Reconstructing the biology of extinct horses from hard-tissue histology:

The case of a South African hipparionine

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Introduction – Hard-tissue histology and life history

Bone and dental histology are useful tools to obtain **palaeobiological information** from extinct animals. They provide information about different life history traits

Photo: C. Nacarino-Meneses

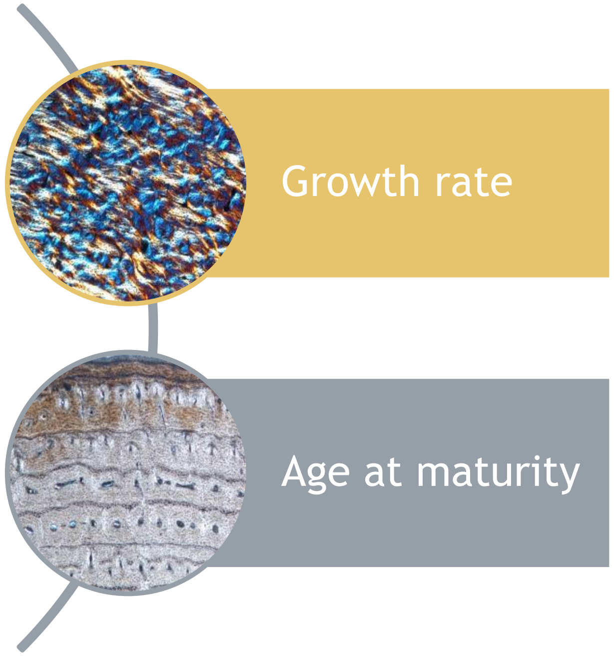
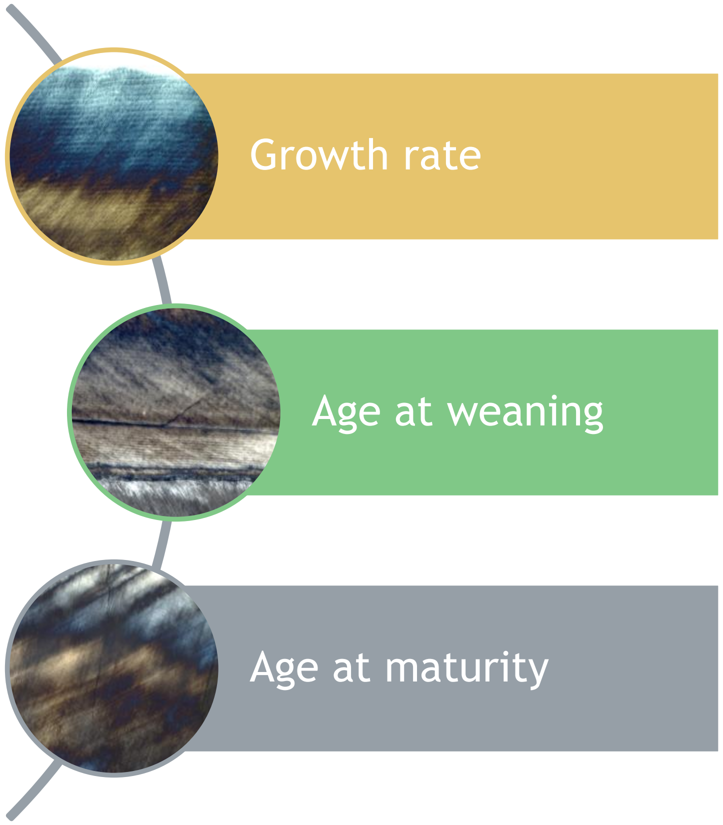


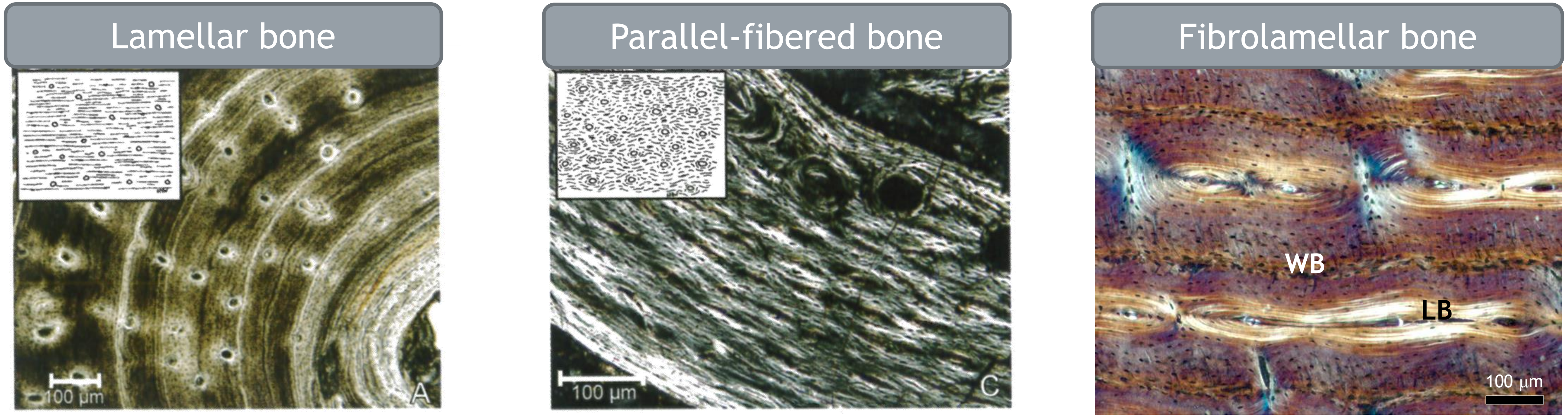
Photo: C. Nacarino-Meneses



Introduction – Bone histology and growth rate

Bone tissue is classified into **different typologies** based on the number and density of bone cells, the distribution of collagen fibers within the bone matrix and the quantity of vascular canals

Primary bone tissue types **differ in their rate of deposition (Amprino's rule)** ❯ Differences in the rate of growth among species

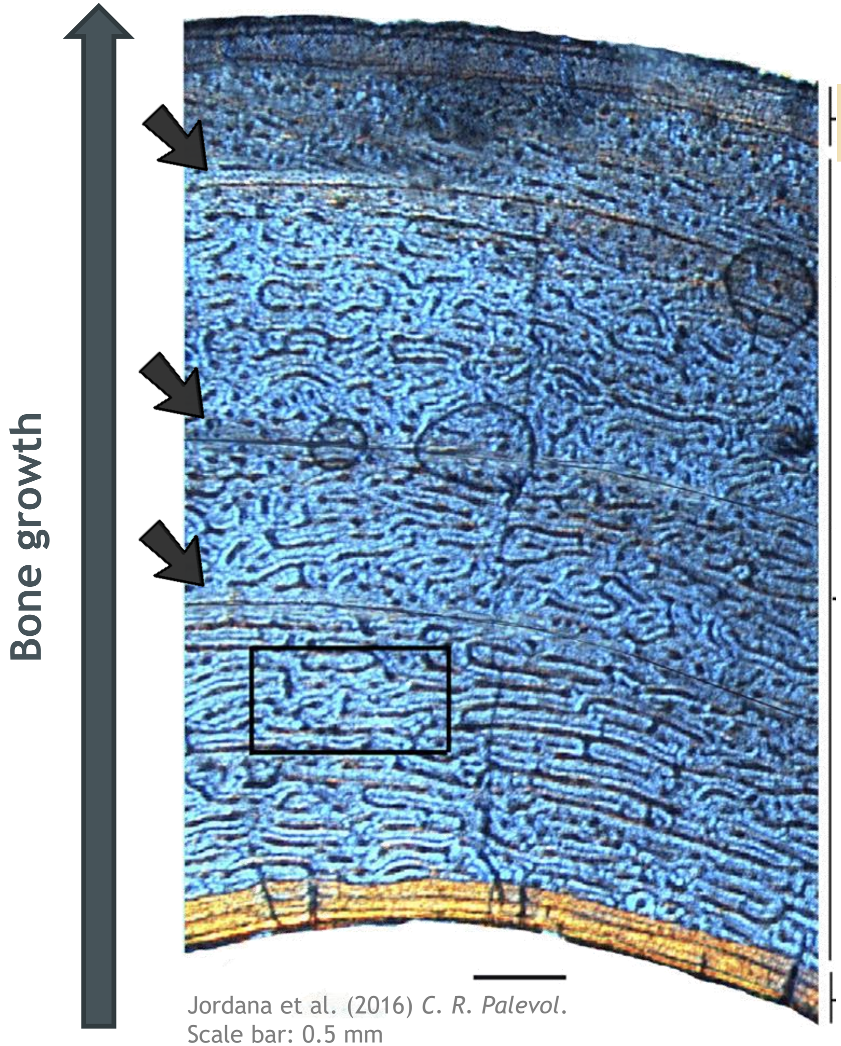


Images of lamellar and parallel-fibered from Huttenlocker et al. (2013), fibrolamellar bone from Nacarino-Meneses (2018)

Slower deposition ⟵ ⟶ Faster deposition

Introduction – Bone histology and age at maturity

Primary bone tissue types also vary **during ontogeny**, recording growth and development



Jordana et al. (2016) *C. R. Palevol*.
Scale bar: 0.5 mm

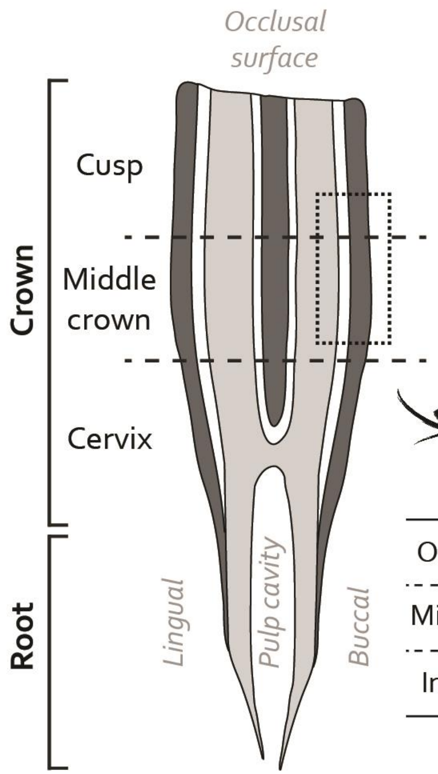
EFS/OCL = External fundamental system / Outer circumferential layer = lamellar bone

Lamellar bone in the outer cortex **(EFS/OCL)** appears when growth rate decreases

