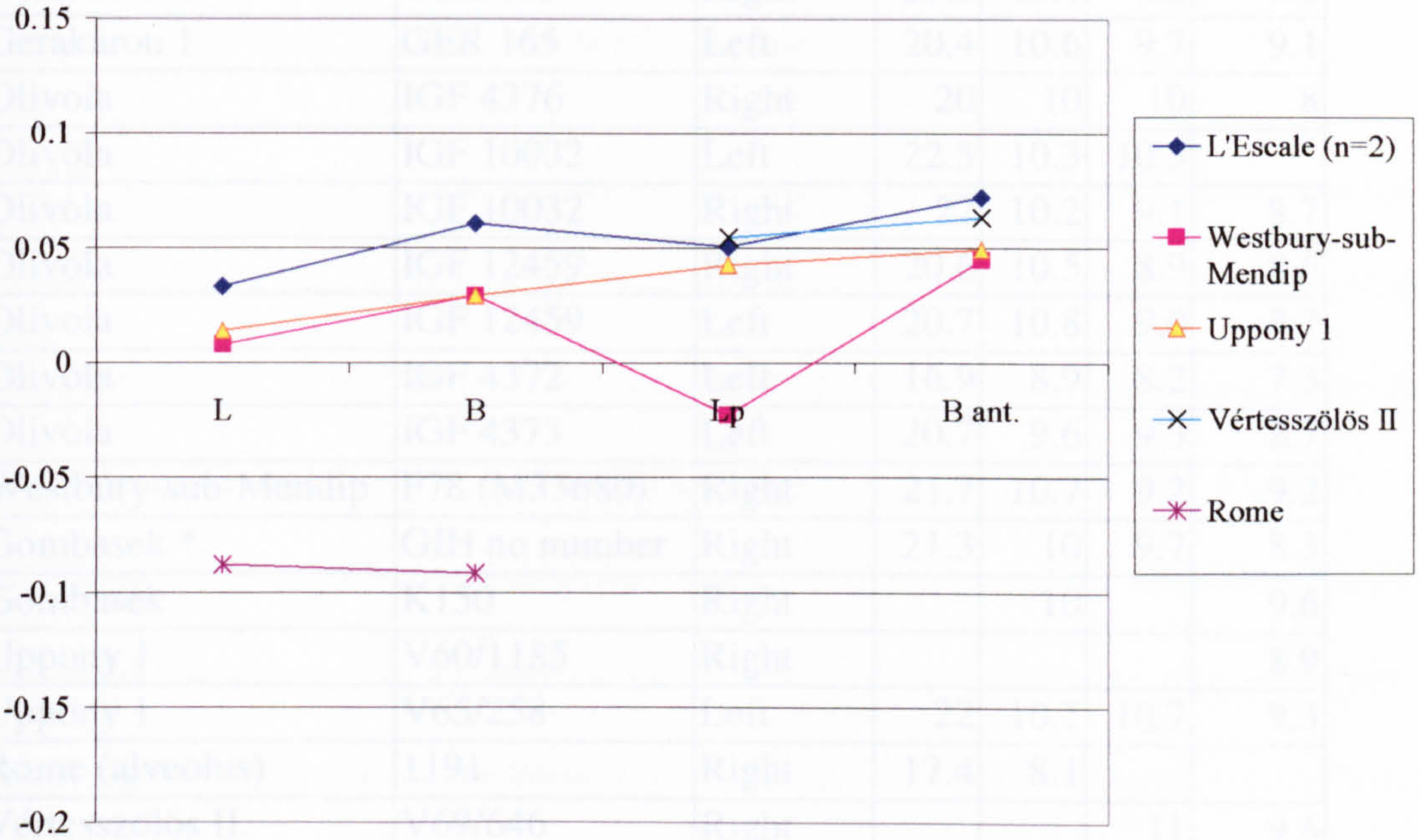

Figure 4.2b. Log ratio diagram of all Late (0.8 – 0.3Ma) *P. gombaszoegensis* P^3 with Gombasek specimen (GIH no number) as standard.

Figure 4.2. Log ratio diagrams of the P^3, using Gombasek specimen (GIH no number) as standard.

The P^3 has very variable morphology. It consists of three cusps - the protocone is the largest whilst the anterior and posterior cusps vary in size. All P^3 specimens have a large anterior cusp, with the exception of Gerakarou 1 (GER 165) in which the anterior border of the tooth slopes upwards to the protocone with no indication of the anterior cusp. Westbury specimen M33680 has a small but defined anterior cusp. The posterior cusps also vary in size, but not to such a great degree. Table 4.2. lists all P^3 specimens studied and Figure 4.2 shows a log ratio diagram of all complete specimens

Site	specimen	Side	L	B	Lp	B ant.
L'Escale	CD 1142	Right		11.7		
L'Escale (alveolus)	C-D 795	Right	21.5	11.2		
L'Escale	C-D 765	Right	23.0	11.4	10.8	9.6
L'Escale	C-D 7634	Left	23.0	11.5	11	9.9
L'Escale	C-D 768	Left		10.8		
Gerakarou 1	GER 165	Right	20.0	10.4	8.8	9.0
Gerakarou 1	GER 165	Left	20.4	10.6	9.7	9.1
Olivola	IGF 4376	Right	20	10	10	8
Olivola	IGF 10032	Left	22.5	10.3	10.5	
Olivola	IGF 10032	Right	22	10.2	9.1	8.7
Olivola	IGF 12459	Right	20.6	10.5	8.9	8.6
Olivola	IGF 12459	Left	20.7	10.8	9.0	8.7
Olivola	IGF 4372	Left	16.9	8.9	8.2	7.3
Olivola	IGF 4373	Left	20.7	9.6	9.3	8.7
Westbury-sub-Mendip	F78 (M33680)	Right	21.7	10.7	9.2	9.2
Gombasek *	GIH no number	Right	21.3	10	9.7	8.3
Gombasek	K150	Right		10		9.6
Uppony 1	V60/1185	Right				8.9
Uppony 1	V65/258	Left	22	10.7	10.7	9.3
Rome (alveolus)	1191	Right	17.4	8.1		
Vértesszölös II.	V69/646	Right			11	9.6

Table 4.2. P^3 measurements in millimetres, all specimens. * indicates specimen used as standard in log ratio diagrams. Abbreviations explained in Table 2.2.

The upper log ratio diagram (Figure 4.2a) shows that both of the older sites follow the same morphological pattern and have slightly broader teeth than the Gombasek standard. The smaller Olivola specimen (IGF 4372) has exactly the same proportions as the larger specimens. The older cats have shorter, broader teeth with smaller protocones than the standard Gombasek cat. The second diagram of younger cats (Fig. 4.2b) shows that they all have similar proportions but that the Gombasek tooth is shorter and broader than the other specimens. The majority of younger specimens have longer protocones and are slightly longer overall when compared with the older animals. The Westbury P^3 (M33680) has a much shorter protocone and smaller anterior cusp than all the other later specimens and is more similar to the proportions of the older Olivola and Gerakarou 1 cats. The Rome specimen (1191) is substantially smaller than the standard and all other *P. gombaszoegensis* fossils.

4.2.3. P^2

L'Escale (n=1) one central cusp.

Uppony 1 (n=1) one central cusp; small cingulum.

The P^2 is a small, single rooted tooth that is often lost in modern specimens. Koufos (1992) describes the Gerakarou 1 P^2 alveolus as being small and single rooted, which is the normal state for this tooth. However, Rome (1191) is unusual in having a very large alveolus on the right hand side, the shape of which indicates that it was originally double rooted. Of 1308 cats examined by Miles & Grigson (1990) a double rooted P^2 is mentioned twice, once in a Geoffroy's cat (*Felis geoffroyi*) and once in a jungle cat (*Felis chaus*). A maxillary fragment with P^2 alveolus and right P^3 from Westbury-sub-Mendip (M33680) also exhibits an interesting trait. The P^2 alveolus is present and it appears to have been a large, well-rooted tooth. Buccal to the P^2, there is second smaller alveolus which may have belonged to a supernumerary tooth. This is quite unusual but is it has been recorded in several of the modern cat species. Miles & Grigson (1990) examined 383 *Panthera* crania and found supernumerary P^2s in 4 specimens. Another possibility is that it was a retained deciduous tooth, but without the tooth itself it is difficult to confirm this.

Site	**Specimen**	**Side**	**Length**	**Breadth**
Gerakarou 1 (alveolus)	GER 163	Left	6.5	4.1
Gerakarou 1 (alveolus)	GER 163	Right	7.0	4.2
L'Escale (alveolus)	CD 795	Right		5.9
L'Escale	CD no number		7.2	5.3
Rome (alveolus)	1911	Left	3.8	2.6
Rome	1911	Right	9.3	3.2
Uppony 1	V60/1185	Right	6.2	5.1

Table 4.3. P^2 measurements in millimetres, all specimens.

4.2.4. C^s

Olivola. C^s (n=5) three specimens with large crowns (over 35mm), two others fragmentary, but much smaller (IGF 1226V and IGF 1227V). No measurements of IGF 1227V possible.

Huéscar. C^s (n=1) small.

Gombasek. C^s (n = 2) very robust.

L'Escale. C^s (n=1) long crown, slight crenelations on lingual ridge.

Westbury-sub-Mendip. C^s (n=4) M33669 has very long crown (over 45mm), other specimens smaller.

Rome. C^s (n=1) short crown

Uppony 1. C^s (n=1) too damaged to see morphology.

The C^s morphology is a contentious issue in *P. gombaszoegensis* studies, as there appears to be some confusion over the length and height of these teeth – in some cases they are short crowned, whereas other specimens are over 45mm in height (see Table 4.4). Bishop (1982:51) states that '[one of the] most obvious morphological differences are the relatively higher crowns of the canines which reach up to 50% of the entire length of the tooth' and this appears to have been followed in many papers. However, few complete crowns exist and many height measurements used are estimates. Reliance on this feature is also problematic because it is the most sexually dimorphic tooth (see section 3.3).

Site	Specimen	Side	L	B	H
L'Escale	C-D 795	Right	21.5	17	40.7
Huéscar	HU1/86/A12.	Right	17.5	13.7	
Ceyssaguet †	CEY 2 658		17.8	14.8	
Gerakarou 1 (alveolus)	GER 165	Right	20.8	17.6	
Olivola *	IGF 4376	Right	17.7	15.1	36 +
Olivola	IGF 4376	Left		14.2	
Olivola *	IGF 10032	Left	19.4	15.9	36 +
Olivola	IGF 1225 V	Left	18.5 +	12 +	39 +
Olivola	IGF 1226 V	Left	16.9	13.4	
Rome	Rome 1191	Right	15.5	12.2	33.1
Rome (alveolus)	Rome 1191	Left	15.4	12.1	
Westbury-sub-Mendip	F62	Left	21.1	16.0	
Westbury-sub-Mendip	M33669	Left	22.9	17.8	
Westbury-sub-Mendip	M33670	Right	21.5	16.9	
Westbury-sub-Mendip	F53	Left	18.2	14.3	
Gombasek	GIH no number	Left	20.0	15.5	
Gombasek	GIH no number	Left	21.2	17.7	
Uppony 1	V60/1185	Right	18.1	14.2	

Table 4.4. Upper canine measurements in millimetres. * denotes specimens used as standard in log ratio diagrams. † indicates specimens measured by A. Turner; these are not included in the morphological analyses. + shows that the specimen is broken or worn and that this is a minimum measurement. Abbreviations explained in section 2.3.1.1.

The log ratio diagram in Figure 4.3 shows all upper canines plotted against the mean of two Olivola specimens as standard. These teeth (indicated in Table 4.4) were used as the standard because of the paucity of fossil specimens for which height measurements were available. In this case the ranges of both the older and younger age groups cluster around the standards. The Gerakarou 1 canine is larger than the Olivola standards and the Ceyssaguet individual. It is possible that GER 165 is a male cat, as it also possesses a large sagittal crest. The later sites are equally spaced about the standard, with three sites larger and three sites smaller than the Gombasek specimen.

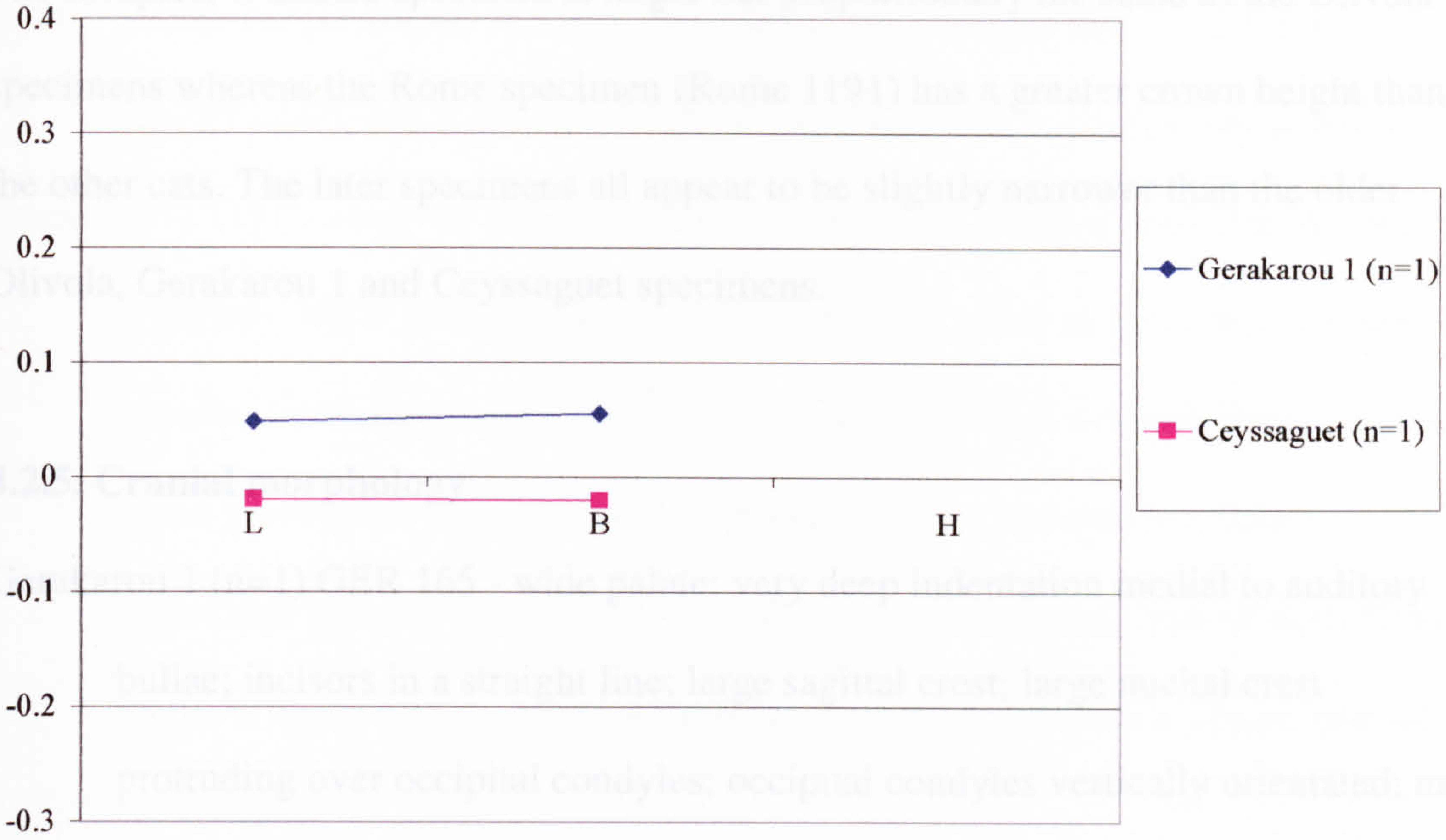

Figure 4.3a. Log ratio diagram of all Early (2.0 – 0.8Ma) *P. gombaszoegensis* C^s with mean of Olivola canines (n=2) as standard.

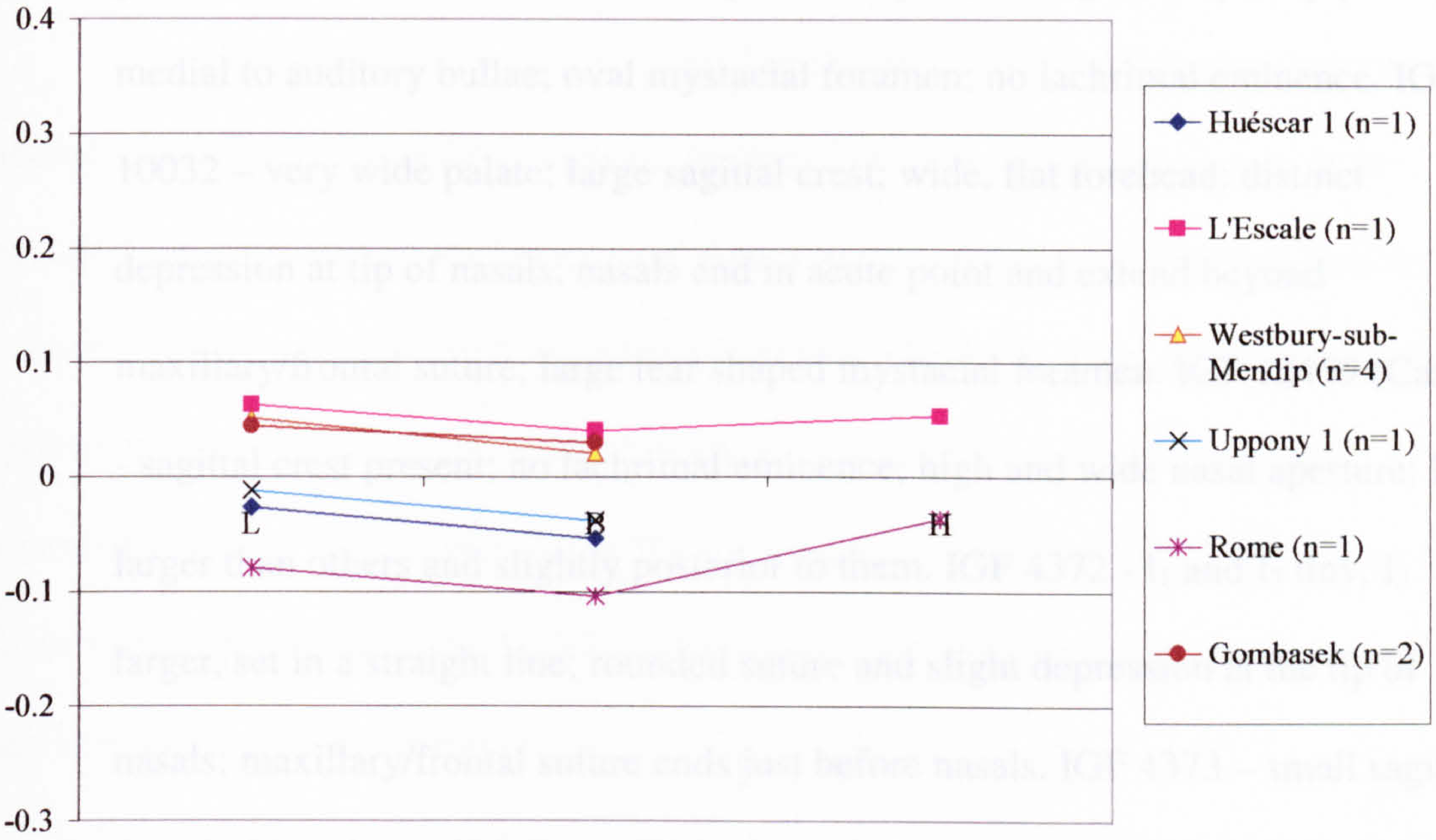

Figure 4.3b. Log ratio diagram of all Late (0.8 – 0.3Ma) *P. gombaszoegensis* C^s with mean of Olivola canines (n=2) as standard.

Figure 4.3. Log ratio diagrams of *P. gombaszoegensis* C^s, using mean of Olivola canines (IGF 4376 and IGF 10032) (n=2) as standard.

The complete L'Escale specimen is larger but proportionally the same as the Olivola specimens whereas the Rome specimen (Rome 1191) has a greater crown height than the other cats. The later specimens all appear to be slightly narrower than the older Olivola, Gerakarou 1 and Ceyssaguet specimens.

4.2.5. Cranial morphology

Gerakarou 1 (n=1) GER 165 - wide palate; very deep indentation medial to auditory bullae; incisors in a straight line; large sagittal crest; large nuchal crest protruding over occipital condyles; occipital condyles vertically orientated; nasal aperture wide and rounded; large oval mystacial foramen; pointed mastoid process.

Olivola (n=5) all specimens quite distorted. IGF 4376 – strong sagittal crest; pronounced nuchal crest; small occipital condyles, damaged; very deep pits medial to auditory bullae; oval mystacial foramen; no lachrimal eminence. IGF 10032 – very wide palate; large sagittal crest; wide, flat forehead; distinct depression at tip of nasals; nasals end in acute point and extend beyond maxillary/frontal suture; large tear shaped mystacial foramen. IGF 12459 (Cast) - sagittal crest present; no lachrimal eminence; high and wide nasal aperture; I^3 larger than others and slightly posterior to them. IGF 4372 - I_1 and I_2 tiny, I_3 larger, set in a straight line; rounded suture and slight depression at the tip of nasals; maxillary/frontal suture ends just before nasals. IGF 4373 – small sagittal crest; wide palate; oval mystacial foramen.

Halykés (n=1) Ah 200 - occipital fragment, large sagittal crest; very pronounced nuchal crest protruding over occipital condyles; occipital condyles large and upright; shallow dip medial to auditory bullae; pointed mastoid process.

L'Escale (n=3) all juvenile. CD898 premaxilla with I_1, I_2 and I_3. CD896 premaxilla with alveoli for permanent incisors. Incisors set in a straight line in both cases.

CD795 - occipital fragment, occipital condyles wide and vertically orientated.

Rome (n=1) 1191 - occipital condyles slanted; distinct postorbital constriction; small braincase; short, narrow palate; I^3 set slightly posterior to other incisors; small lachrimal eminence; nasal aperture heart shaped with a defined groove; nasal bones just extend beyond maxillary/frontal sutures and end in a point; depression at tip of nasals; small round mystacial foramen; base of skull flexed forward; slight dip medial to auditory bullae; mastoid process square; nuchal crest weak.

Based on the above descriptions it is apparent that there is a remarkable degree of similarity between those specimens which have been identified as *P. gombaszoegensis*. Table 4.5 provides measurements of all specimens.

The Greek specimens (Halykés and Gerakarou 1) have a more pronounced nuchal crest than the Olivola specimens, perhaps indicating slightly larger or more powerful neck muscles in the Greek cats. Again, this might suggest that the Gerakarou 1 cat was male. It is interesting that, in the specimens where the orbits are preserved, it appears that the lachrimal eminences are absent. Large lachrimal eminences are regarded as one of the characteristics of the modern jaguar (Seymour, 1989). Only two fossil jaguar specimens in the Smithsonian Museum collections had orbits preserved and both possessed this feature.

The position of the end of the nasals in relation to the maxillary/frontal suture was investigated by Boule (1906). He found that tigers had nasal bones which extend beyond the maxillary/frontal suture, whilst the nasals of lions end before this suture. The specimens of *P. gombaszoegensis* with nasals preserved follow the tiger pattern.

The majority of specimens have the following cranial characteristics in common: a strong sagittal crest; an oval mystacial foramen; absence of lachrimal eminences; vertically orientated occipital condyles; pointed mastoid processes; nasals extending beyond the maxillary frontal suture and a wide and rounded nasal aperture. These features can be contrasted against those of the Rome cat, which has entirely different morphology. The specimen gives the impression of a small cat with a slightly domed cranium and a short face. It also has lachrimal eminences, sloping occipital condyles and a heart shaped nasal aperture.

Site	Specimen	BL	PL	RB	MB	ZB	IO	POP	POC	CB
L'Escale	CD66 C-D 795									54.1
Gerakarou 1	GER 165	231	115	68	98				55.4	45.2
Olivola	IGF 4376	232								
Olivola	IGF 10032						59.2	94	53.3	
Olivola	IGF 12459		124	62+						
Rome	1191	211	105	60.4	88	154	48.1	82	48.9	48.0

Table 4.5. All cranial measurements in millimetres. + indicates that this is a minimum measurement.

Very few specimens were available that had not been significantly altered by post depositional deformation and this is reflected in the lack of fossil material in Figure 4.4. This log ratio diagram uses as standard the mean of all complete crania in the modern jaguar sample. The width of the palate was emphasised by Koufos (1992) in his description of the Gerakarou 1 material and it was also noticeable in the Olivola material. However, Figure 4.4 does not appear to show this; if anything, *P. gombaszoegensis* appears to have a narrow rostral breadth in comparison with the modern jaguar. Although Koufos (1992) does not explicitly state this, the Gerakarou 1 specimen is slightly deformed, as are the Olivola crania and this may indicate that post depositional processes have affected the appearance of the palate in these specimens. Figure 4.4 does show that the fossil specimens are all larger than the modern jaguar. Olivola specimen IGF 10032 is shown to have a much greater interorbital breadth (IO) than the other cats, which is confirmed by the morphological study.

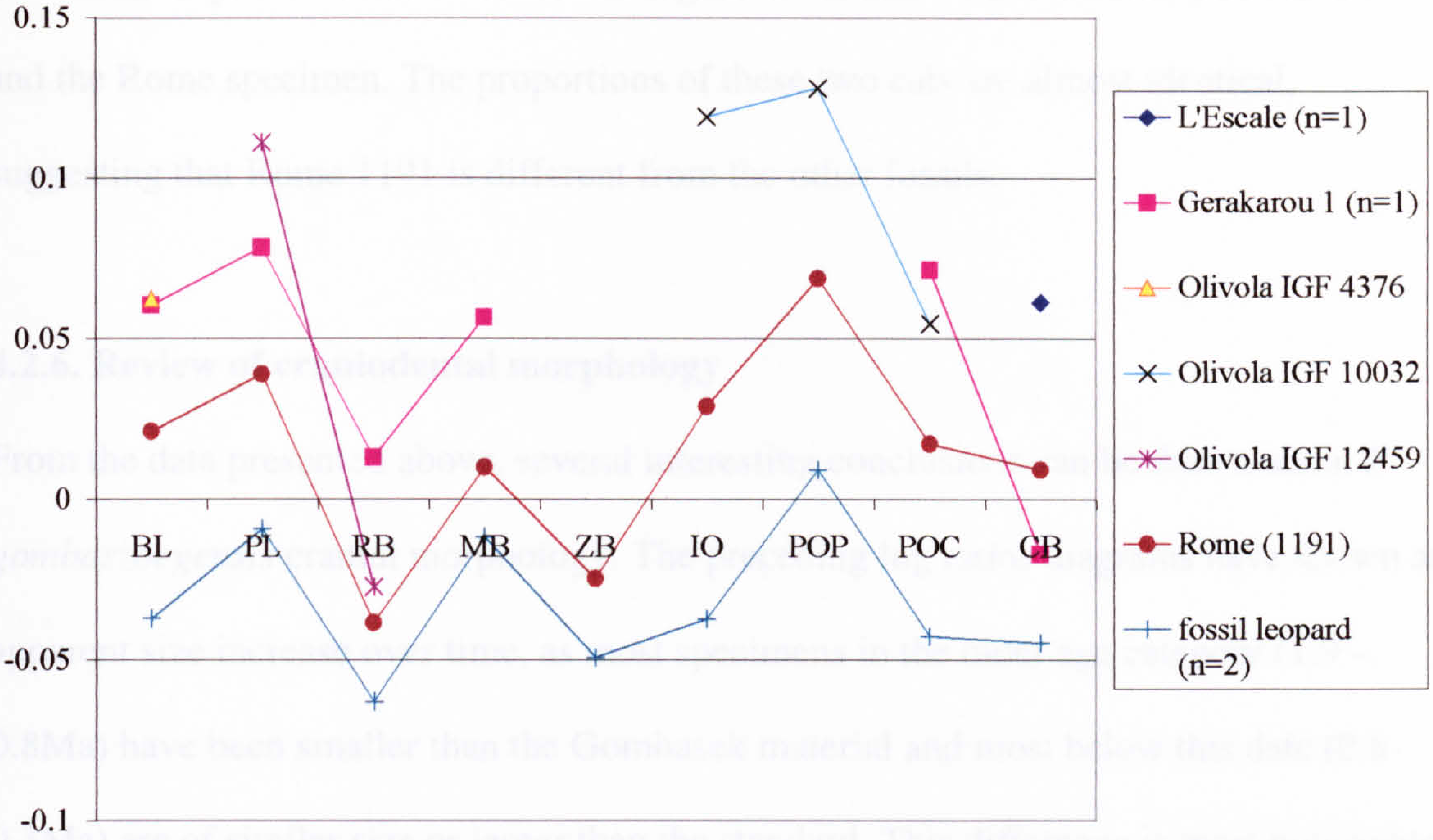

Figure 4.4. Log ratio diagram of all *P. gombaszoegensis* crania with the mean of modern jaguar sample (n=54) as standard. The fossil leopard has been included here for comparison with the Rome specimen.

The fossil leopard has been included in Figure 4.4 to show the similarities between it and the Rome specimen. The proportions of these two cats are almost identical, suggesting that Rome 1191 is different from the other fossils.

4.2.6. Review of craniodental morphology

From the data presented above, several interesting conclusions can be drawn about *P. gombaszoegensis* cranial morphology. The preceding log ratios diagrams have shown an apparent size increase over time, as most specimens in the older age category (1.9 – 0.8Ma) have been smaller than the Gombasek material and most below this date (0.8-0.3Ma) are of similar size or larger than the standard. This difference is most noticeable in the P^3 (Figure 4.2).

On all of the log ratio diagrams, three sites have been shown to be very similar to each other in both size and proportions. These are Westbury-sub-Mendip, L'Escale and Gombasek, the latter two sites are of roughly the same date, although Westbury is slightly later (see Appendix 2).

The one striking difference is the Rome specimen, which has been shown to be proportionally different in all preceding log-ratio diagrams. Figure 4.5 shows a log ratio diagram for the largest and smallest skulls of two modern cat species, calculated from the lion (n=98) and leopard (n=110) datasets using the Gerakarou 1 cranium as standard. As can be seen the lion shows less variation in size than the leopard, although this may be due to the effects of geographic variation on the leopard sample (see section 3.2). Overall the maximum variation for each species is approximately 0.25 on the $\log_{10}$ scale. If the Rome specimen fell outside this range then it would be beyond the extreme range of variation seen in a modern species and could confidently be excluded from *P. gombaszoegensis*. However, although it is much smaller than the other specimens it is not so small that size alone automatically excludes it from *P. gombaszoegensis*.

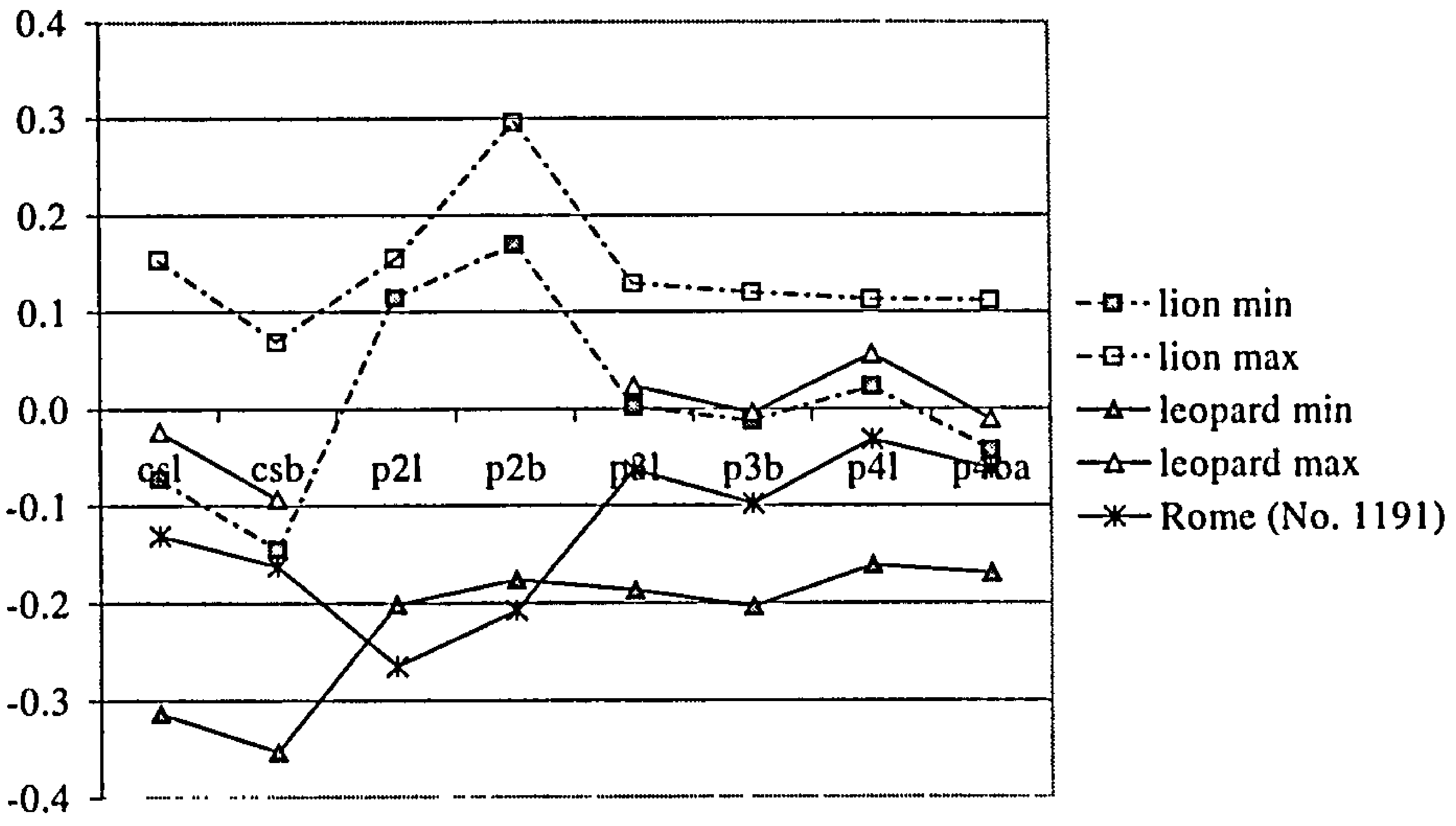

Figure 4.5. A Log_{10} ratio diagram to show the degree of maxillary variation within species using the smallest and largest individuals in a sample of modern lions (n=98) and modern leopards (n=110). Gerakarou 1 cranium as standard.

The Rome specimen has a much narrower P^4 than any of the *P. gombaszoegensis* specimens, a much smaller P^3 and an upper canine that is relatively longer for its cross section than in most other cats. In the majority of cases it is most similar to the modern leopard, although the P^4 is different from all other cats. In cranial proportions it is most similar to the fossil leopards from Equi cave (Figure 4.4), and in cranial morphology it is strikingly different from the other fossil specimens. Therefore, based on both morphological and morphometric characters I do not think that Rome specimen 1191 is *Panthera gombaszoegensis* and that the referral of this specimen to *P. gombaszoegensis* by Hemmer & Schütt (1969) was erroneous. It appears similar to the leopard in most analyses, and is probably *Panthera pardus*, as suggested by Kotsakis & Palombo (1979). Following this conclusion Rome specimen 1191 has been excluded from all following morphological analyses.

4.2.7. M_1

Tegelen. M_1 (n=4) one specimen (ST 103142) has a slight lingual bulge; no talonid; slight cingulum.

Santa Maria nr. Il Tasso (n=1) talonid and cingulum present; no lingual bulge.

Olivola. M_1 (n=4) small cingulum; no lingual bulge; large protoconid in comparison with paraconid.

Halykés. M_1 (n=1) too damaged to see morphology

Gombasek. M_1 (n = 7) protoconid strong and large in comparison with paraconid; talonid absent; small cingulum; two teeth have very small lingual bulges; of the five paraconids present three have a tiny cusp on the mesial surface – an ectoparaconid (two of which are paratypes, β915 and M9); two specimens could not be measured (both GIH no number).

L'Escale. M_1 (n=4) weak cingulum; tiny lingual bulge; ectoparaconid present; no talonid. CD5 unerupted within mandible, morphology not scored.

Westbury-sub-Mendip. M_1 (n=8) one specimen (MF58) has a tiny talonid (no measurements possible); M47340 and MF57 have slight lingual bulges; cingulum variable from weak to pronounced.

Mosbach. M_1 (n=1) defined lingual bulge; paraconid smaller than protoconid.

Rabenstein. M_1 (n=1) slight cingulum; upright paraconid, protoconid slopes back.

Uppony 1. M_1 (n=1) slight lingual bulge; tiny cingulum.

Koneprusy. M_1 (n=1) defined lingual bulge, pronounced cingulum.

The lower carnassial (M_1) has a conservative shape, primarily consisting of two cusps - the protoconid and paraconid – although occasionally a talonid or lingual bulge is present. Measurements of all teeth are given in Table 4.6 and a log ratio diagram of these specimens is shown in Figure 4.6.

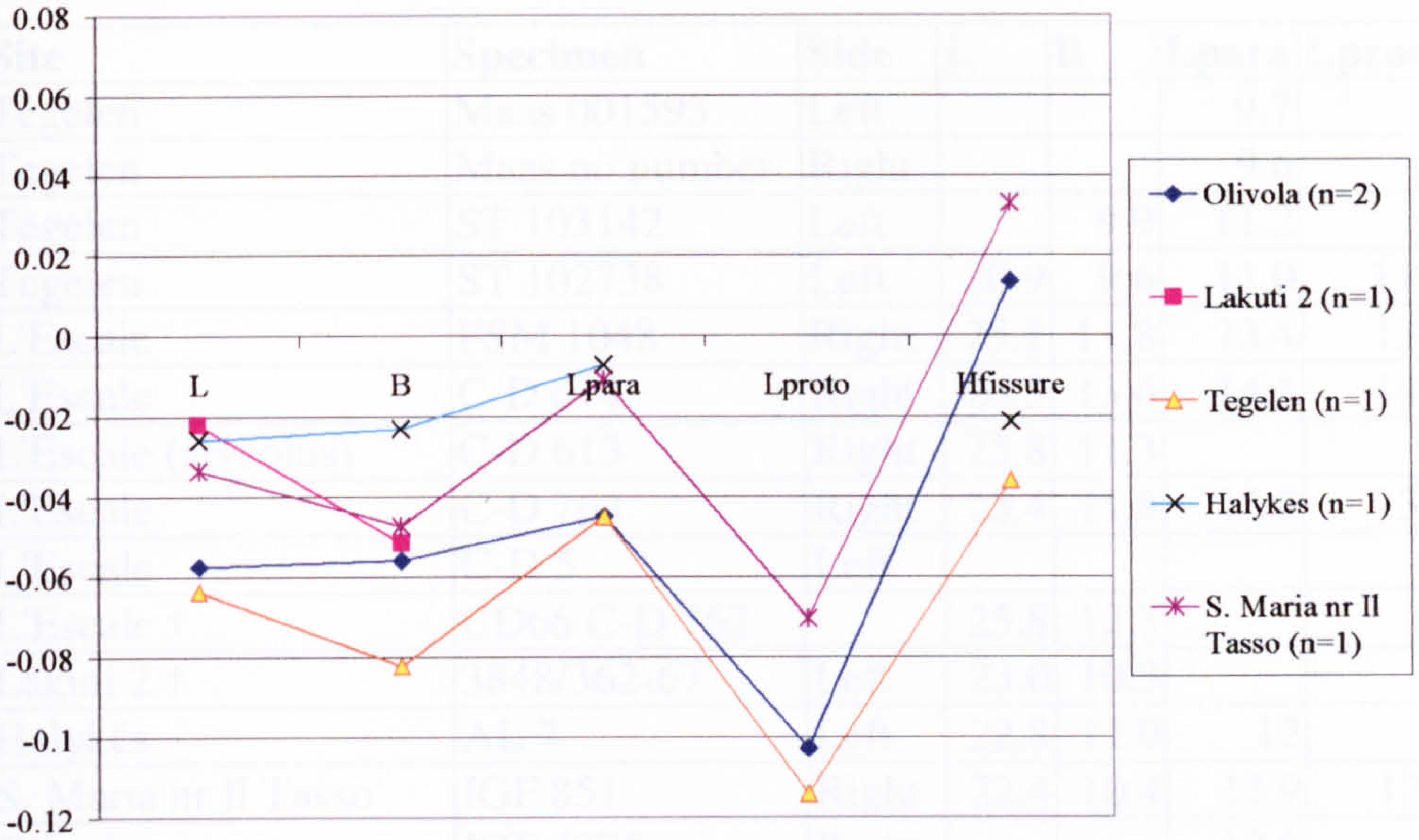

Figure 4.6a. Log ratio diagram of all Early (2.0 – 0.8Ma) *P. gombaszoegensis* M_1 with Gombasek mandible (GIH no number) as standard.

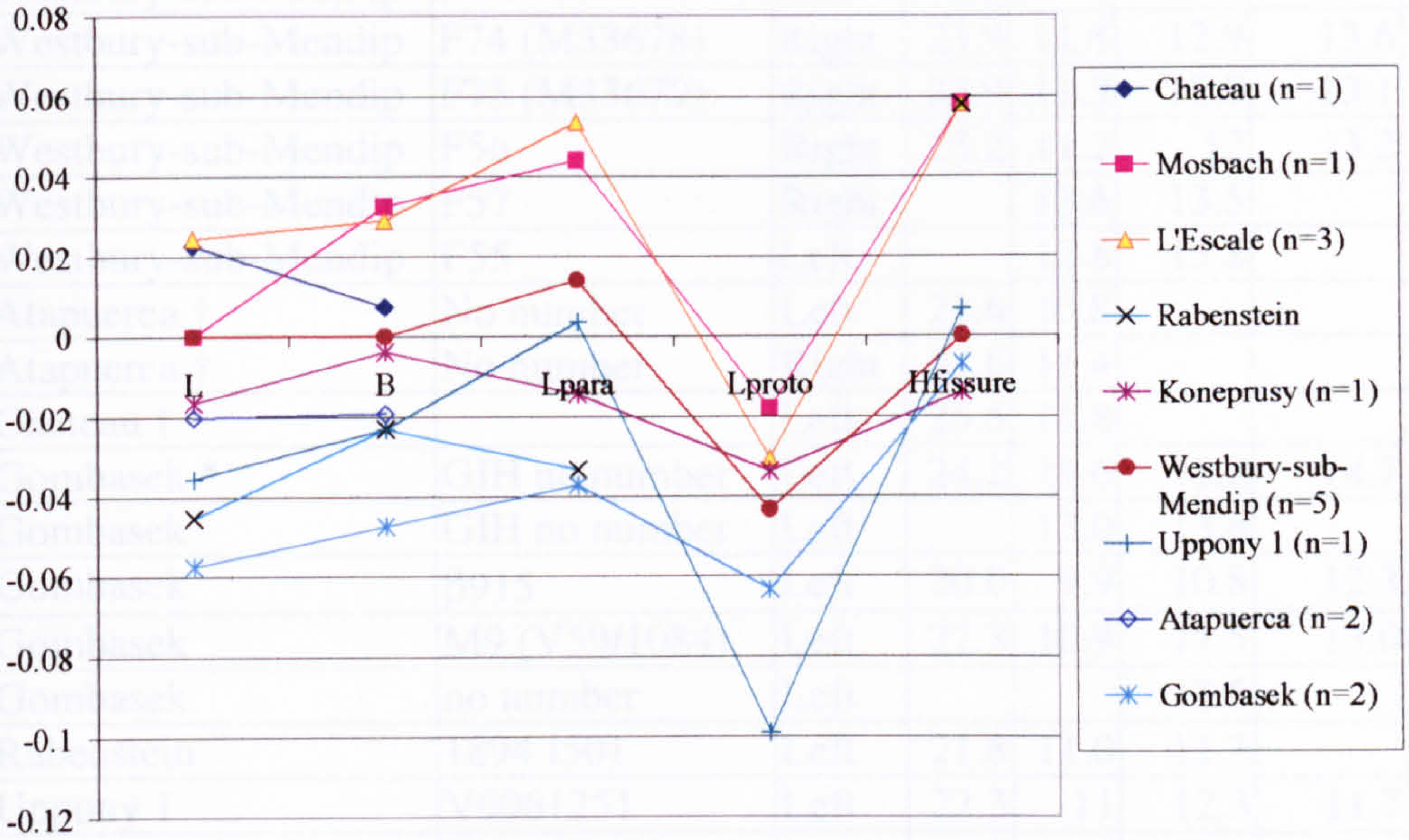

Figure 4.6b. Log ratio diagram of all Late (0.8 – 0.3Ma) *P. gombaszoegensis* M_1 with Gombasek mandible (GIH no number) as standard.

Figure 4.6. Log ratio diagrams of the M_1, using Gombasek mandible (GIH no number) as standard.

Site	Specimen	Side	L	B	Lpara	Lproto	Hfiss
Tegelen	Maas 001593	Left			9.7		6.5
Tegelen	Maas no number	Right			9.6		6.5
Tegelen	ST 103142	Left		9.9	11.2		5.9
Tegelen	ST 102738	Left	20.9	9.6	11.0	11.3	5.8
L'Escale	FSM 1048	Right	25.2	11.8	13.4	13.4	7.1
L'Escale	C-D 614	Right	26.3	13.6	14.1	14.2	7.6
L'Escale (alveolus)	C-D 613	Right	25.8	11.3			
L'Escale	C-D 763	Right	25.4	11.8	13.8	13.6	6.9
L'Escale	C-D 5	Left				14	4.7
L'Escale †	CD66 C-D 762		25.8	12.3			
Lakuti 2 †	3848/362-67	Left	23.0	10.3			
Halykés	AL 7	Left	22.8	11.0	12		6
S. Maria nr Il Tasso	IGF 851	Right	22.4	10.4	11.9	12.5	6.8
Olivola	IGF 4375	Right			12.6		
Olivola	IGF 853	Left	21.1	10.4	10.6	11.6	6.4
Olivola	IGF 852	Left	21.3	10.0	11.4	11.5	6.5
Olivola (Cast)	IGF 12458	Right		9.9	11.5		5.9
Mosbach	1968-398	Right	24.2	12.5	13.5	14.1	7.2
Westbury-sub-Mendip	M47598	Left	26.2	12	13.5	14.3	5 +
Westbury-sub-Mendip	M47340	Left	22.9	11.5	12.5	12.4	6.4
Westbury-sub-Mendip	F74 (M33678)	Right	23.9	11.8	12.9	13.6	6.7
Westbury-sub-Mendip	F75 (M33679)	Right	22.9	11.3	12.0	13.1	5.7
Westbury-sub-Mendip	F56	Right	25.2	11.2	12	13.2	5 +
Westbury-sub-Mendip	F57	Right		13.6	13.5		7.3
Westbury-sub-Mendip	F55	Left		12.8	13.8		7
Atapuerca †	No number	Left	22.6	10.8			
Atapuerca †	No number	Right	23.6	11.4			
Chateau †		Left	25.5	11.8			
Gombasek *	GIH no number	Left	24.2	11.6	12.2	14.7	6.3
Gombasek	GIH no number	Left		12.0	13.6		7.2
Gombasek	β915	Left	20.0	9.9	10.8	12.3	5.8
Gombasek	M9 (V59/1084)	Left	22.3	10.9	11.5	13.0	6.5
Gombasek	no number	Left			12.5		
Rabenstein	1894 I501	Left	21.8	11.0	11.3		7.2
Uppony 1	V6061251	Left	22.3	11	12.3	11.7	6.4
Koneprusy	IGF 851 V	Left	23.3	11.5	11.8	13.6	6.1

Table 4.6. Measurements in millimetres of all M_1 specimens seen in this analysis. * denotes specimen used as standard in log ratio analysis. † indicates specimens measured by A. Turner; these are not included in the morphological analyses. + shows that the specimen is broken or worn and that this is a minimum measurement. Abbreviations explained in Table 2.3.

The morphology of *P. gombaszoegensis* specimens is quite variable, only two specimens – IGF 851 from Santa Maria nr. Il Tasso and MF58 from Westbury sub

Mendip have talonid cusps and these are both very small, but the lingual bulge is more common. Out of a total of 25 teeth with this area preserved, 12 had lingual bulges, giving a total of 48% presence within the entire sample (discussed further in section 4.3.11). Another very interesting feature is the presence of an ectoparaconid on three out of five specimens from Gombasek and all specimens (n=3) from L'Escale. This feature has not been seen on teeth from any other sites and was not present in any of the fossil jaguar material examined. It is expressed as a small cusplet on the anterior edge of the paraconid.

The length and breadth proportions of the teeth are all very similar to the Gombasek standard, as shown in Table 4.6 and illustrated in Figure 4.6. Again, the older sites (pre 0.8Ma) are smaller than the Gombasek specimen, while the younger sites tend to be larger. There is distinct variation in the length of the protoconid (Lproto) and it appears that the Gombasek specimen has a larger protoconid than most other sites. It is most similar to the other Gombasek, Koneprusy and Westbury-sub-Mendip specimens.

4.2.8. P_4

Tegelen. P_4 (n=3) large protocone; robust posterior cusp; cingulum varies from slight to strong. No measurements of Maas 001593 possible.

Santa Maria nr. Il Tasso (n=1) strong cingulum; large anterior and posterior cusps.

Olivola. P_4 (n=5) large, robust anterior and posterior cusps; defined cingulum; IGF 12458 has small 'basin'.

Halykés. P_4 (n=1) strong protocone

Gombasek. P_4 (n = 3) strong cingulum; very large protocone; two teeth have a slight lingual 'basin'.

L'Escale. P_4 (n=5) low cingulum; very large, slightly backwards-sloping protocone;

anterior and posterior cusps vary from small to strong. One specimen has slight 'basin' (FSM 1048).

Westbury-sub-Mendip. P_4 (n=6) large, robust anterior and posterior cusps and cingulum except M33679 where the cusps and cingulum are smaller; large protocone.

Rabenstein. P_4 (n=1) anterior cusp large and defined; posterior cusp low and small; pronounced cingulum; small 'basin'.

Uppony 1. P_4 (n=1) very strong protocone; anterior cusp larger than posterior; slight 'basin'.

Koneprusy. P_4 (n=1) large, robust anterior and posterior cusps; pronounced 'basin'; large protocone, strong cingulum.

P_4 morphology appears quite conservative. The majority of specimens have a large protocone and large anterior and posterior cusps, with the exception of Westbury (M33679) and some L'Escale specimens in which these features are more variable. The Rabenstein mandible and the Uppony 1 specimen (V6061251) both have smaller posterior cusps when compared with the anterior.

A small proportion of the P_4 sample have a lingual 'basin'. This is seen as a lingual expansion of the posterior of the P_4 and is usually accompanied by a robust cingulum.

The log ratio diagrams in Figure 4.7 show that the earlier specimens are all of a similar size to the standard specimen from Gombasek, but they are slightly shorter and broader overall. There is also some variation in the length of the protocone within the sample. The later specimens have a slightly shorter protocone than the standard but are of a similar size. Most P_4 specimens with the exception of Rabenstein are slightly wider across the anterior of the tooth. The Rabenstein mandible is proportionally most similar to the Gombasek standard. The specimens from Westbury-sub-Mendip and L'Escale are very similar, as are those from Koneprusy and Uppony 1. Measurements of all P_4 specimens are listed in Table 4.7.

Site	Specimen	Side	L	B	Lp	B ant.
Tegelen	ST 103142	Left	20.2	9.7	11.2	7.9
Tegelen	ST 102738	Left	21	10.5	12.0	8.7
L'Escale	FSM 1048	Right	23.7	11.5	11.5	9.6
L'Escale (alveolus)	C-D 613	Right	22	11		
L'Escale ‡	C-D 763	Right	23.3	11.5	11.2	9.7
L'Escale ‡	C-D 763	Left	23.5	11.4	11.3	9.8
L'Escale	C-D 766	Right	24.1	12.0	12.2	10.4
L'Escale	C-D 767	Left	24.4	12.0	12.0	10.7
Lakuti 2 †	3848/362-67	Left	22.8	10.2	11.0	
Zasuhino †	978/389-11		21.4	9.5		
Halykés	AL 7	Left	21.7	10.7	11.4	9.6
S. Maria nr Il Tasso	IGF 851	Right	20.9	10.9	11.3	8.4
Olivola	IGF 4375	Right		10.5	11.2	
Olivola	IGF 4374	Left	18.9	9.6	10	8.1
Olivola	IGF 853	Left	20.7	10.3	11.0	8.5
Olivola	IGF 852	Left	19.4	10.1	8.3	9.6
Olivola (Cast)	IGF 12458	Right	22.0	10.3	11.1	9.5
Mosbach (alveolus)	1968-398	Right	23.5	9.9		
Westbury-sub-Mendip	M47471	Right	24.1	11.3	12	10.6
Westbury-sub-Mendip	M47572	Left	22.4	10.1	11	9
Westbury-sub-Mendip	M33678	Right	23.4	11.0	11.1	9.8
Westbury-sub-Mendip	M33679	Right	21.6	10	10.4	9
Westbury-sub-Mendip	M33682	Right		10 +	11	
Westbury-sub-Mendip	M33680	Right		11.3		
Atapuerca †	No number	Left	20.8	10.4	10.7	
Atapuerca †	No number	Right	21.8	10.2	10.6	
Chateau †	Chateau	Left	24.0	11.7	11.8	
Gombasek *	GIH no number	Left	21.9	10.3	10.8	8.7
Gombasek (alveolus)	GIH no number	Right	22.3	10.4		9.3
Gombasek	M51	Left		10.9	9.9	
Gombasek	no number	Left		11.4	11	
Rabenstein	1894I501	Left	21.2	10.5	8.6	10.5
Uppony 1	V6061251	Left	22.7	10.8	10.2	9.2
Koneprusy	IGF 851 V	Left	21.5	11.0	9.9	9.2

Table 4.7. All P_4 measurements in millimetres. * denotes the standard used in log ratio diagrams. † indicates specimens measured by A.Turner; these are not included in the morphological analyses. + shows that the specimen is broken or worn and that this is a minimum measurement. ‡ same specimen numbers but not necessarily the same individual, scored separately in morphological analysis. Abbreviations explained in Table 2.2.

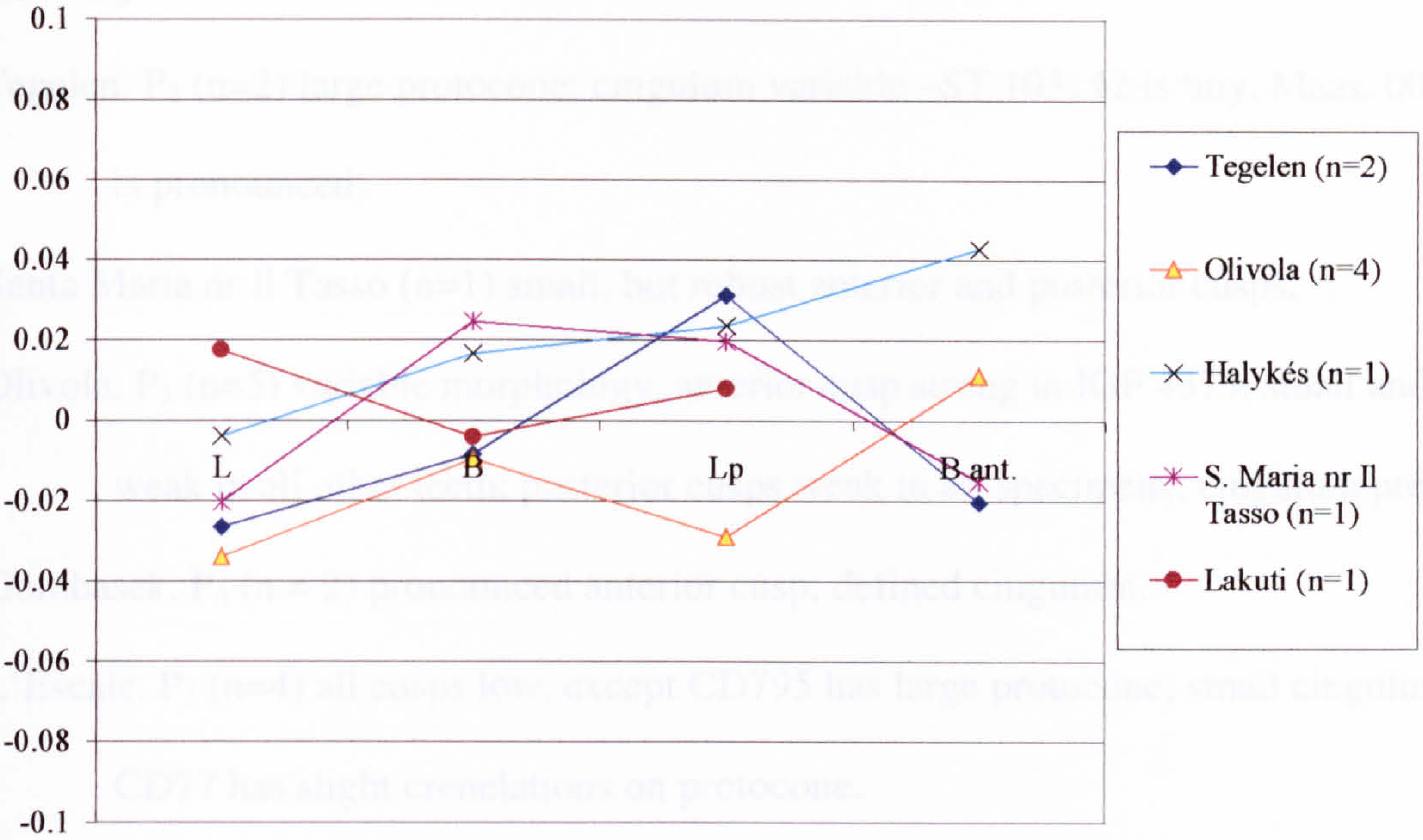

Figure 4.7a. Log ratio diagram of all Early (2.0 – 0.8Ma) *P. gombaszoegensis* P_4 with Gombasek mandible (GIH no number) as standard.

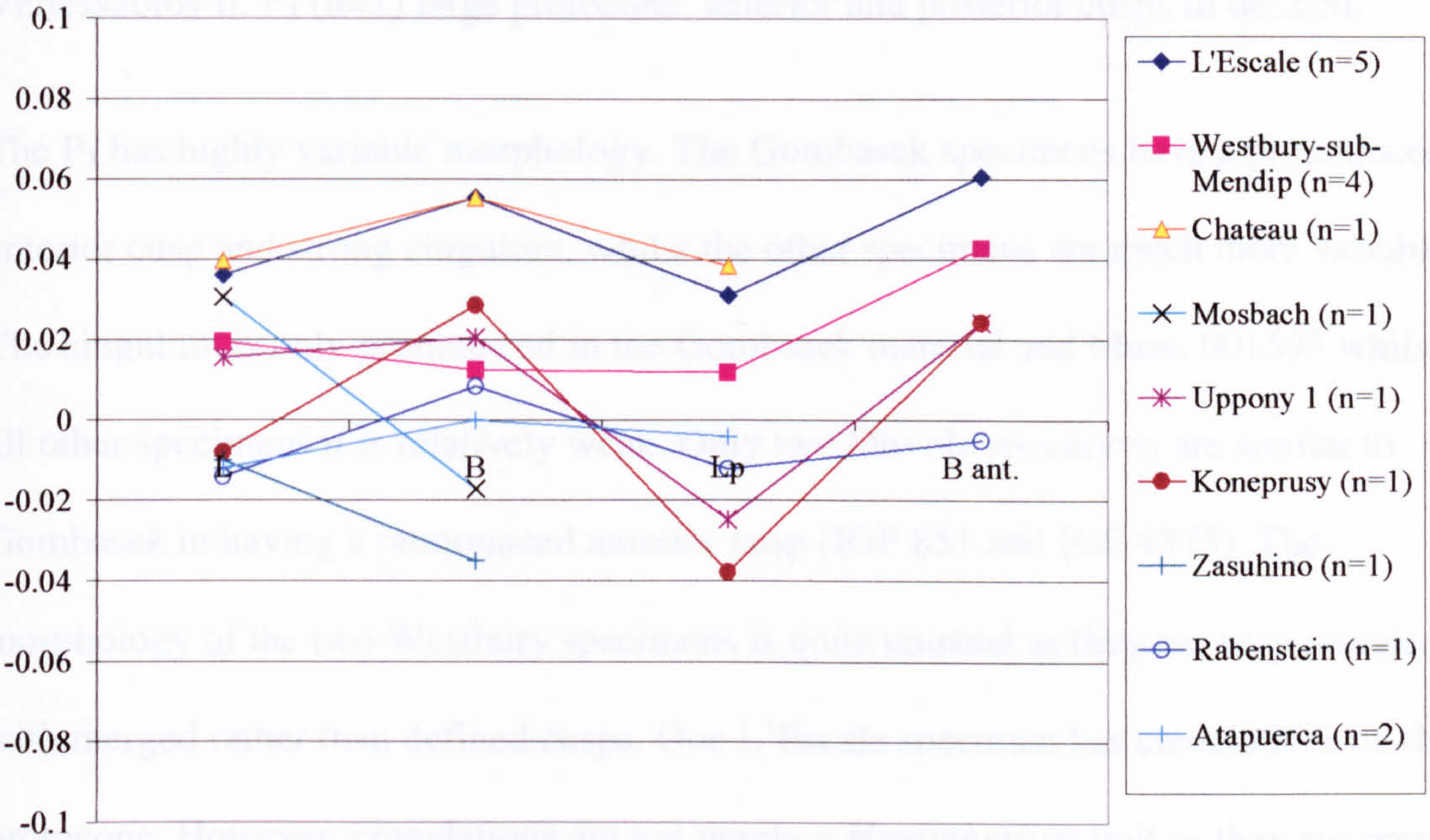

Figure 4.7b. Log ratio diagram of all Late (0.8 – 0.3Ma) *P. gombaszoegensis* P_4 with Gombasek mandible (GIH no number) as standard.

Figure 4.7. Log ratio diagrams of the P_4, using Gombasek mandible (GIH no number) as standard.

4.2.9. P_3

Tegelen. P_3 (n=2) large protocone; cingulum variable –ST 103142 is tiny, Maas. 001593 is pronounced.

Santa Maria nr Il Tasso (n=1) small, but robust anterior and posterior cusps.

Olivola. P_3 (n=5) variable morphology, anterior cusp strong in IGF 4375, small and weak in all other teeth; posterior cusps weak in all specimens; cingulum present.

Gombasek. P_3 (n = 2) pronounced anterior cusp; defined cingulum.

L'Escale. P_3 (n=4) all cusps low, except CD795 has large protocone; small cingulum; CD77 has slight crenelations on protocone.

Westbury-sub-Mendip. P_3 (n=2) very rounded; all cusps merge; tiny cingulum.

Rabenstein. P_3 (n=1) large anterior cusp; small posterior cusp and cingulum.

Stránská Scála 1. P_3 (n=1) small, weak anterior and posterior cusps and cingulum.

Vértesszölös II. P_3 (n=1) large protocone; anterior and posterior cusps ill defined.

The P_3 has highly variable morphology. The Gombasek specimens have a pronounced anterior cusp and strong cingulum, whilst the other specimens are much more variable. The cingulum is only pronounced in the Gombasek material and Maas. 001593 whilst in all other specimens it is relatively weak. Only two Olivola specimens are similar to Gombasek in having a pronounced anterior cusp (IGF 851 and IGF 4375). The morphology of the two Westbury specimens is quite unusual as they are very rounded, with merged rather than defined cusps. One L'Escale specimen has crenelations on the protocone. However, crenelations are not purely a *Homotherium* trait as they are present in some specimens of modern *Panthera* (pers. obs.). Measurements of the P_3 are given in Table 4.8.

In this case on the log ratio diagrams (Figure 4.8) an isolated Gombasek tooth [Fvz 24 (V59/1041)] is used as the standard as the mandible measurements are taken on the alveolus. The older specimens are similar to the standard but appear to be broader

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than the Gombasek specimen. In the younger age group there is a distinct split between sites which have P_3s that are broader than the standard and those that are narrower.

Site	Specimen	Side	L	B	Lp	B ant
Tegelen	Maas 001593	Left		5.8		
Tegelen	ST 103142	Left	14			
L'Escale (alveolus)	C-D 613	Right	17	8		
L'Escale ‡	C-D 763	Left	17.0	8.1	9.4	6.7
L'Escale ‡	C-D 763	Right	17.1	8.7	9.3	7.1
L'Escale	C-D 771	Right	17.6	8.7		
L'Escale	CD 795	Left	17.2	9.2	9.9	7.3
L'Escale †	C-D 762		16.9	8.5		
L'Escale †	C-D 772		16.7	9.0		
Lakuti 2 †	3848/362-67	Left	15.5	7.1		
Zasuhino †	978/389-11		14.0	6.9		
S. Maria nr Il Tasso	IGF 851	Right	16.4	9.3	8.8	7.2
Olivola	IGF 4375	Right	16.7	9.3	8.5	
Olivola	IGF 4374	Left	13.9	8.0	7.9	6.8
Olivola	IGF 853	Left	14.6	7.9	8.2	6.0
Olivola	IGF 852	Left	15.0	8.2	7.9	6.5
Olivola (Cast)	IGF 12458	Right	16.4	8.3	8.7	6.9
Mosbach (alveolus)	1968-398	Right	16.4	7.4		
Westbury-sub-Mendip	M47378	Right	16.6	7.2	9.0	7.1
Westbury-sub-Mendip	M47379	Right	17.1	8.2	9.4	7.2
Westbury-sub-Mendip (alveolus)	M33678	Right	14.5	6.7		
Atapuerca †	No number	Left	16.1	7.3		
Atapuerca †	No number	Right	15.3	6.8		
Chateau †	Chateau	Left	17.7	8.6		
Gombasek (alveolus)	GIH no number	Left	16	7		
Gombasek	GIH no number	Right	16.5	7.4		
Gombasek *	Fvz 24 (V59/1041)	Right	17.1	8	8.6	7.3
Rabenstein	1894 I501	Left	13.5	7.2	7.4	6.2
Stránská Scála 1 (Cast)	1938	Right	12.0	5.9	6.4	5.6
Vértesszölös II	V69/643	Right	19.2	9.8	10.4	8
Koneprusy (alveolus)	IGF 851 V	Left	16.6	7.5		

Table 4.8. All measurements of P_3 in millimetres. * indicates tooth used as standard in log ratio diagrams. † indicates specimens measured by A. Turner; these are not included in the morphological analyses. ‡ same specimen numbers but not necessarily the same individual, scored separately in morphological analysis. Abbreviations are explained in Table 2.2.

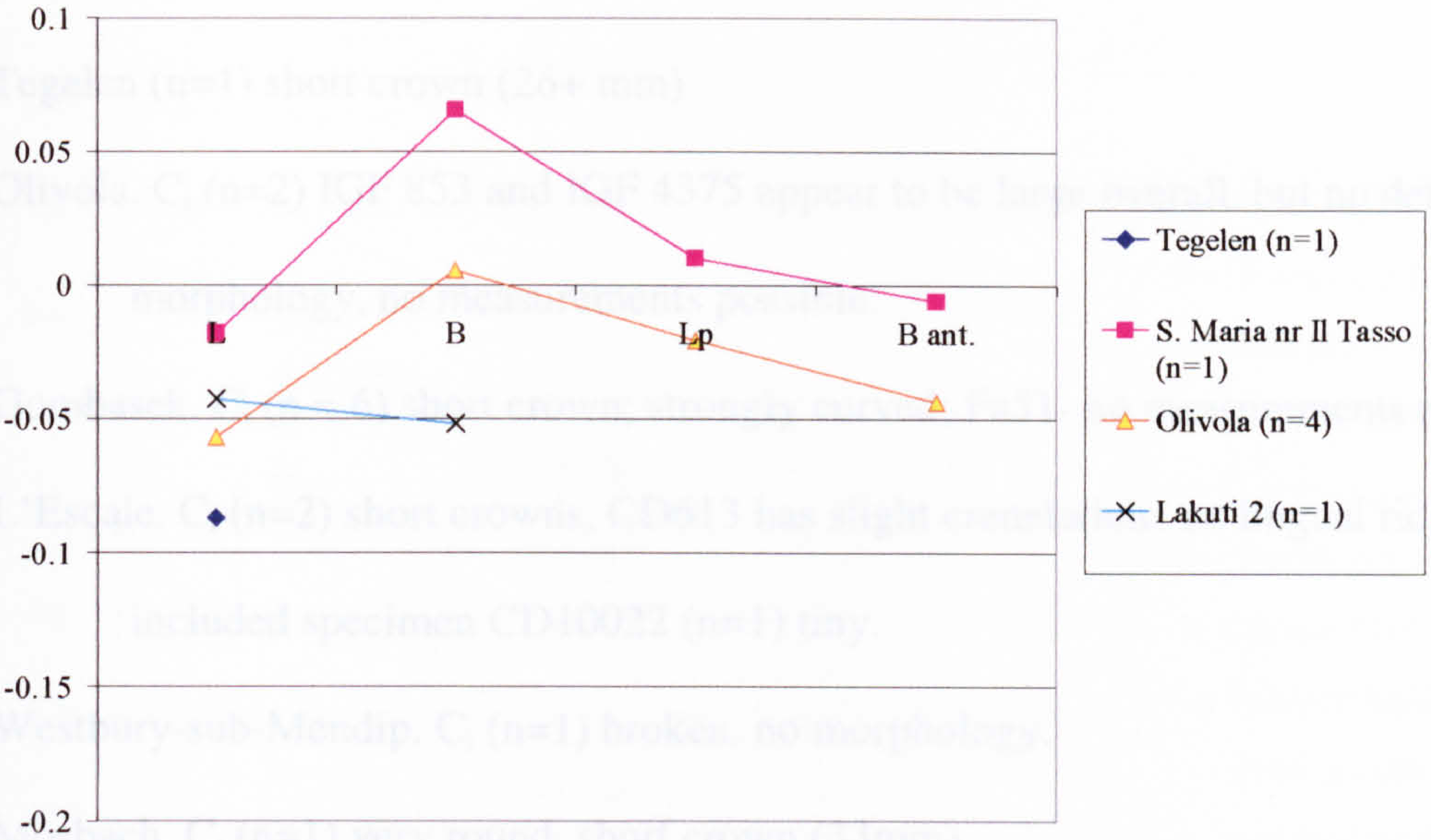


Figure 4.8a. Log ratio diagram of all Early (2.0 – 0.8Ma) *P. gombaszoegensis* P_3 with Gombasek tooth [Fvz 24 (V59/1041)] as standard.

