

# Forelimb Anatomy and the Discrimination of the Predatory Behavior of Carnivorous Mammals: The Thylacine as a Case Study

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**ABSTRACT** Carnivorous mammals use their forelimbs in different ways to capture their prey. Most terrestrial carnivores have some cursorial (running) adaptations, but ambush predators retain considerable flexibility in their forelimb movement, important for grappling with their prey. In contrast, predators that rely on pursuit to run down their prey have sacrificed some of this flexibility for locomotor efficiency, in the greater restriction of the forelimb motion to the parasagittal plane. In this article, we measured aspects of the forelimb anatomy (44 linear measurements) in 36 species of carnivorous mammals of known predatory behavior, and used multivariate analyses to investigate how well the forelimb anatomy reflects the predatory mode (ambush, pursuit, or pounce-pursuit). A prime intention of this study was to establish morphological correlates of behavior that could then be applied to fossil mammals: for this purpose, five individuals of the recently extinct thylacine (*Thylacinus cynocephalus*) were also included as unknowns. We show that the three different types of predators can be distinguished by their morphology, both in analyses where all the forelimb bones are included together, and in the separate analyses of each bone individually. Of particular interest is the ability to distinguish between the two types of more cursorial predators, pursuit and pounce-pursuit, which have previously been considered as primarily size-based categories. Despite a prior consideration of the thylacine as a “pounce-pursuit” or an “ambush” type of predator, the thylacines did not consistently cluster with any type of predatory carnivores in our analyses. Rather, the thylacines appeared to be more generalized in their morphology than any of the extant carnivores. The absence of a large diversity of large carnivorous mammals in Australia, past and present, may explain the thylacine’s generalized morphology. *J. Morphol.* 000:000–000, 2014. © 2014 Wiley Periodicals, Inc.

**KEY WORDS:** carnivores; thylacine; forelimb anatomy; predatory behavior; locomotion

## INTRODUCTION

In a previous publication (Figueirido and Janis, 2011), we showed (following Andersson and Werdelin, 2003; Andersson, 2004a) how the morphology of the distal humerus of carnivorous mammals

could be used to distinguish among different predatory strategies. We noted that the recently extinct thylacine, (*Thylacinus cynocephalus*: commonly known as the “marsupial wolf” or “Tasmanian tiger”), despite its overall “dog-like” appearance, fit better among the extant ambush predators (mostly felids) rather than with the extant specialized cursorial predators (mostly canids). The aim of this article is to further investigate the correlation of carnivore forelimb anatomy with predatory behavior, both to illustrate the ecomorphological correlations in extant taxa, and to serve as a template for investigations of the probable behavior of extinct taxa. For the latter purpose, we use the thylacine to further investigate its probable behavior.

There is a considerable history of publications that correlate the limb anatomy of mammals with their locomotor behavior. Studies on mammals in general include Howell (1944); Maynard Smith and Savage (1956); Brown and Yalden (1973); Gambaryan (1974); Hildebrand (1985); and Polly (2007). Carnivores have been a particular popular group to study in this regard: for example, Gonyea (1978); Van Valkenburgh (1985, 1987); Taylor (1989); Anyonge (1996); Iwaniuk et al. (1999); Polly (2008); Samuels et al. (2013); Martín-Serra et al. (2014), and many other references therein. The forelimb in general, and the humerus in

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particular, is especially informative as to carnivorous locomotor behavior (see e.g., Andersson and Werdelin, 2003; Figueirido and Janis, 2011; Walmsley et al., 2012). Different types of morphology are adaptive for different uses of the forelimb (Samuels et al., 2013): arboreal and scansorial forms use the forelimb for climbing, as well as for general locomotion, and terrestrial carnivores must balance out the demands of a forelimb designed for efficient locomotion for prey capture versus one adapted for handling and dispatching of the prey once it has been caught (see Iwaniuk et al., 2000).

A number of recent papers use aspects of the morphology of the forelimb of carnivores to examine ecomorphological correlates in extant taxa, and to apply these to the determination of the probable behavior of extinct ones: for example, Andersson and Werdelin (2003); Andersson (2004a); Meachen-Samuels and Van Valkenburgh (2009); Figueirido and Janis (2011); Ercoli et al. (2012); Meachen-Samuels (2012); Samuels et al. (2013); and Walmsley et al. (2012). Most of these, and previous, papers attempt to determine morphological correlates of substrate use and/or habitat preference, with a division of the taxa into categories such as cursorial, terrestrial, scansorial, arboreal, semiaquatic, and semifossorial. Body size is also an important consideration, especially in felids: while all felids use their forelimbs to handle their prey, the larger taxa grapple with their prey while the smaller ones merely swipe, and larger felids have proportionally more robust limbs with features indicative of greater use of the manus (e.g., proportionally larger humeral epicondyles for the origin of manual flexor and extensor muscles; Meachen-Samuels and Van Valkenburgh, 2009).

Phylogeny is, of course, also an important consideration in predatory behavior. Most felids are moderately cursorial ambushers whereas many canids are highly cursorial pursuers. However, there are some taxa that overcome their phylogenetic legacy, such as the pursuit predatory behavior of the cheetah (*Acinonyx jubatus*: see below), and such taxa are critical for determining ecomorphological correlations that are independent of phylogenetic associations.

The more cursorial predators can be distinguished into two types: pursuit predators and pounce-pursuit predators, following Van Valkenburgh (1985). Pursuit predators pursue their prey over a long distance (>500 m), usually in packs, and do not grapple with their prey. Pounce-pursuit predators pursue their prey for a longer distance than an ambusher, with the pursuit ending in a pounce or a short chase, and they rely less on the forelimbs for manipulating the prey than do ambushers. Pack hunting pursuit predators may be of relatively recent ancestry, essentially a Plio-Pleistocene phenomenon (Janis and Wilhelm, 1993).

Today pursuit predators can be found among the canids (larger species of *Canis* [such as the grey wolf, *Canis lupus*], the dhole, *Cuon alpinus*, and the African hunting dog, *Lycaon pictus*); the hyenas (the spotted hyena, *Crocuta crocuta*); and the felids (the cheetah, *Acinonyx jubatus*). The cheetah is an anomalous form here: it is a solitary hunter lacking the endurance of the canid and hyenid pursuit predators, and it will bring down its prey with the swipe of a forelimb. However, the cheetah is a felid that is clearly more specialized toward running than others in its family, pursuing its prey for a distance of up to 200 m, at least twice as far as does a lion, and has been classified by other authors as a pursuit predator (see Ewer, 1973; Andersson and Werdelin, 2003; Figueirido and Janis, 2011).

Pounce-pursuit predators are the least clearly defined of the three categories. Most pounce pursuit predators are canids, but the striped and brown hyenas (*Hyaena hyaena*; *Hyaena brunea*) are also considered to be pounce predators (Van Valkenburgh, 1985), and we have included some felids in this category (see below).

Few papers on the correlation of limb morphology and behavior specifically attempt to determine the ecomorphological aspects of the predatory behavior of carnivores, although of course there is a general correlation with substrate use and predatory mode: only terrestrial and cursorial predators can have pursuit or pounce types of predatory behavior. The notable exceptions are those of Andersson and Werdelin (2003) and Andersson (2004a), where they used the morphology of the distal humerus to distinguish cursorial predators from less cursorial ambushers (but did not distinguish between pounce and pursuit predators); and the one of Meachen-Samuels (2012), where she determined the “super-ambush” nature of sabertooth carnivores. To the best of our knowledge, since the 1985 paper of Van Valkenburgh we are the only authors (Figueirido and Janis, 2011) who have shown that morphology can distinguish among ambush, pounce and pursuit predators. Here, we extend this study to consider aspects of the anatomy of the entire forelimb. As detailed below, we restrict our study to larger, terrestrial carnivores because our interests are in the determination of the behavior of the more cursorial predators.

We had originally made the observation that, because of its humeral anatomy, the thylacine might be better termed the “Tasmanian tiger” than the “marsupial wolf” (Figueirido and Janis, 2011). However, this led to some misunderstanding in the popular press that we were suggesting that this animal had a behavior similar to a present-day large felid. In contrast, our data merely showed that thylacines, like most felids, retained the generalized condition of the distal humerus that allows for a degree of supination of the forelimb, and did not have a forelimb locked into a more prone position, as in extant canids. Our

TABLE 1. List of measurements taken in this study with comments on their significance (see also Fig. 1)

Measure	Description	Importance in analysis	Comments
<b>Scapula</b>			
S1	Length of scapular blade from glenoid to dorsal border measured along the length of the scapular spine	+	
S2	Width of scapular base across narrowest point (above glenoid)	-	
S3	Length (AP) of posterior portion of the glenoid from medial posterior border to the point of ventral inflexion with the anterior portion of the glenoid (on the back of the coracoid process)	+	
S4	Length (AP) of from the junction of anterior and posterior portions of the glenoid to the anterior border of the coracoid process	++	Serves a measure of the size of the coracoid process, which is the point of insertion of the coracobrachialis (flexes and adducts humerus, may act as shoulder stabilizer)
S5	Width (ML) of the scapular glenoid at the point of inflexion between the anterior and posterior portion (i.e. at the "waist")	-	
S6	Maximum width (ML) of the posterior portion of the scapular glenoid	-	
S7	Length of supraglenoid tubercle	+	Insertion of the biceps brachii, forearm flexor and supinator
S8	Length of acromion process	++	Acromion process is area of insertion of acromiodeltoid, a forearm abductor
S9	Width of acromion process at base	+++	
S10	Width of acromion process at tip	+	
S11	Length of the dorsal scapula border	-	
S12	Height of the scapula spine above the blade, near point of projection of acromion process)	++	Reflects area of insertion of spinotrapezius, important in scapular rotation
<b>Humerus</b>			
H1	Articular length	++	
H2	Height of greater tubercle above humeral head	++	The greater tubercle is the point of insertion of the supraspinatus and infraspinatus muscles.
H3	Length (AP) of the ridge along the top of the greater tubercle in dorsal view	-	These muscles are important in stabilizing the shoulder
H4	Width (ML) of the greater tubercle across the base in dorsal view, measured from point of projection from the body of the humerus, from the lateral edge of the bicipital groove to the lateral edge of the tubercle	+	carnivores the infraspinatus in particular also aids in supination and abduction of the humerus
H5	Width (ML) of the lesser tubercle in dorsal view, measured in a similar fashion as for H4	+	The lesser tubercle is the point of insertion of the subscapularis muscle. It acts as a shoulder stabilizer and also may participate in flexion and extension of the shoulder joint
H6	Height (DV) of the proximal humerus articular surface from the top of the humeral head to the base of the articulation	+	
H7	Width of humeral head	-	
H8	Midshaft diameter (ML) at base of deltopectoral crest		Not used directly, used to calculate H-AV (see below)
H9	Midshaft diameter (AP) at base of deltopectoral crest.		Not used directly, used to calculate H-AV (see below)
H-AV	Average midshaft humerus diameter	-	
H10	Depth (D/V) of distal articular surface, measured on the anterior face of the articulation	++	
H11	Maximum width across the distal humerus including the epicondyles.		Not used directly in analysis, used to generate variable H11-H12 (see below)
H12	Maximum width across the distal articular surface		Not used directly in analysis, used to generate variable H11-H12 (see below)
H11-H12	Effectively the width of the distal epicondyles	++	Origin for supinators, plus carpal extensors (lateral epicondyle) and flexors (medial epicondyle)
H13	Maximum width of the olecranon groove on the posterior side of the humerus	++	

Table 1. (continued).