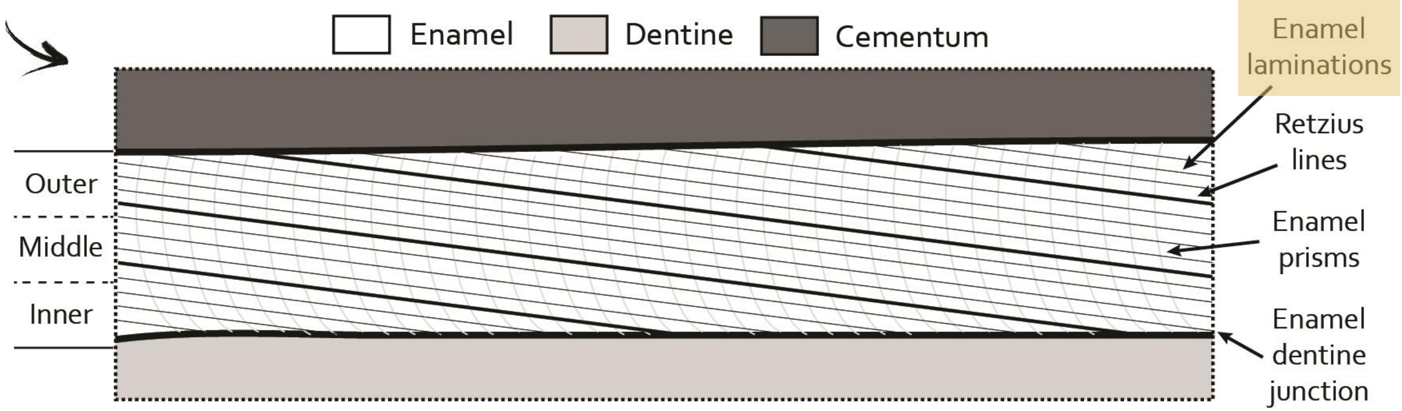
FLB = Fibrolamellar complex = fibrolamellar bone

Age at maturity › Estimated by counting the number of cyclical growth marks (CGMs) before the EFS/OCL

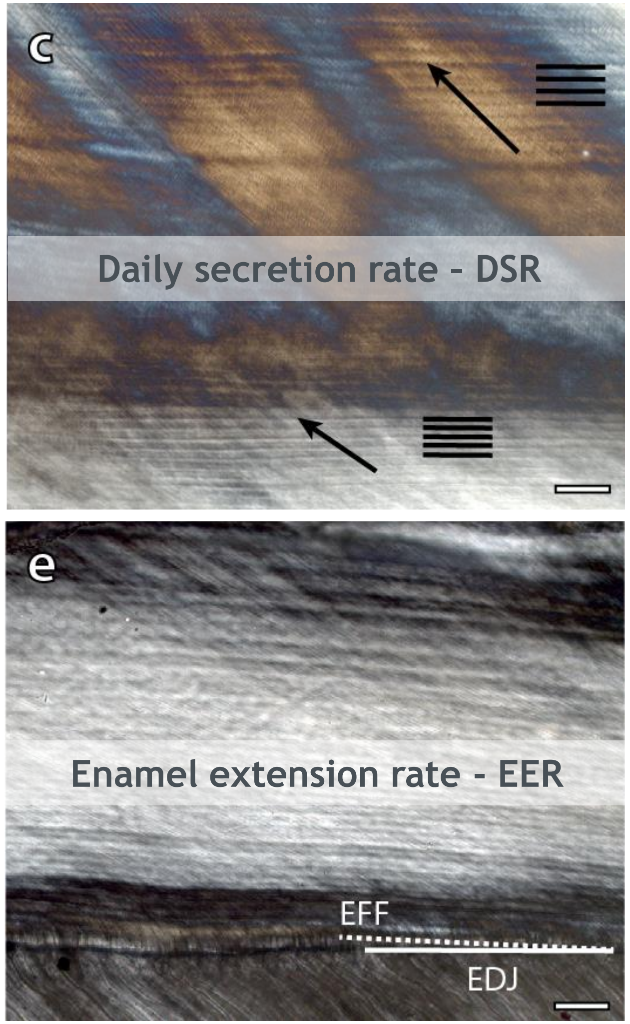
Introduction – Dental histology and growth rate



Dental enamel registers incremental lines of daily periodicity named **laminations**, which can be counted and analysed to estimate **rates of tooth formation**



Nacarino-Meneses & Chinsamy (In rev)



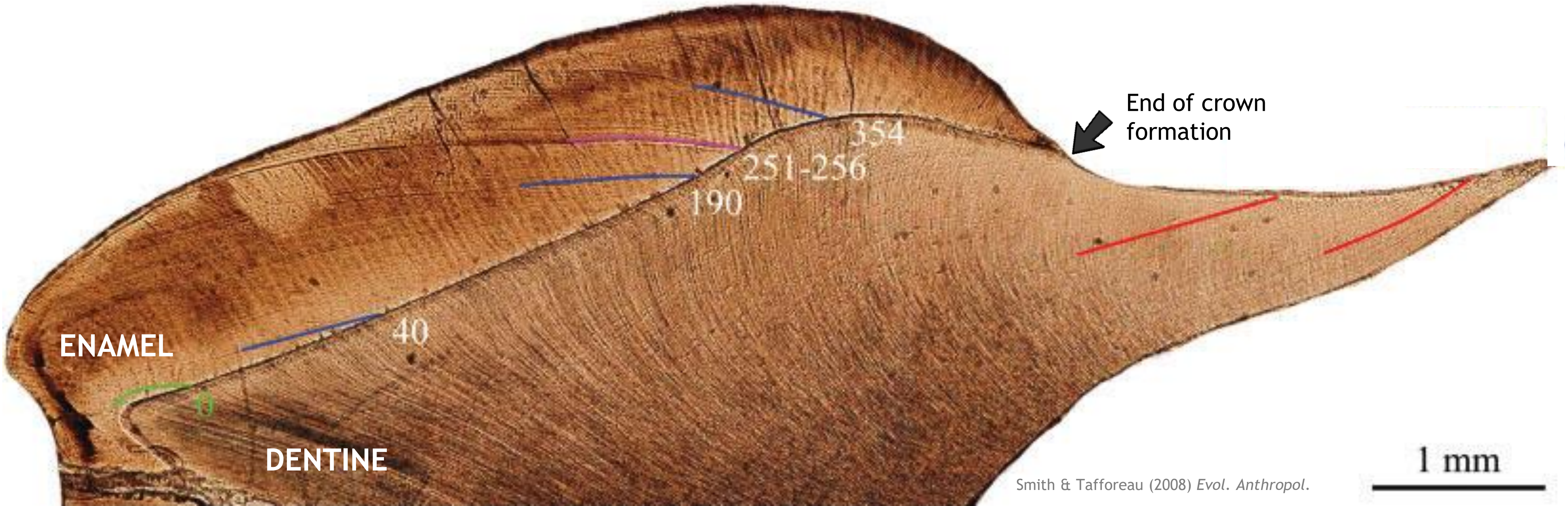
Nacarino-Meneses et al. (2017) *Sci. Rep.*

Differences in EER might reflect **differences in the life history** of the species, as this parameter is considered a proxy of the organism's growth rate

Introduction – Dental histology and maturity

Counting the **total number of incremental lines** within a crown provides an estimation of the crown formation time

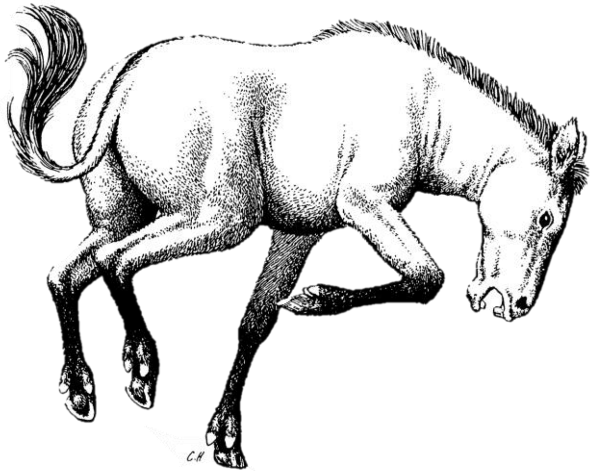
In several mammals, the **end of crown formation** correlates with the **eruption** of the tooth. The **time of eruption of the first and third molar**, in turn, correlates with key LH traits such as age at weaning and age at skeletal maturity respectively



Smith & Tafforeau (2008) *Evol. Anthropol.*

Introduction – *Eurygnathohippus hooijeri* Bernor & Kaiser, 2006

Photo & Map: C. Nacarino-Meneses



Bernor & Kaiser (2006) *Mitt. Hamb. Zool. Mus. Inst.*

Its morphology and palaeodiet is well studied but what about other aspects of its **biology**?

Material & Methods

iziko museums of South Africa

III-metacarpi

III-metatarsi

femora

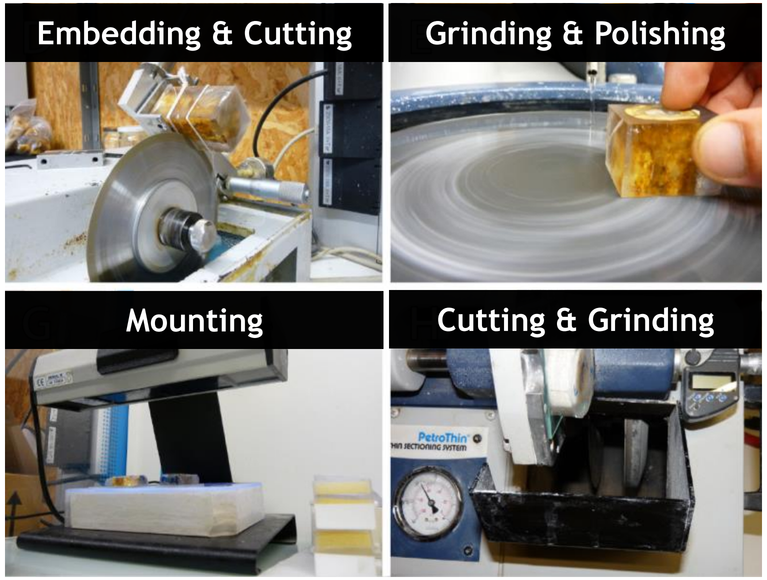
first lower molars

third lower molars

Photos: C. Nacarino-Meneses

Histological slides

Procedures detailed in Chinsamy & Raath (1992)