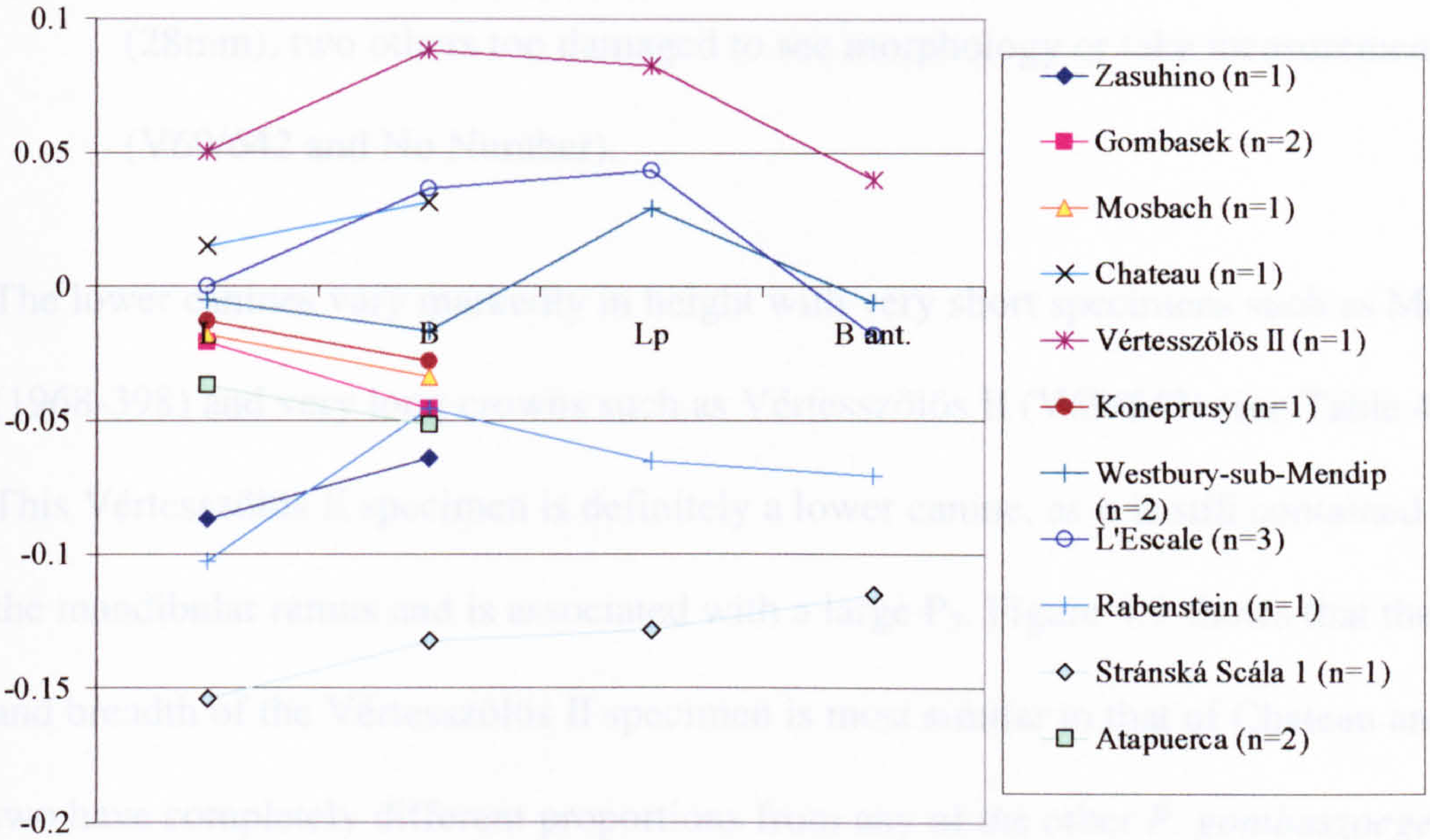


Figure 4.8b. Log ratio diagram of all Late (0.8 – 0.3Ma) *P. gombaszoegensis* P_3 with Gombasek tooth [Fvz 24 (V59/1041)] as standard.

Figure 4.8. Log ratio diagrams of the P_3, using Gombasek tooth [Fvz 24 (V59/1041)] as standard.

4.2.10. C_i

Tegelen (n=1) short crown (26+ mm)

Olivola. C_i (n=2) IGF 853 and IGF 4375 appear to be large overall, but no definable morphology, no measurements possible.

Gombasek. C_i (n = 6) short crown; strongly curved; Fa51- no measurements possible.

L'Escale. C_i (n=2) short crowns, CD613 has slight crenelations on lingual ridge. Also included specimen CD10022 (n=1) tiny.

Westbury-sub-Mendip. C_i (n=1) broken, no morphology.

Mosbach. C_i (n=1) very round, short crown (33mm).

Stránská Scála 1. C_i (n=1) tiny

Uppony 1. C_i (n=1) small; short crown.

Vértesszölös II. C_i (n=4) V69/643 has a long crown (39mm); V69/642 has short crown (28mm); two others too damaged to see morphology or take measurements (V69/642 and No Number).

The lower canines vary markedly in height with very short specimens such as Mosbach (1968-398) and very long crowns such as Vértesszölös II (V69/643) (see Table 4.9). This Vértesszölös II specimen is definitely a lower canine, as it is still contained within the mandibular ramus and is associated with a large P_3. Figure 4.9 shows that the length and breadth of the Vértesszölös II specimen is most similar to that of Chateau and these two have completely different proportions from any of the other *P. gombaszoegensis* specimens. In sharp contrast, the second Vértesszölös II specimen (V69/642) has completely different morphology with a greatly reduced canine height. This reduction is not seen in any of the other specimens in Figure 4.9. Comparison of tooth heights and widths in Table 4.9 again shows that this tooth is different. Although it possesses grooves, these may be a result of damage or wear and it is likely that Vértesszölös II specimen V69/642 is from a bear.

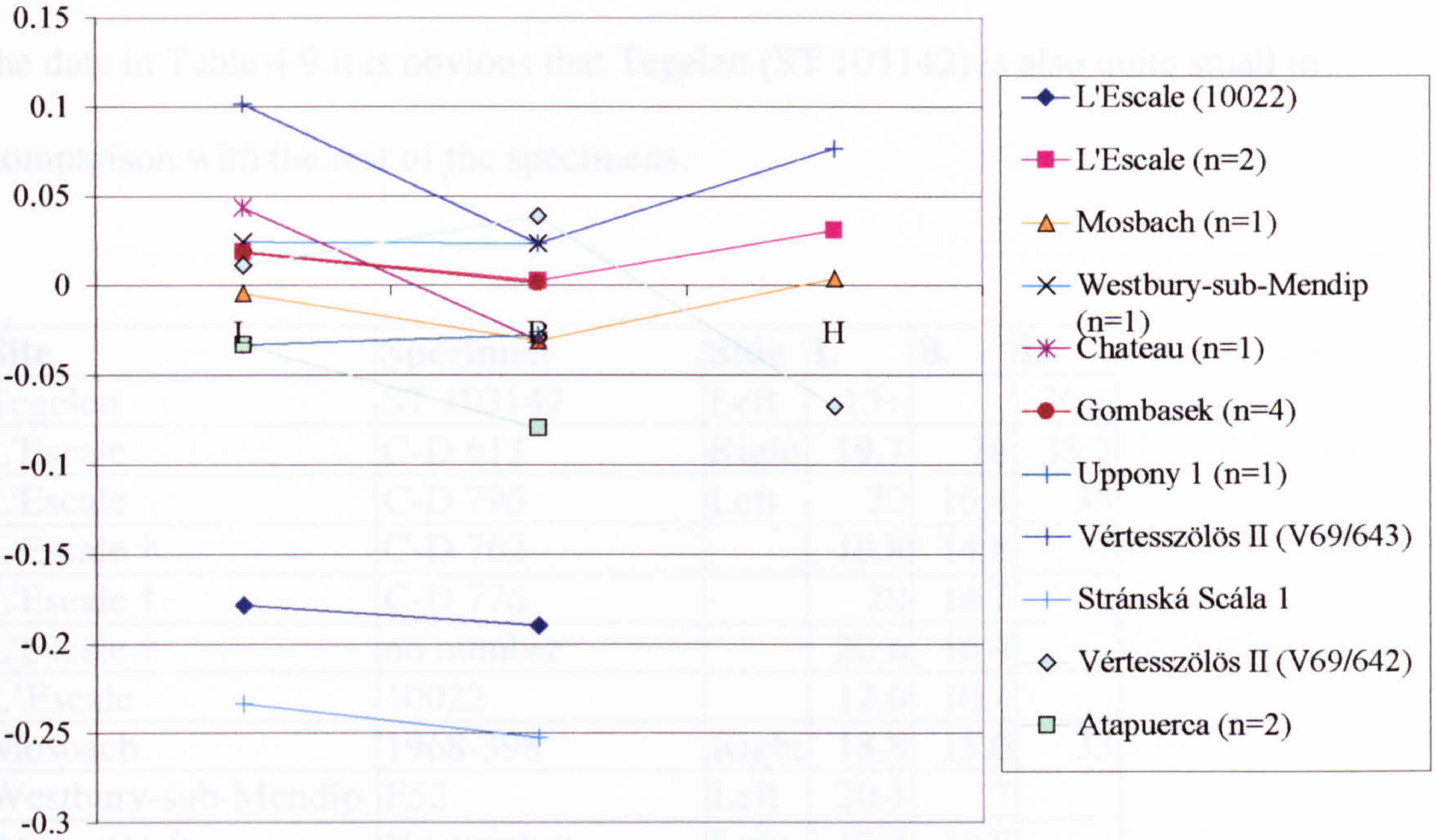


Figure 4.9. Log ratio diagram of all *P. gombaszoegensis* C_i with Gombasek mandible (GIH no number) as standard.

Figure 4.9 also shows that the Stránská Scála 1 cat is very different, and that it and L'Escale (CD10022) have much smaller canines than any of the other specimens. From the data in Table 4.9 it is obvious that Tegelen (ST 103142) is also quite small in comparison with the rest of the specimens.

Site	Specimen	Side	L	B	H
Tegelen	ST 103142	Left	15+		26 +
L'Escale	C-D 613	Right	19.7	16	35.2
L'Escale	C-D 796	Left	20	16.4	35
L'Escale †	C-D 762		19.8	14.8	
L'Escale †	C-D 776		20	14.7	
L'Escale †	no number		20.6	16.4	
L'Escale	10022		12.6	10.4	
Mosbach	1968-398	Right	18.8	15.0	33
Westbury-sub-Mendip	F52	Left	20.1	17	
Atapuerca †	No number	Left	17.7	12.8	
Atapuerca †	No number	Right	17.4	14.0	
Chateau †	Chateau	Left	21	15	
Gombasek *	GIH no number	Left	19.0	16.1	32.7
Gombasek	GIH no number	Right	21.7	17.3	
Gombasek	GIH no number	Right	19.8	16.8	
Gombasek	fa53 (V 59/1044)	Left	17	14.4	
Gombasek	no number	Left	20.8	16.1	
Stránská Scála 1 (Cast)	1938	Right	11.1	9	
Uppony 1	V60/1249	Left	17.6	15.1	
Vértesszölös II	V69/643	Right	24	17	39
Vértesszölös II	V69/642	Left	19.5	17.6	28

Table 4.9. Lower canine measurements in millimetres. * denotes standard used in log ratio diagrams. † indicates specimens measured by A. Turner; these are not included in the morphological analyses. + shows that the specimen is broken or worn and that this is a minimum measurement. Abbreviations explained in section 2.3.

4.2.11. Mandible morphology

Tegelen (n=1) inferior border of ramus curved; masseteric fossa ends before M_1; two mental foramina, one below anterior root of the P_3, one below diastema; curved symphysis; no symphyseal bulge; P_4 most buccal tooth.

S. Maria nr Il Tasso (n=1) straight symphysis; symphyseal bulge present; inferior border of ramus straight; masseteric fossa ends before M_1; two mental foramina, one below canine, one below P_3 centre. P_3 and P_4 most buccal teeth.

Olivola (n=5) IGF 4375 – curved then vertical symphysis; no symphyseal bulge; masseteric fossa ends at M_1; two mental foramina, one is enormous and below diastema, one below P_3 anterior root. IGF 4374 – masseteric fossa ends under M_1; straight symphysis; slight symphyseal bulge; pronounced breadth below P_4; two mental foramina, one below diastema, one below anterior P_3; P_3 most buccal tooth. IGF 853 (juvenile) masseteric fossa ends before M_1; curved symphysis. IGF 852 – one mental foramen visible below anterior P_3, P_3 posterior most buccal. IGF 12458 – one mental foramen visible below anterior P_3.

Halykés (n=1) masseteric fossa ends at or just below M_1; flat lingual surface; P_3 and P_4 posterior most buccal.

L'Escale (n=3) all juvenile. Masseteric fossa ends under M_1; no symphyseal bulge; straight symphysis; (CD613) two mental foramina, one double beneath P_3, one below diastema.

Westbury sub Mendip (n=2) M33679 – masseteric fossa ends under M_1. M33678 – masseteric fossa ends at M_1; two mental foramina one below diastema, one below anterior root of P_3; inferior border of ramus slightly curved; no symphyseal bulge; symphysis straight; P_4 most buccal tooth.

Gombasek (n=2) no symphyseal bulge; masseteric fossa ends at M_1; P_4 most buccal tooth, enormous mental foramen beneath P_3.

Mosbach (n=1) straight inferior border of ramus; straight symphysis; no symphyseal bulge; masseteric fossa ends at M_1. Two mental foramina, one below diastema, one below middle P_3.

Stránská Scála (n=1) vertical symphysis; no symphyseal bulge; two foramina, one below diastema, one below middle P_3.

Koneprusy (n=1) masseteric fossa ends beneath M_1; straight symphysis; distinct symphyseal bulge; pronounced breadth below P_4; two mental foramina, one below diastema, one below anterior P_3. P_4 most buccal.

Rabenstein (n=1) curved inferior border; masseteric fossa ends under M_1; two large mental foramina, one below diastema, 1 below anterior P_3; P_4 most buccal tooth.

It has been suggested in the past that a variety of features of the mandibular corpus can be used to identify *P. gombaszoegensis* such as the depth of the mandible (Spassov & Raichev, 1997). The thickness of the ramus was suggested as a diagnostic feature of *P. gombaszoegensis* by Bishop (1982). This seemed a reasonable suggestion as there were only two mandible fragments known from Westbury sub Mendip and one of these showed great ramal thickening. This is specimen M33679 which is a right mandible fragment containing the P_4 and M_1 The lingual surface of this mandible has a distinct bulge of smooth bone, just beneath the alveolus separating the M_1 and P_4. This is the position in which the BP/4 measurement is taken, but in this case the bulge is greatly exaggerated. After examining many other specimens from different sites, this is the only one to possess such an extreme bulge. However, a specimen from Gombasek (GIH no number) also shows mandibular thickening, in this case on the buccal surface (Figure 4.10). Table 4.10 shows the BP/4 measurements from a variety of specimens and it is apparent that the Westbury specimen is larger than any of these. These bulges are very smooth and show no signs of sinuses that would indicate an abscess within the ramus and they are therefore regarded as non-specific pathologies, rather than diagnostic *P. gombaszoegensis* features. The question of an abscess within the ramus may be resolved in the future by X-raying these specimens and checking for sinus development.

Site	Specimen	BP/4
Westbury *	M33679	22.3
Chateau	No number	21.5
Gombasek *	No number	20.1
Westbury	M33678	18.8
Olivola	IGF 853	15.9
Tegelen	ST 103142	11.9

Table 4.10. Measurements in millimetres of pathological (*) and non pathological specimens showing the range of BP/4 in *Panthera gombaszoegensis* specimens. (Abbreviations follow Table 2.6).

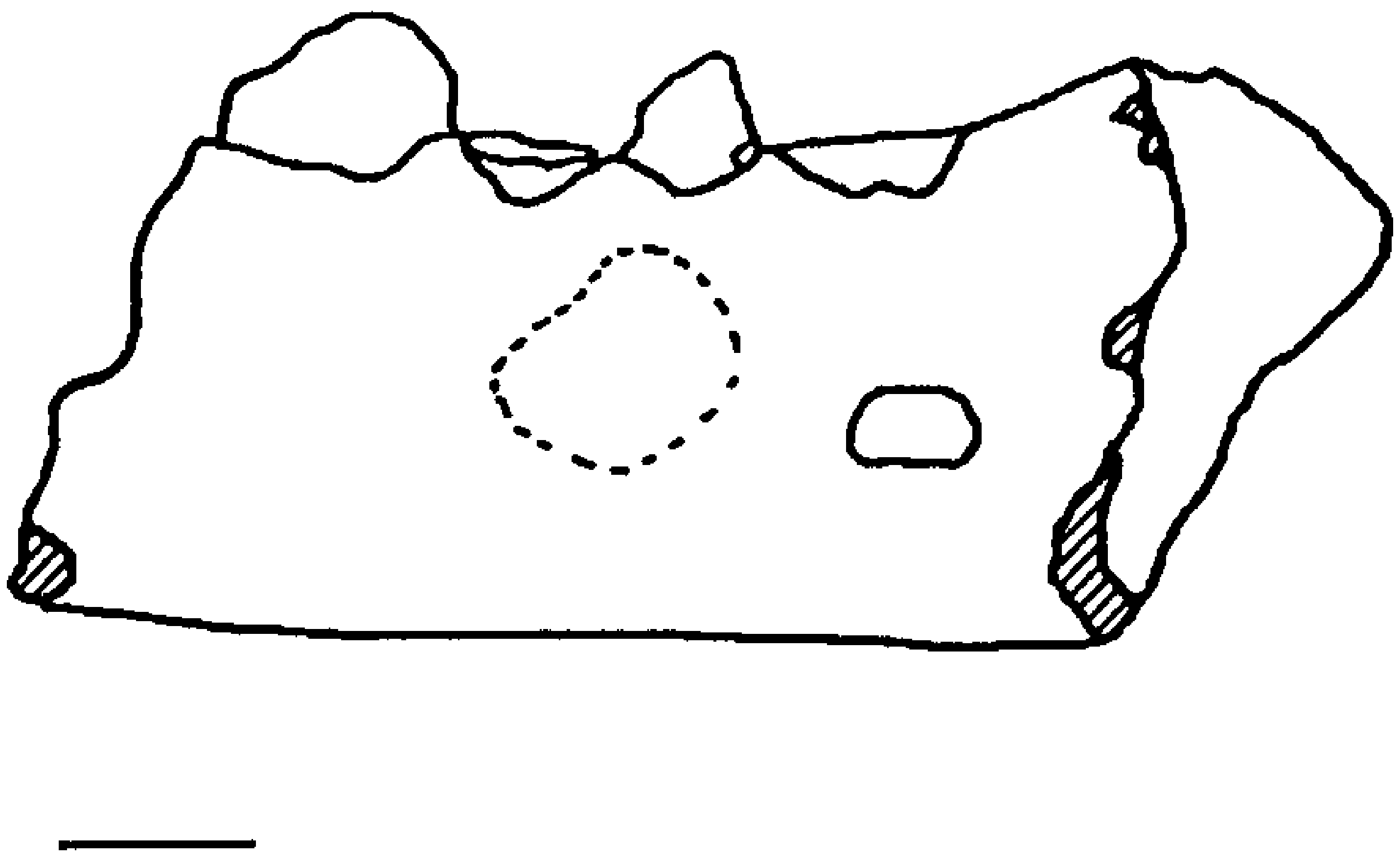


Figure 4.10. Buccal view of right mandibular ramus (Gombasek, no number). The pathological bulge is indicated by dotted lines. Hatching denotes areas of breakage.

All measurements of mandibles are given in Table 4.11. Figure 4.11 shows a log ratio diagram of *Panthera gombaszoegensis* mandibular measurements with the Gombasek mandible as standard. This graph indicates that animals in the older age group had shallower mandibles, without a great lingual thickening but with a relatively long diastema in comparison with the Gombasek specimen. The younger age category cluster around the standard, with two striking exceptions, both of which were in Smuts category 1 (C_i below full eruption). The L'Escale specimen (CD613) has a tiny diastema in comparison with the other specimens, probably because major remodelling still has to take place. The same is true of the Vértesszölös specimen, but in this case the diastema is larger than that of all the other adult cats.

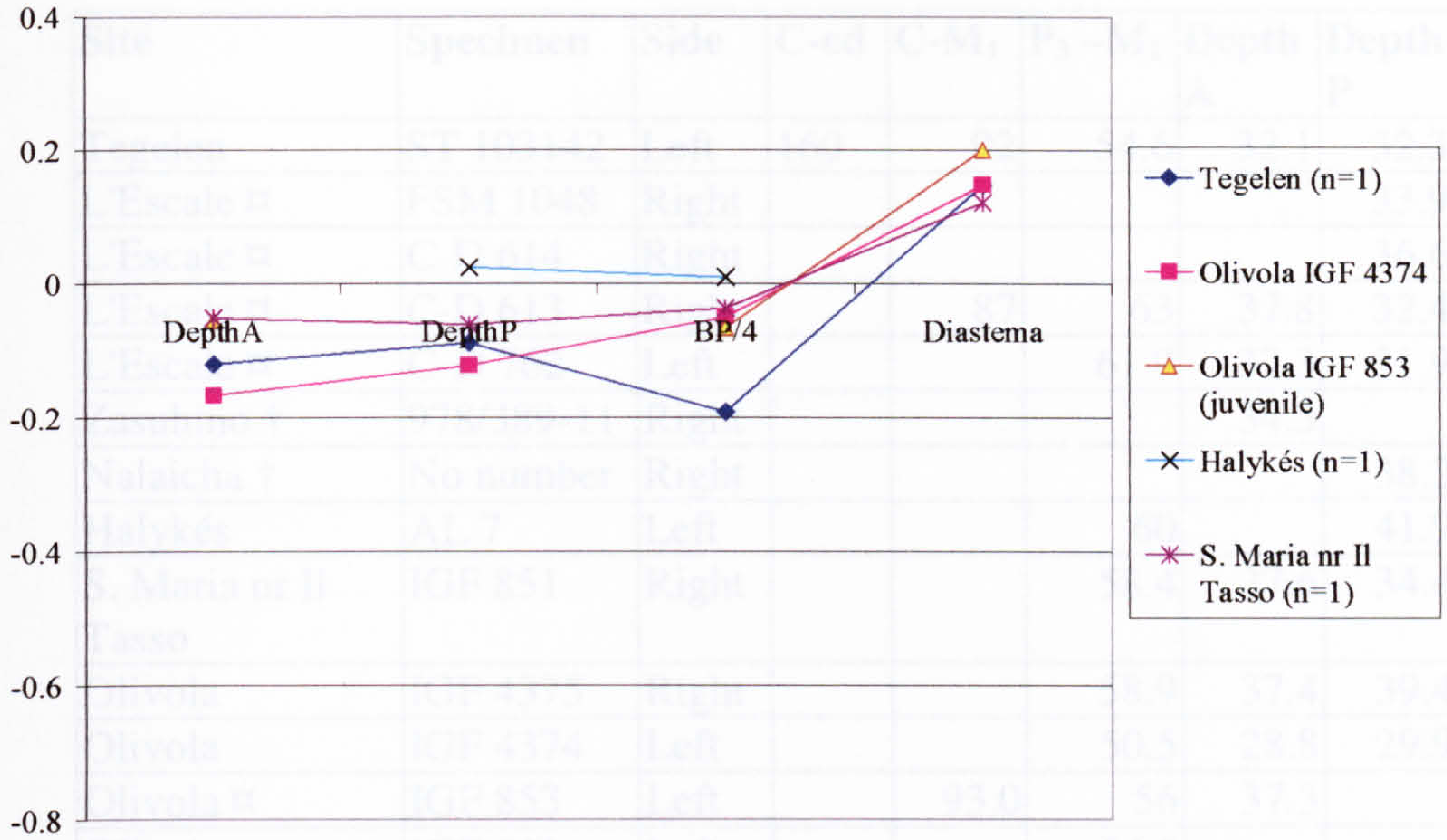


Figure 4.11a. Log ratio diagram of all Early (2.0 – 0.8Ma) *P. gombaszoegensis* mandibular corpus measurements. Gombasek mandible (GIH no number) as standard.

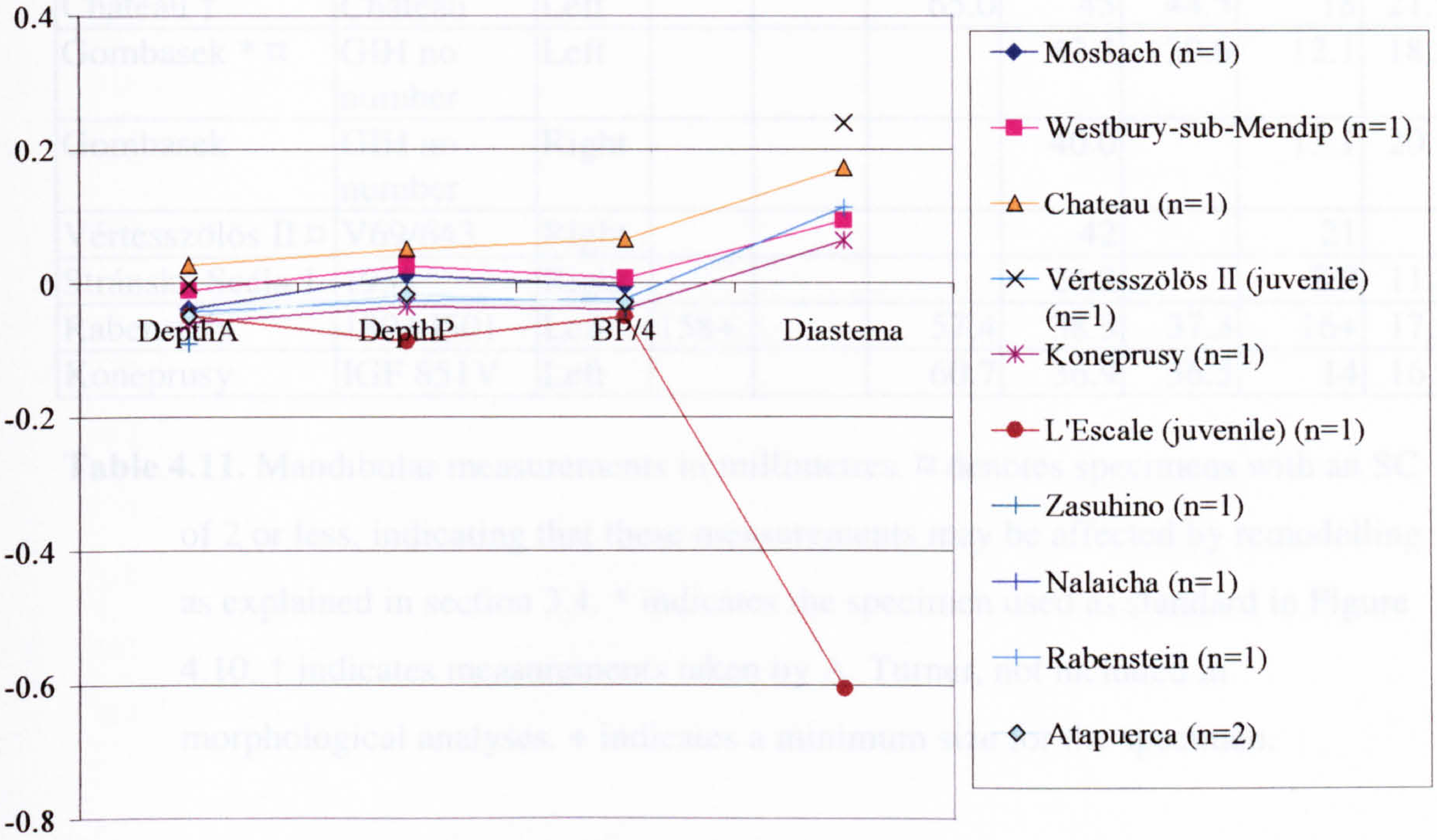


Figure 4.11b. Log ratio diagram of all Late (0.8 – 0.3Ma) *P. gombaszoegensis* mandibular corpus measurements. Gombasek mandible (GIH no number) as standard.

Figure 4.11. Log ratio diagram of all *P. gombaszoegensis* mandibular corpus measurements. Gombasek mandible (GIH no number) as standard.

Site	Specimen	Side	C-cd	C-M_1	P_3 -M_1	Depth A	Depth P	Diast.	BP/4
Tegelen	ST 103142	Left	160	92	54.6	32.1	32.3	17	11.9
L'Escale ¤	FSM 1048	Right					33.9		16.7
L'Escale ¤	C-D 614	Right					36.6		17.8
L'Escale ¤	C-D 613	Right		87	63	37.8	32.4	3.0	16.5
L'Escale ¤	C-D 762	Left			61.9	37.3	31.9		15.9
Zasuhino †	978/389-11	Right				34.3			16.9
Nalaicha †	No number	Right					38.2		
Halykés	AL 7	Left			60		41.9		18.9
S. Maria nr Il Tasso	IGF 851	Right			58.4	37.6	34.4	16	17.0
Olivola	IGF 4375	Right			58.9	37.4	39.4		18.4
Olivola	IGF 4374	Left			50.5	28.8	29.9	17	16.5
Olivola ¤	IGF 853	Left		93.0	56	37.3		19.2	15.9
Olivola	IGF 852	Left			54.5				15.5
Olivola	IGF 12458	Right							15.5
Mosbach ¤	1968-398	Right		98.6	63.2	38.7	40.7	19+	18.3
Westbury-sub-Mendip	M33678	Right				41.2	42.0	15	18.8
Atapuerca †	No number	Left			58.7	37.8	35.7		16.5
Atapuerca †	No number	Right			59.1	37.5	40.2		18.0
Chateau †	Chateau	Left			65.0	45	44.5	18	21.5
Gombasek * ¤	GIH no number	Left				42.3	39.6	12.1	18.5
Gombasek	GIH no number	Right				40.0		13.1	20.1
Vértesszölös II ¤	V69/643	Right				42		21	
Stránská Scála 1	1938	Right				24.2		8.9	11.8
Rabenstein	1894 I501	Left	158+		57.4	38.3	37.3	16+	17.5
Koneprusy	IGF 851V	Left			60.7	36.9	36.5	14	16.9

Table 4.11. Mandibular measurements in millimetres. ¤ denotes specimens with an SC of 2 or less, indicating that these measurements may be affected by remodelling as explained in section 3.4. * indicates the specimen used as standard in Figure 4.10. † indicates measurements taken by A. Turner, not included in morphological analyses. + indicates a minimum size for the specimen.

4.2.12. Review of mandibular morphology

As a general trend it appears that the majority of the older specimens are smaller than the Gombasek standard, while those of the younger age category (0.8 – 0.3Ma) are larger. It also appears that the older specimens have slightly shorter, broader teeth than the younger cats.

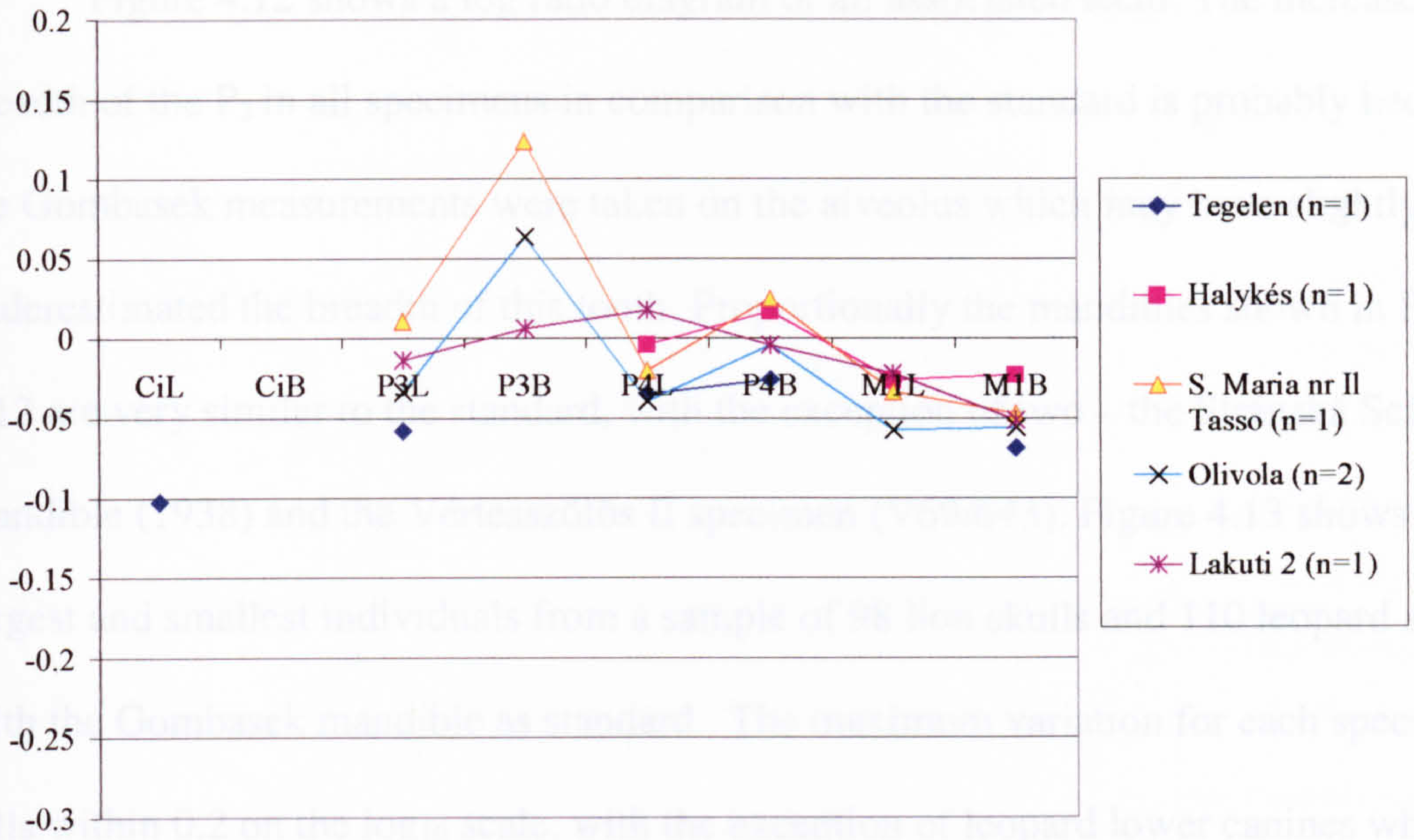


Figure 4.12a. Log ratio diagram of all Early (2.0 – 0.8Ma) *P. gombaszoegensis* mandibles with Gombasek mandible (GIH no number) as standard

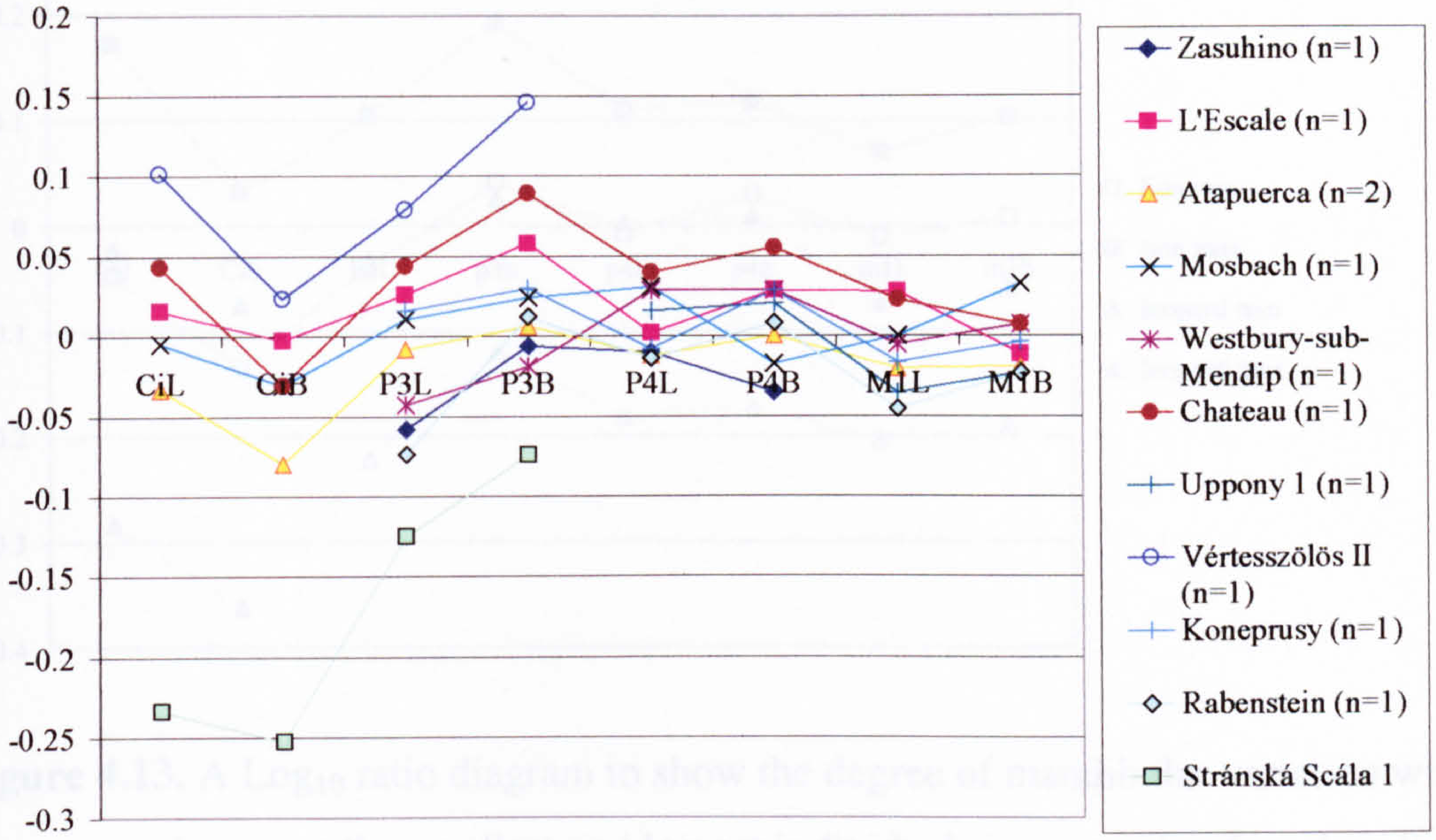


Figure 4.12a. Log ratio diagram of all Late (0.8 – 0.3Ma) *P. gombaszoegensis* mandibles with Gombasek mandible (GIH no number) as standard

Figure 4.12. Log ratio diagram of all *P. gombaszoegensis* mandibles with Gombasek mandible (GIH no number) as standard.

Figure 4.12 shows a log ratio diagram of all associated teeth. The increased breadth of the P_3 in all specimens in comparison with the standard is probably because the Gombasek measurements were taken on the alveolus which may have slightly underestimated the breadth of this tooth. Proportionally the mandibles shown in Figure 4.12 are very similar to the standard, with the exception of two – the Stránská Scála 1 mandible (1938) and the Vértesszölös II specimen (V69/643). Figure 4.13 shows the largest and smallest individuals from a sample of 98 lion skulls and 110 leopard skulls with the Gombasek mandible as standard. The maximum variation for each species falls within 0.2 on the $\log_{10}$ scale, with the exception of leopard lower canines which have a range of approximately 0.3 on the $\log_{10}$ scale.

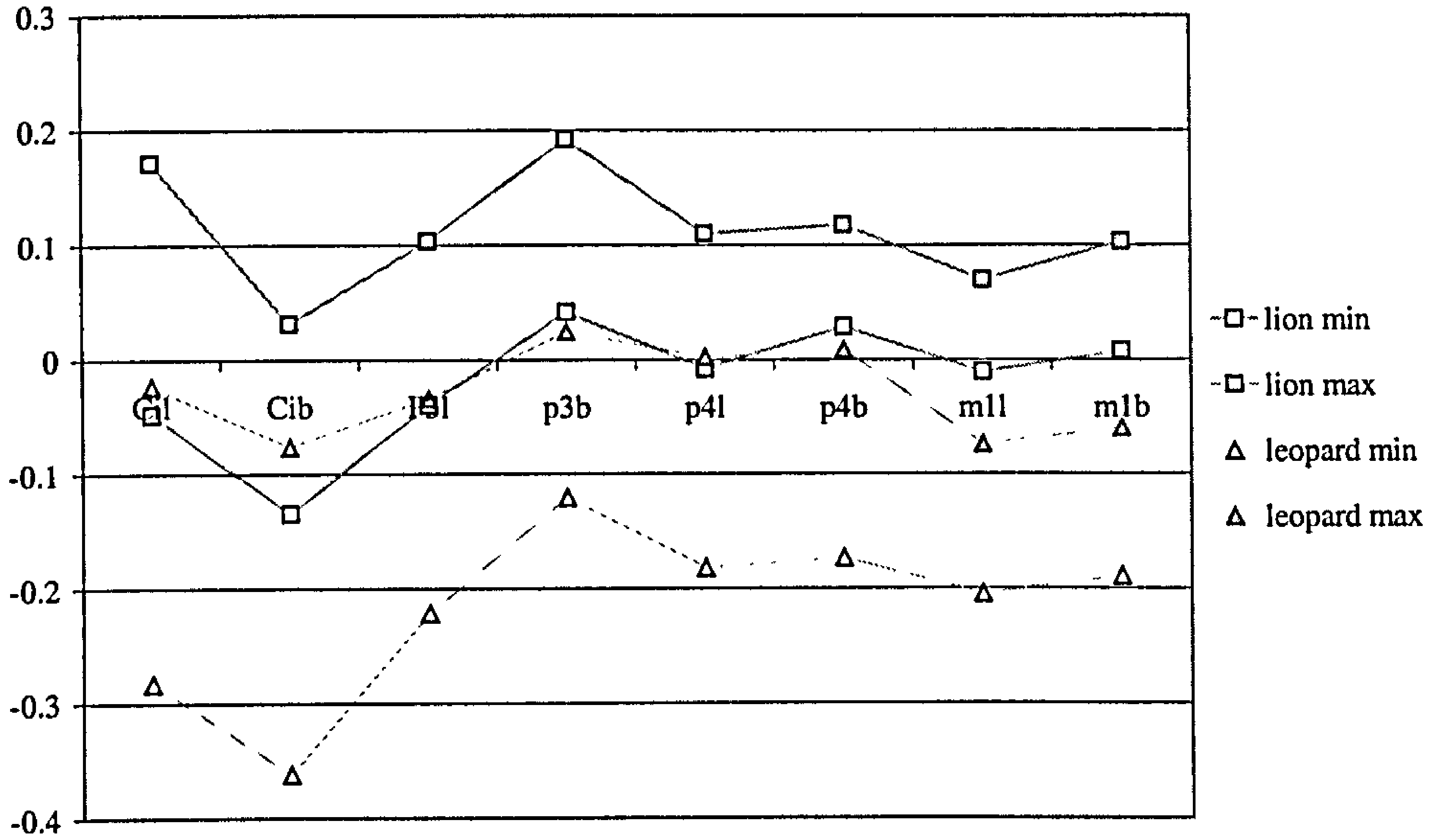


Figure 4.13. A Log_{10} ratio diagram to show the degree of mandibular variation within species using the smallest and largest individuals in a sample of modern lions (n=98) and modern leopards (n=110). Gombasek mandible as standard.

If we apply these values to the Stránská Scála specimen in comparison with the rest of the *P. gombaszoegensis* sample, we can see that it falls below -0.2 on the $\log_{10}$ scale in Figure 4.12. If we assume that variation in fossil cats was no greater than that in the modern species then this indicates that the Stránská Scála specimen cannot be the same species as the rest of the sample. However, its identification still remains unclear.

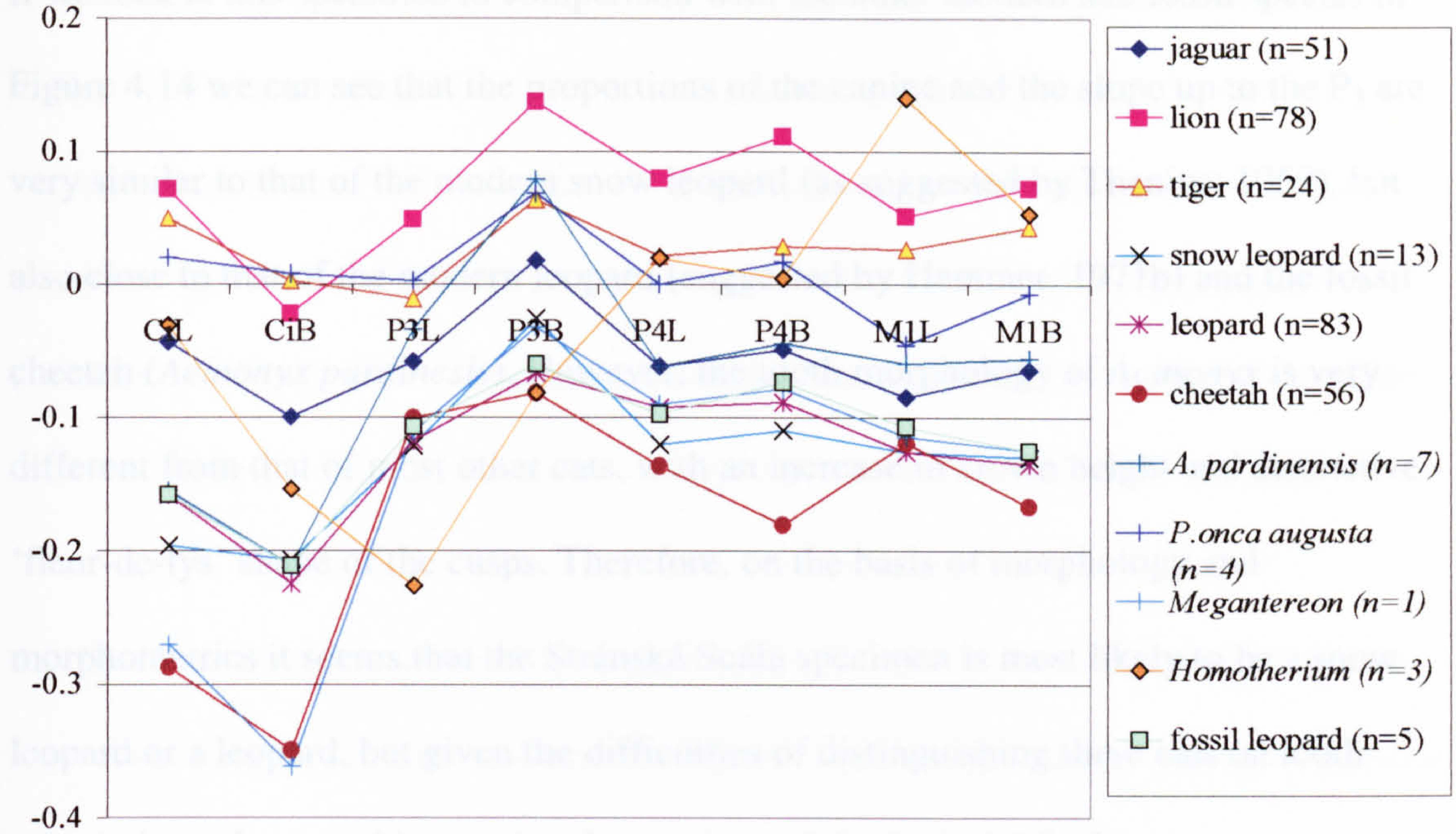


Figure 4.14. Log ratio diagram of all modern and fossil species complete mandibles, using Gombasek mandible (GIH no number) as standard.

If we look at this specimen in comparison with the other modern and fossil species in Figure 4.14 we can see that the proportions of the canine and the slope up to the P_3 are very similar to that of the modern snow leopard (as suggested by Thenius, 1969), but also close to that of the modern leopard (suggested by Hemmer, 1971b) and the fossil cheetah (*Acinonyx pardinesis*). However, the tooth morphology of *Acinonyx* is very different from that of most other cats, with an increase in crown height and distinctive 'fleur-de-lys' shape of the cusps. Therefore, on the basis of morphology and morphometrics it seems that the Stránská Scála specimen is most likely to be a snow leopard or a leopard, but given the difficulties of distinguishing these cats on tooth morphology, I am unable to solve the mystery of the Stránská Scála cat.

The Vértesszölös II specimen is larger than those of the other cats and has a much narrower canine breadth than the Gombasek standard. It is very similar to the Chateau specimen whereas most of the other specimens have a slightly flatter profile on the graph. It is similar to the profile of the modern lion in Figure 4.14, but is still within the overall size range of *P. gombaszoegensis*. One feature that does appear pronounced is the length of the diastema in an animal in which the C_i is just below full eruption. This may suggest that it is not *Panthera gombaszoegensis* at all, but is in fact *Panthera leo.* This interpretation is further supported by the overall morphology of the P_3 which has a very low cusped appearance which may be characteristic of the lion (see section 3.7). Therefore Vértesszölös specimen V69/643 has been removed from all further studies of *P. gombaszoegensis* morphology and is regarded as *Panthera* cf. *P. leo.*

In contrast, the Rabenstein mandible (1894 I501) has remained within the range of variation for *P. gombaszoegensis* in all analyses, despite being classified as a 'robust' leopard by Hemmer (1971b). Spassov & Raichev (1997) postulated that the 'robust' leopards might simply be very late *P. gombaszoegensis* specimens [Rabenstein is dated to approximately 50,000BP (according to the specimen label)], but they had little firm evidence to support this hypothesis. Without studying all of the specimens that have been placed in the 'robust' category it is difficult to judge the merits of dividing *Panthera pardus* into two races. But for these specimens to be assigned to *Panthera gombaszoegensis* it would require this cat to have survived some three hundred thousand years beyond its last known occurrences at Vértesszölös II and Swanscombe (See Appendix 2). This problem will be discussed further in section 4.6.

4.2.13. Morphological change over time

One of the most interesting results of the above morphological study was the realisation that there were changes in the size and morphology of *P. gombaszoegensis* during the Pleistocene. The work of Hemmer (1972a) indicated that the cats from the older sites had narrower premolars than those from the younger. However, as noted in the reviews of morphology above, my data show that there is a general trend for the older specimens from sites dating between 1.9 and 0.8Ma to be shorter but broader than those from the later sites (0.8 – 0.3Ma).

The teeth were reanalysed to see if there had been morphological as well as morphometric change through time. Four features were chosen as being of potential significance:

1) The presence of an M_1 talonid cusp.
2) The presence of a lingual bulge on the M_1.
3) The presence of an ectoparastyle on the P^4.
4) The presence of the P_4 lingual basin.

These four traits were chosen as they are immediately diagnostic and there are a large number of these teeth in the dataset.

The results of this analysis are shown in the following bar charts. These graphs have been created by dividing the fossils into the old and young categories and counting the number of teeth with and without particular features. Specimens were paired, in the same way as the morphological analysis, so that a cranium with two P^4 would only contribute one (n=1) to the sample. The presence of a trait was then calculated as a percentage of the total for each age category and the results were displayed graphically. Specimens which the previous analysis has shown not to be *P. gombaszoegensis* have been removed from the dataset. In order to be confident that only *P. gombaszoegensis* specimens have been analysed, the Rabenstein mandible has not been included in the charts and its morphology will be discussed separately in Section 4.8.

Figure 4.15 shows the percentage count of the presence of an M_1 talonid cusp in the sample. It appears that more specimens in the older age category have this feature, but this apparent reversal is probably due to small sample sizes. There are only four M_1s in the older age category, one of which has a talonid, so this specimen contributes 25% to the overall count. The specimens with this feature are from Santa Maria nr. Il Tasso and Westbury-sub-Mendip; these sites are separated by approximately one million years, indicating that this feature was present at a low level in the species.

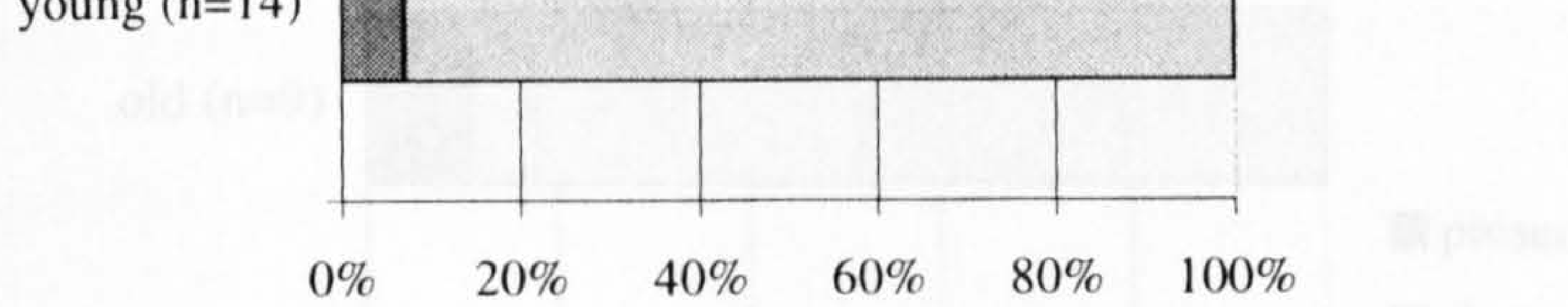


Figure 4.15. Bar chart showing total number of M_1s with a talonid as a percentage for two separate age classes (Old = pre 0.8Ma; Young = post 0.8Ma). Categories calculated on individual animals, not individual teeth.

All specimens in both age categories had an ectoparastyle (100% presence); suggesting that this feature has not altered over time (no graph shown). It is interesting to note that twelve teeth had a lingual bulge, eleven of which were from sites younger than 0.8Ma (the exception is a very small lingual bulge on Tegelen specimen ST103142). These results are too small to test for significance, but do not appear to be the result of low sample numbers in the early material. Figure 4.16 shows these results as a bar chart.

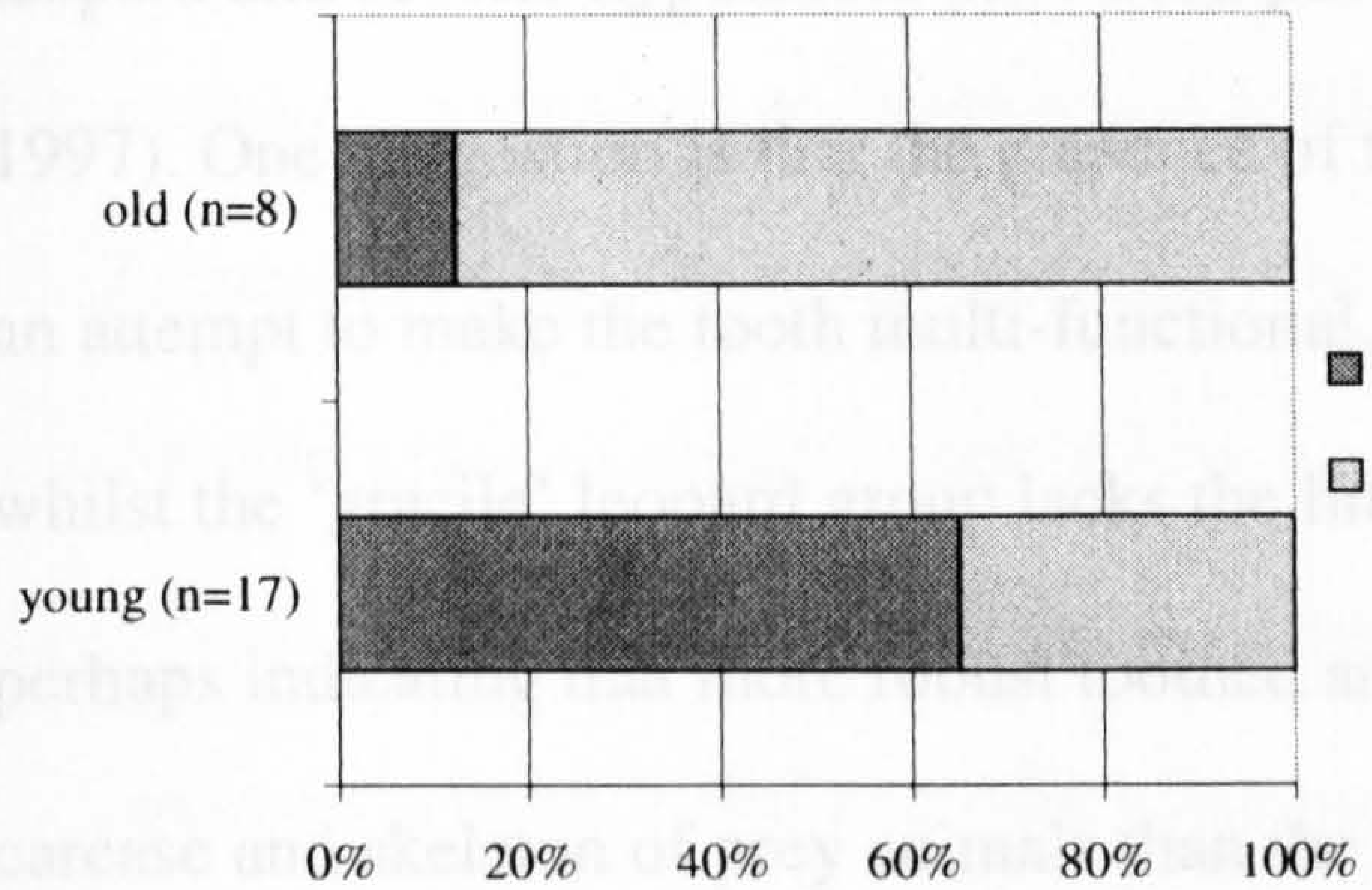


Figure 4.16. Bar chart showing total number of M_1 in sample with and without lingual bulges as a percentage for two separate age classes (Old = pre 0.8Ma; Young = post 0.8Ma). Categories calculated on individual animals, not individual teeth.

The majority of specimens exhibiting a P_4 basin are in the younger age category (0.8 – 0.3Ma) with the exception of IGF 12458 from Olivola. Again, this sample is too small to test for statistical significance between the two groups, but the results are shown in Figure 4.17.

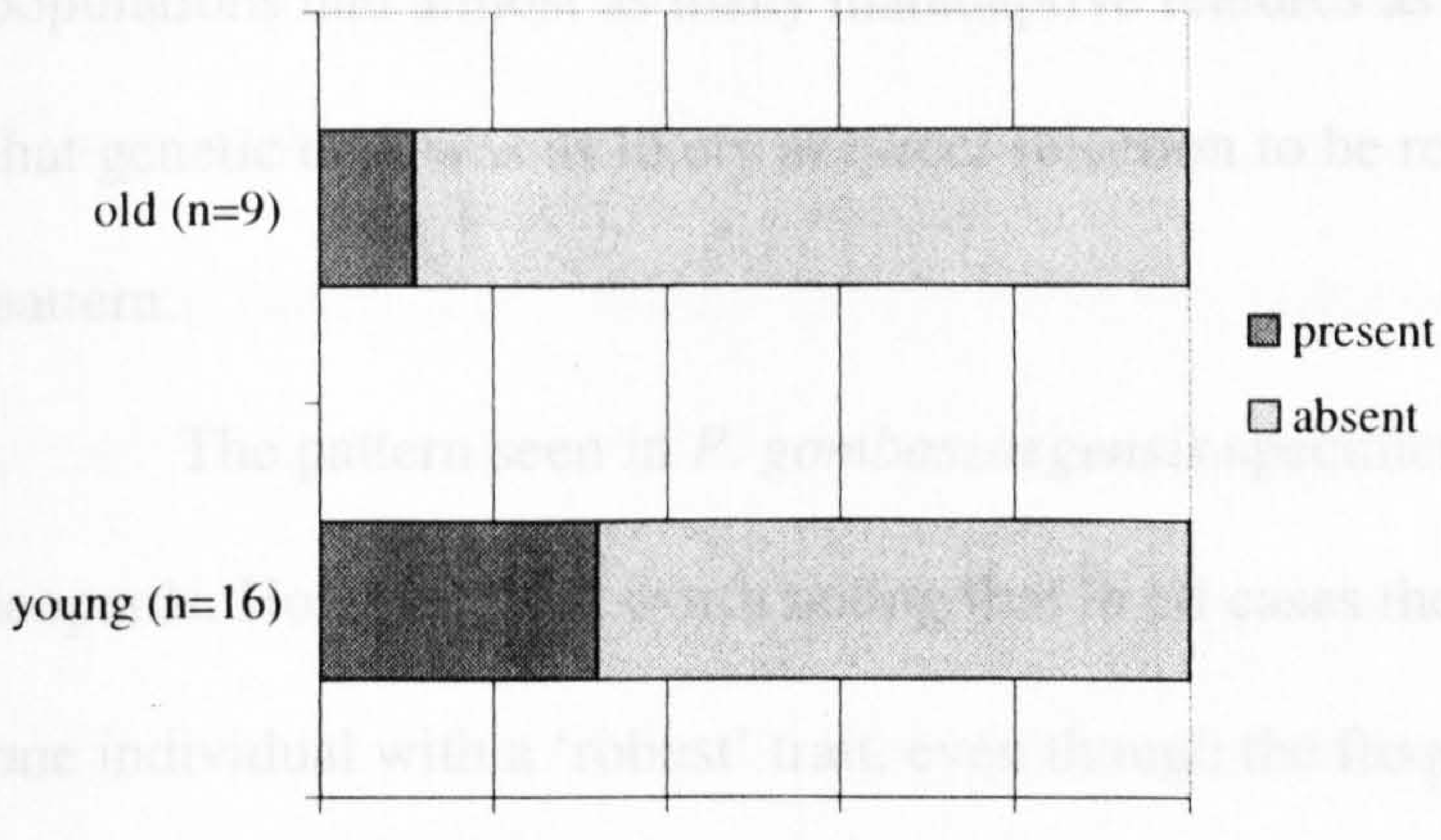


Figure 4.17. Bar chart showing total number of P_4 in sample with and without a lingual 'basin' as a percentage for two separate age classes (Old = pre 0.8Ma; Young = post 0.8Ma). Categories calculated on individual animals, not individual teeth.

On the basis of the above results it appears that the morphology of *P. gombaszoegensis* has become more robust through time as two teeth have shown an increase in the more robust morphologies, although the presence of the talonid and ectoparastyle have remained constant. This change to more robust morphologies has also been noted in the leopard and several hypotheses have been put forward to explain it (Spassov & Raichev, 1997). One suggestion is that the presence of the lingual bulge in fossil leopard M_1s is an attempt to make the tooth multi-functional, able to cut and crush at the same time, whilst the 'gracile' leopard group lacks the lingual bulge and is adapted for cutting only; perhaps indicating that more robust toothed animals were capable of eating more of the carcase and skeleton of prey animals than the gracile group (Spassov & Raichev, 1997). Interestingly it appears that the gracile leopards appear first, with the robust animals emerging later, possibly evolving from the gracile form to become a European subspecies (Spassov & Raichev, 1997). C.G.Turner (1987) found increased expression of 'robust' traits in the dentition of human populations from the Late Pleistocene of Northern Asia. He suggested that direct selection for these traits was possible, as there might be some adaptive advantage in having teeth that were capable of crushing small bones and that were more resistant to damage. However, he also found that these populations had almost as many maladaptive features as adaptive ones and concluded that genetic drift was as likely as direct selection to be responsible for the observed pattern.

The pattern seen in *P. gombaszoegensis* specimens is similar to that of the fossil leopards. However, it is worth noting that in all cases the earlier groups contain at least one individual with a 'robust' trait, even though the frequency of occurrence does appear to increase over time. This suggests that we are not looking at a new subspecies or drastic morphological changes but simply that traits which were present in older groups became more commonly expressed within later populations. This could occur for several reasons, which will be outlined here and discussed further in Chapter 6:

a) The more robust morphologies were adaptive for the individuals concerned as they could extract nutrients from bones or suffer less tooth breakage than their more gracile contemporaries.

b) Repeated glaciations and population bottlenecks led to localised morphologies becoming more pronounced through genetic drift – each glaciation producing a founder effect in isolated populations.

c) The fossilisation process and the selection of sites for this thesis has led to an apparent pattern in the data which is purely due to chance and will disappear when further sites are analysed.

4.3. REVIEW OF *P. GOMBASZOEGENSIS* MORPHOLOGY AS A RESULT OF THIS STUDY

The preceding analysis of *Panthera gombaszoegensis* has led to the definition of the following morphological characters which will be compared with other *Panthera* species in section 4.4.

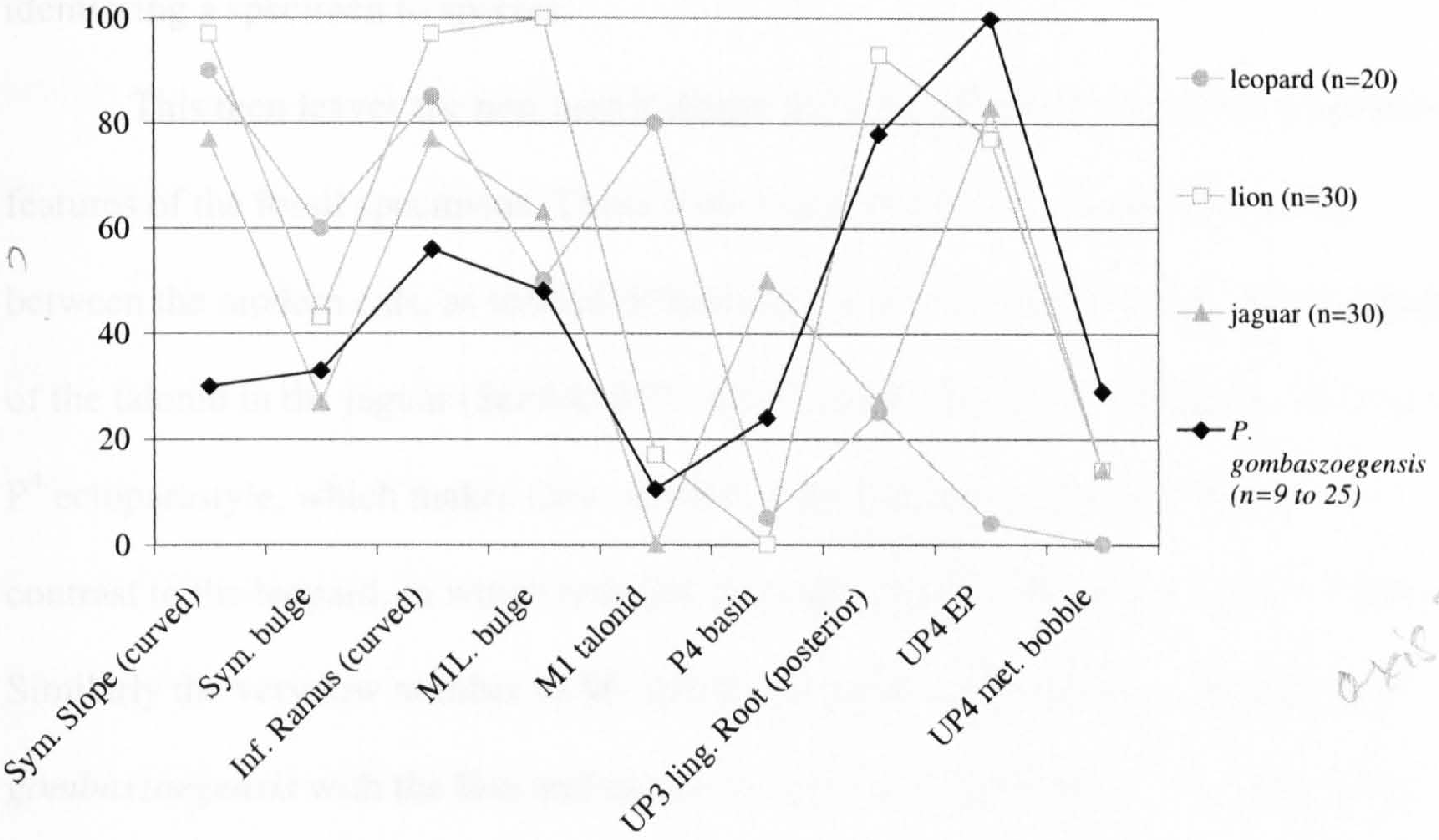
Panthera gombaszoegensis can be characterised as a cat with a P^4 ectoparastyle; a straight anterior edge and a curved metacone. The anterior and posterior cusps of the P^3 are variable in size, but are usually large with a pronounced cingulum. The upper canine is robust. The cranium usually has a large sagittal crest and a strong nuchal crest projecting back over vertically orientated occipital condyles. The incisors are positioned in a straight line and the I^3 is the largest. There will be a large oval mystacial foramen, a wide nasal aperture and the nasal bones extend to or beyond the frontomaxillary suture. The nasals usually have a depression at their distal tip with a defined groove running up between the bones.

In terms of the mandible, the M_1 protoconid is larger than the paraconid, often with a slight lingual bulge in later (post 0.8Ma) specimens. The cingulum is usually present and a talonid is very rare. The P_4 has a large protocone, with distinct and usually large anterior and posterior cusps and cingulum and later specimens may have a 'basin' on the posterior lingual surface. The P_3 is highly variable and of little diagnostic use, although cusps are usually ill-defined with a small posterior cusp. The lower canine tends to have a short crown and a rounded cross section. There are no determining mandibular corpus features, except that all specimens have two mental foramina and usually have a straight (but not upright) symphysis.

