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LIFE HISTORY OF THE PLEISTOCENE, INSULAR, RUMINANTS OF JAVA (**AXIS LYDEKKERI** AND **DUBOISIA SANTENG**)

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Πτυχιούχος Γεωλόγος

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ΚΥΚΛΟΣ ΖΩΗΣ ΤΩΝ ΠΛΕΙΣΤΟΚΑΙΝΙΚΩΝ, ΝΗΣΙΩΤΙΚΩΝ ΜΗΡΥΚΑΣΤΙΚΩΝ ΤΗΣ ΙΑΒΑΣ (**AXIS LYDEKKERI** ΚΑΙ **DUBOISIA SANTENG**)

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LIFE HISTORY OF THE PLEISTOCENE, INSULAR RUMINANTS OF JAVA (AXIS LYDEKKERI AND DUBOISIA SANTENG) - *Master Thesis*

ΚΥΚΛΟΣ ΖΩΗΣ ΤΩΝ ΠΛΕΙΣΤΟΚΑΙΝΙΚΩΝ, ΝΗΣΙΩΤΙΚΩΝ ΜΗΡΥΚΑΣΤΙΚΩΝ ΤΗΣ ΙΑΒΑΣ (AXIS LYDEKKERI AND DUBOISIA SANTENG) - *Μεταπτυχιακή Διπλωματική Εργασία*

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ABSTRACT

In the present thesis, I studied fossil material of two endemic ruminant species, the deer *Axis lydekkeri* (Cervini, Cervidae) and the antelope *Duboisia santeng* (Boselaphini, Bovidae) belonging to the world-famous Dubois collection. The fossils include dozens of mandibles and isolated molars from both species, assembled mostly from Trinil as well as other sites all over Java. They date back to the Middle Pleistocene and are part of the *Stegodon-Homo erectus* fauna. The life history of endemic mammal species has long been of interest as a means of studying the effect of insularity on mammals. The present study was a unique opportunity to gather new data from a historic collection and contribute to the ongoing discussion about the life history strategies of endemic species. The data were obtained by measuring the crown height of the molars of each mandible and then adjusting the measurements for the isolated molars since the whole tooth is visible this time. The raw measurements were then translated into age estimations using the Quadratic Crown Height Method. Mortality profiles and mortality curves based on these estimations were then produced in order to address the life-history strategies of these two species. The results correspond well with what is known about life history traits of other endemic ungulates and indicate a shift towards a slow life, with maximum survivability around 70-80% of potential ecological longevity. The mortality profiles for both species are attritional, U-shaped, and with high mortality for juveniles. Based on the profile, in which mortality is almost constant throughout the age groups, it seems that *Duboisia* was targeted more by predators and/or hominid hunters. This could be attributed to its lifestyle (gregarious, moving in herds) or even more likely, the type of environment (more open habitat compared with the deer). Finally, potential cases of osteophagia are presented here and discussed.

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1. INTRODUCTION

1.1 AIMS OF THE STUDY

This study aims to achieve two things: One is to collect individual age data of two endemic Javanese ruminants (*Axis lydekkeri*, Stremme, 1911 and *Duboisia santeng*, Stremme, 1911) for the purpose of constructing mortality profiles and mortality curves in order to be able to extract data on life history traits. These results will be interpreted and compared with life history data of other endemic as well as continental ungulate species from published literature, obtained with the same or comparable methods. This will help us to interpret life history traits and strategies that island ungulates have developed in response to an insular environment. As part of this research project, a critical assessment of the age estimation based on tooth crown height decrease through wear during life is indispensable, not only because such methods are known to under- or overestimate ages depending on either species or the used molar of choice, or even both, but also because the result of the project's outcome relies heavily on these age estimations and so making error prediction is of paramount importance. The Middle Pleistocene of Java is famous for its *Stegodon* - *Homo erectus* fauna which is impoverished when compared to mainland faunas of the same time period and region, but not exactly unbalanced, as larger mammalian carnivores are present (tigers, hyenas and a canid), but with a high level of endemism (Van Den Bergh et al., 2001; Van Der Geer et al., 2018; Vos, 1984, 1983). Based on this, the expectation would be for the mortality profiles of endemic ruminants of this fauna to approach the average of insular and mainland ruminants. Regarding mortality profiles, there are two broad categories: attritional and catastrophic mortality profiles (Caughley, 1966; Klein, 1982; Klein and Cruz-Uribe, 1983). Catastrophic profiles represent the living community (population) that perished during a catastrophic event (calamity), while attritional profiles represent a metapopulation that spans hundreds or thousands of years from which individuals died gradually over time, due to natural causes. Since the specimens were gathered from different sites of Java, the profiles produced should be averaged over space and time. Similarities between the profiles of the deer and the bovid are to be expected since they probably were affected by the isolated environment in similar ways. At the same time, their mortality profiles might also differ, based on differences in lifestyle (such as small or large herds or solitary) and habitat preferences (such as open grass versus closed forest).