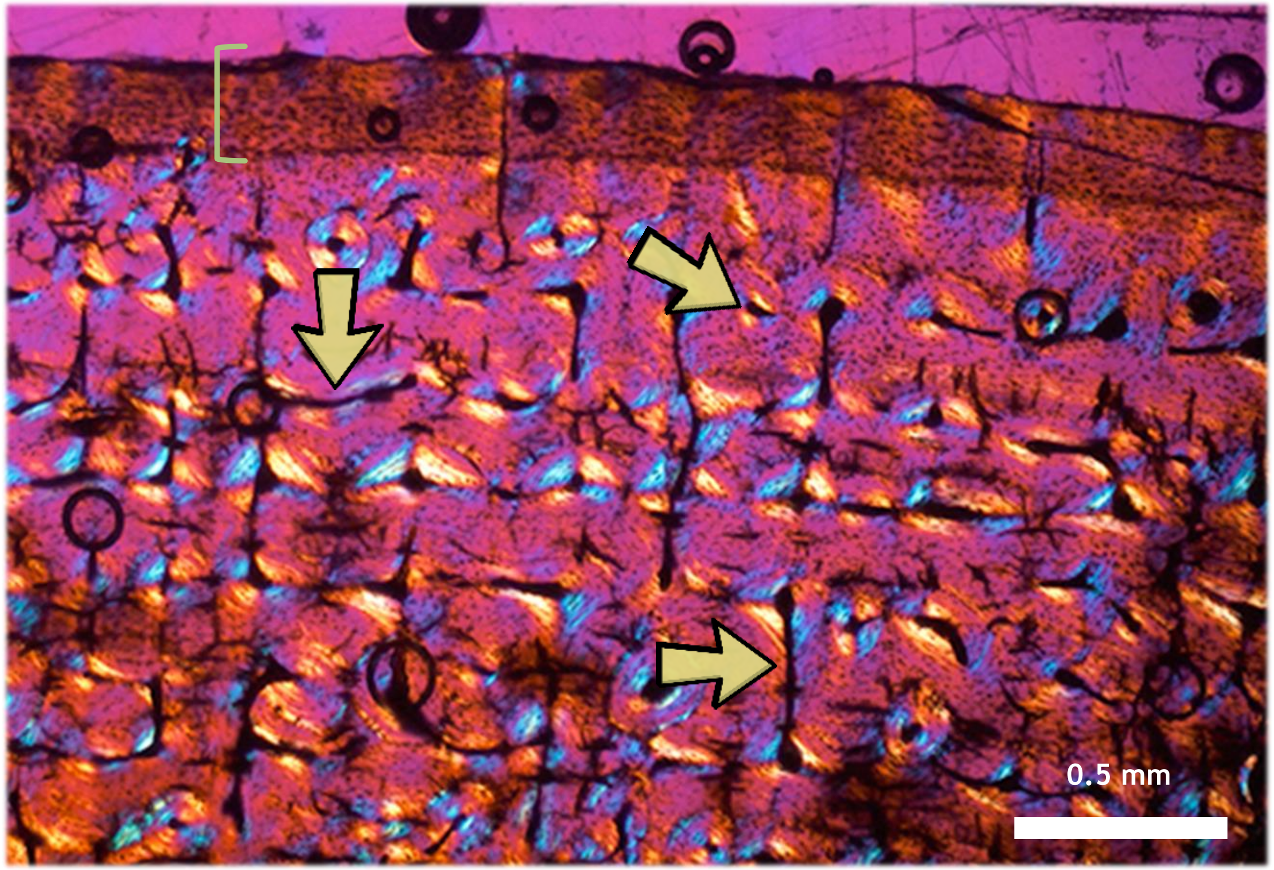
Photos: M. Fernández

Body mass estimations

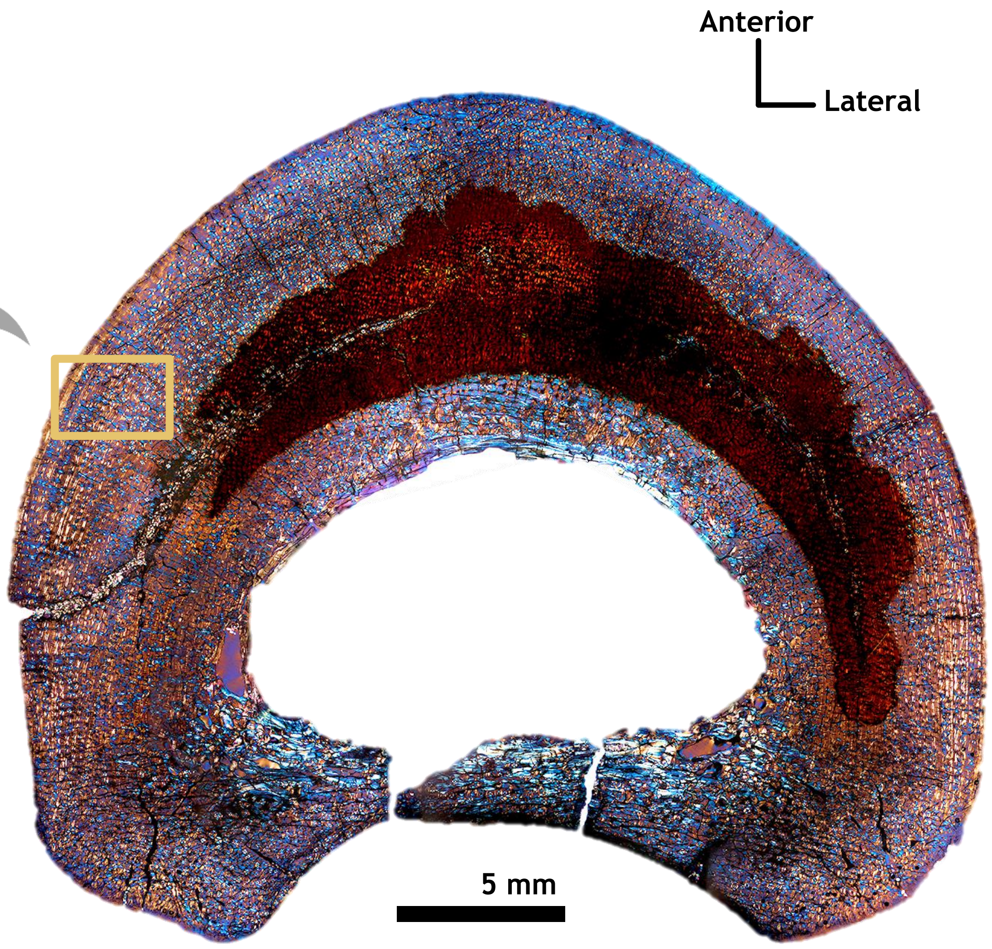
Equations in Eisenmann & Sondaar (1998)

Results & Discussion – Primary bone tissue types - Metacarpus

- Highly vascularized **fibrolamellar bone**
- Longitudinal, circumferential and radial **vascular canals**
- **Outer circumferential layer**

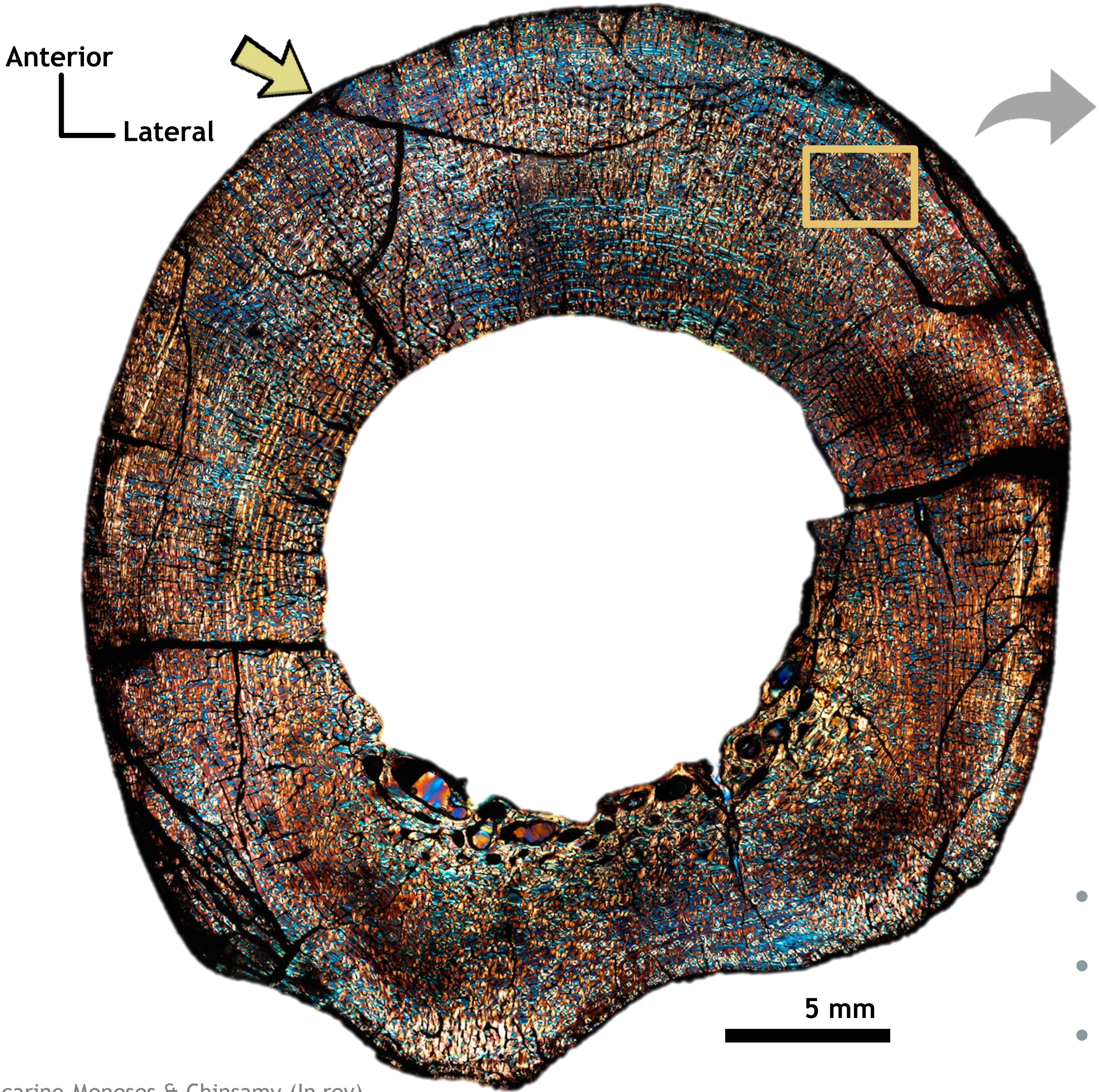


Nacarino-Meneses & Chinsamy (In rev)

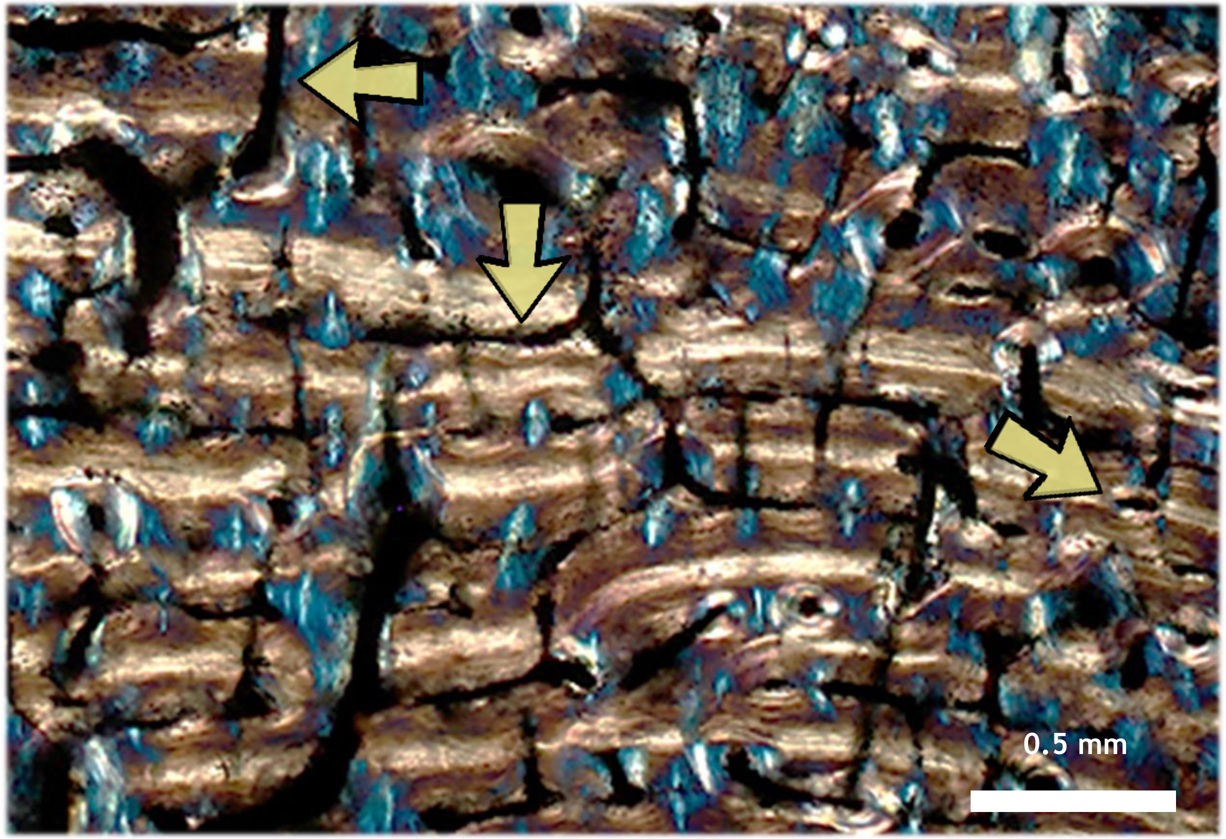


Nacarino-Meneses & Chinsamy (In rev)