4.4. COMPARISON OF *P. GOMBASZOEGENSIS* WITH MODERN *PANTHERA* SPECIES

Panthera gombaszoegensis specimens were analysed using the methods and features that are described in section 3.7.1. but not all of the morphological features were appropriate for use on the fossil specimens. The results of this analysis are illustrated in Figure 4.18 which shows Figure 3.22 with *Panthera gombaszoegensis* presence and absence scores overlying those of the modern species.

It appears from the results in Figure 4.18 that the slope of the mandible is much straighter in *P. gombaszoegensis* than in any of the modern cats, but this result may be due to estimating the curve of the mandible based on a few partial specimens of the fossil species (n = 10). Often only a small portion at the base of the canine was present making it difficult to judge this angle effectively. It has been suggested that the shape of the symphysis can be diagnostic, but this either requires complete specimens, or a study of this portion of the mandible taking the angular measurement at the base. The symphyseal bulge was present in several *P. gombaszoegensis* specimens in the sample and this is an unequivocal feature which was either present in the mandible or not, so this result can be regarded as a true reflection of the presence of this feature in the *P. gombaszoegensis* sample.



axis?

Figure 4.18. Morphological presence and absence features of *P. gombaszoegensis* craniodental specimens. These overlie the modern *Panthera* results, which are illustrated and explained in section 3.7.2.

The curvature of the inferior ramus is another feature that is hard to judge on fossil remains, as a bulge in the centre of the mandible may well be offset by a symphyseal bulge and a large angular process, which would make it straight according to the criteria of Boule (1906). This feature has to be estimated on the fossil material because few specimens have both ends of the mandible preserved and therefore it is likely that the *P. gombaszoegensis* results for this feature are misleading. Other features noted in the morphological review such as the position of the masseteric fossa and the number of mental foramina were also investigated. All *P. gombaszoegensis* specimens were found to have two mental foramina. The modern cats are quite variable in this respect with animals having a range of two to five foramina each. No complete specimen of the modern or fossil species had a single foramen. The masseteric fossa was found in any one of three positions in *P. gombaszoegensis.* Again, as concluded for the modern specimens, it does not appear that mandibular features alone provide reliable criteria for identifying a specimen to species.

This then leaves the non-metric dental traits as potentially the most informative features of the fossil specimens. These were much more useful in differentiating between the modern cats, as several of them lack particular features (e.g. 100% absence of the talonid in the jaguar (Section 3.7). All *P. gombaszoegensis* specimens possess a P^4 ectoparastyle, which makes them similar to the lion and jaguar and in marked contrast to the leopard, in which only 5% of modern specimens possessed this feature. Similarly the very low number of M_1 specimens possessing a talonid, also groups *P. gombaszoegensis* with the lion and jaguar as opposed to the leopard. In addition, the high number of cats with a posteriorly placed P^3 root makes them lion like, in contrast to the leopard and jaguar. However, in terms of the presence of an M_1 lingual bulge it is most like the modern jaguar and leopard.

4.5. COMPARISON WITH OTHER MODERN AND FOSSIL SPECIES

It is unfortunate that few authors have provided full morphological descriptions of large cat teeth. Notable exceptions include Barry (1987), von Koenigswald (1960) and Koufos (1992). The following review of morphological features is based on my own observations and information culled from the literature. Log ratio diagrams were also plotted and are included here if they showed distinct differences between species.

4.5.1. P^4

All *P. gombaszoegensis* specimens were found to possess an ectoparastyle feature. Barry (1987) found that lions and jaguars are variable in this trait, whilst leopards tend to have no ectoparastyle or a very faint trace of one. Tigers on the other hand always have an ectoparastyle feature and this is often very well developed (Mazak, 1981). My results agree with those of the above authors, the lion and jaguar possess an ectoparastyle, whilst in the leopard it is only very rarely present. All fossil jaguar specimens in the Smithsonian Institution had well developed ectoparastyles (n=5).

Nagel (1999) drew attention to the position of the protocone in leopards, noting that it is positioned beside the fissure between the parastyle and paracone, which suggests that it is set back from the anterior of the tooth. The majority (although not all) of *P. gombaszoegensis* specimens have a straight anterior margin [e.g. the holotype illustrated in Kretzoi (1938)]. The fossil leopard from Rome (1191) has a posteriorly placed protocone, with a curved anterior margin.

The log ratio diagram of all modern and fossil species in Figure 4.19 shows that *Homotherium* is the most distinctive cat, with a greatly reduced anterior breadth of the tooth and a much larger metacone. The fossil cheetah *Acinonyx pardinensis* and the smaller sabre-toothed species, *Megantereon*, also follow this pattern, although not in such an extreme way. The other pantherine cats are all proportionally very similar to the standard, with the fossil jaguar and the modern tiger closest in terms of size and these two species plus the modern jaguar and fossil leopard proportionally most similar.

These results indicate the similarity between *Panthera gombaszoegensis* and the fossil jaguar and modern tiger.

4.5.2. P^3

The P^3 morphology is variable across all species. Much attention has been given to the relative size of the anterior cusp in the different species. Barry (1987) noted that this cusp is small in jaguars, leopards and tigers and large in lions. On the other hand, Nagel (1999) found that lions and tigers both have prominent anterior cusps.

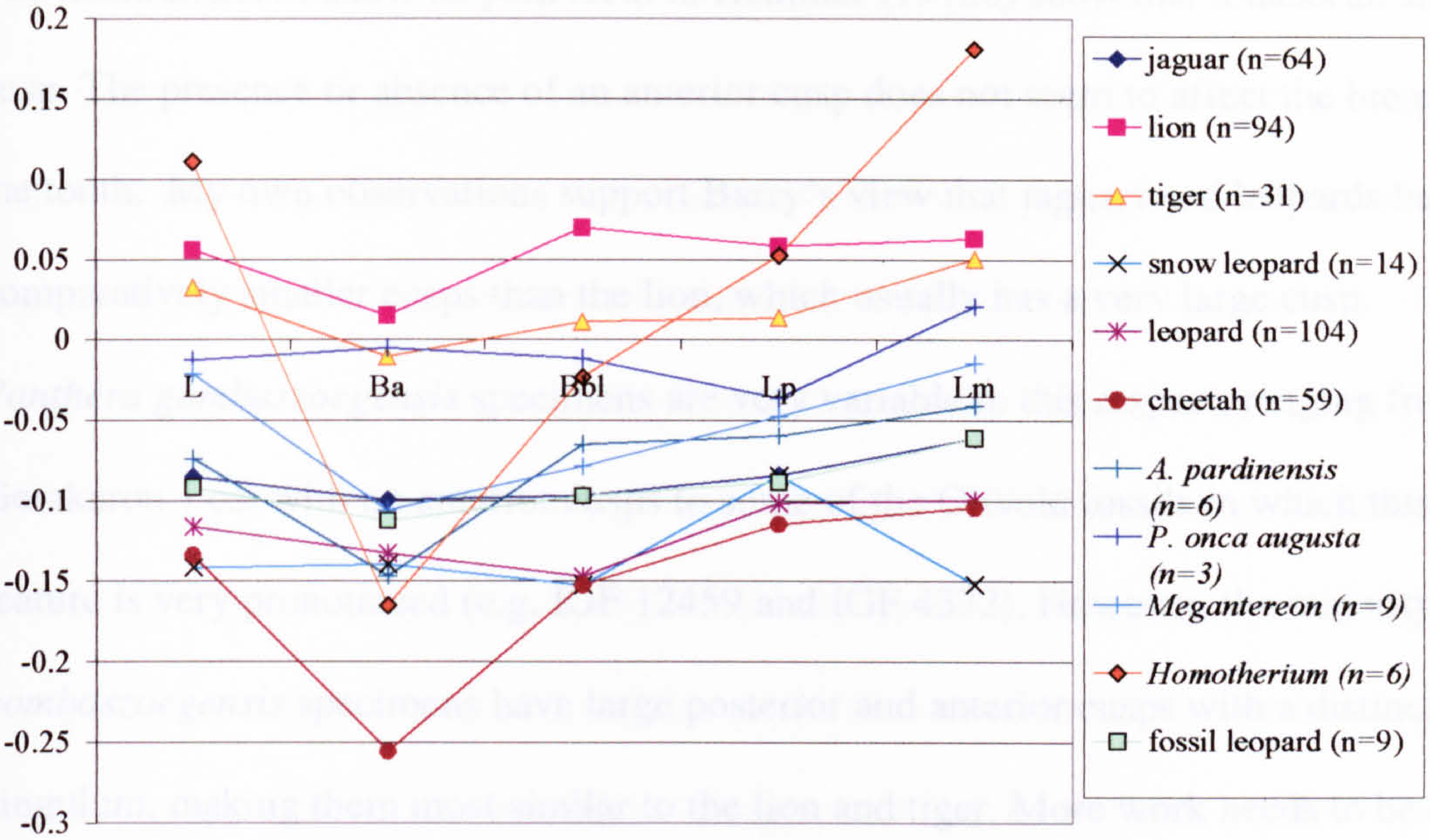


Figure 4.19. Log ratio diagram of all modern and fossil species P^4 with Gombasek specimen (ß 767) as standard.

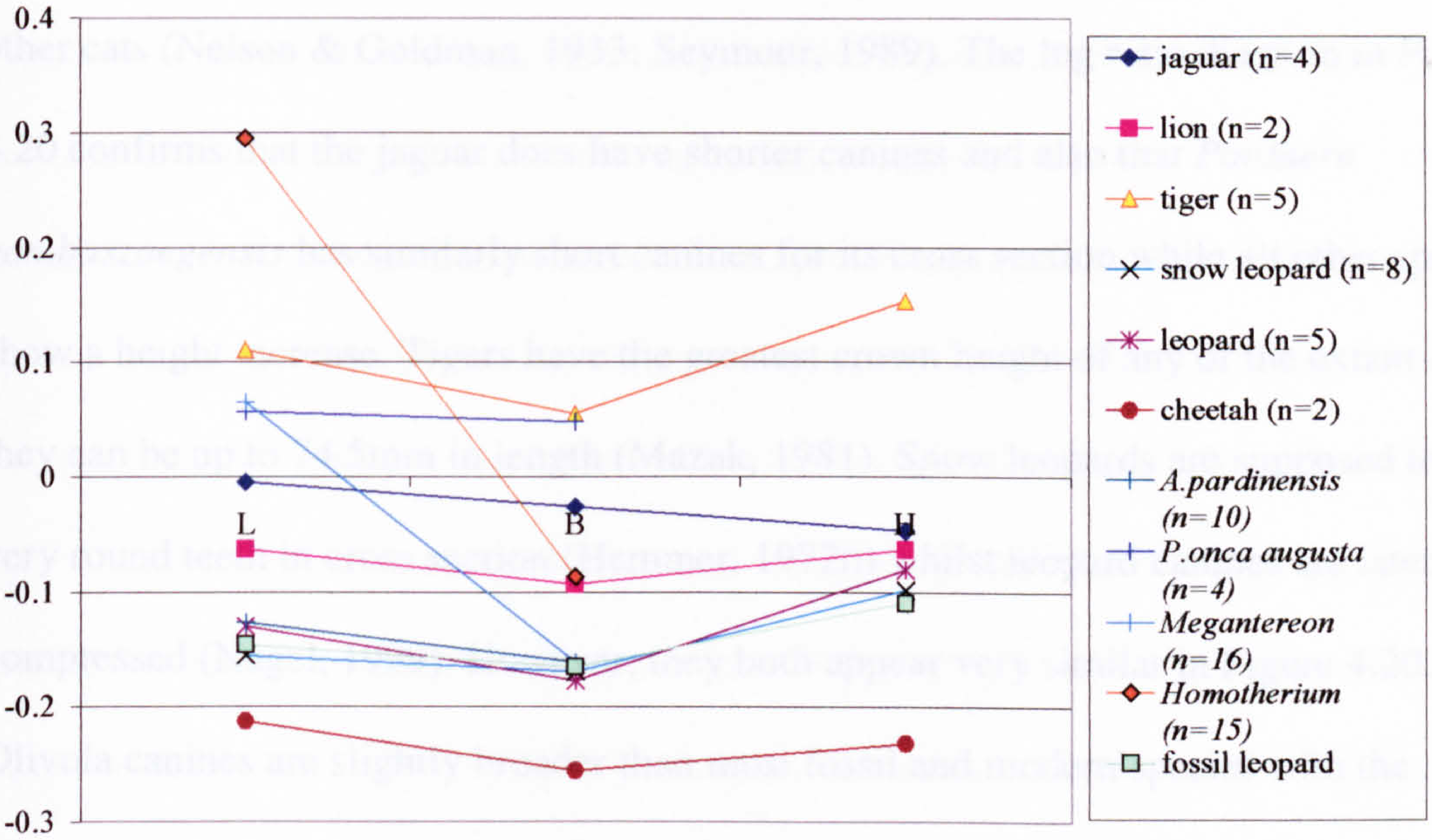


Figure 4.20. Log ratio diagram of all modern and fossil species C^s with Olivola canines (n=2) as standard.

The illustrations of snow leopard teeth in Hemmer (1972b) show that it lacks an anterior cusp. The presence or absence of an anterior cusp does not seem to affect the breadth of the tooth. My own observations support Barry's view that jaguars and leopards have comparatively smaller cusps than the lion, which usually has a very large cusp. *Panthera gombaszoegensis* specimens are very variable in this respect, ranging from the Gerakarou 1 cat with no anterior cusps to some of the Olivola fossils in which this feature is very pronounced (e.g. IGF 12459 and IGF 4372). However, the majority of *P. gombaszoegensis* specimens have large posterior and anterior cusps with a distinct cingulum, making them most similar to the lion and tiger. More work needs to be done on these features before their phylogenetic importance can be fully assessed.

4.5.3. C^s

It has traditionally been reported that jaguars have relatively shorter canines than the other cats (Nelson & Goldman, 1933; Seymour, 1989). The log ratio diagram in Figure 4.20 confirms that the jaguar does have shorter canines and also that *Panthera gombaszoegensis* has similarly short canines for its cross section while all other species show a height increase. Tigers have the greatest crown height of any of the extant cats – they can be up to 74.5mm in length (Mazak, 1981). Snow leopards are supposed to have very round teeth in cross section (Hemmer, 1972b) whilst leopard canines are laterally compressed (Nagel, 1999). However, they both appear very similar in Figure 4.20. The Olivola canines are slightly broader than most fossil and modern species with the exception of *P. onca augusta* which is larger and the snow leopard which is smaller than the standard, but are proportionally the same. *Homotherium* and *Megantereon*, the two saber-toothed species, are obviously proportionally different, with medio-laterally compressed canines.

The crown height of *P. gombaszoegensis* has been thought to be diagnostic of this species (e.g. Bishop, 1982). Jánossy (1969) plotted the canine heights of Hungarian *Panthera gombaszoegensis* specimens against fossil and modern lion teeth and found a distinct difference between the groups. However, this study was performed on estimated crown heights as the majority of teeth were damaged and he did not attempt to differentiate between any species other than the lion and *P. gombaszoegensis.* My data for complete *P. gombaszoegensis* canines plotted against all complete modern and fossil specimens are shown in Figure 4.21. This graph shows that *Panthera gombaszoegensis* falls in a group with the other medium to large sized pantherines and is distinct from the cheetah, leopard and snow leopard. However, there is no clear distinction between *P. gombaszoegensis* and the modern lion.

4.5.4. Maxillary review

Figure 4.22 shows all maxillary teeth in fossil and modern species, plotted against Gerakarou 1 as standard. This graph shows that the tiger, modern jaguar and *P. onca augusta* are proportionally most similar to *P. gombaszoegensis.* There is also a marked split in the pantherines over canine proportions which indicate that the Gerakarou 1 cat has very large canines in comparison with its postcanine dentition, a position mirrored by the jaguar and *P. onca augusta*, whereas all other cats show a decrease in absolute canine size when compared with the postcanine dentition. This is interesting and may indicate that the postcanine teeth in pantherines are more evolutionarily stable than the canines as these teeth are used in intraspecific aggression (Schaller, 1972); as a means of crushing skulls (Schaller & Vasconcelos, 1978) or possibly as sexually selected characters [e.g. lions have the most dimorphic canines (Section 3.3)].

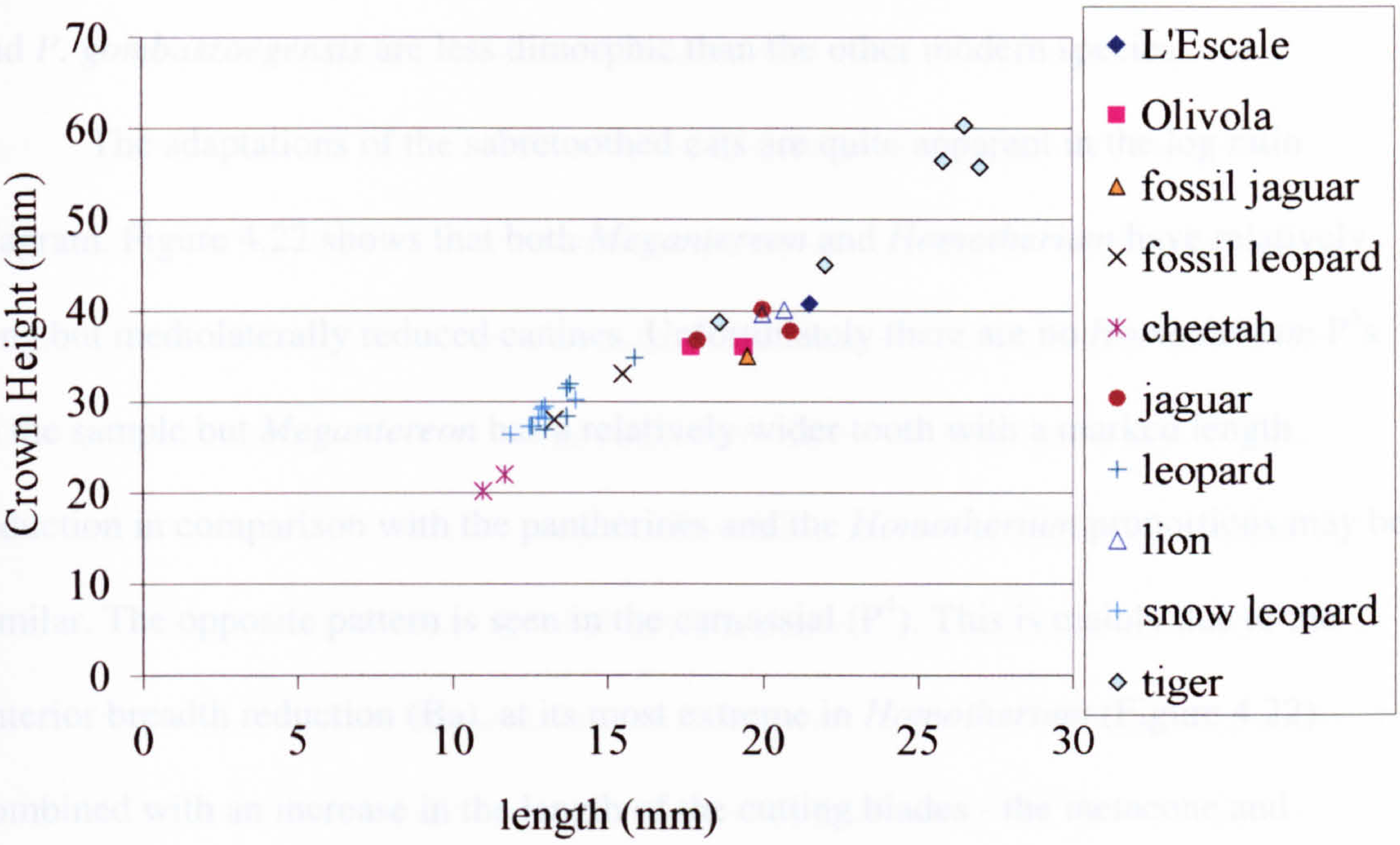


Figure 4.21. Scatterplot of upper canine (C^s) crown height, using all modern and fossil specimens.

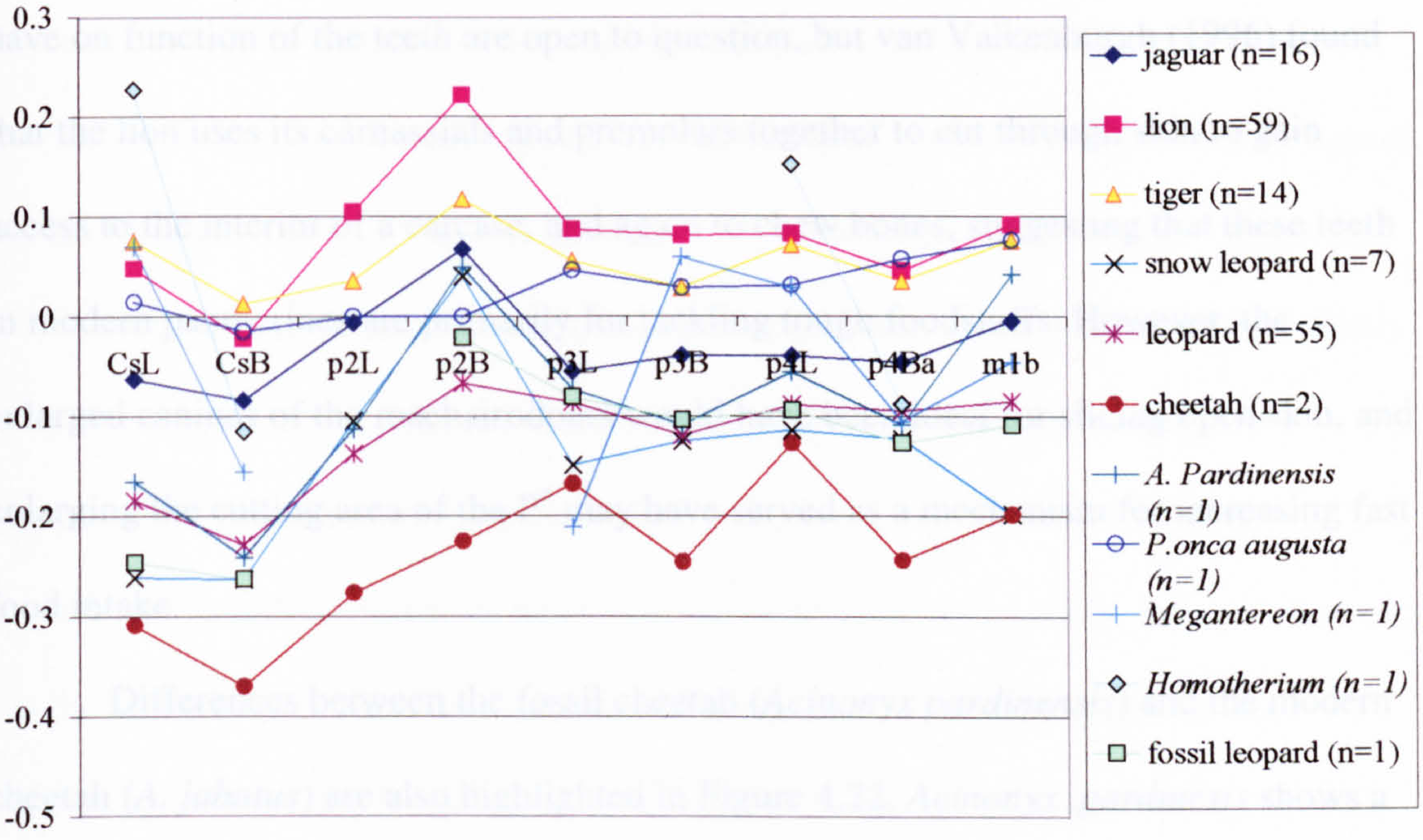


Figure 4.22. Log ratio diagram of all modern and fossil species maxillae. Gerakarou 1 cranium (GER 165) as standard.

This difference in canine size may indicate that canines have come under different selection pressures from the postcanine dentition and that the jaguar, *P. onca augusta* and *P. gombaszoegensis* are less dimorphic than the other modern species.

The adaptations of the sabretoothed cats are quite apparent in the log ratio diagram. Figure 4.22 shows that both *Megantereon* and *Homotherium* have relatively long but mediolaterally reduced canines. Unfortunately there are no *Homotherium* P^3s in the sample but *Megantereon* has a relatively wider tooth with a marked length reduction in comparison with the pantherines and the *Homotherium* proportions may be similar. The opposite pattern is seen in the carnassial (P^4). This is mainly due to the anterior breadth reduction (Ba), at its most extreme in *Homotherium* (Figure 4.22) combined with an increase in the length of the cutting blades - the metacone and paracone [Lm and Lp respectively (shown in Figure 2.22)]. These changes illustrate the major differences between the Machairodontinae and the Felinae, with the machairodonts showing a loss of general crushing functions of the teeth and overall increase in the length and height of the canines. The effects that such changes would have on function of the teeth are open to question, but van Valkenburgh (1996) found that the lion uses its carnassials and premolars together to cut through skin to gain access to the interior of a carcase, and again to chew bones, suggesting that these teeth in modern pantherines are primarily for tackling tough foodstuffs. However, the enlarged canines of the machairodonts would have been ideal for slicing open skin, and enlarging the cutting area of the P^4 may have served as a mechanism for increasing fast food intake.

Differences between the fossil cheetah (*Acinonyx pardinensis*) and the modern cheetah (*A. jubatus*) are also highlighted in Figure 4.22. *Acinonyx pardinesis* shows a tendency towards tooth breadth reduction (seen as a zig-zag pattern on the graph), but it is not much greater than that of the modern tiger, whereas the modern cheetah shows a much more extreme breadth reduction.

In terms of cranial morphology, *P. gombaszoegensis* has strong sagittal and nuchal crests, traits that have also been noted in the tiger (Mazak, 1981) and the jaguar (Ficcarelli & Torre, 1968). No *P. gombaszoegensis* specimens were found to have lachrimal eminences although large lachrimal eminences are regarded as one of the defining features of the modern jaguar (Seymour, 1989) and are also present in the fossil jaguar (pers. obs). Inflation of the forehead is a feature of the snow leopard (Hemmer, 1972b) and the cheetah (O'Regan, in press b) the first may be an adaptation to cold climates, whilst the cheetahs morphology may be related to increasing air intake and reducing overheating whilst hunting (Taylor & Rowntree, 1973). McCrady *et al* (1951) found that inflation of the frontals differed between modern and fossil jaguar specimens. Unfortunately no specimens of *P. onca augusta* from which reliable measurements could be obtained were available for study, so this difference could not be evaluated. However, Pocock (1939) observed that inflation of the interorbital breadth (IO) and postorbital process (POP) was down to individual variation within a species. The *Panthera gombaszoegensis* specimens studied also showed variation in this respect, one cat from Olivola (IGF 10032) has a very wide forehead, but most other specimens do not. Taking Pocock's observations into account, it seems that this feature is unlikely to be diagnostic except when faced with a cheetah or snow leopard cranium, as it appears variable in all other species. Figure 4.23 shows that the inflation of the interorbital breadth is seen at its most extreme in *Megantereon*, whilst in most other cats it is the postorbital process that has expanded. Again it is interesting to note the differences between the modern and fossil cheetah in Figure 4.23, the modern cheetah has greatly reduced facial measurements in comparison with the fossil species.

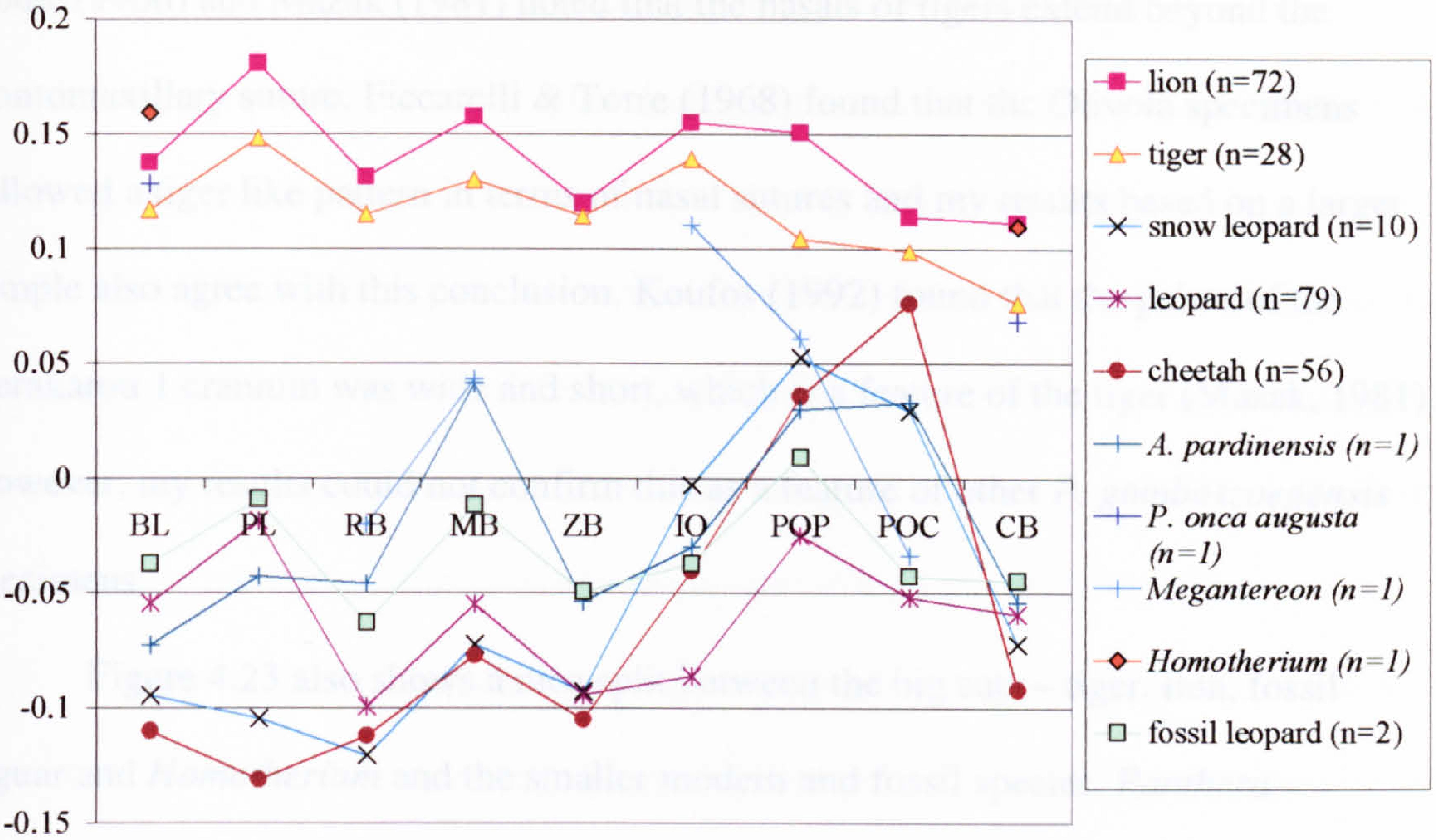


Figure 4.23. Log ratio diagram of all modern and fossil crania, using the mean of the modern jaguar sample (n=55) as standard.

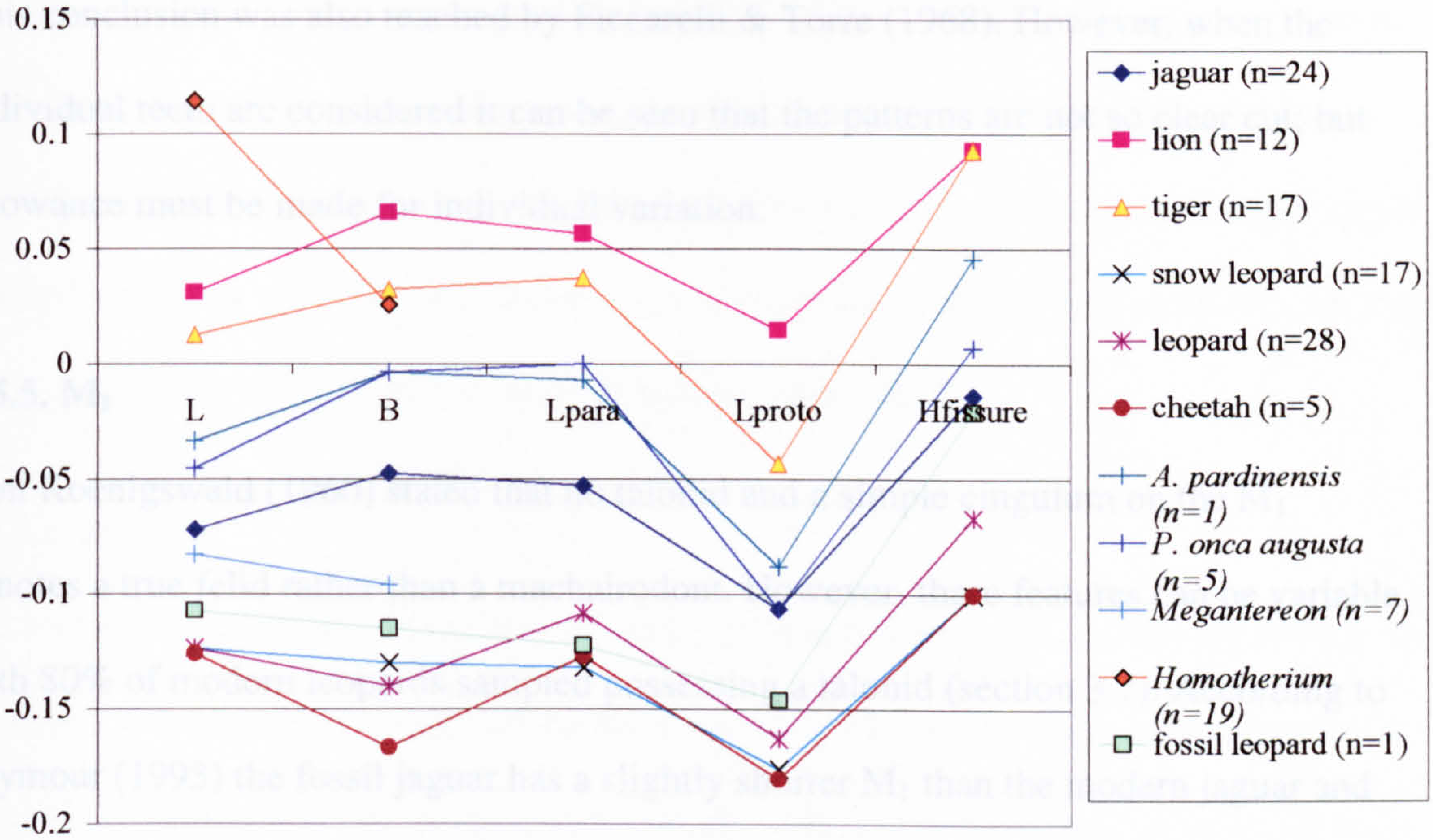


Figure 4.24. Log ratio diagrams of all fossil and modern M_1, using Gombasek mandible (GIH no number) as standard.

Boule (1906) and Mazak (1981) noted that the nasals of tigers extend beyond the frontomaxillary suture. Ficcarelli & Torre (1968) found that the Olivola specimens followed a tiger like pattern in terms of nasal sutures and my results based on a larger sample also agree with this conclusion. Koufos (1992) found that the palate of the Gerakarou 1 cranium was wide and short, which is a feature of the tiger (Mazak, 1981). However, my results could not confirm this as a feature of other *P. gombaszoegensis* specimens.

Figure 4.23 also shows a nice split between the big cats – tiger, lion, fossil jaguar and *Homotherium* and the smaller modern and fossil species. *Panthera gombaszoegensis* is precisely placed between these two groups. The lion and the tiger are most similar to the jaguar in terms of proportions as well as size.

To summarise, in cranial dimensions and morphology *P. gombaszoegensis* is most similar to the tiger, jaguar and *P. onca augusta* based on the data presented here. This conclusion was also reached by Ficcarelli & Torre (1968). However, when the individual teeth are considered it can be seen that the patterns are not so clear cut; but allowance must be made for individual variation.

4.5.5. M_1

Von Koenigswald (1960) stated that no talonid and a simple cingulum on the M_1 denotes a true felid rather than a machairodont. However, these features can be variable, with 80% of modern leopards sampled possessing a talonid (section 3.7). According to Seymour (1993) the fossil jaguar has a slightly shorter M_1 than the modern jaguar and this is borne out by the results in Figure 4.24, which show that the fossil jaguar has a more acute slope between length and breadth of the tooth than the modern individuals, but in all other respects it is almost exactly the same. It is interesting to note that there is a distinct split between species with an increase in breadth and those with a decrease.

The modern lion, tiger, jaguar and fossil jaguar have wider teeth than *P. gombaszoegensis* whilst smaller species such as the leopard, snow leopard and cheetah are proportionally similar to the standard, or show a breadth decrease.

The difference between the modern and the fossil cheetah is of note, as there has been a great breadth reduction from the fossil to the modern form. It is unfortunate that *Acinonyx* fossils are so rare, but if *A. pardinensis* is ancestral to *A. jubatus*, it should be possible to trace this relationship over the course of the Plio-Pleistocene.

Differences in tooth proportions have been noted for many species. *Panthera uncia* is regarded as having a short paraconid (Hemmer, 1972b) whilst *Panthera gombaszoegensis* is thought to have a long paraconid (Spassov & Raichev, 1997). It is difficult to determine this on Figure 4.24 as the standard is unusually large in this respect and many of the other *P. gombaszoegensis* teeth have shorter paraconids (see Figure 4.7). Many *P. gombaszoegensis* specimens were found to have a lingual bulge, especially in the younger age category. Spassov & Raichev (1997) found that the snow leopard often has a lingual bulge and a broad M_1, a trait which is similar to the lion, whilst the leopard has a much narrower tooth. The ectoparaconid seen on the specimens from Gombasek and L'Escale has been noted in the modern tiger and snow leopard, but not in any other species, either fossil or modern (pers. obs.).

4.5.6. P_4

In terms of P_4 morphology the size of the anterior and posterior cusps has attracted most interest. Mazak (1981) found that the tiger has a large posterior cusp and small anterior cusp. The opposite is true of the leopard (Barry, 1987). The snow leopard has relatively increased anterior breadth and a short protocone (Hemmer, 1972b). The Tegelen fossils have large and well defined anterior and posterior cusps with a strong cingulum (von Koenigswald, 1960). The presence of the P_4 basin has been discussed previously, but to recap, the lion and leopard rarely if ever have this feature, whilst it is common in the jaguar and the later specimens of *P. gombaszoegensis*.

The log ratio diagram in Figure 4.25 shows that the Gombasek specimen has a much longer protocone for its length than any of the other cats. Again, *P. onca augusta* is most similar to the standard in size and proportions and the leopard and snow leopard are also proportionally similar, but smaller. The tiger specimen used in this analysis (Budapest museum: 77.8.1) is very small in comparison with most other tiger specimens; this explains the apparent size reduction of this species when compared to the lion on the graph. The sabretooths *Megantereon* and *Homotherium* and the modern cheetah have narrower teeth with a reduced protocone, whereas the pantherines tend to be broader. The lion and the jaguar are most similar to each other and are very different to the other cats as both have a reduced length and protocone when compared with the breadth of the teeth.

4.5.7. P_3

The P_3 is highly variable. Seymour (1993) noted that jaguars have a smaller P_3 than other cats. However, Hemmer (1971a) and Spassov & Raichev (1997) consider that the modern jaguar and *Panthera gombaszoegensis* have a relatively long P_3 in comparison with other cats. The log ratio diagram in Figure 4.26 shows that the tiger, the leopard, the jaguar and *P. onca augusta* are very similar to each other with a longer protocone and narrower anterior breadth than the standard. Mazak (1981) observed that the anterior and posterior cusps are small and indistinct in tigers, whilst leopards have large anterior cusps and increased posterior breadths (Barry, 1987). Nagel (1999) noted that snow leopards have wider P_3s than the modern leopard. This can also be seen in Figure 4.26 as the snow leopard has a relatively wider anterior breadth.

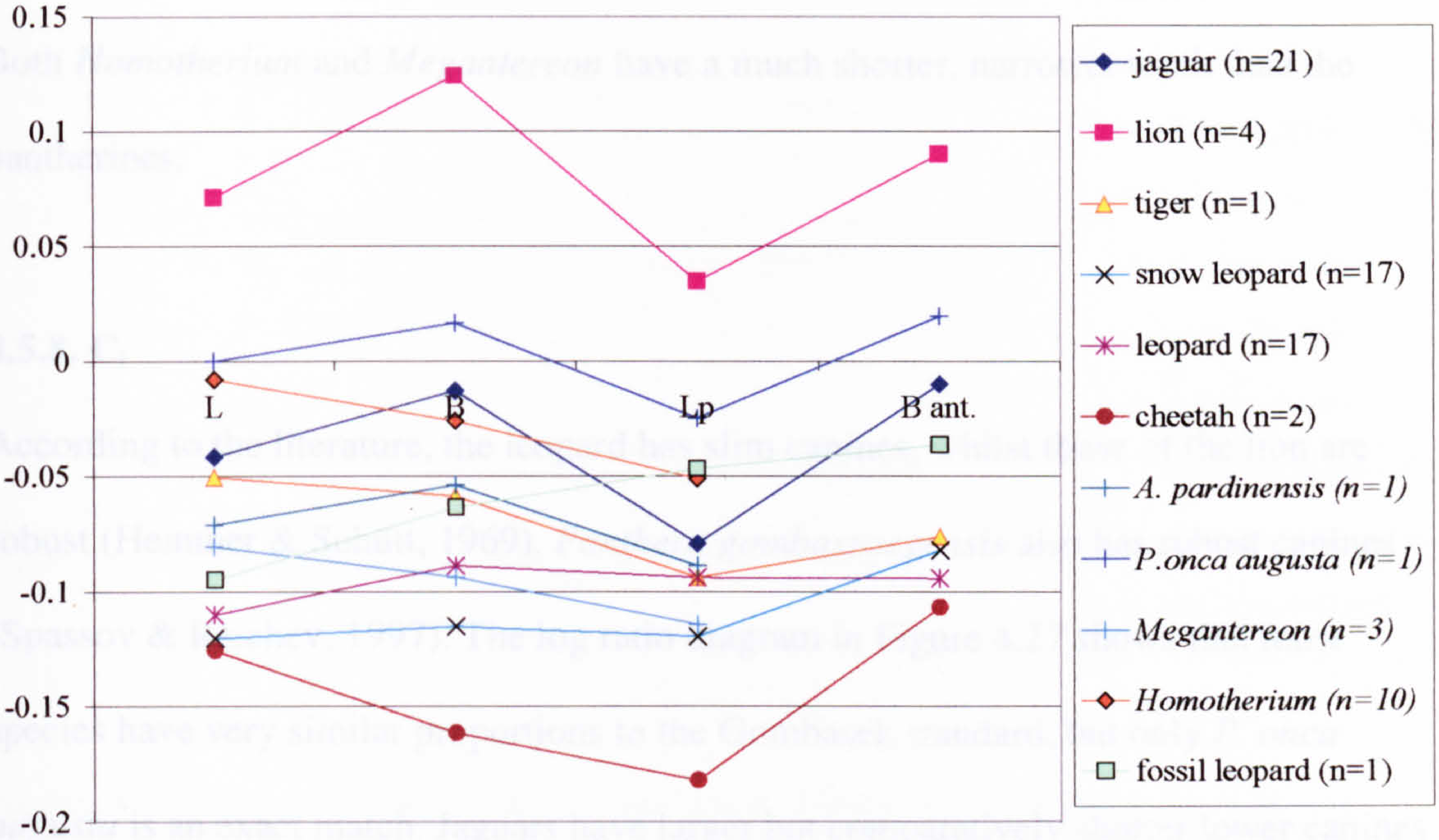


Figure 4.25. Log ratio diagram of all modern and fossil P_4 with Gombasek mandible (GIH no number) as standard.

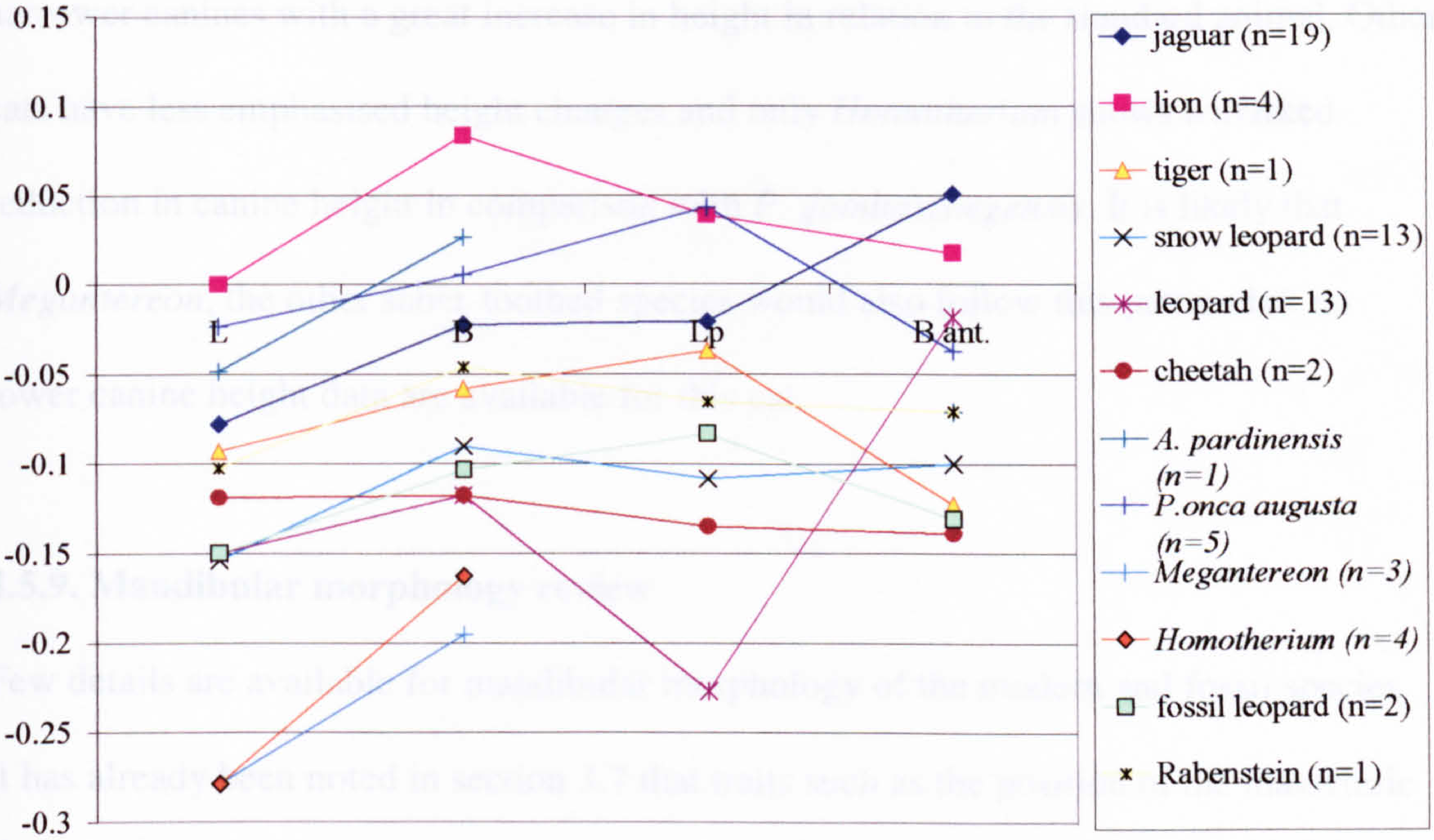


Figure 4.26. Log ratio diagram of all modern and fossil species P_3 with Gombasek tooth [Fvz 24 (V59/1041)] as standard.

The Rabenstein specimen has a pattern similar to that of the modern snow leopard, while the modern cheetah is proportionally the most similar to the Gombasek standard. Both *Homotherium* and *Megantereon* have a much shorter, narrower tooth than the pantherines.

4.5.8. C_i

According to the literature, the leopard has slim canines, whilst those of the lion are robust (Hemmer & Schütt, 1969). *Panthera gombaszoegensis* also has robust canines (Spassov & Raichev, 1997). The log ratio diagram in Figure 4.27 shows that most species have very similar proportions to the Gombasek standard, but only *P. onca augusta* is an exact match. Jaguars have larger but comparatively shorter lower canines than the other pantherine species (Nelson & Goldman, 1933; Seymour, 1989). This is confirmed by the log ratio diagram that shows that only the modern jaguar and cheetah have a very small height increase. The tiger, snow leopard and leopard all have slightly narrower canines with a great increase in height in relation to the standard animal. Other cats have less emphasised height changes and only *Homotherium* shows a marked reduction in canine height in comparison with *P. gombaszoegensis*. It is likely that *Megantereon*, the other saber-toothed species would also follow this pattern but no lower canine height data are available for this cat.

4.5.9. Mandibular morphology review

Few details are available for mandibular morphology of the modern and fossil species. It has already been noted in section 3.7 that traits such as the position of the masseteric fossa in relation to the M_1 have no taxonomic value. Two features of the snow leopard that are thought to have diagnostic value are a short diastema (Nagel, 1999) and a vertical mandibular symphysis (Spassov & Raichev, 1997).

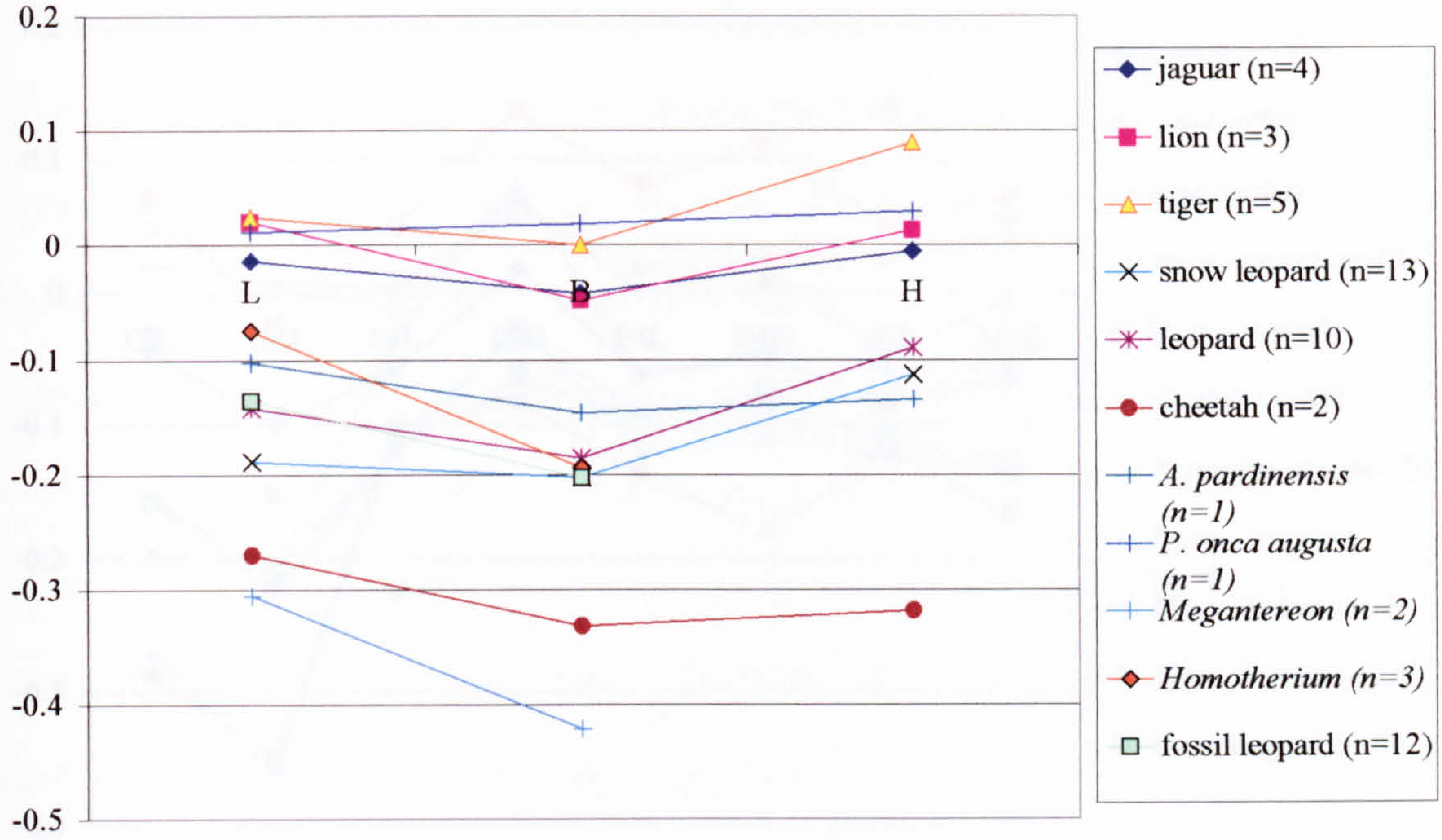


Figure 4.27. Log ratio diagram of all modern and fossil C_i measurements with Gombasek Mandible (GIH no number) as standard.

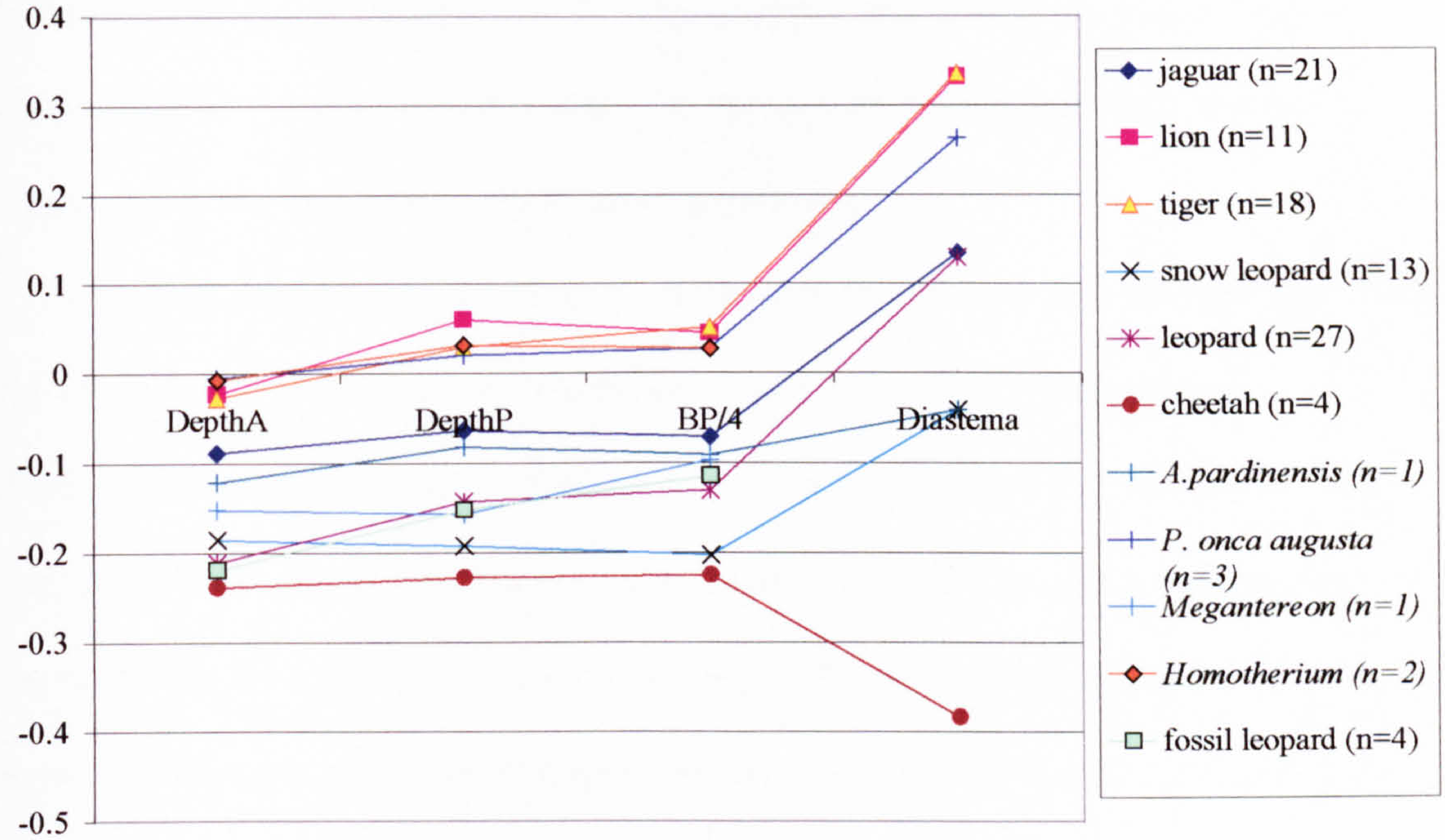


Figure 4.28. Log ratio diagram of all modern and fossil species mandibular corpus measurements. Gombasek mandible (GIH no number) as standard.

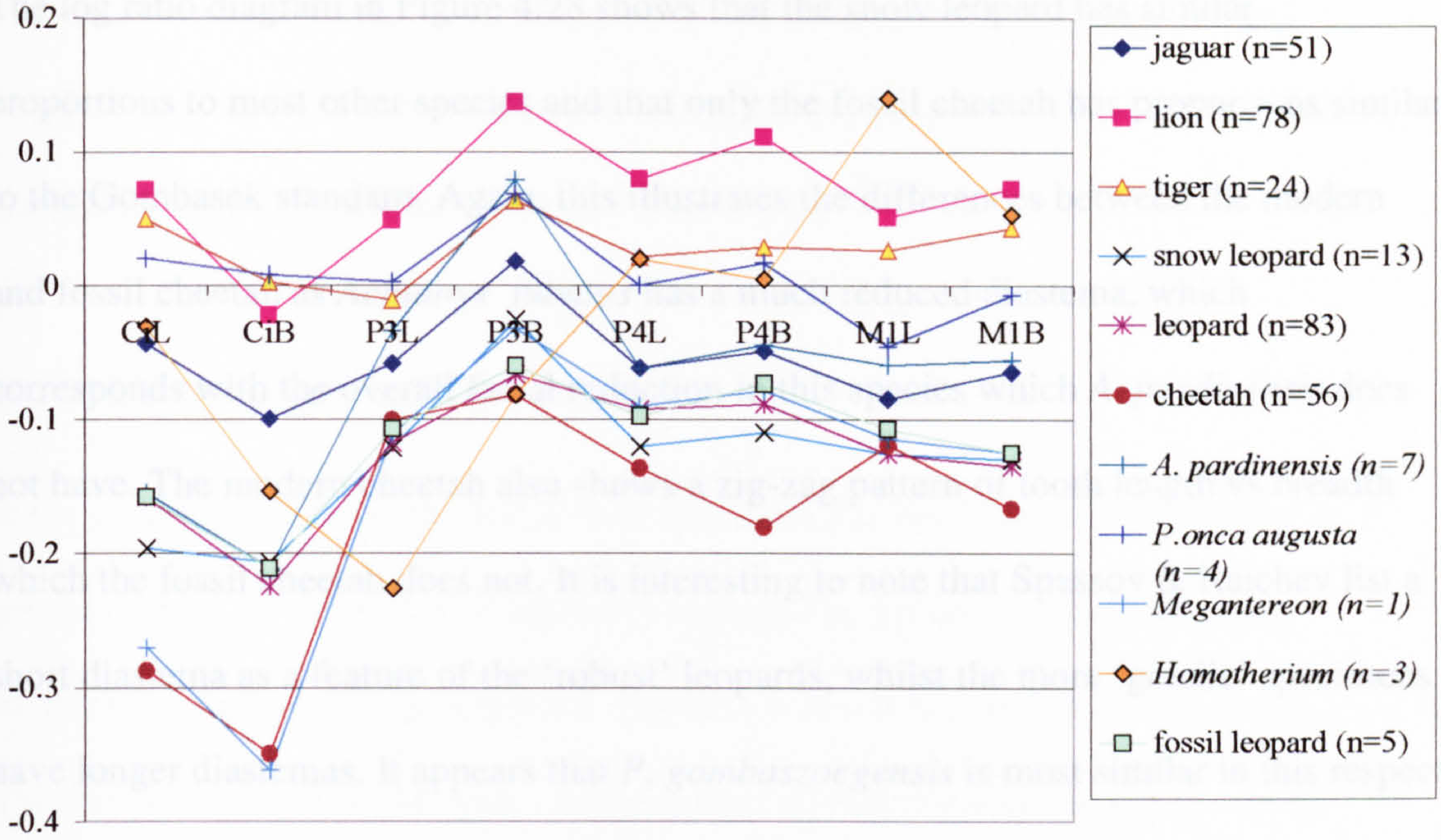


Figure 4.29. Log ratio diagram of all modern and fossil species complete mandibles, using Gombasek mandible (GIH no number) as standard.

The log ratio diagram in Figure 4.28 shows that the snow leopard has similar proportions to most other species and that only the fossil cheetah has proportions similar to the Gombasek standard. Again, this illustrates the differences between the modern and fossil cheetah as *Acinonyx jubatus* has a much reduced diastema, which corresponds with the overall facial reduction in this species which *A. pardinensis* does not have. The modern cheetah also shows a zig-zag pattern of tooth length vs breadth which the fossil cheetah does not. It is interesting to note that Spassov & Raichev list a short diastema as a feature of the 'robust' leopards, whilst the more 'gracile' specimens have longer diastemas. It appears that *P. gombaszoegensis* is most similar in this respect to the 'robust' rather than the 'gracile' leopards, as Figure 4.12 shows the Rabenstein mandible is very similar to the standard.

In comparison with the other extinct and extant species the pattern shown in Figure 4.29 is comparable to that of the cranium, with the standard Gombasek mandible being most similar to the tiger and *P. onca augusta.* In this case the lion and jaguar show a similar pattern, but they follow the opposite line, with relatively broader but shorter teeth in comparison with *P. gombaszoegensis.*

All of the cats discussed here are alike in terms of the postcanine dentition, with the exception of *Homotherium*, which has an entirely different morphology. *Homotherium* exhibits mediolaterally compressed canines and a huge reduction in P_3 length, with a P_4 of similar dimensions to the standard and a greatly lengthened but narrowed M_1. This pattern is akin to that seen in the maxillary teeth (Section 4.7.4) and again indicates the adaptation to hypercarnivory, with a reduction of the C_i and P_3 to accommodate the greatly enlarged upper canine. It appears that *Homotherium* was adapted to slicing and cutting prey but had no real ability to crush or grip its food with the postcanine teeth. These adaptations parallel those of the North American sabretooth *Smilodon* which is regarded as a separate tribe – the Smilodontini, whose likely ancestor was *Megantereon* (Turner & Antón, 1997). The modern and fossil cheetahs and *Megantereon* all show a similar canine size reduction, but none have a corresponding reduction of the P_3 or enlargement of the carnassial

4.6. THE RABENSTEIN MANDIBLE

In the preceding analysis the Rabenstein mandible has been consistently similar to *P. gombaszoegensis* although it is currently regarded as a leopard. There are three possibilities that need to be explored. The first is that it is *Panthera gombaszoegensis*; if it is then it is some 300,000 years younger than all other specimens which seems unlikely given that no other late specimens have been found despite the volume of work which has been focussed on the last 100,000 years. However, there is the possibility that because *P. gombaszoegensis* is presumed to be extinct after this date then all medium sized pantherine fossils are automatically assigned to *P. pardus*. This brings us to the second possibility - that a future review of the Late Pleistocene leopards might find a greater similarity between *P. gombaszoegensis* and the 'robust' leopards which may, in fact, turn out to be late *P. gombaszoegensis* as tentatively suggested by Spassov & Raichev (1997). A third possibility is that after the extinction of *P. gombaszoegensis* the leopard was able to expand to fill the empty niche, becoming larger and more robust as it did so. However, I studied only one mandible of the robust type of leopard, so more data will be required to investigate these hypotheses further and it is also possible that a larger sample would show conclusively that they are *P. pardus*. The non metric traits discussed in section 3.7 could be applied to this problem.

CHAPTER 5 -POSTCRANIA, JUVENILES AND SITE REVIEW

The postcrania of a fossil animal can be very informative about its habits, such as locomotion or hunting strategies. However it is often difficult to confidently assign isolated postcranial material to species. This Chapter considers all postcranial *P. gombaszoegensis* specimens that I have seen at first hand and discusses the identification of this material and issues such as sexual dimorphism. In Section 5.3 all juvenile *P. gombaszoegensis* specimens are reviewed and the potential palaeoecological information that can be gained from an analysis of this material is addressed. All published *P. gombaszoegensis* specimens that have not yet been discussed are critically reviewed in section 5.4. Finally, the presence of *P. gombaszoegensis* in Africa [suggested by Barry (1987) and Dietrich (1968)] is considered in section 5.5.

5.1. POSTCRANIA

No associated postcranial *Panthera gombaszoegensis* remains were available for study. Therefore, to allow direct comparison of the postcranial graphs, the mean of the jaguar sample (n=11) has been used as the standard in all log ratio diagrams. For morphological discussions, a modern jaguar skeleton and a modern leopard skeleton have been used for comparison with the fossil material. Observations of these two skeletons have been supplemented with morphological details of other specimens or species where appropriate.

5.1.1. Scapula

The scapula is a very delicate bone; in modern specimens it is sometimes possible to see through it when held up to the light. For this reason it does not survive well in the palaeontological record and even fragments may be rare. Only one putative *Panthera gombaszoegensis* scapula has been studied and this is from Uppony 1. Measurements of the length and breadth of the glenoid cavity are given in Table 5.1. As these are both estimated measurements a log ratio diagram was not constructed.

Site	Specimen	TL	TW
Uppony 1	V60/1211	45+	32+

Table 5.1. Measurements of the glenoid cavity in millimetres. + indicates a minimum measurement.

5.1.2. Humerus

Olivola (n=2) IGF 4358 – wide olecraneon fossa; large medial epicondylar expansion; small coronoid fossa. IGF 4357 – very deformed; distinct radial fossa.

Halykés (n=1) AL 24 - very damaged; large medial epicondylar expansion; very steep slope from trochlea to capitulum.

Westbury-sub-Mendip (n=4) F3 - wide, olecraneon fossa; deep radial fossa; moderately expanded medial epicondyle; shallow coronoid fossa, deep dip in lateral epicondyle. F1 - shallow coronoid fossa; large trochlea; distinct lateral condylar ridge; wide, low olecraneon fossa; deep dip in lateral epicondyle. M47489 - very long, low olecraneon fossa; very strong lateral condylar ridge; shallow condylar fossa; distinct radial fossa; deep dip in lateral epicondyle. M47621 - long, low olecraneon fossa; slight coronoid fossa; deep radial fossa; deep dip in lateral epicondyle.

Swanscombe (n=1) M16501- lateral condylar ridge begins strong then peters out; long, low epicondylar fossa with distinct break in slope; coronoid and radial fossae absent; shallow dip in lateral epicondyle.

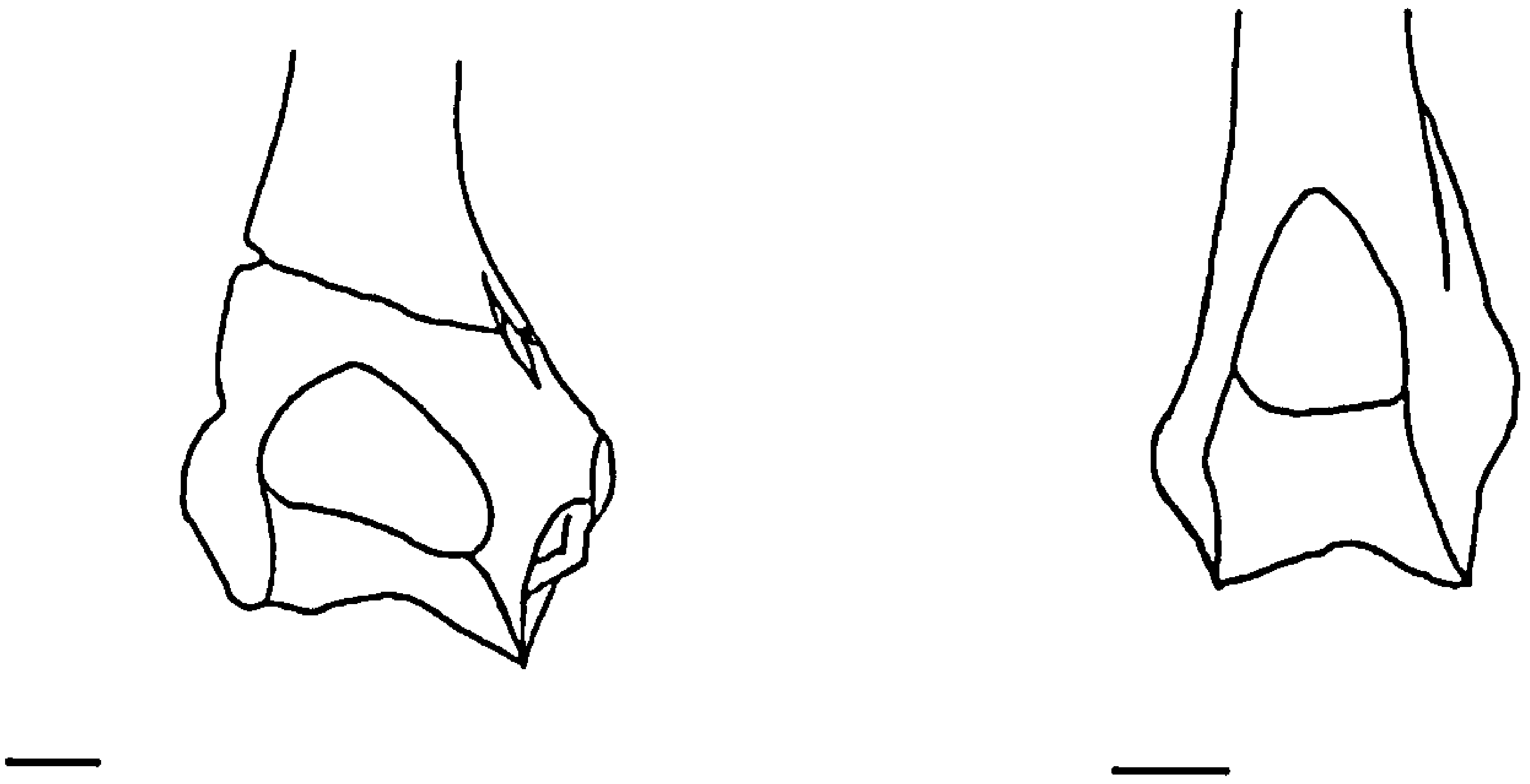
Süssenborn (n=1) Süß 10295 - long, low olecraneon fossa; deep dip in lateral epicondyle; deep radial fossa; shallow coronoid fossa.