Measure	Description	Importance in analysis	Comments
H14	Maximum width (ML) of the capitulum of the distal articular surface (articulation of radius)	++	A short and deep capitulum reflects a limb more locked into a prone position
H15	Maximum width (ML) of the trochlea of the distal articular surface (articulation of ulna)	+++	A long and slender trochlea reflects a limb capable of a large amount of supination
H16	Maximum height (DV) of the capitulum	+	
H17	Maximum height (DV) of the trochlea	+	
Ulna			
U1	Total length	–	
U2	Articular length, from center of proximal articulation to distal tip.	+++	
U3	Height (i.e., proximo-distal length) of the olecranon process above the dorsal lip of the trochlear notch	+	A measure of the moment arm of the triceps and anconeus muscles for the extension of the forelimb
U4	Length (AP) across the olecranon process, measured from the anterior edge just above the trochlea obliquely to the posterior edge of the top of the process	++	Provides an estimate of the degree to which the olecranon process is posteriorly deflected
U5	Length (AP) along the dorsal border of the olecranon process	++	
U6	Maximum width (AP) of the ulna just ventral to the trochlear notch	–	
U7	Maximum width of the base of the ulna, above the styloid process	++	
Radius and Manus			
R1	Maximum width (ML) of proximal articular surface	+	
R2	Minimum width (AP) of proximal articular surface	+	
R3	Length (ML) of distal articular surface.		Not used directly in analysis, used to generate variable R5-R3 (see below)
R4	Width (AP) of distal articular surface	–	
R5	Maximum width (ML) across the distal radius, including the styloid process		Not used directly in analysis, used to generate variable R5-R3 (see below)
R5-R3	Effectively the length of the styloid process	+++	Insertion point of the brachioradialis, acts as powerful forearm flexor when the limb is in a prone position
R6	Maximum midshaft width	–	
R7	Maximum length of radius	+++	
R8	Distance between proximal end of radius and base of radial tuberosity.	++	The radial tuberosity is the insertion for the biceps brachii, and thus this is a measure of the moment arm of the biceps brachii around the radius
M1	Length of longest metacarpal	++	
M2	Width (ML) of longest metacarpal	+	
P1	Length of first phalanx of longest digit	++	
P2	Width (ML) of first phalanx of longest digit	–	

investigation into further aspects of carnivore forelimb anatomy is with the intent of seeing if thylacines do indeed share any specialized aspects of their anatomy with felids, or if their anatomy is merely generalized in relation to that of extant placental carnivores; eye-witness observations of thylacines suggest that they did not pursue their prey over any great distance, but neither did they have specialized felid-like ambushing (Smith, 1982).

## MATERIALS AND METHODS

We took 44 linear measurements, using digital calipers to the nearest 0.01 mm, on a total of 57 specimens of extant carnivorous mammals (including 54 placentals [34 species] and three

marsupials [two species]), and five specimens of the thylacine, *Thylacinus cynocephalus*. The specimens were measured from the collections at the American Museum of Natural History (AMNH), and the Museum of Comparative Zoology (MCZ), with a few additions from the Museum Victoria and Queensland Museum. Specimens from zoos were avoided, except in the case of the thylacines, where no wild-caught specimens are available in any institution. Table 1 and Figure 1 show details of the measurements. Table 2 lists the specimens measured, and provides the guide to the numbers on Figures 3 and 4. Figure 2 shows a phylogeny of the taxa included here, and also notates their predatory behavior and average species body mass.

Our choice of measurements was based in part on those chosen in other works, and in part from our own determinations of potentially important morphological features (related to muscle attachments and biomechanical considerations). We originally took measurements of the length of the deltopectoral crest of

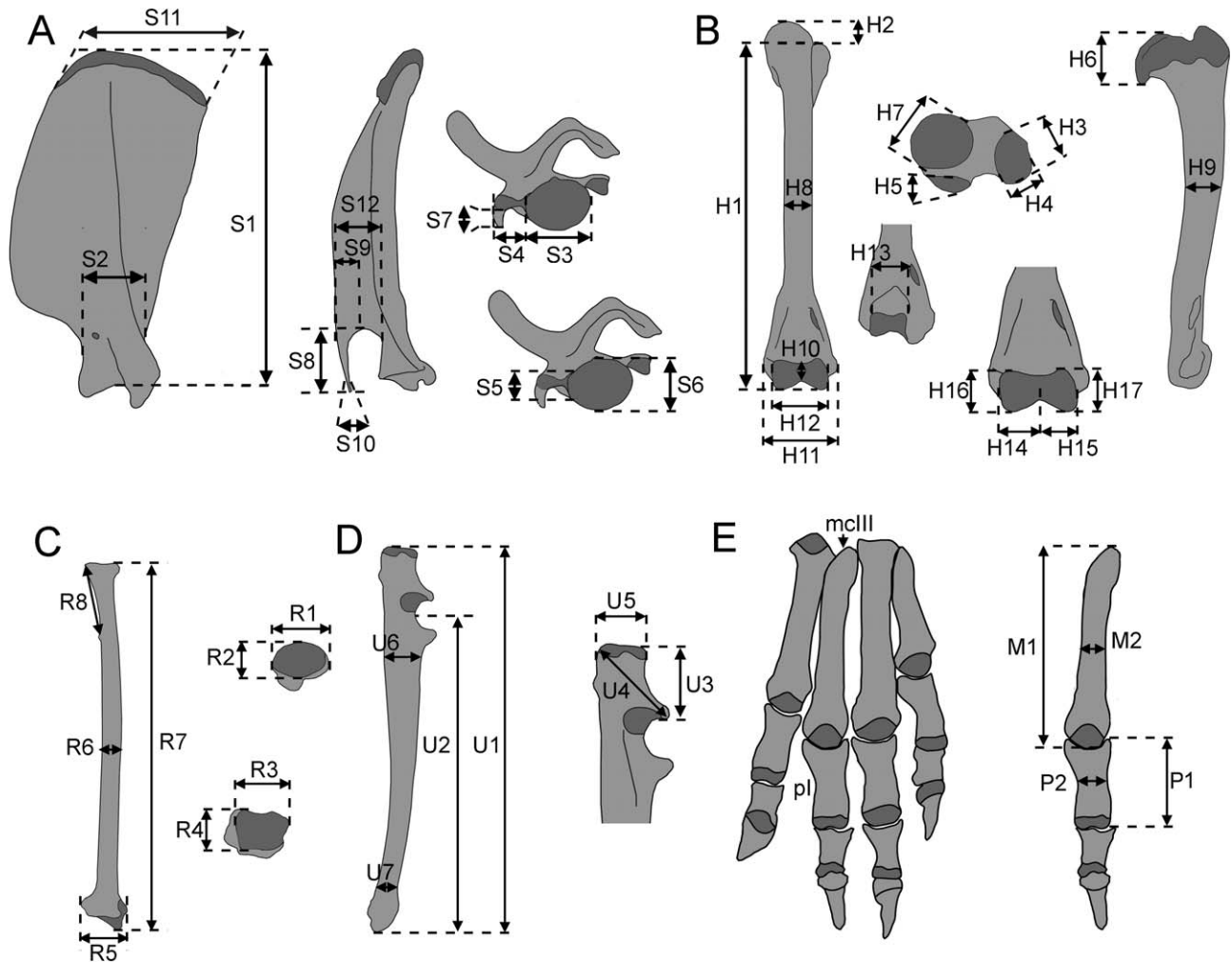


Fig. 1. Measurements taken on the forelimb anatomy (based on *Thylacinus cynocephalus*, AMNH 35244).

the humerus, a potentially important indicator of forelimb strength (e.g., Samuels et al., 2013), but we found this variable to be too subject to measurement error across taxa, as the more cursorial taxa had a rather poorly defined distal end to the crest, and we dropped it from the analysis.

Our choice of specimens of extant mammals was determined as follows. First, only terrestrial forms were selected; more arboreal taxa (e.g., the clouded leopard, *Neofelis nebulosa*) were excluded. Second, we considered primarily large cursorial or scansorial taxa, so almost all of our specimens are from the Canidae, Felidae, and Hyaenidae (see below for a couple of exceptions). However, as we wanted to include other marsupials (to make sure that any positioning of the thylacines within the morphospace was not due to phylogenetic affinities alone), we also included the extant larger dasyurids: the Tasmanian devil (*Sarcophilus harrisi*) and two spotted-tailed quolls (*Dasyurus maculatus*), both noncursorial forms that we classified as ambush predators. To balance the selection of these marsupials we included a placental of similar size and locomotor type (i.e., noncursorial, more plantigrade) in each case: the wolverine (*Gulo gulo*) was selected to compliment the Tasmanian devil (body mass 6–13 kg, Jones et al., 2001), and the marsh mongoose (*Atilax paludinosus*) to complement the spotted-tailed quolls (body mass 1.8–3.5 kg, Nowak, 1999).