Results & Discussion – Primary bone tissue types - Metatarsus



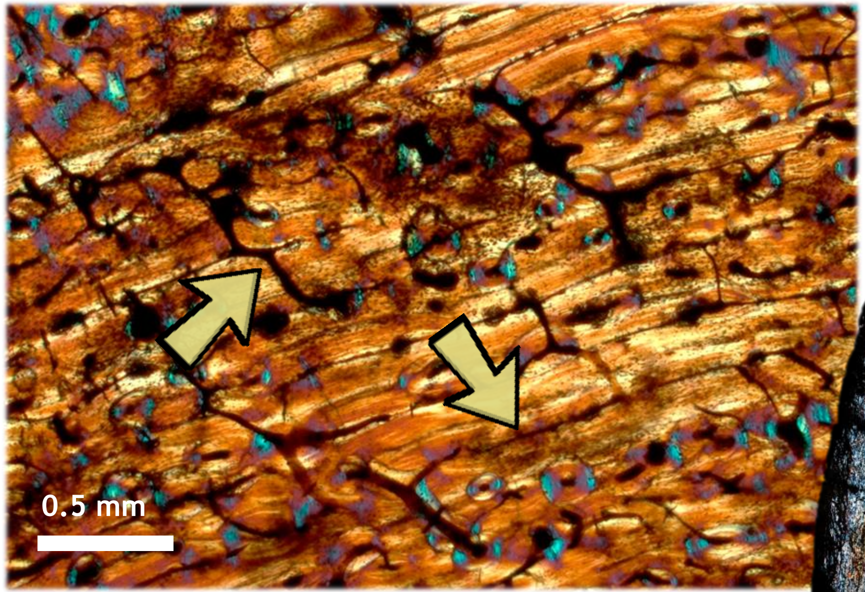
Nacarino-Meneses & Chinsamy (In rev)



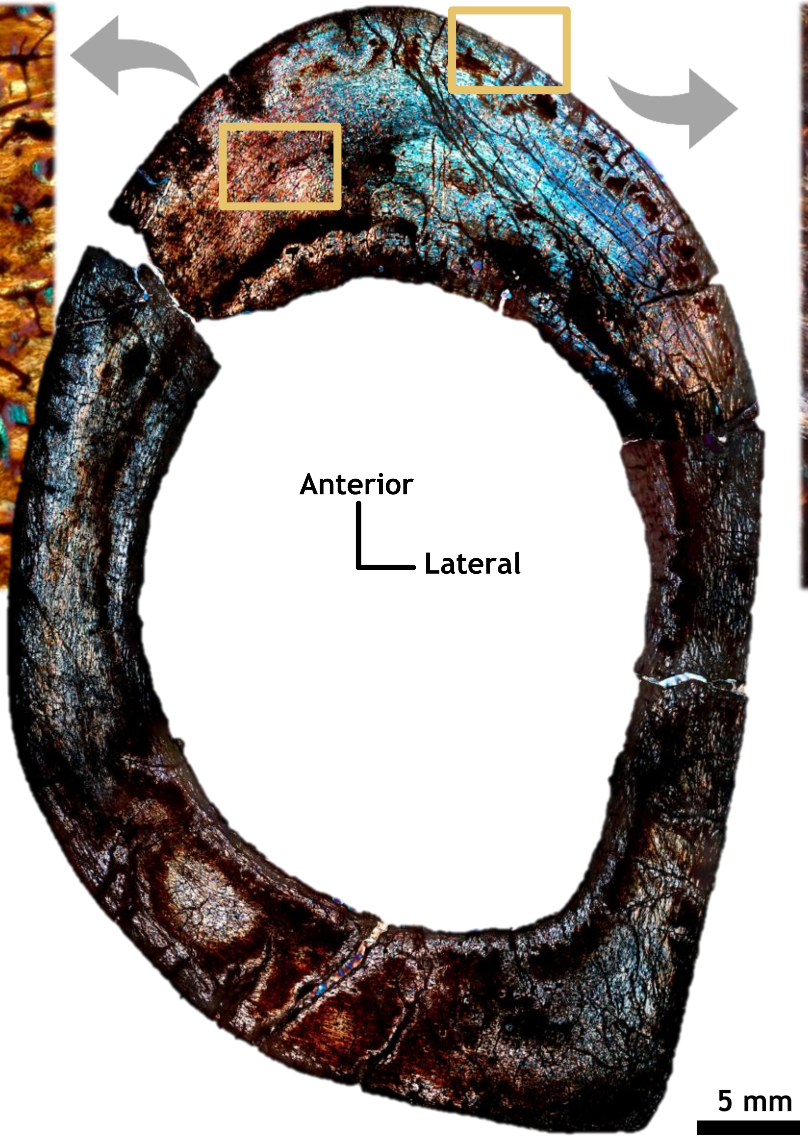
Nacarino-Meneses & Chinsamy (In rev)

- Highly vascularized **fibrolamellar bone**
- Longitudinal, circumferential and radial **vascular canals**
- **Outer circumferential layer**

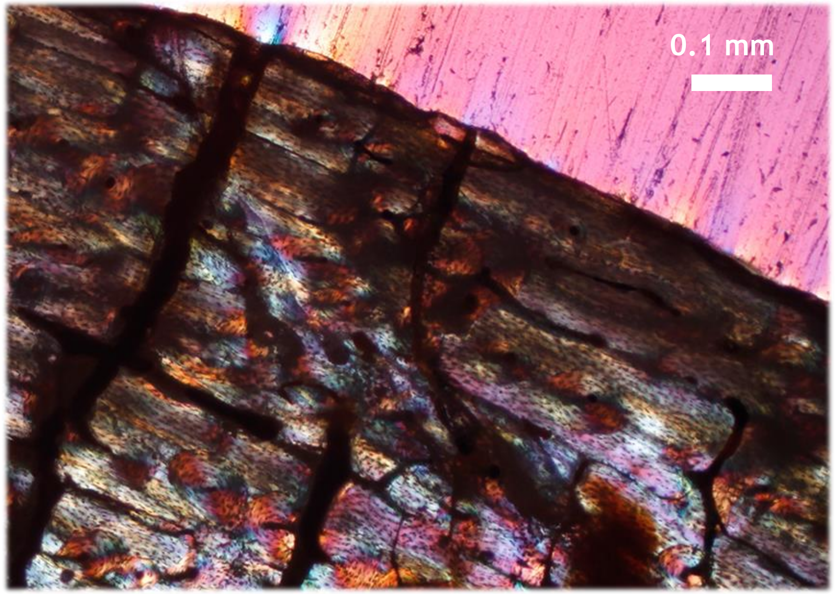
Results & Discussion – Primary bone tissue types - Femur



Nacarino-Meneses & Chinsamy (In rev)



Nacarino-Meneses & Chinsamy (In rev)

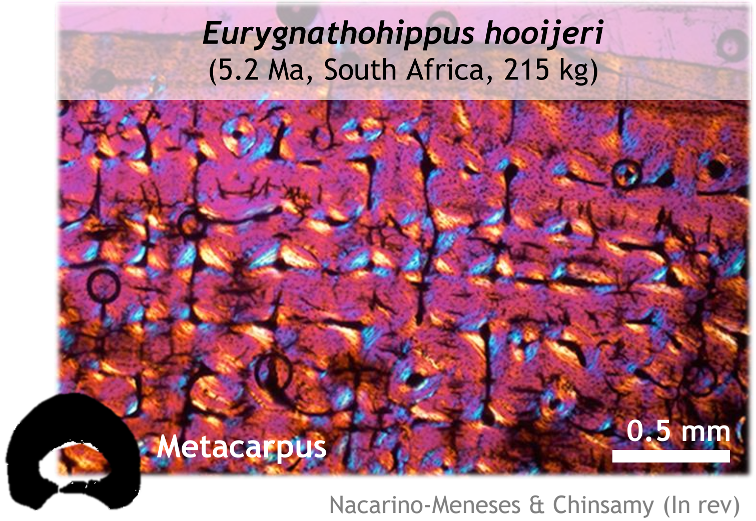


Nacarino-Meneses & Chinsamy (In rev)

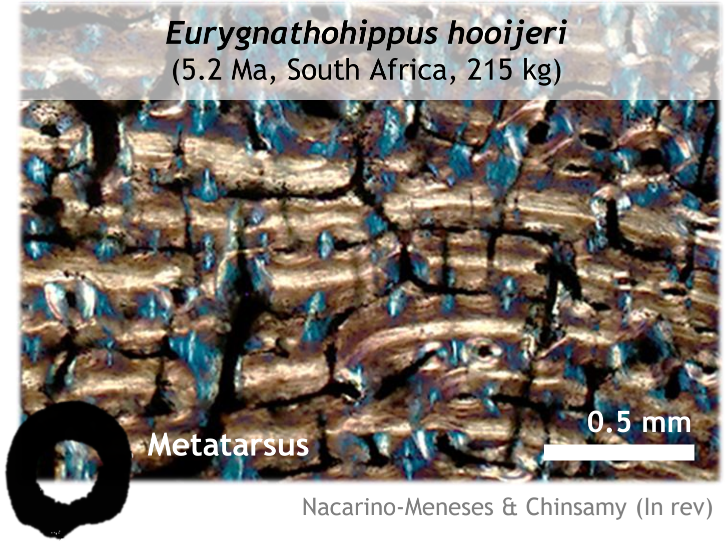
- Highly vascularized **fibrolamellar bone**
- Circumferential and radial **vascular canals**

No outer circumferential layer

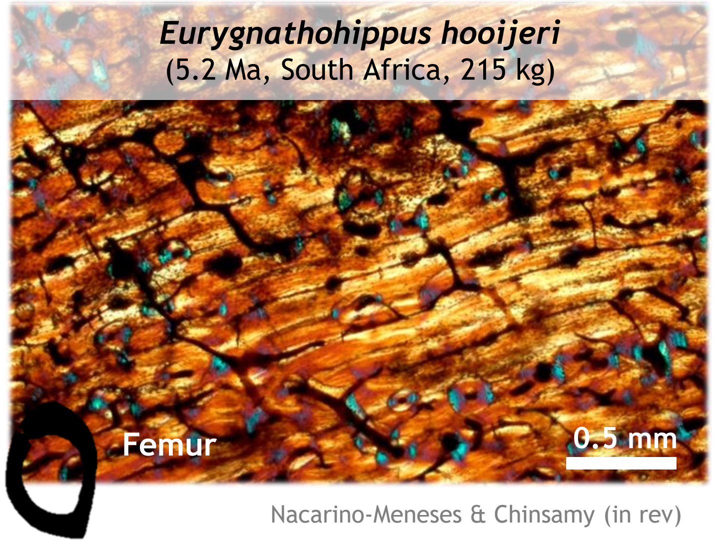
Results & Discussion – Primary bone tissue types - Comparisons