No proximal articulations or complete humerii have been found, but the distal humerus is quite a common *P. gombaszoegensis* element; at least nine have been recovered. Measurements of the specimens included in this study are given in Table 5.2. The paper of Kurtén & Poulianos (1977) gives measurements of a humerus from the type site of Gombasek - EPW 73mm and TrochW 53mm. These are very similar to the measurements given below and it is probable that this specimen is *P. gombaszoegensis.*

Site	Specimen	side	SW min	EPW	TrochW
Halykés	AL 24	Right		76.1	
Olivola	IGF 4358	Right		80.4	54.2
Süssenborn	Süß 10295	Left		67.7	45
Swanscombe	M16501	Left	27.4	79.4	55
Westbury-sub-Mendip	F3	Right		81.7	52
Westbury-sub-Mendip	F1	Right		75	50
Westbury-sub-Mendip	M47489	Left	27.4	76.0	52.0
Westbury-sub-Mendip	M47621	Right		80.8	51

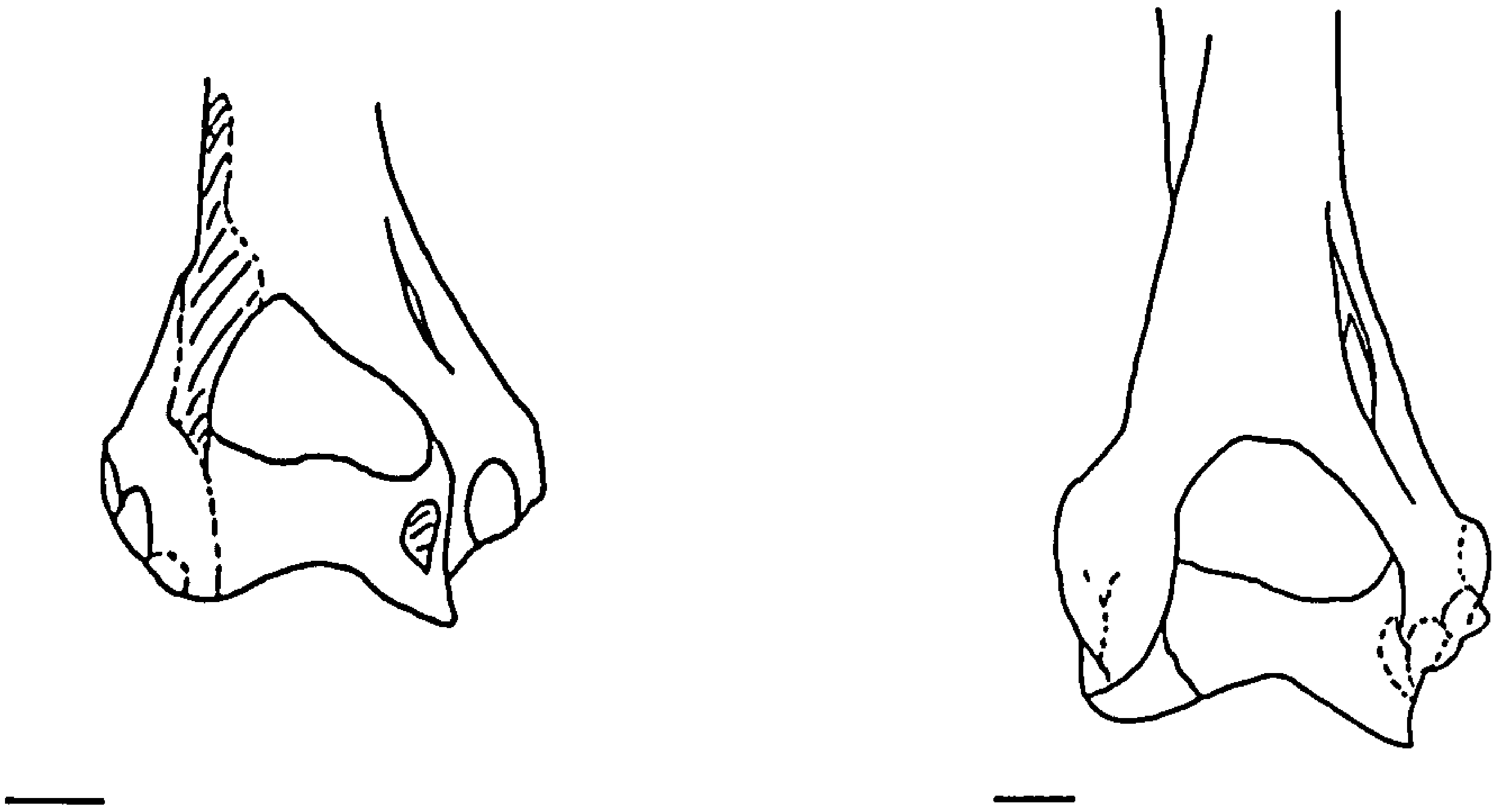
Table 5.2. Measurements of all *P. gombaszoegensis* humerii in millimetres. Abbreviations explained in section 2.3.4.1. + indicates a minimum measurement.

The morphology of the olecraneon fossa in *P. gombaszoegensis* is considered quite distinctive, as it is long and low whilst in the lion it is wide and high (Kurtén, 1969; Turner, 2000). Figure 5.1 shows the anterior view of the distal humerus for five fossil species: *P. gombaszoegensis*; *Acinonyx pardinensis*; *Homotherium*; fossil jaguar and fossil lion. It can be seen from this illustration that the shape of the articulation and olecraneon fossa morphology is quite different in these species and that specimens can be confidently assigned to *Panthera* if nothing else. *Homotherium* morphology is distinctive as it is a large animal, with a high, wide olecraneon fossa and an acute angle between the trochlea and capitulum. This articulation also has an 'hourglass' appearance in profile, as there is a distinct dip between the two condyles.



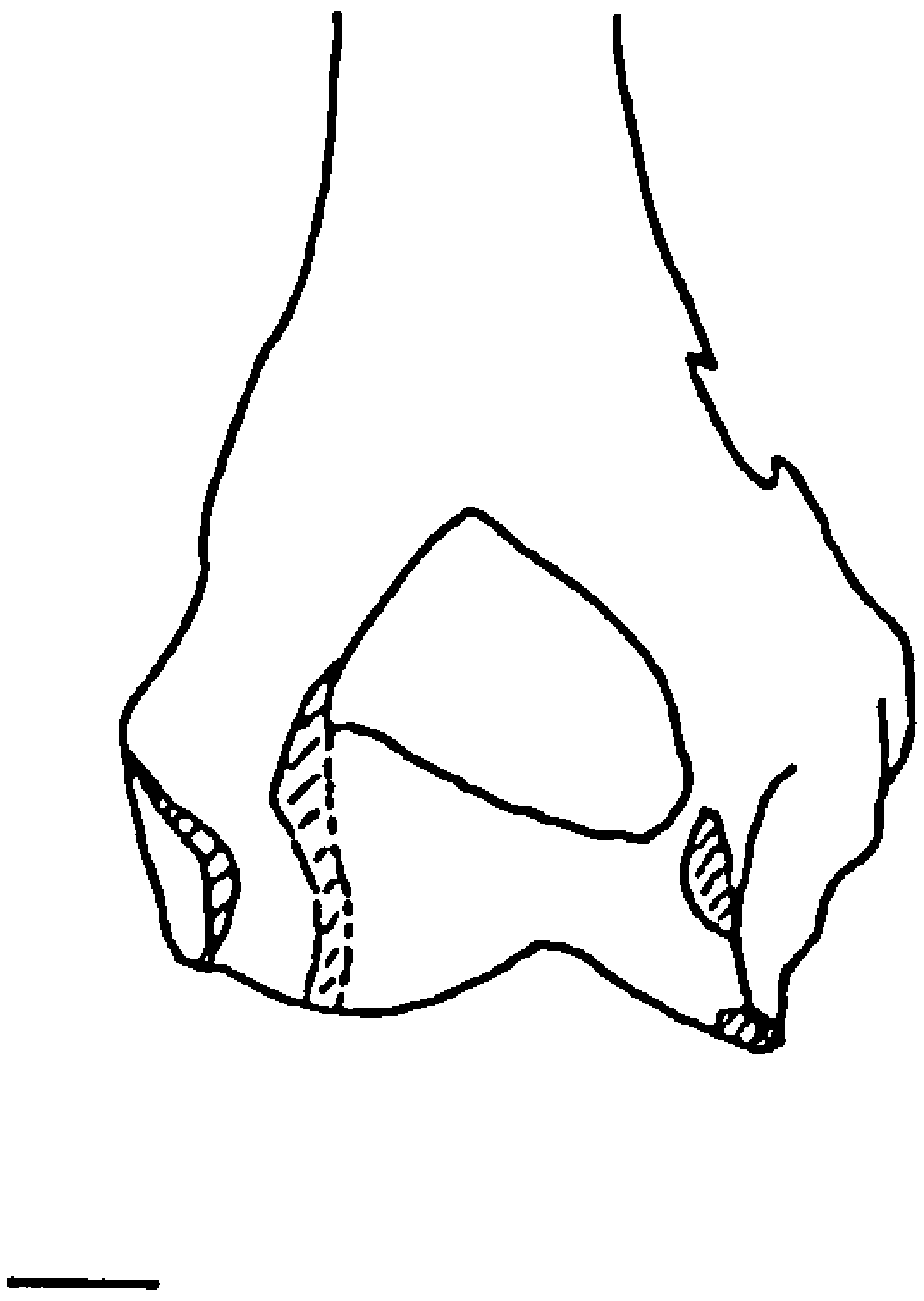
a. *P. gombaszoegensis*. Süssenborn (Süß 10295)

b. *A. pardinensis*. Mosbach



c. fossil jaguar – Salt River (18262)

d. fossil lion – Mosbach (1960/101)



e. *Homotherium* – Mosbach (1950/298)

Figure 5.1. Comparative left humerii shown in posterior view. Scale bar equals 15mm. Hatched areas represent damage.

Kurtén & Poulianos (1977) indicate that the distinct angle of the trochlea is diagnostic of all machairodontinae, suggesting that this feature would be present in *Megantereon* as well. In contrast, *Acinonyx* has a mediolaterally compressed joint, with barely any epicondylar expansion on either side. It also has a very high, narrow olecraneon fossa, which is similar to the domestic dog illustrated in Gonyea (1978).

The pantherine humerii are very similar to each other, but there do appear to be differences. Kurtén & Poulianos (1977) give the following features as being characteristic of *P. gombaszoegensis* – medial part of the trochlea is relatively larger than the lion, large supracondylar foramen, weakly developed supinator ridge, large olecraneon fossa. The lion has a large articulation, with a high and wide olecraneon fossa (confirming the observations of Kurtén, 1969 and Turner, 2000). In contrast the fossil (and modern) jaguar has a very low, wide olecraneon fossa and a greatly expanded medial epicondyle. *Panthera gombaszoegensis* lies somewhere between the two, with a low olecraneon fossa and moderate medial expansion. The medial epicondyle is the insertion point for the medial ligament which attaches the humerus to the posterior surface of the radius (Sisson, 1914). An increase in the depth of this area may indicate that the medial ligament is relatively more important in *P. gombaszoegensis* than in some of the other species. To see if the medial expansion affects the overall shape of the humerus the EPW and Troch W were scatterplotted for the five fossil species. The results are shown in Figure 5.2 and it can be seen that although a lateral expansion appears obvious when looking at the bone, it really is a function of scaling and the larger the cat, the larger the epicondylar width.

The preceding morphological analysis of fossil species is interesting as it highlights the differences between specimens that are currently referred to *P. gombaszoegensis*, which were reviewed at the start of this section. In particular the suggestion that the Halykés specimen is *P. gombaszoegensis* looks suspicious as it has the steep slope from trochlea to capitulum that is normally associated with the machiarodonts. However, it is not so pronounced as in *Homotherium* and it lacks the anteroposterior compression that is seen in this species. Overall I believe it to be a pantherine. The second doubtful attribution is the specimen from Swanscombe, as it lacks the deep insertion point in the lateral epicondyle and has no radial fossa. However, it does possess the classic long, low olecraneon fossa which is seen in all other specimens and it has a break in the proximal slope of this fossa which is very similar to that of the fossil jaguar in Figure 5.1.

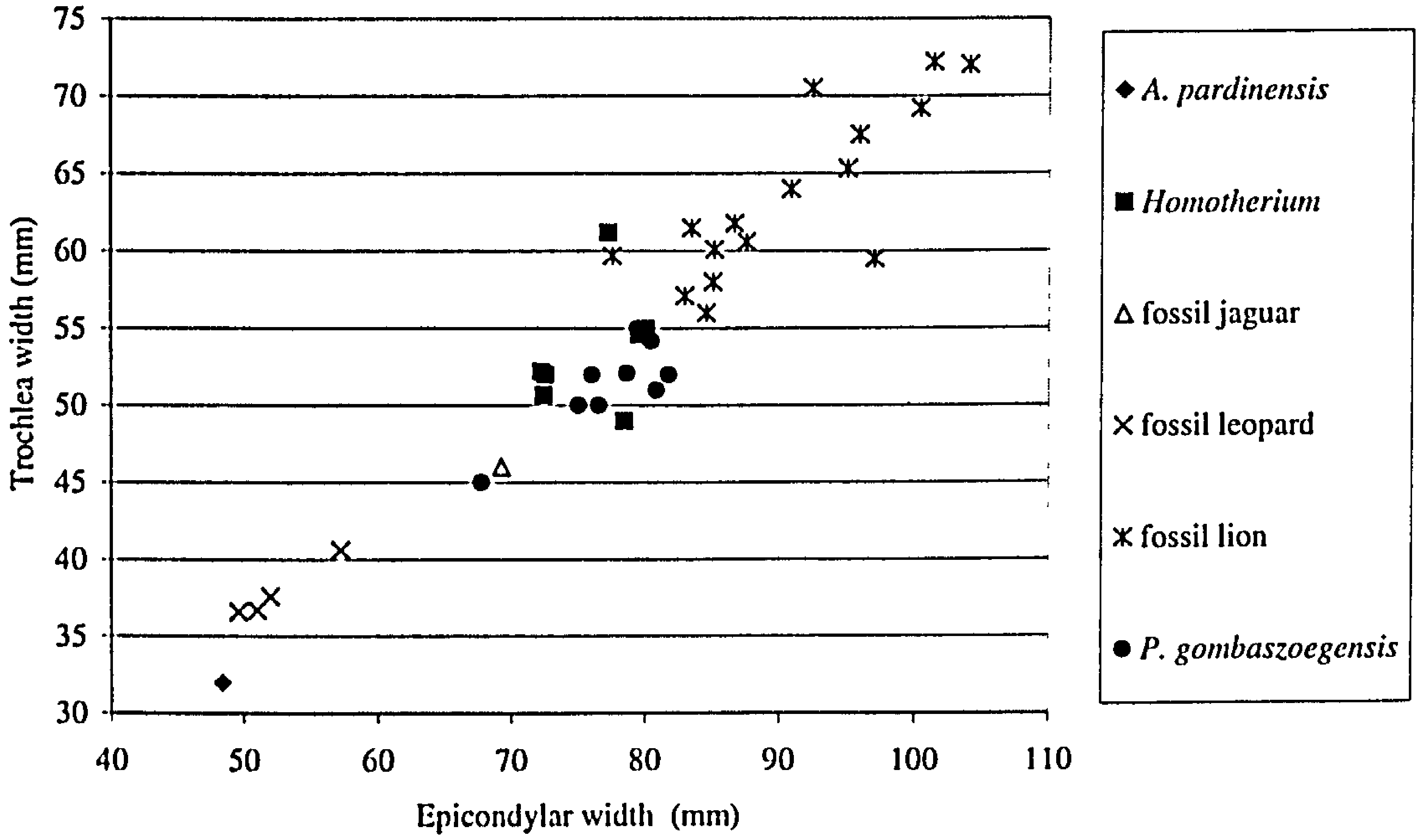


Figure 5.2. Scatterplot of EPW vs Troch W to investigate the effects of epicondylar expansion on six fossil species.

Another interesting specimen is Westbury M47489 (Published by Turner, 2000) which shows slight eburnation of the capitulum in the area in contact with the radial head. Eburnation is often indicative of arthritis (Rogers & Waldron, 1995), although it is not possible to diagnose the specific type on such a small feature. It is unlikely to have interfered with the animal's ability to capture prey and as such is simply evidence of this type of pathology in the population.

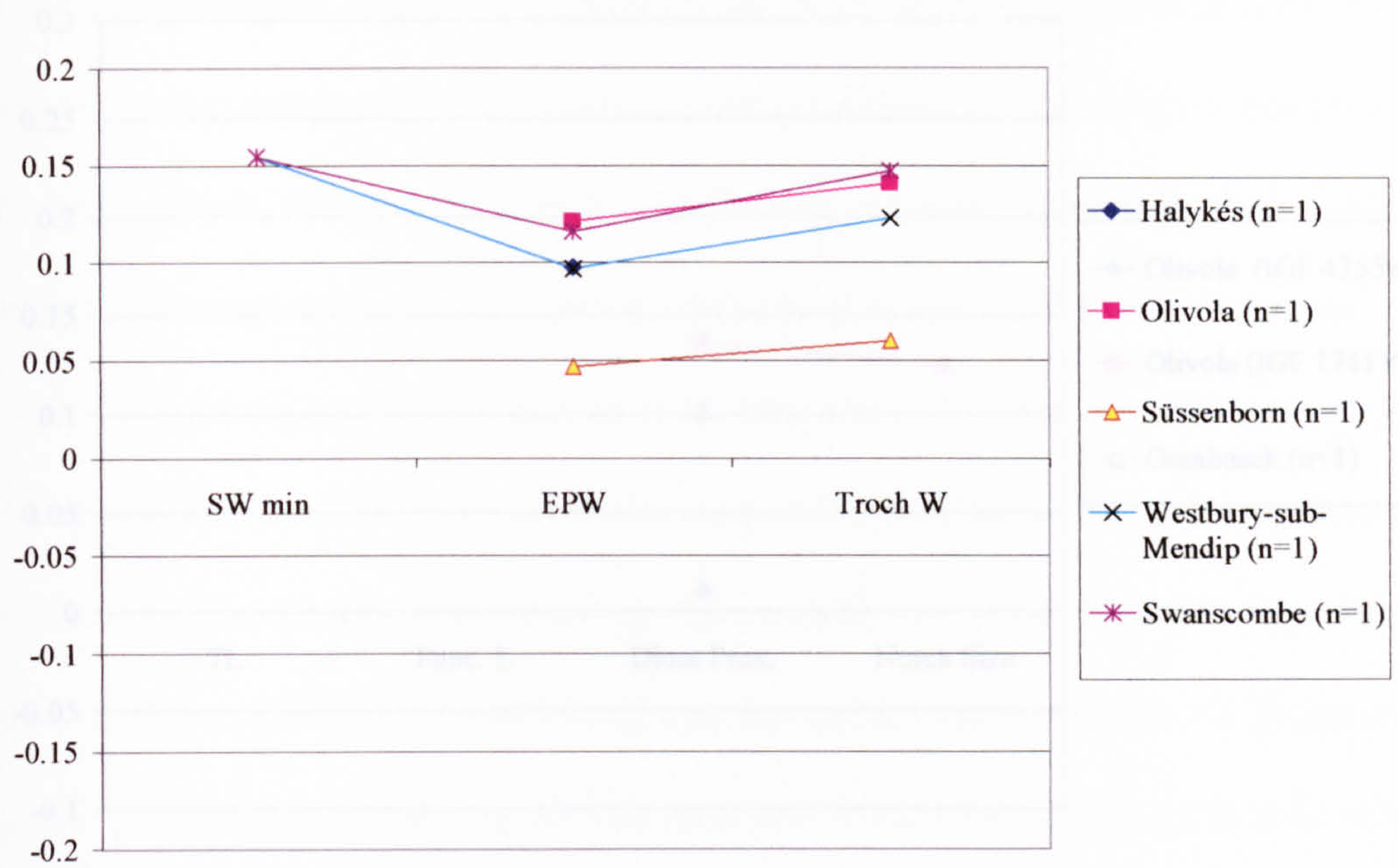


Figure 5.3a. Log ratio diagram of all *P. gombaszoegensis* humerii with mean of modern jaguar sample as standard (n=11)

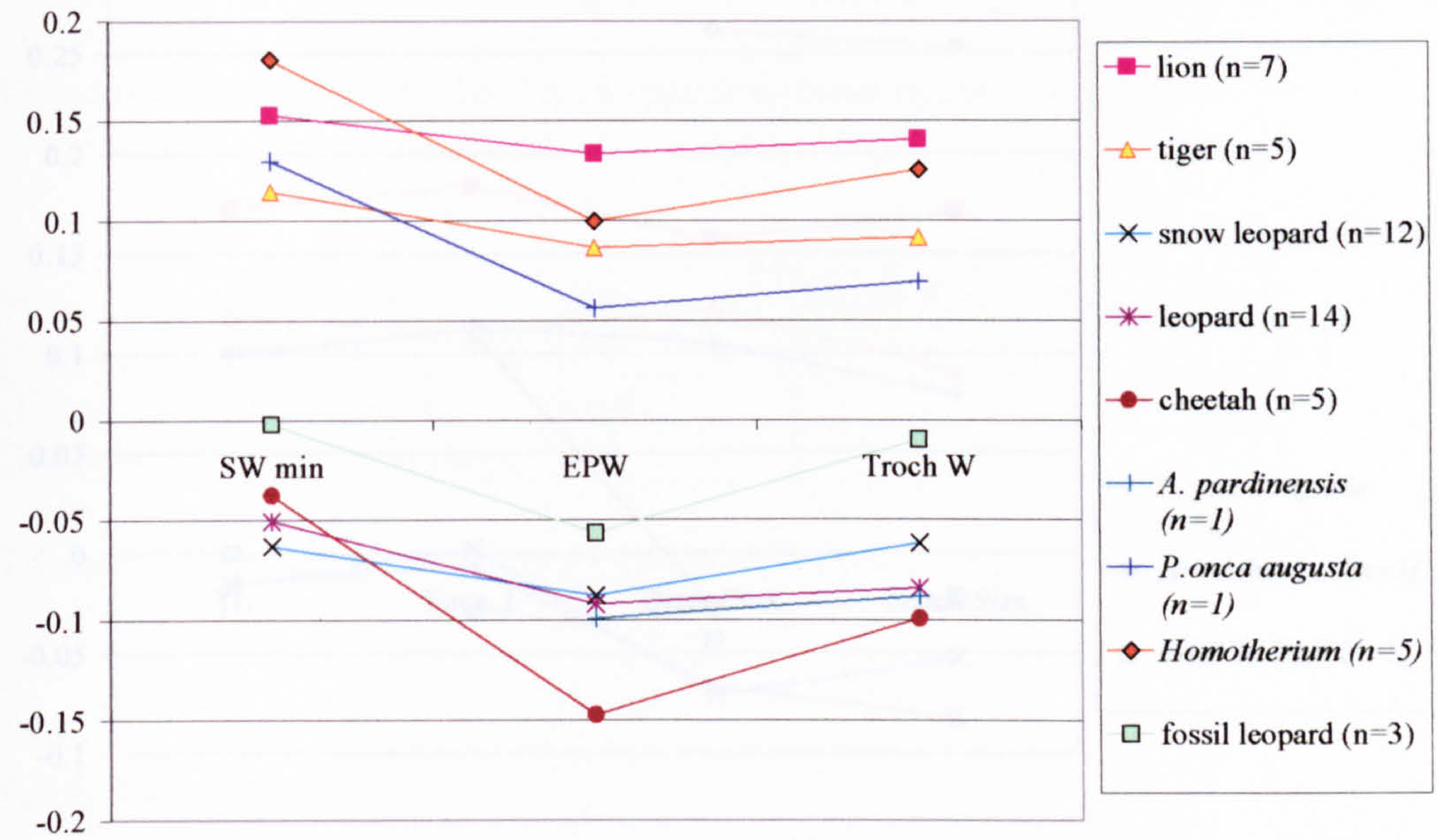


Figure 5.3b. Log ratio diagram of all modern and fossil species humerii with mean of modern jaguar sample as standard (n=11)

Figure 5.3. Log ratio diagrams of the humerus, using the mean of the modern jaguar sample as standard (n=11)

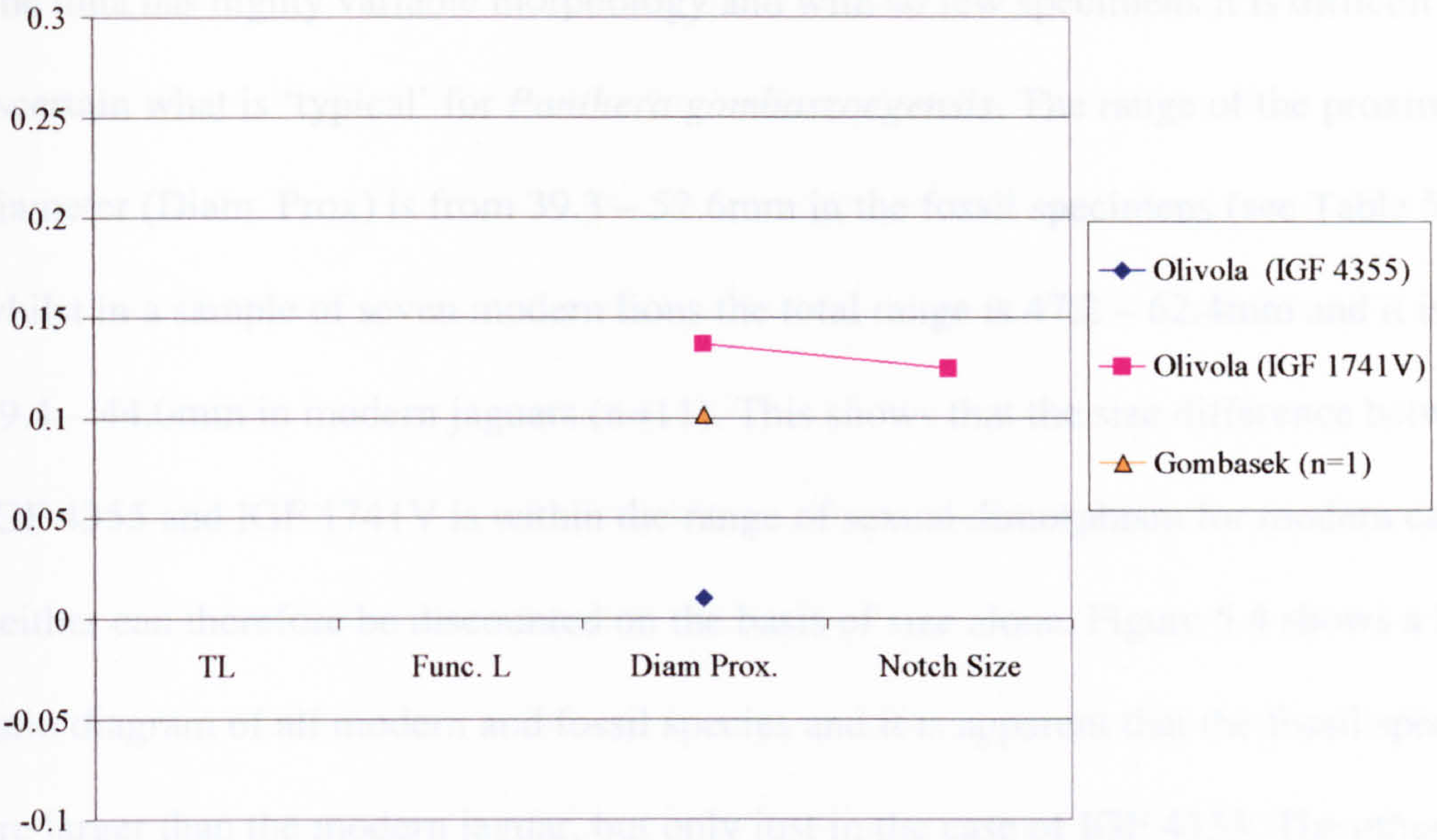


Figure 5.4a. Log ratio diagram of all *P. gombaszoegensis* ulnae with mean of modern jaguar sample as standard (n=11)

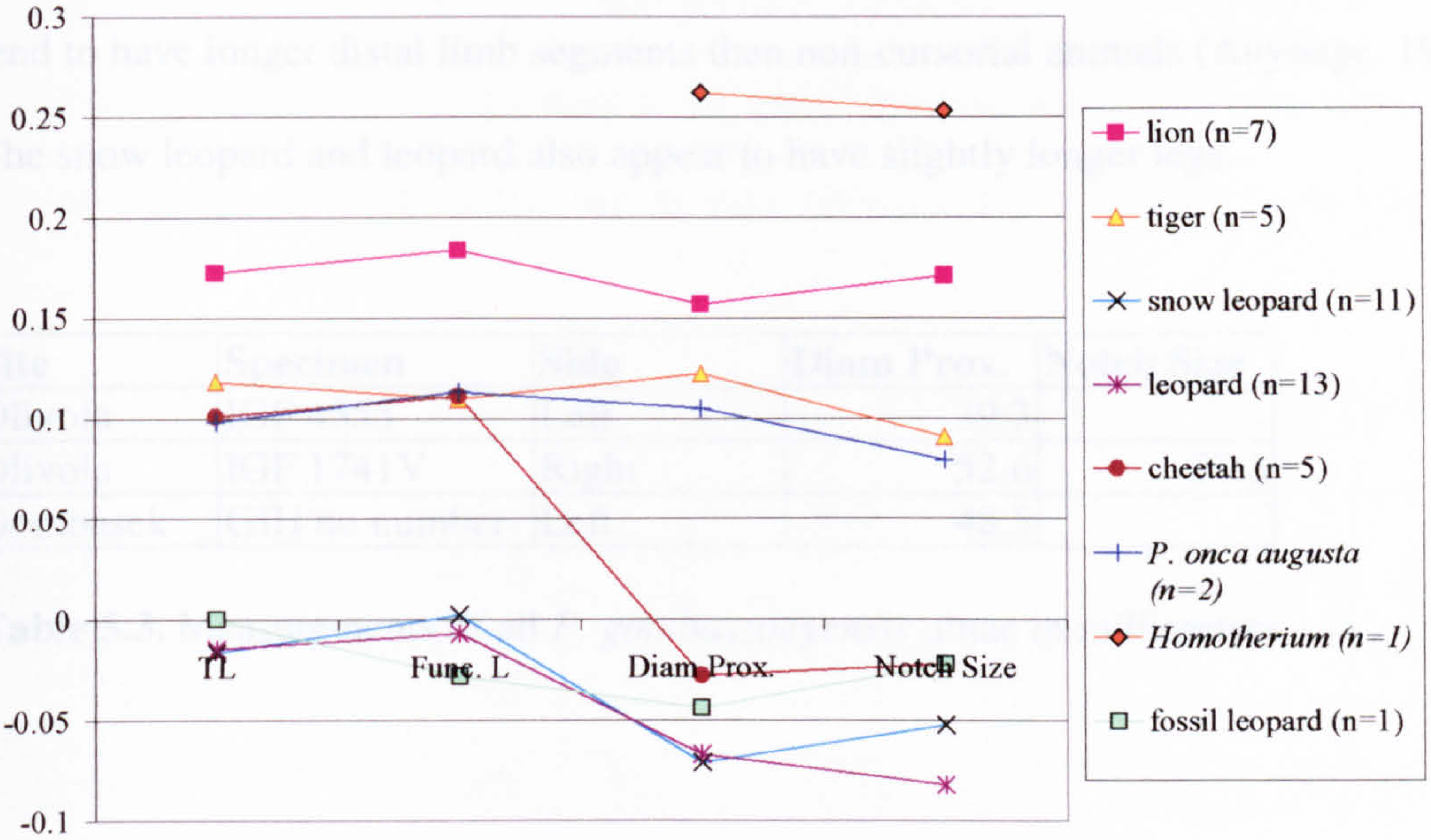


Figure 5.4b. Log ratio diagram of all modern and fossil species ulnae with mean of modern jaguar sample as standard (n=11)

Figure 5.4. Log ratio diagrams of the ulna, using the mean of the modern jaguar sample as standard (n=11)

The ulna has highly variable morphology and with so few specimens it is difficult to ascertain what is 'typical' for *Panthera gombaszoegensis*. The range of the proximal diameter (Diam. Prox) is from 39.3 – 52.6mm in the fossil specimens (see Table 5.3), whilst in a sample of seven modern lions the total range is 47.2 – 62.4mm and it is from 29.4 – 44.0mm in modern jaguars (n=11). This shows that the size difference between IGF 4355 and IGF 1741V is within the range of sexual dimorphism for modern cats and neither can therefore be discounted on the basis of size alone. Figure 5.4 shows a log ratio diagram of all modern and fossil species and it is apparent that the fossil specimens are larger than the modern jaguar, but only just in the case of IGF 4355. The other felids all have similar proportions to the standard, with the exception of the modern cheetah which shows an increase in total length without expanding the size of the proximal articulation. These results agree with other studies that have shown cursorial mammals tend to have longer distal limb segments than non-cursorial animals (Anyonge, 1996). The snow leopard and leopard also appear to have slightly longer legs.

Site	Specimen	Side	Diam Prox.	Notch Size
Olivola	IGF 4355	Left	39.3	
Olivola	IGF 1741V	Right	52.6	29.3
Gombasek	GIH no number	Left	48.5	

Table 5.3. Measurements of all *P. gombaszoegensis* ulnae in millimetres.

5.1.5. Metacarpals

5.1.5.1. Second metacarpal

Olivola (n=1) IGF 1224V – straight edge on Mc1 articulation; in anterior view both sides curve upwards; distinct groove across proximal anterior surface; Mc3 articulation has large bulge beneath facet; facet is very deep and fully beneath the overhanging proximal surface.

L'Escale (n=2) CD814 – unfused; thick shaft; distinct groove across proximal anterior surface; deep anterior profile; Mc1 articulation has two distinct bumps beneath it; Mc3 articulation has slight bump on posterior of shaft; large facet. CD 2514 – slender shaft; Mc3 facet is very pronounced; one bump beneath Mc1 articulation; shallow anterior profile.

Gombasek (n=1) ß823 – broken; deep Mc3 articulation but top does not overhang the facet; two raised areas beneath the facet.

Kövesvárad (n=2) V63/244 – damaged; very steep curve in anterior profile; Mc3 articulation relatively shallow. V63/244 – strong bulge beneath Mc1 articulation; distinct groove across proximal anterior surface.

Uppony 1 (n=1) V65/182 – no morphology recorded.

The morphology of the Mc3 facet appears quite variable, with the Olivola and Gombasek specimens having a deep facet, whilst this feature is shallow in the Kövesvárad material. The fossils are all quite similar in terms of size (Table 5.4).

Site	Specimen	Side	TL	PWML	PWAP	SWML	SWAP	DW
L'Escale	C-D 814	Left		19.5	24.1			
L'Escale	C-D 2514	Right		18.4	23.6			
Olivola	IGF 1224 V	Right	92.2	16.5	28.4	10.8	12.2	17.6
Gombasek	ß823	Right	78.7	16.1		12.4	12.3	18.4
Kövesvárad	V63/244	Right		17	24.8			
Kövesvárad	V63/244	Left			25			
Uppony 1	V65/182	Left	82.6	18.2		14.2	13.6	20.1

Table 5.4. Measurements of all *P. gombaszoegensis* 2nd metacarpals in millimetres. Abbreviations explained in section 2.3.4.5.

The log ratio diagram in Figure 5.5 shows that the specimens are also proportionally similar, although the L'Escale metacarpals show a distinct anteroposterior reduction in comparison with the Kövesvárad and Olivola specimens. This may be because the L'Escale specimens have unfused epiphyses and are therefore juvenile.

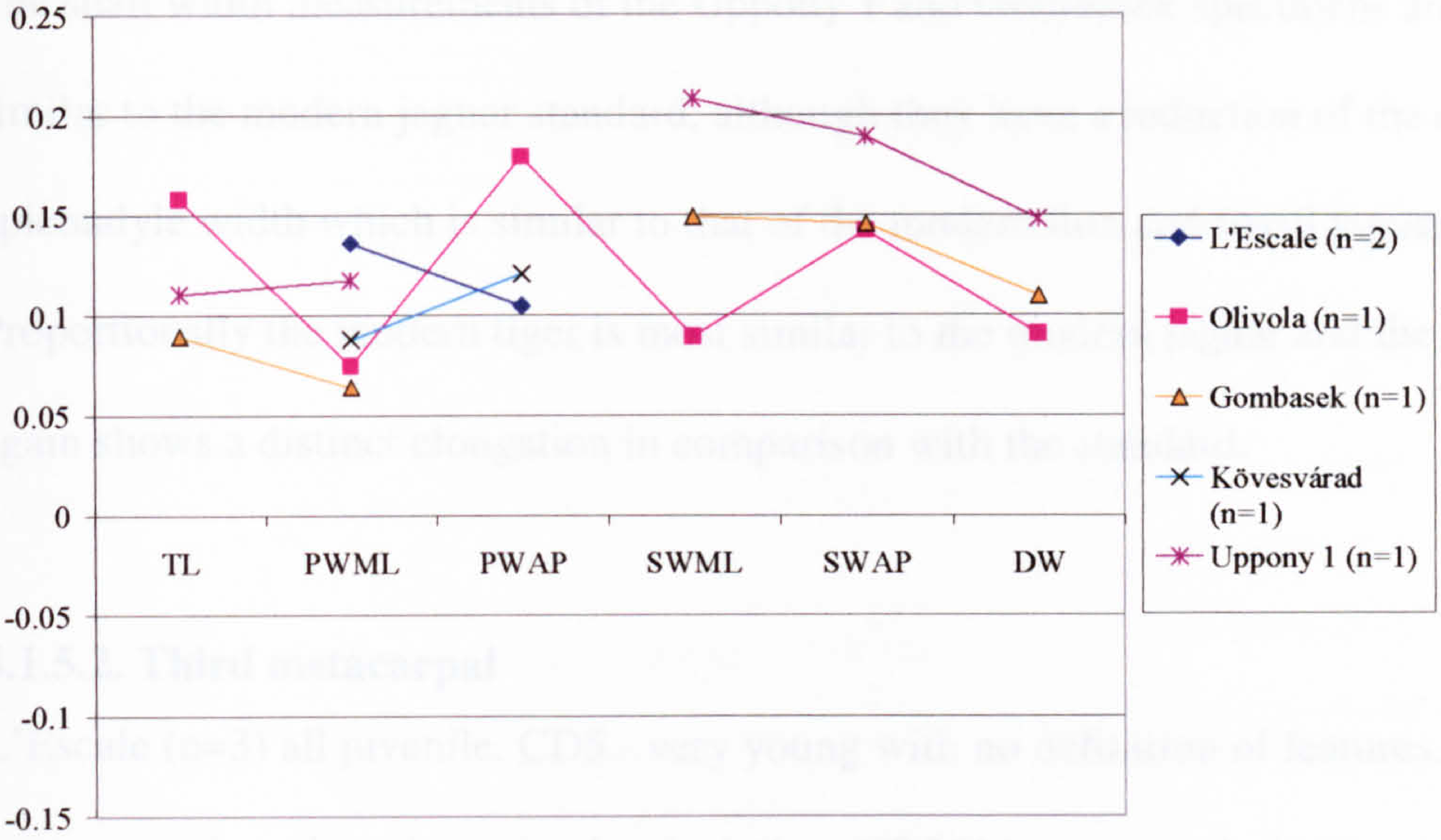


Figure 5.5a. Log ratio diagram of all *P. gombaszoegensis* 2nd metacarpals with mean of modern jaguar sample as standard (n=10)

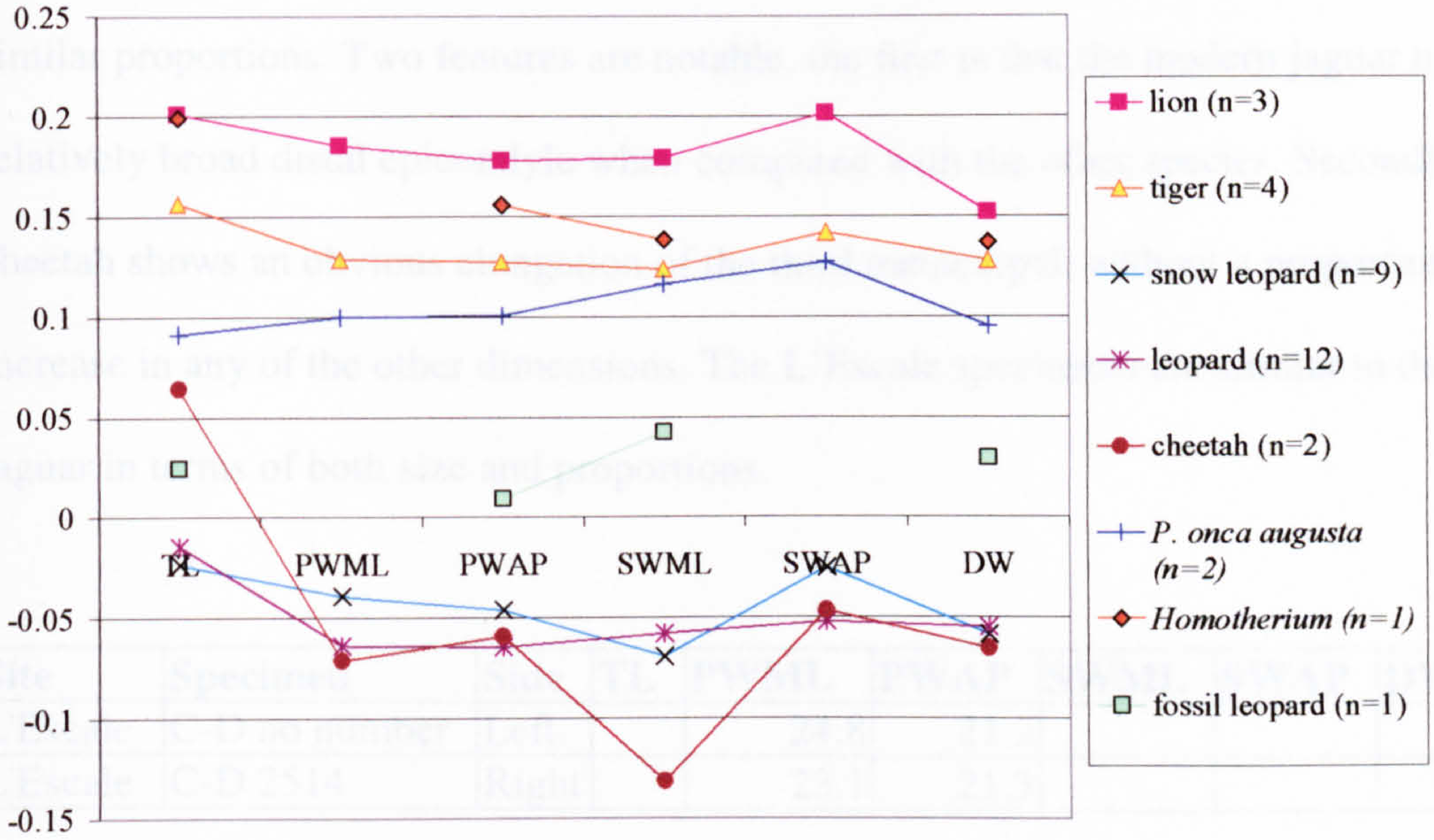


Figure 5.5b. Log ratio diagram of all modern and fossil species 2nd metacarpals with mean of modern jaguar sample as standard (n=10)

Figure 5.5. Log ratio diagrams of the 2nd metacarpal using the mean of the modern jaguar sample as standard (n=10)

The shaft width measurements of the Uppony 1 and Gombasek specimens are very similar to the modern jaguar standard, although they have a reduction of the distal epicondyle width which is similar to that of the modern lion and fossil jaguar. Proportionally the modern tiger is most similar to the modern jaguar and the cheetah again shows a distinct elongation in comparison with the standard.

5.1.5.2. Third metacarpal

L'Escale (n=3) all juvenile. CD5 - very young with no definition of features. CD no number - broad proximal articulation. CD2514 - no morphology recorded.

Measurements of the L'Escale specimens are given in Table 5.5 and shown in the log ratio diagram in Figure 5.6. It can be seen from this graph that all of the cats have very similar proportions. Two features are notable, the first is that the modern jaguar has a relatively broad distal epicondyle when compared with the other species. Secondly, the cheetah shows an obvious elongation of the third metacarpal, without a proportional increase in any of the other dimensions. The L'Escale specimens are similar to the fossil jaguar in terms of both size and proportions.

Site	Specimen	Side	TL	PWML	PWAP	SWML	SWAP	DW
L'Escale	C-D no number	Left		24.8	21.2			
L'Escale	C-D 2514	Right		23.1	21.3			

Table 5.5. Measurements of all *P. gombaszoegensis* 3rd metacarpals in millimetres. Abbreviations explained in section 2.3.4.5.

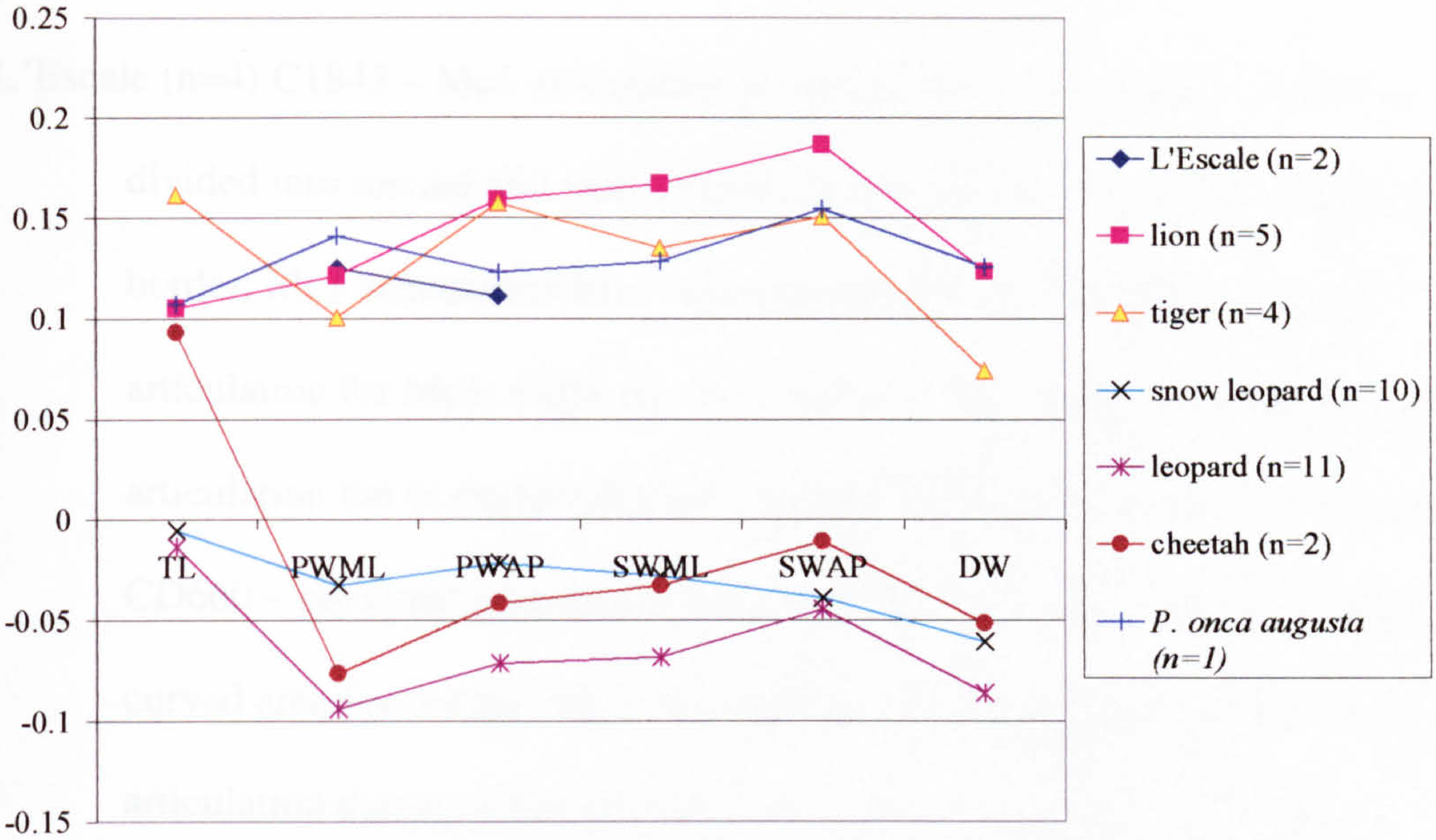


Figure 5.6. Log ratio diagram of all 3rd metacarpals with mean of modern jaguar sample as standard (n=10)

5.1.5.3. Fourth metacarpal

L'Escale (n=4) C1843 – Mc5 articulation is very curved; Proximal articulation is divided into medial and lateral facets by a slightly raised area; straight anterior border; Mc3 articulation has a squared anterior facet. CD661 – curved articulation for Mc5; slight dip on anterior border; facets undivided on proximal articulation but is slightly dipped; Anterior facet of Mc3 articulation is pointed. CD660 – proximal articulation undivided but has distinct change in slope; curved anterior border; Mc3 articulation has squared anterior facet; Mc5 articulation damaged but appears curved. CD2514 – very curved Mc5 articulation; no division of facets on proximal articulation.

Gombasek (n=1) M1 - very strongly curved Mc5 articulation; dipped anterior border; large, raised areas for muscle attachment on shaft; distinct insertion points above the posterior surface of distal condyle.

The Gombasek and L'Escale specimens are very like a modern jaguar in the BMNH (No. 117f. 1858.5.26.9). The Mc5 articulation is less curved in the fossil jaguar (Hamilton Cave cat). Many of the features observed are not consistent in any of the modern or fossil species studied, for example the Mc5 articulation in a modern jaguar specimen (Liverpool Museum No. 1.11.1853) is divided into two distinct facets, a difference that may be thought to be diagnostic. However, no other modern and fossil jaguar had this feature. It appears that the morphology of the fourth metacarpal is too variable to be diagnostic which leaves morphometric data as the most likely way of discriminating between species. Table 5.6 contains measurements of all *P. gombaszoegensis* specimens and these are plotted with other fossil and modern species in the form of a log ratio diagram in Figure 5.7. The log ratio diagram shows that the L'Escale metacarpals are proportionally the same as the modern jaguar, while the other two sites are not directly comparable to any of the other species.

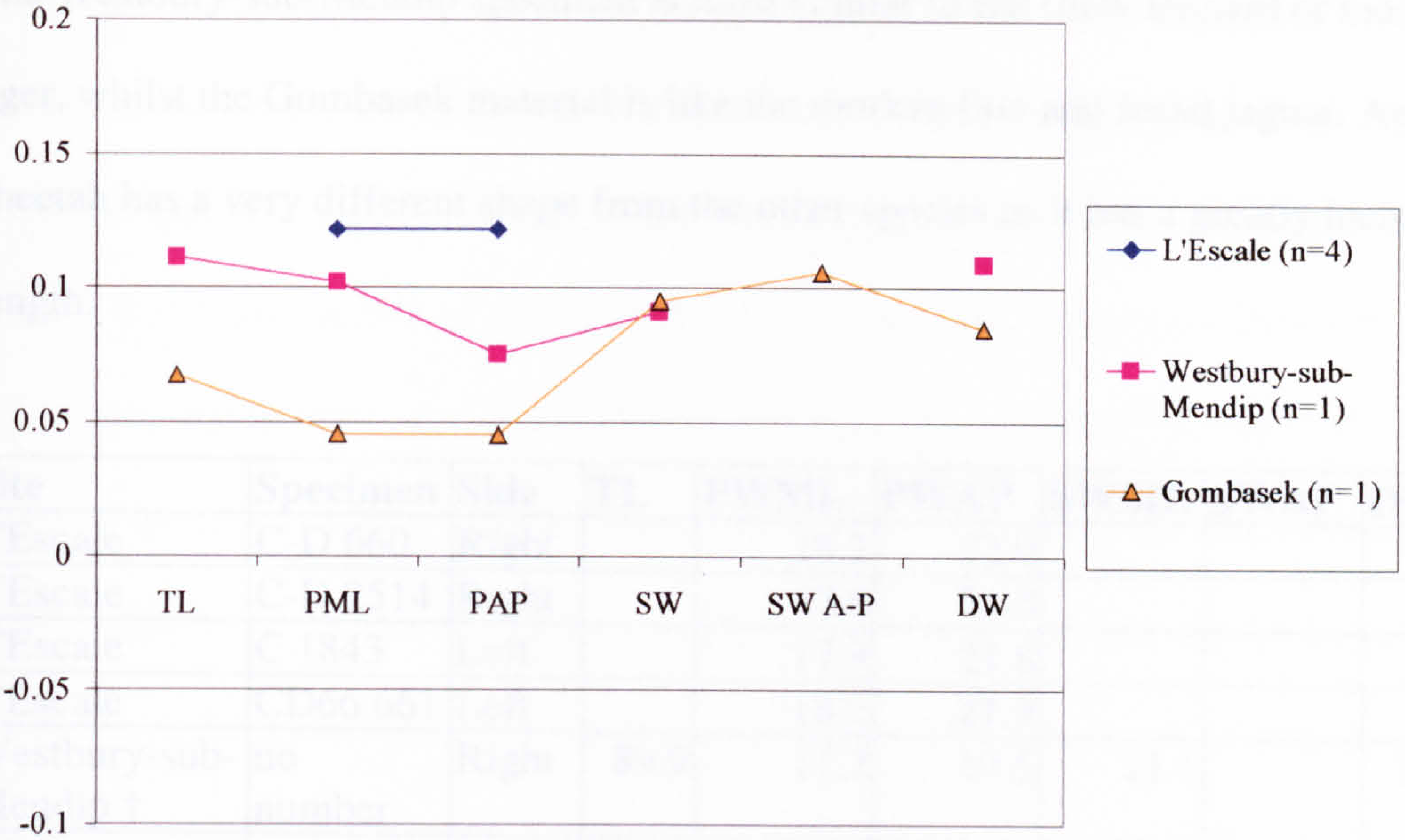


Figure 5.7a. Log ratio diagram of all *P. gombaszoegensis* 4th metacarpals with mean of modern jaguar sample as standard (n=10)

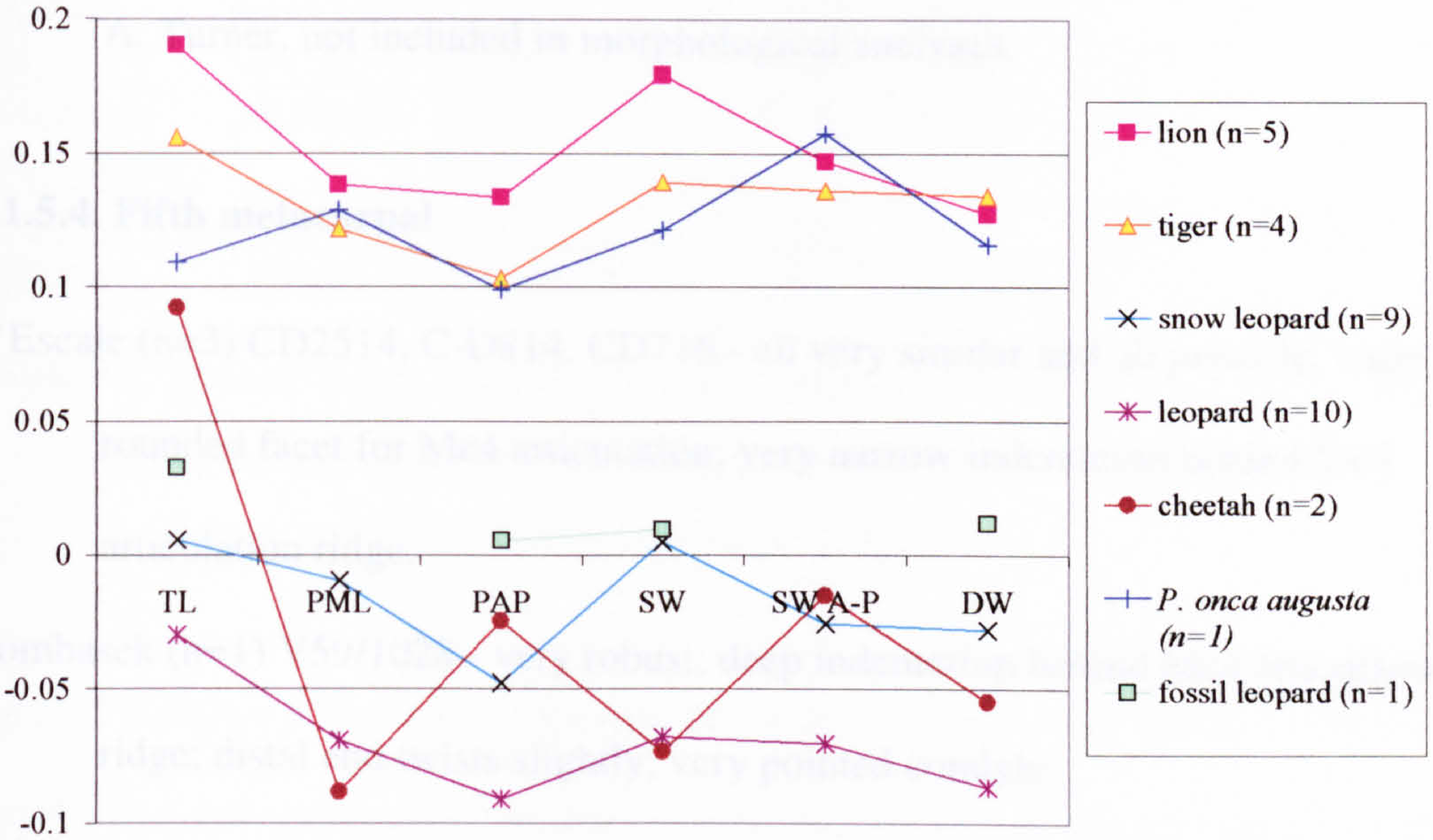


Figure 5.7b. Log ratio diagram of all modern and fossil species 4th metacarpals with mean of modern jaguar sample as standard (n=10)

Figure 5.7. Log ratio diagrams of the 4th metacarpal, using the mean of the modern jaguar sample as standard (n=10)

The Westbury-sub-Mendip specimen is most similar to the snow leopard or modern tiger, whilst the Gombasek material is like the modern lion and fossil jaguar. Again, the cheetah has a very different shape from the other species as it has a greatly increased length.

Site	Specimen	Side	TL	PWML	PWAP	SWML	SWAP	DW
L'Escale	C-D 660	Right		18.2	22.0			
L'Escale	C-D 2514	Right		17.8	21.0			
L'Escale	C 1843	Left		17.9	21.8			
L'Escale	CD66 661	Left		18.2	21.9			
Westbury-sub-Mendip †	no number	Right	89.9	17.2	19.5	11.1		18.5
Westbury-sub-Mendip †	M51500	Right	90.2	16.7		12.8		19.4
Gombasek	M1	Left	81.3	15.1	18.2	11.2	11.1	17.5

Table 5.6. Measurements of all *P. gombaszoegensis* 4th metacarpals in millimetres. Abbreviations explained in section 2.3.4.5. † indicates measurements taken by A. Turner, not included in morphological analyses.

5.1.5.4. Fifth metacarpal

L'Escale (n=3) CD2514, C-D814, CD716 - all very similar and all juvenile; large, rounded facet for Mc4 articulation; very narrow indentation behind Mc4 articulation ridge.

Gombasek (n=1) V59/1028 - very robust; deep indentation behind Mc4 articulation ridge; distal end twists slightly; very pointed condyle.

Halykés (n=1) Ah29 - wide indentation behind Mc4 articulation ridge; lateral edge expanded and squared off.

Uppony 1 (n=1) V60/1193 - reconstructed; no morphology recorded.

The Gombasek specimen (V59/1028) was marked '*Epimachairodus*' in the museum catalogue (*Epimachairodus* = *Homotherium*). However it is much too small to be

Homotherium and appears a good match for *P. gombaszoegensis* (see Table 5.7). The Halykés specimen is very different from the others. This could be because all the L'Escale specimens are juvenile, but it is very similar to the leopard illustrated in Nagel (1999). It is a similar size to the other *P. gombaszoegensis* specimens shown in Table 5.7. Again, the morphology of the Mc5 is very variable, with the Liverpool Museum jaguar (No. 1.11.1853) having the Mc4 articulation divided into two distinct areas, but BMNH No. 117f. 1858.5.26.9 does not. Therefore I have not assigned the Halykés specimen to *P. pardus* as I do not believe that metapodials have sufficiently reliable features on which to diagnose species.

Site	Specimen	Side	TL	PWML	PWAP	SWML	SWAP	DW
L'Escale	C-D 2514	Right		18.3	20.2			
L'Escale	C-D 841			20.4	19.0			
L'Escale	C-D 716	Left		20.2	20.6			
Halykés	Ah 29	Left		18.8	17.4			
Westbury-sub-Mendip †	M51488	Left	71.8	17.6	19.7	12.2		18.2
Gombasek	V59/1028	Right	73	15.6	20.3	12.6	12.6	18.2
Uppony 1	V60/1193	Right	69.7	15.2	21.3	11.7	11.4	18

Table 5.7. Measurements of all *P. gombaszoegensis* 5th metacarpals in millimetres. Abbreviations explained in section 2.3.4.5. † indicates measurements taken by A. Turner, not included in morphological analyses.

Figure 5.8 shows a log ratio diagram of all modern and fossil specimens, it can be seen that the Halykés specimen is similar to the L'Escale material and that these two sites are very different from the other fossil specimens. Proportionally they are most similar to the modern cheetah, but the fossil specimens are certainly pantherine. This may be an indication that the Halykés specimen is juvenile, like the L'Escale material, and that the anterioposterior width of the fifth metacarpal alters before adulthood. The Uppony 1 specimen is most similar to the fossil jaguar, while the Gombasek and Westbury-sub-Mendip are very different to all other cats.

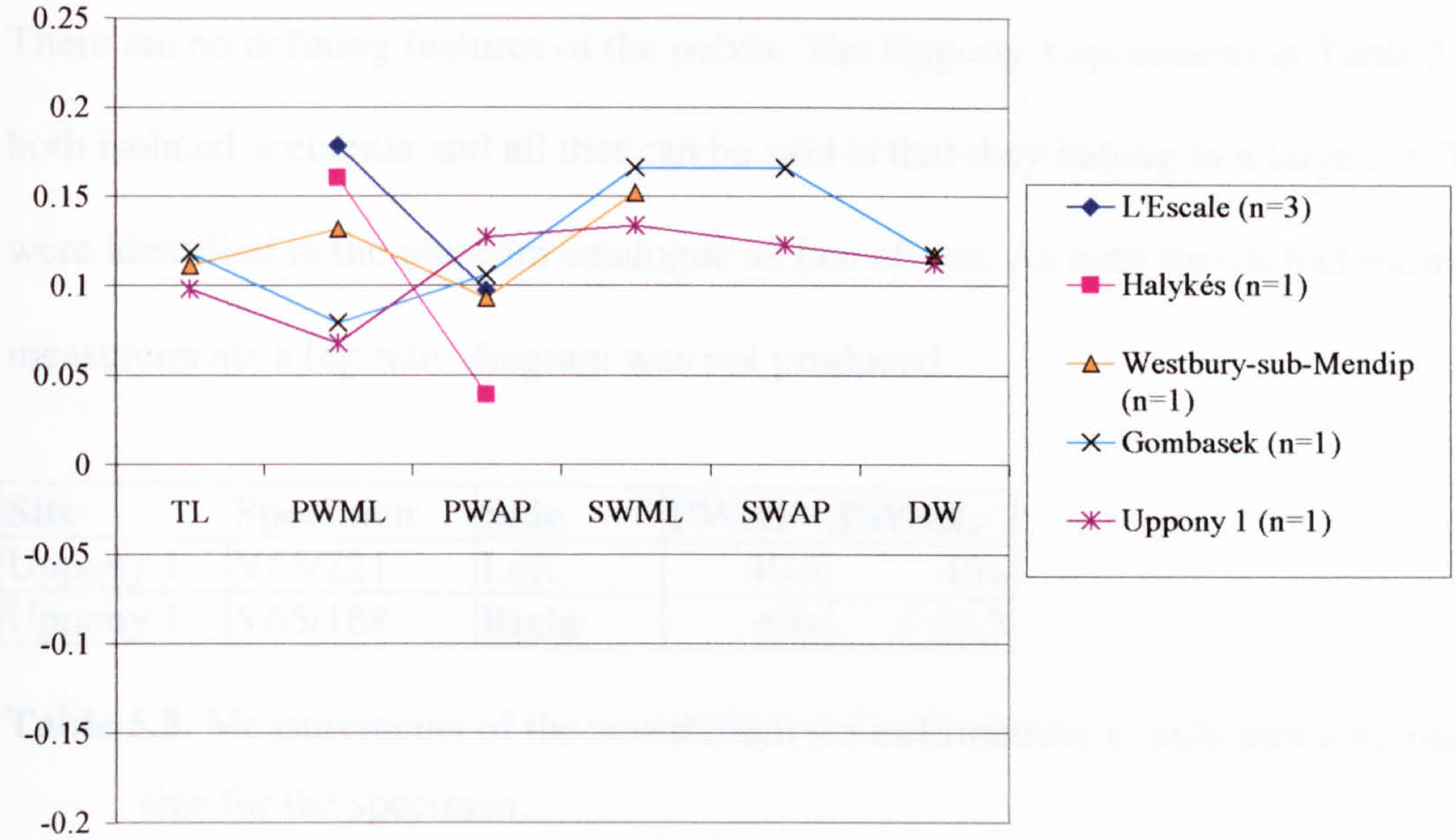


Figure 5.8a. Log ratio diagram of all *P. gombaszoegensis* 5th metacarpals with mean of modern jaguar sample as standard (n=10)

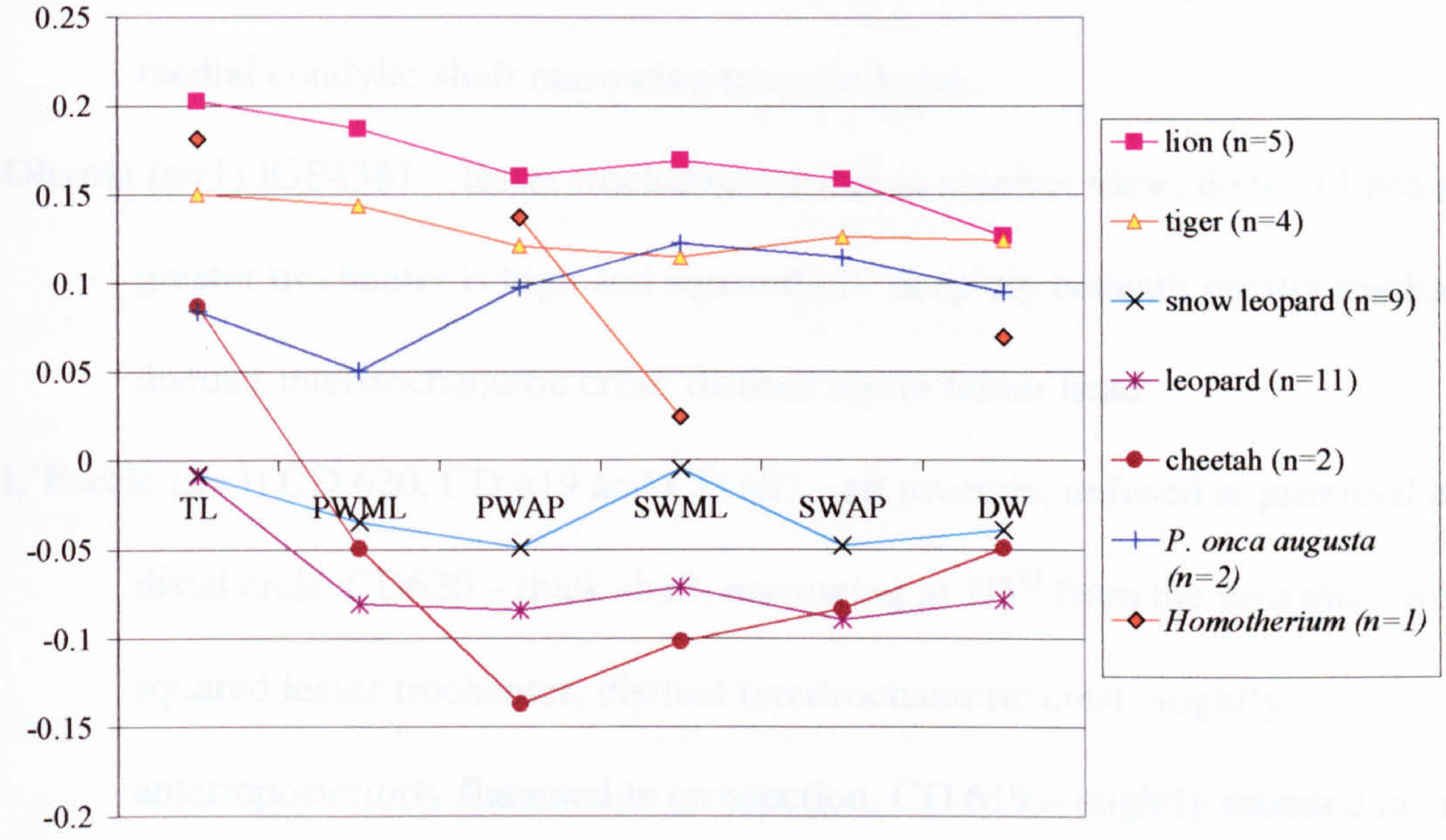


Figure 5.8b. Log ratio diagram of all modern and fossil species 5th metacarpals with mean of modern jaguar sample as standard (n=10)

Figure 5.8. Log ratio diagrams of the 5th metacarpal, using the mean of the modern jaguar sample as standard (n=10)

5.1.6. Pelvis

There are no defining features of the pelvis. The Uppony 1 specimens in Table 5.8 are both isolated acetabula and all that can be said is that they belong to a large cat. They were identified in the museum catalogue as *Leo* cf. *leo*. As both fossils had estimated measurements a log ratio diagram was not produced.

