THE PLIO-PLEISTOCENE ANCESTOR OF WILD DOGS, *LYCAON SEKOWEI* N. SP.

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ABSTRACT—African wild dogs (*Lycaon pictus*) occupy an ecological niche characterized by hypercarnivory and cursorial hunting. Previous interpretations drawn from a limited, mostly Eurasian fossil record suggest that the evolutionary shift to cursorial hunting preceded the emergence of hypercarnivory in the *Lycaon* lineage. Here we describe 1.9–1.0 ma fossils from two South African sites representing a putative ancestor of the wild dog. The holotype is a nearly complete maxilla from Coopers Cave, and another specimen tentatively assigned to the new taxon, from Gladysvale, is the most nearly complete mammalian skeleton ever described from the Sterkfontein Valley, Gauteng, South Africa. The canid represented by these fossils is larger and more robust than are any of the other fossil or extant sub-Saharan canids. Unlike other purported *L. pictus* ancestors, it has distinct accessory cusps on its premolars and anterior accessory cuspids on its lower premolars–a trait unique to *Lycaon* among living canids. However, another hallmark autapomorphy of *L. pictus*, the tetradactyl manus, is not found in the new species; the Gladysvale skeleton includes a large first metacarpal. Thus, the anatomy of this new early member of the *Lycaon* branch suggests that, contrary to previous hypotheses, dietary specialization appears to have preceded cursorial hunting in the evolution of the *Lycaon* lineage. We assign these specimens to the taxon *Lycaon sekowei* n. sp.

INTRODUCTION

THE FAMILY Canidae (dogs, wolves, jackals, foxes, etc.) is an important component of the open-habitat African carnivore guild of today. However, the fossil record of Canidae on the continent is very poor, even when compared to other carnivoran families such as the Felidae and Hyaenidae. This is especially true of large-bodied canids (above ca 10–15 kg body weight). Such canids are known only from a handful of records throughout the continent. Therefore, any find of a large-bodied canid from Africa is of great interest and important to understanding the evolution of the family on the continent.

The only large-bodied canid in Africa today is the "wild" or "painted" or "hunting" dog, *Lycaon pictus* (Brookes, 1827 in Griffith, et al., 1827), which has a scattered distribution across parts of arid and semi-arid east, central and southern Africa (Fanshawe et al., 1997). Like other living canids, it is cursorial and for a canid extremely hypercarnivorous (Van Valkenburgh, 1991), with anatomical adaptations that make it the most highly derived of all of the canids for this lifestyle; *L. pictus* teeth are high-crowned and sectorial, and its postcranial skeleton is slender and gracile–suited for distance running and not grappling (Andersson and Werdelin, 2003; Andersson, 2004). The most widely appreciated anatomical feature related to this cursorial behavior is the putative loss of the first manual digit (Dallas, 1856; Flower and Lydekker, 1891; Nowak, 1991; Rook, 1994; Tedford et al., 1995), a trait that is unique among canids.

The evolutionary origin of *L. pictus* is poorly understood. Despite numerous morphological (Tedford et al., 1995; Van Valkenburgh and Koepfli, 1993; Zrzavý and Řičánková, 2004) and molecular studies (Bardeleben et al., 2005; Lindblad-Toh et al., 2005; Zrzavý and Řičánková, 2004), its phylogenetic relationship to other canids, especially the genera *Canis* (Linnaeus, 1758; wolf-like dogs) and *Cuon* (Hodgson, 1838; the Asiatic dhole), has remained controversial (see also