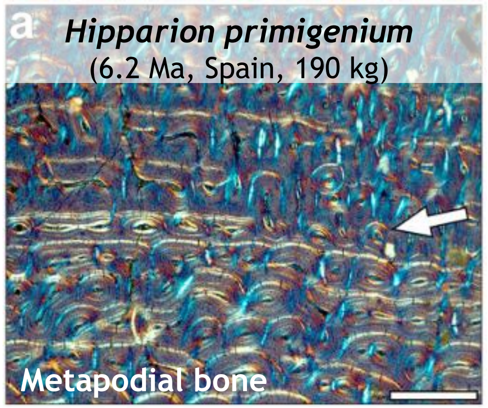
Nacarino-Meneses & Chinsamy (In rev)



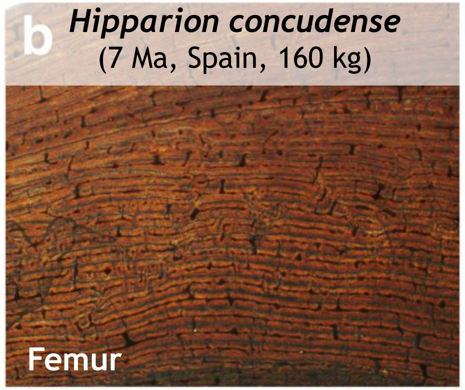
Nacarino-Meneses & Chinsamy (In rev)



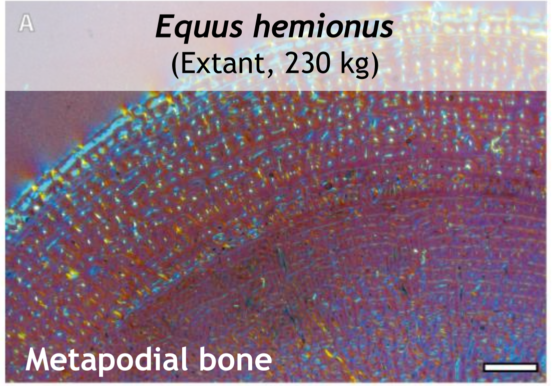
Nacarino-Meneses & Chinsamy (in rev)



Orlandi-Oliveras et al. (2018) *Sci Rep*



Martínez-Maza et al. (2014) *PLoS ONE*



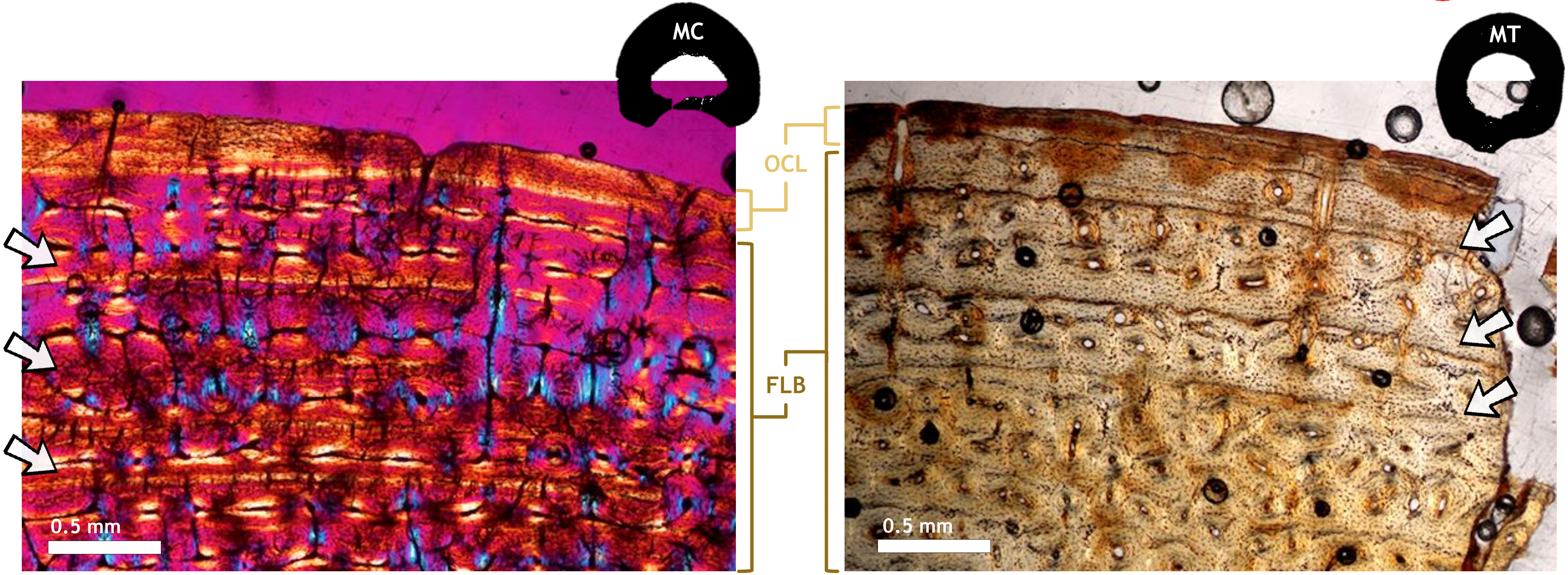
Nacarino-Meneses et al (2016) *PeerJ*

Bone tissue is **more vascularized** in *E. hooijeri* than in Late Miocene European hipparionines and *Equus*

⬇

Higher growth rate in *E. hooijeri*

Results & Discussion – Bone growth marks - Metapodia



Nacarino-Meneses & Chinsamy (In rev)

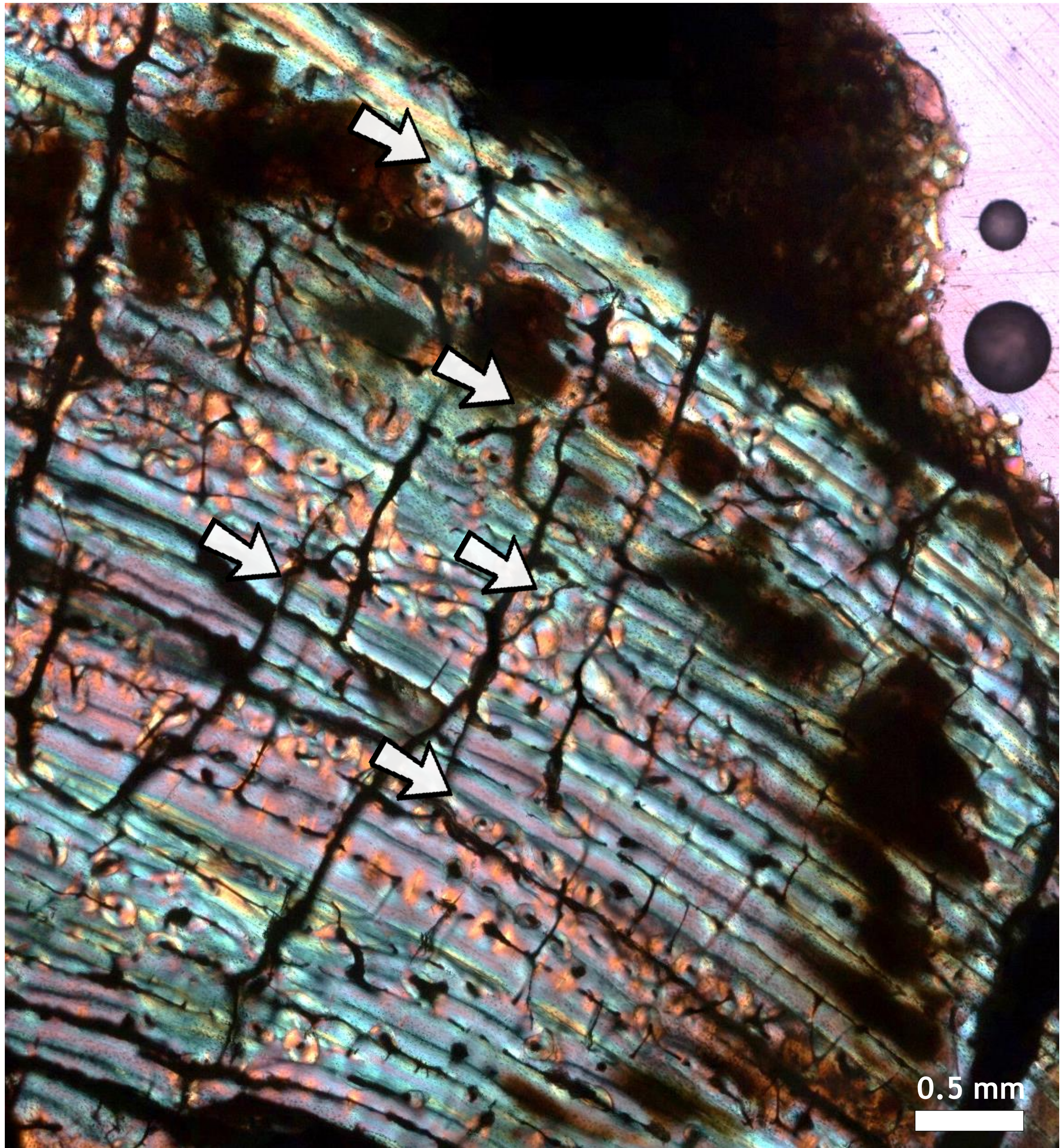
Nacarino-Meneses & Chinsamy (In rev)

3 cyclical growth marks in metacarpi and metatarsi before the OCL

Metapodia **finish most of their growth after the 3rd cycle**/year of growth

Results & Discussion – Bone growth marks – Femur

FLB



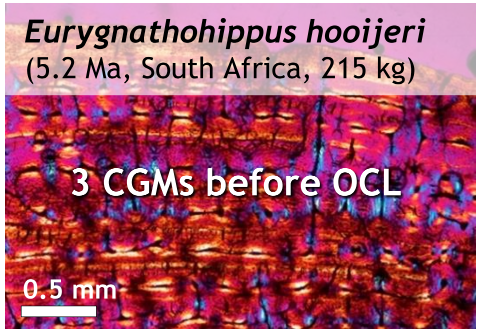
5 cyclical growth marks in femur and **NO OCL**

⬇

Femur is still growing after the **5th cycle**/year of growth

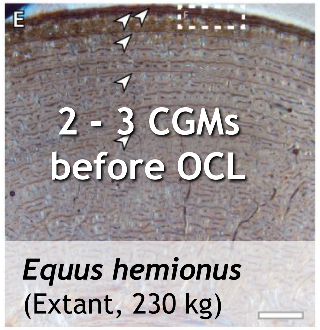
Nacarino-Meneses & Chinsamy (In rev)

Results & Discussion – Bone growth marks - Comparisons



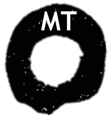
Nacarino-Meneses & Chinsamy (In rev)