Site	Specimen	Side	PWAP	PWML
Uppony 1	V65/221	Left	40.4	40+
Uppony 1	V65/168	Right	40+	39.3

Table 5.8. Measurements of the acetabulum (in millimetres).+ indicates a minimum size for the specimen.

5.1.7. Femur

Slivnitsa (n=1) SL107 FM1507 - distal femur and half shaft; large medial condyle; wide patellofemoral joint; narrow intercondylar fossa; distinct squaring off above medial condyle; shaft narrowing towards break.

Olivola (n=1) IGF4381 – lesser trochanter visible in anterior view; distinct linea aspera; greater trochanter is high and squared off; deep dip beneath greater trochanter; distinct intertrochanteric crest; distinct dip in femur head.

L'Escale (n=3) CD 620, CD 619 and CD 627 - all juvenile, unfused at proximal and distal ends. CD620 – thick shaft, narrowing at 1/3rd from the proximal end; squared lesser trochanter; distinct intertrochanteric crest; slightly anterioposteriorly flattened in crossection. CD 619 – slightly rounded in cross section; heavily reconstructed; marginally less robust than CD620. CD 627 – very young animal; morphology not defined.

Westbury-sub-Mendip (n=1) WSM77W5R3 – proximal femur, lacking femoral head; large lesser trochanter, visible in anterior view of the shaft; large greater trochanter; deep and narrow hollow beneath greater trochanter.

Uppony 1 (n=2) V601221 and V601210 – both very similar; large; very deep dip in femoral head; femoral head is not rounded but squared off in the distal posterior quarter; very deep dip before the greater trochanter; lesser trochanter large and well defined.

Certain features are common to the *P. gombaszoegensis* specimens: a large lesser trochanter that is visible in anterior view; a deep dip beneath the greater trochanter and a strong intertrochanteric crest. The two Uppony 1 specimens stand out for two reasons – the deep insertion point and the squaring off of the femoral head. In the fossil jaguar and all *P. gombaszoegensis* specimens the dip is present but is not pronounced and the femoral head is slightly rounder. This indicates that the Uppony 1 specimens are not jaguars or *P. gombaszoegensis*. It is possible that these two specimens may be lions, as they are the right size to fit the two pelves identified as *Panthera* cf. *leo* in section 5.1.7. Figure 5.9 shows a log ratio diagram of all potential *P. gombaszoegensis* specimens. This shows that the Olivola specimen is very small and similar to the modern jaguar in size, while the Westbury and Uppony 1 cats are much larger. Interestingly, only *P. gombaszoegensis* shows a reduction in femoral head size when compared with the modern jaguar. The cheetah, snow leopard and modern tiger have a slightly narrower shaft than the other cats, but for the most part they are all very similar to the standard.

Site	**Specimen**	**Side**	**PW Max**	**Neck Diam**	**Head Diam**	**SW Min**	**DW**
Olivola	IGF 4381	Right	59.7	24.3	27.8		
Slivnitsa	SL107 FM1507	Left					53.6
Westbury-sub-Mendip	WSM77W5R3 161	Right		30+		29.5+	
Uppony 1	V60/1221	Left		29.8	35.2		
Uppony 1	V60/1210	Right		30.8	35.3		

Table 5.9. Measurements of all *P. gombaszoegensis* femora in millimetres. + indicates a minimum measurement.

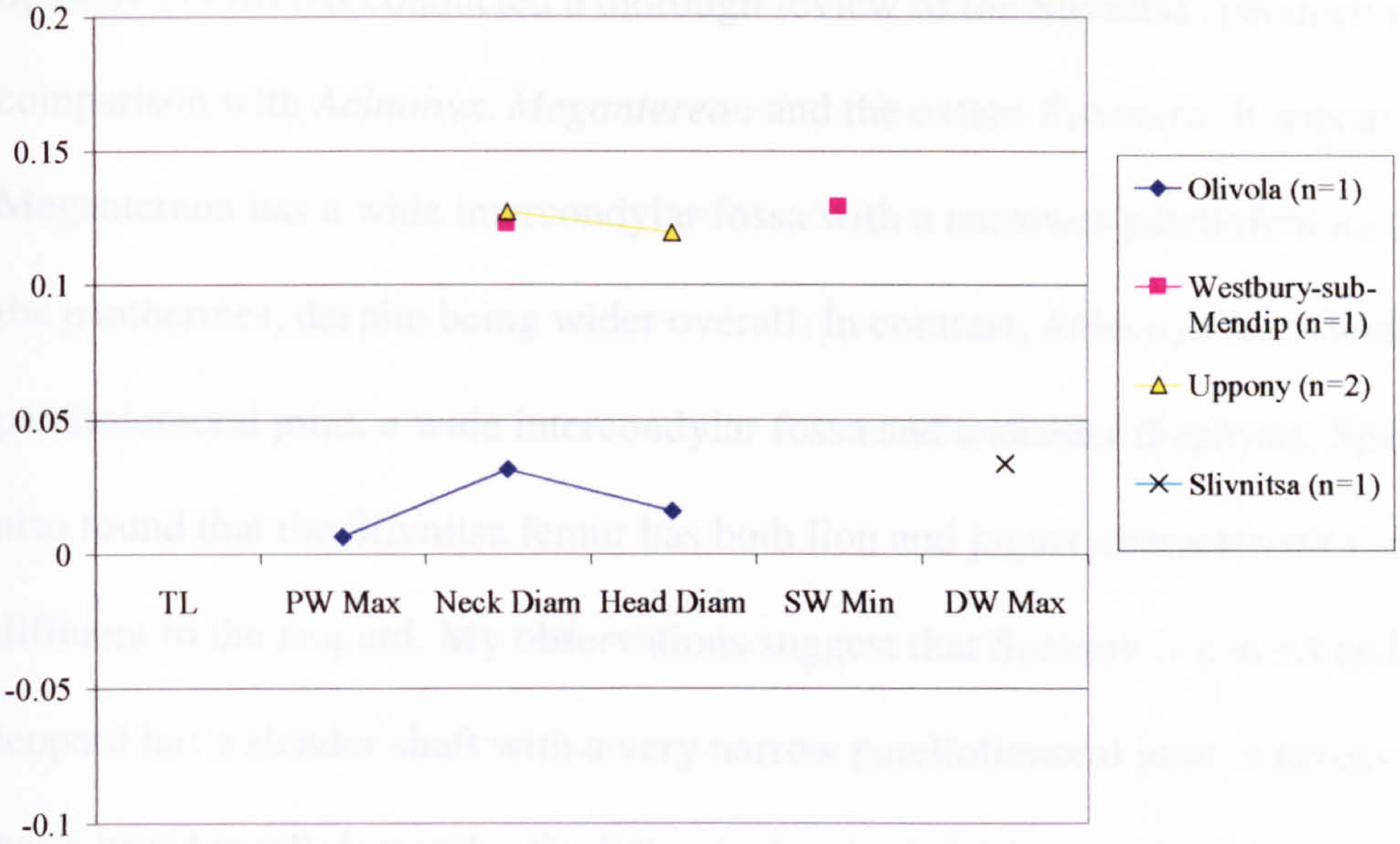


Figure 5.9a. Log ratio diagram of all *P. gombaszoegensis* femora with mean of modern jaguar sample as standard (n=11)

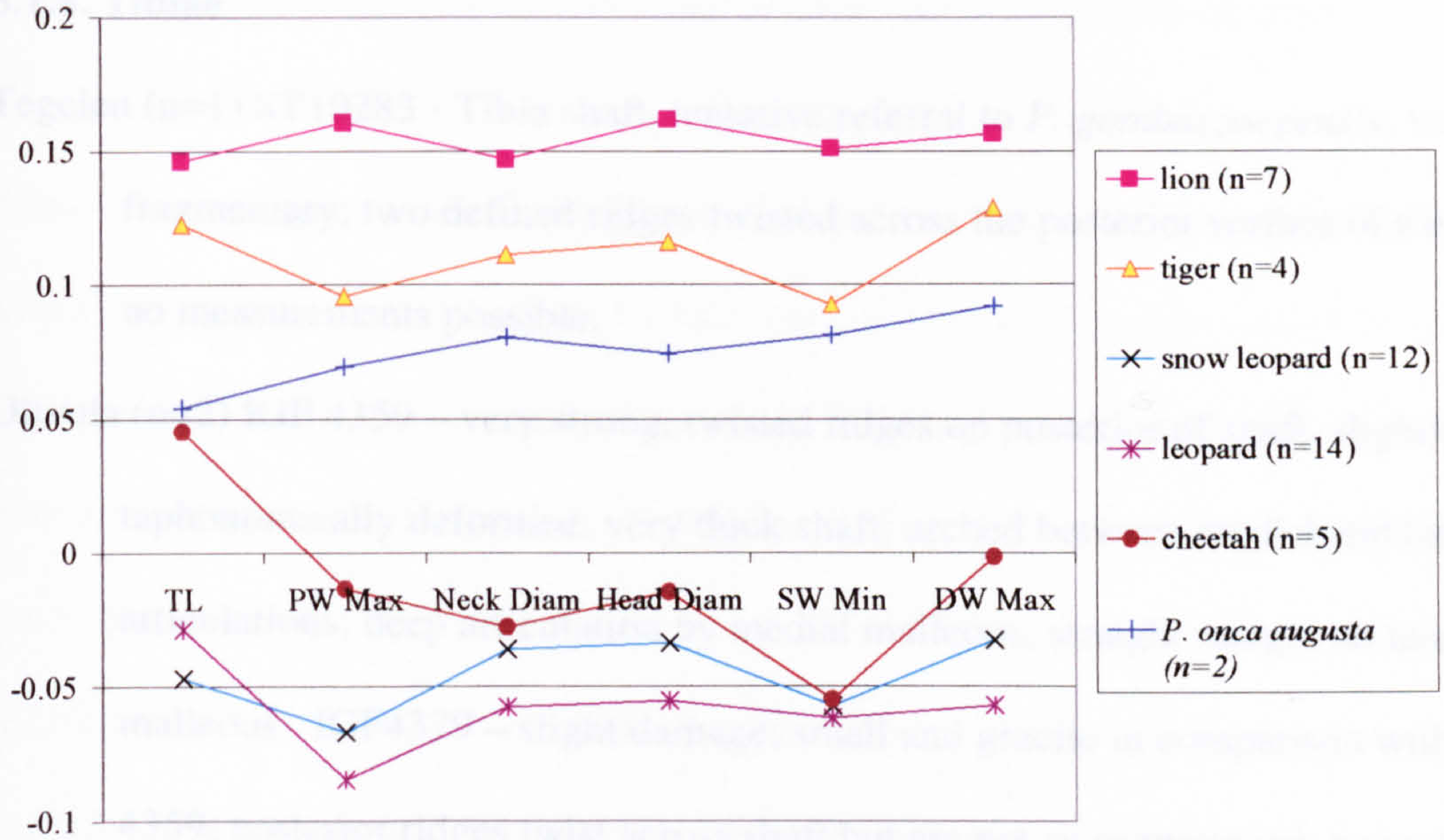


Figure 5.9b. Log ratio diagram of all modern and fossil species femora with mean of modern jaguar sample as standard (n=11)

Figure 5.9. Log ratio diagrams of femora, using the mean of the modern jaguar sample as standard (n=11)

Spassov (1998) has conducted a thorough review of the Slivnitsa specimen in comparison with *Acinonyx*, *Megantereon* and the extant *Panthera*. It appears that Megantereon has a wide intercondylar fossa with a narrower patellofemoral joint than the pantherines, despite being wider overall. In contrast, *Acinonyx* has a wide patellofemoral joint, a wide intercondylar fossa and a slender diaphysis. Spassov (1998) also found that the Slivnitsa femur has both lion and jaguar characteristics and was very different to the leopard. My observations suggest that Spassov is correct and that the leopard has a slender shaft with a very narrow patellofemoral joint, whereas the jaguar has a broad patellofemoral articulation and a much thicker shaft. In view of this, the Slivnitsa femur does have jaguar-like characteristics.

5.1.8. Tibiae

Tegelen (n=1) ST10283 - Tibia shaft, tentative referral to *P. gombaszoegensis*; very fragmentary; two defined ridges twisted across the posterior surface of the shaft; no measurements possible.

Olivola (n=2) IGF 4359 – very strong, twisted ridges on posterior of shaft; slightly taphonomically deformed; very thick shaft; arched between medial and lateral articulations; deep articulation by medial malleous; straight margin on lateral malleous. IGF4379 – slight damage; small and gracile in comparison with IGF 4359; posterior ridges twist across shaft but are not so pronounced; no real dip beneath tibial tuberosity. Proximal end - lateral crest is set slightly posterior to and slightly higher than, the medial crest; two dips and a small bump orientated anterioposteriorly separate the proximal facets. Distal end – straight border between lateral and medial articulations; very deep medial articulation.

Monte Carlo (n=1) IGF 1220V - very large; Proximal – large ridge surrounds the anterior part of the proximal articulation; medial crest is higher than lateral crest but both are well defined; one small depression between the articulations; very deep dip beneath tibial tuberosity; lateral border above proximal tibiofibular articulation is very square; entire shaft is twisted. Distal end – low projection of medial malleolus; very straight lateral border; straight border between lateral and medial articulations.

Slivnitsa (n=1) SL109 FM1506 – distal tibia fragment; relatively high medial malleolus; shallow slope to lateral side; medial articulation also quite shallow; straight border between the medial and lateral articulations; lateral border straight, but has a large protrusion just proximal to it.

L'Escale (n=1) CD66 1527 - distal tibia, slightly damaged; very robust; quite rectangular in cross section; long, shallow slope to tibiofibular joint.

Morphologically the tibiae all appear very similar, with the exception of the Slivnitsa and Monte Carlo specimens. Two features are common to *P. gombaszoegensis* and the modern and fossil jaguar - a deep, distinct dip beneath the tibial tuberosity and a deep articulation by the medial malleolus (distal end). The Slivnitsa specimen appears to be very slender when compared with the other cats and Spassov (1998) noted that it is similar to the fossil cheetah, *Acinonyx pardinensis*. The Monte Carlo specimen appears enormous, but is of a similar size to IGF 4359 from Olivola (Table 5.10).

Site	Specimen	Side	TL	PML	SW	DML	DAP
L'Escale	CD66 1527	Right				49+	34.6
Slivnitsa (cast)	FM1506 SL109	Left				42.5	27.5
Atapuerca	Sabadell	Right	270	60.0	25.3	48.8	31.1
Olivola	IGF 4379	Right	249	52+	21.6	47+	30+
Olivola	IGF 4359	Left	306+		28+		32+
Monte Carlo	IGF 1220 V	Left	309	73.7	26.5	50.7	37.5

Table 5.10. *P. gombaszoegensis* tibiae, all measurements in millimetres. Abbreviations as in section 2.3.4.2. + indicates a minimum size for the specimen.

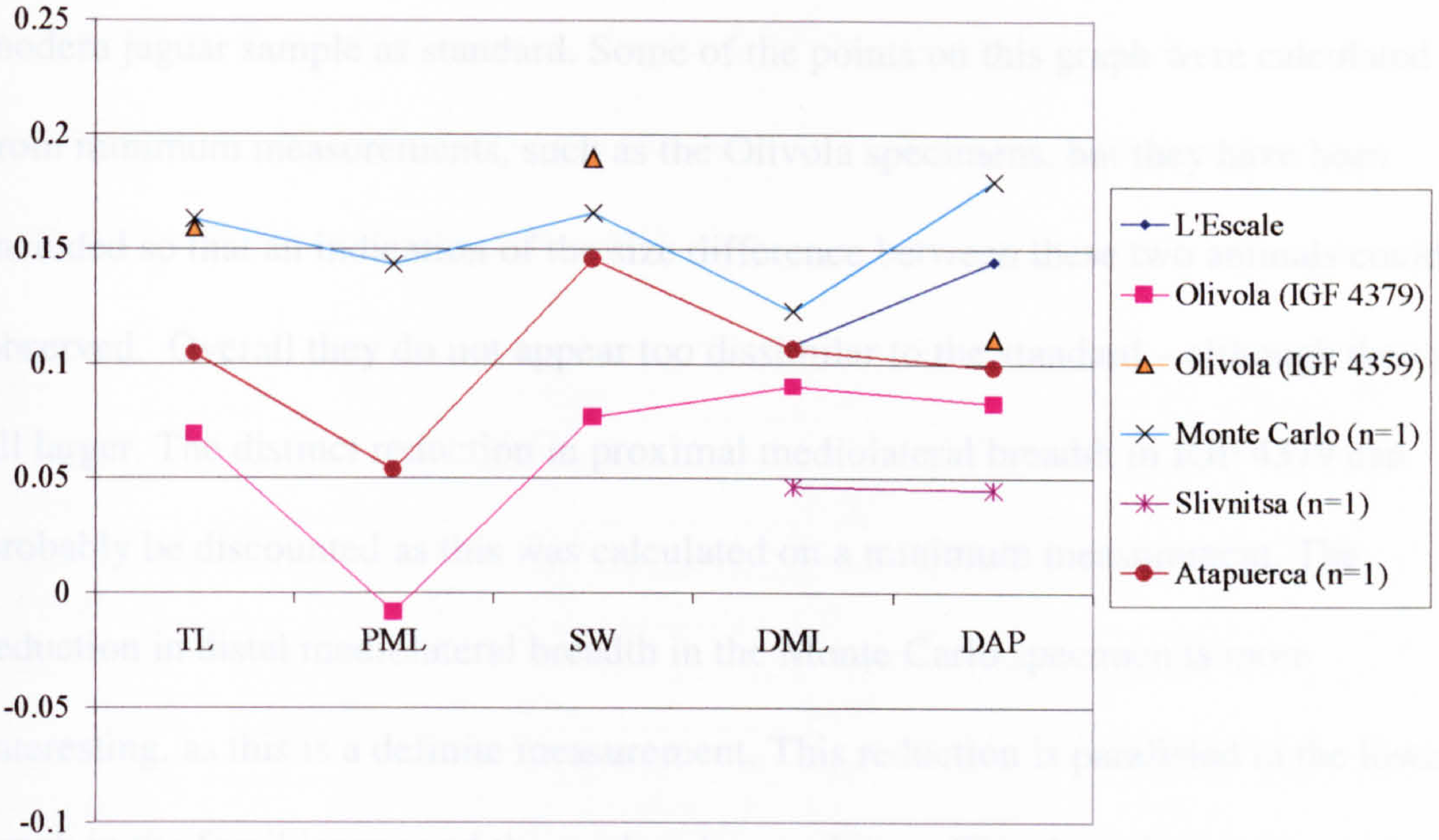


Figure 5.10a. Log ratio diagram of all *P. gombaszoegensis* tibiae with mean of modern jaguar sample as standard (n=9). Some measurements estimated, see Table 5.11 for details.

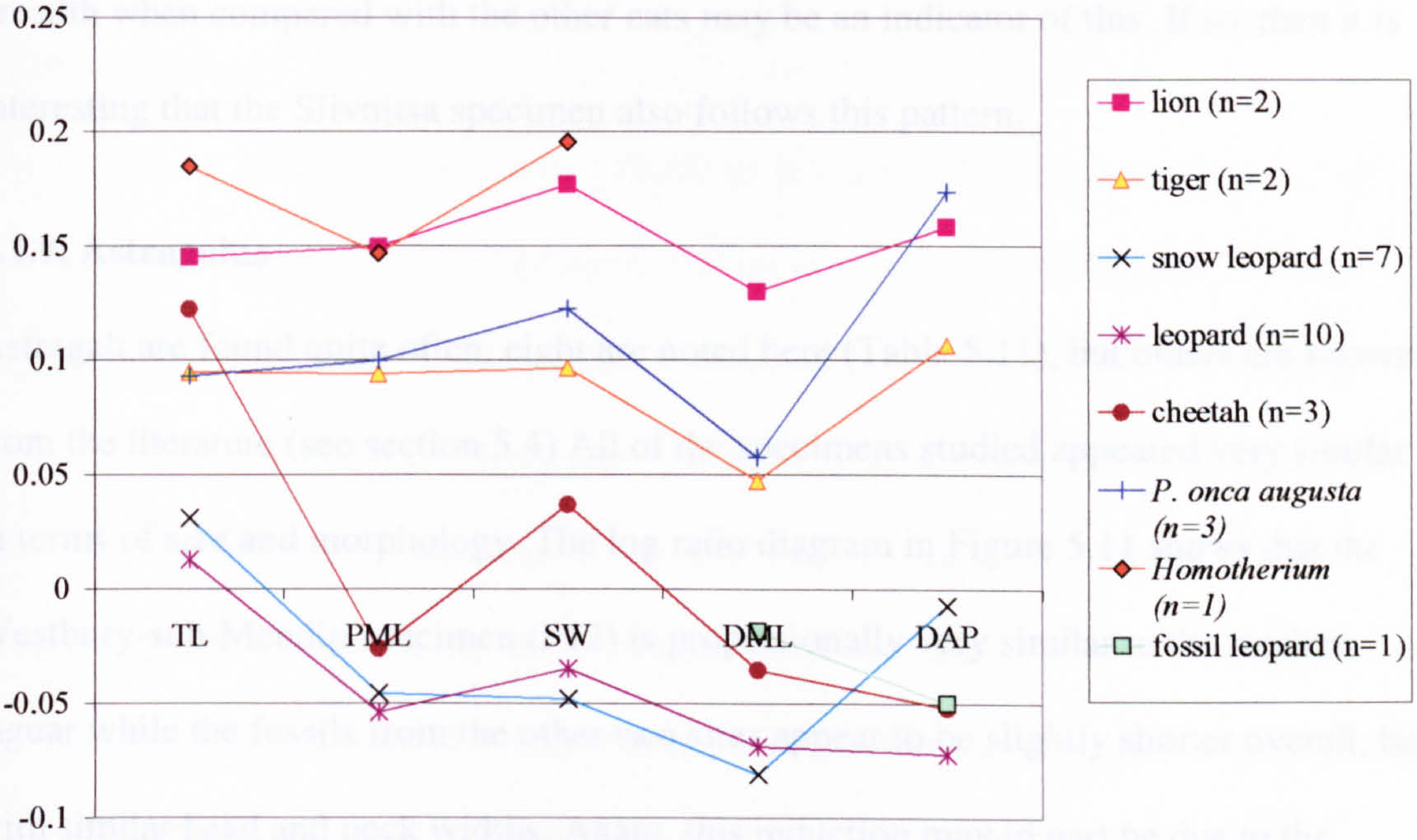


Figure 5.10b. Log ratio diagram of all modern and fossil species tibiae with mean of modern jaguar sample as standard (n=9)

Figure 5.10. Log ratio diagrams of the tibia, using the mean of the modern jaguar sample as standard (n=9)

Figure 5.10 shows a log ratio diagram of all *P. gombaszoegensis* specimens with the modern jaguar sample as standard. Some of the points on this graph were calculated from minimum measurements, such as the Olivola specimens, but they have been included so that an indication of the size difference between these two animals could be observed. Overall they do not appear too dissimilar to the standard – although they are all larger. The distinct reduction in proximal mediolateral breadth in IGF 4379 can probably be discounted as this was calculated on a minimum measurement. The reduction in distal mediolateral breadth in the Monte Carlo specimen is more interesting, as this is a definite measurement. This reduction is paralleled in the lower graph in the fossil jaguar and the modern lion and tiger. The cheetah is again very different, with a greater increase in total length than would be expected from the size of the articulations. Only the modern leopard has distal proportions that are similar to the jaguar. These are both tree climbing cats and this relative increase in mediolateral breadth when compared with the other cats may be an indicator of this. If so, then it is interesting that the Slivnitsa specimen also follows this pattern.

5.1.9. Astragalus

Astragali are found quite often, eight are noted here (Table 5.11), but others are known from the literature (see section 5.4) All of the specimens studied appeared very similar in terms of size and morphology. The log ratio diagram in Figure 5.11 shows that the Westbury-sub-Mendip specimen (F12) is proportionally very similar to the modern jaguar while the fossils from the other two sites appear to be slightly shorter overall, but with similar head and neck widths. Again, this reduction may in part be due to the presence of juvenile specimens amongst the L'Escale material. The small Gombasek specimen (b in Figure 5.11) is interesting because it is smaller than the rest, as is Westbury specimen M51484. However, they are of a similar size to a modern female tiger (Edinburgh PH4.99: TL = 46.6mm and Neck W = 19.1mm) and are therefore within the range of variation seen in a modern species, so they can be referred, with confidence, to *P. gombaszoegensis*. Figure 5.11 also shows that the fossil jaguar and modern tiger are proportionally very similar, whilst the snow leopard and leopard are most similar to the modern jaguar standard.

Site	Specimen	Side	TL	Neck W	Head W
L'Escale	C-D 728	Left	48.9	22.4	28.0
L'Escale	C-D 631	Right	49.6	21.8	27.9
L'Escale	C-D 753	Right	51	21.9	29.0
L'Escale	C-D 633	Left	51.2		
Westbury-sub-Mendip	F12	Right	53.6	22.3	28.9
Westbury Sub Mendip †	M51484	Left	45.5		
Gombasek	GIH no number (a)	Right	53.3	24.5	32.2
Gombasek	GIH no number (b)	Left	43.5+	19.1	

Table 5.11. Measurements of *P. gombaszoegensis* astragali in millimetres. Abbreviations explained in Table 2.9. † indicates measurements taken by A. Turner, not included in morphological analyses. + indicates a minimum size for the specimen.

5.1.10. Calcaneus

The morphology of the calcaneus is difficult to describe. Of the four calcanea studied, two are from subadults – CD 629 from L'Escale is unfused (no measurements taken) and the fusion line is still visible on IGF 854 (Table 5.12). The log ratio diagram in Figure 5.12 shows that the Olivola and Uppony 1 specimens are very similar to each other and that they follow a pattern that is also seen in several modern cats. The Mosbach specimen is most similar in proportions to the modern cheetah and *Acinonyx pardinensis* is known from this site (Wolsan, 1993). The fossil cheetah has been proved to be substantially different to the modern cheetah on many of the graphs, so similarities with the modern cheetah cannot be used to definitely assign a specimen to the fossil species. Also, two of the measurements of the Mosbach specimen are minimum estimates, so for these reasons it cannot be referred to *Acinonyx* with confidence.

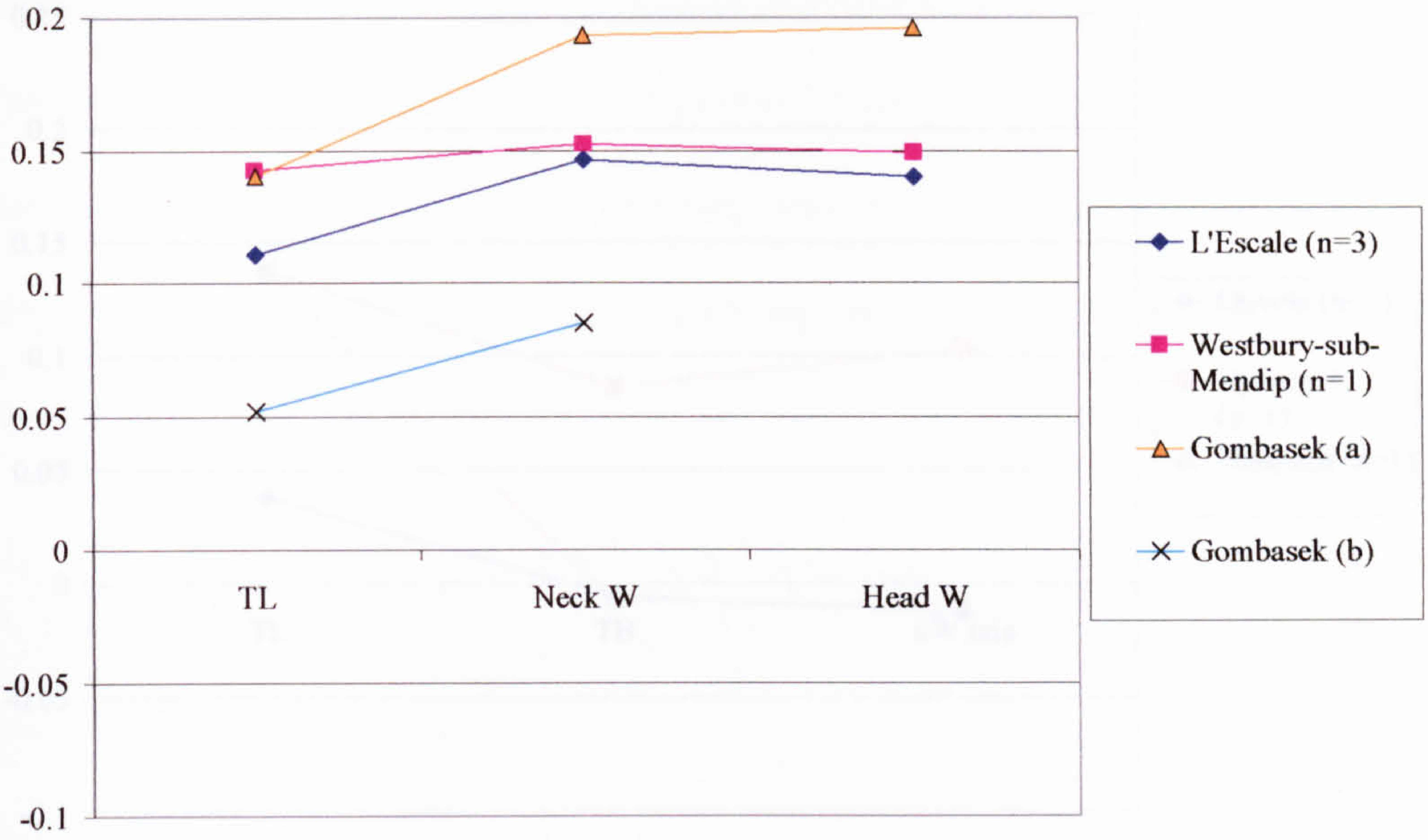


Figure 5.11a. Log ratio diagram of all *P. gombaszoegensis* astragali with mean of modern jaguar sample as standard (n=11)

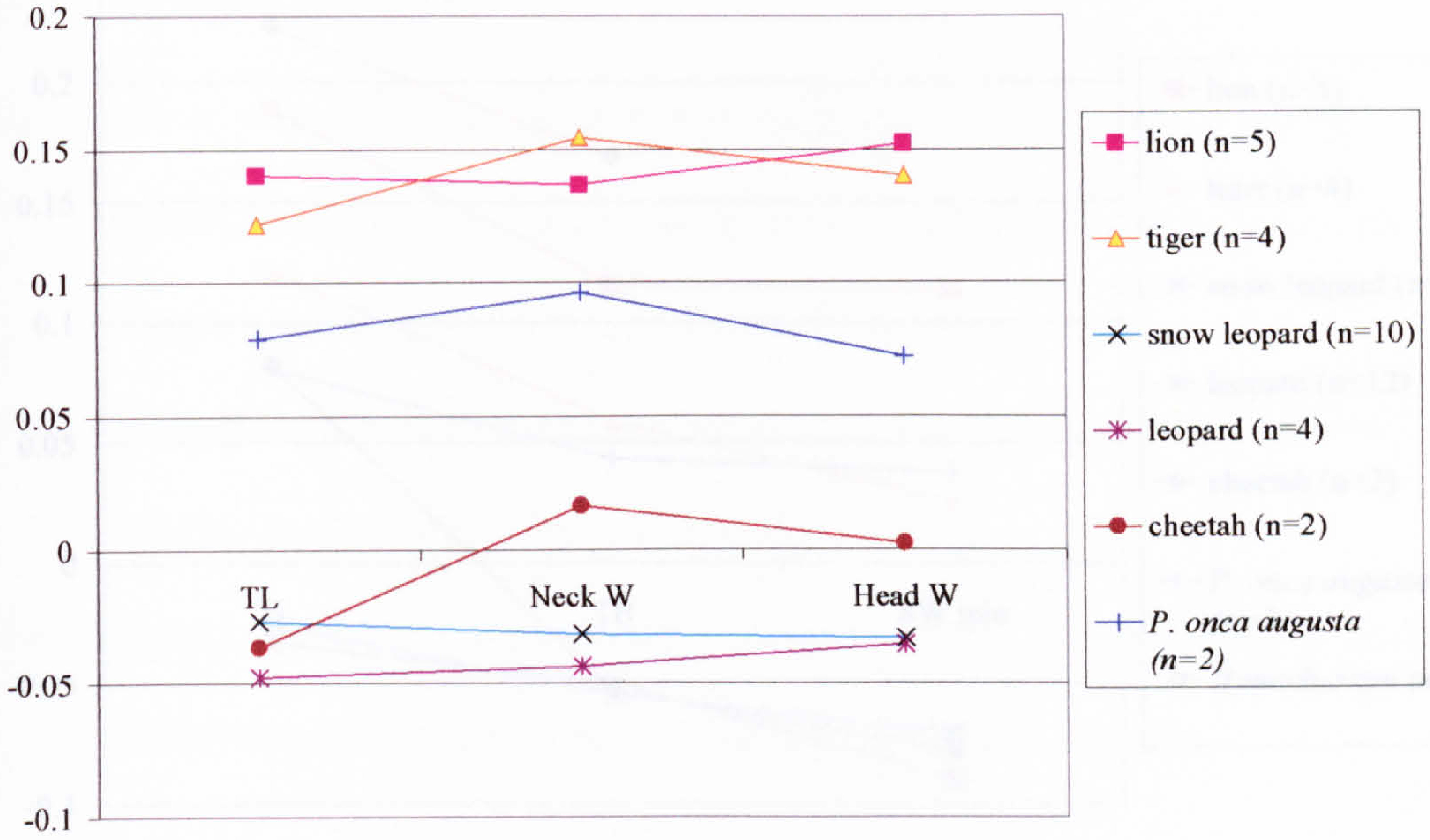


Figure 5.11b. Log ratio diagram of all modern and fossil species astragali with mean of modern jaguar sample as standard (n=11)

Figure 5.11. Log ratio diagrams of astragali, using the mean of the modern jaguar sample as standard (n=11)

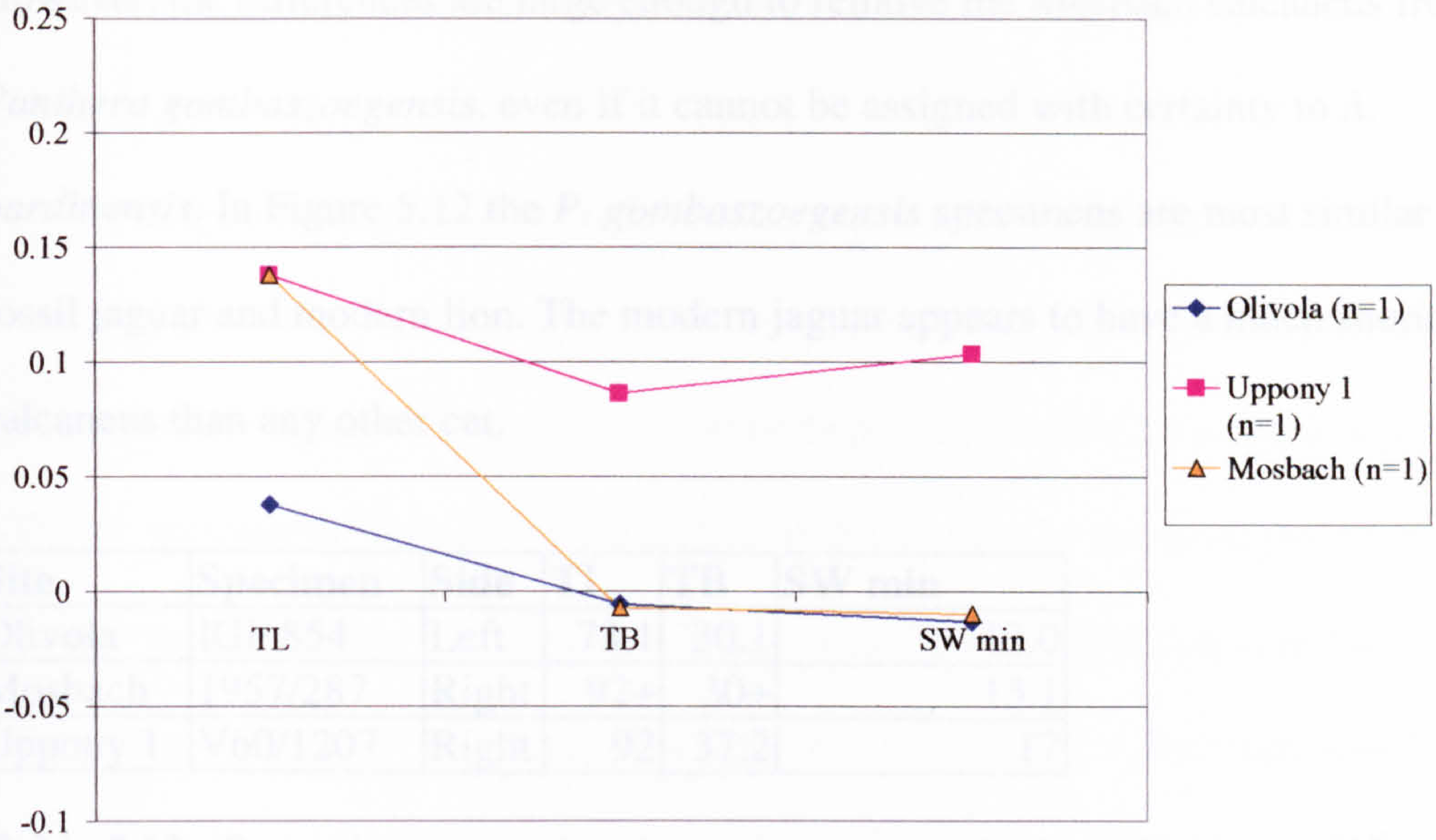


Figure 5.12a. Log ratio diagram of all *P. gombaszoegensis* calcanea with mean of modern jaguar sample as standard (n=11)

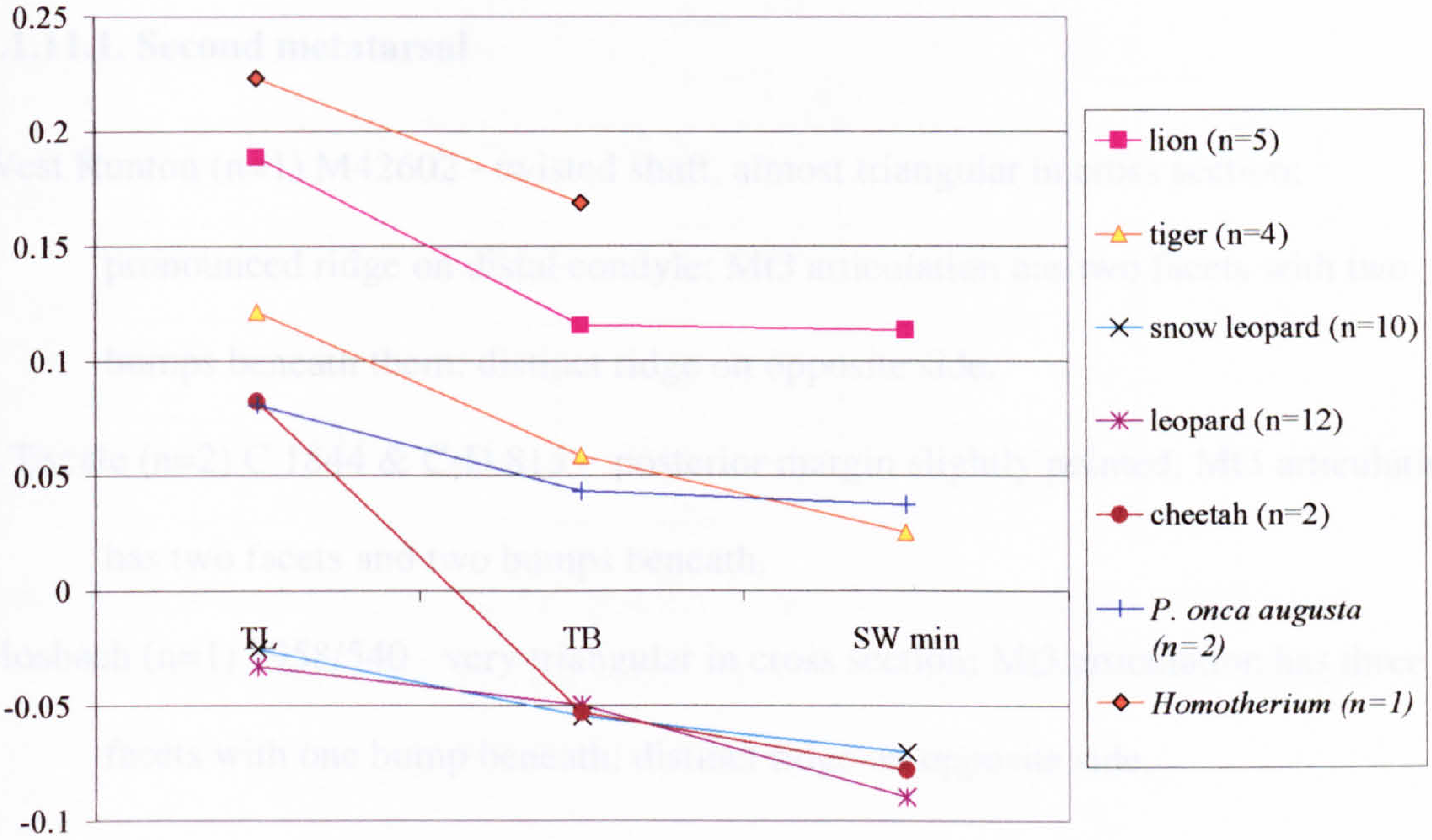


Figure 5.12b. Log ratio diagram of all *P. gombaszoegensis* calcanea with mean of modern jaguar sample as standard (n=11)

Figure 5.12. Log ratio diagrams of calcanea, using the mean of the modern jaguar sample as standard (n=11)

However, the differences are large enough to remove the Mosbach calcaneus from *Panthera gombaszoegensis*, even if it cannot be assigned with certainty to *A. pardinensis*. In Figure 5.12 the *P. gombaszoegensis* specimens are most similar to the fossil jaguar and modern lion. The modern jaguar appears to have a much shorter calcaneus than any other cat.

Site	Specimen	Side	TL	TB	SW min
Olivola	IGF 854	Left	73.1	30.1	13.0
Mosbach	1957/287	Right	92+	30+	13.1
Uppony 1	V60/1207	Right	92	37.2	17

Table 5.12. *P. gombaszoegensis* calcanea measurements in millimetres. Abbreviations explained in section 2.3.4.4. + indicates a minimum size for the specimen.

5.1.11. Metatarsals

5.1.11.1. Second metatarsal

West Runton (n=1) M42602 - twisted shaft, almost triangular in cross section; pronounced ridge on distal condyle; Mt3 articulation has two facets with two bumps beneath them; distinct ridge on opposite side.

L'Escale (n=2) C 1844 & C-D 815 - posterior margin slightly pointed; Mt3 articulation has two facets and two bumps beneath.

Mosbach (n=1) 1958/540 - very triangular in cross section; Mt3 articulation has three facets with one bump beneath; distinct ridge on opposite side.

The Mosbach specimen is different from the other two specimens in having three facets on the Mt3 articulation. However, the same morphological pattern of three facets and one bump is also seen in the fossil jaguar specimen from Hamilton Cave (pers obs). The leopard illustrated in Nagel (1999) and the leopard from Liverpool Museum (No. 18.5.97.4) also have this feature. Both modern jaguar specimens are the same as the L'Escale and West Runton specimens with only two facets. Table 5.13 contains measurements of the fossil specimens and shows that all specimens are similar in terms of size.

A log ratio diagram (Figure 5.13a) shows that the Westbury-sub-Mendip, West Runton and Mosbach specimens are very similar in terms of proportions, with a reduction in proximal mediolateral breadth when compared with the modern jaguar and L'Escale specimens. This reduction is similar to that seen in the fossil jaguar, modern tiger and modern leopard in the graph below, although the reduction is not so extreme in these animals (Figure 5.13b). Proportionally, the fossil leopard, tiger and fossil jaguar are most similar to the modern jaguar standard. The cheetah again shows an overall elongation of the metatarsal without a corresponding increase in other dimensions.

Site	Specimen	Side	TL	PWML	PWAP	SWML	SWAP	DW
L'Escale	C 1844	Right		16.3	23.6			
L'Escale	C-D 815	Right		15.0	23.6			
Atapuerca †	Sabadell	Left	102.3		19.2	10.7		17.3
Mosbach	1958/540	Left		12.8	22.4			
West Runton (Cast)	M42602	Left	94.4	12.1	22.5	11.5	11.4	17.2
Westbury-sub-Mendip †	M33987	Right		14.3	26.6	13.7		
Westbury-sub-Mendip †	M33981	Right		14.3	26.6	13.7		
Westbury-sub-Mendip †	M47364	Left	100.6	13.1	25.6	12.9		19.4

Table 5.13. Measurements of all *P. gombaszoegensis* 2^{nd} metatarsals. † indicates measurements taken by A. Turner, not included in morphological analyses. Abbreviations explained in section 2.3.4.5.

5.1.11.2. Third metatarsal

Olivola (n=3) IGF 4360 – too damaged to discern morphology. IGF 4361 – some damage; proximal articulation very angular. IGF 1221V – small and slender; juvenile; wide, squared opening for Mt2 articulation; Mt4 facet under proximal articulation, but quite shallow.

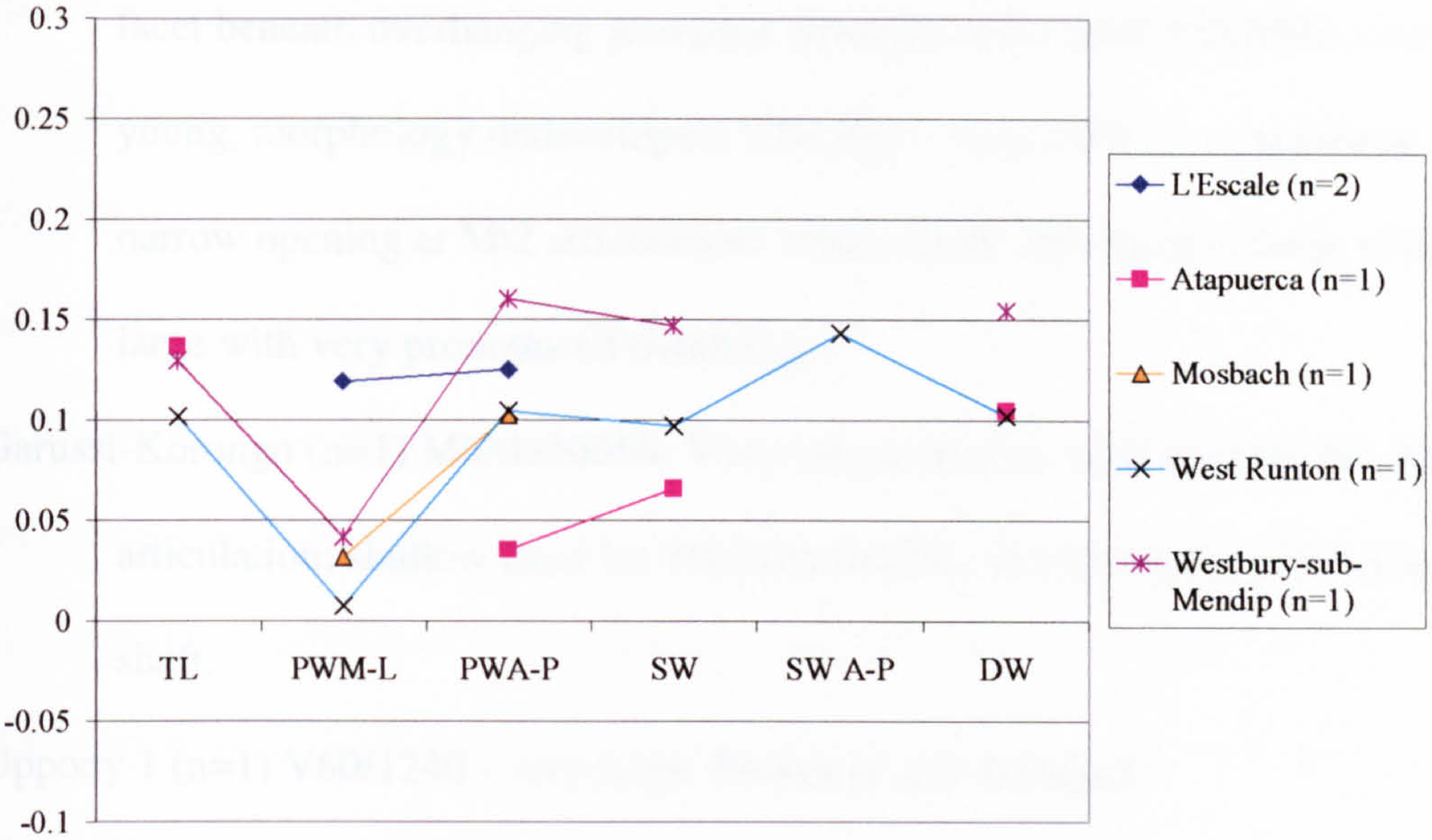


Figure 5.13a. Log ratio diagram of all *P. gombaszoegensis* 2nd metatarsals with mean of modern jaguar sample as standard (n=10)

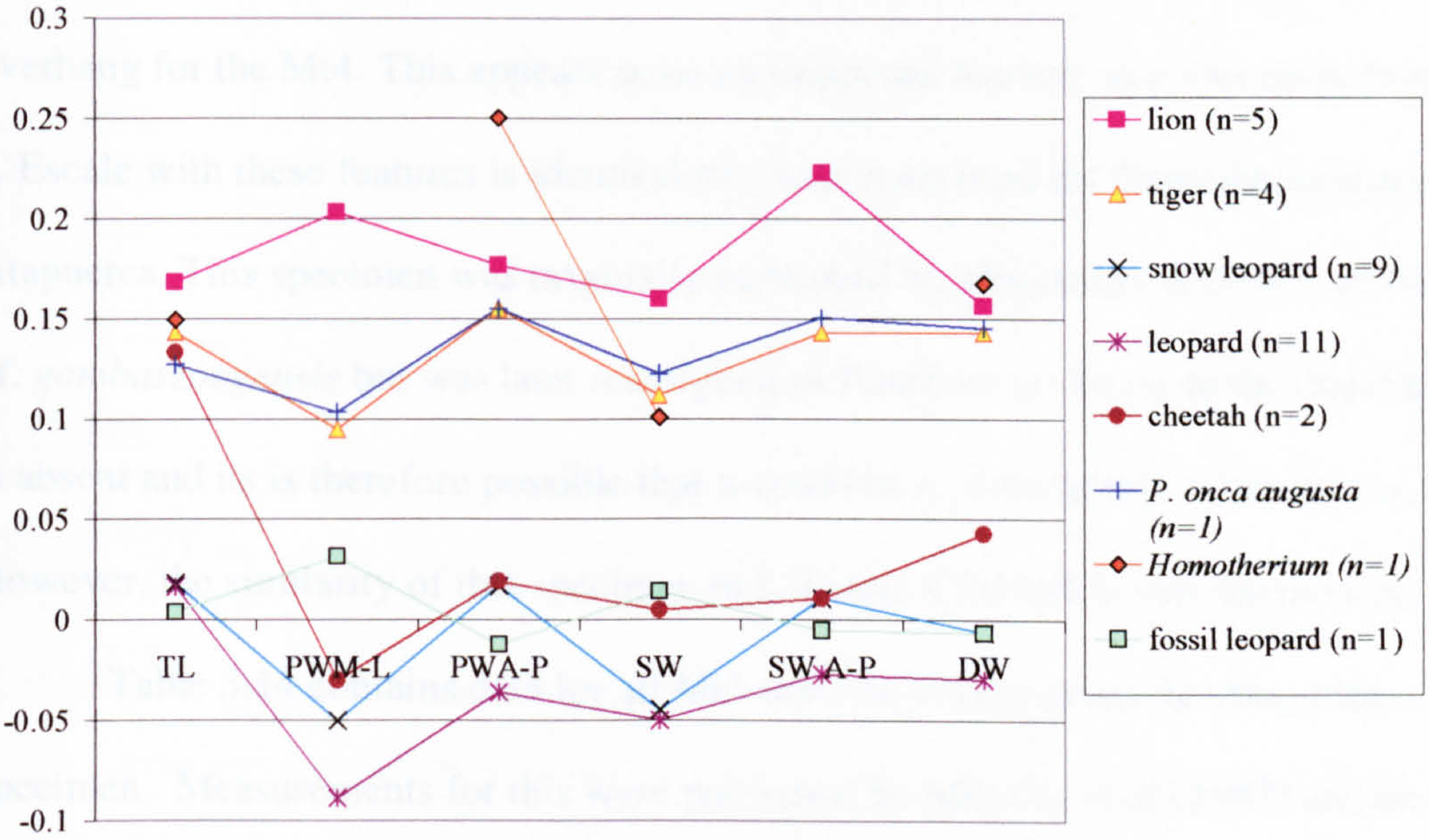


Figure 5.13b. Log ratio diagram of all modern and fossil species 2nd metatarsals with mean of modern jaguar sample as standard (n=10)

Figure 5.13. Log ratio diagrams of the 2nd metatarsal using the mean of the modern jaguar sample as standard (n=10)

L'Escale (n=3) All juvenile. CD 7640 – narrow opening for Mt2 articulation; shallow facet beneath overhanging proximal articulation for Mt4. CD 2594 – very young, morphology undeveloped. CD1209 – very different to previous; very narrow opening at Mt2 articulation; robust shaft; Mt4 facet is deep, wide and large with very pronounced overhang.

Garussi-Korongo (n=1) MbMa30050- Very robust animal; wide opening for Mt2 articulation; shallow facet for Mt4 articulation; strong, backwards curve on shaft.

Uppony 1 (n=1) V60/1240 - very large. Proximal end damaged.

A wide notch at the Mt2 articulation and a shallow facet for the Mt4 is found in the modern and fossil jaguar and the modern lion (Walker, 1985). In contrast the modern leopard has a narrow opening for the Mt2 articulation and a deep facet beneath an overhang for the Mt4. This appears quite an important feature, as a specimen from L'Escale with these features is identical to a specimen from the Sima de los Huesos, Atapuerca. This specimen was originally published by Morales *et al* (1987) as *Panthera* cf. *gombaszoegensis* but was later reassigned to *Panthera* sp. because the distal portion is absent and its is therefore possible that it could be a juvenile lion (García *et al*, 1997). However, the similarity of this specimen to L'Escale CD1209 is very interesting.

Table 5.14 contains data for all Mt3 with the exception of the Atapuerca specimen. Measurements for this were published by Morales *et al* (1987) and are given as PWML = 21.5mm and PWAP = 28.6mm. These dimensions are similar to the other *P. gombaszoegensis* specimens in Table 5.14, although slightly smaller than the estimated PWAP of 23.5 for CD 1209. Unfortunately, the L'Escale specimen is damaged and could not be included in the log ratio diagram in Figure 5.14, but because of the potential importance of the material the Atapuerca measurements were included. This shows that the other L'Escale specimens and the Atapuerca specimen have similar proportions to each other and to the Olivola and Garussi Korongo material. In terms of the modern species they are most like the lion, tiger, cheetah and leopard. Again, it is possible that because the L'Escale specimens are juvenile they have not fully developed the adult morphology. However, the similarity with the Atapuerca specimen and the morphological differences between CD1209 and the other L'Escale material, may indicate that the Atapuerca and L'Escale metatarsals are not *P. gombaszoegensis*. Morphologically they are most similar to the modern leopard, but the early leopard was substantially smaller than *P. gombaszoegensis* (see Figure 4.3 for an illustration of differences in C^s size between these two species). Therefore, although the size of these specimens is consistent with other *Panthera gombaszoegensis* material they cannot be referred to this species with confidence.

Site	**Specimen**	**Side**	**TL**	**PWML**	**PWAP**	**SWML**	**SWAP**	**DW**
L'Escale	C-D 7640	Left		22.1	29.1			
L'Escale	C-D 2594	Right		22.2	29.2			
L'Escale	C-D 1209	Left		23.5+				
Atapuerca †	Sabadell	Left	114.7		25.1	13.6		18.5
Olivola	IGF 4360	Left	94.5		23+		12+	16+
Olivola	IGF 4361	Right	93.3	20.3	28.1	14+	13.5	20.5
Olivola	IGF 1221V	Left		18.8	23.7	12.7	9.3	
Garussi Korongo	MbMa30050	Left	109.6	22.2	30.9	16.5	13.4	21.4
Westbury-sub-Mendip †	M51212	Right		24.0	30.5			
Uppony 1	V60/1240		110+			13.0	12.5	18.7

Table 5.14. Measurements of all *P. gombaszoegensis* 3rd metatarsals in millimetres. † indicates measurements taken by A. Turner, not included in morphological analyses. + indicates a minimum size for the specimen. Abbreviations explained in section 2.3.4.5.

The second interesting specimen here is that from Garussi Korongo, Serengeti. This was originally published by Dietrich (1968) as *Panthera* cf. *toscana* and was the first African specimen to be referred to this species. It is very large in comparison with even the latest *P. gombaszoegensis* specimens in Table 5.14.

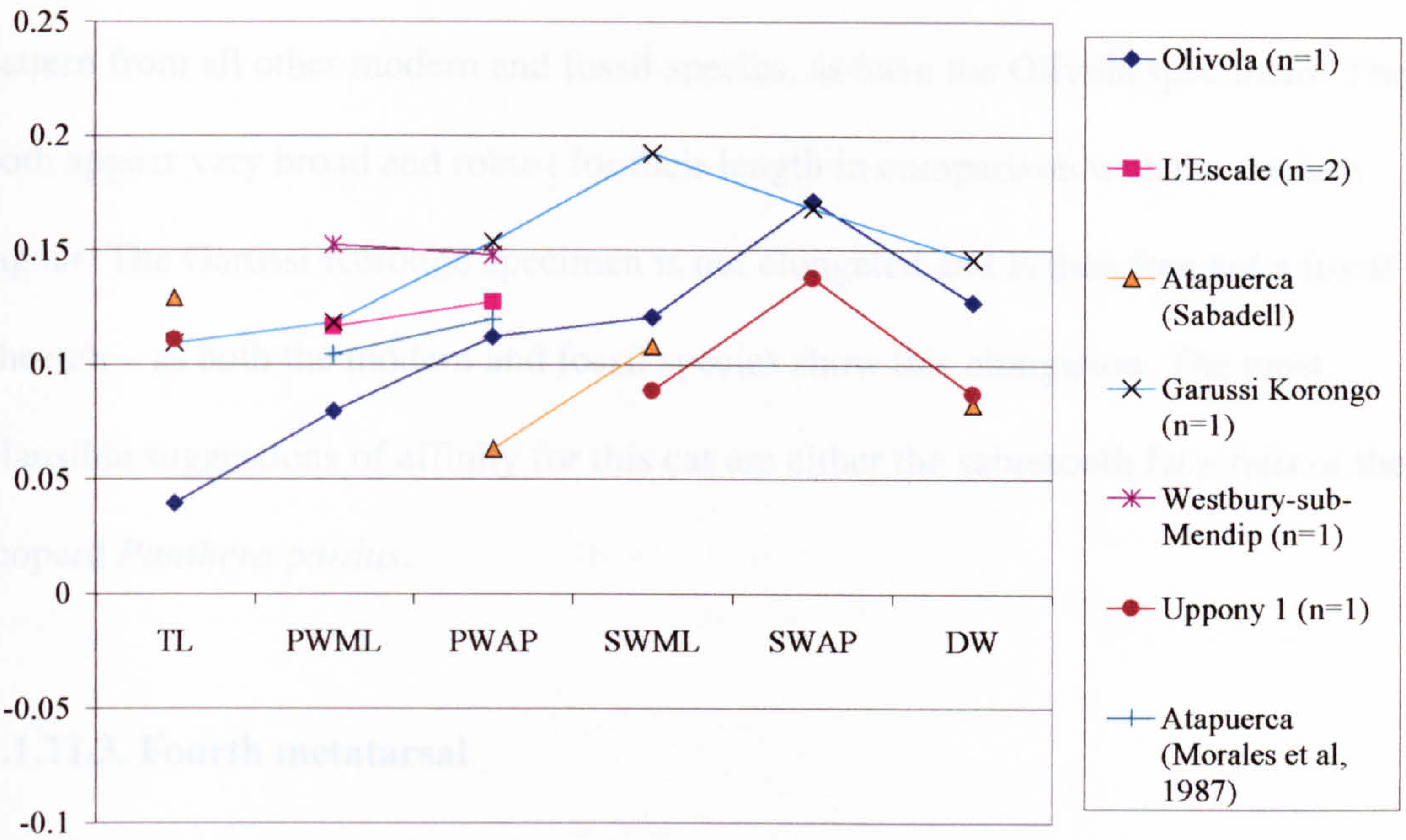


Figure 5.14a. Log ratio diagram of all *P. gombaszoegensis* 3rd metatarsals with mean of modern jaguar sample as standard (n=11)

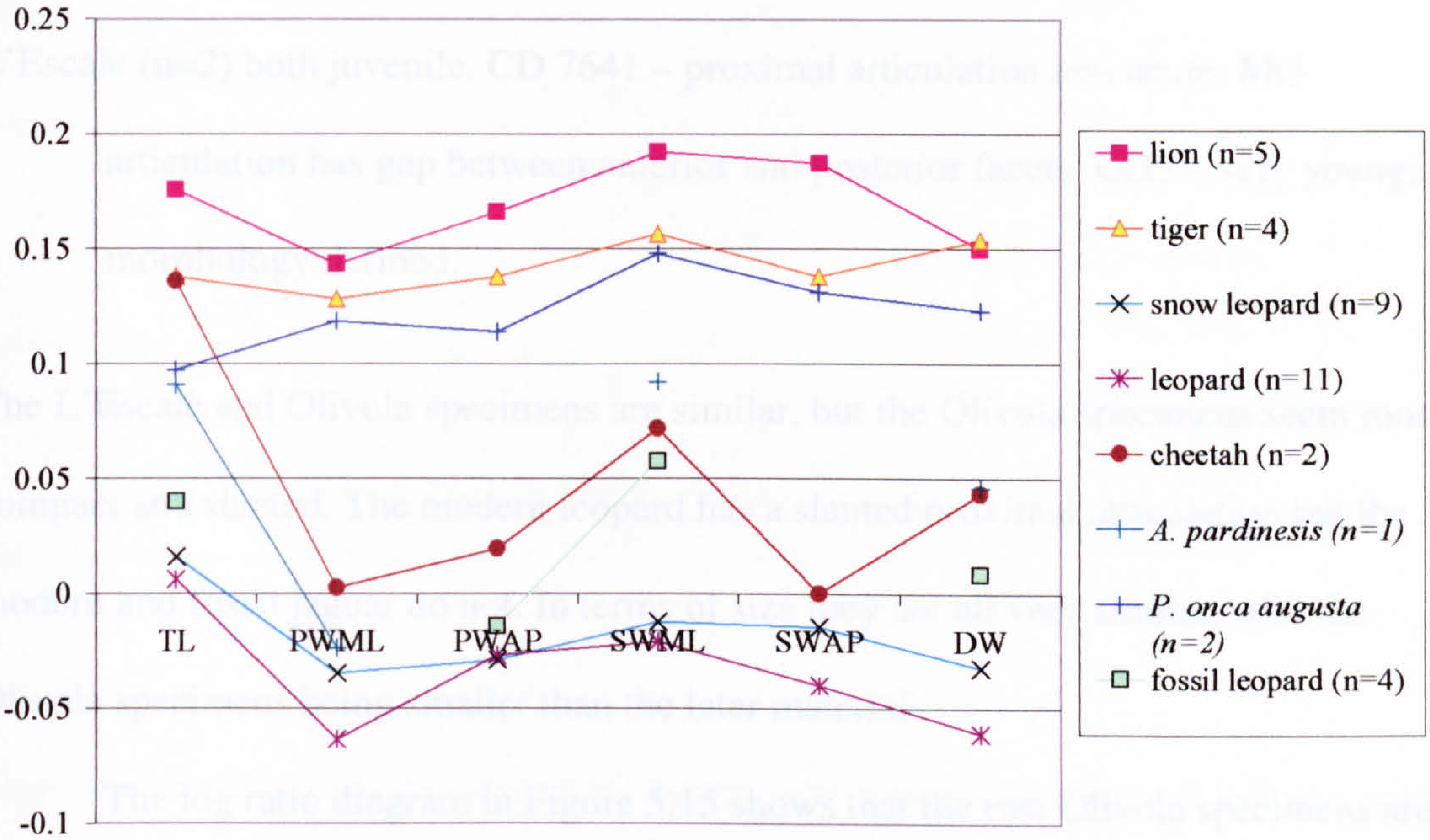


Figure 5.14b. Log ratio diagram of all modern and fossil 3rd metatarsals with mean of modern jaguar sample as standard (n=11)

Figure 5.14. Log ratio diagram of the 3rd metatarsal with mean of modern jaguar sample as standard (n=11)

In Figure 5.14 it can be seen that the Garussi Korongo specimen has a very different pattern from all other modern and fossil species, as have the Olivola specimens. They both appear very broad and robust for their length in comparison with the modern jaguar. The Garussi Korongo specimen is not elongated and is therefore not a fossil cheetah – as both the modern and fossil species show this elongation. The most plausible suggestions of affinity for this cat are either the sabretooth *Dinofelis* or the leopard *Panthera pardus*.

5.1.11.3. Fourth metatarsal

Olivola (n=3) IGF 1222V – distal epiphysis just fusing; narrow and very slanted proximal articulation; Mt3 articulation has gap between proximal and posterior facet; Mt5 articulation has deep dip. IGF 4361 – damaged and rolled; no morphology visible. IGF 4357 – damaged.

L'Escale (n=2) both juvenile. CD 7641 – proximal articulation less acute; Mt3 articulation has gap between anterior and posterior facets. CD5 – very young; no morphology defined.

The L'Escale and Olivola specimens are similar, but the Olivola specimens seem more compact and slanted. The modern leopard has a slanted proximal articulation but the modern and fossil jaguar do not. In terms of size they are all very similar, with the Olivola specimens being smaller than the later material.

The log ratio diagram in Figure 5.15 shows that the two Olivola specimens are very different from each other, IGF 1222 is similar to the modern jaguar standard whilst IGF 4361 appears most similar to the modern cheetah, or to the less extreme pattern of the fossil jaguar and modern lion. The modern tiger and modern leopard are most like the modern jaguar in terms of proportions. Westbury-sub-Mendip specimen 1982/64 is also notable as it shows a pattern that is very similar to that of *A. pardinensis*.

