by muscles that attach to the scapula and humerus, with the clavicle providing stability and support for the position of the shoulder joint. Thylacines, however, had a very reduced clavicle, which enabled the forelimb to move more easily in line with the body for rapid running locomotion. Similar adaptations are found in other running mammals.

As mentioned before, marsupials generally possess an elongate epipubic bone that is connected to the front of the pelvis and the muscles of the abdominal wall. This bone is also found in monotremes and reptiles but has been lost in the evolution of eutherian ('placental') mammals. It has been suggested that epipubic bones may help to stabilise the trunk during locomotion. Thylacines, however, had very reduced epipubic bones in comparison with all other marsupials (except the very unusual marsupial moles), which suggests that thylacines evolved quite different adaptations to locomotion than other marsupials, with the reduced epipubic bones presumably allowing greater flexibility of the trunk for rapid running locomotion.

Collectively, these features demonstrate remarkable specialisation in the thylacine skeleton for cursorial running locomotion that, evolutionarily, is convergent with other running mammals. There is still much to be learnt about the evolution and development of the thylacine skeleton though. It would be interesting to examine the rate of growth of the different parts of the skeleton and also to examine the early development of features such as the reduced clavicle and epipubic bones, so that we can better understand the forces that influenced the evolution of this unique and beautiful marsupial.

How thylacines walked

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Animals with legs use them to propel themselves, often in irregular bursts of movement. When they repeat a regular pattern of propulsive limb movements over and over at a constant speed, the pattern is called a 'gait'. Gaits are either symmetrical, in which the pattern in the second half of each cycle is a mirror image of the first half (with left and right reversed, as in a human walking: left, right, left, right), or asymmetrical (e.g. a kangaroo hopping with both legs moving together). As an animal walks faster and faster, each foot stays planted for a smaller percentage of the cycle, until there is a part of the cycle ('aerial phase') when the animal is flying through the air with all feet off the ground. At that point, the animal is no longer walking, but running.

Any symmetrical four-footed gait can be specified by just two numbers: duty factor (the percentage of time that a foot is planted on the ground, which is usually about the same for all four feet and varies roughly as the inverse of speed) and diagonality (the phase difference between fore- and hindlimbs: the percentage of total-cycle duration by which the forelimb repeating left-right cycle lags that of the hindlimb). In a symmetrical gait with very low or very high diagonality, the animal puts both left feet down together and then both right feet,