Orlandi-Oliveras et al. (2018) *Sci Rep*

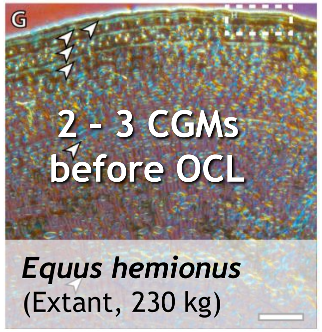


Nacarino-Meneses et al. (2016) *PeerJ*

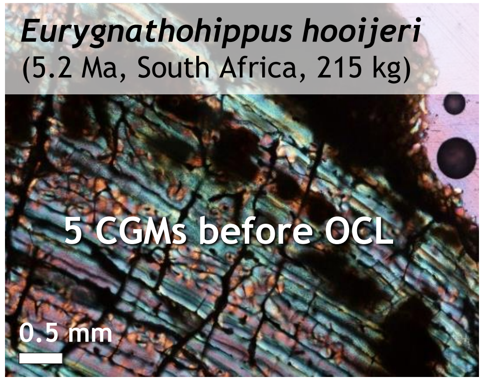
Nacarino-Meneses & Chinsamy (In rev)



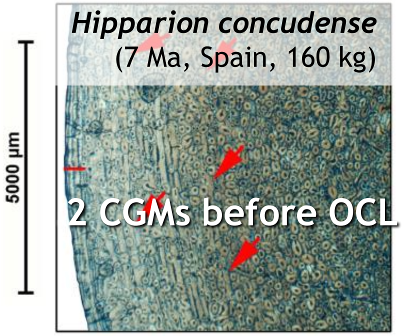
Orlandi-Oliveras et al. (2018) *Sci Rep*



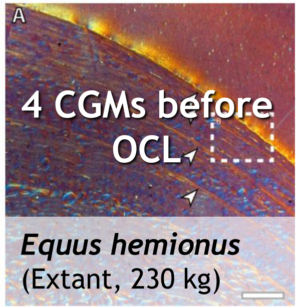
Nacarino-Meneses et al. (2016) *PeerJ*



Nacarino-Meneses & Chinsamy (In rev)



Martínez-Maza et al. (2014) *PLoS ONE*



Nacarino-Meneses et al. (2016) *PeerJ*

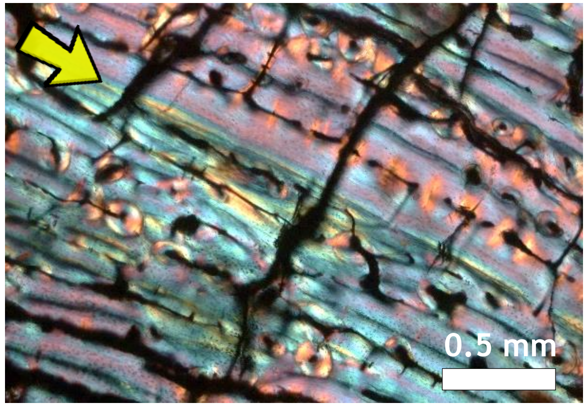
OCL appears later in *E. hooijeri* than in medium- and large-sized European hipparionines and in similar-sized extant *Equus*

⬇

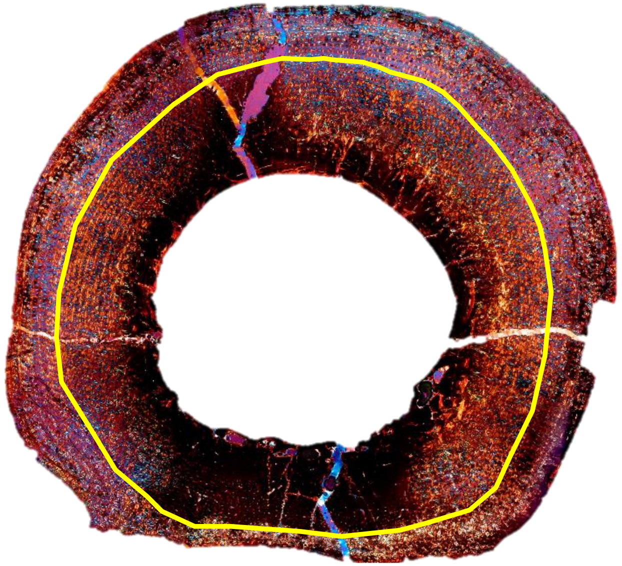
Delayed
age at skeletal and reproductive maturity

Age at reproductive maturity: + 5 years

Results & Discussion – Size at birth

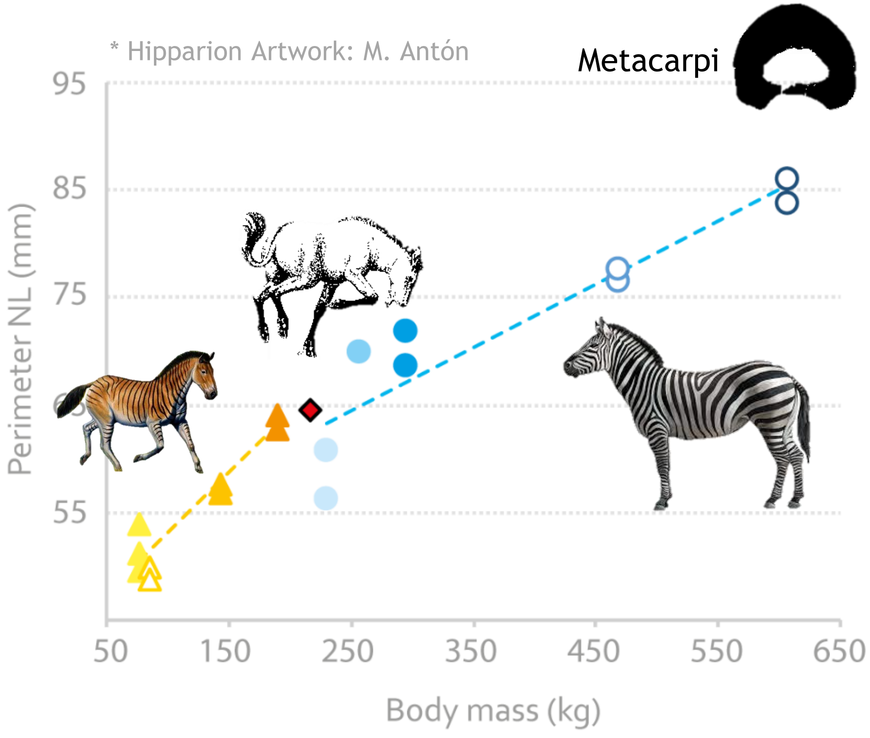


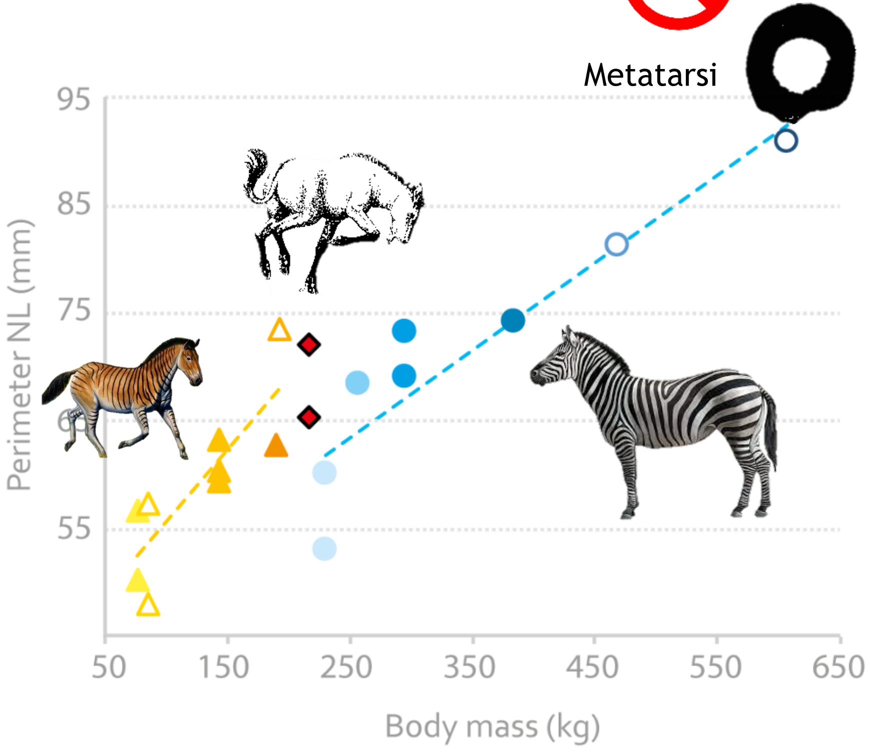
Nacarino-Meneses & Chinsamy (In rev)



Nacarino-Meneses & Chinsamy (In rev)

* Hipparion Artwork: M. Antón





Nacarino-Meneses & Chinsamy (In rev)

Tribe Hipparionini

- *macedonicum* morphotype
- *dietrichi* morphotype
- *primigenium* morphotype
- *Hipparion gromovae*
- *Hipparion truyolsi*
- *Eurygnathohippus hooijeri*

Tribe Equini

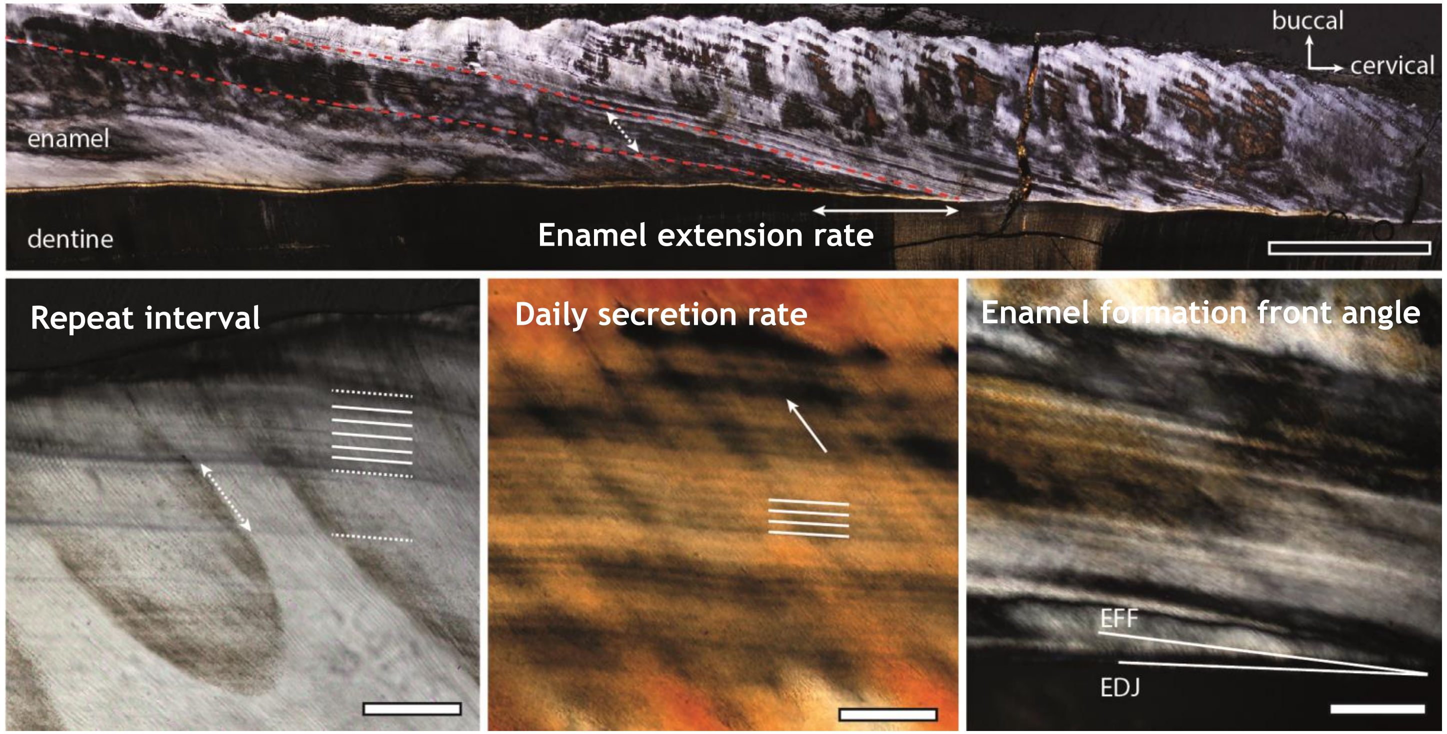
- *Equus hemionus*
- *Equus quagga*
- *Equus zebra*
- *Equus grevyi*
- *Equus steinheimensis*
- *Equus mosbachensis*