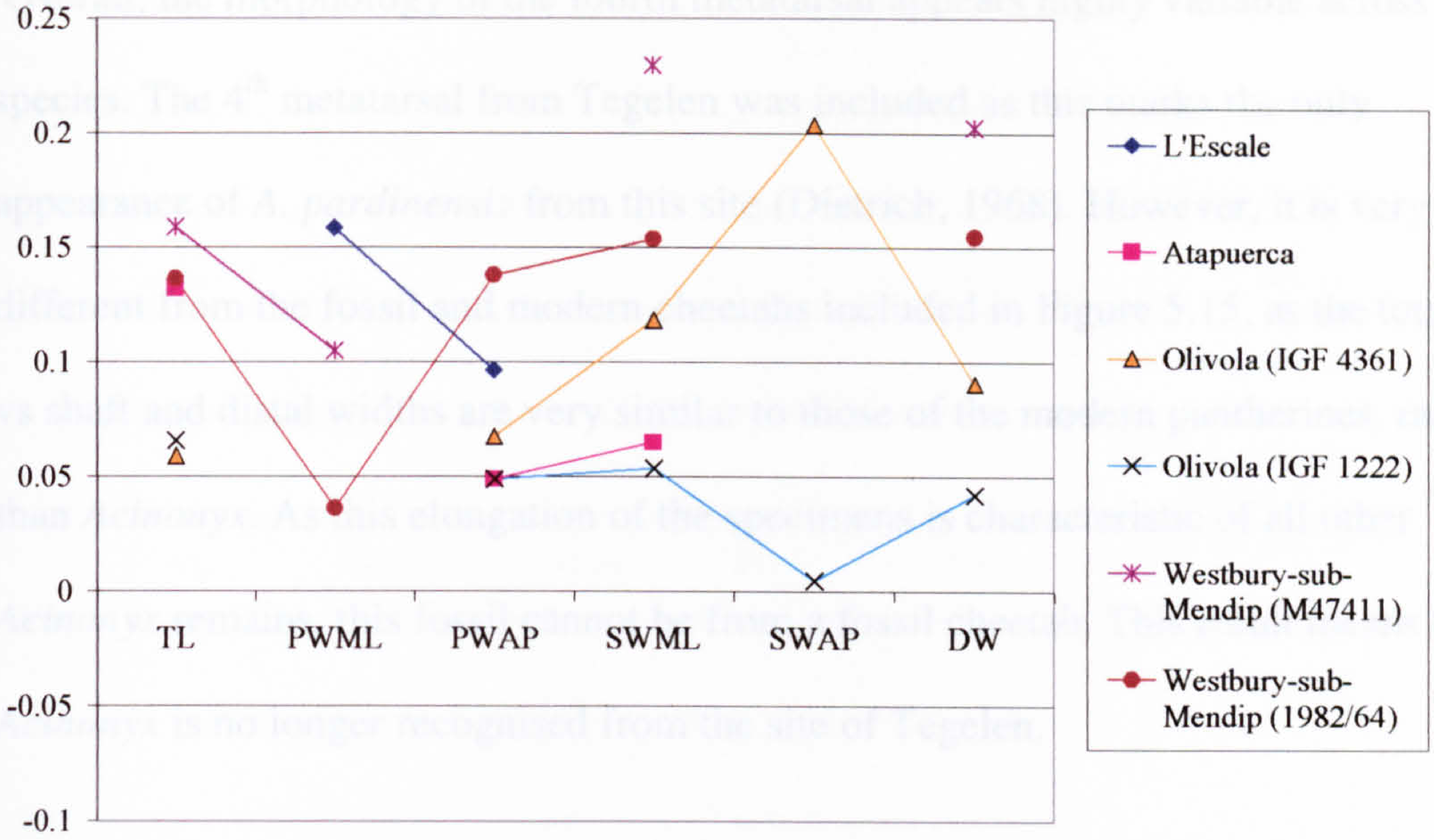


Figure 5.15a. Log ratio diagram of all *P. gombaszoegensis* 4th metatarsals with mean of modern jaguar sample as standard (n=10)

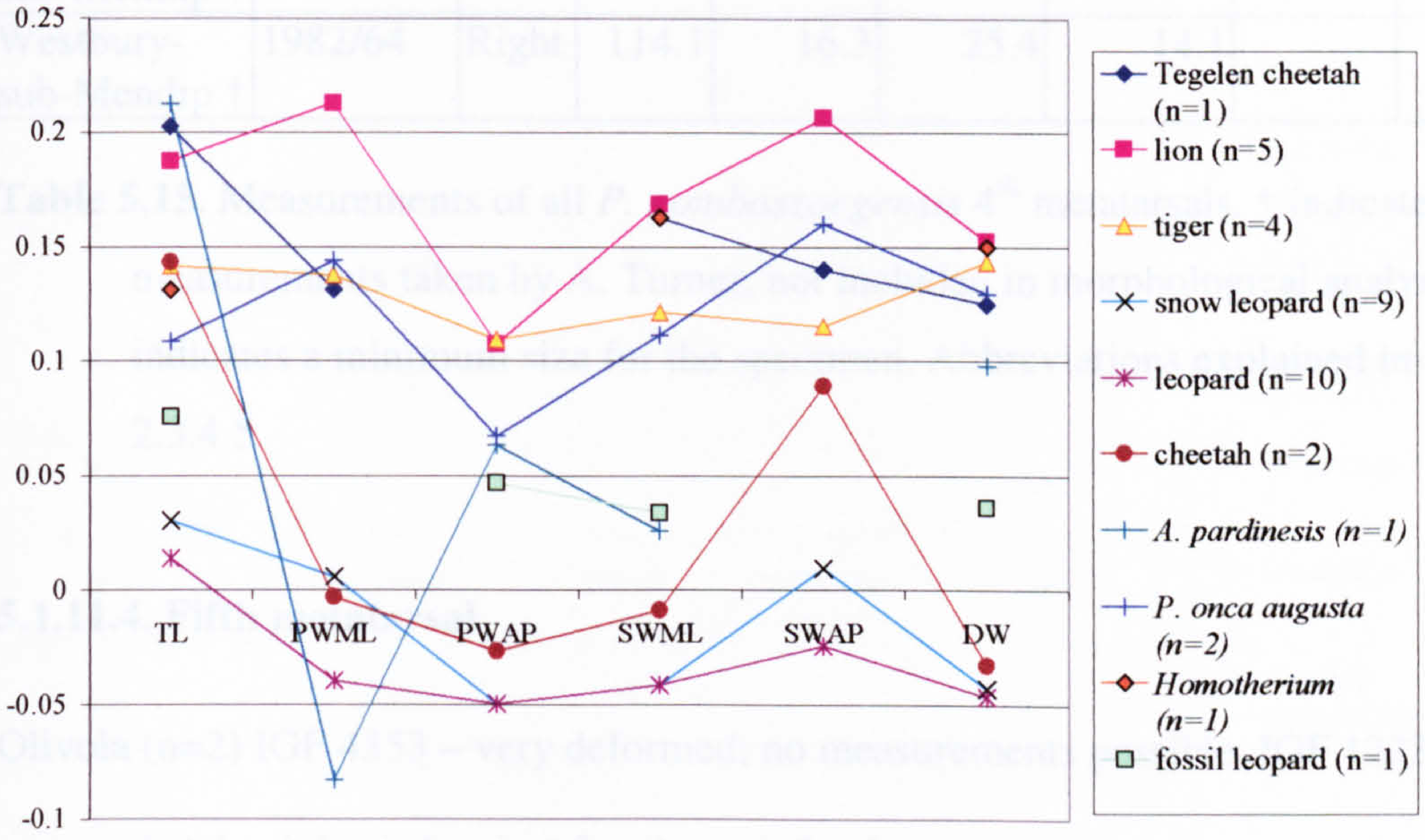


Figure 5.15b. Log ratio diagram of all modern and fossil 4th metatarsals with mean of modern jaguar sample as standard (n=10)

Figure 5.15. Log ratio diagram of the 4th metatarsal with mean of modern jaguar sample as standard (n=10)

Overall, the morphology of the fourth metatarsal appears highly variable across all species. The 4th metatarsal from Tegelen was included as this marks the only appearance of *A. pardinensis* from this site (Dietrich, 1968). However, it is very different from the fossil and modern cheetahs included in Figure 5.15, as the total length vs shaft and distal widths are very similar to those of the modern pantherines, rather than *Acinonyx*. As this elongation of the specimens is characteristic of all other *Acinonyx* remains, this fossil cannot be from a fossil cheetah. This result means that *Acinonyx* is no longer recognised from the site of Tegelen.

Site	Specimen	Side	TL	PWML	PWAP	SWML	SWAP	DW
L'Escale	C-D 7641	Left		21.6	23.1			
Atapuerca †	Sabadell	Left	113.0		20.7	11.5		
Olivola	IGF 4361	Right	95.5		21.6	13+	14.7+	17.0
Olivola	IGF 1222	Left	97		20.7	11.2	9.3	15.2
Westbury-sub-Mendip †	M47411	Right	120.2	19.1		16.8		22.0
Westbury-sub-Mendip †	1982/64	Right	114.1	16.3	25.4	14.1		19.7

Table 5.15. Measurements of all *P. gombaszoegensis* 4th metatarsals. † indicates measurements taken by A. Turner, not included in morphological analyses. + indicates a minimum size for the specimen. Abbreviations explained in section 2.3.4.5.

5.1.11.4. Fifth metatarsal

Olivola (n=2) IGF 4353 – very deformed; no measurements possible. IGF 1223V – distal epiphysis has just fused; very slender.

Gombasek (n=1) No number - very strong backwards curve.

L'Escale (n=1) CD662 - juvenile; broken.

Uppony 1 (n=1) V60/1264 – broken; similar to Gombasek specimen. V60/1268 very slender, similar to Gombasek.

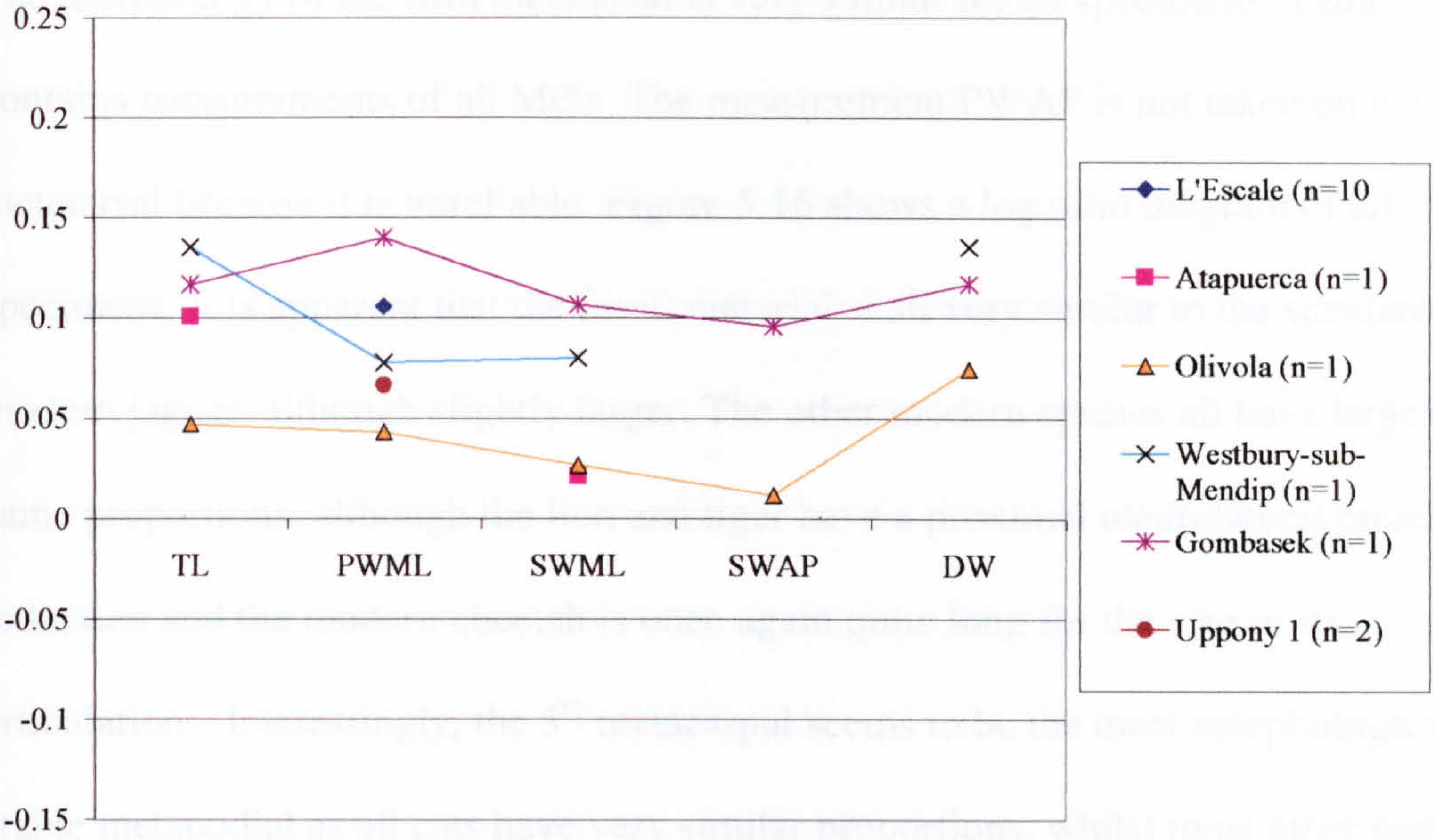


Figure 5.16a. Log ratio diagram of all *P. gombaszoegensis* 5th metatarsals with mean of modern jaguar sample as standard (n=10)

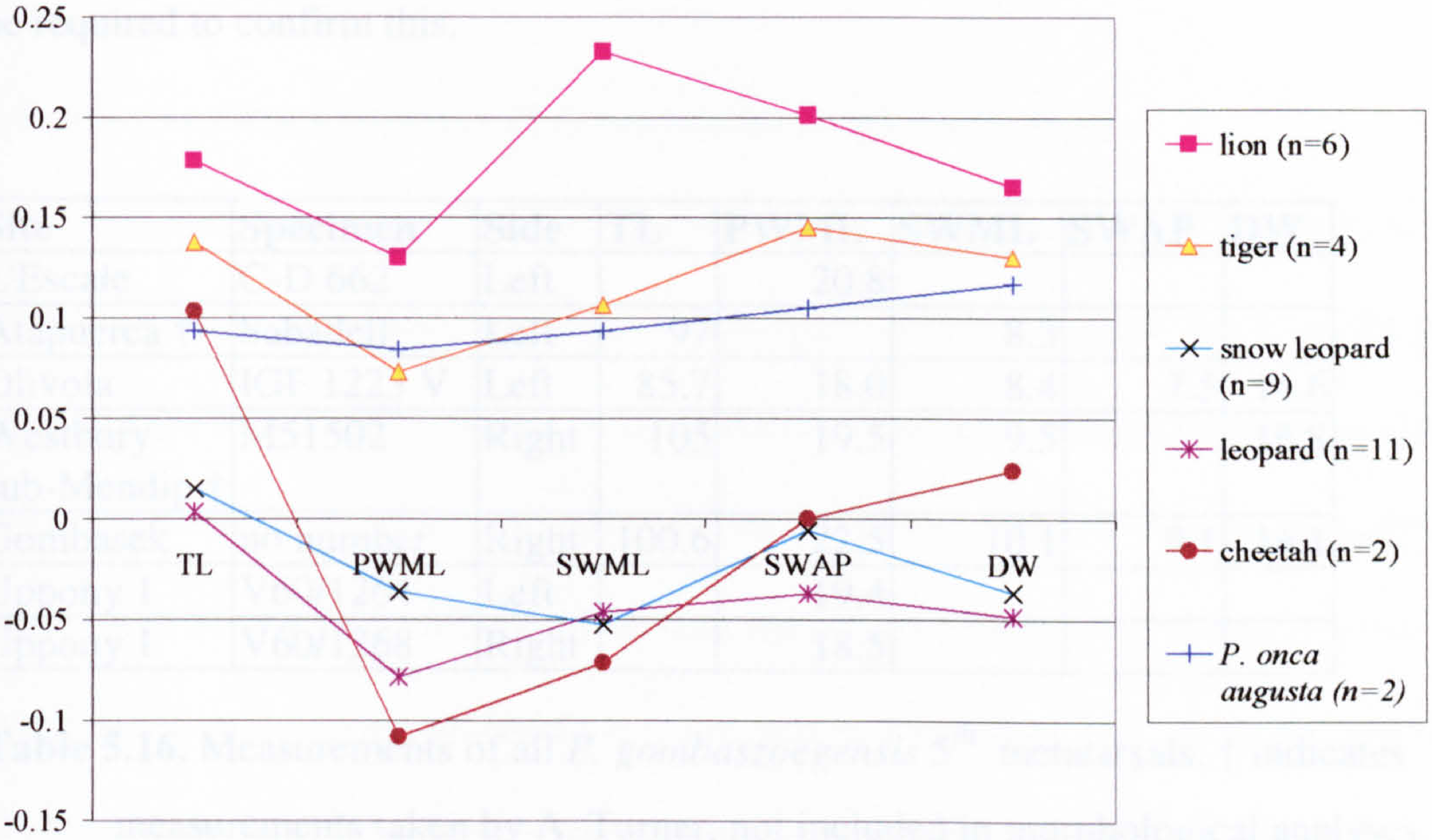


Figure 5.16b. Log ratio diagram of all modern and fossil 5th metatarsals with mean of modern jaguar sample as standard (n=10)

Figure 5.16. Log ratio diagram of the 5th metatarsal with mean of modern jaguar sample as standard (n=10)

The morphology of the fifth metatarsal is very similar for all specimens. Table 5.16 contains measurements of all Mt5s. The measurement PWAP is not taken on the 5th metatarsal because it is unreliable. Figure 5.16 shows a log ratio diagram of all specimens. It is apparent that the fossil material is all very similar to the standard modern jaguar, although slightly larger. The other modern species all have largely the same proportions, although the lion and tiger have a proximal mediolateral breadth reduction and the modern cheetah is once again quite long for the size of its articulations. Interestingly, the 5th metacarpal seems to be the most morphologically stable metapodial as all cats have very similar proportions, whilst most other metapodia show distinct differences between both individuals and species. It is possible that this may be related to the biomechanics of the foot as the 5th metatarsal is not really weight bearing and therefore is not under so much selective pressure, but further work would be required to confirm this.

Site	Specimen	Side	TL	PWML	SWML	SWAP	DW
L'Escale	C-D 662	Left		20.8			
Atapuerca †	Sabadell	Left	97		8.3		
Olivola	IGF 1223 V	Left	85.7	18.0	8.4	7.5	14.6
Westbury-sub-Mendip †	M51502	Right	105	19.5	9.5		16.8
Gombasek	no number	Right	100.6	22.5	10.1	9.1	16.1
Uppony 1	V60/1264	Left		19.4			
Uppony 1	V60/1268	Right		18.5			

Table 5.16. Measurements of all *P. gombaszoegensis* 5th metatarsals. † indicates measurements taken by A. Turner, not included in morphological analyses. Abbreviations explained in section 2.3.4.5.

5.1.12. Conclusion

Overall, the postcranial remains of the large felids do not appear to be particularly informative. Certain diagnostic features of the humerus do appear to distinguish

Panthera gombaszoegensis reliably from the lion and leopard, and the elongation of the bones of cheetah is distinctive. However, the morphology of most other bones was found to be highly variable both within and between species indicating that a very large sample size will be required to fully understand the possible range of variation within the modern cats. Without this, a study of the postcrania of extinct animals is hampered by not knowing if the features under discussion are of phylogenetic importance or simply reflect individual variation. When the partial skeletal remains from Dmanisi and Koneprusy are published some of the problems will be resolved as it will, for the first time, be possible to associate postcranial and cranial *P. gombaszoegensis* material directly, which will provide a benchmark for future research in this area. Until then, however, the mechanism for referring postcranial specimens to *P. gombaszoegensis* will continue to be size related rather than based on specific morphologies.

5.2. SEXUAL DIMORPHISM IN *P. GOMBASZOEGENSIS* POSTCRANIA

The ulnae and tibiae from Olivola come in two distinct sizes, but the size range is within that of a modern population of sexually dimorphic animals. Measurements of the total length of the largest and smallest tibiae in each sample of modern pantherine species are shown in Table 5.17. In order to quantify the sexual dimorphism of these specimens and make them comparable with the fossil data the largest (?male) was divided by the smallest (?female) individual and the result was multiplied by 100. It can be seen that all samples are small, so these results are unlikely to represent the true level of dimorphism seen within the modern species, but they provide a good indicator of the range. From the results in row 4, it can be seen that the snow leopard sample has the least dimorphism and the leopard the most. The same formula applied to the Monte Carlo and Olivola tibiae gives a result of 124.1%, or the larger tibia is 24.1% larger than the smaller specimen. This is well within the range of variation seen in Table 5.17 and they can therefore be regarded as coming from one species.

	Lion (n=7)	**Jaguar (n=11)**	**Leopard (n=14)**	**Snow leopard (n=12)**	**Tiger (n=5)**	**Olivola & Monte Carlo**
Largest	327	241	243	248	341	309
Smallest	279	180	178	214	263	249
Total (%)	117	134	137	116	130	124

Table 5.17. Largest and smallest tibiae in the modern and fossil dataset. The formula used for calculating percentages is explained in the text

5.3. JUVENILE *PANTHERA GOMBASZOEGENSIS*

5.3.1. Cranial specimens

Tegelen (n=2) Both Maas. No number - dC^S, crowns and roots broken., no measurements possible.

L'Escale (n=3) CD795 - maxilla fragment with large bulge to accommodate erupting permanent C^s. CD 7637 - dC^s root fragment. CD5 - juvenile mandible, dpm_4 (carnassial) has large backwards-sloping paraconid; protoconid much larger than paraconid; talonid cusps and cingulum are very pronounced. dpm_3 is very high cusped; large anterior and posterior cusps; pronounced cingulum; permanent M_1 unerupted but visible within ramus.

Gombasek (n=2) Fa56 (V59/1102) - right mandible; permanent C_i emerging; permanent M_1 unerupted but visible within ramus; dpm_4 and dpm_3 very damaged. Fa55 - right mandible with dc_i, dpm_3 and dpm_4; teeth unworn; dpm_3 has backsloping protocone; very high pointed cusps; dpm_4 damaged; large talonid cusp and cingulum.

The morphology of the juvenile dentition is regarded as being potentially informative about the phylogeny of the animals (Broom, 1949). However, one of the problems associated with identifying juvenile material is making sure that it is indeed related to the species under discussion. This problem is compounded by a lack of good comparative data for modern and fossil juvenile cats. It is sometimes possible – depending on the biological age of the specimen – to find that the permanent dentition has begun to form and on these teeth a reliable identification can be made. This is the case with *Panthera gombaszoegensis*, as both specimen CD5 from L'Escale and Fa55 from Gombasek have the permanent molars visible, although unerupted. The shape of the permanent M_1 in specimen CD5 confirms that the mandible is that of a felid. The measurements of permanent teeth given in Table 4.6 when compared with those in Table 5.18 show that the L'Escale M_1 protoconid is well within the size range of the adult *P. gombaszoegensis* specimens in the assemblage (M_1Lproto range from 13.4 to 14.2 mm). This confirms that specimen CD5 is a juvenile *Panthera gombaszoegensis* and the teeth of this specimen can then be used for comparison with other putative *P. gombaszoegensis* material.

Site	Specimen	dpm_3 L	dpm_4 L	dpm_4 B	dpm_4 Lp	M_1 Lproto
L'Escale	CD5	13.7	17.8	6.2	7.4	14
Gombasek	Fa55	14	17.6	6.6	7.5	
Atapuerca*	E VI 4		18.9			

Table 5.17. Measurements (in millimetres) of the deciduous and permanent dentition of *P. gombaszoegensis*. * data from Morales *et al* (1987).

Morphologically, the teeth from Gombasek are very like those from L'Escale and are of a similar size (Figure 5.17 and Table 5.17). Few descriptions of deciduous teeth of modern specimens are available for comparison with this material. However, Broom (1949) illustrated the milk dentition of the lion, leopard and cheetah in a comparative study of the morphology of these teeth. Ewer (1973) noted that the deciduous canines have a lingual groove, which allows the permanent canines to erupt beside the milk canines, so that for a brief period both are functional, until the juvenile teeth are shed. All of the fossil dC^s specimens have this groove. They have been identified as upper canines using Broom's illustrations and descriptions which show that the lower deciduous canines have a subsidiary cusp on the lingual surface of the tooth; the fossil specimens lack this cusp. They are also very similar to the dC^s of a fossil *Panthera leo* specimen that is illustrated in García *et al* (1997). Broom's (1949) illustrations also show that the leopard dpm_4 has a talonid and tiny metaconid and lacks the cingulum; Plate 3b (a juvenile leopard mandible) in Ewer (1973) again shows that the metaconid is very small. This photograph also shows that the dpm_3 has a large protocone but all other cusps are small and indistinct. In contrast, the *P. gombaszoegensis* specimens have large and very pointed cusps on the dpm_3 and a distinct metaconid on the dpm_4. The lion illustrated by Broom (1949) has a much more robust dpm_3 with slightly larger cusps. In the lion and leopard the protoconid of the dpm_4 is large and backwards-sloping. The cheetah looks most similar to the *P. gombaszoegensis* specimens with high pointed cusps on the dpm_3 and a distinct talonid and metaconid at the rear of the dpm_4.

Figure 5.17. Illustration of right dpm_4 in buccal view from two sites: a) L'Escale and b) Gombasek (broken protoconid). Not to scale.

Several features of juvenile *P. leo* are described in García & Arsuaga (1998) [based on the work of Dawkins & Sanford, 1866] and include morphologies such as the lingual depression on the deciduous canines, extra cusps on the dpm_3 and the presence of a talonid and metaconid on the dpm_4. Yet, the review of literature above has shown that all of these features have been found in the lion, leopard and cheetah and are therefore valid only to identify the specimens as felids. However, this literature review was based on a sample of n=1 for the lion and cheetah and n=2 for the leopard and *Panthera gombaszoegensis*. On such a small sample it is not possible to make valid diagnostic decisions on the size and position of cusps as these may prove to be highly variable when a larger sample is studied. Despite this I believe for the reasons discussed above that the Gombasek and L'Escale specimens are very similar and can be referred to *Panthera gombaszoegensis*. It is more difficult to identify the Tegelen canines to species as there are few morphological landmarks on these teeth. However, only *P. gombaszoegensis* is present in the Tegelen assemblage and it is likely that these teeth can be assigned to this species. This referral marks the first recognition of juvenile *P. gombaszoegensis* remains from the site of Tegelen.

5.3.2. Age of specimens

The Felidae have two sets of teeth, the permanent and deciduous dentition (diphodonty). No *Panthera gombaszoegensis* specimens have erupting deciduous teeth, so they have been aged using the permanent dentition.

5.3.2.1. Eruption sequences of the permanent dentition in modern species

Different species appear to have different permanent tooth eruption sequences and this may prove to be of phylogenetic use. Also for some species individual tooth eruption dates are known and this provides a rough guideline for the age at death of the juvenile specimens of *P. gombaszoegensis*. Several permanent tooth eruption sequences for the modern *Panthera* have been published and are summarised below. Bracketed teeth indicate that the eruption times are grouped for those particular teeth. It is worth noting that all tooth eruption sequences refer to the first gingival emergence of the teeth, rather than at their point of eruption through the maxilla or mandible. Therefore fossil specimens are likely to be slightly younger than the ages calculated on gum eruption dates.

5.3.2.2. Tiger

$I^1\ I_1\ (I^2\ I^3\ I_2\ I_3)\ (P^4\ M_1)\ (C^s\ C_i)\ P^3\ (P^2\ M^1)\ (P_3\ P_4)$

Eruption of the permanent dentition begins at 8.5 – 9.5 months and is finished by 12 – 14 months (data from Mazak, 1981).

5.3.2.3. Lion

$I^1\ I_1\ I^2\ I_2\ (I^3\ I_3)\ M_1\ C\ P^2\ P^4\ M^1\ P^3\ P_4\ P_3$

Eruption of the permanent dentition begins at 8-9 months and is finished by 15-20 months. The eruption times of particular teeth appear to vary greatly between individual cubs and no differentiation is made in the notation of the upper and lower canines in the paper (data from Smuts *et al*, 1978).

5.3.2.4. Snow leopard

Upper $I^1\ I^2\ (P^2\ M^1)\ I^3\ (C^s\ P^4)\ P^3$

Lower $I_1\ I_2\ I_3\ M_1\ C_i\ P_3\ P_4$

The data from Pocock (1916b) (above) was reconstructed by Hemmer (1972b) into the following sequence (no I_3 eruption data given):

$I^1\ I_1\ I^2\ I_2\ M_1\ P^2\ M^1\ I^3\ (C^s \text{ or } C_i)\ P^4\ P^3\ P_3\ P_4$

This sequence is based on two skulls of captive cats from London Zoo; no indication of the age of the animals is given beyond their surviving only ‘a few months in captivity’ (Pocock, 1916b:306).

5.3.2.5. Discussion

It can be seen that some teeth erupt at approximately the same time in all species. The time of eruption for the first and last teeth (I^1 and I_1 and the P_3 and P_4) is fairly stable within the sequence. However, other teeth erupt at different times in different species. The tiger carnassial pair for example (P^4 M_1) erupt at approximately the same time, which would perhaps be the logical way of approaching the shedding of the deciduous teeth and getting the major slicing teeth into occlusion as quickly as possible. However, neither the lion nor snow leopard follow this pattern and instead appear to delay the eruption of the P^4 until after the M_1 is fully in place. This may, in fact, be a more sensible strategy as it allows at least one of the carnassial pair to be fully in place before the other erupts, perhaps increasing the stability of the jaw and allowing eruption to proceed effectively. Ewer (1973) noted that a carnivore must never be without its canines or carnassials; this results in the M_1 erupting before the dpm_4 is shed and the P^4 erupting to replace the dpm^4 before the permanent P^3 replaces the milk carnassial (dpm^3). On the basis of this observation and that of the lion and snow leopard eruption sequences discussed above, it is more likely that the tiger eruption sequence in Mazak (1981) is erroneous and that the pattern of eruption is very similar in all modern cats.

5.3.3. Juvenile *Panthera gombaszoegensis* specimens

Few juvenile *P. gombaszoegensis* specimens are known with enough teeth for an eruption sequence to be established. The material from L'Escale is largely from young animals, as shown by the lack of apical root closure in most specimens, but they are all isolated teeth. Table 5.18 lists all juvenile *Panthera gombaszoegensis* specimens included in this study. Unfortunately there are not enough associated specimens for a tooth eruption sequence to be calculated, but information on the palaeoecology of these animals can still be gained.

Site	Specimen	Description
L'Escale	CD795	P^4 in place, C^s below full eruption
L'Escale	CD5	dpm_3 dpm_4 present I_1 just emerging, M_1 encrypted but visible
L'Escale	CD 614	M_1 (P_3 &P_4 alveoli) C_i root still open
L'Escale	CD 7637	A dC^s
Olivola	IGF 853	M_1 P_4 P_3 present C_i just below full eruption
Gombasek	Fa55	dC_i dpm_3 dpm_4, M_1 encrypted, enamel forming
Gombasek	Fa56	C_i and M_1 encrypted, dpm_2 dpm_3 present, I_1 just emerging
Tegelen	Maas no number	Two dC^s (damaged)

Table 5.18. All *P. gombaszoegensis* specimens with deciduous dentition or permanent teeth below full eruption that have been included in this study.

5.3.3.1. Ageing fossil specimens

The *P. gombaszoegensis* fossils have been aged using the eruption data from Smuts *et al* (1978) for the modern lion. It has been assumed that the eruption dates for *P. gombaszoegensis* would have been similar to that of the modern cats and detailed eruption dates of the permanent teeth have only been published for the lion. It is possible that the lion, as a social carnivore, may have slightly delayed maturation in comparison with the other cats (see eruption ages, above) and that therefore by using the gingival eruption data for this cat the ages of the fossil animals are likely to be overestimated.

L'Escale. No L'Escale specimens appear to be fully adult since, as noted above, the majority of teeth had not reached apical closure. There are also two distinct age groups within the assemblage; specimens CD795 and CD614 are likely to be between 28 and 36 months based on the apical closure rates of the upper and lower canines respectively, whilst in specimen CD5 the I_1 is just beginning to emerge, giving an age of approximately 8-9 months. The isolated dC^s is would have belonged to a cat below 12-15 months of age, as at this point the permanent canines erupt. This difference is also seen in the metapodials from the site - there is a very young animal, with an unfused

Mc4 shaft length of only 50.8mm and a second group of older animals (MNI=2 based on two left Mt3) that are still unfused but of almost adult proportions.

Olivola. The Olivola specimen is a complete mandible with the C_i just below full eruption. This is equivalent to 18 – 24 months of age in modern lions (Smuts *et al*, 1978).

Tegelen. The two deciduous upper canines from Tegelen can be given a maximum age, as in neither case had the roots begun to be reabsorbed, indicating that they were not due to be shed. Smuts *et al* (1978) found that the deciduous upper canines in lion cubs erupt between 20-30 days and are replaced at 12-15 months.

Gombasek. Both the Gombasek specimens are very young, with the M_1 visible in its crypt but still some way from full eruption. In specimen Fa56 the eruption of the I_1 has begun which implies an age of 8-9 months for this animal. The lack of erupting permanent teeth but the presence of a full set of deciduous teeth suggests an age between 2 months and 8 months for Fa55. However, the dpm_3 is only slightly worn and the M_1 is much less developed than that of Fa56, suggesting that this cat is in the younger part of this age range.

5.3.4. Juvenile postcrania

Several of the sites studied had juvenile postcrania in the assemblages. However, as no information is available for epiphysial fusion rates in the larger Felidae I have not attempted to age these animals. Sites at which juvenile postcrania have been found include Olivola (illustrated in del Campana, 1915; 1916) and L'Escale (all L'Escale postcranial specimens are unfused). The juvenile postcrania has the potential to be informative - as mentioned above, there are distinct similarities between the 3rd metatarsals from Atapuerca and L'Escale but it is not known how much these bones change during ontogeny so they cannot be assigned to species with certainty. Future work could include measuring juvenile specimens of known age to see exactly how much these bones alter before maturity. The astragalus, for example, has no epiphyses so the maturity of the animal can only be gauged by looking carefully at the bone surface. It would be interesting to find out whether these areas do increase in size or alter morphologically through the animals growth phase. It may be possible to draw an analogy with dogs, as there is a well known theory that the size of a puppies paws gives an indication of the size of the adult animal, although I am not aware of a scientific study which has demonstrated this.

5.3.5. Palaeoecology

Several palaeoecological questions can be addressed when looking at the juvenile specimens of a fossil species. Although the *P. gombaszoegensis* remains discussed above are few in number, some interesting information can still be gleaned on the denning behaviour and the age at independence of this cat.

5.3.5.1. Denning

No evidence was found of denning behaviour, or of cats young enough to still be in their dens just after birth. Table 5.19 shows life history data for modern big cat species. It can be seen that in the modern species of *Panthera* cubs begin to follow their mothers between one and three months of age. None of the *P. gombaszoegensis* remains studied were this young, although it is possible that Fa55 from Gombasek was not much older than 3 months. In addition no shed deciduous teeth or those with reabsorbed roots were found at any site, indicating that all specimens were still rooted within the oral cavity at the time of the animals death. Shed teeth and juvenile bones may be able to provide information on denning behaviour in other species such as bears (Andrews & Turner, 1992), but there is no such information for *P. gombaszoegensis*, perhaps indicating that these animals were not living in cave sites but were simply dying there.

Species	**Leave den (months)**	**Independence (months)**	**Sexual maturity (years)**	**Reference**
Lion	1 – 1.5	30	3 – 3.5	Schaller (1972)
Jaguar	1.5 - 2	18 - 24	2 – 4	Rabinowitz & Nottingham (1986); Mondolfi & Hoogesteijn (1986)
Leopard		20 - 22	3	Schaller (1972)
Tiger	2	20 - 24	3-5	Schaller (1972); Mazak (1981)
Snow Leopard	3		2	Summarised in Hemmer (1972b)

Table 5.19. Life history data for the extant pantherines.

5.3.5.2. Age at independence

The younger cats from L'Escale (CD5) and Gombasek (Fa55 and Fa56) would probably still have been dependent on their mothers, if they were similar to the modern *Panthera* species (see Table 5.19). Using modern cat data we can see that the Olivola individual may have just become independent at approximately 20 months, whilst the older L'Escale specimens would have been fully independent by 28 months (Table 5.19). Although it is dangerous to assume that specimens are related because of the vagaries of site formation processes, it is possible that the two older L'Escale specimens identified by metapodials may have been littermates, as they were almost exactly the same size. Although this is plausible it might just be coincidence that two specimens of the same size were found together, but close associations between independent littermates are known in several of the modern species [e.g. lions (Kitchener, 1991); cheetahs (Caro, 1994) and jaguars (Hoogesteijn & Mondolfi, 1992)].

5.4. SPECIMENS FROM OTHER SITES

The preceding analysis of *Panthera gombaszoegensis* features has been based entirely on specimens that I have observed at first hand. As well as these specimens, additional material is also available for study in the literature and these are reviewed below. For further details of the environment and dating of each site see Appendix 2.

5.4.1. Austria

Panthera gombaszoegensis was included in the faunal list from the site of Deutsch Altenburg 4 (Wolsan, 1993). This material consists of an astragalus and a second metatarsal (D.Nagel, pers comm)

5.4.2. Azerbaijan

The site of Palan-Tyukan was published in Russian with an short English summary by Sotnikova & Sablin (n.d.). The specimen referred to *Panthera* ex. gr. *gombaszoegensis* is a calcaneum measuring approximately 83mm in length and 34mm in width (measurements calculated from a photograph in the publication). The size of this specimen puts it within the size range of *P. gombaszoegensis* calcaneii listed in Table 5.12. The photograph shows a bone with a very pointed tuber calcis, similar to the specimen from Mosbach, but it appears very flattened across the sustentaculum. The inclusion of ex. gr. in the referral of this specimen indicates that the authors were unsure about the validity of the designation and the validity of this species. The validity of the species has already been discussed, but I am similarly doubtful about the referral of this specimen to *P. gombaszoegensis*.

5.4.3. Belgium

La Belle Roche. The specimens from the site of La Belle Roche have yet to be fully published. Nevertheless, the original site report of 1981 contained an illustration of three teeth attributed to *Panthera gombaszoegensis* – a P_3, P_4 and M_1 (Cordy, 1981:96).

From this illustration it is apparent that both premolars have a large protocone, the P_3 has very low anterior and posterior cusps whilst the P_4 has a low cingulum and quite pronounced accessory cusps. The M_1 is obviously damaged but there is no sign of a talonid. Measurements taken from the photograph indicate that the teeth are very large, with approximate lengths of 18mm, 24mm and 27mm respectively. Both the P_3 and M_1 fall outside the size range of *P. gombaszoegensis* specimens that I have studied (see Table 4.6 and 4.8 for these measurements), but it is a matter of some tenths of a millimetre. At 24mm the P_4 falls within the range of the largest specimens from Westbury sub Mendip and L'Escale (Table 4.7). As these measurements are very roughly calculated and are very close to the rest of the sample it would be unwise to exclude them from *P. gombaszoegensis* on the basis of size. The morphology of the teeth is consistent with that previously described for *P. gombaszoegensis* (section 4.4) and therefore I retain them as *P. gombaszoegensis* with the proviso that a full examination has not been conducted. The website of this site also contains a photograph of a complete cranium identified as *P. gombaszoegensis*, unfortunately it is too pixellated for morphology to be identified (Anon, 2001a). However, it does provide evidence for some very nice material that will be available for study in the future.

5.4.4. Czech Republic

Holstejn. The synthesis of Kahlke (1975) listed *Panthera gombaszoegensis* as being present at Holstejn in the Czech Republic. No further information is available about this site.

Koneprusy. A partial skeleton collected from Koneprusy in the 1950s has been referred to *P. gombaszoegensis*. A cast of a mandible in the collections of the Firenze museum is from this site and has been discussed in Chapter 4. The mandible is notable for the robust traits it displays, with a P_4 lingual basin, etc. Other material from this site remains unpublished. All information from Professor Fejfar (pers comm).

5.4.5. France

Many French sites have *P. gombaszoegensis* present but few have been fully published. The L'Escale monograph is a notable exception (Bonifay, 1971) and its contents have already been discussed above (Section 4.3). Five other sites with *P. gombaszoegensis* will be reviewed below.

Vallonnet has been the cause of much interest. Both *Panthera gombaszoegensis* and *Panthera pardus* have been identified from Vallonnet, making it the earliest arrival of the leopard in Europe (Moullé *et al*, 2000). However, the material has yet to be fully published.

Grotte 14 in the Dordogne has only recently been discovered and is not yet fully published. Details of the site are given by Guadelli (2001). This publication has a photograph of a right mandible containing the C_i, P_3, P_4 and M_1 which has been referred to *Panthera gombaszoegensis*. Few morphological features can be discerned, as the mandible is still in situ in the breccia, but it is apparent that the both the P_3 and P_4 have very large protocones with small anterior cusps. Little can be said about the affinities of this specimen until a full report is available, but it is certainly a pantherine cat.

The site of Artenac-en-Charante is still under investigation but a preliminary faunal list has been published, indicating that two *P. gombaszoegensis* skulls were found at this locality (Delagnes *et al*, 1999). *Panthera gombaszoegensis* is described as 'abundant' in the deposit (Delagnes *et al*, 1999). Quantities of any large carnivore are unusual, so this site promises to be very interesting when the full report is published. A photograph of one of the *P. gombaszoegensis* specimens has been published on the internet (Becq-Giraudon, 1999). From this photograph it is apparent that a complete skull with both maxillary and mandibular dentition has been recovered. Although it is crushed and distorted the direct association of the upper and lower jaws is unparalleled amongst *P. gombaszoegensis* specimens, so a detailed analysis will allow aspects such as the morphology of both upper and lower teeth in a single individual to be fully understood. It is difficult to see details on the photograph, but it appears that the P^3 either lacks or has a very small anterior cusp, the posterior cusp is slightly larger and the tooth has a low cingulum. The P_3 and P_4 have very low cusps, similar in appearance to the Westbury-sub-Mendip specimens. The P_4 has a low cingulum and a slightly larger posterior cusp when compared with the anterior. The mandible has a large diastema; two mental foramina, one below the diastema and one below the middle of the P_3 and the masseteric fossa ends at or just before the M_1. In these respects it is similar to the *P. gombaszoegensis* specimens I have studied, but the teeth are slightly less robust than those from most other sites.

Chateau. One of the specimens from Chateau was included in the log ratio diagrams in Section 4.3. All of the other specimens from this site are postcranial and were illustrated by Argant (1980; 1991). As already noted the Chateau mandible is quite large and is similar to the Vértesszölös II specimen that was re-identified as *Panthera* cf. *P. leo*. Of all the Chateau specimens described in Argant (1980) only three have measuremnst which are comparable with mine. The femoral head width of specimen H6-10 is given as 36.1mm, which is of a similar size to the Uppony 1 specimens (which may be *P. leo*) in Table 5.9 and larger than the other *P. gombaszoegensis.* specimens. Measurements of a calcaneum (H5–73) are also large, with a TB of 41.4mm and a SWmin of 19.5mm, again these are bigger than the specimens listed in Table 5.12. However, an astragalus (F7-7) has a total length of 51.0mm and a head width of 27.6mm; which is well within the size range of *P. gombaszoegensis* specimens in Table 5.11. On the basis of the measurements I consider that the majority of Chateau specimens which have been referred to *P. gombaszoegensis* are likely to be *P.leo.* However, the presence of the small astragalus indicates that *P. gombaszoegensis* may also have been present.

Cessaguet. An unpublished upper canine, tentatively referred to *Panthera pardus* has been recovered from Cessaguet (Turner, 1995a). This tooth was included in the log ratio diagrams in Chapter 4. It was apparent from this study that this canine, although small, is within the size range of the earlier *P. gombaszoegensis* specimens and is similar to the slightly later C^s from Huéscar. It cannot therefore be excluded from *Panthera gombaszoegensis* on the basis of size alone.

5.4.6. Georgia

Dmanisi. The site of Dmanisi has attracted much attention as *Panthera gombaszoegensis* has been discovered there, as well as *Homo erectus* fossils (Gabunia *et al*, 2000). Thirty one *P. gombaszoegensis* specimens have been reported, with a minimum number of one individual (Gabunia *et al*, 2000). This assemblage consists of a mandible, scapula, humerus, radius, carpals, metacarpals and a phalange (D. Lordkipanidze, pers comm).

Akhalkalaki. The material from this site was originally identified as *Panthera tigris* (Vekua, 1986) but a more recent publication has listed it as *P. gombaszoegensis* (Moullé *et al*, 2000). The specimens in question include a mandible containing C_i, P_3, P_4 and M_1; isolated C_i, P_3, P_4; M_1; 1 proximal radius and a dpm^4. These specimens are illustrated in Vekua (1986) and a new report on this material will be published shortly (D. Lordkipanidze, pers comm).

5.4.7. Germany

Erpfinger Höhle. Two specimens are known from this site, the first is a P^4 attributed to *Felis toscana* (Lehmann, 1953) and the second is a left C^s referred to *Felis* cf. *toscana* (Lehmann, 1957). Measurements and illustrations of the P^4 and measurements of the C^s are given in their respective publications. The P^4 has a length of 30.1mm and an anterior breadth of 15.0 mm, these dimensions are well within the range of the *Panthera* *gombaszoegensis* specimens in Table 4.1. The illustration (Lehmann, 1953:440) shows a tooth with a heavily worn or broken parastyle and protocone and a chipped metacone, indicating that the P^4 length may be unreliable. The breadth of the tooth across the blade and behind the protocone appears very similar, there is little evidence of narrowing until the rear of the metacone is reached. The protocone is small and distinctly separate from the parastyle with a distinct dip on the anterior edge of the tooth. The is a small but very defined ectoparastyle. Overall it appears quite squat with low cusps and the paracone and metacone appear equally sized. The morphology of this tooth is unusual, but it is within the range of variation seen in specimens from Olivola, Gerakarou 1 and Westbury sub Mendip, although no one tooth provides an exact match. On the basis of the drawing I refer this specimen to *Panthera* cf. *P. gombaszoegensis*. The canine has a length of 17.8mm and a breadth of 14.7mm (Lehmann, 1957:68). This is quite a small tooth, but it is comparable with the teeth from Huéscar, Cessaguet and Olivola (IGF 4376), so it is within the size range of the specimens listed in Table 4.4. Lehmann (1957) suggested that it might be a female canine and this is a distinct possibility. One cause for concern is the canine height which is given as 20mm. This is far too short for a felid, but the tooth is said to be heavily worn, so this may be a measurement of the remaining crown height rather than the total tooth. I agree with Lehmann's diagnosis, but given that *Felis toscana* is a synonym of *Panthera gombaszoegensis* I would refer this specimen to *Panthera* cf. *Panthera gombaszoegensis*.

Meiningen. *Panthera gombaszoegensis* was included in the Meiningen faunal list published by Kahlke (1982) but no further information is available.

Untermassfeld. Another site at which *P. gombaszoegensis* is said to be relatively common is that of Untermassfeld (Kahlke, 1995). This locality is of great interest as it is one of the few sites dated to the Jaramillo event (Kahlke, 2000). A full report on the felid material is expected shortly (R.D. Kahlke, pers comm).

No Locality. An unpublished specimen which lacks a provenance has been referred to *P. gombaszoegensis*. It consists of the forepart of a cranium and is stored in the collections of the Naturhistorisches Museum, Mainz (Specimen WO59). Having studied this material at first hand I feel that it is unlikely to be *P. gombaszoegensis* and is moreover a modern specimen; this conclusion is based on two observations. The first is that the P^3 has a very large anterior cusp which is a lion-like trait. It also has a very distinct cingulum all around the tooth. On the P^4 the protocone is set posterior to the parastyle, so that there is a distinct step on the anterior edge of the tooth; in addition, the metacone has a distinct enamel 'bobble'. These traits are not seen in *Panthera gombaszoegensis*. Although it is within the size range of *P. gombaszoegensis* ($P^4L = 29.7$; $P^3L = 22.1$; $C^sL = 18.9$), it is also within the range of the extant species of *Panthera*. The second feature is the presence of fine cutmarks around orbits and the rear of the palate, some of which contain soil. I suspect that this is the remains of a modern hunting trophy that had been buried and then 'discovered'. For these reasons I have removed it from the list of potential *Panthera gombaszoegensis* specimens.

5.4.8. Greece

Petralona. Two reports have been published on the Carnivora from the site of Petralona (Kurtén & Poulianos, 1977; 1981). The assemblage referred to *Panthera* cf. *gombaszoegensis* consists of a distal humerus (No 79) and an Mt3, Mt4 and Mc2 (Kurtén & Poulianos, 1977). The second paper referred specimens to *Panthera gombaszoegensis* and reported a distal humerus (TB 1698); 2P^3s; a P^4 and a calcaneum (Kurtén & Poulianos, 1981). Measurements of all specimens are given in the appropriate publications. A plate shows the distal humerus (specimen No. 79) in anterior view (Kurtén & Poulianos, 1977). It is apparent from this photograph that there is no medial expansion, although this part of the specimen is slightly damaged. Both a coronoid and a radial fossa are visible. The second humerus (TB 1698) is illustrated in both anterior and posterior views (Kurtén & Poulianos, 1981). These show a robust humerus, with a moderate medial expansion, a deep radial fossa and a wide, low olecraneon fossa and a strongly developed lateral condylar ridge. It appears to have classic *Panthera gombaszoegensis* morphology.

Site	Specimen	Side	SWmin	EPW	Troch W
Petralona	No 79	Left	35.0	# 85	# 64
Petralona	TB 1698	Right	32.4	86	
Westbury-sub-Mendip	F3	Right		81.7	52

Table 5.20. Measurements (in millimetres) of the Petralona humerii and the largest *P. gombaszoegensis* specimen from Table 5.2. # indicates an estimated measurement (data from Kurtén & Poulianos, 1977; 1981).

Table 5.20 contains measurements of these humerii and the largest *P. gombaszoegensis* specimen that I have recorded (see Table 5.2 for full details). When these data are compared it can be seen that both Petralona specimens are larger than any of the *P. gombaszoegensis* specimens that I have studied.

The calcaneus was referred to *P. gombaszoegensis* because it is of a similar size to a specimen from Westbury-sub-Mendip (Kurtén & Poulianos, 1981). The measurements given for this specimen are: total length 104mm and total breadth 44mm (Kurtén & Poulianos, 1981). These measurements are much larger than any other specimens that I have studied (details in Table 5.12) and I have been unable to find a record of a calcaneus from Westbury. The Petralona specimen seems too robust when compared with the other *P. gombaszoegensis* specimens. It is most similar to the specimen from Mosbach, which has been removed from *P. gombaszoegensis* and may be *Acinonyx*.

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The three teeth are potentially more informative. Measurements of the specimens are given in Table 5.21. Again, we can see that these teeth are quite large when compared to the other *P. gombaszoegensis* specimens in Table 4.1 and 4.2. The P^4Ba falls between the two largest *P. gombaszoegensis* specimens, while the P^4Lp measurement is much larger than any other tooth. Likewise the P^3 length is greater than any *P. gombaszoegensis* specimen that I have measured, but only just – the largest P^3L is from L'Escale (23.0mm). However, the breadth of OM71 is much larger than any other tooth.

Specimen	**P^3L**	**P^3B**	**P^4Ba**	**P^4Lp**
TD 403	23.6	11.9		
OM 71		13.0	17.8	14.1

Table 5.21. Measurements (in millimetres) of isolated teeth from Petralona. Data from Kurtén & Poulianos (1981).

No morphological details are given for these specimens, which is unfortunate as they are two of the more diagnostic teeth. They may be *P. gombaszoegensis* as they fall just outside the size range of the other fossils, but it is also possible that they are small *P. leo* specimens, although this cannot be proven without morphological evidence.

Three metapodials were also referred to *Panthera* cf. *gombaszoegensis*. The Mt3 is not mentioned, after the initial reference, but measurements of the Mc2 are given, as well as a brief morphological description of the Mt4 (Kurten & Poulianos, 1977: 115 – 118). These measurements are given in Table 5.22. In comparison with the other *P. gombaszoegensis* specimens in Tables 5.4 and 5.14 the Mc2 is very short and robust, but the Mt4 is of a similar size to a specimen from Westbury (1982/64). The Mc2 is illustrated in a photograph in Kurtén & Poulianos (1977) and the overall shortness and increased breadth of the specimen is obvious when looking at this picture. It also has very strong muscle markings on the anterior surface and large distal epicondyles. I accept the original diagnosis of this specimen as *Panthera* cf. *gombaszoegensis*, but note that it is very robust in comparison with the specimens seen previously.

The most recent faunal lists from Petralona have not referred any specimens to *Panthera gombaszoegensis* (Tsoukala, 1992; Sen & Leduc, 1996).

Specimen	Bone	TL	PWML	PWAP	SWmin	DW
No. 90	Mc2	74	16.6	24.7	12.8	18.3
No. 88	Mt4				14.6	

Table 5.22. Measurements of metapodials from Petralona. Data from Kurtén & Poulianos, 1977.

Volos. The site of Volos was included in a review of Greek sites by van der Meulen & van Kolfschoten (1986) and has subsequently been referred to by Koufos (2001) However no faunal descriptions have been published and there appears to be some confusion as to which site is meant by the name 'Volos' as there are several localities in this area (Athanassiou, 1993 - 1994).

5.4.9. Hungary

Kisláng. Jánossy (1986) listed *Leo* sp. cf. *toscana* as being present at Kisláng in Hungary. The same site is listed as having *Leo* sp. by Wiegank (1983). I have no further information about this site, but there is obviously some doubt over assigning these specimens to species.

Kövesvárad. Eight specimens referred to *Panthera gombaszoegensis* are known from Kövesvárad. I have studied two proximal metacarpal fragments (discussed in section 5.16) and an M^1 (V63/246). This M^1 does not appear to be from a felid, it is certainly not *P. gombaszoegensis* and is more likely to be a canid M_3. As well as these specimens, an additional five specimens were reported by Jánossy (1963), including the medial epicondyle of a humerus, a carpal and two phalanges. A complete femur was also recovered but this was destroyed by fire in 1956. The total length of this femur is given as 340mm (Jánossy, 1963), unfortunately no other complete femora have been recovered so the relationship of this femur to *P. gombaszoegensis* cannot be assessed.

The only specimen fully described and figured in the original publication is a second phalange (Jánossy, 1963: Plate 1, Figure 20). He suggests that it is of a similar size to those of modern female lions and tigers, whilst those of the sabretoothed cats are wider. He then goes on to state that the other specimens are not suitable for a full morphological analysis and that they are assigned to *Leo* cf. *gombaszoegensis* as they are of a similar size and date to those from Gombasek. Without further data it is impossible to evaluate this statement, so the Kövesvárad specimens have simply been updated to reflect current taxonomic views and are assigned to *Panthera* cf. *P. gombaszoegensis.*

Somssich Hill, Locality 2. The material from Somssich Hill referred to *Panthera gombaszoegensis* by Jánossy (1986) consists of a fragmentary premolar. I was not able to determine exactly which premolar it was, so measurements were not taken. However, it does appear to be a felid.

Jánossy (1986) referred a specimen from the site of Villany 3 (= Villany-Kalkberg-Nord) to *P. gombaszoegensis.* This material currently missing.

5.4.10. Israel

Two specimens are reported from the site of Oubeidiyeh (also called 'Ubeidiya), a first phalange and a 4th metacarpal; these are illustrated and measurements are given in the original carnivore report by Ballesio (1986). The total length of the Mc4 is given as 92.0mm and the distal width as 18.2mm, which is slightly longer, but narrower than the *Panthera gombaszoegensis* specimens listed in Table 5.7. It was assigned to *P. gombaszoegensis* because it was intermediate in size between the lion and leopard. The illustration of this specimen shows a complete metacarpal with small distal epicondyles. The Mc5 articulation is curved and appears quite shallow. The surface of the proximal articulation is smooth, with no trace of a stepped profile. It is therefore similar to the *P. gombaszoegensis* specimens from L'Escale.

5.4.11. Italy

Ellera of Corciano. A left calcaneum has been reported from this site by Ambrosetti *et al* [(1995a) cited in Gentili *et al* 1997]. No further information is available.

Pantalla. *Panthera* cf. *P. gombaszoegensis* has been reported from the site of Pantalla (Gentili *et al*, 1997). These specimens are still under preparation but may be available for study in 2002 (P. Argenti, pers comm).The site report refers to two skulls and an isolated left mandible from this locality; a photograph of the mandible is included in the publication (Gentili *et al*, 1997). This photograph is very dark and shows the mandible in situ. It is difficult to see any details but the protocones of the P_3 and P_4 are very large and appear to slope backwards. The M_1 also appears to be large with a distinct fissure between the paraconid and protoconid. No accurate measurements can be taken from the photograph and it may be that breccia is obscuring some morphological features. However, on the evidence presented I have doubts about referring this specimen to *Panthera gombaszoegensis*.

Pietrafitta. The lignite mine at Pietrafitta has yielded specimens referred to *Panthera gombaszoegensis* (Gentili *et al*, 1996). These consist of two partial metapodials and have yet to be published (P. Argenti, pers comm).

Slivia. The material from Slivia was published by Ambrosetti *et al* (1979) and consists of an isolated left C_i which was identified as *Panthera* cf. *toscana*. Unfortunately no measurements or illustrations of this specimen are available so the validity of this assignation cannot be assessed.

5.4.12. Saudi Arabia

An Nafud. The preliminary report on this site listed an Mc3 that was diagnosed as *Panthera* cf. *gombaszoegensis* on the dubious basis of being of similar size and proportions to the Mc4 from Oubeidiyeh (Thomas *et al*, 1998). No measurements or pictures of this specimen were included so this identification cannot be further evaluated.

5.4.13. Spain

As well as Huéscar which has been discussed previously, *P. gombaszoegensis* has also been reported from Atapuerca, Venta Micena, Cueva Victoria and Cullar Baza 2.

Atapuerca -Trinchera, Sabadell collection. The unstratified Atapuerca material collected by Dr. Crusafont is held in the collections of the Sabadell museum. Despite being unstratified, they are known to come from the Trinchera, from which other *P. gombaszoegensis* material has been recovered. This material has been discussed at the appropriate points in the text, but to recap, it consists of two mandibles, a complete tibia and a complete set of metatarsals, all of which appear to be *Panthera gombaszoegensis.*

Atapuerca - Gran Dolina. A complete tibia from the Gran Dolina was referred to *P. gombaszoegensis* by Morales *et al* (1987) and retained as such by García & Arsuaga (1999). It is slightly damaged and has been reconstructed. It has many features in common with the tibiae discussed in section 5.1.9. such as a deep depression beneath the tibial tuberosity and a deep dip beside the medial malleolus. However, neither of these features is diagnostic. Morales *et al* in their original diagnosis noted that it was of a similar size and morphology to the distal tibia from L'Escale. The measurements of the Atapuerca specimen are given as TL 270mm and SWmin of 24.7mm which are almost exactly the same as the unstratified specimen from Sabadell discussed previously. I therefore accept the referral of this specimen to *P. gombaszoegensis.*

Atapuerca - Sima de los Huesos. Morales *et al* (1987) identified a proximal third metatarsal from the Sima de los Huesos as *Panthera gombaszoegensis*, but this was subsequently reassigned to *Panthera* sp. by García *et al* (1997). Measurements and photographs of this specimen were included in the original publication (Morales *et al*, 1987). This specimen is very interesting as it is morphologically an exact match for specimen CD 1209 from L'Escale and it has been fully discussed in Section 5.1.11.2.

Atapuerca - Tres Simas. A juvenile mandible (E VI 4) from the Tres Simas was originally identified as *P. gombaszoegensis* by Morales *et al* (1987), but has since been reassigned to *Panthera leo* by García & Arsuaga (1998). The photograph of this specimen in García & Arsuaga (1998) shows a dpm_4 with a large talonid and smaller cingulum. The specimen is larger than the specimens from L'Escale and Gombasek (see Table 5.a) with a dpm_4 length of 18.9mm. It was also found in association with a large number of other *Panthera leo* specimens (García & Arsuaga, 1998). The features listed in Section 5.2.1. did not prove to be useful in identifying specimens to species, so I accept the referral of specimen E VI 4 from Atapuerca to *P. leo*, pending a more detailed investigation of the juvenile dentition in the extant cats.

Venta Micena. Two mandible fragments from Venta Micena were identified as *P.* cf. *gombaszoegensis* and published by Pons-Moyà (1987). This material consisted of a mandible fragment containing the roots of a P_4 and M_1 and a second specimen with fragmentary C_i and the roots of a P_3. The lengths of the teeth were given as C_i-16mm; 17mm for the premolars and 20mm for the M_1 (Pons-Moyà, 1987:119). The mandibles were from juveniles so corpus measurements were not taken. They were assigned to *P.* cf. *gombaszoegensis* largely because of their size. A later study illustrated one of the specimens and reassigned them to juvenile *Pachycrocuta brevirostris* (Navarro, 1992). The photograph shows a specimen with an anterior depth of approximately 30mm (measurement taken from the photograph in Navarro, 1992: Plate 14b). The adult *P.*

gombaszoegensis specimens listed in Table 4.10 all have an anterior depth of 32mm or over, whilst L'Escale specimen CD5 had a Depth A of 29.4mm. So it cannot be excluded from *P. gombaszoegensis* simply on the grounds of size. However, the photograph also shows a large deciduous canine, which is almost as large as a small adult *P. gombaszoegensis* specimen – Pons-Moyà gave a C_i length of 16mm for the Venta Micena mandible while the smallest *P. gombaszoegensis* specimens are only just over 17mm (see Table 4.9). These measurements indicate that this animal could not be *P. gombaszoegensis* and I therefore accept the referral of this specimen to *Pachycrocuta brevirostris.*

Cueva Victoria. A mandible with P_4 and M_1 and two isolated P^3s were identified as *P. gombaszoegensis* from the site of Cueva Victoria (Carbonell *et al*, 1981). They are said to be similar to those from Olivola, but no further information is given.

Cullar Baza 2. The site of Cullar Baza 2 is interesting as *P. gombaszoegensis* was included in the faunal list from this site in review of Spanish material (Alberdi *et al*, 1998). However, no further information was given and the material does not appear to have been published.

5.4.14. Tadjikistan

The mandible from Lakhuti 2 was included in the logratio diagrams in section 4.3. The specimen itself was figured in a publication by Sotnikova & Vislobokova (1990). This illustrates a mandible with complete dentition, lacking only the ascending ramus. However, it does not indicate that the P_3 and P_4 are still in the process of erupting (A. Turner, pers comm). As an aside, an animal with P_3 and P_4 still erupting is likely to have been below 20 months of age and therefore is likely to have still been with its mother (see Section 5.2.2). The specimen appears to have been crushed but from the photograph it is possible to see that the C_i is very short, the P_4 has a large protocone and posterior cusp with a distinct cingulum and the M_1 has a high protoconid and lower paraconid. The distance from the cemento-enamel junction to the base of the fissure appears quite large. The M_1 has a small cingulum but no talonid cusp. The features of the Lakhuti 2 cat correspond with those of *P. gombaszoegensis* and therefore I regard this specimen as *Panthera gombaszoegensis*.

5.4.15. Turkey

Yarimburgaz Cave. *Panthera gombaszoegensis* was included in a faunal list from Yarimburgaz (Darlas, 1995). However, a subsequent publication lists the felid material as *P. leo* and possibly *P. pardus* (Stiner *et al,* 1996). The specimens themselves have not been published.

5.4.16. Western Transbaikalia

Panthera cf. *tigris* has been identified from member three of Zasuhino (Vangengejm *et al*, 1990). This specimen was included in the log ratio diagrams in Section 4.3 and is of a similar size with a slightly narrower P_3 and a shorter P_4 protocone than the standard. It is most similar to the Lakhuti 2 specimen (Figures 4.8, 4.9 and 4.13). No morphological details of this specimen are given in Vangengejm's publication and it is not figured so the morphology of this specimen cannot be examined in detail.

5.4.17. Yugoslavia (Former)

Panthera cf. *toscana* is reported from the site of Tongruben von Strimica in a review of former Yugoslavian sites (Malez, 1986). I have been unable to find any further information on this site.

5.5. *PANTHERA GOMBASZOEGENSIS* IN AFRICA

Panthera gombaszoegensis has been reported twice from Africa. The first report was in 1968 by Dietrich who referred a 3rd metatarsal to *P. toscana*. This specimen was discussed with all other Mt3s in Section 5.1.11.2. The second suggestion that *P. gombaszoegensis* was in Africa came with the publication of the Laetoli specimens, in which Barry (1987) referred eight fragmentary teeth, a radius and a calcaneum to *Leo* aff. *gombaszoegensis* or *Leo palaeosinensis*. This diagnosis is largely based on a maxilla fragment with P^3 and P^4. However, I have grave doubts assigning the Laetoli specimens to this species. The estimated length of the P^4 is given as 35.5mm and the P^3 as 24.3mm which puts it outside the size range of even the largest of the *P. gombaszoegensis* specimens listed in Section 4.3. In terms of morphology the specimen is unlike any of the European *P. gombaszoegensis* material - the P^4 lacks an ectoparastyle when this feature was found in all European specimens. In addition, the P^3 has a tiny anterior cusp when most European specimens have quite large defined cusps (with the exception of Gerakarou 1).

It is obvious from these results that the Laetoli specimens cannot be *Panthera gombaszoegensis*. However, although it is the size of the modern lion it does not have any of the morphological features associated with this species, such as a large ectoparastyle and a large anterior cusp on the P^3. Another interesting feature is the very large P^2 alveolus which is given by Barry as approximately 10mm in length and 7.3mm in breadth, again this is the size of the modern lion. Therefore, we have a cat that is the size of the modern lion but morphologically very different. Barry realised this and assigned the specimens to *P. gombaszoegensis*, as this cat is of similar size to the fossils. However, I have shown that the morphology of these specimens does not match *Panthera gombaszoegensis* either. *Felis crassidens* Broom, 1948 was discussed by Barry as a possible candidate, but this species has been shown to be a chimera, based on the erroneous amalgamation of leopard and cheetah specimens (Turner, 1984b). Barry then compared the material to *Felis palaeosinensis*, but found that this cat is smaller than the Laetoli material. It must be remembered that the Laetoli deposits are some 3.6 million years old and therefore these fossils are amongst the earliest known of the pantherine cats. It is possible that the features observed in the modern lion are derived and there is no reason to assume that the earliest forms of a species must be exactly the same as the latest examples. Therefore we may be wrong in rejecting these specimens from *P. leo* on the basis of the morphology of the modern lion. Whatever the outcome of a review of the African material, it is certain that the Laetoli specimens are not *Panthera gombaszoegensis*.

CHAPTER 6 - BIOGEOGRAPHY AND PALAEOECOLOGY OF LARGE PLEISTOCENE CARNIVORES

The presence or absence of a species at a particular site or the regular co-occurrence of groups of animals may be very informative about ecology in the past; if a true pattern can be discerned from palaeontological evidence. This chapter attempts to address these issues by looking at the biogeography, potential for competition or exclusion and the effects of refugia on Pleistocene hyaenids and felids. Full details of the sites, publications and dates used in this section are given in Appendix 4.

6.1. BIOGEOGRAPHY

After many years of research the biogeography of European animals is largely understood in terms of arrival and extinction (e.g. Turner, 1995b); but there may be more detailed information about the distributions of animals to be gained by studying the overall pattern on a continental scale. For example, Kurtén (1968) suggested that *Megantereon* had a restricted circum-Mediterranean distribution and the absence of *Pliohyaena perrieri* from Spain, Italy and Britain after ~1.6Ma has also been noted (Turner, 1995a). By constructing a database of 195 European Pleistocene sites the accuracy of these observations can be tested and their implications assessed with a much greater degree of confidence.

The list of sites in the following analysis is not comprehensive but represents the amalgamation of site reports and syntheses from many different authors that have come to my attention (see Appendix 4 for further details). As such it is vulnerable to misidentifications and wrongly dated sites, but it is a first stage in assessing large scale change within the carnivore guild. The majority of this thesis has focussed on the larger cats, and it is likely that there is some bias toward sites with cats or extinct hyaenids in the dataset because of this. For this reason the following analysis is restricted to the felids and hyaenids because it is considered a representative sample of sites with these particular animals.

6.1.1. Method

All European Plio-Pleistocene localities with at least one carnivore species (with the exception of small mustelids) were included in this study. The dataset was constructed using published faunal lists which were entered into a Microsoft Access database. This gave a total of 195 sites dating between 1.9Ma and 0.3Ma. Many sites did not have exact dates attached to them and in order to include as many as possible in the analysis all sites were grouped into one of the four age categories shown in Table 6.1. These ranges were chosen because 1.4Ma is a useful boundary point in the Early Pleistocene, 0.8Ma was used because many sites are dated to the Cromerian (which began just after) and also because this is close to the Brunhes/Matuyama boundary. The 0.5Ma date was chosen because it is the date after which many of these species are considered extinct and so that this study could address the validity of this assumption. These categories were used to construct biogeographic maps of Europe. Where the age range of a site crossed a category boundary it was given the date code in which the majority of the date range fell. The total number of sites in each date category is shown in Table 6.1.

Date code	Date	Total (n)
Early	1.99 – 1.41 Ma	56
Middle	1.40 – 0.81 Ma	41
Late	0.80 – 0.50 Ma	69
Very Late	0.49 – 0.30 Ma	29

Table 6.1. Date codes, dates and total number of sites in each age category used for the construction of biogeographic maps.

The presence or absence of a particular species is indicated in the following maps by one of the shades listed in Table 6.2. In order to give more detail a grey scale is used so that the number of sites with a certain animal in one country can be quickly compared with others. Figure 6.1. shows the total number of sites in each country for individual age categories.

Colour		**Sites**	**Description**
White		0	No sites of this date with this species known from this country.
Light grey	░	1 - 3	One to three sites of this date with this species known from this country.
Dark grey	▒	4 – 6	Four to six three sites of this date with this species known from this country.
Very dark grey	▓	7 – 9	Seven to nine sites of this date with this species known from this country.
Black	█	10 - 12	Ten to twelve sites of this date with this species known from this country.

Table 6.2. Colours used in the following biogeographic maps to indicate the number of sites with a particular species in each country.

These maps can then be used as a quick visual reference to see where animals have been found, or where they are absent. Outlines of modern countries are used to show where particular species have been found. These are usually based on geopolitical boundaries such as mountain ranges or rivers and are therefore appropriate as such obstacles may have hindered migration in the past. They also have the advantage of being easily recognisable and those sites which were only referable to country or region can be included in the dataset.

It is important to realise when looking at the maps that the absence of a particular species does not mean anything if there are no sites of that age in the country (cf. Portugal in Figure 6.1 and 6.2). This will be taken into account in the analysis. Also, sites outside Europe such as 'Ubeidiyah in Israel are included in analyses and totals but are not shown on the maps. Site totals mentioned in the following account are those from my database, e.g. Megantereon is reported from 21 sites that are included in this study.