Third we included only taxa within the general broad size range of the thylacine (average species body mass noted listed in Fig. 2): in general we sought to include only carnivores of the size of the thylacine (~25 kg) or greater, as there is a size threshold of around 15–25 kg below which placental carnivores primarily hunt prey much smaller than themselves (Carbone et al., 1999), and are usually more generalized in their behavior and morphology. However, because we also included some smaller marsupials, we also included some smaller carnivores in addition to the ones mentioned above, such as the little spotted cat (*Leopardus tigrinus*) and red fox (*Vulpes vulpes*). As the largest of the canids (*Canis lupus*) and the hyenids (*Crocuta crocuta*) are around 40 and 60 kg on average body mass (Nowak, 1999), we excluded the two felids that are significantly larger than this (the lion, *Panthera leo*, and the tiger, *Panthera tigris*), so as to avoid a bias where specimens from a single family and predatory mode dominated the large body size range in the data, especially as there are pronounced allometric effects on the forelimb bones at larger body sizes in felids especially (see Walmsley et al., 2012). Other than this, the specimens chosen for measurement reflect the availability in the institutions that we visited (primarily the Harvard MCZ and the AMNH).

Our sample sizes vary slightly between the various taxa, and largely reflect the availability of specimens in museum

TABLE 2. Taxa used in analyses. Taxonomy from Nyakatura and Binida-Emonds (2012) for the placental order Carnivora, and Cardillo et al. (2004) for the marsupial order Dasyuromorphia

ID #	Family	Taxon	Common name	Specimen no.	Sex	Predatory behavior
1	Felidae	<i>Puma concolor</i>	Puma	AMNH 135341	M	Ambush
2	Felidae	<i>Puma concolor</i>	Puma	MCZ 28614	U	Ambush
3	Felidae	<i>Leptailurus serval</i>	Serval	AMNH 119207	U	Pounce
4	Felidae	<i>Leopardus tigrinus</i>	Little spotted cat	MCZ 28678	M	Ambush
5	Felidae	<i>Leopardus pardalis</i>	Ocelot	AMNH 35734	M	Ambush
6	Felidae	<i>Leopardus pardalis</i>	Ocelot	MCZ 9351	U	Ambush
7	Felidae	<i>Caracal caracal</i>	Caracal	AMNH 113794	M	Pounce
8	Felidae	<i>Panthera onca</i>	Jaguar	MCZ 9371	U	Ambush
9	Felidae	<i>Panthera onca</i>	Jaguar	AMNH 90254	M	Ambush
10	Felidae	<i>Panthera onca</i>	Jaguar	AMNH 1135928	F	Ambush
11	Felidae	<i>Uncia uncia</i>	Snow leopard	AMNH 35303	F	Ambush
12	Felidae	<i>Uncia uncia</i>	Snow leopard	AMNH 100110	U	Ambush
13	Felidae	<i>Panthera pardus</i>	Leopard	MCZ 13666	M	Ambush
14	Felidae	<i>Panthera pardus</i>	Leopard	AMNH 347746	U	Ambush
15	Felidae	<i>Panthera pardus</i>	Leopard	AMNH 704085	U	Ambush
16	Felidae	<i>Panthera pardus</i>	Leopard	AMNH 54462	M	Ambush
17	Felidae	<i>Acinonyx jubatus</i>	Cheetah	AMNH 119654	U	Pursuit
18	Felidae	<i>Acinonyx jubatus</i>	Cheetah	MCZ 13667	M	Pursuit
19	Felidae	<i>Acinonyx jubatus</i>	Cheetah	MCZ 59279	F	Pursuit
20	Felidae	<i>Lynx rufus</i>	Bobcat	AMNH 141192	U	Pounce
21	Felidae	<i>Lynx canadensis</i>	Canada lynx	AMNH 80188	F	Pounce
22	Canidae	<i>Lycaon pictus</i>	African hunting dog	AMNH 82081	F	Pursuit
23	Canidae	<i>Lycaon pictus</i>	African hunting dog	AMNH 35177	F	Pursuit
24	Canidae	<i>Lycaon pictus</i>	African hunting dog	AMNH 82086	M	Pursuit
25	Canidae	<i>Cuon alpinus</i>	Dhole	AMNH 54976	M	Pursuit
26	Canidae	<i>Cuon alpinus</i>	Dhole	AMNH 102803	F	Pursuit
27	Canidae	<i>Cuon alpinus</i>	Dhole	AMNH 35929	U	Pursuit
28	Canidae	<i>Canis lupus</i>	Gray wolf	AMNH 134941	M	Pursuit
29	Canidae	<i>Canis lupus</i>	Gray wolf	AMNH 98227	U	Pursuit
30	Canidae	<i>Canis lupus</i>	Gray wolf	AMNH 98226	M	Pursuit
31	Canidae	<i>Canis familiaris dingo</i>	Dingo	MCZ 21590	U	Pounce
32	Canidae	<i>Canis familiaris dingo</i>	Dingo	MCZ 21591	U	Pounce
33	Canidae	<i>Canis familiaris dingo</i>	Dingo	QM 6963	U	Pounce
34	Canidae	<i>Canis familiaris dingo</i>	Dingo	QM 11500	U	Pounce
35	Canidae	<i>Canis simensis</i>	Ethiopian wolf	AMNH 81001	M	Pursuit
36	Canidae	<i>Canis aureus</i>	Golden jackal	MCZ 9342	U	Pounce
37	Canidae	<i>Canis mesomelas</i>	Black-backed jackal	MCZ 56858	M	Pounce
38	Canidae	<i>Canis latrans</i>	Coyote	MCZ 51124	U	Pounce
39	Canidae	<i>Canis latrans</i>	Coyote	MCZ 51692	M	Pounce
40	Canidae	<i>Urocyon cinereoargenteus</i>	Gray fox	MCZ 64708	F	Pounce
41	Canidae	<i>Alopex lagopus</i>	Arctic fox	MCZ 56778	F	Pounce
42	Canidae	<i>Cerdocyon thous</i>	Crab-eating fox	MCZ 3915	F	Pounce
43	Canidae	<i>Vulpes vulpes</i>	Red fox	AMNH 69550	U	Pounce
44	Canidae	<i>Lycalopex culpaeus</i>	Andean fox	AMNH 1427547	M	Pounce
45	Canidae	<i>Chrysocyon brachyurus</i>	Maned wolf	MCZ 28615	U	Pounce
46	Canidae	<i>Nyctereutes procyonoides</i>	Raccoon dog	MCZ 24860	U	Pounce
47	Canidae	<i>Speothos venaticus</i>	Bush dog	MCZ 28056	F	Pounce
48	Hyaenidae	<i>Crocuta crocuta</i>	Spotted hyena	AMNH 83593	M	Pursuit
49	Hyaenidae	<i>Crocuta crocuta</i>	Spotted hyena	AMNH 18776	M	Pursuit
50	Hyaenidae	<i>Proteles cristata</i>	Aardwolf	AMNH 70261	F	Pounce
51	Hyaenidae	<i>Hyaena hyaena</i>	Striped hyena	AMNH 35431	U	Pounce
52	Hyaenidae	<i>Hyaena hyaena</i>	Striped hyena	AMNH 5	U	Pounce
53	Herpestidae	<i>Atilax paludinosus</i>	Marsh mongoose	MCZ 38063	F	Ambush
54	Mustelidae	<i>Gulo gulo</i>	Wolverine	MCZ 5131	U	Ambush
55	Dasyuridae	<i>Sarcophilus harrisi</i>	Tasmanian devil	MCZ 6342	U	Ambush
56	Dasyuridae	<i>Dasyurus maculatus</i>	Spotted-tail quoll	NMV 5778	F	Ambush
57	Dasyuridae	<i>Dasyurus maculatus</i>	Spotted-tail quoll	NMV 25985	M	Ambush
58	Thylacinidae	<i>Thylacinus cynocephalus</i>	Thylacine	AMNH 35866	U	Unknown
59	Thylacinidae	<i>Thylacinus cynocephalus</i>	Thylacine	AMNH 42259	U	Unknown
60	Thylacinidae	<i>Thylacinus cynocephalus</i>	Thylacine	AMNH 35244	M	Unknown
61	Thylacinidae	<i>Thylacinus cynocephalus</i>	Thylacine	AMNH 35504	F	Unknown
62	Thylacinidae	<i>Thylacinus cynocephalus</i>	Thylacine	MCZ 36797	U	Unknown

The ID numbers are the key to the numbers in Figures 3 and 4.