nomenclatural note in Material and Methods, below). The phylogenetic uncertainty of the lineage is heightened by the extremely sparse record of fossil African canids, which means that the evolutionary path leading to *L. pictus* is poorly known. Currently, the best hypothesis of ancestry for the living wild dog is that of Martínez-Navarro and Rook (2003), who suggest an evolution from the late Pliocene *Xenocyon falconeri* (Forsyth Major, 1877) via the early Pleistocene *Xenocyon lycaonoides* (Kretzoi, 1938)–both considered *Canis* by these authors–to the extant *L. pictus* [it should be noted that the demarcation between these two species of *Xenocyon* is at present not clear: the boundary drawn by Rook (1994) differs from that drawn by Martinez-Navarro and Rook (2003), though no new analysis was presented in the latter publication. Herein, we mainly follow Rook (1994) in this respect]. Martínez-Navarro and Rook (2003) based their hypothesis on the gradually increasing similarity in the dentitions between the fossil species and the extant one, on the apparent absence of a first metacarpal (MC I) in *Xenocyon* (based on *X. falconeri* metacarpals from the early Pleistocene of Pirro Nord, Italy)–an autapomorphic feature of *L. pictus*, and on the presence of a fossil *L. pictus* specimen from the late middle Pleistocene of Hayonim in Israel (Rook, 1994). It should be noted that in this scheme, the African "*Canis*" *africanus* (Pohle, 1928)from Olduvai and Kromdraai A is synonymized with *Xenocyon falconeri/lycaonoides*, which is a reasonable suggestion based on the available material. However, this is the only African material relevant to the scenario of Martínez-Navarro and Rook (2003), and the scenario requires a minimum of two separate dispersals: either two dispersals into Africa, first of *Xenocyon* then of *L. pictus*, or a dispersal out of Africa of *Xenocyon* followed by a later dispersal of its descendant, *L. pictus* into Africa. In their scheme, the highly specialized cursoriality of the *Lycaon* lineage preceded the highly specialized hypercarnivory of the *Lycaon* lineage–a hypothesis our specimens apparently refute.
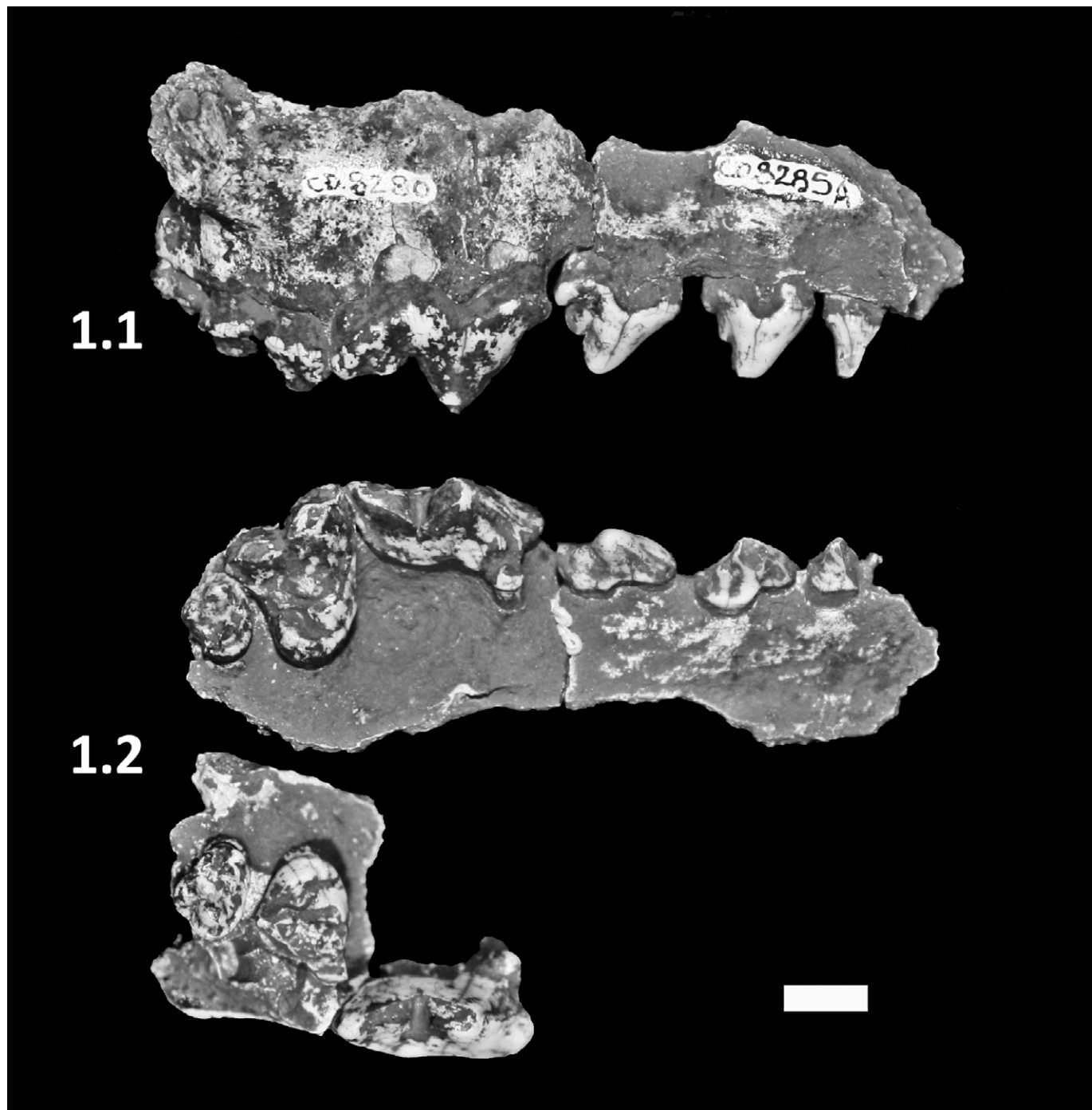
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FIGURE *1*—Holotype specimen in articulation. CD 8280/8281/8285, maxillary sections containing right P1-M2 and left P4, M1, M2. Left P2 is not figured. *1.1*, buccal view of right maxilla; *1.2*, occlusal view. Anterior is right in both specimens. Scale bar = 1cm.

In this paper, we describe new specimens from hominin bearing sites in the Sterkfontein valley, Gauteng, South Africa that shed light on the origins of the *Lycaon* lineage. They represent the oldest large fossil canid species yet recovered in southern Africa. The first specimen (Figs. 1, 3.1I, and 3.1II), from 1.6–1.9 ma deposits (unpublished U-series dates) at Coopers Cave, "Coopers D," (a site that, like Kromdraai A, has a remarkable concentration of carnivore taxa; Hartstone-Rose et al., 2007) is represented by a nearly complete palate with ten teeth. The second (Figs. 2 and 3.1III), from approximately 1 ma sediments from Gladysvale (unpublished

ESR dates), is a partial skeleton (~40% skeletal elements, ~70% when mirror imaged; making it the single most nearly complete mammalian skeleton yet described in publication from the entire Sterkfontein valley), that preserves craniodental and postcranial elements from all regions of the skeleton. The dog represented by these fossils is larger (ca. 10% larger dentally than *L. pictus*) and more robust than any of the known fossil or extant sub-Saharan canids and had a large first metacarpal, distinguishing it from *L. pictus*. In this article, we compare the specimens to two similar extant canids, *L. pictus* and *C. lupus* (Linnaeus, 1758), and the most similar

FIGURE 2—Paratype specimen, GV 466, in anatomical position. Some elements have been omitted for visual clarity.

fossil canids, *X. falconeri* and *X. lycaonoides*. We assert that these specimens represent a new species and we here assign them to the taxon *Lycaon sekowei* n. sp.

MATERIAL AND METHODS

Metric data.—The data used in the metric analyses comes from several sources (Table 1). Data used in Figure 4 on extant *Lycaon* are from specimens in the Swedish Museum of Natural History and that of *C. lupus* from several sources, while data on *Xenocyon* spp. are from Rook (1993). Data used for the metrics described in Table 2 (and for most of the qualitative comparisons) were collected on specimens from the American Museum of Natural History (AMNH), the Transvaal Museum (TM), the Smithsonian (USNM) and the faunal collections held at the University of the Witwatersrand.