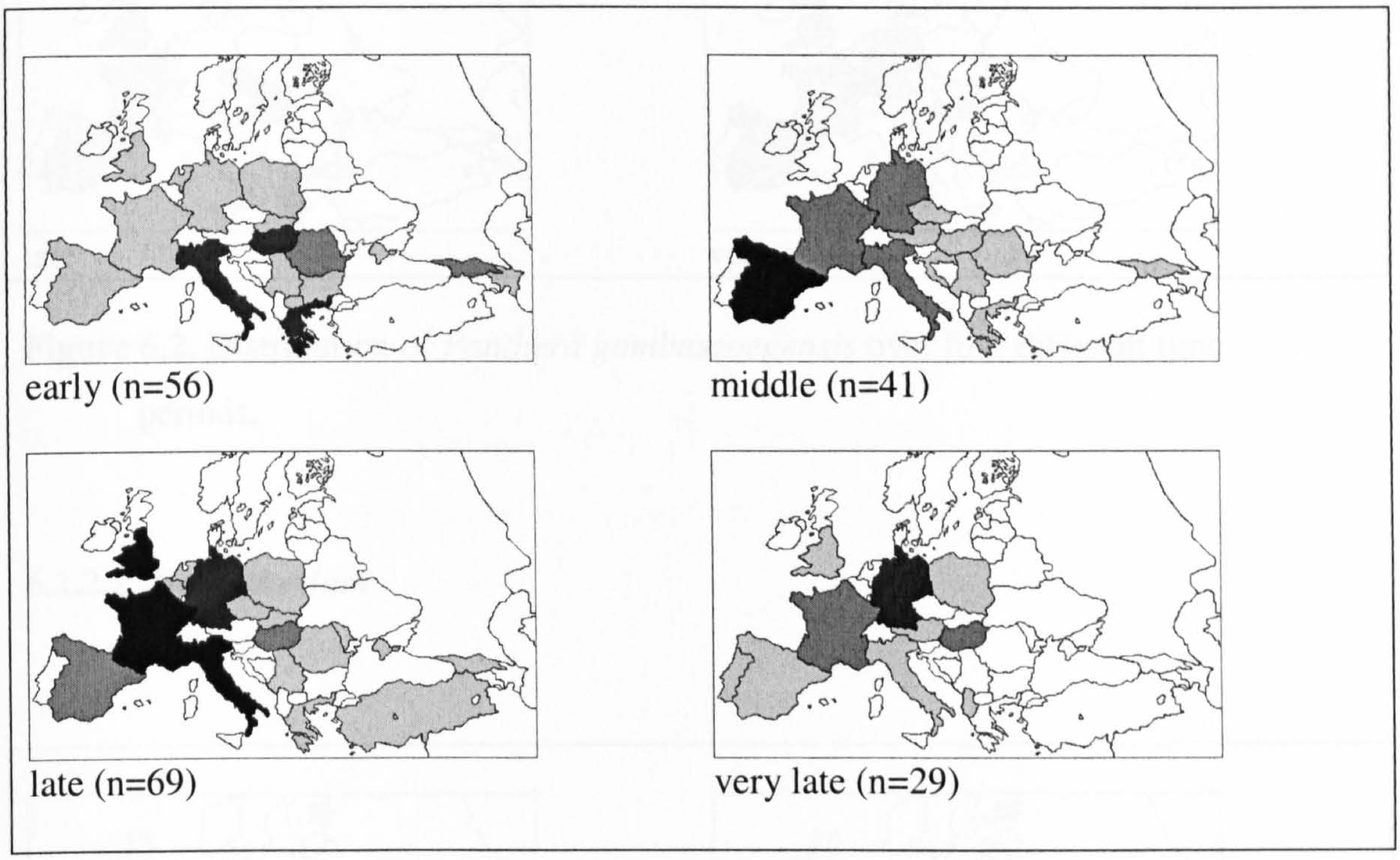


Figure 6.1. Total numbers of sites in each date category for the entire dataset (n=195).

6.1.2. Results

6.1.2.1. *Panthera gombaszoegensis*

Panthera gombaszoegensis appears at many sites (fifty-one in total) but is never common (Figure 6.2). It is most widespread in the middle age category (1.4 – 0.8Ma). It does not appear to reach Spain until after 1.4Ma and it is absent from Italy after 0.8Ma.

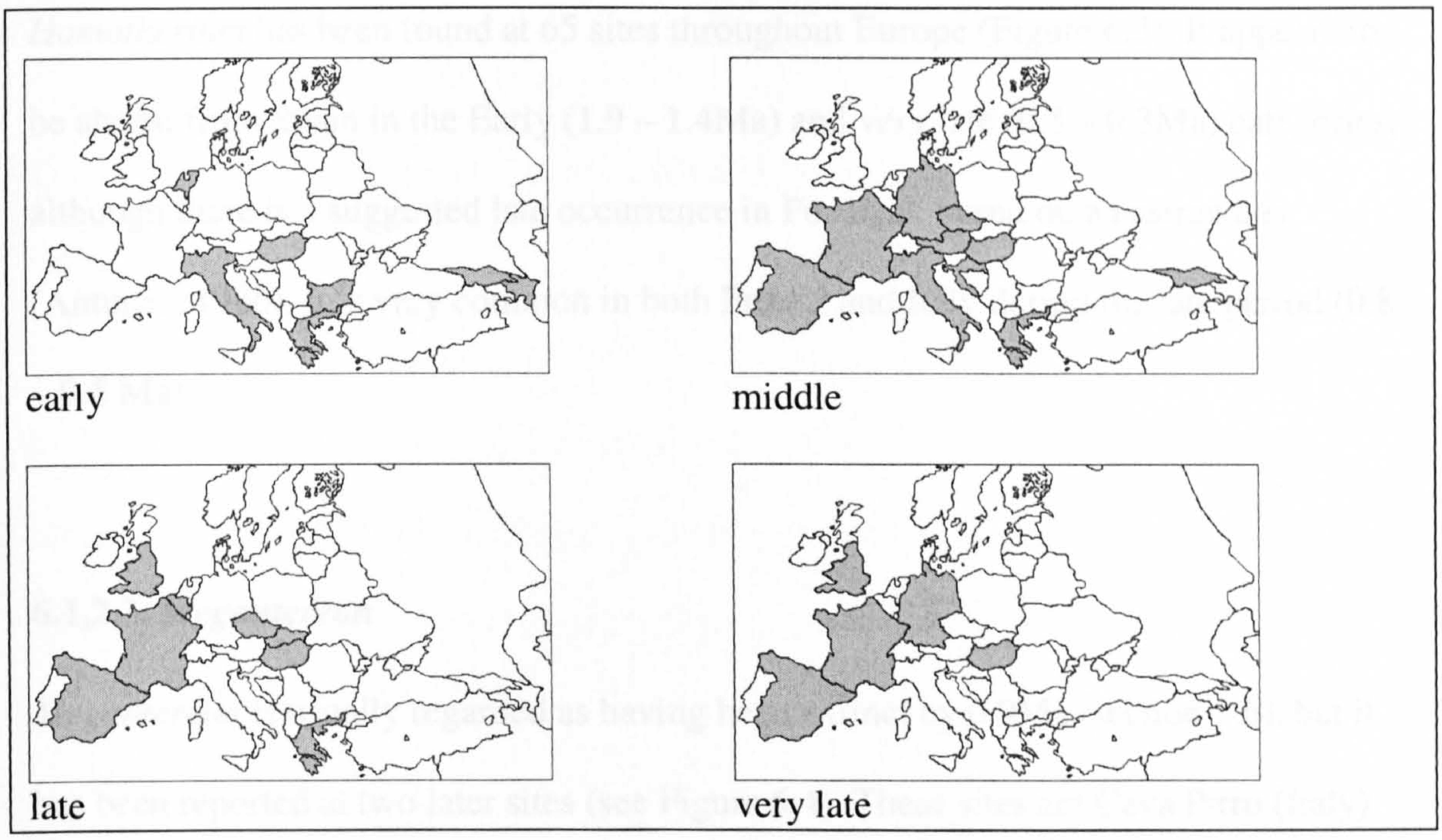


Figure 6.2. Distribution of *Panthera gombaszoegensis* over four different time periods.

6.1.2.2. *Homotherium*

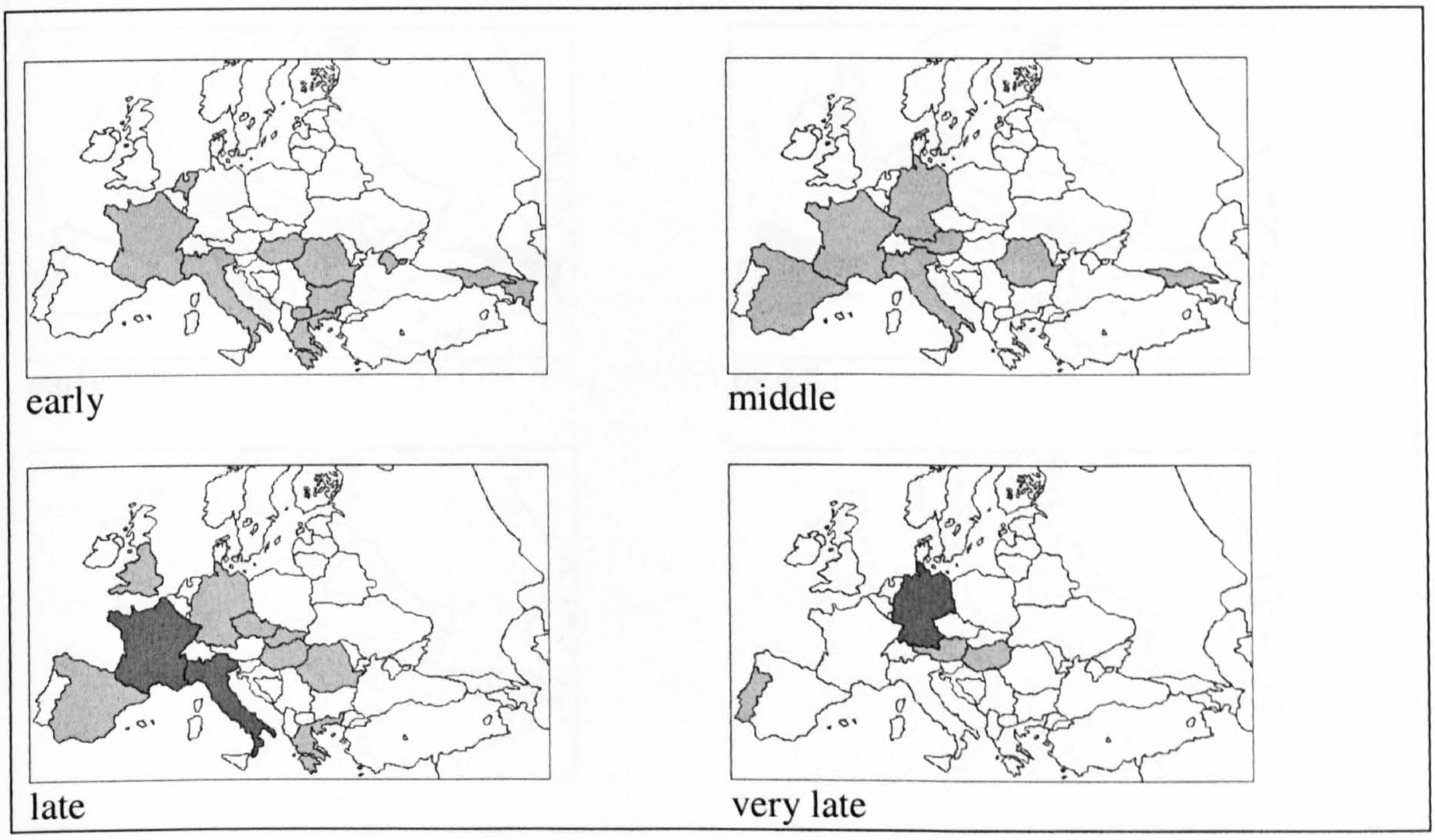


Figure 6.3. Distribution of *Homotherium* over four different time periods.

Homotherium has been found at 65 sites throughout Europe (Figure 6.3). It appears to be absent from Spain in the Early (1.9 – 1.4Ma) and very late (0.5 – 0.3Ma) categories, although there is a suggested late occurrence in Portugal, based on an astragalus (Antunes, 1986). It is very common in both France and Italy during the late period (0.8 – 0.5 Ma).

6.1.2.3. *Megantereon*

Megantereon is usually regarded as having been extinct by 0.9Ma (section 1.6), but it has been reported at two later sites (see Figure 6.4). These sites are Cava Pirro (Italy) and Abbeville (France). It has been found at 21 Pleistocene sites and was certainly extinct by 0.5Ma. Interestingly, it appears to have been relatively common in Italy, but was only present in Spain between 1.4 and 0.8Ma and has never been reported from the UK.

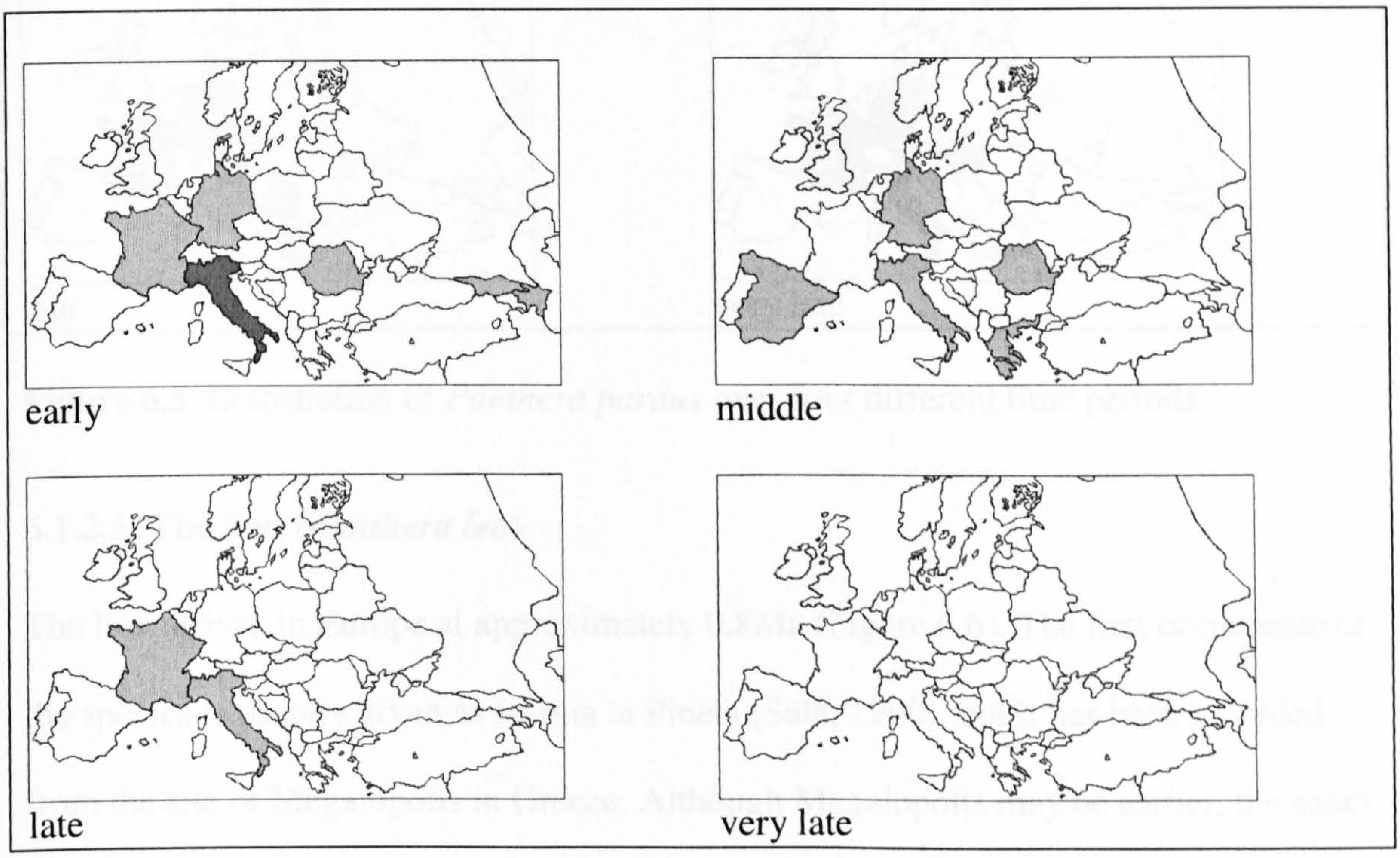

early
middle
late
very late

Figure 6.4. Distribution of *Megantereon* over four different time periods.

6.1.2.4. The leopard (*Panthera pardus*)

The leopard is always rare in Europe and has only been reported from 18 sites. It is found in France and Austria prior to 0.8Ma and subsequently reaches eastern and central Europe. It arrives in Italy after 0.5Ma and is only recorded at one Late Pleistocene site In Iberia (Turner, 1995a). It is interesting to compare this distribution with that of *Megantereon* above, which is present in Italy until the arrival of the leopard. A possible interaction between these two species will be considered later in the chapter.

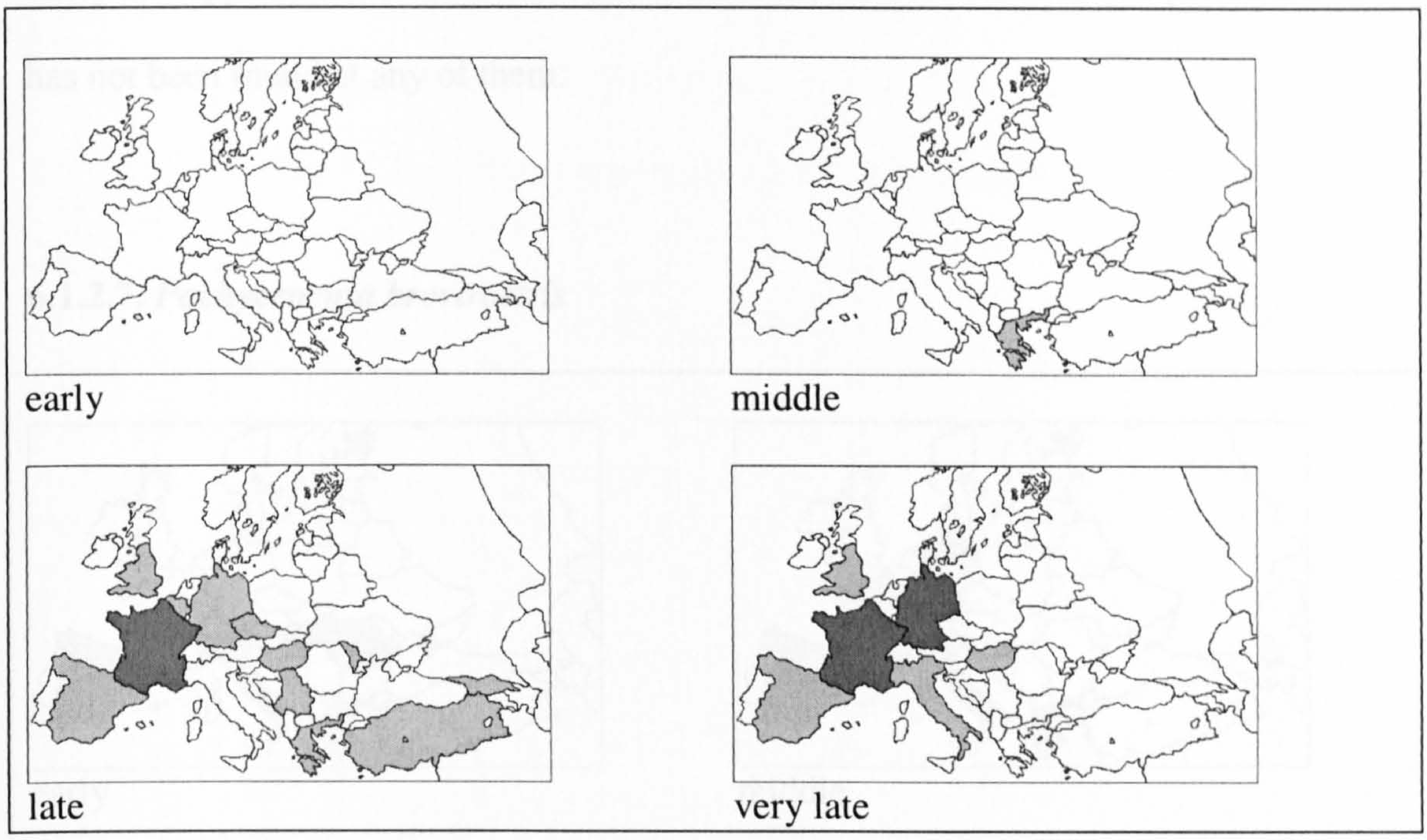
early middle

late very late

Figure 6.5. Distribution of *Panthera pardus* over four different time periods.

6.1.2.5. The lion (*Panthera leo*)

The lion arrives in Europe at approximately 0.8Ma (Figure 6.6). The first occurrence of the species is usually given as Isernia la Pineta (Sala, 1990), but it has been recorded from the site of Megalopolis in Greece. Although Megalopolis may be earlier, the exact date of this site is uncertain (Koufos, 2001), therefore no great significance can be attached to this find until the dating issue is resolved. Following its arrival the lion quickly becomes widespread and is relatively common in France and Germany. It became a very common European taxa and persisted in the Balkans until the Holocene (Guggisberg, 1975).



early

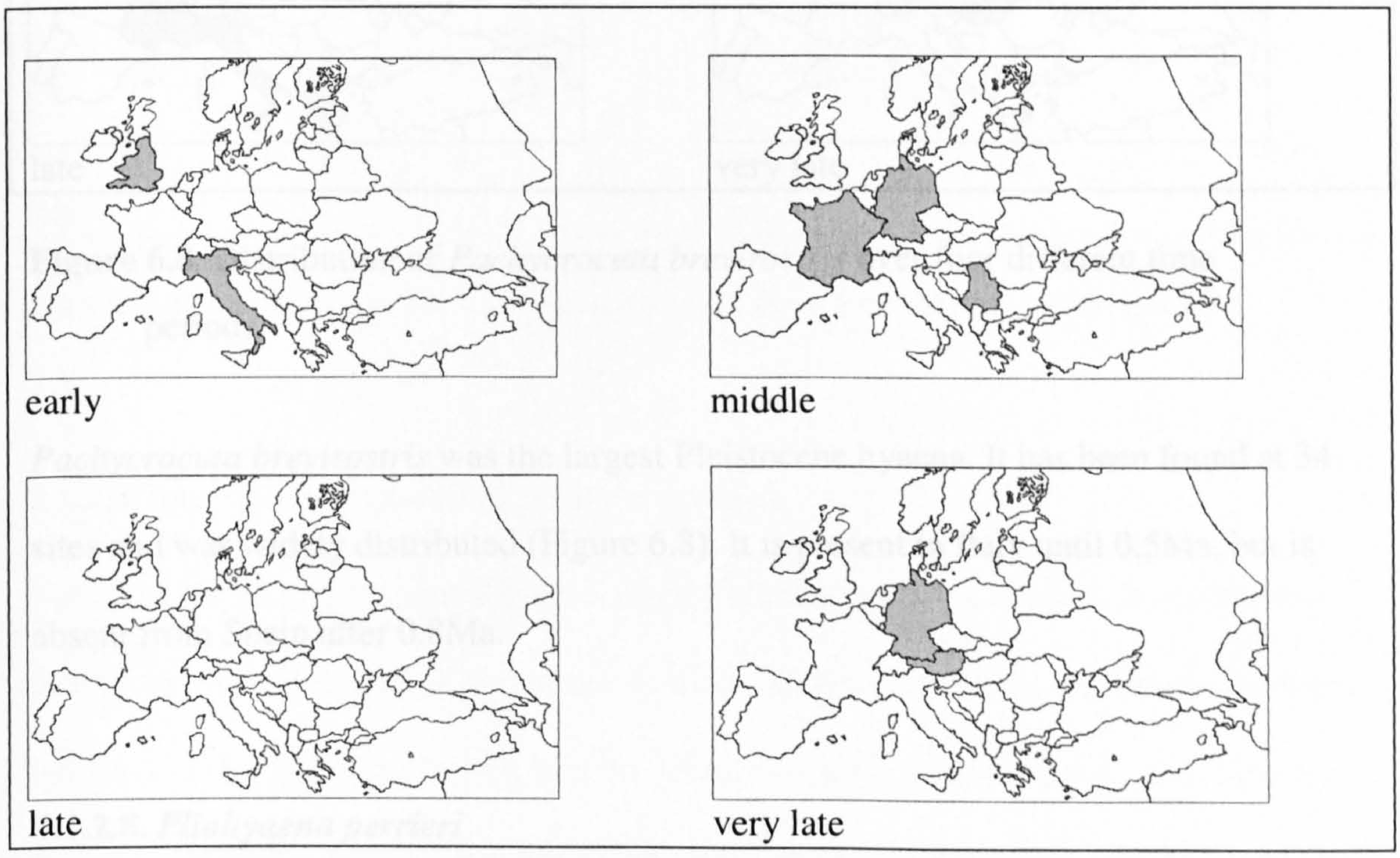
middle

late

very late

Figure 6.6. Distribution of *Panthera leo* over four different time periods.

6.1.2.6. The cheetah (*Acinonyx pardinensis*)



early

middle

late

very late

Figure 6.7. Distribution of *Acinonyx pardinensis* over four different time periods.

The cheetah is always scarce and has been found at only 9 Pleistocene sites (Figure 6.7). There are no records at all of it in the late category (0.8 - 0.5Ma). Despite its overall rarity this appears to be a true absence, as there are 69 sites dated to this period and it has not been found at any of them.

6.1.2.7. *Pachycrocuta brevirostris*

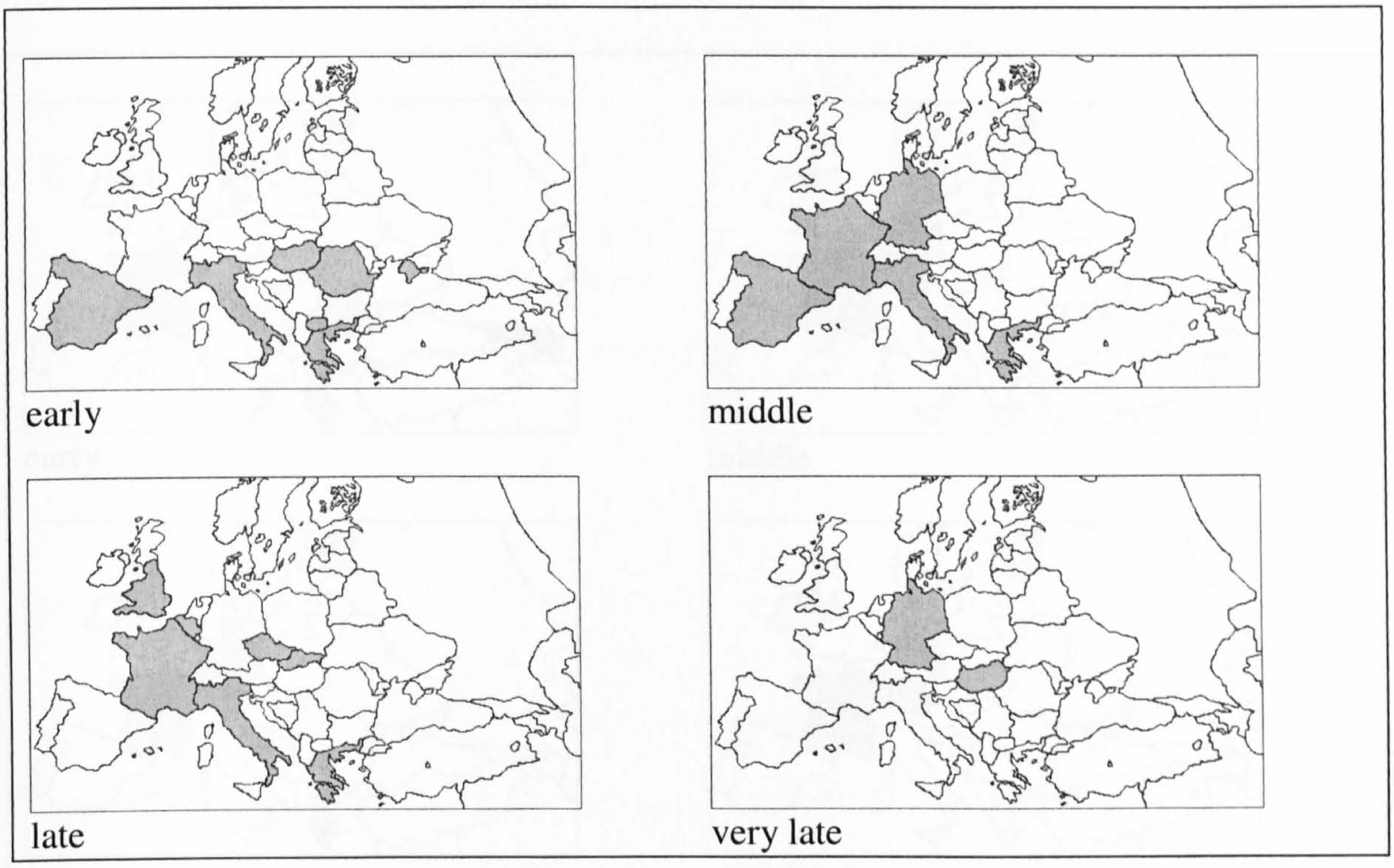


Figure 6.8. Distribution of *Pachycrocuta brevirostris* over four different time periods.

Pachycrocuta brevirostris was the largest Pleistocene hyaena. It has been found at 34 sites and was widely distributed (Figure 6.8). It is present in Italy until 0.5Ma, but is absent from Spain after 0.8Ma.

6.1.2.8. *Pliohyaena perrieri*

Pliohyaena perrieri is an extinct hyaenid. It is never common (reported from 26 sites) but it is persistent in France and Germany (Figure 6.9). There is a hiatus in the

European distribution of this species between 1.6 – 0.7Ma (Turner & Antón. 1997) but this has not been picked up here. In fact, it has been reported from two sites between these dates: Courterolles in France (dated between 0.8 and 1.3Ma [Argant, 1991]) and Erpfingen in Germany (dated to ~1.4Ma [Azzaroli *et al*, 1988]). It is found in Spain at Puebla de Valverde (2.1Ma) but is absent thereafter. It has not been found at any Italian sites.

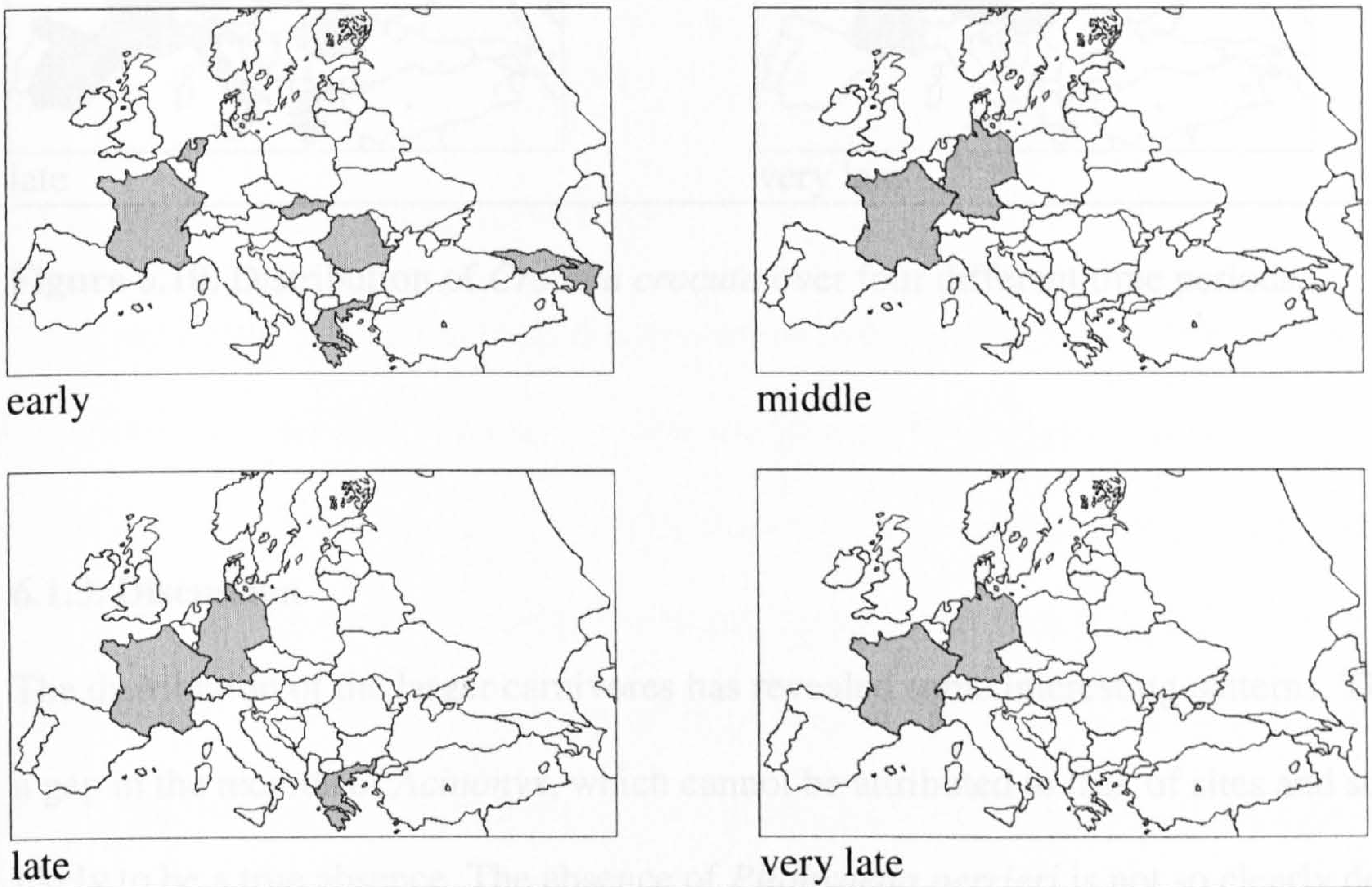
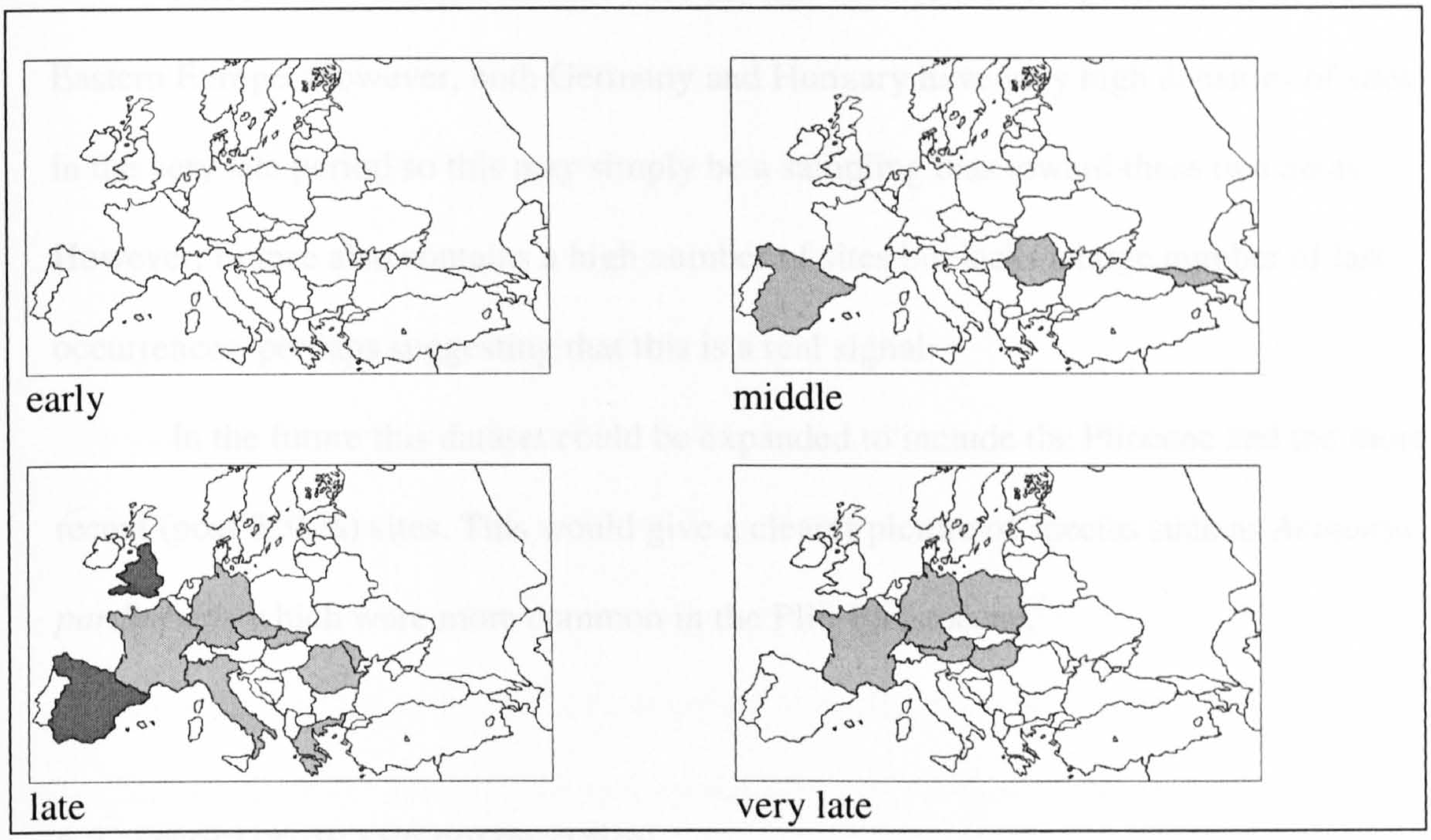


Figure 6.9. Distribution of *Pliohyaena perrieri* over four different time periods.

6.1.2.9. The spotted hyaena (*Crocuta crocuta*)

The distribution of the spotted hyaena is very interesting (Figure 6.10). It arrives in Europe in the middle period and becomes quite common in France and Britain between 0.8 and 0.5Ma. It is most common in the Iberian peninsula between 0.5 – 0.3Ma when both *Pachycrocuta brevirostris* and *Pliohyaena perrieri are* absent.



early

middle

late

very late

Figure 6.10. Distribution of *Crocuta crocuta* over four different time periods.

6.1.3. Discussion

The distribution of the larger carnivores has revealed some interesting patterns. There is a gap in the records of *Acinonyx*, which cannot be attributed to lack of sites and so is likely to be a true absence. The absence of *Pliohyaena perrieri* is not so clearly defined as previously thought but it is still very scarce between 1.4 and 0.8Ma. The circum-Mediterranean distribution of *Megantereon* noted by Kurtén (1968) is not quite so clear cut, as it has now been identified in Germany and Romania. On a very broad scale there appears to be replacement of some species by others, for example the two extinct hyaenids by *Crocuta crocuta* in Spain. In addition there is some evidence that classic refugia such as the Iberian peninsula and Italy may not have been inhabited by all species. The possible causes and implications of this observation will be discussed in section 6.4.

There is also a slight tendency for the last occurrences of species to be in North Eastern Europe. However, both Germany and Hungary have very high densities of sites in the very late period so this may simply be a sampling bias toward these two areas. However, France also contains a high number of sites but lacks a large number of last occurrences, perhaps suggesting that this is a real signal.

In the future this dataset could be expanded to include the Pliocene and the more recent (post 0.3Ma) sites. This would give a clearer picture of species such as *Acinonyx pardinensis* which were more common in the Plio-Pleistocene.

6.2. ASSOCIATION AND COMPETITION

The preceding section has looked at species in isolation but there will have been some degree of competition between the different groups. In the past it has been suggested that *Panthera gombaszoegensis* and *Pachycrocuta brevirostris* tend to occur together and that there may be some sort of relationship between them (Kurtén, 1968). In addition modern taphonomic work on West Runton hyaenid coprolites assumed that *Crocuta crocuta* was more likely to be responsible than *Pachycrocuta* because of the scarcity of this animal (Larkin *et al*, 2000). Work on modern felids has shown that cheetahs will deliberately move away from lions and hyaenas, their principle predators (Durant, 2000). Again, ideas and observations such as these can be directly tested using the database of Pleistocene sites.

6.2.1. Method

A large data matrix was constructed for all 195 sites in the dataset, including non-European sites such as those of An Nafud (Saudi Arabia) and 'Ubeidiya (Israel). Pairs of taxa were tested for associations by taking the number of sites at which the they co-occurred, the number of sites at which each species was present and the total number of sites in the dataset. A chi-squared test was then performed on these results to see if there were any significant associations between the species. Each pair was examined in this way, resulting in a total of 36 tests for the entire dataset of six cat and three hyaenid species.

It is recognised that some species became extinct before others or that the ranges of particular animals partially overlap. Only the portion for which both species were present together was included in the analysis. For this purpose the four date codes described in section 6.1 were used to define overlapping time bands. For example, the lion initially appears in the middle category and is present in the late and very late section whilst *Megantereon* is extinct by the very late category. Therefore only those sites dating to the middle and late time periods (when the two species overlapped) were included in the sample.

6.2.2. Results

The result of the chi-squared analyses are shown in Table 6.3. It can be seen from this table that there are very few significant associations between pairs of taxa (significant results are shown in bold). Many samples had an observed cell count of less than five, which makes the results invalid (Fowler *et al*, 1998), therefore these pairings cannot be evaluated. However, of these pairings six were significant and they are noted separately in Table 6.3.

It is interesting to note that the pairings which showed a positive association were between the cats and hyaenids. This would make sense in that the sabretoothed cats are likely to have left flesh on carcasses which could be scavenged by the hyaenids (Turner & Antón, 1997). There were no significant associations between the hyaenids despite the hypothesised competition in the Iberian peninsula.

	P. gombaszoe	Leopard	Lion	Cheetah	*Homotherium*	*Megantereon*	*P. brevirostris*	*P. perrieri*	*Crocuta*
P. gombaszoe	–	X	X	<5	**0.002**	X	**0.009**	X	**0.044**
Leopard		–	X	<5	X	<5	<5	<5 sg	<5 sg
Lion			–	<5	X	<5	X	<5 sg	X
Cheetah				–	<5 sg	<5	<5 sg	<5	<5
Homotherium					–	X	**0.000**	X	**0.015**
Megantereon						–	<5	<5 sg	<5
P. brev							–	<5	X
P. perrieri								–	<5
Crocuta									–

Table 6.3. Chi squared test results for pairs of Pleistocene carnivores. Significant and non significant associations are shown in **bold**, invalid results are shown in plain type, sg indicates an invalid but significant result.

Although a significant association has been observed between the cats and hyaenids we cannot be sure of the cause. It is possible that they are animals that existed in the same environments, e.g. *Homotherium* and *Pachycrocuta* are both thought to be characteristic of open environments. However, a significant relationship between *Homotherium* and *P. gombaszoegensis* was also observed and *P. gombaszoegensis* is usually thought to be a forest dweller (Alberdi *et al*, 1998). It also appears from these results that Kurtén (1968) was correct and that there is a significant association between *Pachycrocuta brevirostris* and *P. gombaszoegensis.*

If we look at the significant results that were invalid (Table 6.3), it appears that there is a relationship between *Pliohyaena perrieri* and the leopard, lion and *Megantereon*; while *Pachycrocuta brevirostris* is associated with *Homotherium*, *Acinonyx* and *Panthera gombaszoegensis*. The cheetah is another open environment animal.

6.3. COMPETITIVE EXCLUSION

As noted in Chapter 3, patterns of size separations exist within communities which are consistent with theories of competitive exclusion (Krebs, 2001). It was hypothesised that if similar size differentiation was found to exist within fossil cat communities then patterns of competition could be inferred.

Of the six measurements used in Chapter 3, three were plotted for all available Pleistocene large cat fossils. It is hypothesised that there may be size overlap between cats with different strategies, for example between a group living and a solitary animal as they will not be in direct competition, but there should not be a marked overlap between cats with similar lifestyles. If there is an overlap this indicates that there may have been some niche differentiation in order for the cats to successfully co-exist.

6.3.1. Results

It can be seen from the graphs in Figure 6.11 that *Megantereon* and the older (1.9 - 0.8Ma) *Panthera gombaszoegensis* specimens were of a similar size, although *Megantereon* had a slightly longer P^4 and a narrower C^sB, both of which are sabretooth adaptations. However, it is interesting to see that the leopard P^4 length substantially overlaps the lower part of the range of *Megantereon* and the older *P. gombaszoegensis* specimens. However, the later (0.8- 0.3Ma) *P. gombaszoegensis* teeth are slightly larger than the early specimens and they are only just within the range of the largest leopard specimens. The lower carnassial exhibits a similar pattern, although there is a slightly increased overlap between the young *P. gombaszoegensis* specimens and the leopard. *Homotherium* and the lion also have similar ranges, although *Homotherium* tends to be slightly larger.

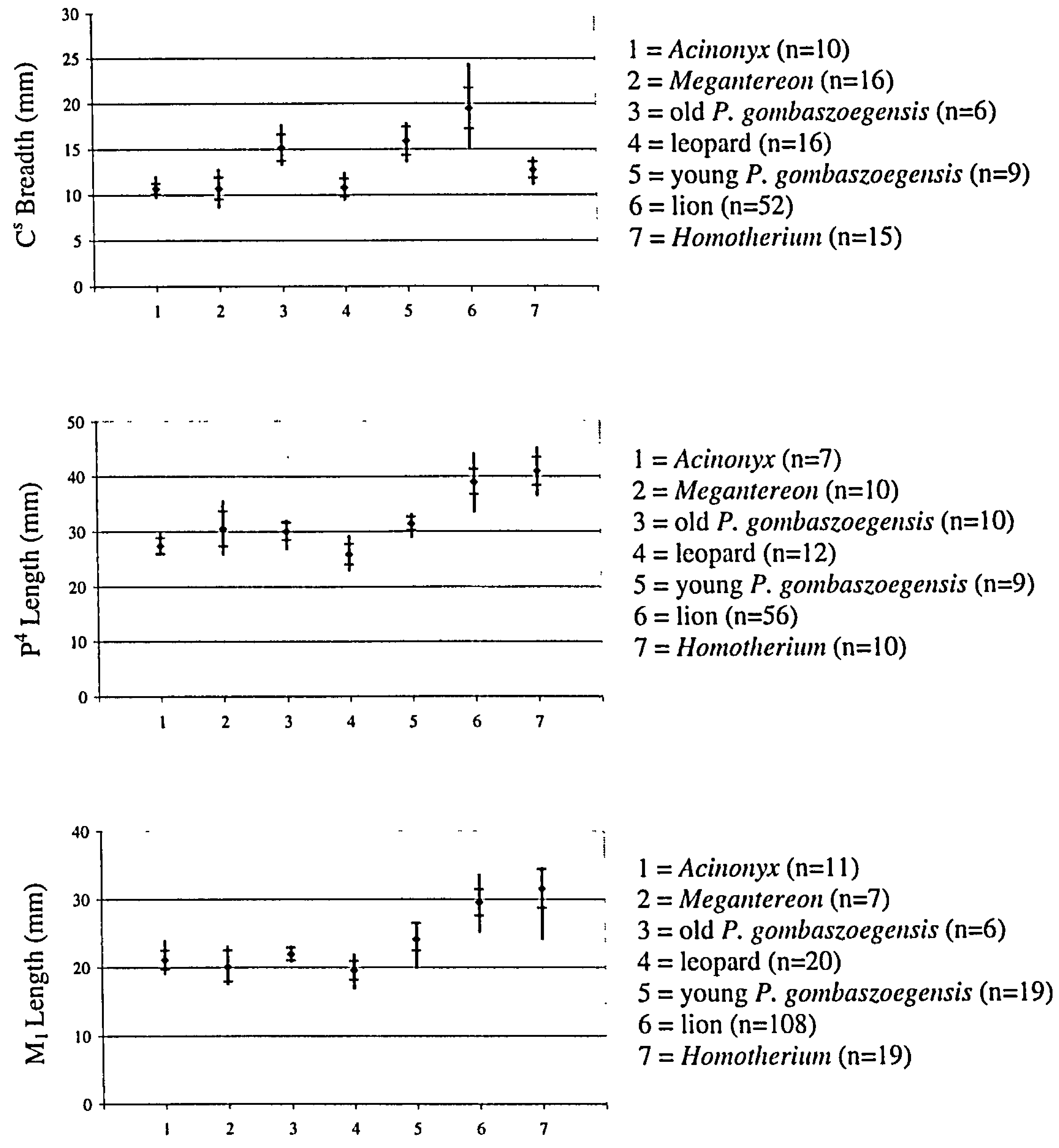


Figure 6.11. Comparative dental measurements for 6 species of fossil cat. Horizontal bars indicate one standard deviation from the mean (shown as a diamond) and vertical bars show the range in each sample.

The conclusions that can be drawn from this study are that *Megantereon* and *P. gombaszoegensis* were of a very similar size but *Megantereon* was a sabretoothed cat and therefore inhabited a slightly different niche. However the arrival of the leopard which is of a similar size to *Panthera gombaszoegensis* may have led to niche overlap between the two species and *Panthera gombaszoegensis* subsequently became larger.

This is not to suggest a direct causal relationship between these two events, but it is an interesting observation of a size change which is a plausible consequence of competition.

6.4. REFUGIA

Much attention has been paid to the patterns of postglacial migration in Europe (e.g. Hewitt, 1996; 2000) and the role of refugia in supporting temperate species until they were able to recolonise previously glaciated areas. However, the majority of this work has concentrated on the potential for speciation in refugia and the postglacial migration patterns of a variety of species such as grasshoppers, bears and oaks (Taberlet *et al*, 1998).

Very little has been said on the possible role of refugia in extinctions on either a regional or continental scale. Obviously an animal's chances of survival in a refugium is of paramount importance if it is to subsequently recolonise its former range. It is possible that this aspect of Pleistocene palaeoecology has been overlooked because of a focus on small mammals and insects which are still extant and have many subspecies. I have applied the concepts of modern population biology to the large cats to see if the European Pleistocene refugia would have been able to accommodate sufficient animals to prevent extinction.

Following on from the preceding biogeographical analysis, the absence of several species from the Iberian peninsula and Italy is of interest. It is possible that these gaps reflect true absences that may be related to the difficulties of getting into, and subsequently out of, these areas. Figure 6.12 shows a hypothesised vegetational map of Europe at the last glacial maximum (Circa 20,000BP).

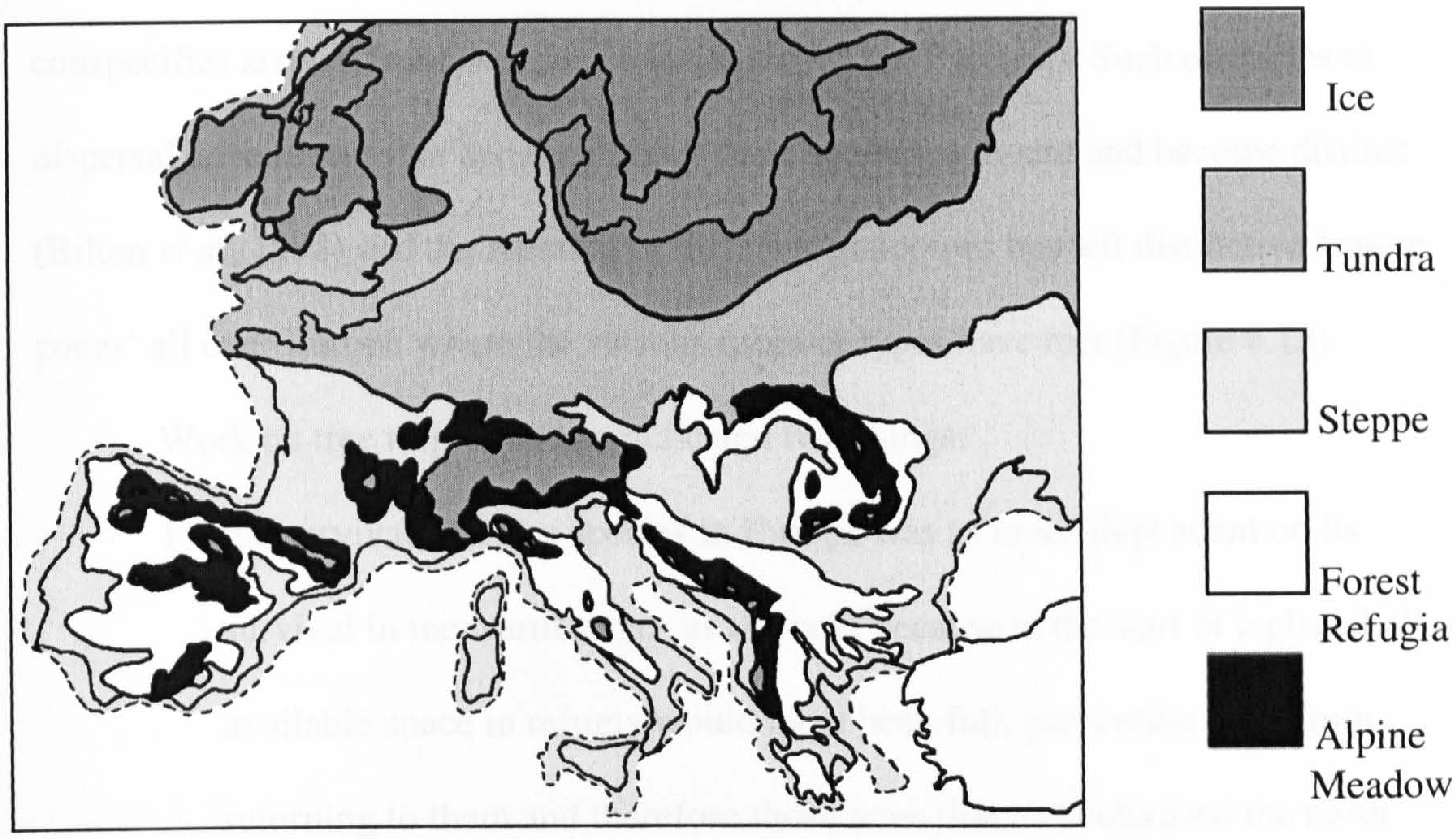


Figure 6.12. Palaeovegetation map of Europe during the last glacial maximum (~20,000BP). The dotted line represents sea level, areas outside the dotted line have not been considered. Modified from Zagwijn (1992).

Figure 6.12 shows that there were major ice masses across northern Europe, the Alps and the Pyrenees, with tundra extending as far south as Austria. Three major forested refugia in Southern Europe have been identified - the Balkans, Italy and the Iberian peninsula which are shown in white on the map. It is apparent that these areas are small in comparison with the overall area of the continent that would have been habitable during an interglacial.

What effect would such a range contraction have had on the fauna? There is a lot of information available about the last glaciation through studies of the MtDNA of different European mammals, trees and insects. These analyses have also highlighted the presence of three main refugia in Italy, Iberia and the Balkans as well as showing the importance of animals migrating in from the East (Taberlet *et al*, 1998). The colonisation of Europe by different genotypic groups has left a distinctive pattern which can still be picked up some 13,000 years later, because of varying rates of dispersal from particular areas. Few animals appear to have crossed the Alps before their conspecifics arrived from the East or made it over the Pyrenees. Such obstacles to dispersal have meant that certain animals have speciated in-situ and become distinct (Bilton *et al*, 1998) and the meeting of different genotypes has left distinctive 'suture zones' all over Europe where the various races or types have met (Figure 6.13).

Work on tree migration has indicated two things:

1. the survival of a tree species in Europe was as much dependant on its survival in the warm stages as the cold because at the start of a glacial all available space in refugia would have been full, preventing trees from returning to them and therefore those trees that had colonised the north would have died in situ (Bennett *et al*, 1991).
2. the survival of a particular species in a refugium may simply have been a matter of chance (Birks & Line, 1993).

Both of the above points are applicable to mammals. If we consider the large carnivores, animals at the top of the food chain, we see that they require three things – suitable habitat, appropriately sized prey and conspecifics to mate with. The interruption of any of these factors may have been enough to cause extinction, perhaps not on a wide scale, but locally. A local extinction may have led to their absence in a refugium during a particular glaciation. The subsequent absence of an important ecological competitor may have allowed another species to survive, through a lack of both direct and indirect competition as the prey resource would be under less pressure.

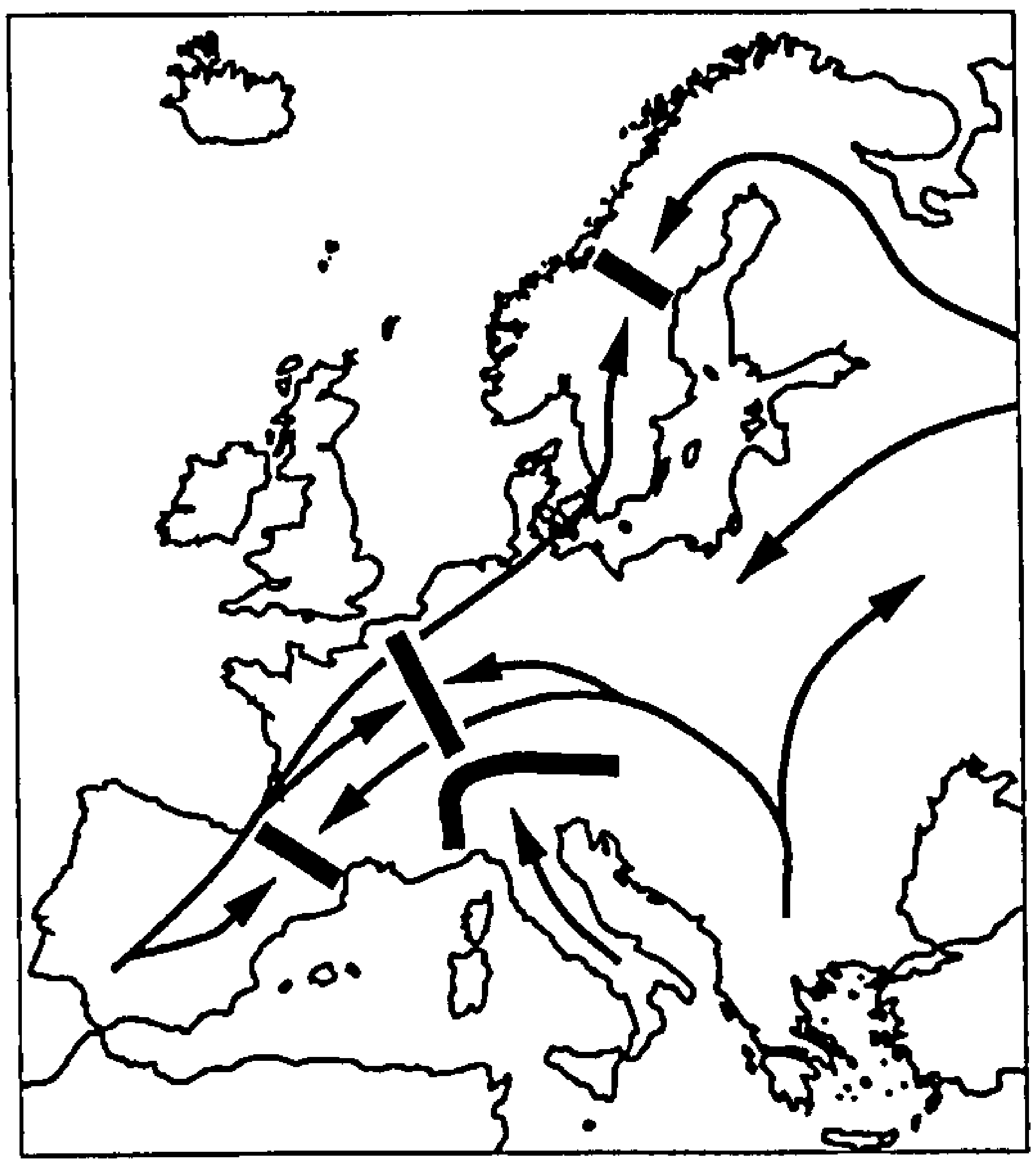


Figure 6.13. Major postglacial colonisation routes and suture zones in Europe· (From Taberlet et al, 1998). For a more detailed examination of suture zones see Hewitt (2000).

So can a refugium promote extinction? Genetic bottlenecks are known to occur when animals reach a low population level, but recovery from these can be swift, for example the Northern elephant seal was reduced to a population of ~15 individuals and has now increased to ~120,000 in 100 years (Hoelzel, 1999). It has been suggested that 12% of the Middle and Late Pleistocene was spent at glacial maximum (van Kolfschoten, 1995). Within a Milankovich cycle of 100,000 years this would be approximately 12,000 years at glacial maximum per cycle. During these times there would have been little opportunity for animals to migrate in and out of the refugia as both Iberia and Spain were cut off from the rest of Europe by glaciers on the Pyrenees and Alps (Figure 6.12). Therefore, although the bottleneck would not have been as extreme as that of the northern elephant seal, it would have been much more prolonged.

I will now illustrate the idea that the indirect effects of glaciations such as small population sizes and lack of migration may have led to localised extinctions in large mammals. The area chosen for this example is the Italian peninsula. This is not intended to be a fully comprehensive model, but to simply highlight the potential effects of a glaciation on a population of large cats.

6.4.1. Calculating effective populations

Modern conservation biologists have been faced with the potential extinction of many species and have created models that can be used to calculate the minimum population size required to keep a population genetically viable for a period of two hundred years (Ballou & Foose, 1996).

Using these formulae and data on modern big cats I have calculated the maximum number of territories which would have been available in Italy during a glacial maximum and compared these figures to the effective population size that is considered the minimum for a viable population of modern mammals. It must be noted that this is a minimum population for genetic health, but this estimate does not take into account prey availability, competition or migration, which would in all likelihood increase the required numbers of individuals considerably.

The area of Italy was calculated using the distance from Genoa to the sole of the boot and greatest breadth of the country. This gave an approximate total area of 180,000km^2. This figure does not take into account the topography of the country or the Pleistocene sea level change, but as can be seen in Figure 6.12 large amounts of land are likely to have been unsuitable for habitation.

Range size data are available for five species of modern cat – the lion, leopard, jaguar, tiger and cheetah and three of these were present in Pleistocene Europe. The total area of Italy was divided by the minimum, median and maximum range size for the extant cats to work out the total number of territories available within Italy. The median range size was calculated by taking the mid point between the maximum and minimum. The results are shown in Table 6.4.

Cat	Sex	Range (km^2)	Number of territories		
			Min	Median	Max
Lion	Female	19 – 400	450	859	9473
Jaguar	Male	28.5 – 158.5	1135	1925	6315
	Female	9.5 – 168	1071	2031	18947
Leopard	Male	9 – 63	2857	5000	20000
	Female	8 – 60	3000	5294	22500
Siberian tiger	Male	800 – 1000	180	200	225
	Female	100 – 400	450	720	1800
Cheetah	Female	50 – 65	2769	3130	3600

Table 6.4. Range size of modern large cats and calculations of the number of territories available in Italy during a glacial maximum (range size data from Hoogesteijn & Mondolfi, 1992).

These calculations can be used to calculate the effective population size (N_e) which is the number of animals that will pass their genes onto the next generation and is usually smaller than the total population size. The formula for calculating the effective population size is:

$$N_e = \frac{4 \times N_m \times N_f}{N_m + N_f}$$

where N_f and N_m are the total number of female and male adults (respectively) in the population in one generation (Ballou & Foose, 1996)

The assumptions made in this calculation are that the population is not growing, that generations do not overlap and that all individuals have an equal opportunity to breed (Ballou & Foose, 1996). The first assumption is fulfilled here as migration would have been zero. More complex equations cannot be used as we do not have detailed data on family history for extinct mammals, therefore this is an appropriate test.

Using the mean values in Table 6.4 we can calculate the effective population size for cats where data are available for both sexes; the results are shown in Table 6.5. These show that the leopard potentially has a large population size and would survive well in Italy. However, many assumptions have been made when producing these figures which would probably reduce the number of territories and therefore the number of individuals.

Cat	N_e
Jaguar	3953
Leopard	10285
Tiger	626

Table 6.5. Effective population sizes for modern cats, calculated from data in Table 6.4.

The vegetation of Italy has been assumed to be homogeneous, yet we know that this was not the case. Certain areas are likely to have been preferred by particular species, in much the same way as we see today; so the leopard may well have been found in mosaic habitats, whilst *Homotherium* is more likely to have been in more open areas. In addition, although large areas are shown as forest in Figure 6.12 this was more likely to have been a mosaic of forested patches, perhaps separated by great distances (Willis, 1996). This would lead to even smaller, isolated populations, within the refugium. All available territories have been calculated as being occupied, although there are likely to have been vacancies at some point. Also it was not simply a case of animals moving into Italy when the glaciations began as the territories would already have been occupied. Therefore population increase could not take place, so the population size of approximately 4000 calculated for the jaguar would have been isolated for some 10 – 12,000 years. Once glacial maximum was reach emigration and immigration would be severely limited, meaning that the genetic stock that was present would be the entire population with little possibility of outbreeding. Animals which were born would not have been able to emigrate, perhaps leading to increased competition for territories and prey. The observation that you do not get large numbers of similarly sized big cats living together today may be even more important if we consider that there were five big cats and three large hyaenids co-existing at ~0.5Ma and it is unlikely that all would have been able to survive together in such a small land mass for some 10,000 years. Inter- and intra- species avoidance strategies may have broken down because of increased pressure on limited resources. Animals which require territories in order to breed successfully would have been particularly disadvantaged, as the resulting displaced males would not have contributed to the genepool, reducing the effective population size even further. The other very important thing to consider is that animals prey on particular species or prey sizes and if these animals became extinct then the predators would either have to switch prey or be vulnerable to extinction themselves.

6.4.2. The broader picture

The effects of an extended bottleneck could be inbreeding depression, morphological changes and local extinctions. If localised morphologies had developed it might be possible to see this and trace migration patterns when Europe was recolonised after the glaciations. Evidence for this is extremely tenuous, but as observed in Chapter 4, two contemporaneous sites – Gombasek in Slovakia and L'Escale in France - have a similar tooth morphology which was not seen at any other site. These two sites lie on one of the colonisation routes from the Balkans (Figure 6.14). Although this is not a large body of evidence upon which to base a hypothesis, if glacial refugia are a factor in extinction as well as speciation, the following predictions can be made:

1. repeated bottlenecks might lead to local extinctions and resulting in loss of diversity, or different morphologies might become expressed in isolated groups which may be traceable if sufficient, well dated material is available for study.
2. Larger animals will be more vulnerable to extinction or inbreeding (i.e. proboscideans and large carnivores) because they require more space to reach an effective population size, whilst small mammals may be more likely to speciate.

3. Animals which require territories in order to be able to breed successfully will be more vulnerable to extinction than those that do not, as territorial behaviour will reduce the effective population size.
4. Specialised animals that require certain conditions or are reliant on particular prey types will be especially vulnerable, should that prey become extinct.

These predictions can be tested using our knowledge of similar, extant organisms. Prediction one could be tested by studying the morphology of subpopulations of modern species in which mtDNA studies have already demonstrated isolation, e.g. the European brown bear (Taberlet *et al*, 1998). Predictions two and three can be tested using more rigorous techniques devised to study modern populations of conservation concern. For species such as the large cats, where data on the extant species have been collected (e.g. Schaller, 1967; 1972) it should be possible to model the effects of isolation on the populations to calculate chances of extinction. These models will also permit different strategies for extinct species to be tested, for example territorial vs. non-territorial, to see what effects this will have on the probability of species survival.

6.5. THE PALAEOECOLOGY OF *PANTHERA GOMBASZOEGENSIS*

It may be seen from the ideas discussed above that the environment *P. gombaszoegensis* inhabited will have greatly affected its chances of survival. If it was a forest dwelling species during the glacial maxima (as suggested by Alberdi *et al*, 1998) it could have been vulnerable to extinction. So what is the evidence for forest dwelling? It seems to be largely based on the supposition that *P. gombaszoegensis* is most closely related to the jaguar and that the jaguar is a forest species. However, as previously noted, the jaguar has become restricted to a closed environment fairly recently as a result of hunting pressure and was capable of surviving in more open environments (Hoogesteijn

& Mondolfi, 1996). Alberdi *et al* (1998) listed *P. gombaszoegensis* as a woodland species, whilst most other carnivores were categorised as open area or limited tree cover species. The exception to this was *Megantereon* which was regarded as inhabiting areas with intermediate tree cover, in contrast to Marean (1989) who described it as a forest species. Environmental data is available for 20 of the fifty one sites reported to have *P. gombaszoegensis* (Appendix 2), of these fourteen are listed as cold, dry or steppe habitats whilst only 6 are said to be forested or warm environments. Whilst this is not conclusive, it is strong evidence that there is no clear association between *P. gombaszoegensis* and forested environments. In addition the results presented in Table 6.3 found significant associations between *P. gombaszoegensis* and two open environment species – *Homotherium* and *Pachycrocuta brevirostris.*

Considering these results, I propose that *Megantereon* is more likely to have been a forest dweller and that the largescale reduction of this habitat during the glacial maxima may have contributed to its extinction. In contrast, the persistence of *P. gombaszoegensis* despite these changes suggests that it was a more adaptable species and less dependant on forest environments. The arrival of the modern leopard in Europe at ~0.9Ma may have placed pressure on *P. gombaszoegensis* as *P. pardus* would have focussed upon the smaller bodied animals, which were at the lower end of the *P. gombaszoegensis* prey size range. As noted in section 1.6, the Middle Pleistocene is characterised by an increase in the body size of prey animals. It is plausible to suggest that the arrival of the leopard, the reduction of tree cover and an increase in prey size were factors in the decline and subsequent disappearance of *Megantereon.* Similarly, the larger size of the later *P. gombaszoegensis* specimens noted in Chapter 4 may have been a response to the size increase of the prey species combined with direct competition from the leopard.

CHAPTER 7 - DISCUSSION AND CONCLUSIONS

7.1. REASSIGNED SPECIMENS

This study found that non metric dental traits used in combination with morphometrics can be used to discriminate between modern and fossil *Panthera* species. The interpretation of the canines as being unusually high-crowned in *P. gombaszoegensis* was not supported by this analysis. In addition, mandibular features such as the position of the masseteric fossa were found to be of no diagnostic value. Following this analysis, several specimens have been reassigned and doubts expressed over others. Rome specimen 1191 was shown to be a leopard, a result which agrees with the diagnosis of Kotsakis & Palombo (1979). The referral of African specimens to *P. gombaszoegensis* was found to be erroneous. The 3rd metatarsal from Tegelen referred to *Acinonyx* by Dietrich (1968) has been reassigned as *P. gombaszoegensis*; juvenile specimens have also been recognised from this site. Doubts were raised about the affinities of the Chateau, Vértesszölös II and Uppony 1 material which may in the future prove to be *P. leo*. The Mosbach calcaneus was removed from *P. gombaszoegensis* and may be *Acinonyx*. The Halykés material is also interesting as the humerus displays some machairodontine features, whilst the 5th metacarpal is leopard-like.

7.2. REVISED DIAGNOSIS

The last list of synonyms was published by Hemmer & Schütt (1969) and remains largely unchanged. However some new names have been added. This analysis found no differences between species such as *Jansofelis vaufreyi* Bonifay, 1971 and *Felis (Panthera) schreuderi* von Koenigswald, 1960 and *Panthera gombaszoegensis*. Therefore these taxa are regarded as junior synonyms of *P. gombaszoegensis* as recommended by Hemmer & Schütt (1969) and Hemmer (1972a). The revised taxonomy of *Panthera gombaszoegensis* is as follows :

Order CARNIVORA Bowditch, 1821

Family FELIDAE Gray, 1821

Subfamily PANTHERINAE Pocock, 1917

Genus *PANTHERA* Oken, 1816

Species *GOMBASZOEGENSIS* Kretzoi, 1938

Junior synonyms: *Felis toscana* (Schaub, 1949); *Felis* (*Panthera*) *schreuderi* (von Koenigswald, 1960); *Janosfelis vaufreyi* (Bonifay, 1971).