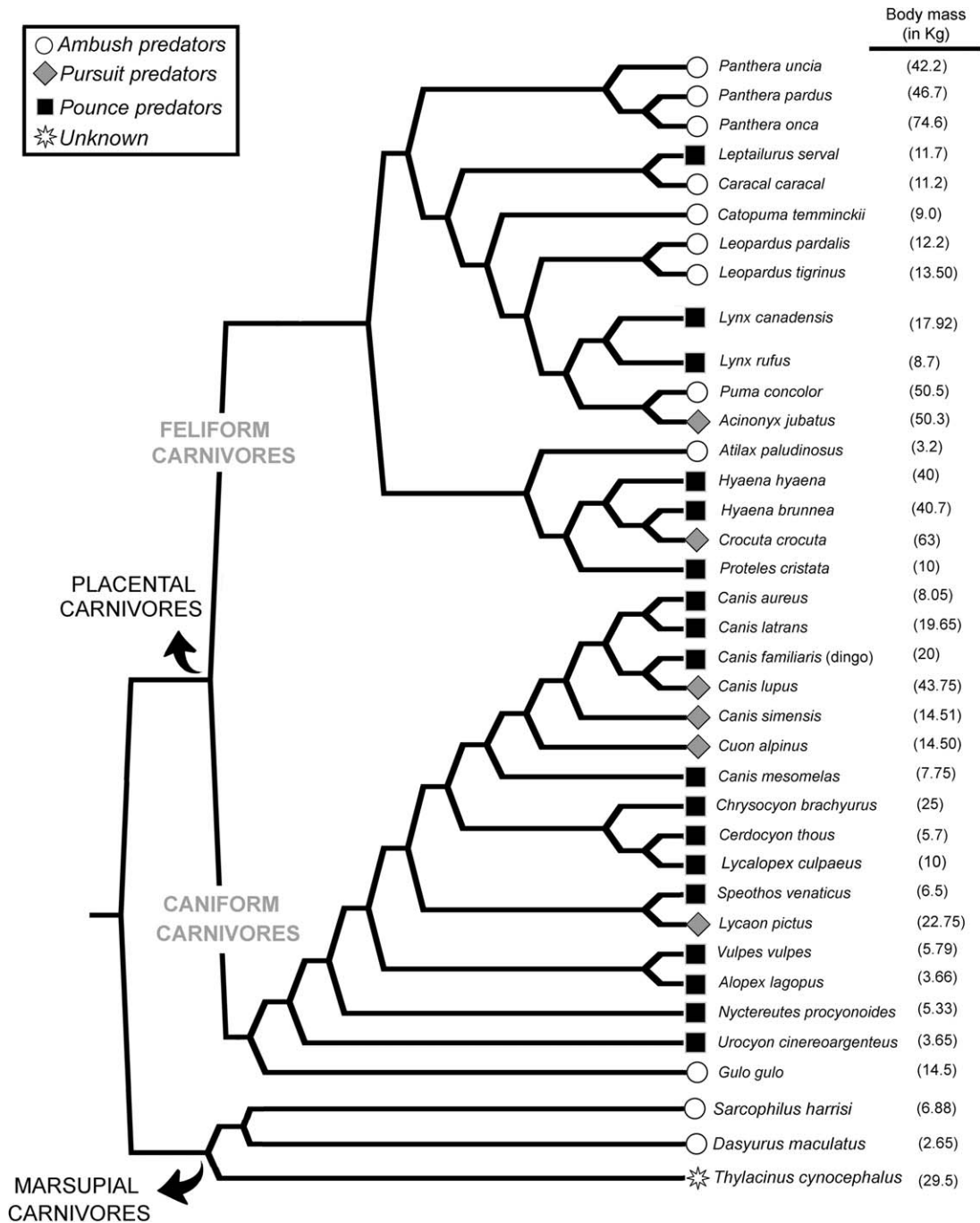


Fig. 2. Phylogeny and average body mass for the taxa used in this article. The tree topology and taxonomy was taken from Nyakatura and Binida-Emonds (2012) and Cardillo et al. (2004) for the placental order Carnivora and for the marsupial order Dasyuromorphia, respectively. The body mass was taken from the following sources: Tumilson (1987), Koehler and Richardson (1990), Jones (1997), Jones et al. (2001), Murray and Gardner (1997), Paddle (2000), Andersson et al. (2004b), Torregrosa et al. (2010), Figueirido et al. (2011a), Letnic et al. (2012).

collections. We obtained as many specimens of the thylacine as possible (five individuals). However, for the other taxa, the number of specimens varies from one to four. Although using individuals rather than species averages in the analyses could introduce some bias in ecomorphological analysis, such as the effects of static allometry, we used individuals in the analyses for the following reasons: i) In both canonical variates analysis (CVA) and discriminant analysis the reliability of group separa-

tion depends directly on the number of specimens included per group and ii) To explore if the intraspecific variability of the thylacine is similar to that seen in other predators. In any event, as the differences in the number of specimens included per species in our study are small, this difference is not enough to bias the various multivariate analyses. In fact, nowadays, it is a common practice to include the specimens measured as individuals, rather than to create species means (see e.g.,

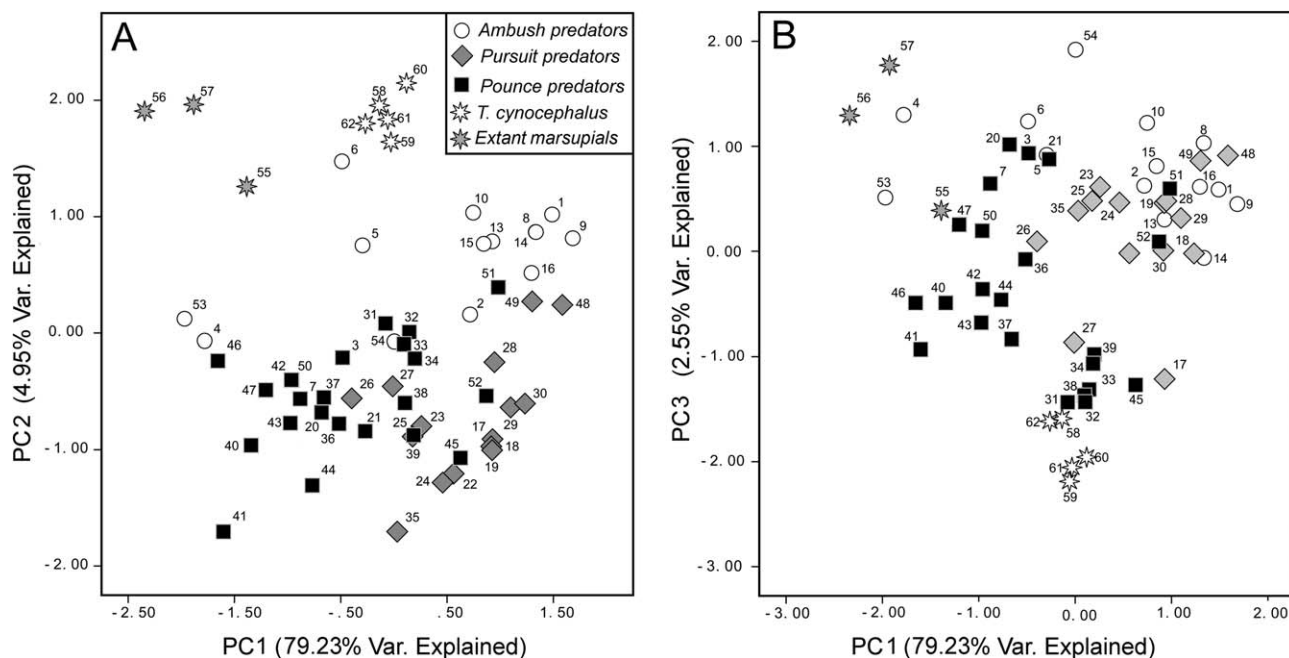


Fig. 3. Results of the principal components analyses. (A) Morphospace depicted from the bivariate graph of the scores of PC1 on PC2. (B) Morphospace depicted from the bivariate graph of the scores of PC1 on PC3.

Meachen-Samuels and Van Valkenburgh, 2009; Figueirido et al., 2011b; Meachen-Samuels, 2012).

We assigned predatory behaviors to the taxa largely following Van Valkenburgh (1985), but with a few exceptions. As noted in the previous section, we classified the cheetah (*Acinonyx jubatus*) as a pursuit predator. While felids are usually classified as ambush predators, because we sought to reduce phylogenetic bias in our sample, we re-evaluated the hunting behavior of felids from the literature and decided, at least for the purposes of this article, to classify some of the more cursorial felids as being pounce pursuit predators: the serval (*Leptailurus serval*, #3 on Figs. 3 and 4), the caracal (*Caracal caracal*, #7), the bobcat (*Lynx rufus*, #20) and the Canadian lynx (*Lynx canadensis*, #21). Note that in the principal components analysis (PCA) analysis these taxa cluster along the second factor with the pounce pursuit canids rather than with the other felids (see Fig. 3A). Note also that a recent study (Martín-Serra et al., 2014) analyzing the three dimensional shape of the forelimb in carnivores showed that two of these taxa have more slender limb bones than other living felines, with the exception of the cheetah. The ambush predators falling in this same part of the morphospace as the proposed “pouncer” felids in the PCA are the very small ones: the little spotted cat [*Leopardus tigrinus*, #4], and the marsh mongoose [*Atilax paludinosus*, #53]. The other felid of a similar size, the ocelot [*Leopardus pardalis*, #5, 6] clusters with the larger ambushing felids on factor 2.

We performed a PCA of log-transformed data of the complete set of measurements (Table 1; Fig. 1) to generate a phenotypic space based on forelimb anatomy. However, as PC-axes reflect the greatest variance in the whole dataset, and the specimens are ordered on these axes according to the major patterns of shape variation, PCA is not an appropriate method for separating a priori defined groups of specimens.

To investigate those skeletal features that best distinguish between the three hunting techniques displayed by extant terrestrial predators (i.e., ambush, pounce pursuit, and pursuit predators), we performed several canonical variates analyses (CVA): first from the complete set of measurements, and subsequently for each bone separately [i.e., scapula, humerus, ulna,

radius, and those of the manus (fourth metacarpal and first phalanx)]. We used the stepwise procedure instead of the direct method because it uses only the best set of variables to distinguish among the groups compared (Davis, 1986). This procedure reduces the dimensionality of the data and it is thus more appropriate when the samples within groups are not particularly large. The sole exception was the case of the manus as only four variables were included, and the direct method was preferred over the stepwise one. In addition, we performed different linear discriminant analyses (LDA) to discriminate between all possible pairings of the groups (i.e., ambush versus pursuit, ambush versus pounce, and pursuit versus pounce): again, first from the complete set of measurements, and subsequently for each bone separately (i.e., scapula, humerus, ulna, radius, and those of the manus [fourth metacarpal and first phalanx]). The power of the discrimination was evaluated with the percentage of correct assignments provided by the functions adjusted with the leave-one-out method of cross validation, and also with the Wilk’s lambda ( $\lambda$ ) and  $F$  statistic. As a selection criterion, the stepwise model included variables with  $F$  probability  $<0.05$  and excluded variables with  $F$  probability  $>0.1$ . In those cases where a large number of variables were incorporated into the functions, we restricted the inclusion of variables to an  $F$  probability of  $<0.005$ . We performed all the analysis (PCA, CVA, and LDA) with IBM SPSS statistics v.19.