Nomenclatural note.—The most recent studies of extant canid phylogeny place the dhole (*Cuon*) and wild dog (*Lycaon*) in a monophyletic clade with some members of the genus *Canis*, while placing some species traditionally assigned to *Canis* (specifically black-backed and side-striped jackals) outside that clade. This has consequences for the nomenclature of these taxa. Previously, one of us (LW) has advocated including the dhole and wild dog in *Canis*. However, due to the complexities of the phylogeny of this clade when fossils are included in the picture, we here adopt the alternative option, which is to recognize the validity of the genera *Cuon* and *Lycaon*. This also requires placing the black-backed and side-striped jackals in their own genus, for which the nomen *Lupulella* (Hilzheimer, 1906) is available. Further, due to the uncertain position of the genus *Xenocyon* (often used as a

subgenus for "*Canis*" *falconeri* and "*Canis*" *lycaonoides*) vis-à-vis *Canis* sensu stricto, this genus is also considered valid herein. These nomenclatural decisions are reflected throughout the text.

SYSTEMATIC PALEONTOLOGY

Family CANIDAE Fischer, 1817
Genus LYCAON Brookes, 1827 (*in* Griffith, et al., 1827)
LYCAON SEKOWEI new species

Diagnosis.—A canid intermediate in dental size between *Lycaon pictus* and *Canis lupus*; dentition stoutly built and relatively high-crowned; P^1 lacking distal shelf, P^2 and P^3 short and comparatively broad, with tall, short distal accessory cusps; P^4 less high-crowned than anterior premolars, with substantial but low protocone; M^1 long, with wide basin.

Description.—(Based on holotype only) Dental metrics are provided in Table 2. The morphology of the P^1 is very similar to that of *L. pictus* in that the paracone is high crowned and conical with only the slightest indication of a metastyle or cingulum. It is very different from that of *X. falconeri* or *C. lupus*: in *C. lupus*, the low-crowned paracone occupies only the mesial half of the tooth, while the distal half slopes off into a nearly horizontal portion; *Xenocyon* spp. is intermediate between the states seen in *L. pictus* and *C. lupus*, though it is more similar to that of *C. lupus*.

The P^2 crown is taller than in *C. lupus* and lower than in *L. pictus*, yet in overall morphology is more similar to that of *L. pictus* (Table 3). In both the Coopers maxilla and *L. pictus*, the P^2 has a high paracone and two substantial distal accessory
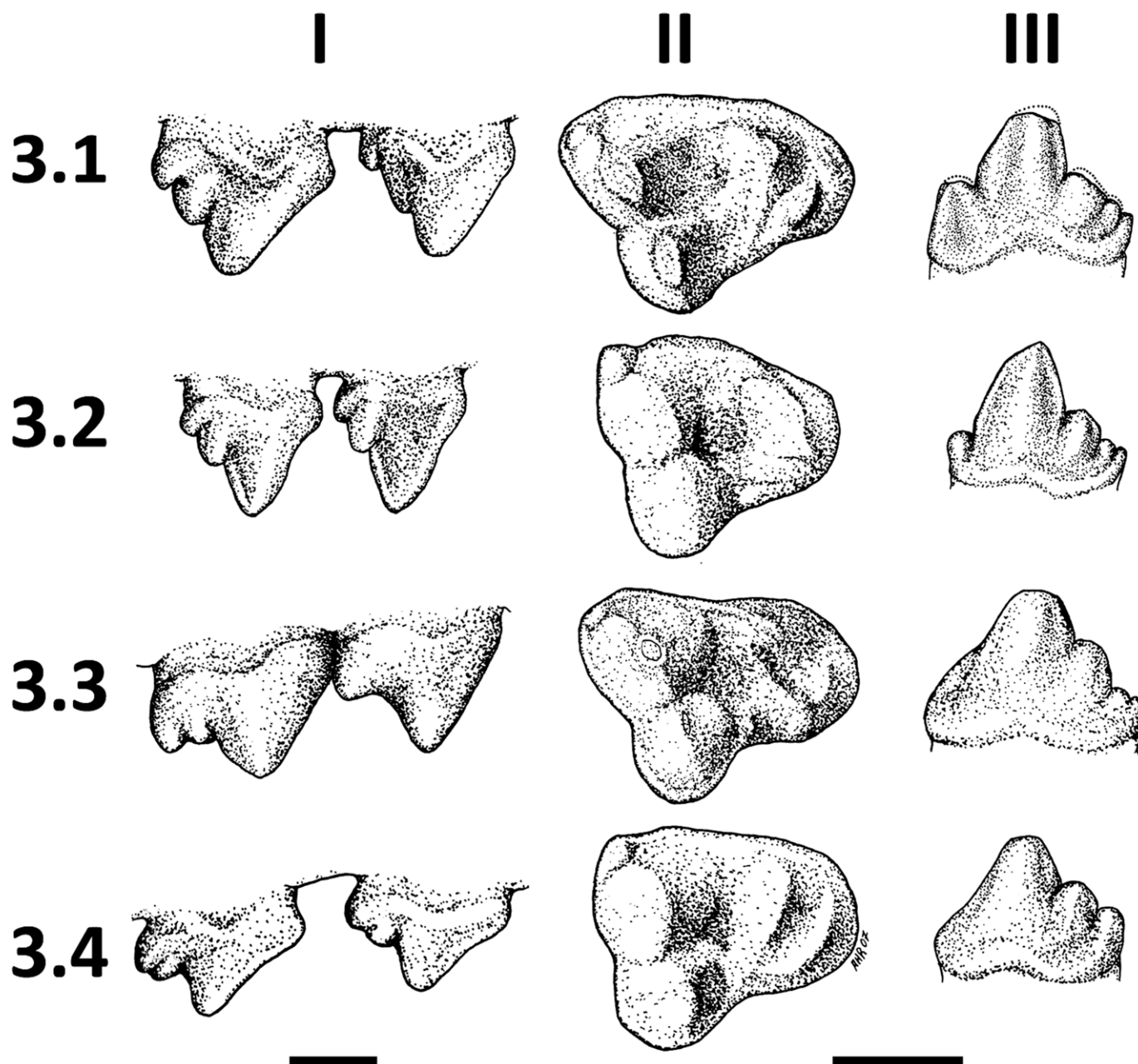
FIGURE 3—Comparative dentition of: *1, Lycaon sekowei*; *2, L. pictus*; *3, Xenocyon* spp.; *4, Canis lupus*. Column I = RP2 and RP3, buccal view. Mesial is to the right. Column II = RM1, occlusal view. Buccal is to the left. Column III = LP4 buccal view. Mesial is to the left. Scale bars = 1cm. I.3.1. CD 8285a; I.3.2 USNM 470144 ♂; I.3.3 (AMNH) FAM 97952; I.3.4 USNM 265101 ♂; II.3.2 CD 8280; II.3.2 USNM 470144 ♂; II.3.3 KA 1556 (reversed); II.3.4 USNM 64960 ♂; III.3.1 GV 466-1b; III.3.2 USNM 470144 ♂; III.3.3 AMNH 102520; III.3.4 USNM 64960 ♂.

cusps. In *C. lupus* the paracone is lower and longer, the first distal accessory cusp is lower and the second indistinct or absent. In *X. falconeri* the paracone is as in *C. lupus* and the distal accessory cusps are absent altogether.