Holotype: ß991- Upper fourth premolar (illustrated in Kretzoi, 1938, currently missing).

Type locality: Gombasek (= Gombaszög) Czech Republic, Middle Pleistocene.

Diagnosis:

P^4: ectoparastyle present; a straight anterior edge and a curved metacone.

P^3: variable anterior and posterior cusps, but usually large with a pronounced cingulum.

C^s: robust.

The cranium: large sagittal crest and strong nuchal crest projecting back over vertically orientated occipital condyles; incisors positioned in a straight line; I^3 is largest; large oval mystacial foramen; wide nasal aperture; nasal bones extend to or beyond the frontomaxillary suture.

M_1: protoconid larger than paraconid; later specimens often have a slight lingual bulge; cingulum usually present; talonid very rare.

P_4: large protocone; anterior and posterior cusps and cingulum are distinct and usually large; later specimens may have a 'basin' on the posterior lingual surface.

P_3: highly variable morphology, although cusps usually ill-defined with a small posterior cusp.

C_i : tends to have a short crown; rounded cross section.

Mandible: no determining features, but all specimens have two mental foramina and usually have a straight (but not upright) symphysis.

Postcrania: the only diagnostic bone of the postcranial skeleton is the humerus which has a long, low olecraneon fossa.

Distribution: Europe and Western Asia.

7.3. SUBSPECIFIC DISTINCTIONS

Hemmer (1972a) described two separate chronosubspecies – *P. gombaszoegensis toscana* and *P. gombaszoegensis gombaszoegensis* – on the basis of narrower premolars and a more robust build in the former. However my results do not support his diagnosis, in fact I found that the older material (*P. gombaszoegensis toscana*) had broader but shorter premolars than the younger (*P. gombaszoegensis gombaszoegensis*) and were slightly smaller overall. In addition, an increase in the robusticity of the cats was also seen, as the younger specimens more commonly had features such as an M_1 lingual bulge. However, these were not new morphologies, as each feature had been observed in at least one older specimen. This suggests that this is not a new species but simply that certain traits that had always been present in the population became more commonly expressed over time. So, Hemmer (1972a) was correct in observing differences between the older and younger specimens, but my results have been unable to replicate his diagnosis and have in fact emphasised very different traits. However, it is not possible to diagnose a specimen to a particular subspecies with certainty as it is a trend rather than an absolute difference. Given that there is much confusion over the identity of Pleistocene pantherine fossils (and that it is difficult to identify them to species let alone subspecies) I reject the suggestion of two subspecies, but acknowledge that there is a morphological difference between the two age groups.

7.4. THE TAXONOMIC AFFINITIES OF *P. GOMBASZOEGENSIS*

I initially felt that *Panthera gombaszoegensis* was likely to be a leopard, but the analysis of modern and fossil material has shown that this is not the case. However, it does not have the very rounded or robust morphology seen in the modern or fossil lion, suggesting that it is not directly ancestral to this cat either. Surprisingly, the tiger and modern and fossil jaguar proved to be most similar to the *P. gombaszoegensis* in the log ratio diagrams and in most morphological features it corresponds to Boules' tiger criteria much more than the lion. This result is in accordance with a recent phylogenetic study which also found that the jaguar and tiger were most closely related (Mattern & McLennan, 2000). Modern biogeography may also indicate similarities as the ancestral tiger ranged into Beringia and fossil tigers have been identified in North America (Herrington, 1987).

On the basis of my study, I suggest that *Panthera gombaszoegensis* may be ancestral to or closely related to the modern tiger and jaguar as it exhibits traits of both that are not shared by the lion or leopard. However, I do not think that it was *P. gombaszoegensis* per se that moved into North America but was perhaps a part of a pantherine radiation at approximately 2Ma which led one group to become the tiger and remain in Asia (subsequently giving rise to the jaguar at 1Ma or thereabouts) and a second to follow a movement of Asian bovids into Europe (Spassov, 1998). No evidence of *P. gombaszoegensis* has been found in Africa, indicating that it may be an Asian species.

7.5. PALAEOECOLOGY

No information was discovered to suggest that *P. gombaszoegensis* was a social cat. It is no more sexually dimorphic than the modern leopard or jaguar and it has not been found in large numbers at any one site. It is therefore likely to have been a solitary ambush hunter, like most of the modern *Panthera* species. Given that the ancestral coat pattern of the pantherines is flecked (Werdelin & Olsson, 1997) and that the majority of extant species have a spotted coat pattern [even juvenile lions have spots (Schaller, 1972)], it is likely that *P. gombaszoegensis* was also a spotted cat.

Unlike previous suggestions this study found that there was no direct link between *P. gombaszoegensis* and forested environments. In fact it was found to be significantly associated the presumed open country species *Homotherium* and *Pachycrocuta*. The size increase seen in the more recent *P. gombaszoegensis* specimens may be related to a number of factors such as the arrival of the leopard and the overall increase in prey body size after ~0.8Ma. These changes combined with a reduction of forested habitat may have led to the extinction of *Megantereon*. Of all the sites at which *P. gombaszoegensis* is present, at only six did the environmental data indicate warm or wooded areas, showing that this cat was adaptable to a variety of conditions and was not a specialised forest dweller. The occurrence of a specific morphology in two sites of similar date may indicate migration patterns in this species, as the small sizes of glacial refugia may have lead to inbreeding or localised extinctions.

7.6. FUTURE WORK

This study has provoked a large number of questions which may be answerable with future work. The hypothesis that *P. gombaszoegensis* is closely related to the tiger can be tested by studying fossil tiger material to see if similar morphological traits are found. The collection of data on non-metric dental traits will be widened to include all modern *Panthera* species. The European faunal database will be augmented, to increase sample sizes and test the distribution of other species; in particular the addition of prey species may yield some interesting results. The potential for extinction or inbreeding in glacial refugia will be tested using more rigorous models developed for use in conservation biology. The study of known age juvenile postcrania would be of interest, to see what changes occur during ontogeny and whether or not the differences seen in the Atapuerca and L'Escale metatarsals can be ascribed to this. The distinct differences between the modern and fossil cheetah shown in the log ratio diagrams could prove informative, as it appears that the modern cheetah is a much more specialised animal than the fossil species. However, larger sample sizes and a full study of the fossil material would be required to investigate this further. The final possibility of future work is based on the observation that captive animals exhibit significant cranial differences to their wild conspecifics. This will be studied further using a variety of techniques as it has implications both for comparative studies and conservation biology.

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APPENDIX 1 - AUTHORITIES LIST

Common name	Species	Authority
Grey Wolf	*Canis lupus*	Linnaeus, 1758
	Canis arnensis	Del Campana, 1913
	Canis etruscus	Forsyth Major, 1877
	Canis lupus mosbachensis	Soergel, 1925
	Xenocyon lycaonoides	Kretzoi, 1938
Puma	*Puma concolor*	(Linnaeus, 1771)
Cheetah	*Acinonyx jubatus*	(Schreber, 1775)
Fossil cheetah	*Acinonyx pardinensis*	(Croizet & Jobert, 1859)
Clouded leopard	*Neofelis nebulosa*	Raffles, 1821
Tiger	*Panthera tigris*	(Linnaeus, 1758)
Leopard	*Panthera pardus*	(Linnaeus, 1758)
Jaguar	*Panthera onca*	(Linnaeus, 1758)
Lion	*Panthera leo*	(Linnaeus, 1758)
Snow leopard	*Panthera uncia*	(Schreber, 1775)
Fossil Jaguar	*Panthera onca augusta*	(Leidy, 1872)
Fossil tiger	*Panthera palaeosinensis*	(Zdansky, 1924)
	Homotherium latidens	(Owen, 1846)
	Megantereon cultridens	(Cuvier, 1824)
	Dinofelis	Zdansky, 1924
Marbled cat	*Pardofelis marmorata*	Martin, 1836
Temmincks cat	*Felis temminckii*	Vigors & Horsfield, 1828
King cheetah	*Acinonyx rex*	Pocock, 1927
Geoffroys cat	*Felis geoffroyi*	d'Orbigny & Gervais, 1844
Jungle cat	*Felis chaus*	Gueldenstaedt, 1776
Spotted hyaena	*Crocuta crocuta*	(Erxleben, 1777)
Brown hyaena	*Hyaena brunnea*	Thunberg, 1820
	Pachycrocuta brevirostris	(Aymard, 1846)
	Pliocrocuta perrieri	(Croizet & Jobert, 1828)

APPENDIX 2 - A list of all sites at which *Panthera gombaszoegensis* has been reported.

Akhalkalaki
Location: Georgia
Date: 1.1Ma
P. gombaszoegensis remains: 1 mandible (originally *P.* cf. *tigris*)
Environment: dry, steppe
Published: Vekua (1986); Vekua & Lordkipanidze (1998); Gabunia *et al* (2000); Moullé *et al* (2000).

An Nafud
Location: Saudi Arabia
Date: Early Pleistocene
P. gombaszoegensis remains: an McIII
Published: Thomas *et al* (1998)

Artenac
Location: Charente, France
Date: 0.7 – 0.5 Ma
P. gombaszoegensis remains: 2 nearly complete skulls
Environment: cold
Published: Delagnes *et al* (1999); Becq-Giraudon (1999).

Atapuerca - Gran Dolina (=Trichera Dolina)
Location: Atapuerca, Spain
Date: OIS 21-20 (~0.8Ma)
P. gombaszoegensis remains: A complete tibia
Environment: Cold/warm transition
Material stored: Geology Department of the Universidad de Complutense, Madrid, Spain
Published: Morales *et al* (1987); García & Arsuaga (1999)

Atapuerca - Sima de los Huesos
Location: Atapuerca, Spain
Date: OIS 9-11 (~0.4Ma)
P. gombaszoegensis remains: a proximal Mt3
Material stored: Geology Department of the Universidad de Complutense, Madrid, Spain
Published: Morales *et al* (1987); García *et al* (1997).

Atapuerca - Tres Simas
Location: Atapuerca, Spain
Date: post 0.6Ma
P. gombaszoegensis remains: a juvenile mandible (now *P. leo*)
Material stored: Geology Department of the Universidad de Complutense, Madrid, Spain
Published: Morales *et al* (1987); García & Arsuaga (1998)

Belle Roche
Location: Sprimont, Belgium
Date: 0.5 Ma (ISO 13 – 15)
P. gombaszoegensis remains: unknown, at least some dental specimens
Environment: cold to warm
Material stored: Vertebrate and Human Research Group, University of Liège
Published: Cordy (1981); Cordy *et al* (1992).

Cessaguet
Location: France
Date: ~1.0Ma (older than Vallonnet)
P. gombaszoegensis remains: 1 C^s
Published: Turner (1995a)

Chateau
Location: Cluny, France
Date: 0.4 – 0.35 Ma
P. gombaszoegensis remains: Many, cranial and postcranial
Environment: cool
Material stored: 1 specimen in Earth Science Dept. University of Lyon,
Published: Argant (1980, 1991).

Cueva Victoria
Location: Murcia, Spain
Date: 0.8Ma (ISO 22)
P. gombaszoegensis remains: 1 mandible and 2 P^3.
Published: Carbonell *et al* (1981); Carbonell & Rodriguez (1994)

Cullar Baza 2
Location: Orce, Spain
Date: 0.9 (Colle Curti, F.U.) Galerian
P. gombaszoegensis remains: yes
Published: Alberdi *et al* (1998)

Deutsch Altenburg 4
Location: Austria
Date: ~1.4Ma
P. gombaszoegensis remains: an Mt2 and an Astragalus
Material stored: Vienna University
Published: Wolsan (1993); D. Nagel (pers comm).

Dmanisi
Location: Georgia
Date: 1.7Ma
P. gombaszoegensis remains: Thirty one specimens including a Mandible, Scapula, Humerus, Radius, Carpals, Metacarpals and a Phalanx.
Environment: mosaic landscape – arid and warm
Published: Gabunia *et al* (2000); D. Lordkipanidze (pers. comm); Gabunia *et al* (2001)

Ellera
Location: Corciano, Italy
P. gombaszoegensis remains: a calcaneum
Published: Ambrosetti *et al* (1995a).

Erpfinger Höhle
Location: Germany
Date: Early Pleistocene (~1.4Ma in Azzaroli *et al*, 1988)
P. gombaszoegensis remains: isolated P^4 and C^s
Published: Lehmann (1953; 1957)

Garussi Korongo
Location: Serengeti, Africa
Date: Pliocene
P. gombaszoegensis remains: Mt3.
Material stored: Museum für Naturkunde, Humboldt University, Berlin, Germany
Published: Dietrich (1968)

Gerakarou 1
Location: Macedonia, Greece
Date: 1.9 – 1.6 (Seneze-Olivola Faunal Unit)
P. gombaszoegensis remains: A nearly complete cranium
Material stored: Department of Geology & Physical Geography, Aristotle University of Thessaloniki, Greece
Published: Koufos (1992).

Gombasek (= Gombaszög)
Location: Slovakia
Date: 0.8 – 0.7 Ma (Lower Cromerian)
P. gombaszoegensis remains: $2P^4$; $1P^3$; $1I^1$; $3M_1$; $2C^s$; $5C_i$; $1P_3$; $2P_4$; 2 juvenile mandibles; 2 maxilla frags; 2 mandible frags; 1 mandible; 2 astragalus; 1 ulna; 1Mt5; 1Mc2; 1Mc4; 1Mc5. 1 humerus (missing).
Material stored: Hungarian Geological Institute, Budapest (unpublished); Palaeontological Department, National Museum of Natural History, Budapest, Hungary (Holotype (missing) and Paratypes).
Published: Kretzoi (1938); Wolsan (1993).

Holstejn 1
Location: Czech Republic
Date: 1.35 – 0.95
P. gombaszoegensis remains: yes
Published: Kahlke (1975); Wolsan (1993)

Grotte 14
Location: Dordogne, France
Date: ISO 11 – 17 (= 0.4 - 0.7Ma [Shackleton, 1995])
P. gombaszoegensis remains: at least 1 mandible
Environment: temperate/moist
Published: Guadelli (2001)

Halykés (= Alikes)
Location: Thessaly, Greece
Date: ?MNQ 19, Lower Pleistocene (possibly Tasso Faunal Unit)
P. gombaszoegensis remains: 1 mandible; 1 cranial fragment; 1 distal humerus; 2 metacarpals.
Material stored: Department of Geology at the University of Athens, Greece
Published: Athanassiou (1993-1994, 1996); Koufos (2001).

Huéscar
Location: Spain
Date: 0.7Ma (García *et al*, 1999)
P. gombaszoegensis remains: P^4 and C^s
Material stored: Museo de Ciencias Naturales, Madrid (MNCN), Spain
Published: Alcala & Morales (1989)

Kisláng
Location: Hungary
Date: 2.0 – 1.5
P. gombaszoegensis remains: identification uncertain
Published: Jánossy (1986); Wiegank (1983).

Koneprusy (= Zlaty Kon)
Location: Czech Republic
Date: *Mimomys savini* (= 0.45 - 0.8Ma [see Table 1.1])
P. gombaszoegensis remains: 1 mandible and partial skeleton (unpublished)
Material stored: Department of Palaeontology, Charles University, Prague, Czech Republic.
Published: Jánossy (1969); Wolsan (1993); Professor Fejfar (pers comm).

Kövesvárad
Location: Hungary
Date: 0.8 - 0.7 Ma
P. gombaszoegensis remains: studied - 2 proximal metacarpals and a reassigned M^1 (canid). Not seen - Humerus frag; carpal; 2 phalanges; 1 femur (destroyed 1956).
Material stored: Palaeontological Department, National Museum of Natural History, Budapest, Hungary
Published: Jánossy (1963); Kordos (1994).

Lakhuti 2
Location: Tadjikistan
Date: 0.9 – 0.8Ma (between the Jaramillo event and the Brunhes/Matuyama boundary).
P. gombaszoegensis remains: 1 mandible
Environment: open
Material stored: Moscow
Published: Sotnikova & Vislobokova (1990)

Laetoli
Location: Serengeti, Africa
Date: Pliocene – 3.6Ma
P. gombaszoegensis remains: none – originally 8 teeth, a radius and a calcaneum.
Published: Barry (1987)

L'Escale
Location: Southern France
Date: 0.8 -0.7 Ma
P. gombaszoegensis remains: many - cranial and postcranial (all juvenile)
Material stored: Maison Méditerranéenne des Sciences de l'Homme (MMSH), Aix-en-Provence, France
Published: Bonifay (1971); Hemmer (1972a).

Meiningen
Location: Germany
Date: 1.05 – 0.95Ma
P. gombaszoegensis remains: yes
Published: Wolsan (1993); Wiegank (1983)

Mosbach 2
Location: Germany
Date: 0.5 – 0.3 (Wolsan, 1993); 0.60 - 0.55 (Maul *et al*, 1998)
P. gombaszoegensis remains: 1 mandible; Mt2 (possibly leopard); 1 calcaneum (possibly *Acinonyx*).
Environment: temperate & steppe fauna
Material stored: Naturhistorisches Museum, Mainz, Germany
Published: Hemmer & Schütt (1969), Maul *et al* (1998).

Naliacha
Location: Mongolia
P. gombaszoegensis remains: 1 mandible fragment
Material stored: Moscow
Published: unpublished

Olivola
Location: Valdarno, Italy
Date: 1.8 – 1.6Ma
P. gombaszoegensis remains: many - cranial and postcranial
Material stored: Museo di Storia Naturale, Department of Geology and Palaeontology, Florence, Italy
Published: del Campana (1915, 1916); Ficcarelli & Torre (1968).

Oubeidiyeh (= 'Ubeidiya)
Location: Israel
Date: 1.4 - 0.8 Ma
P. gombaszoegensis remains: 1 phalange, 1 McIV
Published: Ballesio (1986), Aguirre *et al* (1997).

Palan-Tyukan
Location: Eastern Transcaucasia, Azerbaijan
Date: Late Villafranchian (Olivola, Tegelen correlation) Pre 1.6 Ma.
P. gombaszoegensis remains: 1 calcaneum
Environment: Marine coastal lagoon
Published: Sotnikova & Sablin (n.d.)

Pantalla
Location: Perugia, Italy
Date: Late Villafranchian = 1.0 - 1.7Ma (see Table 1.1)
P. gombaszoegensis remains: Two skulls and a left mandible
Material stored: Perugia University
Published: Gentili *et al* (1997)

Petralona
Location: Greece
Date: Middle Pleistocene = 0.5 – 0.75
P. gombaszoegensis remains: 2 distal humerii; Mt3; Mt4; Mc2; $2P^3$; $1P^4$ and calcaneum.
Environment: Warm, Savannah/forest
Material stored: currently unknown
Published: Kurtén & Poulianos (1977, 1981); Darlas (1995); Tsoukala (1992)

Pietrafitta
Location: Perugia, Italy
Date: 1.6 – 1.4 Ma (Farneta Faunal Unit)
P. gombaszoegensis remains: 2 metapodial fragments (unpublished) (P. Argenti, pers comm)
Environment: Locally open areas, colder climate
Material stored: On site museum at Pietrafitta lignite mine
Published: Gentili *et al* (1996)

Rome (Monte Sacro)
Location: Rome, Italy
Date: 0.42 – 0.16Ma
P. gombaszoegensis remains: none, cranium reassigned as *P. pardus*.
Material stored: Palaeontological Museum, Department of Earth Sciences, University of Rome "La Sapienza", Italy
Published: Portis (1907); Hemmer & Schütt (1969); Kotsakis & Palombo (1979).

Santa Maria nr Il Tasso
Location: Tuscany, Italy
Date: ~ 1.7Ma (approximately the same as Olivola)
P. gombaszoegensis remains: 1 mandible
Material stored: Museo di Storia Naturale, Department of Geology and Palaeontology, Florence, Italy
Published: Schaub (1949); Ficcarelli & Torre (1968)

Slivia
Location: Italy
Date: ~0.9Ma (Sardella *et al*, 1998)
P. gombaszoegensis remains: isolated C_i
Environment: temperate and damp
Published: Ambrosetti *et al* (1979); Palombo & Mussi (2001)

Slivnitsa
Location: Slivnitsa, Bulgaria
Date: 1.9 Ma (Seneze Faunal Unit)
P. gombaszoegensis remains: 1 distal femur; 1 distal tibia; 1 phalange.
Environment: cooling
Material stored: National Museum of Natural History, Sofia, Bulgaria
Published: Spassov (1998).

Somssich Hill, Locality 2
Location: Southern Hungary
Date: 1.1 – 0.8
P. gombaszoegensis remains: a partial $P_?$
Material stored: Palaeontological Department, National Museum of Natural History, Budapest, Hungary
Published: Jánossy (1986); Kordos (1994).

Stránská Scála 1
Location: Czech Republic
Date: 0.6 – 0.5 Ma (upper Cromerian)
P. gombaszoegensis remains: possibly.
Material stored: ? cast of specimen 1938 studied at Vienna University, Austria.
Published: Thenius (1972); Musil (1968); Wolsan (1993)

Süssenborn
Location: Thuringia, Germany
Date: 0.5 – 0.4 Ma
P. gombaszoegensis remains: 1 distal humerus
Environment: temperate to cold
Material stored: Forschungsinstitut und Museum Senckenberg, Weimar, Germany.
Published: Kurtén (1969); Wolsan (1993).

Swanscombe
Location: UK
Date: OIS 11 = ~0.3Ma (Lowe & Walker, 1997)
P. gombaszoegensis remains: 1 distal humerus
Material stored: British Museum (Natural History), London, UK.
Published: Turner & O'Regan (n.d.)

Tegelen
Location: Russel-Tiglia-Egypte Quarry, Tegelen, Netherlands
Date: 2.2 – 1.7 Ma
P. gombaszoegensis remains: studied - $3M_1$; $2P_4$; $1P_3$; 2 dc^s; 1 maxilla with P^4; 1 mandible. Missing specimens – $2M_1$; $3P_4$; $3P_3$; $1C_i$; $1P^3$.
Material stored: Naturalis Museum, Leiden (unpublished); Natuurhistorisch Museum, Maastricht; Missing specimens: Zoology Museum, Amsterdam and Biology Institute, Groningen.
Published: von Koenigswald (1960); van Kolfschoten (2001)

Tongruben von Strmica

Location: Former Yugoslavia
Date: Lower Pleistocene = 1.75 – 0.8Ma (see Table 1.1)
P. gombaszoegensis remains: yes
Published: Malez (1986)

Untermassfeld

Location: Thuringia, Germany
Date: 1.0 Ma (Early Jaramillo)
P. gombaszoegensis remains: cranial and postcranial
Environment: warm and humid
Material stored: Forschungsinstitut und Museum Senckenberg, Weimar, Germany.
Published: Kahlke (1995; 2000).

Uppony 1

Location: Hungary
Date: 8 different layers ranging from 0.35 – 0.1
P. gombaszoegensis remains: possibly lion – mandible with P_3 & P_4; maxilla wth C^s & P^2; C_i; P^3; M^1; Mt3; Mt4; Mt5; 2 x Mc2; Mc5; 1 calcaneum; 2 femur heads; 2 radii; 1 scapula frag.
Environment: cooling to glacial
Material stored: Palaeontological Department, National Museum of Natural History, Budapest, Hungary
Published: Kordos (1994); Wolsan (1993)

Vallonnet

Location: South-East France
Date: 1.0 (Jaramillo event); ISO 30.
P. gombaszoegensis remains: yes
Environment: cold and dry
Published: de Lumley (1988); Moullé *et al* (2000); Anon (2001b).

Venta Micena

Location: Guadix-Baza Basin, Spain
Date: 1.4 – 1.0Ma (Biostratigraphic)
P. gombaszoegensis remains: none – 2 mandible fragments reassigned as *Pachycrocuta brevirostris* (Navarro, 1992).
Environment: Dried freshwater lake bed
Material stored: Museo Paleontológico de Orce, Granada, Spain
Published: Pons-Moyà (1987); Navarro (1992); Arribas & Palmqvist (1998)

Vértesszölös II

Location: Nr. Budapest, Hungary
Date: 0.35 Ma (biostratigraphic)
P. gombaszoegensis remains: P^4; P^3; $2C_i$; 2C. 1 mandible (reassigned *P. leo*)
Environment: cool
Material stored: Palaeontological Department, National Museum of Natural History, Budapest, Hungary
Published: Kretzoi & Vertes (1965); Kordos (1994)

Villany 3 (= Villany-Kalkberg-Nord)
Location: Hungary
Date: 2.0 – 1.5Ma
P. gombaszoegensis remains: 1 specimen, currently missing
Material stored: Hungarian Geological Institute, Budapest
Published: Jánossy (1986)

Volos
Location: Greece
Date: MNQ 21 = 1.4Ma (Sen & Leduc, 1996)
P. gombaszoegensis remains: yes
Published: Koufos (2001); van der Meulen & van Kolfschoten (1986).

Westbury-sub-Mendip
Location: Somerset, England.
Date: 0.6 – 0.4 Ma (ISO 11, 13 or 15)
P. gombaszoegensis remains: Many - cranial and postcranial
Environment: Warm.
Material stored: Natural History Museum, London
Published: Bishop (1982), Turner (2000)

West Runton
Location: UK
Date: late Cromerien = Voigstedt (Stuart, 1995) = 0.5 – 0.6 (Maul *et al*, 1998)
P. gombaszoegensis remains: 1 Mt2
Material stored: British Museum (Natural History), London, UK.
Published: Turner (2000); Turner & O'Regan (n.d.).

Yarimburgaz
Location: Northwestern Turkey
Date: Probably late Middle Pleistocene
P. gombaszoegensis remains: none - reassigned to *P.leo* or *P. pardus*
Published: Darlas (1995), Stiner *et al* (1996)

Zasuhino
Location: Western Transbaikalia
Date: Early Cromerian
P. gombaszoegensis remains: 1 mandible
Material stored: Moscow
Published: Vangengejm *et al* (1990)

APPENDIX 3 – COMPARATIVE SPECIMENS

† indicates measurements taken by A. Turner

Cheetah (*Acinonyx jubatus*)

Crania:

† **Transvaal Museum**, Pretoria, South Africa: TM 13275; TM No 55; TM 870; AZ 162; AZ 159; AZ 379; AZ T3; AZ 339; TM 18758; AZ T13; TM 25602; TM 16525; TM 16526; TM 16523; TM 747; TM 12159; TM 16524; TM 16522.
† **South African Museum**, Cape Town, South Africa: ZM 37408; ZM 39034; ZM 39079; ZM 39047; ZM 36703; ZM 36719; ZM 36704; ZM 38746; ZM 39046; ZM 39424; ZM 37658; ZM 39080; ZM 38747; ZM 39048; ZM 39035; ZM 38781; ZM 39049; ZM 39477; ZM 39081; ZM 39375; ZM 36684; ZM 37411; ZM 36702; ZM 36849; ZM 33374; ZM 39034; ZM 36701; ZM 38733; ZM 38630; Uncatalogued.
† **University of the Witwatersrand**, Johannesburg, South Africa: BPI/C 201; 58; 59.
Liverpool Museum, Merseyside, UK:1963.173.104; 1982.398.104; 1963.173.105.
National Museum of Scotland, Edinburgh, UK: 16/95; 1990.044.003.
Cambridge Zoology Museum, Cambridge, UK: K5442; K5443; K5444.

Postcranial specimens:
National Museum of Scotland, Edinburgh, UK: 16/95; 1990.044.003.
† **Transvaal Museum**, Pretoria, South Africa: TM Ia 1092; AZ T3; AZ T13.

Lion (*Panthera leo*)

Crania:

† **Transvaal Museum**, Pretoria, South Africa: Bailey 53; TM 24004; TM 24119; 5604; TM 978; TM 1023; TM 927; TM 964; TM 869; TM 1024; TM 3186; TM 4402; TM 926; TM 3187; TM 4403; TM 1026; TM 385; TM 765; TM 868; TM 3187; AZ 771; Bailey Col. No.350; TM 973; TM 12428; CR 9; TM 16736.
† **South African Museum**, Cape Town, South Africa: ZM 36111; ZM 3983; ZM 35041; ZM 35113; ZM 35060; ZM 35527; ZM 36741; ZM 37770; ZM 38824; ZM 38844; ZM 38845; ZM 39870; ZM 14573; ZM 17671; ZM 33413; ZM 33428; ZM 35042; ZM 35114; ZM 35115; ZM 36873; ZM 39231; ZM 39241; ZM 39302; ZM 14893; ZM 33360; ZM 33368; ZM 33363; ZM 33376; ZM 33426; ZM 34266; ZM 33429; ZM 33427; ZM 35125; ZM 35126; ZM 35122; ZM 35127; ZM 36876; ZM 36875; ZM 36874; ZM 36900; ZM 38222.
† **University of the Witwatersrand**, Johannesburg, South Africa: BPI/C 187; BPI/C 184 BPI/C 185; BPI/C 186; BPI/C 183.
Liverpool Museum, Merseyside, UK: 10.1.67; 1963.173.107; 1929.73.1; 1963.173.108 1982.173.106; 1982.573; 1982.576; 1982.488; 1982.546.7; 46.6;1982.489;1989.123.30.
National Museum of Scotland, Edinburgh, UK: 1869/15/29; lion; 1945-60; 1995.005.
Cambridge Zoology Museum, Cambridge, UK: K5465; K5465.1; K5467; K5467.2; K5467.3; K5472; K5473; K5474; K5475; K5463.
National Museum of Hungary, Budapest: 60.186.1; 64.265.1.

Postcrania:
National Museum of Scotland, Edinburgh, UK: lion; 1995.005; 1945.6; 1869/15/2A.
National Museum of Hungary, Budapest: 64.265.1; 60.186.1.
Cambridge Zoology Museum, Cambridge, UK: K5463.

Jaguar (*Panthera onca*)

Crania:
British Museum (Natural History), London, UK: 1845.8.25.22; 1899.3.2.1; 87.236; 1935.3.6.2; 1935.3.6.1; 28.5.2.13q; 1874.4.8.2; 1936.5.26.3; 1926.12.4.29; 77.857; 76.671; 1995.64.
† **Institute of Biology**, Mexico: 39974; 39975; 39976; 39977; 39978; 39980; 39981; 39982; 39983; 39984; 39985; 39986; 39987; 39988; 39989; 39990; 39991; 39969; 39970; 39971; 39972; 39973; 39993; 5024; 24564; 20106; 26635; 9154; (214) 15984.
Smithsonian Institution, Washington DC, USA: A49393; A12296/010390; 155603.
† **Mexico Polytechnic**, Mexico City: 5147; 5148; 5149; 11194.
† **INAH,** Mexico: 5613; 643; 642; 641; 4945.
National Museum of Scotland, Edinburgh, UK: *P.onca* Edinburgh Zoo; 1906-172; PH07.96.
Cambridge Zoology Museum, Cambridge, UK: K5781; K5782; K5783; K5784.
Liverpool Museum, Merseyside, UK: D.Ost.2.
National Museum of Hungary, Budapest: 60.302.1; 57.127.1; 77.302.1.
Natural History Museum, Vienna, Austria: 6050.
Museum für Naturkunde, Humboldt University, Berlin, Germany; MaMb30007.

Postcrania:
British Museum (Natural History), London, UK: 117f. 1858.5.26.9.
National Museum of Scotland, Edinburgh, UK: PH07.96; *P. onca* Edinburgh Zoo.
Liverpool Museum, Merseyside, UK: D.Ost.2.
National Museum of Hungary, Budapest: 77.302.1; 57.127.1; 60.302.1.
Smithsonian Institution, Washington DC, USA: A49393; A12296/010390; 141897/A49762; 155603.

Leopard (*Panthera pardus*)

Crania:
† **Transvaal Museum**, Pretoria, South Africa: TM 981; TM 1005; TM 19199; TM 918; TM 12162; TM 13277; TM AZ/420; TM AZ/501; TM 19198; TM 12161; TM 13276; TM 982; TM 928; TM 12017; TM 36725; TM 746; TM 20420; TM 13548; TM 92; TM 11746; TM AZ/ 431.
† **South African Museum**, Cape Town, South Africa: ZM 39868; ZM 6856; ZM 7211; ZM 35821; ZM 36051; ZM 36949; ZM 37390; ZM 39051; ZM 38608; ZM 38609; ZM 39123; ZM 39812; ZM 39695; ZM 39694; ZM 38167; ZM 38610; ZM 33357; ZM 33358; ZM 14580; ZM 33345; ZM 33346; ZM 14579; ZM 33433; ZM 33430; ZM 35128; ZM 36305; ZM 36324; ZM 38752; ZM 37730; ZM 37427; ZM 37751; ZM 38606; ZM 38607; ZM 38784.
† **University of the Witwatersrand**, Johannesburg, South Africa: BPI/C 190; BPI/C 189; BPI/C 188; BPI/C 259; BPI/C 191; BPI/C 258; BPI/C 193; BPI/C 192; BPI/C 194; BPI/C 253; BPI/C 200; BPIc 252.
Liverpool Museum, Merseyside, UK: 31.12.06.3; 1938.55.8g; 1963.173.113; 1963.173.114; 1963.173.118; 1963.173.117; 1963.173.116; 1963.173.115; 20.12.66.19; 1982.937; 18.5.97.4.
Cambridge Zoology Museum, Cambridge, UK: K5844; K5848; K5849; K5850; K5855; K5848.2; K5854; K5841; K5858; K5851.
National Museum of Scotland, Edinburgh, UK: 23.4.95; PH09.96; PH1/98 or Z1998.45; 23.95; PH31.96; 7; 1950.101.41.

National Museum of Hungary, Budapest: 60.187.1.
Natural History Museum, Vienna, Austria: NMW 2843; NMW 4042; NMW 8350.
British Museum (Natural History), London, UK: 1952.10.20.9; 1952.10.20.10; 1927.2.9.7; 36.2.28.24; 1952.10.20.11; 23.12.10.1; 44.67.
† **Mammal Research Institute**, Pretoria, South Africa: uncatalogued; uncatalogued.
† **Sheffield University**, UK: A 1900.1.
MNCN, Madrid, Spain: 3984.

Postcrania:
National Museum of Scotland, Edinburgh, UK: PH1/98 or Z1998.45; 23.95; PH31.96; PH09.96; 23.04.1995
† **Transvaal Museum**, Pretoria, South Africa: AZ 574.
† **University of the Witwatersrand**, Johannesburg, South Africa: BPIc 258.
Liverpool Museum, Merseyside, UK: 18.5.97.4.
National Museum of Hungary, Budapest: 68.83.1; 68.82.1; 60.187.1.
Natural History Museum, Vienna, Austria: 4042; NWW2843; 8350.

Tiger (*Panthera tigris*)

Crania:
National Museum of Scotland, Edinburgh, UK: PH3.99; PH4.99.
Liverpool Museum, Merseyside, UK: 1963.173.110; 1963.173.112; 1963.173.111; 1938.55.7a; 1982.487; 1982.574; TN 4623; TN 4622 (A52); 1938.55.7c; 1938.55.7d; 1938.55.7e; 59.82; 1938.55.7b; 1938.55.7g; 1982.587.
Cambridge Zoology Museum, Cambridge, UK: K5626.4; K5623.2; K5623; K5626.10; K5627; K5622; K5626.2; K5626.5; K5626.7; K5626.8; K5626.9; K5628; K5638; K5625; K5621.
† **South African Museum**, Cape Town, South Africa: ZM 38777; ZM 33367; ZM 33362; ZM 33361.
National Museum of Hungary, Budapest: 77.8.1.

Postcrania:
National Museum of Scotland, Edinburgh, UK: PH3.99; PH4.99.
Cambridge Zoology Museum, Cambridge, UK: K5627; K5621.
National Museum of Hungary, Budapest: 77.8.1.

Snow Leopard (*Panthera uncia*)

Crania:
National Museum of Scotland, Edinburgh, UK: 1995.235.002; RL34/97; PH33.96 PH54/96; 1993.009; 1995.302.003; 1997.5;1999.277; 2000.132.2; 2000.132.1; 1995.114.
Smithsonian Institution, Washington DC, USA: 252543; 337500; 176048; 241212; 321948; 84091.
† **British Museum (Natural History)**, London, UK: 1963.2.25.1

Postcrania:
National Museum of Scotland, Edinburgh, UK: 1995.235.002; RL34/97; PH33.96; PH54/96; 1995.302.003; 1997.5;1999.277; 1995.114.
Smithsonian Institution, Washington DC, USA: 176048; 241212; 321948.
† **British Museum (Natural History)**, London, UK: 1963.2.25.1.

APPENDIX 4 - LIST OF SITES USED IN THE BIOGEOGRAPHIC ANALYSIS

Early (1.9 – 1.41Ma) sites

Country	Site	source of species list
Azerbaijan	Palan-Tyukan	Sotnikova & Sablin (n.d.)
Azov penninsula,	Port Katon	Bajgusheva *et al* (2001)
Azov penninsula,	Semibalki	Bajgusheva *et al* (2001)
Bulgaria	Slivnitsa	Spassov (1998)
France	Chagny	Argant (1991)
France	Chilac	Turner (n.d); Boeuf (1990)
France	Coupet	Turner (n.d)
Georgia	Diliska	Vekua & Lordkipanidze (1998)
Georgia	Dmanisi	Gabunia *et al* (2000)
Germany	Schernfeld	Turner (n.d)
Greece	Gerakarou 1	Koufos (1992)
Greece	Halykes	Athanassiou (1993 - 1994)
Greece	Kastritsi	Koufos (2001)
Greece	Kiafias	Koufos (2001)
Greece	Livakos	Koufos (2001)
Greece	Makinia	Koufos (2001)
Greece	Pyrgos	Koufos (2001)
Greece	Vassiloudi	Koufos (2001)
Holland	Oosterschelde	van Kolfschoten (2001)
Hungary	Beremend 16/17	Jánossy (1996)
Hungary	Kislang	Jánossy (1986)
Hungary	Nagyharsanyhegy 2	Wolsan (1993)
Hungary	Osztramos 8	Wolsan (1993)
Hungary	Sutto	Jánossy (1986)
Hungary	Villany 3	Jánossy (1986)
Hungary	Villany 5	Wolsan (1993)
Italy	Casa Frata	Turner (n.d)
Italy	Collepardo	Turner (n.d)
Italy	Costa San Giacomo	Turner (n.d)
Italy	Fontana Acetosa	Turner (n.d)
Italy	Matassino	Turner (n.d)
Italy	Monte Riccio	Mazzini *et al* (2000)
Italy	Olivola	Turner (n.d)
Italy	Pietrafitta	Gentili *et al* (1996)
Italy	Tasso	Turner (n.d)
Macedonia	Kastoria-Becken	Steensma (1990)
Netherlands	Scheldt	Mol & de Vos (1996)
Netherlands	Tegelen	Richter & Thomassen (1996)
Poland	Kamyk	Wolsan (1993)
Poland	Zabia Cave	Wolsan (1993)
Romania	Betfia 13	Terzea (1996)
Romania	Fintina Alortitei	Radulesco & Samson (1990)
Romania	La Pietris	Radulesco & Samson (1990)
Romania	La Seci	Radulesco & Samson (1990)
Romania	Tetoiu (Bugiulesti)	Ghenea (1997)
Romania	Valea Graunceanului	Radulesco & Samson (1990)
Slovakia	Strekov & Nova	Holec (1996)

Country	Site	source of species list
Spain	Casablanca 1	Soto & Morales (1985); Turner (n.d.)
Spain	Cueva de las Yedras	Aguirre & Morales (1990)
Spain	Cueva Victoria	Navarro (1992)
UK	Easton Bavents	Turner (n.d).
UK	Red Crag	Turner (n.d)
Yugoslavia	Sandalja 1	Malez (1986) Turner (n.d.)

Middle (1.40 – 0.8Ma)

Country	Site	source of species list
Austria	Deutsch Altenburg 2	Wolsan 1993
Austria	Deutsch Altenburg 4	Wolsan, 1993
Croatia	Tongruben von Strmica	Malez (1986)
Czech	Holstejn 1	Kahlke (1975); Wolsan (1993)
France	Ceyssaguet	Turner (n.d)
France	Chaintre	Argant (1991)
France	Courterolles	Argant (1991)
France	Soleihac	Bonifay (1996)
France	Vallonnet	Kahlke (1975); Bonifay (1996)
Georgia	Akhalkalaki	Vekua & Lordkipanidze (1998)
Germany	Erpfinger	Lehmann (1953; 1957)
Germany	Jockgrim	Wolsan (1993); Kahlke (1975)
Germany	Meiningen	Wolsan (1993)
Germany	Mosbach 1	Wolsan (1993)
Germany	Untermassfeld	Kahlke (2000)
Greece	Apollonia	Koufos (2001)
Greece	Megalopolis	Koufos (2001)
Greece	Volos	Koufos (2001)
Hungary	Osztramos 2	Wolsan (1993); Jánossy (1986)
Hungary	Somssich Hill 2	Wolsan (1993); Kordos (1994)
Israel	Ubediyah	Ballesio (1986) Aguirre *et al* (1997)
Italy	Colle S. Andrea	Ambrosetti *et al* (1995b)
Italy	Monte Tendavi	Palombo & Mussi (2001)
Italy	Pantalla	Gentili *et al* (1997)
Italy	Piro Nord	Turner (n.d)
Italy	Slivia	Ambrosetti (1979)
Italy	Villa S. Faustino	Ambrosetti *et al* (1995b)
Romania	Betfia 5	Terzea (1996)
Romania	Betfia 7	Terzea (1996)
Romania	Betfia 7	Terzea (1996)
Saudi Arabia	An Nafud	Thomas *et al* (1998)
Spain	Cullar Baza 1	Alcala & Morales (1989)
Spain	Cullar Baza 2	Alberdi *et al* (1998)
Spain	Fuente Nueva 3	Navarro *et al* (1998)
Spain	Incarcal	Turner (n.d)
Spain	Ponton de la Oliva	Turner (n.d)
Spain	Trinchera Dolina	García & Arsuaga (1999)
Spain	Venta Micena	Arribas & Palmqvist (1998)
Tajikistan	Lakhuti 2	Sotnikova & Vislobokova (1990)
Transbaikalia	Zasuhino	Vangengejm *et al* (1990)
Yugoslavia	Zadar-Archipels	Malez (1986)

Late (0.8-0.5Ma)

Country	Site	source of species list
Belgium	Belle Roche	Cordy *et al* (1992); Tuffreau & Antoine (1995)
Black Sea, USSR	Taman Peninsula	Kahlke (1975)
Czech	Koneprusy	Kahlke (1975); Wolsan (1993)
Czech	Stranska Skala 1	Kahlke (1975); Wolsan (1993)
Czech	Zirany 1 - 3	Wolsan (1993)
France	Abbeville	Bonifay (1996)
France	Aldene	Bonifay (1996)
France	Artenac	Delagnes *et al* (1999)
France	Carpentier, Abbeville	Tuffreau & Antoine (1995)
France	Grotte 14	Guadelli (2001)
France	L'Escale	Kahlke (1975)
France	La Nauterie	Bonifay (1996)
France	Rosieres	Kahlke (1975)
France	Sainzelles	Kahlke (1975); Turner (n.d)
France	Vergranne	Bonifay (1996)
Georgia	Cona	Ljubin & Bosinski (1995)
Germany	Achenheim	Bosinski (1995)
Germany	Grotte Sackdillinger	Wolsan (1993)
Germany	Mauer	von Koenigswald (1995)
Germany	Miesenheim 1	van Kolfschoten & Turner (1995)
Germany	Steinheim 2	Kahlke (1975); Turner (n.d)
Germany	Steinheim 3	Kahlke (1975); Turner (n.d)
Germany	Voigstedt	Wolsan (1993)
Greece	Petralona	Darlas (1995)
Holland	Maasvlakte 1	van Kolfschoten (2001)
Hungary	Kovesvarad	Jánossy (1963); Wolsan (1993)
Hungary	Nagyharsanyhegy 4	Wolsan (1993)
Hungary	Varhegy	Kahlke (1975)
Hungary	Villany (Csarnota 1)	Kahlke (1975)
Italy	Cava Pirro	Ficcarelli *et al* (1996)
Italy	Cesi	Ficcarelli *et al* (1997)
Italy	Colle Curti	Ficcarelli *et al* (1996)
Italy	G.R.A. Roma	Palombo & Mussi (2001)
Italy	Isernia la Pineta	Mussi (1995)
Italy	Notachino	Palombo & Mussi (2001)
Italy	Selvella	Ficcarelli *et al* (1996)
Italy	Soave	Kahlke (1975)
Italy	Valdemino	Palombo & Mussi (2001)
Italy	Visogliano	Palombo & Mussi (2001)
Moldavia	Tiraspol	Kahlke (1975); Turner (n.d)
Montenegro	Crvena Stijena	Malez (1986)
Poland	Zalesiaki 1A	Wolsan (1993)
Romania	Betfia 7	Terzea (1996)
Romania	Draghici	Kahlke (1975)
Slovakia	Gombasek 1	Wolsan (1993); Kahlke (1975)
Spain	Huescar 1	Alcala & Morales (1989); Turner (n.d)
Spain	Mestas de Con	Kahlke (1975); Wiegank (1983)
Spain	Torralba	Turner (n.d)

Country	Site	source of species list
Spain	Trinchera Dolina	García & Arsuaga (1999)
Turkey	Yarimburgaz	Darlas (1995)
UK	Boxgrove	Anon (1997)
UK	Little Oakley	Stuart (1996)
UK	West Runton	Turner & O'Regan (n.d)
UK	Westbury-sub-Mendip	Turner (2000)
USSR (Sea of	Nogaisk	Kahlke (1975)
USSR (Volga	Khazar	Kahlke (1975)
Yugoslavia	Split	Kahlke (1975)
Yugoslavia	Vindija Hohle (Donja	Malez (1986)

Very late (0.5 – 0.3Ma)

Country	Site	source of species list
Albania	Gajtan	Darlas (1995)
Austria	Hundsheim	Wolsan (1993)
France	Arago (Tautavel)	Turner (n.d)
France	Chateau	Argant (1991)
France	Jaurens	Turner (n.d)
France	L'Igue des Rameaux	Bonifay (1996)
France	Lunel-Viel	Kahlke (1975); Bonifay (1996)
Germany	Bilzingsleben	Mania (1995)
Germany	Erpfingen 3	Wolsan (1993)
Germany	Heppenloch	Turner (n.d)
Germany	Karlich	van Kolfschoten & Turner (1995)
Germany	Mauer 5	Wolsan (1993)
Germany	Mosbach 2	Wolsan (1993)
Germany	Sussenborn	Kahlke (1975); Wolsan (1993)
Germany	Wurzburg-Schalksburg	Wolsan (1993); Turner (n.d)
Hungary	Tarko	Wolsan (1993)
Hungary	Uppony	Wolsan (1993)
Hungary	Uppony 1	Wolsan (1993)
Hungary	Vertesszollos 1 & 2	Kordos (Date) (1994), Wolsan (fauna) (1993)
Hungary	Villany 8	Wolsan (1993)
Israel	Bears Cave	Tchernov & Tsoukala (1997)
Italy	Fontano Ranuccio	Mussi (1995)
Italy	Rome (Monte Sacro)	Portis (1907); Kotsakis & Palombo (1979)
Italy	Venoso Loreto	Palombo & Mussi (2001)
Poland	Kozi Grzbiet	Wolsan (1993)
Portugal	Mealhada	Raposo & Santonja (1995)
Spain	Sima de los Huesos	García *et al* (1997)
Spain	Trinchera-Galeria	García & Arsuaga (1998)
UK	Swanscombe	Stuart (1982)

APPENDIX 5 - PUBLISHED WORK

Morphological effects of captivity in big cat skulls

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Abstract

Captive animals are a vital resource for analyses of wild animal morphology as they are often the only provenanced specimens with postcrania available for study in museum collections. Despite this many researchers choose not to use captive animal remains in their studies as they are considered to be pathological or non-representative of the species as a whole. This idea can be traced back to a paper by Hollister (1917) on East African lions in which he found that cranial proportions in captive lions were different to their wild counterparts. However, these results have not, to my knowledge, been tested using modern statistical techniques. This paper uses additional morphometric data of lion (*Panthera leo*) and leopard (*Panthera pardus*) skulls to see if differences can be found between wild and captive animals. Changes are observed in both species, in the same areas and it is concluded that captivity may induce cranial changes in the large *Panthera*. Although present, these changes do not affect the overall value of captive specimens to morphometric studies, they simply illustrate the need for caution when using them and a need for more studies. These can only be carried out if more materials are made available through museum collections.

Introduction

Animals in captivity may be externally similar to their wild counterparts, but are they the same on the inside?

Pocock as far back as 1916 recognised that captivity could alter morphology, in this case the crania of snow leopards (*Panthera uncia*) "The animals themselves lived only a few months in captivity. Hence the features the skulls present may be regarded without hesitation as normal" (Pocock, 1916:306). Shortly after this Hollister (1917) published his paper "*Some effects of environment and habit on captive lions*" which has since become a standard reference for the dismissal of captive felines from morphological and morphometric studies (e.g. Miththapala, 1992). However, I feel that this approach is short sighted. The bones of exotic captive animals are often the only ones available to people studying these species in countries where the animals are not indigenous. In addition, when so many species are in decline it is not practicable nor desirable to obtain modern specimens from the wild. Therefore zoo animals represent the only readily available and provenanced source of materials for the osteologist who works on endangered species. Rather than dismissing these specimens out of hand as being unrepresentative of the wild morphology, I believe it is better to compare the wild and captive specimens we have at our disposal in museum collections around the world and quantify any changes that are found to have occurred. In this way, those anatomical areas that are affected by captivity can be identified. If changes are not present, or are found in a minority of areas, then these can be noted and caution can be exercised when using data from these sites, but these will not negate the information that can be gained from the rest of the animal.

Captivity is known to affect the behaviour of cats and attempts are being made to overcome this (e.g. Williams *et al*, 1996). However, it can also affect the osteology of the animals in two ways. The first is the increased incidence of disease – certain types of arthritis have only been found in captive felids, suggesting a higher incidence of these diseases in captive animals than in wild ones (Rothschild *et al*, 1998). The second type of change is more subtle; for example Duckler (1998) reported a non-metric change in captive lion (*Panthera leo*) and tiger (*Panthera tigris*) skulls, which may be related to overuse of the head and neck muscles in excessive grooming behaviours. Schaller (1972) mentions that a wild caught lion cub raised in captivity was much larger than cubs of the same age which had remained in the wild. He attributed this to better nutrition in captivity, without periods of starvation which the wild lions had endured. Smuts *et al* (1978) found that the skulls of captive lion cubs were larger than wild cubs of similar ages and they also suggested that this may have been due to better nutrition.

Methods

The measurements in this study are described in Table 1 and illustrated in Figure 1. Four measurements are used, three from the cranium and one from the mandible. Two separate but directly comparable datasets have been utilised. The first are male lion measurements taken from Hollister (1917). These dimensions were originally given in millimetres so no conversions were necessary. The second dataset is of lion and leopard (*Panthera pardus*) skull measurements collected by Dr Alan Turner and myself. All measurements were recorded to the nearest 0.1mm using vernier scale callipers, with the exception of condylobasal length (BL) which was measured to the nearest 1mm with a steel tape.

Measurement	Abbreviation	Description
Condylobasal Length	BL	From the anterior of the first incisor to the anterior of the foramen magnum
Zygomatic Breadth	ZB	Greatest width across the zygomatic arches
Interorbital Breadth	IO	Least width between the orbits
Canine to Condyle length	C-Cd	Length of the mandible from the anterior of the lower canine to the posterior of the mandibular condyle

Table 1. Skull measurements used in this study. Illustrated in Figure 1.

Cats are sexually dimorphic so the data were split into male and female for each species, before being divided by provenance (zoo vs. wild). Not all datasets were normally distributed, so they were all tested with the Mann-Whitney U test to make the results comparable.

Results

The original study by Hollister (1917) focussed on captive and wild lions from East Africa. The captive animals were found to have larger cranial dimensions, with the exception of condylobasal length which was smaller. This study was carried out before tests of statistical significance were commonly used. Only the sample of male lions was large enough to be tested with the Mann-Whitney U test and the results of this are given in Table 2.

Measurement	Wild n	Zoo n	Wild median	Zoo median	α
BL	5	5	324.0	309.0	0.2963
ZB	6	5	233.5	261.0	0.0137*
IO	6	5	71.0	75.0	0.2633
C-Cd	6	5	251.0	248.0	0.5219

Table 2. Results of Mann-Whitney U test for captive and wild ♂ East African lions (Data from Hollister, 1917). * = $P<0.05$.

These results show that zygomatic breadth (ZB) is the only measurement that shows a significant difference (P=<0.05) between wild and captive male lions. Reference to the medians (Table 2) shows that the zygomatic breadth is greater in captive cats.

The same analysis was then performed on the modern dataset of male and female lions and leopards. The results of this are given in Table 3.

Measurement	Species	Sex	Wild n	Zoo n	Wild median	Zoo median	α
BL	*P. pardus*	♂	19	6	181.0	180.0	1.0000
		♀	13	5	157.0	171.0	0.1519
	P. leo	♂	11	9	295.0	311.0	0.1022
		♀	11	8	254.0	269.0	0.2643
ZB	*P. pardus*	♂	19	5	135.0	137.0	0.6695
		♀	13	4	119.0	137.5	0.0312*
	P. leo	♂	11	8	223.0	249.5	0.0286*
		♀	11	9	198.0	210	0.0365*
IO	*P. pardus*	♂	19	6	38.4	38.0	0.9493
		♀	13	5	33.2	35.7	0.3243
	P. leo	♂	11	8	66.5	69.3	0.5357
		♀	11	9	61.7	59.7	0.5949
C-Cd	*P. pardus*	♂	19	6	136.0	136.5	1.0000
		♀	13	5	118.0	132.0	0.0542
	P. leo	♂	10	9	234.0	248.0	0.1777
		♀	11	8	201.0	207.5	0.4328

Table 3. Mann-Whitney U Test results for differences between modern captive and wild lions and leopards. * = $P<0.05$

Again, this shows that for the majority of cases there are no significant differences between the two groups. However both male and female lions and female leopards all show a significant (P=0.05) difference between wild and captive zygomatic breadths. Once again, reference to the medians shows that the captive animals are larger, supporting the results from Hollister's data. The fact that two different datasets and two separate species show the same changes indicates that this is a real difference between wild and captive animals.

Conclusion

The results of this study are important for two reasons:

1. The majority of dimensions show no significant differences between the two groups, indicating that, for the most part, captive cat data can be used in morphometric analyses.
2. The increase in zygomatic breadth in captive animals of both species suggests that captivity has some impact on this area of the skull. If nutritional causes, as suggested by Schaller (1972) and Smuts *et al* (1978), were responsible then a global increase in measurements would be expected rather than localised changes.

It appears that captivity does alter large cat cranial morphology in (at least) one specific area, but how and why this occurs merits further investigation. In addition, this study has shown that not all areas of the skull are affected by captivity, it is therefore wrong to dismiss captive animals from morphological studies entirely. However, caution should be exercised in deciding which dimensions are used and many more comparative studies are needed to establish what the changes are in each group of animals or species. Captive animal bones have as much to tell us as those from wild animals but we can only learn more if this valuable material is collected and stored in museum collections; they are a very valuable resource and it is important not to disregard or discard them.

Acknowledgements

I would like to thank Dr Alan Turner for allowing me to use unpublished measurements of modern lions and leopards. I would also like to thank the curators of museums in Europe and South Africa for allowing myself or Dr Turner to measure specimens in their care.

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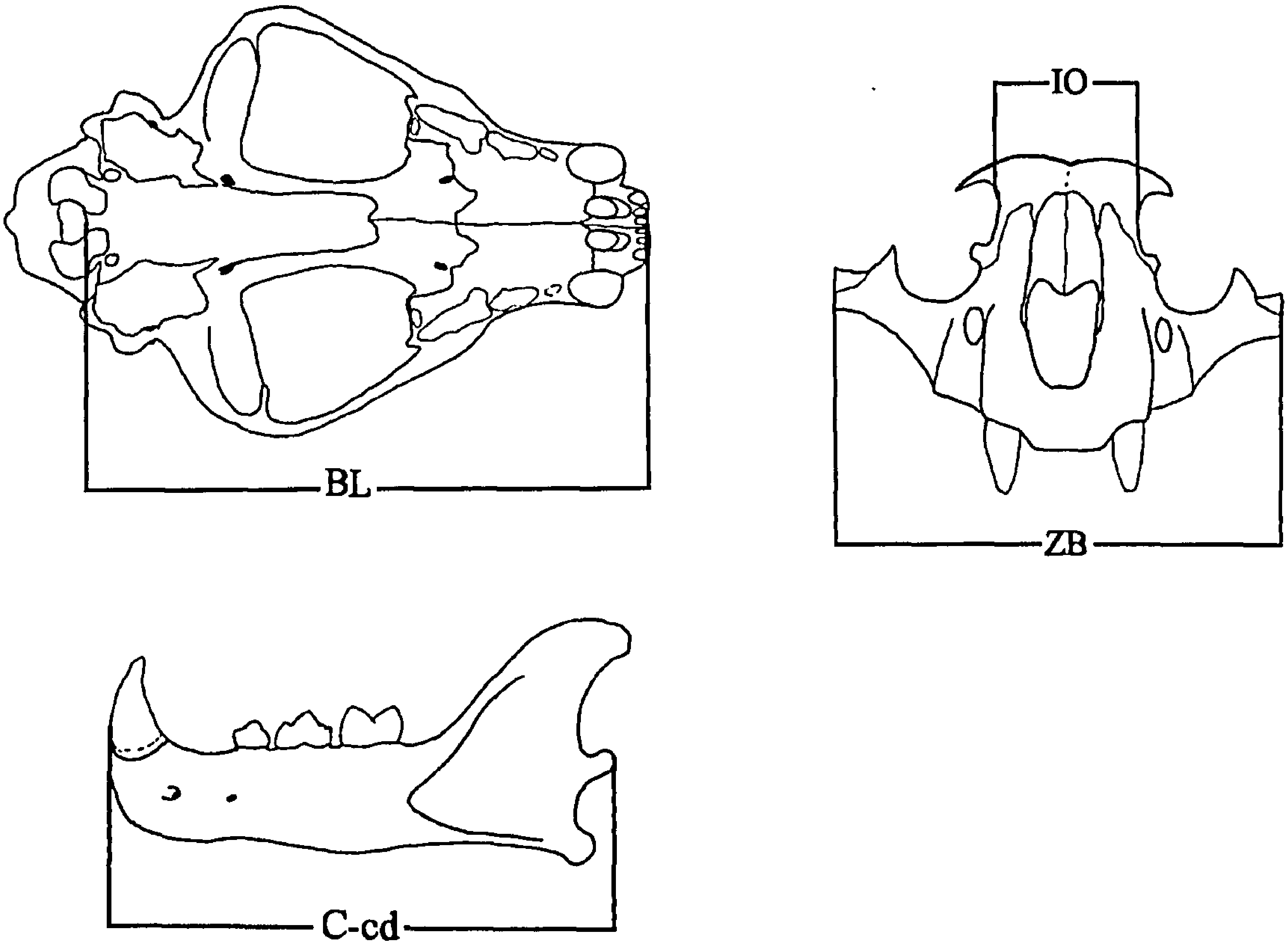

Figure 1. Skull measurements used in this study. Abbreviations listed in Table 1.

Defining Cheetahs, a multivariate analysis of skull shape in big cats

Hannah J. O'Regan.

Abstract

The skulls of six species of large cat were measured to compare the Cheetah (*Acinonyx jubatus*) to the five members of the genus *Panthera.* A total of 34 measurements were taken on 152 skulls of all species. These were analysed using Principal Components Analysis (PCA) to determine size and shape differences between the cats. Only 13 variables showed shape differences, all others scaled with size. The shape changes can be related to the Cheetahs adaptations to running and the overall proportions of cat crania. Cheetahs have wider braincases and narrower teeth than pantherines of a similar size. The differences in cranial variables can be explained by two factors: the inflation of the nasal bones and a wider postorbital process and postorbital constriction. The narrowness of the teeth is explained as a means of weight reduction.

Keywords: *Panthera*, *Acinonyx*, morphometrics, evolution, felid.

Introduction

The 'big cats' are a group of large felids comprising the five members of the genus *Panthera* (Lion, Leopard, Jaguar, Snow Leopard and Tiger) and the Cheetah (*Acinonyx jubatus*). Molecular phylogenies have been used to date the Cheetahs divergence from the main cat lineage (including *Panthera*), these estimates range from 16.2Ma (Bininda-Emonds, Gittleman & Purvis, 1999) to 8.2Ma (Mattern & McLennan, 2000). Whichever is right, it is apparent that the Cheetah has evolved separately for several million years.

In behaviour the Cheetah is an atypical felid. It commonly chases its prey at high speeds and kills by strangulation, although it is capable of stalking like a typical felid (Ewer, 1973). This study has used a multivariate analysis of morphometric data to define and attempt to explain the differences and similarities between *Acinonyx* and *Panthera*.

Methods

A total of 390 skulls of all six species were measured to the nearest 0.1millimetre (See Appendix 1 for a list of museum collections). Thirty four measurements were taken on each; these are summarised in Table 1. Only cats with complete datasets were included, reducing the total to 152 specimens; consisting of 34 Cheetahs, 26 Jaguars, 36 Leopards, 41 Lions, 10 Tigers and 5 Snow Leopards.

Principal Components Analysis (PCA) was used to highlight differences in shape between the species; this technique creates new axes which are orthogonal to each other and combines the variables to show the maximum variation between individuals. (Fowler, Cohen & Jarvis, 1998).

Results and discussion

The results of the PCA are shown in Table 2. Only two axes were produced with eigenvalues greater than 1 and these encompassed 93.6% of the variation. All variables showed a high positive loading on Axis 1 (PC1), suggesting that these are size-related differences. Only 13 of the original 34 variables had values greater than 0.1 on PC2, these are shown in Table 3. The majority of these were related to dentition or measurements of the braincase. Although the second axis contains only

3.6% of the total variance, it clearly separates *Acinonyx* from *Panthera* when these axes are plotted with species labels (Figure 1).

This analysis shows that the major difference between the pantherine cats is on PC1. The cats fall into two groups, with the Snow Leopard (*P. uncia*), Leopard (*P. pardus*) and Jaguar (*P. onca*), clustering to the left of the graph, as a smaller size grouping in comparison with the Lion (*P. leo*) and Tiger (*P. tigris*) group which form a cluster on the right. In 21 out of 34 measurements there were no obvious differences between any of the species, other than size.

The second axis is related to shape and it is here that the greatest difference between the smaller *Panthera* group and the Cheetah can be seen. The Cheetahs form a discrete cluster in the top left-hand corner and examination of the values in Table 3 shows that this is because the teeth of a Cheetah are narrower than would be predicted from its cranial breadth (PP and PC). These changes may be related to the Cheetahs running adaptations and felid biomechanics. The Cheetah is built for speed and any adaptation that would increase this would be of benefit. Its teeth have lost the crushing function that many of the other cats still retain (Ewer, 1973). This can be seen in the upper P4 which has a greatly reduced protocone (Martin, Gilbert & Adams, 1977), and is highlighted in Table 3 where the anterior breadth of the upper P4 (UP4Ba) has a high negative loading on PC2. Teeth are heavy and dense and a reduction in tooth size would reduce the weight of the skull. In comparison with similar sized Leopard teeth the mean upper P4 breadth (UP4B) in Cheetahs is 0.3mm smaller. The teeth of both cats are made of the same materials - dentine and enamel - therefore a decrease in overall size must result in a reduction in weight. In all cases the breadths of the teeth have altered more than the anteroposterior lengths, with the exception of both the upper and lower canines. The reduction in both the anteroposterior and mediolateral diameters of the canines is due to the fact that they are used to bite and hold struggling prey. A tooth that is circular in cross section is more resistant to damage than a laterally compressed one when the stresses are unpredictable (Biknevicius & Van Valkenburgh, 1996). Therefore to minimise the possibility of breakage in felid canines, a reduction in the mediolateral breadth requires a corresponding decrease in the anteroposterior length. In addition, *Acinonyx* has reduced canine height which may make a throat bite more effective than a neck bite, as the teeth are not large enough to penetrate the vertebral column (Eaton, 1974:143).

The braincase measurements are those variables that are least related to size on Axis 1. The interorbital breadth is greater than would be predicted from the tooth size. This is related to the inflation of the nasal bones in the Cheetah, which allows the cat to breathe rapidly whilst prey is being strangled (Kingdon, 1997). This adaptation may also prevent the brain overheating during and after a sprint (Taylor & Rowntree, 1973). A similar inflation is seen in the Snow Leopard, which cluster towards the Cheetah on PC2; in this case it is interpreted as an adaptation to cold climates (Hemmer, 1972). The Cheetah shows increased breadth of the postorbital process (POP) and postorbital constriction (POC) in comparison with the pantherines. The greater breadths of these dimensions are typical of small felids (Werdelin, 1983). It appears that despite increasing its size to that of a pantherine, the Cheetah has retained small cat cranial proportions. This retention of cranial shape, despite an increase in overall size, has also been observed in the Puma (*Puma concolor*) (Werdelin, 1983).

Conclusions

On the basis of this study, a Cheetah can be defined as a cat with narrow teeth, small canines and a wide braincase for its size. Despite being a highly specialised cat it still follows the generalised large felid form in 21 out of 34 variables analysed. The dental differences seen are adaptations to capturing and killing prey that have occurred in the genus *Acinonyx* alone. In addition the Cheetah has retained some cranial features of the smaller cats, despite increasing its overall size. In view of this, it is not so much that Cheetahs have altered that is surprising, but how apparently conservative the feline cranial shape has been over the last few million years.

Acknowledgements

Alan Turner kindly allowed me to use unpublished measurements taken on Cheetahs, Jaguars and Leopards. I thank Sally Reynolds and Dave Wilkinson for discussion of ideas and Alan Turner for reading and commenting on the manuscript. I am grateful to the many museum curators who have allowed myself or Dr Turner to measure specimens in their collections.

Appendix 1.

UK - British Museum (Natural History), London; Liverpool Museum, Liverpool; Manchester Museum, Manchester; University Museum of Zoology, Cambridge; National Museums of Scotland, Edinburgh. Europe – Hungarian Natural History Museum, Budapest; Natural History Museum, Vienna, Austria. South Africa - Mammal Research Institute, Pretoria; Transvaal Museum, Pretoria; Bernard Price Institute, Johannesburg; Zoology Museum, University of the Witwatersrand, Johannesburg; South African Museum, Cape Town. USA – Smithsonian Institute, Washington D.C. Mexico - Institute of Biology, Mexico City; Polytechnic, Mexico City; INAH, Mexico City.

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Measurement Abbreviation	Description of measurement
CSL *	Upper Canine, greatest anteroposterior length at Cemento-enamel junction
CSB *	Upper Canine, greatest mediolateral breadth at C-E junction
UP2B *	Upper 2nd Premolar, greatest mediolateral breadth
UP3L	Upper 3rd Premolar, greatest anteroposterior length
UP3B *	Upper 3rd Premolar, greatest posterior mediolateral breadth
UP4L	Upper 4th Premolar, greatest anteroposterior length
UP4Ba *	Upper 4th Premolar, anterior mediolateral breadth
UP4BBL	Upper 4th Premolar, mediolateral breadth at carnassial notch
UP4Lp	Upper 4th Premolar, anteroposterior length of the protocone
UP4Lm	Upper 4th Premolar, anteroposterior length of the metastyle
UM1B	Upper 1st molar, mediolateral breadth
BL	Basal length, from anterior of incisors to the foramen magnum
PL	Palate length, from buccal edge of incisors to the farthest edge of the palate
RB	Rostral breadth, greatest distance between buccal edges of the upper canines
MB	Muzzle breadth, greatest distance between posterior buccal edge of upper P4's
ZB	Zygomatic breadth, greatest width of the zygomatic arches
IO *	Least distance between the orbits
PP *	Greatest breadth of the postorbital process
PC *	Least width of the postorbital constriction
CONDB	Breadth of the occipital condyles, from the outer edges, across the foramen magnum
CIL *	Lower Canine, greatest anteroposterior length at C-E junction
CIB *	Lower Canine, greatest mediolateral breadth at C-E junction
P3L	Lower 3rd Premolar, greatest anteroposterior length
P3B	Lower 3rd Premolar, greatest posterior mediolateral breadth
P4L	Lower 4th Premolar, greatest anteroposterior length
P4B *	Lower 4th Premolar, greatest posterior mediolateral breadth
M1L	Lower 1st molar, greatest anteroposterior length
M1B	Lower 1st molar, greatest mediolateral breadth
C-cd	Length from buccal edge of lower canine to mandibular condyle
HPC *	Height of the coronoid process
P3-M1	Distance from anterior edge of lower P3 to the posterior edge of lower M1.
A	Anterior depth of the mandible, anterior to P3
P	Posterior depth of the mandible, posterior to M1
Bp/4	Greatest mandibular breadth below lower P4

Table 1. Description and abbreviations of measurements used in this study. Those marked with an asterisk are highlighted on PC2.

	Initial Eigenvalues			Extraction Sums of Squared Loadings		
Component	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	30.582	89.948	89.948	30.582	89.948	89.948
2	1.230	3.617	93.565	1.230	3.617	93.565
3	.645	1.896	95.461			
4	.281	.826	96.287			
5	.211	.620	96.906			
6	.150	.440	97.346			
7	.139	.407	97.754			

Table 2. Principal components extracted. Two have eigenvalues above 1, accounting for 93.6% of the variance.

Variable	PC 1	PC 2
CSL	.972	-.138
CSB	.951	-.183
UP2B	.922	-.135
UP3B	.957	-.187
UP4BA	.941	-.283
ZB	.956	.101
IO	.933	.288
PP	.804	.522
PC	.643	.707
CIL	.967	-.199
CIB	.916	-.249
P4B	.971	-.132
HPC	.939	.144

Table 3. Results of PCA. Only those measurements with values above 0.1 are shown.