## RESULTS

### Principal Components Analysis

The PCA gave three significant PCs (i.e., eigenvalue  $[\lambda] > 1.0$ ), which jointly explained more than 85% of the original variance. The first PC (explaining  $\sim 79\%$  of the variance) reflects clearly a size axis. The second PC (explaining  $>5\%$  of the variance) largely separates ambushers from the others (Table 3 and Fig. 3). Note that the cheetah clusters with other pursuit predators along the



TABLE 3. Summary of results of Principal Components Analysis and Canonical Variates Analysis (with all three predatory categories)

Bone(s)	% CC	Variables loading positively	Variables loading negatively	Groups distinguished	Reflects size?	Overlap	Thylacines cluster with?	Thylacines cluster with marsupials?
All bones (PCA2)		S8, S7, S10, H13, S9, H5, U7, H4, U3	M1, R5-R3, P1, H2, H1, R7, U2, U5, H10	Ambush (+)	No	Slight	Ambush	Yes
All bones (PCA3)		R5-R3, H11-H12, S4, H15, S7, P1, R8, R2, H13	S9, H2, R7, U2, U4, S1, S12	Pounce (-)	No	Slight	Pounce	No
All bones (CVA 1)	86	U4, M1	H11-H12, S8, S9	Ambush (-) Pursuit (+) Pounce (-)	No	Slight	Ambush	No
(CVA 2)		U4	S9, M1	Pounce (-)	In part	Considerable	Ambush & pursuit	No
Scapula (CVA1)	70.2	S8	S4	Pursuit (+)	No	Moderate	Ambush	Yes (with <i>S. harrisi</i> )
(CVA2)		S4, S8	-	Pounce (-)	Yes	Considerable	Ambush & pursuit	Yes (with <i>S. harrisi</i> )
Humerus (CVA1)	71.9	H16, H2	H11-H12, H15	Ambush (-)	No	Moderate	Pursuit & pounce	No
(CVA2)		H15, H16	H11-H12, H2	Pounce (-)	Yes	Considerable	None	No
Ulna (CVA1)	59.6	U7, U4	U5	Ambush (+)	No	Slight	Ambush	No
(CVA2)		U4	U5, U7	Pounce (-)	Yes	Considerable	Ambush & pursuit	No
Radius (CVA1)	71.9	R8, R3-R5	R7	Ambush (+)	No	Moderate	Pursuit & pounce	No
(CVA2)		R3-R5	-	Pursuit (-)	Yes	Considerable	Pounce	Yes (with <i>D. maculatus</i> )
Manus (CVA1)	68.4	M1	M2, P1	Ambush (-)	No	Moderate	Ambush	Yes
(CVA1)		M2	-	None	Yes	Considerable	Ambush & pursuit	Yes (with <i>D. maculatus</i> )

CC means correct classification following the leave-one-out cross-validation procedure.

second component of the PCA. Thylacines cluster on PC2 with more positive scores than most ambush placentals, as do the other marsupials (although this is not necessarily entirely a phylogenetic issue, as one of the ocelots, *Leopardus pardalis* [#6 on Fig. 3] also clusters with them). Those pursuit and pounce predators with high scores on PC2 (thus encroaching into the ambush predator morphospace) are all hyenids. Those ambush predators that score lower on PC2 are either the small placentals (the marsh mongoose *Atilax paudinosus*, and the little spotted cat, *Leopardus tigrinus*), as previously mentioned, or the plantigrade wolfverine (*Gulo gulo*, #54).

The variables loading with high values on PC2 reflect a forearm that is not specialized for cursoriality and where flexibility and some ability to supinate the hand is retained. The various measures of the acromion process reflect the retention of prominent limb abductors, such as the deltoids. The supraglenoid tubercle serves for the origin of the biceps brachii, so a large tubercle indicates a powerful forearm flexor. High values for the distal ulnar shaft reflect a relatively unreduced ulna, and the wide distal humeral trochlea relates to supination around the elbow. The lesser tubercle of the humerus is the point of insertion of the subscapularis muscle, one of the rotator cuff shoulder-stabilizing muscles, and a long olecranon process reflects a long moment arm for the triceps that maximizes power at the expense of speed. In summary, this component reflects ways in which both the marsupials, and the ambushing placental predators, have not modified their forearm from the more generalized mammalian condition.

In contrast, those factors loading negatively on PC2 reflect limb specializations that are generally indicative of a greater degree of cursoriality than in generalized mammals, reflecting longer distal limb segments, and an elbow that is more constrained for movement in the parasagittal plane. The inclusion of the radial styloid process (insertion of the brachioradialis muscle) is a little puzzling, as this usually reflects the powerful forelimb of ambush predators (see discussion of PC3, below). However, we also found this to be an important variable in distinguishing pursuit predators from pouncers (see later discussion), as if the forelimb is locked in a more prone position it acts as a flexor rather than a pronator/supinator.

The third PC (explaining 2.5% of the variance) separates thylacines and pounce predators from the others. Note that, on this axis, the possibly "pouncer" felids [#3, 7, 20, 21] cluster with the ocelots [#5, 6], and other ambushing felids; but the pounce hyenas (*Hyaena hyaena* [#51, 52] and *Proteles cristata* [#50]), also have high values on PC3, suggesting that this axis may in part be one distinguishing canids (lower values, at least the pouncer canids) from other carnivores

TABLE 4. Summary statistics of the results obtained from the Canonical Variates Analysis performed to separate among the three predatory groups using first, all forelimb bones together and secondly, each bone individually

		All the bones	Scapula	Humerus	Ulna	Radius	Manus
Function 1	<i>Eigenvalue</i>	3.309	0.896	1.547	0.792	1.264	0.982
	<i>Wilks' lambda</i>	0.113	0.393	0.270	0.409	0.323	0.385
	<i>Chi-square</i>	113.169	49.903	68.813	47.433	59.875	50.560
	<i>P-value</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
	<i>variance explained</i>	76%	72.5%	77.2%	68.4%	77.5%	76%
Function 2	<i>Eigenvalue</i>	1.045	0.340	0.456	0.365	0.367	0.310
	<i>Wilks' lambda</i>	0.489	0.746	0.687	0.732	0.731	0.764
	<i>Chi-square</i>	37.210	15.674	19.728	16.506	16.578	14.296
	<i>P-value</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
	<i>variance explained</i>	24%	27.5%	22.8%	31.6%	22.5%	24%

(although the bush dog, *Speothos venaticus*, [#57], also has fairly high scores). Of the pursuit predators, one cheetah (*Acinonyx jubatus*, #17) and one dhole (*Cuon alpinus*, #27) also score low on PC3, falling with the majority of the pounce predator canids.

The variables loading with high values on PC3 mainly denote forelimbs modified for a greater degree of power than seen in more generalized mammals, reflecting the use of the forelimbs either in grappling and restraining prey (in the case of the ambush predators), or in more sustained rapid locomotion (in the case of the pursuers). The radial styloid process is the site of insertion of the brachioradialis muscle, which acts to flex the forearm and supinate the hand; the coracoid process is the point of origin of the coracobrachialis muscle, a shoulder extensor and adductor; the larger humeral epicondyles are the origin of the hand flexor muscles and extensor muscles; a long supraglenoid tubercle is for the origin of the muscle biceps brachii (see above); and the position of the radial tuberosity, where the muscle biceps brachii inserts, denotes a long moment arm for the action of this muscle, reflecting power in forelimb flexion and protraction. Large felids, in particular, tend to have a long first phalanx. The low scores of the thylacines for these variables reflect the fact that, while they share many generalized features of the forelimb with ambush predators, they lack the specialized features related to forearm strength.

The variables loading with negative values on PC3 include length measures of the ulna and radius, and reflect the elongation of the forearm in more cursorial predators. The wide base of the acromion process indicates the retention of a more generalized condition, and this may be the reason why the pounce-pursuit predators tend to plot with lower values on PC3 than the more cursorial pursuit ones. The larger greater tubercle of the humerus (point of insertion of the supraspinatus and infraspinatus muscles) in more cursorial forms may reflect greater stabilization of the arm on the shoulder during faster locomotion. The

more caudally deflected olecranon process reflects a less crouched limb posture, as this morphology allows for the retention of the moment arm of the triceps with a more erect stance (Taylor, 1989; Van Valkenburgh, 1987). The longer scapular blade is a derived condition that may reflect the restriction of scapular motion to the parasagittal plane and/or allow for a greater stride length.

### Canonical Variates Analysis

**All forelimb bones.** The first canonical axis (see Tables 3 and 4, and Fig. 4A) provides an almost complete separation of ambush predators (positive scores) from pursuit predators (more negative scores) and from the pounce predators (intermediate scores). The two ambushers that fall within the pounce/pursuit grouping are both small placentals (the marsh mongoose, *Atilax paludinosus* [#53] and the little spotted cat, *Leopardus tigrinus* [#4]). The one pounce predator with very low scores, clustering with the pursuit predators, is the maned wolf (*Chrysocyon brachyurus*, #45), a position that can be explained by its extremely long metapodials. Interestingly, the Andean fox (*Lycalopex clupaeus*, #44) also clusters more with the pursuit predators on the first axis. The thylacines cluster with the ambushers (but with overlap with some of the pounce predators in this first canonical axis).

As in the PCA, the variables with positive high loadings on the first component reflect features of more generalized forelimbs that have not been specialized for cursoriality: large distal humeral epicondyles and a robust acromion process. The variables with high negative loadings reflect more derived features of the limbs: a less crouched limb posture (more caudally deflected olecranon process), and longer distal limb segments (metacarpals; see Supporting Information Table S1).