The P^3 is similar in overall morphology to P^2, but all the cusps are larger. The paracone is considerably taller than in *X. falconeri* or *C. lupus*, though not as tall as in *L. pictus*. There are two well developed distal accessory cusps in the Coopers specimen with the mesial-most (i.e., the one directly distal to the paracone) being the larger of the two. This mimics the condition in *L. pictus*. In *X. falconeri* the cusps are of about equal size, where they are developed at all. In *C. lupus* the cusps are quite indistinctly developed and of about equal size.

In both P^2 and P^3, the Coopers specimen represents an intermediate between *L. pictus* and *Canis* spp. in that the intermediate accessory cusps (between the paracone and the distalmost accessory cusp) are less well defined than in most *L. pictus* but far moreso than in *Canis* spp., the postparacristae are less sharply crested than in *L. pictus*, and the distal accessory cusp is more substantial (i.e., the distal aspect of the tooth is relatively more emphasized than is the case in *L. pictus*). While this distal accessory cusp is buccally displaced in *L. pictus* and less so in *Canis* spp., it is extremely so in the Coopers specimen, particularly in the P^3 (Fig. 3I and Table 3).

As in *L. pictus*, *X. falconeri* and *C. lupus*, the P^4 of the Coopers specimen has a tall paracone with a strong

TABLE 1—List of specimens used in metric analyses (alphabetical by species and then by locality). AMNH: American Museum of Natural History, New York; DE University of Florence, Institute of Earth Sciences, Cava Dell'Erba collection; GIN: Academy of Sciences, Russia, Institute of Geology; IGF University of Florence, Museum of Geology and Paleontology; Lok: Chinese specimens (viewed at the AMNH); MUC: Colle Curti, Spain (Viewed at the AMNH); NRM VE: Swedish Museum of Natural History, Department of Vertebrate Zoology; PMU: Evolution Museum, Uppsala University, Paleontological collection; PN University of Florence, Institute of Earth Sciences, Pirro Nord collection; TM: Transvaal Museum, Pretoria; UH ZM: University of Helsinki, Zoological Museum; VM: Venta Micena, Spain (viewed at the American Museum of Natural History, AMNH); *s.n.*: no number.

Species	Catalog number	Origin
Canis lupus	Inari 1914/19, Inari 1914/17, Inari 1914/23, Inari 1914/18, Inari 1913/29, Inari 1912/26, Inari 1912/30, UH ZM 1351, UH ZM 1348, UH ZM 1347, UH ZM 1349,	Finland
Lycaon pictus	NRM VE A584153	Africa
	NRM VE A583668, A583670, A583671, A593669, A595102	Congo
	TM AZ 221*, TM AZ 223*	South Africa
Xenocyon antonii (sensu Rook 1994)	Lok 64*	Chihli Province, China
	Lok 33*	Honan Province, China
Xenocyon falconeri	DE 11-1 *s.n.***	Cava Dell'Erba, Italy
	MUC 204*	Colle Curti, Italy
	TM KA 1556**, TM KA 1288*	Kromdraai A
	PP 186**, PN 22*, PN 23, PN 25*, PN 2c *s.n.***, PN 2 *s.n.***	Pirro Nord, Italy
	IGF 883**, IGF 865*,	Valdarno Superior, Italy
	VM 2255*, VM 2256*, VM 2257*	Venta Micena, Spain
	PMU M3514	Yang Shao Tsun, China
Xenocyon lycaonoides	IGF *s.n.*	Gombaszög
	GIN 3722/141, GIN UZK 2291	Tologoi, Russia
*Xenocyon spp.**	AMNH 96570, 96570, 96571a, 96571b, 96575, 96579, 96579, 96580, 96581a, 96581b, 96585, 97052, O15017, O1519	Various