Size at birth of *E. hooijeri* agrees with allometric predictions

Results & Discussion – Enamel growth

m1

Photo: C. Nacarino-Meneses

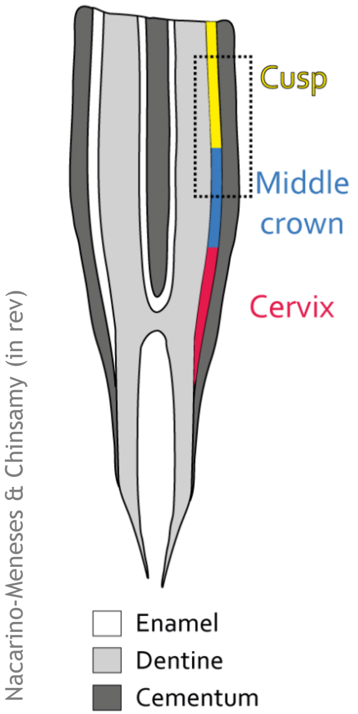


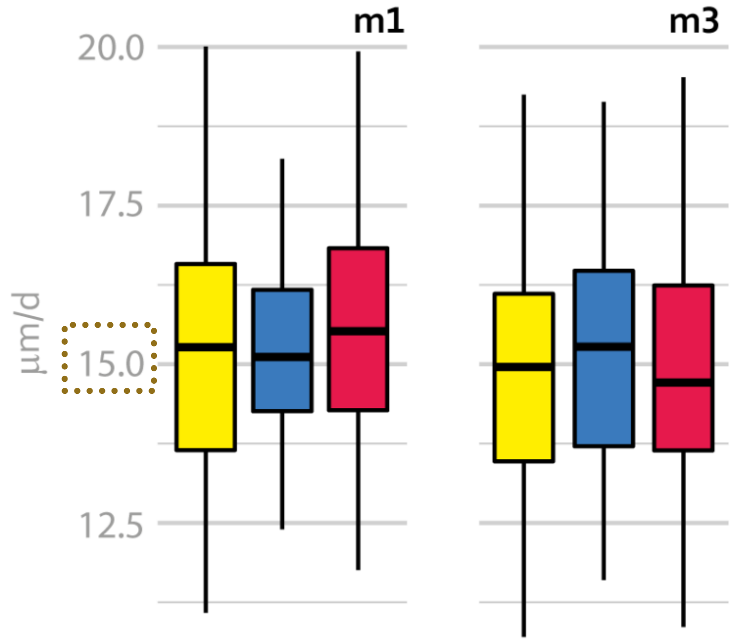
Nacarino-Meneses & Chinsamy (In rev)

m3

Photo: C. Nacarino-Meneses

Results & Discussion – Daily secretion rate



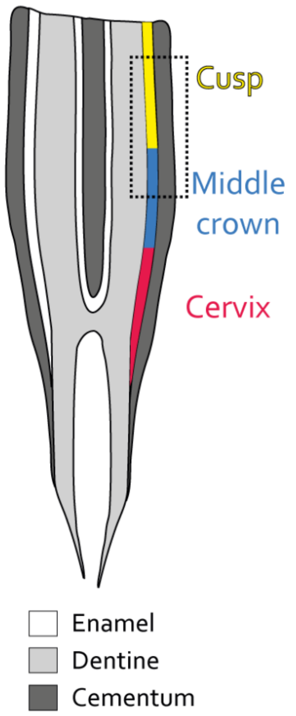


Nacarino-Meneses & Chinsamy (in rev)

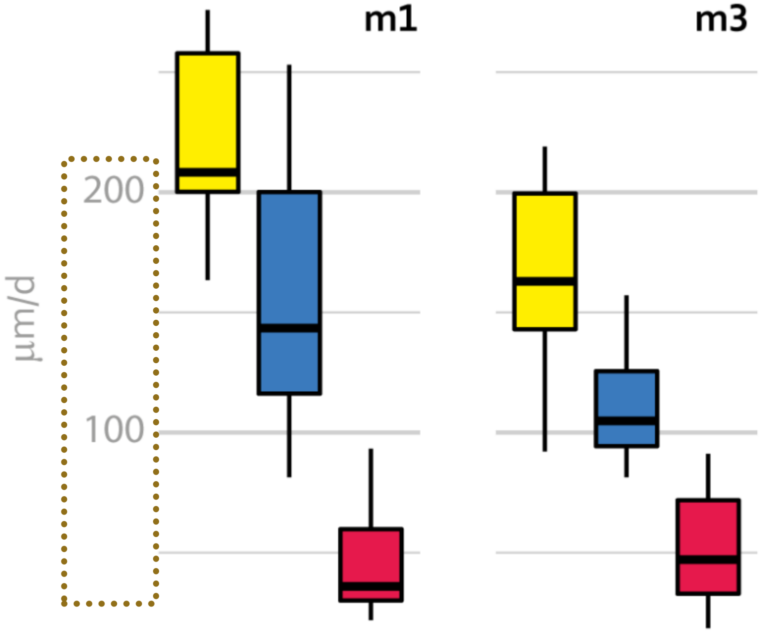
Artwork: Mauricio Antón

Dental enamel in *E. hooijeri* grew at **similar rates** to Old World hipparionines rather than *Equus*

Results & Discussion – Enamel extension rate



Nacarino-Meneses & Chinsamy (in rev)



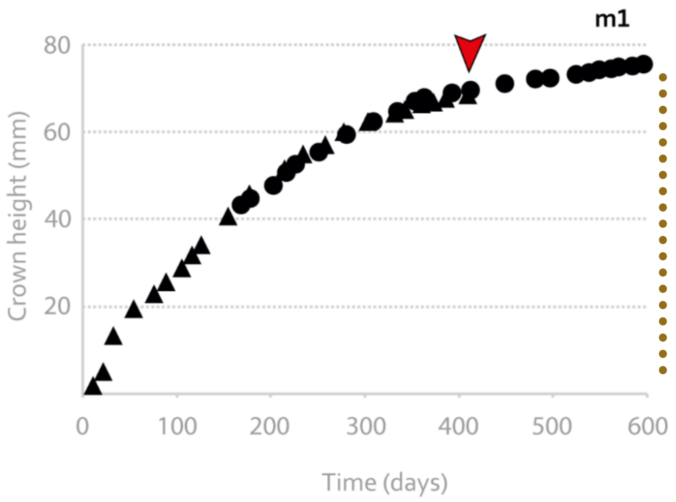
Nacarino-Meneses & Chinsamy (in rev)

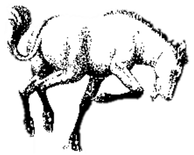
Artwork: Mauricio Antón

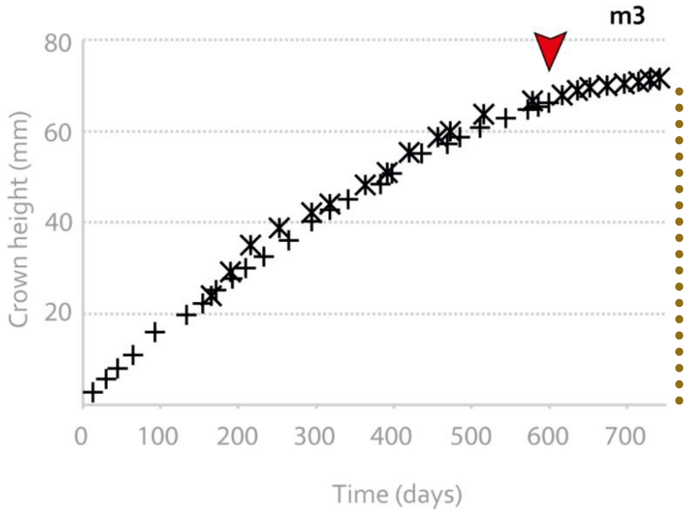
Dental enamel in *E. hooijeri* grew at **similar rates** to Old World hipparionines rather than *Equus*

Results & Discussion – Crown formation time

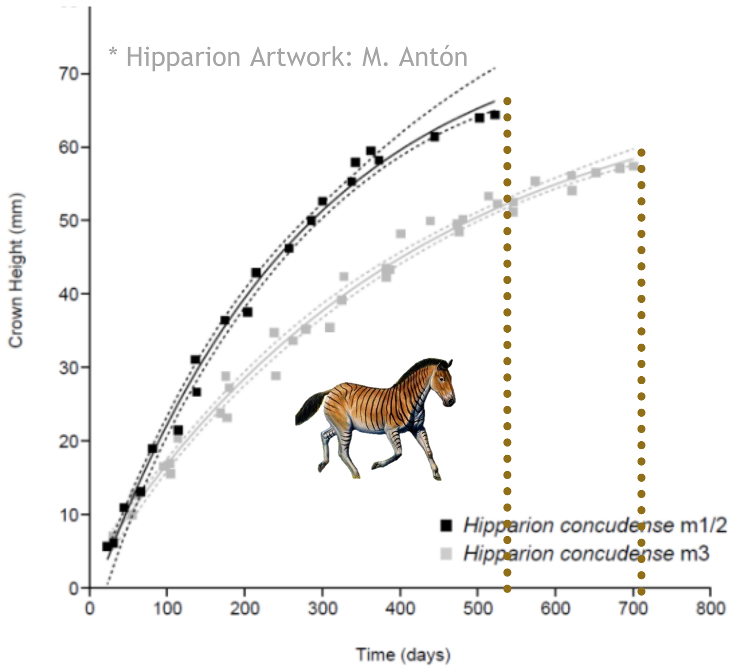
Photo: C. Nacarino-Meneses







Nacarino-Meneses & Chinsamy (in rev)