The second canonical axis separates the pounce pursuit predators (low scores) from the others, and may be selecting aspects of size: the combination of variables with positive loadings reflecting larger animals that have proportionally shorter metapodials and a more robust acromion process (see

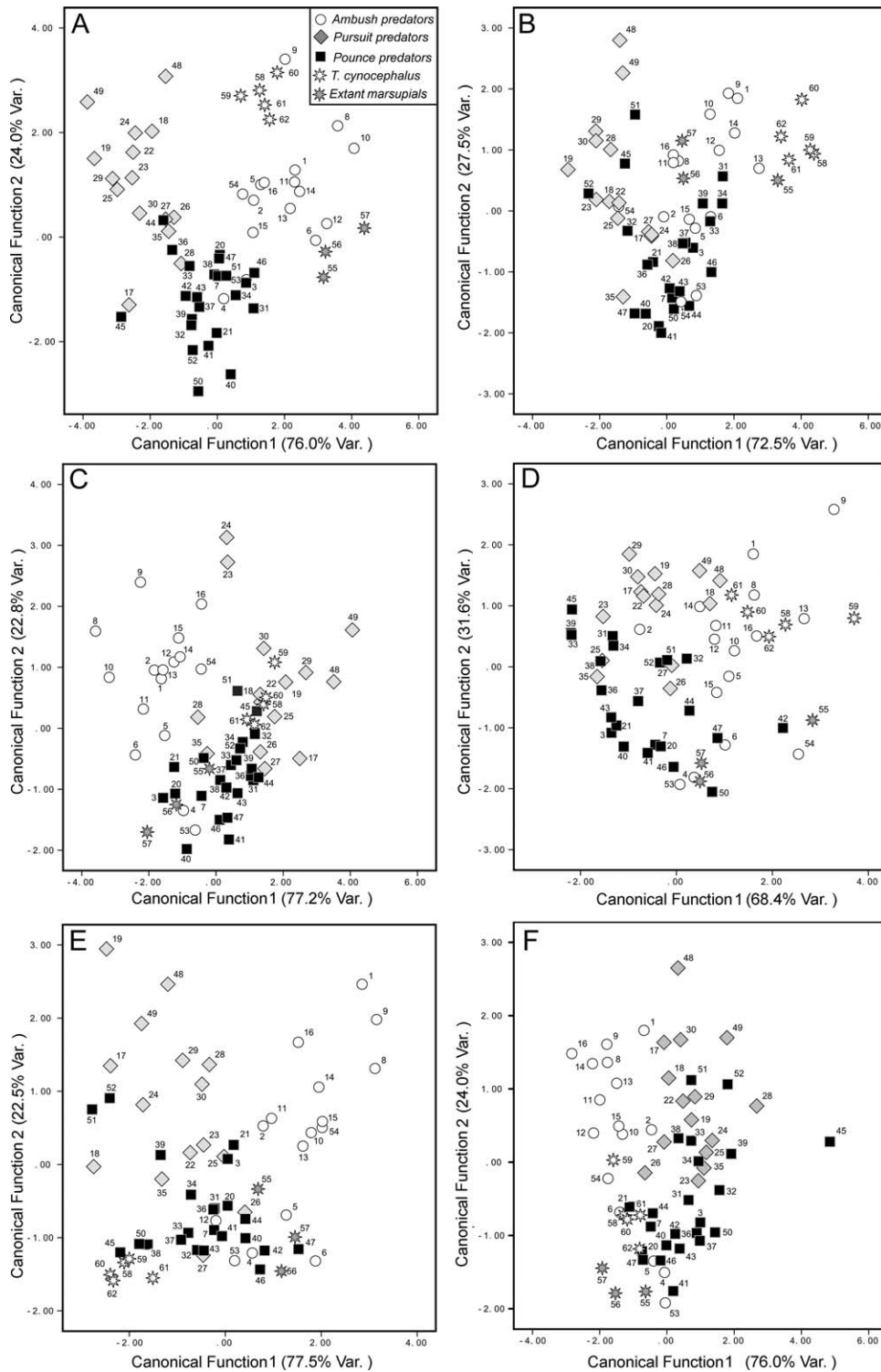


Fig. 4. Results of the canonical variates analyses (CVA) performed to find those morphological features that best distinguish among the three predatory groups (i.e., ambush; pounce-pursuit; and pursuit predators) using (A) the morphology of all the bones, (B) scapula only, (C) humerus only, (D) ulna only, (E) radius only, and (F) manus only.

Supporting Information Table S1). The ambush predators that have lower scores are the smaller ones: again the marsh mongoose and the little

spotted cat, and also the quolls (*Dasyurus maculatus*, #56, 57), and one of the ocelots (*Leopardus pardalis*, #6). One of the cheetahs (*Acinonyx*

*jubatus*, #17), also has low scores on this axis, unlike the other cheetahs (#18, 19): this is the same individual that clustered away from the other cheetahs in Figure 3B, perhaps representing an aberrant individual in some respects. The “pouncer” felids, (#3, 7, 20, 21) cluster with the pounce pursuit canids, away from the other felids. Perhaps surprisingly, the thylacines have high scores on this variable, clustering away from the pounce pursuit predators.

In summary, both canonical functions classified 86% of living taxa correctly following the leave-one out cross validation method. All of the thylacines were classified as ambushers with more than 99% of probability to belong to this predatory grouping.

**Each bone considered individually.** In each case, the distribution of taxa along the second canonical axis is similar: pounce predators have negative scores, except for the larger taxa (the striped hyenas, *Hyaena hyaena* [#51, 52], and, more variably, the maned wolf, *Chrysocyon brachyurus* [#45], the dingoes, *Canis familiaris dingo* [#31–34], and at least one of the coyotes, *Canis latrans* [#38, 39]). The pursuit predators generally have positive scores, except for the smaller forms: the Ethiopian wolf, *Canis simensis* [#35], and the dholes, *Cuon alpinus* [#25–27]. The larger ambushers (all of the *Panthera* species [#8–10, 13–16], and also the snow leopard *Uncia uncia* [#11, 12]) invariably have positive scores, while the smallest forms (the ocelot, *Leopardus pardalis* [#5, 6], the little spotted cat, *Leopardus tigrinus* [#4], the marsh mongoose, *Atilax paludinosus* [#53], and the quolls, *Dasyurus maculatus* [#56, 57]) invariably have negative scores, although the ocelots usually have the least negative of the scores. The two plantigrade taxa, the wolverine (*Gulo gulo* [#54]) and the Tasmanian devil (*Sarcophilus harrisi* [#55]) are more variable in their placement, but usually lie in between the smaller and larger ambushers, as does the puma (*Puma concolor* [#1, 2]). This difference between small and large ambushers may reflect the fact that larger ambush predators are more specialized, and more likely to grapple with their prey (Meachen-Samuels and Van Valkenburgh, 2009; Julik et al., 2012).

The CVA performed from the scapula morphology (see Tables 3 and 4, and Fig. 4B) yielded two canonical axes that correctly classified 70.2% of the living specimens of known predatory group. The first axis (see Table 4) separates the pursuit predators (negative scores) from the ambushers, with the pounce predators falling between the two groups (the one ambusher that clusters with the pursuit predators is the wolverine, *Gulo gulo*, [#54]). Pursuit predators are distinguished by a smaller acromion process (reflecting a limb with less abduction and more parasagittal motion), and a larger coracoid process (indicating a larger cora-

coradialis muscle, a shoulder extensor and adductor, reflecting greater stabilization of the humerus on the scapula during fast running). Here, thylacines cluster with the ambushers, but with even more positive scores than the extant ambush carnivorans, reflecting a relatively long acromion process (the Tasmanian devil, *Sarcophilus harrisi* [#55], has similarly high scores, but the quolls, *Dasyurus maculatus* [#56, 57] do not; see Supporting Information Table S5).

The same morphological variables both load positively on the second canonical axis. Little separation of groups is seen here, but as usual, pounce-pursuit predators tend to have the lowest scores. However, thylacines and the other marsupials have relatively high scores, clustering away from the pounce predators. For this analysis all of the thylacines were classified as ambush predators with a probability to belonging to this group of greater than 98%.

The CVA performed from the humerus (see Tables 3 and 4, and Fig. 4C) correctly classifies 71.9% of living carnivores, performing only slightly better than the scapula. The first canonical function clearly distinguishes ambushers (with negative scores) from other predators, with only the smaller ambush taxa falling into the morphospace of pounce predators. Ambushers are distinguished especially by large distal epiphyses, indicating powerful flexor and extensor musculature, and they retain the primitive feature of a long trochlea on the distal articular surface, indicating the retention of supination of the forearm. In contrast, ambushers lack the larger greater tubercle (stabilization of the shoulder joint during rapid locomotion) and the boxy capitulum (locking of the elbow joint into a more prone position) of the other predators (see Supporting Information Table S9). This axis probably indicates grappling with prey, as this is a feature of large carnivores, but not smaller ones (Julik et al., 2012; Meachen-Samuels and Van Valkenburgh, 2009). There is a degree of overlap between pounce and pursuit predators, but pursuit predators tend to have higher values (especially the spotted hyenas (*Crocuta crocuta*, #48, 49). Thylacines cluster in between the pursuit and pounce predators, and do not group with the other marsupials, which cluster with the ambushers.

The second canonical function separates most of pounce predators from the other carnivores, although there is a considerable overlap between them and some ambush predators. Along this function the thylacines again cluster in the middle of the analysis, while the wolverine (#55) now has positive scores, clustering with the large felids. Both functions classified the thylacines as pursuit predators with a probability ranging from 55 to 93% depending on the individual.

The ulna does not appear to be a particularly informative bone in this analysis, yielding only 59.6% of correct classifications (Tables 3 and 4, and Fig. 4D). The first canonical axis separates ambush predators (positive scores) from the others, largely on the basis of the generalized feature of an unreduced distal ulna, and a relatively narrow olecranon process (reflecting a relatively smaller area for the insertion of the triceps; Supporting Information Table S13). Pounce predators clustering with the ambushers include relatively less cursorial forms: the crab-eating fox (*Cerdocyon thous*, #42), the bush dog (*Speothos venaticus*, #47) and the aardwolf (*Proteles cristata*, #50). The “pouncer” felids (#3, 7, 20, 21) cluster with the pounce pursuit canids, away from the other felids. The thylacines cluster with the ambushers, but not with the other marsupials.

The second canonical axis again reflects size/generalized versus specialized condition, but in this analysis the thylacines have relatively high values, as do many of the larger felids.

The radius appears to be a more informative bone than the ulna for discriminating among predatory types (see Tables 3 and 4, and Fig. 4E), with 71.9% correct classification. On the first canonical axis, ambushers (positive scores) are distinguished by features representing forearm strength: the moment arms of the biceps brachii and brachioradialis muscles (both forelimb flexors), plus the retention of a relatively short radius (see Supporting Information Table S17). The pounce predators with relatively high scores are the less cursorial canids: the bush dog (*Speothos venaticus*, #47), the crab-eating fox (*Cerdocyon thous*, #42), and the raccoon dog (*Nyctereutes procyonoides*, #46). Here also the “pouncer” felids, (#3, 7, 20, 21) cluster with the pounce pursuit canids, away from the other felids. The two specimens of striped hyena (*Hyaena hyaena*, #51, 52) have very low scores, even lower than most of the pursuit predators. Thylacines cluster a large distance away from the ambush predators, lacking the specialized powerful forelimbs.