"*" = Used for qualitative comparisons and table 2 metrics only; "**" = Used in qualitative comparisons, table 2 metrics, and figure 4 bivariate comparisons.
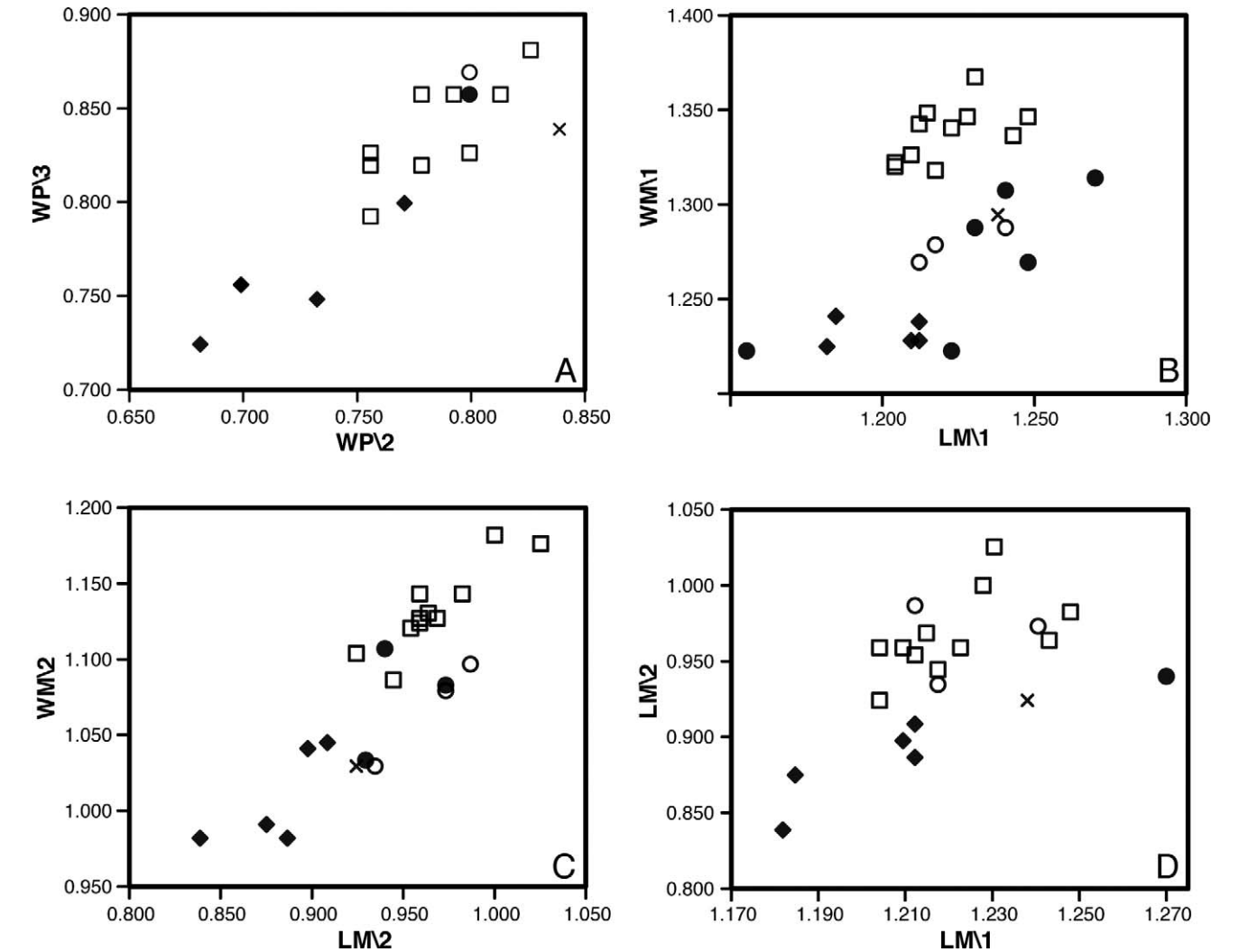

FIGURE 4—Bivariate Dental Metrics. Buccolingual widths (W) and mesiodistal lengths (L) of upper teeth in log mm. X = *Lycaon sekowei*, diamond = *L. pictus*, square = *Canis lupus*, Circles = *Xenocyon*, open = *X. lycaonoides*, and closed = *X. falconeri*.

TABLE 2—Metrics. Measurements of diagnostic morphology of *Lycaon sekowei* in comparison to *Xenocyon spp.*, *L. pictus* and *C. lupus*. Upper dental measurements are from the Coopers specimen, and the lower teeth are from the Gladysvale specimen. Shape variables are lengths/width.

	Lycaon sekowei (mm)	*Xenocyon spp.*			*L. pictus* (N = 4)		*C. lupus* (N = 5)	
		(mm)	N	SD	(mm)	SD	(mm)	SD
P^1 L	7.2	7.3	2	0.5	6.9	0.1	7.7	0.4
P^1 W	6.0	5.0	2	0.8	5.2	0.5	5.6	0.5
P^2 L	12.7	13.9	6	0.7	10.2	0.6	13.9	0.9
P^2 W	6.9	5.8	6	0.5	5.0	0.4	6.0	0.4
P^3 L	15.2	17.1	4	0.5	12.3	0.5	15.7	1.1
P^3 W	6.9	6.7	5	0.5	6.0	0.5	6.6	0.8
P^4 L	25.7	25.9	13	1.7	21.0	1.1	24.4	2.1
P^4 Total W	13.1	13.0	11	1.4	11.2	0.5	13.8	1.4
P^4 Buccal W	10.4	9.9	6	1.0	8.6	0.7	10.2	0.9
M^1 Trigon L	17.3	17.0	15	1.1	15.9	1.3	16.6	1.9
M^1 Waist L	12.2	12.7	9	0.8	10.6	0.5	12.4	1.2
M^1 Tot W	19.7	19.7	15	2.1	16.5	0.8	19.7	1.5
M^1 Buccal W	9.0	10.4	9	0.8	9.7	1.0	11.0	1.6
M^2 Trigon L	8.4	9.2	11	0.9	6.9	0.7	8.6	0.9
M^2 Waist L	7.1	8.4	5	0.8	5.9	0.7	7.9	0.9
M^2 Total W	10.7	12.7	11	1.2	9.0	1.4	12.6	1.4
M^2 Buccal W	5.9	6.8	5	1.0	5.1	0.4	6.6	1.4
P^1 Shape	1.2	1.5	2	0.1	1.4	0.1	1.4	0.1
P^2 Shape	1.8	2.4	6	0.2	2.1	0.1	2.3	0.1
P^3 Shape	2.2	2.5	4	0.2	2.1	0.1	2.4	0.2
P^4 Total Shape	2.0	2.0	11	0.2	1.9	0.0	1.8	0.1
P^4 Buccal Shape	2.5	2.6	6	0.2	2.5	0.1	2.4	0.2
M^1 Total Shape	0.9	0.9	15	0.1	1.0	0.0	0.8	0.1
M^1 Buccal Shape	1.9	1.6	9	0.1	1.6	0.2	1.5	0.2
M^2 Total Shape	0.8	0.7	11	0.1	0.8	0.1	0.7	0.1
M^2 Buccal Shape	1.4	1.4	5	0.1	1.4	0.1	1.3	0.2
P$_4$ L	16.1	16.5	16	1.2	13.2	0.6	15.3	1.0
P$_4$ W	8.3	7.6	15	0.7	6.7	0.4	7.6	0.5
M$_1$ W	10.8	10.9	16	1.0	9.6	0.6	11.4	0.7
M$_1$ Trigonid L	17.6	18.9	14	1.4	17.7	1.5	19.7	1.5
P$_4$ Shape	1.9	2.2	15	0.1	2.0	0.0	2.0	0.2
M$_1$ Trigonid Shape	1.6	1.7	14	0.1	1.8	0.0	1.7	0.1

preparacrista leading to a slight buccomesial cingulum and meeting the preprotocrista lingually. Whereas the protocone in *C. lupus* is mesially positioned, the P^4 protocones of both the Coopers specimen and *L. pictus* lie distal to the anterior edge of the mesial cingulum. The condition in *X. falconeri* is variable in this respect. Like in *C. lupus*, but unlike in *X. falconeri* and *L. pictus*, there is a strong lingual cingulum running the entire length of the metacone.