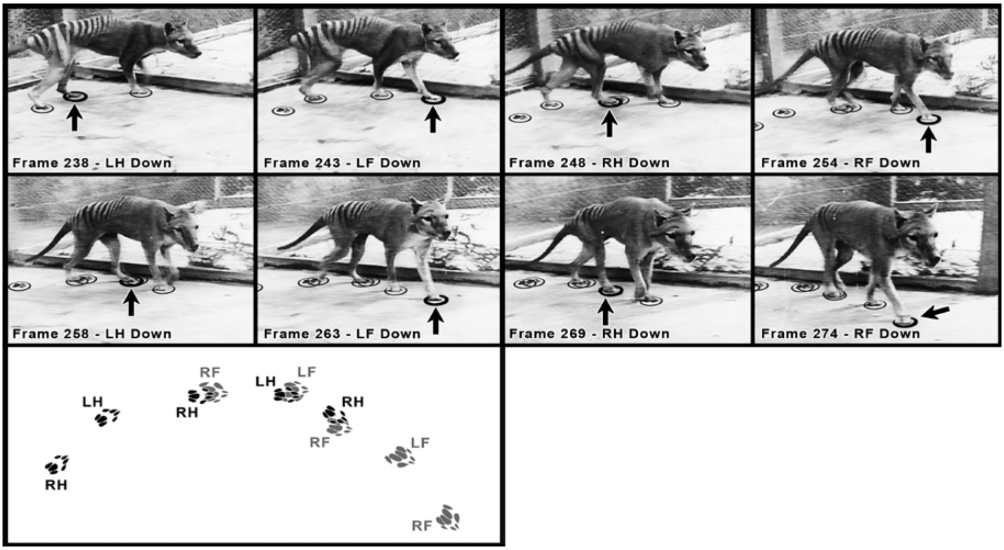

Fig. 3. Eight frames representing the eight footfalls (F = fore, H = hind, L = left, R = right) from two successive strides of the thylacine 'Benjamin'. Arrows indicate the foot that has just touched down in each frame. The superimposed pawprints, added to mark the position of each footfall, present a schematic curved trackway (bottom). In these cycles, the animal's footfalls are almost evenly spaced in time, giving it a diagonality of approximately 25 and placing it near the boundary between diagonal and lateral couplets (see Fig. 4). Film stills courtesy of The Thylacine Museum <http://www.naturalworlds.org/thylacine/>.

similar to a camel walking ('lateral couplets'). In a gait with moderate diagonality, limbs that are diagonally opposite move together, as in a trotting horse ('diagonal couplets').

Different mammals walk symmetrically in different ways, putting their feet down in footfall sequences that vary among orders and families. The few existing films of captive thylacines give us an opportunity to see which of the other mammals the thylacine most resembles. Thylacines resemble the dog family (Canidae) of placental mammals in diet, dentition and body form and so we might expect them to have dog-like locomotion as well. We have described that the two thylacine walking cycles extracted from one of the films resembled the slowest walks of dogs (Cartmill *et al.* 2020). The recent discovery of new films of caged thylacines was an opportunity to increase our sample.

We studied all nine known films of thylacines and identified potentially usable gait cycles from four of them.[2] These cycles were converted into still frames using the 'Render Video' function in Adobe Photoshop and the frame numbers for each footfall and liftoff were determined for calculating duty factor and diagonality (Fig. 3). Because these films were not made with gait analysis in mind, image resolution is low and the camera angles are less than ideal, so different observers sometimes had different estimates of the exact frame in which a foot was lifted or put down. To help correct for interobserver error, we ran four independent

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[2] Eds: this chapter was written before the discovery of the tenth known film (see Chapter 53, pp. XXX–XXX), which unfortunately does not contain a useable gait cycle for the juvenile animal.

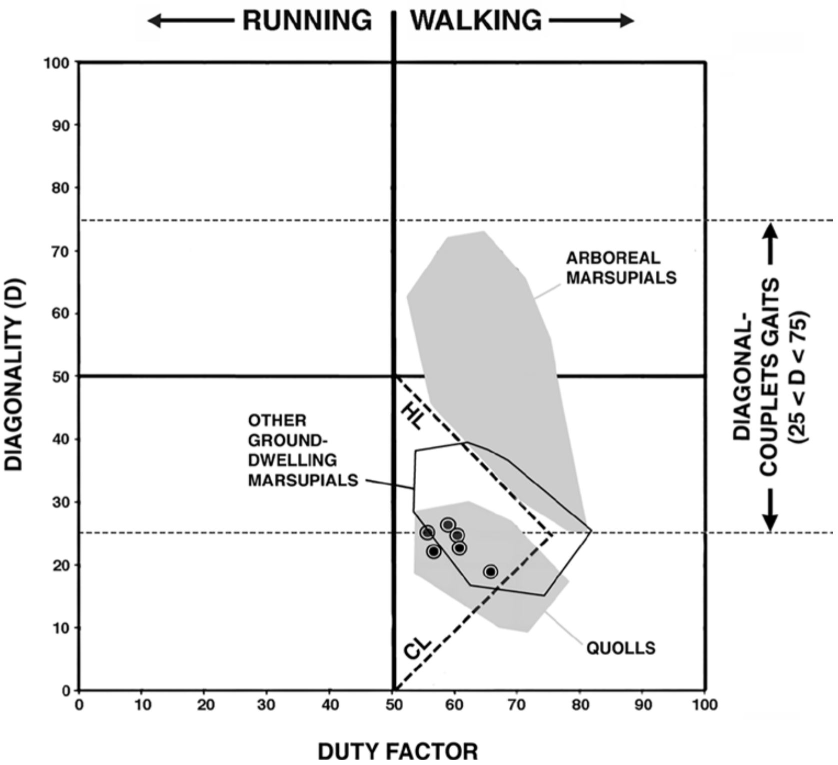

Fig. 4. Estimated duty factor and diagonality in thylacine walking gaits, averaged across four observers for each of six symmetrical walk cycles (circles). Diagonal dashed lines represent the theoretical 'horse line' (HL; see text) and 'camel line' (CL). Lower grey area: spotted-tailed quoll (*Dasyurus maculatus*). Solid outline: other ground-dwelling marsupials. Upper grey area: arboreal marsupials. Non-thylacine data from (Cartmill *et al.* 2020).