In contrast to the other analyses of single bones, thylacines have very low values on the second canonical axis, but interestingly cluster here (and also in the first axis) with the maned wolf, *Chrysocyon brachyurus* (#45), and the aardwolf, *Proteles cristatus* (#50), perhaps indicative of a rather weak forearm in all of these animals.

Only four variables are involved in the analysis of the manus (see Tables 3 and 4, and Fig. 4F) with 68.4% of correct classifications. On the first canonical axis, ambushers (negative scores) are distinguished by the possession of relatively short but broad metacarpals, a generalized condition, but also by the possession of a long first phalanx, which appears to be a specialized feature of the larger felids (see Supporting Information Table

S21). The maned wolf (*Chrysocyon brachyurus* [#45]) is an outlier (positive scores) on this axis, due to its extremely long metacarpals. Here the “pouncer” felids, (#3, 7, 20, 21) cluster with the similarly sized ocelots (#5, 6). Metacarpal width is the only variable with high loadings on the second function (see Supporting Information Table S21). Thylacines group with the ambushers on function one, but close to the area of overlap with the more cursorial predators, and have somewhat negative loadings on function two, here clustering to a certain extent with the other marsupials. All of the thylacines were classified by CVA as ambushers with an average probability to belong to this hunting group of 72% (ranging from 56 to 89% depending on the specimen).

### Linear Discriminant Analysis (Pairwise Comparisons)

Pairwise comparisons revealed additional information about the variables used to separate the different predatory groups. The figures showing the distributions of the taxa along a single axis are included in Supporting Information, but the description of the outcome of the analyses (Table 5) and the summary statistics (Table 6) are included here.

**All forelimb bones.** Ambushers are distinguished from pursuit predators (Supporting Information Fig. S1) by the possession of a less specialized elbow joint (i.e., less restriction of forearm motion to the parasagittal plane), a longer moment arm for the insertion of the biceps brachii (reflecting a limb designed for power rather than speed), and the retention of relatively short metacarpals (Supporting Information Table S2). Thylacines cluster with the ambushers.

Ambushers are distinguished from pounce predators (Supporting Information Fig. S1) based on the retention of a long acromion process and a more generalized elbow joint, while pounce predators have longer forearms (Supporting Information Table S3). Thylacines again cluster with the ambushers.

Pursuit predators are distinguished from pouncers (Supporting Information Fig. S1) by features that may reflect relative size rather than locomotion (Supporting Information Table S4), and thylacines cluster with neither grouping.

**Scapula.** Ambushers can be distinguished from pursuit predators (Supporting Information Fig. S2 and Table S6) by the same two variables as in the previous analysis, and from pounce predators only by virtue of having a longer acromion process (Supporting Information Table S7): thylacines again cluster with the ambushers in both cases.

Different variables are used to distinguish pursuit predators from pouncers (Supporting

TABLE 5. Summary of the results of the Linear Discriminant Analyses on pairwise comparisons of the predatory categories. Analyses performed to distinguish among the three predatory groups using first, all the bones together and second, each bone individually

Bone	Predatory comparison	% CC	Overlap?	Variables used (in order of importance)	Thylacines cluster with?
All bones	Ambush (-) vs. Pursuit (+)	100%	None	H14, R8 (-) M1 (+)	Ambush
All bones	Ambush (+) vs. Pounce (-)	95.2%	Minimal	H15, H6, S8 (+) H2, S3, R7 (-)	Ambush
All bones	Pursuit (-) vs. Pounce (+)	86.8%	Moderate	S9 (-) S15, U3 (+)	Neither
Scapula	Ambush (+) vs. Pursuit (-)	94.1%	Moderate	S8 (+) S4 (-)	Ambush
Scapula	Ambush (+) vs. Pounce (-)	76.2%	Considerable	S8 (+)	Ambush
Scapula	Pursuit (+) vs. Pounce (-)	92.1%	Moderate	S12 (+) S9 (-)	Neither
Humerus	Ambush (-) vs. Pursuit (+)	100%	None	H11-H12, H13 (-) H16, H2, H1 (+)	Neither
Humerus	Ambush (+) vs. Pounce (-)	90.5%	Moderate	H15 (+) H17, H2 (+)	Neither
Humerus	Pursuit (+) vs. Pounce (-)	89.5%	Slight	H10, H4, H15 (+) H17 (-)	Neither
Ulna	Ambush (-) vs. Pursuit (+)	88.2%	Moderate	U7, U3 (-) U5, U2 (+)	Ambush
Ulna	Ambush (+) vs. Pounce (+)	73.8%	Considerable	U2 (+) U7 (-)	Neither/ Ambush
Ulna	Pursuit (-) vs. Pounce (+)	73.7%	Considerable	U4 (+)	Neither
Radius	Ambush (-) vs. Pursuit (+)	91.2%	Slight	R5-R3, R8 (-) R1, R7 (+)	Pursuit
Radius	Ambush (+) vs. Pounce (-)	85.7%	Moderate	R2, R8 (+) R7 (-)	Pounce
Radius	Pursuit (-) vs. Pounce (+)	76.3%	Considerable	R5-R3 (+)	Pursuit

CC means correct classifications following the leave-one-out cross-validation procedure.

Information Fig. S2 and Table S8): here pursuit predators have a taller scapular spine, reflecting a larger spinotrapezius muscle for scapular rotation, but a smaller acromion process (at least, thinner at the base), reflecting a smaller acromiodeltoid for limb abduction. Thylacines do not distinctly cluster with either group.

**Humerus.** Ambushers are again distinguished from pursuit predators (Supporting Information Fig. S3) by virtue of large distal epicondyles, but additional variables are now co-opted. Ambushers have a wide olecranon groove on the posterior distal humerus, which denotes a broad and shallow morphology of this area: pursuit predators are again distinguished by a boxy capitulum, but additionally also show a larger greater tubercle (for the insertion of the supraspinatus and infraspinatus muscles, again indicative of shoulder stability), and they also have a longer humeral shaft (Sup-

porting Information Table S10). Similar indicators of elbow morphology distinguish ambushers (more generalized) from pounce predators (Supporting Information Fig. S3), and the pouncers also have a larger greater tubercle (Supporting Information Table S11).

Finally, pursuit predators are distinguished from pounce predators (Supporting Information Fig. S3) by features denoting greater restriction of rotation about the elbow joint (Supporting Information Table S12). In all of the pairwise comparisons the thylacines cluster in the area of overlap between the two categories.

**Ulna.** Ambushers are again distinguished from pursuit predators (Supporting Information Fig. S4) by a more robust distal ulna and a smaller olecranon process, while the pursuit predators have derived features: a more caudally deflected olecranon process (indicating a less crouched

TABLE 6. Summary statistics of the results obtained from the Linear Discriminant Analyses performed to separate among pairwise predatory groups using first, all the bones together and second, each bone individually

		All the bones	Scapula	Humerus	Ulna	Radius	Manus
Ambush vs. Pursuit	<i>Eigenvalue</i>	5.197	1.552	4.737	2.803	2.239	2.586
	<i>Wilks' lambda</i>	0.161	0.392	0.174	0.263	0.309	0.279
	<i>Chi-square</i>	55.634	29.037	51.534	40.070	36.432	38.946
	<i>P-value</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Ambush vs. Pounce	<i>Eigenvalue</i>	4.618	0.548	1.854	0.789	1.548	1.041
	<i>Wilks' lambda</i>	0.178	0.646	0.350	0.559	0.392	0.490
	<i>Chi-square</i>	63.862	17.256	40.381	22.677	36.016	27.475
	<i>P-value</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Pursuit vs. Pounce	<i>Eigenvalue</i>	2.123	1.524	2.526	0.899	0.682	0.897
	<i>Wilks' lambda</i>	0.320	0.396	0.284	0.527	0.595	0.527
	<i>Chi-square</i>	39.285	32.398	42.849	22.762	18.460	22.095
	<i>P-value</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

posture, as this) and a longer ulna shaft (Supporting Information Table S14). Thylacines cluster with the ambushers. A broad distal ulna also distinguishes the ambushers from the pounce predators, and the thylacines fall in the region of overlap between the two groups (Supporting Information Fig. S4 and Table S15).

The pursuit predators can also be distinguished from the pouncers (Supporting Information Fig. S4) by virtue of a more caudally projecting olecranon process (Supporting Information Table S16), the thylacines again clustering between the two groupings.

**Radius.** Ambushers are again distinguished from the pursuit predators (Supporting Information Fig. S5) by the variables indicative of long moment arms for the forelimb flexors in combination with a short radius, and the thylacines again cluster with the pursuit predators (Supporting Information Table S18). Similar variables distinguish the ambushers from the pouncers (Supporting Information Fig. S5; Table S19), with the thylacines clustering with the latter group.

Pursuit predators and pounce predators (Supporting Information Fig. S5) are weakly distinguished. Maximum width of distal radius is indicative of a more robust forelimb in the pursuit predators (Supporting Information Table S20): thylacines group with the pounce pursuit predators.

## DISCUSSION

### General Ecomorphological Variables

Our determinations of ecological correlates with predatory behavior match those of others to a fair degree. Ambush predators do not have the cursorial specializations of the other carnivores, and in some respects their morphology is more generalized. This is reflected in the retention of a large acromion process of the scapula, relatively short distal limb segments with an unreduced distal ulna, a distal humeral articulation that allows for a degree of supination of the forearm (relatively long and shallow capitulum and trochlea), and an undeflected olecranon process. Their morphology is specialized as evidenced in osteological features that reveal larger muscles with more distal insertions: these include muscles that flex the forelimb (biceps brachii and brachioradialis), with ambushers having a larger supraglenoid tubercle on the scapula, a more distally placed radial tuberosity, and a larger styloid process of the radius; and muscles that flex and extend the digits, reflected by enlarged distal humeral epicondyles. Large felids also have a relatively longer first phalanx, probably reflecting greater use of the hand in prey capture (see also Meachen-Samuels and Van Valkenburgh, 2009).