In many respects the M^1 from Coopers looks like an intermediate between *Canis* and *L. pictus* (Tables 2 and 3 and Fig. 3II). The para- and metastyles of *L. pictus* are well developed, while those of *Canis* are virtually indistinguishable from the cingula that surround the mesiobuccal and distobuccal aspects of the para- and metacones respectively. The Coopers specimen possesses distinct para- and metastyles (as in *L. pictus*), but they are contiguous with adjacent cingula (as in *Canis*). Like that in *L. pictus* (and unlike that in *C. lupus*), the M^1 does not possess a paraconule, and the mesiobuccal cingulum does not continue lingual to the area where the paraconule would exist. Like that in *C. lupus* (and unlike that in *L. pictus*), there is a substantial postprotocrista separating the trigon from the talon. Furthermore, like that in *C. lupus* and unlike that in *L. pictus*, the distobuccal cingulum meets the metaconule lingually, and the talon is further emphasized by substantial pre- and posthypocristae that form a distolingual crest in which the hypocone is barely distinguishable.

It is in this latter trait that the Coopers specimen differs most substantially from the only other large canid fossils described from the Sterkfontein valley, KA 1556 (from the site of Kromdraai locality ''A''), the paratype specimen of *Xenocyon atrox* (Broom, 1948, Fig. 3II) from Kromdraai–synonymized by Rook (1994) with *Xenocyon africanus*–which has a fully separate hypoconule. That is, the distolingual crest

created by the hypocone, hypoconule and their pre- and post cristids is more bifurcated in KA 1556 than in any other canid specimen included in this study. Furthermore, KA 1556 differs from the Coopers M^1 in that it has a relatively narrower distance between the metacone and hypoconule and correspondingly narrower metaconule. KA 1556 also contains a sharper postprotocrista which separates shallower talon and trigon depressions. In all of these regards, the morphology of the Kromdraai specimen is ambiguous as to phylogenetic affinity. This is not surprising, given that the M^1 is not particularly useful for separating the large-bodied canids (Tedford et al., 1995).

The M^2 of the Coopers specimen closely resembles that of *L. pictus*, and not *Xenocyon* or *C. lupus*, in that it is a very simple tooth consisting of three globular cusps and no smaller cuspules. As in *L. pictus*, and not in *C. lupus*, the lingual cusps are united into one mass, though this trait is intraspecifically variable. Unlike in *L. pictus*, however, the protocone and the hypocone cannot be distinguished. Furthermore, in *L. pictus* the protocone is higher and more substantial than the hypocone; however, in the Coopers specimen, the lingual cusp mass maintains its height mesodistally, and thus, the hypocone (if it were distinguished) would be high relative to that in *L. pictus*.

Metric comparisons.—Due to limited comparative material and other factors, only a few metric comparisons between the Coopers specimen and other large-sized Canidae will be made here. These are, however, in some respects quite illuminating.

Of the premolars, the considerable width of P^2 is worth noting. This is seen in Fig. 4.1, comparing the widths of P^2 and P^3. The Coopers specimen has a P^2 that is broader

The proportions of the molars are more illuminating. Fig. 4.2 shows length versus width of M^1. The proportions of this tooth in the Coopers specimen lie within the range of

TABLE 3—Diagnostic morphology of *L. sekowei* in comparison to other canids. Bold indicates comparative morphology most similar to *L. sekowei*.

Morphology	a. *Lycaon sekowei*	b. *C. (Xenocyon)*	c. *L. pictus*	d. *C. lupus*
M^1 Occlusal Outline	Heavy buccal cusps and large basin	Slightly narrower buccal cusps, narrow waist separating and small talon	Narrowest and most crested buccal cusps and smallest talon	**Lowest buccal cusps and large basin**
M^1 Talon Cusps	Deeply crested	Small and not crested	Small and not crested	**Moderately crested**
P^2 and P^3 Crown Shape	Moderately sectorial distal edge of main cusp and fairly high crowns	Slightly sectorial distal edge of main cusp of P^3 and fairly low crowns	**Sectorial mesial and distal edges of main cusp and highest crowns**	Rounded cusps (non-sectorial) with very low crowns
P^2 and P^3 Accessory Cusps	High and fairly narrow	Most bulbous and least numerous	**Highest and narrowest**	Lowest and bulbous
P_4 Crown Shape	Moderately high crowned and relatively sectorial	Moderately high crowned and less sectorial	**Highest crowned and most sectorial**	Lowest crowned and least sectorial
P_4 Anterior Accessory Cusps	Very substantial and sectorial	Not present, though slightly indicated	**Present though small**	Not present
First Metacarpal (MCI)	Almost identical in size and shape to *C. lupus* though much larger relative to MCII length	Not recovered	Not present	**Present**

Xenocyon spp., with *L. pictus* having similar proportions but being smaller. The M^1 of *C. lupus* is markedly broader relative to length. The same is generally true of M^2 (Fig. 4.3), though here the Coopers specimen is intermediate in size between the *Xenocyon spp.* and *L. pictus* samples. Most interesting, however, is the diagram of relative length of M^1 and M^2 (Fig. 4.4). This shows the Coopers specimen to have an M^2 that is short relative to M^1, as in *L. pictus*, whereas in *Xenocyon lycaonoides*. This relationship is close to that in *C. lupus*. Put in other terms, in *L. pictus* and all fossil specimens the upper molar dentitions are reduced relative to that of *C. lupus*. However, in *L. pictus* and the Coopers specimen, this reduction has gone further in M^2, which is reduced in size (particularly length) relative to the condition in *C. lupus* and *Xenocyon lycaonoides*.