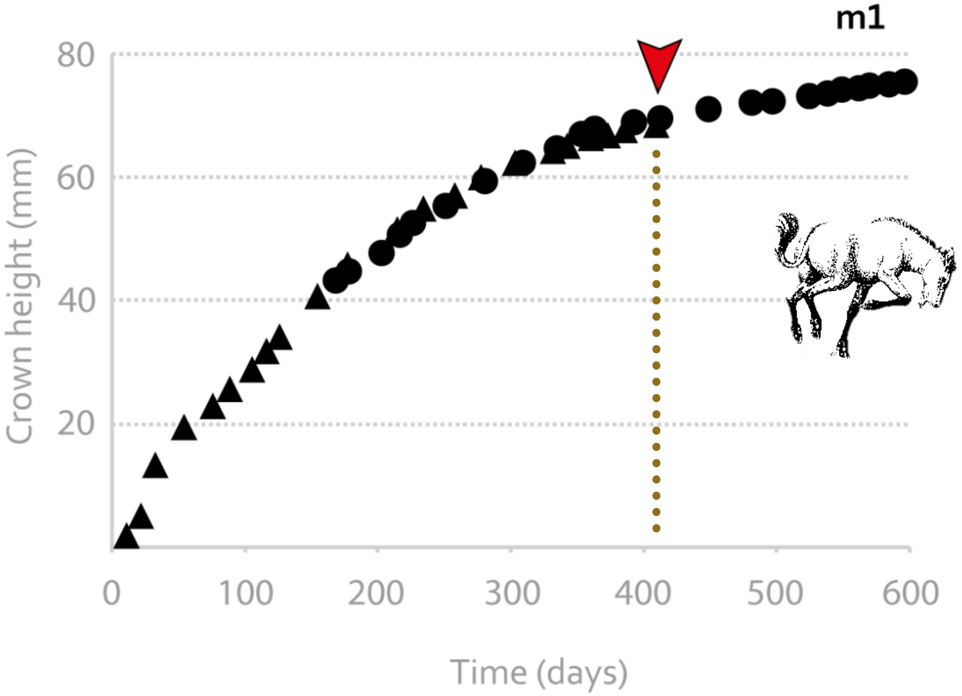


Orlandi-Oliveras et al. (2019) *Palaeogeogr. Palaeoclimatol. Palaeoecol.*

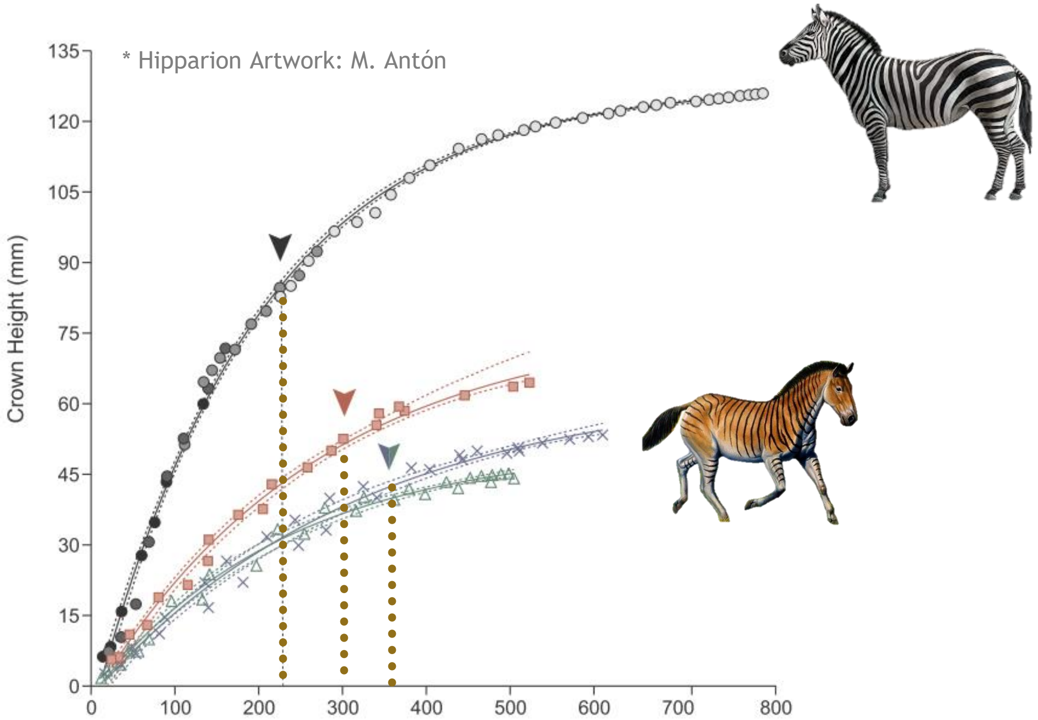
The higher degree of hypsodonty observed in *E. hooijeri* is the result of **longer crown formation times**

Results & Discussion – Age at weaning

Photo: C. Nacarino-Meneses



Nacarino-Meneses & Chinsamy (in rev)



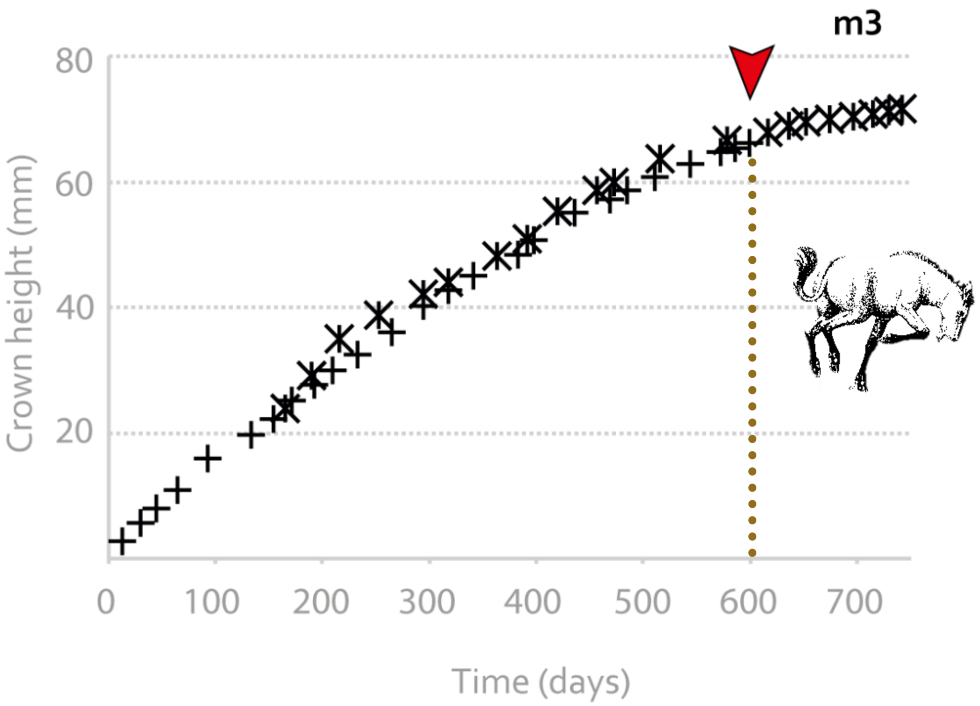
Orlandi-Oliveras et al. (2019) *Palaeogeogr. Palaeoclimatol. Palaeoecol.*

Age at weaning: **13 months**

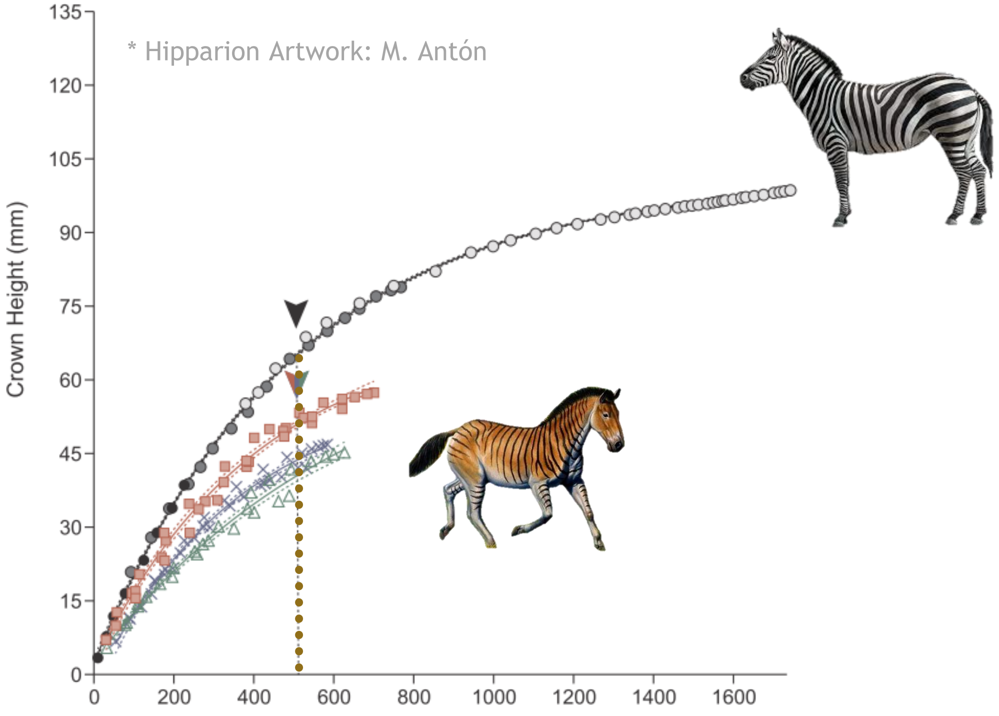
Delayed as compared to Late Miocene hipparionines and *Equus*

Results & Discussion – Age at skeletal maturity

Photo: C. Nacarino-Meneses



Nacarino-Meneses & Chinsamy (in rev)

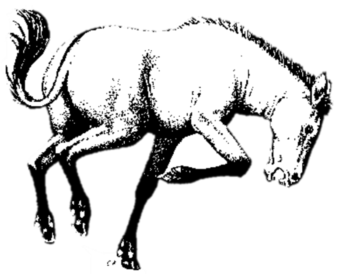


Orlandi-Oliveras et al. (2019) *Palaeogeogr. Palaeoclimatol. Palaeoecol.*

Age at skeletal maturity: **3.5 years**

Delayed as compared to Late Miocene hipparionines and *Equus*

Summary – Life history strategy



Late age at reproductive maturity (+5 years)

Late age at skeletal maturity (3.5 years)

Late age at weaning (13 months)

High rates of growth (vascular canals) ?

Moderate rates of growth (EER)

FAST end — LH continuum — SLOW end

Energy allocated to reproduction

Short life-span
Fast development
Advanced maturity
Short generation times
Low parental investment

Energy allocated to growth & maintenance

Long life-span
Slow development
Delayed maturity
Long generation times
High parental investment

Summary – Palaeoecological inferences


Mauricio Antón


Mauricio Antón


Roman Uchytel


Adam Hartstone-Rose

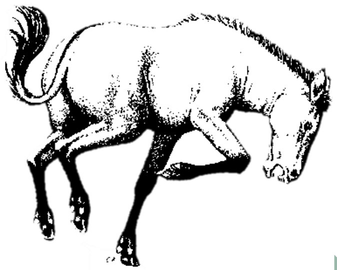
LBW records a number of carnivorans that likely preyed on *E. hooijeri*

Closed **woodland environment** provided protection ✗

Grassland was the preferential habitat of the species

Predation focused on **juveniles** ✓

Observed in **extant** species



FAST end ← **LH continuum** → **SLOW end**

Trigger by **low predation** ← Energy allocated to **growth & maintenance**

Long life-span
Slow development
Delayed maturity
Long generation times
High parental investment

Reconstructing the biology of extinct horses from hard-tissue histology: The case of a South African hipparionine

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