analyses of each of the cycles examined and came up with just six gait cycles determined by all four analysts to be symmetrical. These six cycles are from two films, both of the same individual ('Benjamin') in the Beaumaris Zoo in Hobart (Sleightholme *et al.* 2020).

The values of duty factor and diagonality reported by the four observers were averaged for each of these six cycles and plotted on a 'Hildebrand diagram', a graph of duty factor against diagonality (Fig. 4). Our analyses showed that the surviving records of thylacine locomotion all represent moderately slow walks, clustered around the boundary between lateral-couplets and diagonal-couplets gaits, similar to the recorded gaits of quolls (*Dasyurus* spp.) in captivity and similarto the walks of most other terrestrial marsupials, the observed thylacine gaits all lie below the so-called 'horse line' (Fig. 4). Gaits in this part of the Hildebrand diagram minimise interference between fore- and hindfeet in walking (Cartmill *et al.* 2020).

We predict that thylacines, as with other terrestrial marsupials, would have exhibited higher diagonality values in walking as speed increased and duty factors went down (following the horse line upward), but they would not have displayed the behavioural flexibility seen in the gait-pattern distributions of dogs (i.e. encompassing both horse-type and camel-type gaits: Cartmill *et al.* 2002). We will probably never know for sure unless living thylacines are discovered or new films come to light showing thylacines moving around at more varied speeds in less cramped enclosures. However, our prediction should also hold for Tasmanian devils (*Sarcophilus harrisii*), the thylacine's largest surviving relative – which, happily, are still around to be studied.

Acknowledgements

We are grateful to The Thylacine Museum's Curator, Cameron Campbell, for his generous provision of all the known films of living thylacines and for his kind permission to use the stills reproduced in Fig. 3.

The likely hunting behaviour of the thylacine, as deduced from its forelimb anatomy

Christine M. Janis and Borja Figueirido

The thylacine has been popularly called the 'marsupial wolf', especially in the Northern Hemisphere, and is often used as a classical example of convergent evolution between marsupials and placentals. But despite its superficially dog-like appearance, the thylacine was certainly not an ecological analogue of the placental wolf. Rare observations from the early 20th century report it hunting alone or in pairs, with neither the pursuit chasing of a wolf nor the specialised ambush attack of a large cat (Smith 1982). Were thylacines perhaps like other, more generalised canids, such as coyotes or jackals? These animals hunt via a type of behaviour called 'pounce–pursuit', which involves a short chase before pouncing on the prey.

Could the skeleton of the thylacine inform us as to its predatory behaviour? To answer this question, we must determine whether such behaviours correlate with the anatomical features of living animals with known behaviour. Scientists have been making investigations into the correlation between anatomy and behaviour (and/or performance) in animals for many years. In the past couple of decades techniques have become increasingly sophisticated, including the use of computed tomography scans of bones to image the anatomy in detail, and a diversity of statistical techniques to analyse the data collected.

Some previous studies on general limb proportions (Jones and Stoddard 1998; Jones 2003) showed the thylacine to be a generalised carnivore, less specialised for either running or pouncing than living placental carnivores and more similar to its marsupial relatives, the quolls and the Tasmanian devil. We decided to look specifically at the forelimb, because that reflects whether a carnivore is specialised for running (e.g. wolves) or retains the ability to grapple with its prey (e.g. cats).

A particular feature that we noted was the structure of the elbow joint, specifically the anatomy of the lower end of the humerus (the upper arm bone). When humans rotate a hand from the palm facing down position (prone) to the palm facing up (supine), the movement comes from the rotation of the forearm (comprising the radius and ulna bones) at the elbow