Etymology.—in memoriam of Joseph Sekowe, a second-generation fossil excavator who found and recovered the holotype specimens.

Holotype.—CD 8280/8281/8285 maxillary sections containing right P^1-M^2 and left P^2, P^4, M^1, M^2. CD 8393, an isolated RI^3 may belong to the same individual (Fig. 1).

Occurrence.—Late Pliocene (ca. 1.9 ma) from Coopers Cave, Sterkfontein Valley, Gauteng, South Africa.

Discussion.—We consider the Coopers specimen described above to lie closer to the ancestry of *L. pictus* on the basis of the following features:

1) Its teeth are in general sharper and higher-crowned than those of either *Xenocyon* or *C. lupus*.
2) It has many accessory cusps – a diagnostic feature of *Lycaon* – more than are found in all large fossil or extant canids other than *L. pictus* (Figure 3I).
3) Though its palate is incomplete, *L. sekowei* appears to have had a broad palate, like *L. pictus* and unlike *Xenocyon* which has a palate narrower than that found in *C. lupus* Rook, 1994.
4) Like *L. pictus* its M^1-M^2 buccal cingula are reduced (Figure 3II).
5) Like *Xenocyon* and *L. pictus* its M^1 has been reduced in width (Figure 4B).
6) Like *Xenocyon falconeri* and *L. pictus*, but unlike *X. lycaonoides* and *C. lupus*, M^2 is reduced in length relative to M^1 (Figure 4D).

Tentatively referred specimen.—A second specimen (Fig. 2), from younger (ca. 1 Ma) sediments from Gladysvale (GV), GV 466, a skeleton containing approximately 110 elements, including LP_4 and LM_1, mandibular fragments with alveoli of LM_2 and an apparently small LM_3, as well as postcranial bones from all skeletal regions (notably, both first and second left metacarpals), also shows affinities to *L. pictus* and may belong to *Lycaon sekowei*. This specimen provides additional information on the evolution of the *Lycaon* lineage.

Description.—GV466-1A is a left lower carnassial (LM_1), missing the distal root and part of the talonid. Although the total length of the tooth is not ascertainable due to breakage, the trigonid length is within the size range of *Xenocyon* and *L. pictus* (Table 2). Furthermore, the specimen is relatively bulbous compared to the more bladelike M_1 of *L. pictus* and appears to be relatively stouter than that of *C. lupus* as well. Relative to the protoconid, the paraconid is lower than in *L. pictus* and *C. lupus*, and the metaconid is small. There does not appear to be a cristid obliqua, unlike the condition in *L. pictus* and *C. lupus*.

While the specimen is very similar in size to KA 1288 (referred to *Xenocyon falconeri*), the Gladysvale specimen is
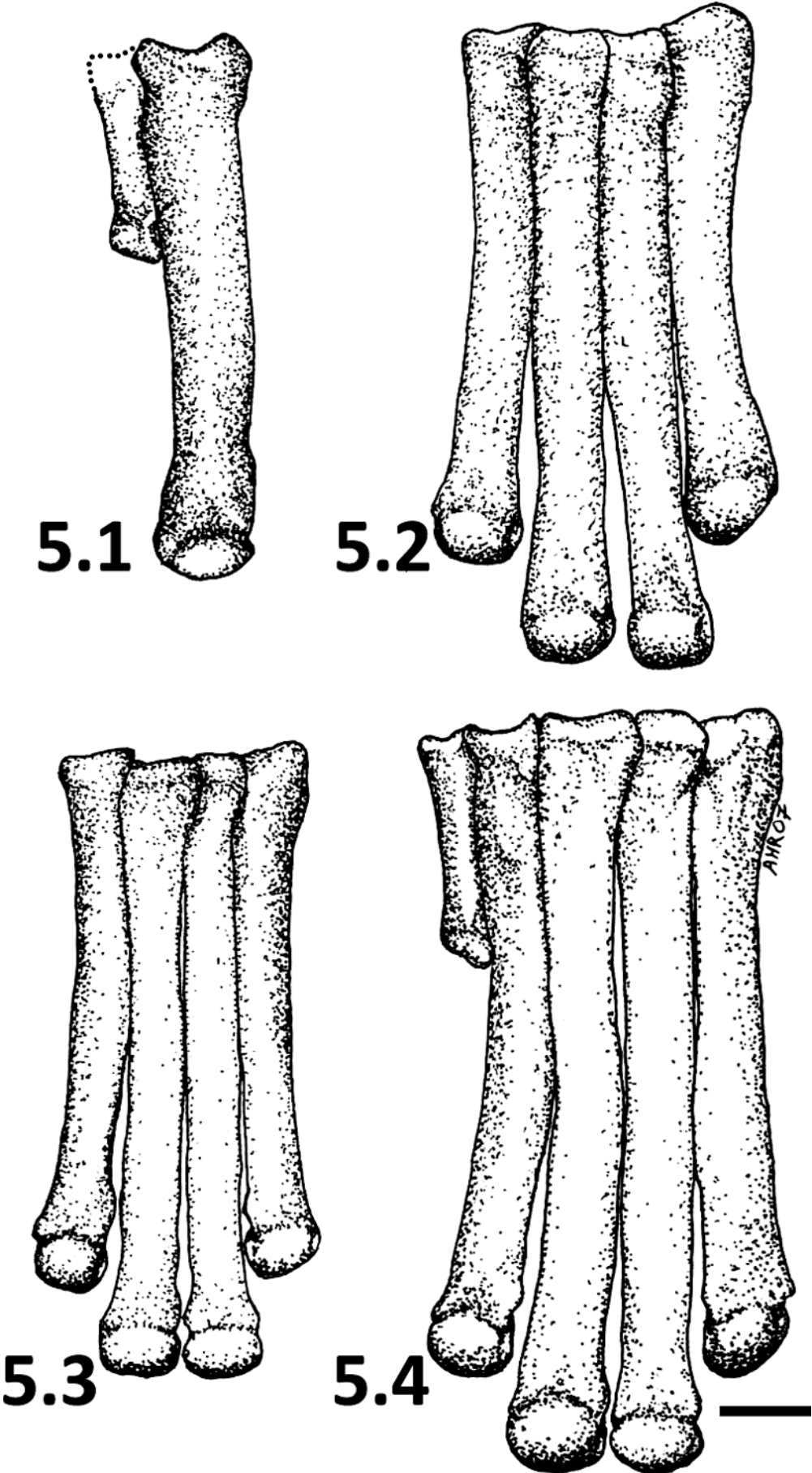
lower-crowned and substantially more bulbous. Furthermore, while the metaconids are of similar size in the two specimens, KA 1288 has a substantial cristid obliqua (moreso than in *L. pictus*) and a very small lingual metaconulid, neither of which are present in GV466-1A. Rook (1994) also notes that specimens of *Xenocyon* tend toward blade-like carnassials, unlike the M_1 from Gladysvale.