More cursorial predators (pursuit and pounce) have forelimbs that are modified for speed rather

than power: they have longer distal limb segments with a reduced distal ulna; a greater restriction of the limb motion to the parasagittal plane (as evidenced by the reduction of the acromion process of the scapula); a distal humeral articulation that reflects the limb locked in to a more prone position (shorter trochlea; deeper, more boxy capitulum, deeper proximal articular surface); an olecranon process of the ulna that is caudally projected (reflecting a less crouched stance); and reduced mobility of the digits (smaller distal humeral epicondyles for the origin of digital flexor and extensors). A new feature that we have identified here is in the morphology of the scapulohumeral joint: cursorial predators tend to have a larger coracoid process (origin of the corabrachialis) and a larger greater tubercle of the humerus (insertion of the supra- and infraspinatus muscles), which perhaps reflects a greater amount of stabilization of this joint during rapid locomotion.

### Can Pounce Predators be Distinguished from Pursuit Predators?

To a certain extent this is a size related issue: smaller cursorial predators (e.g., foxes and jackals) tend to be pouncers, while the larger ones (e.g., wolves) are pursuers. On a number of the plots (e.g., Fig. 4B [CVA scapula], 4C [CVA humerus], and 4E [CVA radius]), the smaller pursuit predators (the dholes, *Cuon alpinus* [#25–27]) tend to cluster more with the pounce predators. We (Figueirido and Janis, 2011) showed a difference (but with some overlap) in the distal humeral morphology between pursuit and pounce predators, but could that again just be related to body size? While body mass scales as a cube function of linear dimensions, joint surface area scales as a square function, and thus larger animals would be expected to have more robust joints (see Meachen-Samuels and Van Valkenburgh, 2009).

Conversely, size cannot be the only factor. The maned wolf (*Chrysocyon brachyurus* [#45], a pounce predator) and the African hunting dog (*Lycaon pictus* [#22–24], a pursuit predator) are of similar body size (~25 kg), but they have different morphologies. While they cluster together in some plots (e.g., Figs. 3A [second component of the PCA] and 4D [CVA ulna]), they do not do so uniformly (note Fig. 4A [CVA all bones included] and 4E [CVA radius]); in general the maned wolf has limb elements that are much more gracile.

So, the question remains: are pursuit predators merely pounce predators writ larger, or have they gone the extra mile in their morphology (as well as in their behavior) to reflect a greater degree of stamina? And, if so, are their osteological correlates that can be used to distinguish between pouncers and pursuers in the fossil record? The results of the pairwise comparisons obtained here

TABLE 7. Summary of the results of the Linear Discriminant Analyses on pairwise comparisons of pounce versus pursuit predators in the canids; first, all the bones together and second, each bone individually

Bone	% CC	Overlap?	Variables used (in order of importance)	Thylacines cluster with?
All bones	83%	moderate	S9 (-) S12, U3 (+)	Neither
Scapula	78%	moderate	S12 (+) S9 (-)	Neither
Humerus	85%	slight	H10, H4, H14 (+) H16 (-)	Neither
Ulna	69%	considerable	U4 (+)	Neither
Radius	67%	considerable	R5-R3 (+)	Pursuit

CC means correct classifications following the leave-one-out cross-validation procedure.

(see Table 5) allow us to identify some morphological features that could help to differentiate between pounce and pursuit predators. For example:

- i. The linear measurements support our geometric morphometric measures of the distal humeral articulation: pursuit predators have a deeper articulatory surface (H10), a more box-shaped capitulum (H14) and a smaller trochlear (H16).
- ii. Pursuit predators have reduced their acromion process (especially the width of the base, S9) to a greater extent than pouncers, possibly reflecting a lesser commitment to the restriction of limb motion to the parasagittal plane.
- iii. Pursuit predators tend to have a taller scapular spine (S12), perhaps reflecting a larger spinotrapezius for scapular rotation during locomotion.
- iv. Pursuit predators have an olecranon process of the ulna that is more caudally projected (U4), but this could merely be a reflection of body size.

To further investigate the possibility that pursuit and pounce predators might be separated by osteological features, we reran the analyses (see Table 7) using the canids only (excluding the maned wolf, *Chrysocyon brachyurus*, with its peculiarly long legs), to see if a similar signal could be picked up with a more restricted group of carnivores (both in terms of phylogeny, and in terms of behavioral classifications). Several variables emerged that separated these two predatory modes among canids. Some were clearly related to body size, such as relatively more robust metacarpals in the pursuit predators. However, some of the determinations above for the full range of carnivores were recovered in this more restricted analysis of the canids, in particular the lower value for the base of the acromion process (S9) in pursuit predators, indicative of a reduction in limb adductor musculature and the restriction of limb motion to a more parasagittal plane, and a taller scapular spine (S12), possibly reflecting a larger spinotrapezius for scapular retraction. In addition, the pursuit canids have a deeper humeral head (H6), also indicative of restriction of the range of

forearm movement. This matches well with the geometric morphometric studies of the distal humerus, which showed that pursuit predators have more restriction of rotatory motion at the elbow joint (Figueirido and Janis, 2011), although perhaps puzzlingly, the pursuit canids also have a less deep distal humerus capitulum (H16) than the pouncers. Other features of pursuit canids include a larger radial styloid process (R5-R3), reflecting speed of forearm flexion, perhaps important for more rapid recycling of the forelimb, and a relatively broad distal ulna (U7), which may reflect overall size and robusticity.

More data, larger sample sizes, greater consideration of the possible effects of body size, and a more rigorous determination of extant taxa into predatory behavior would be needed to determine if these osteological features are valid. We present these observations as interesting but tentative as exploring the differences between these two predatory groups to define what if anything is a pounce is beyond the scope of this article.

### The Predatory Behavior of the Thylacine

Jones and Stoddart (1998) and Jones (2003) made quantitative determinations of thylacine ecomorphology and likely predatory behavior. Various limb ratios of thylacines, such as the metatarsal/femur ratio (a traditional index of speed), the metacarpal/phalangeal ratio (indicative of manus shape and foot posture), and the olecranon process/ulna shaft ratio (indicative of fossorial versus terrestrial versus arboreal activities) all placed this animal, in comparison with extant placental carnivores, as a generalized terrestrial form, less specialized than extant felids and pounce-pursuit canids, and similar to that of the noncursorial extant marsupials quolls and Tasmanian devils. From this, Jones determined that thylacines were not fast runners, certainly unlikely to have been pursuit predators, and she classed them as pounce-pursuit predators.

Jones's data and interpretations certainly agree in general with ours here, but we note that our data do not classify the thylacine within the morphometric range of extant carnivoran pounce-pursuit predators, and that the thylacine rarely clusters with the other marsupials in any of our



analyses (see Table 3, the second component of the PCA [Fig. 3A] being a notable exception). Rather, the thylacine appears to be more generalized in its morphology than any extant placental.

In our geometric morphometrics study of the distal humerus (Figueirido and Janis, 2011) we showed that the thylacine specimens fell within the morphospace of the ambushers, but this was largely because the ambush predators retain a more generalized elbow morphology, while the pursuit and pounce predators are more specialized to restricting forearm supination. In this larger study, a clearer pattern emerges. When the ambush predators are being distinguished on the retention of primitive features, such as a large acromion process and an unreduced distal ulna, and the cursorial predators are being distinguished by derived features such as elongated metacarpals and the caudal deflection of the acromion process, then the thylacines cluster with the ambushers (e.g., second component of PC2 [Fig. 3A], CVA of all the forelimb bones [Fig. 4A], CVA of the scapula [Fig. 4B], CVA of the ulna [Fig. 4D], and CVA of the manus [Fig. 4E]). However, when the ambushers are being distinguished by derived features indicative of forearm strength, such as enlarged distal humeral epicondyles, distal placement of the radial tuberosity, large styloid process of the radius, then the thylacines cluster with the cursorial predators (e.g., the CVA of the humerus [Fig. 4C], and CVA of the radius [Fig. 4D]). In almost no analysis do thylacines cluster specifically with the pounce-pursuit predators (the exception being on the third component of the PCA). In fact, on the second function of the discriminant analyses, where the axis seems to be one reflecting size/robusticity/generalized features, the thylacines usually cluster in the opposite direction from the pouncers (the exceptions being in the case of the radius and the manus, see Fig. 4D,E).

Why should it be the case that thylacines are so much less specialized than placental carnivores? One suggestion has been that marsupials cannot become as specialized in their forelimb anatomy as placentals, due to the constraints of parturition, when they have to make the climb to the pouch (e.g., Sears, 2004). Ercoli et al. (2012), in their study of extinct South American marsupial carnivores (sparassodontids), note that these animals always retain some degree of a lateral epicondylar crest on the humerus, reflecting the role of the digital flexor and extensor muscles in the neonate. However, they nevertheless demonstrate a diversity of different predatory modes among these marsupials, including arboreal and scansorial forms, although none appears to have been a specialized cursor.

However, the ecomorphology of the thylacine needs to be considered in the light of the history of the Australian mammal faunas (see Black et al., 2012). There were two separate lineages of large marsupial carnivores in Australia, both initially

known from the late Oligocene: The thylacoleonids (marsupial “lions”) that did not survive the Pleistocene, and the thylacinids, that survived into the 20th century. Thylacoleonids were always highly specialized, “super-ambush” carnivores, with possibly analogous behavior to placental sabertooths (Wroe et al., 2008); while the thylacinids, although having a moderate diversity of body sizes (ranging from around 1–50 kg), retained a more generalized postcranial morphology. Although a number of genera and species of thylacines have been named, they all retained a generalized postcranial morphology (although some may have been more arboreal than *Thylacinus*), and after the late Miocene no more than one thylacine species (and only of the genus *Thylacinus*) is known from any fossil fauna (this is also true for the thylacoleonids). This is in contrast to the much greater diversity of placental carnivores known from both fossil and recent faunas, a diversity that may have forced divergent specialization among the placentals. In contrast, it appears that Plio-Pleistocene to Recent thylacines, at least, were the only medium sized carnivores in the faunas (with the exception of the highly specialized marsupial lions), and so were never under any selective pressure to specialize their type of predatory behavior, although their craniodental morphology was clearly specialized for meat-eating (e.g., Wroe et al., 2007). Whatever the reason, the morphology of the thylacine shows it to be a more generalist type of predator than any known placental—broadly an “ambush” or “pounce” predator, but lacking the anatomical specialties of those types of placental carnivores.

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