GV466-1B represents a left mandibular premolar, most likely a P_4 based on its size relative to the M_1 (Fig. 3III). Again, as is true with the M_1, the P_4 is relatively larger than that of *L. pictus*. Unlike the M_1, however, the GV 466 P_4 is also larger than that found in *C. lupus*. Furthermore, as with the M_1, the P_4 appears more bulbous and less bladelike than that of *L. pictus*, and the cusps appear more stoutly built and the notches between them not as deep. As in *L. pictus* but no in *Xenocyon* or *C. lupus*, there is a distinct hypoconulid. Both the GV 466 and *L. pictus* P_4 have a large anterior (mesial) accessory cuspid–a trait that is typical of more hypercarnivorous species (Hartstone-Rose, 2008) and recognized as unique among canids to *L. pictus* (Flower and Lydekker, 1891)–not found in any *Xenocyon* or other extant large canids.

The presence of a first metacarpal (MC I) in GV 466 (Fig. 5) is remarkable for an ancestor on the *L. pictus* lineage, as *L. pictus* displays tetradactyly, unique among extant canids (Dallas, 1856; Flower and Lydekker, 1891; Nowak, 1991; Rook, 1994). The presence of MC I distinguishes the Gladysvale specimen from *Xenocyon falconeri*, in which the MC I has not been recovered. This absence has been argued to reflect a close phylogenetic relationship with *L. pictus* (Rook, 1994). However, it is difficult to diagnose the absence of an MC I in the fossil record, and all specimens (even those without any ossified MC I) have MC I facets on their second metacarpals (Rook, 1994). With that said, GV466 represents a very different morphology than the other canids, with an MC I that is larger (when compared to total body size) even than that of *C. lupus* (see Fig. 5). That is, the preserved distal end of the GV 466 MCI is nearly identical in size and shape to that of a large *C. lupus*, though its complete MC II (and the rest of the paw) is much shorter (Fig. 5).

Discussion.—The constellation of morphology represented by the maxilla from Coopers Cave and the skeleton from Gladysvale is unlike any seen in the other extant or extinct Canidae. Prior to their discovery, the wealth of fossils from Eurasia grouped under the various *Xenocyon* species did indeed appear to show the right mix of morphology to be the likely ancestor of *L. pictus* (Martinez-Navarro and Rook, 2003). However, the addition of the new South African taxon makes the picture more complex (Table 3).

Prior to the discovery of *L. sekowei* n. sp., *Xenocyon* spp. was the best candidate for the ancestor of *L. pictus*–linked mainly by its apparent lack of a first metacarpal, as well as some features of the dentition (Rook, 1994). However, this highly variable feature is not a reliable piece of morphology upon which to base phylogenetic relationships–especially when its diagnosis is based solely on the morphology of its facet on the MCII. Furthermore, the dental morphology of *Xenocyon* spp. is very different than that of *L. pictus*, the former being defined by a notable reduction in the number of

accessory cusps of its premolars and the latter by a notable accentuation of those cusps (Fig. 3I), a feature shared with the holotype of *Lycaon sekowei*, described above. In the lower dentition, the relationship between the referred Gladysvale specimen of *L. sekowei* and *L. pictus* is unambiguous: this is the only canid taxon other than *L. pictus* to have a prominent anterior accessory cusp on its lower premolar (Fig. 3III). Furthermore, while its teeth are more robust than those of *L. pictus*, they are higher-crowned and more sectorial than those of *Xenocyon spp.* (Fig. 3I AND 3III). reflecting the adaptive shift to hypercarnivory that characterizes wild dogs. With all of this morphological evidence taken into account, along with its presence in sub-Saharan Africa just after the molecularly supported divergence time between *L. pictus* and the other large canids, *L. sekowei* now becomes the most likely ancestor for *L. pictus*.

Thus, the evolution of the hypercarnivorous and highly cursorial *L. pictus* appears to have followed three phases:

1) The addition of accessory cusps and cuspids – an initial step toward hypercarnivory found to a greater extent in *L. sekowei* than in *Xenocyon*.
2) An increase in the height and acuity of the postcanine dentition. A trend only just begun in *L. sekowei*.
3) Postcranial adaptations to cursorial locomotion, not yet seen in *L. sekowei*.

The *L. sekowei* specimens appear to support an evolutionary progression of behavior and morphology quite different from earlier interpretations based on *Xenocyon*, in which a shift to a cursorial mode of predation would have preceded dietary adaptations to hypercarnivory. *L. sekowei* instead demonstrates that the shift toward hypercarnivory preceded the locomotor shift toward greater cursoriality.

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FIGURE 5—Left manus dorsal view. Medial is to the left. Scale bar = 1 cm. *5.1*, *Lycaon sekowei*, partial MC I and complete MC II, GV 466-3j; *5.2*, *Xenocyon* ex gr. *falconeri*, MC II-V, PN 7-10 Cava dell'Erba Pirro Nord drawn for Rook 1994; *5.3*, *L. pictus*, MC II–V, TM AZ 2232 ♂; *5.4*, *C. lupus*, MC I–V, TM AZ 1570 ♂.

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