1.2 PLEISTOCENE GEOLOGY OF JAVA

The island of Java, along with Sumatra, Borneo, Palawan and associated islands comprise the Sunda Shelf which, today, forms a part of the continental shelf of Asia. Most, if not all, of the southeastern continental blocks of Asia, rifted from northern Gondwana at different periods and the Sunda Shelf itself, is an extensive shallow floor, surrounded in the west and east by a volcanic arc along its margins (Van Gorsel, 2020). Java started to uplift about 2.4 million years ago from west to east, through a stepwise process thanks to both tectonic and volcanic activities. The collision between the Eurasian and the Indian- Australian plates is responsible for most of the geological structures in Java, which largely dictated the sedimentation cycles in the Tertiary and Quaternary. Current tectonic models unanimously agree on the convergence of three major tectonic plates in the Indonesian region, Eurasian, Indian - Australian and the Pacific. According to Baumann (1982), there are five different sedimentation cycles in Java and Sumatra during the Cenozoic, with each of them commencing with a transgression and ending with a volcanic and tectonic phase while lasting for approximately 10 Ma. Sea level fluctuations, however, were the main force in constituting the Javanese geography, floral and faunal compositions in the Pleistocene, determining the time and level of its isolation from the mainland (Moores, 1997; Van Gorsel, 2020).

Indonesia is one of the most volcanically active regions of the world with 128 active and several inactive or extinct volcanoes. Present volcanism in Indonesia can be found along the three main arc segments: Sunda-Banda, Sangihe and Halmahera, with the first two constituting a continuous system related to the subduction of the north-moving Indian-Australian plate (Moores, 1997). On Java in particular, volcano spacing is rather irregular on the west, but fairly regular on the eastern part (~70km). Southwards shifts of the volcanic eruption centers have been observed through time, towards the subduction zone. After volcanic activity ceases, erosion of the edifices is rapid and the geologic record will only preserve the volcanic deposits and the underlying intrusives, even though some of the active volcanoes reach elevations of up to 3000m (Moores, 1997; Van Gorsel, 2020).

The Java Sea on its western part, is a continuation of the Paleozoic - Early Mesozoic continental complexes of Sumatra and Borneo. For the most part, the island of Java is underlain by Late Cretaceous - Eocene complexes and Paleogene arc volcanics. When most of the northern part of Java was a marine basin, the only land of the region was a long belt of old andesite volcanic arc deposits, formed during the late Oligocene and early Miocene. Most of the present-day land was formed during the Pleistocene by a combination of arc volcanism, compressional tectonics and rapid shoreline progradation. Moreover, East and Central Java is rich in oil and gas deposits, while the volcanic belt of West Java has been holding onto a number of gold and silver deposits (Moores, 1997; Van Gorsel, 2020).

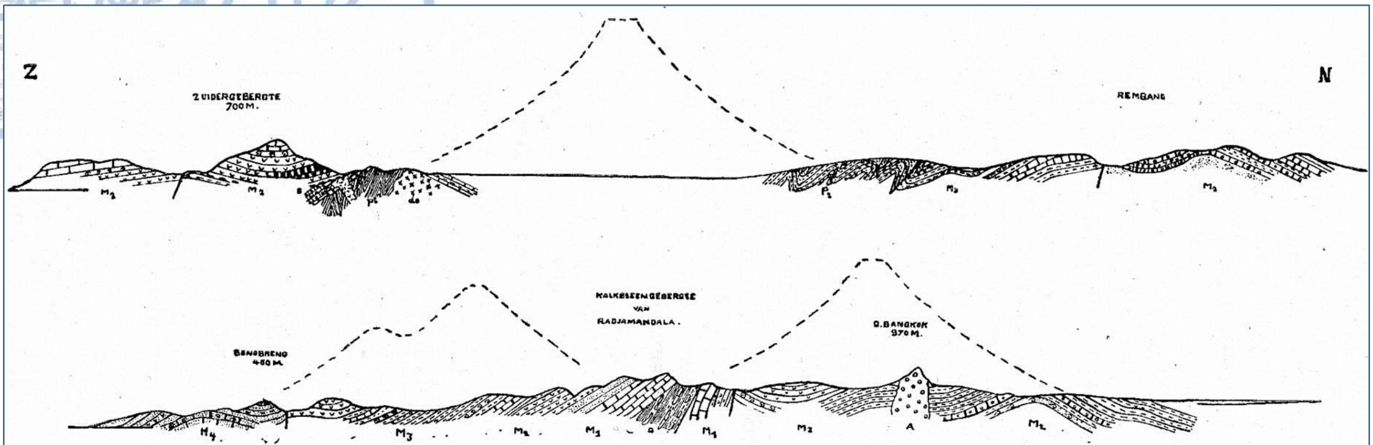

Abb. 3. Zwei schematische Profile durch Ost- und Westjava, ca. 1:1000000, doppelt überhöht.
p = Pliozän, m_1—m_4 = Miozän, o = Oligozän, e = Eozän, pt = Prätertiär, a = Andesit, do = Diorit.

Fig. 1.1 S-N geological cross-sections across East Java (top) and West Java (bottom), (Gerth 1931) (https://vangorselslist.com/java.html).

Indonesia today lies amid the tropical-humid climate belt, which means that, without human intervention, most of the land should be covered by tropical lowlands and rainforests (Moores, 1997). This was not the case however during the glacial periods of the Pleistocene, when the average temperature for the equatorial regions was lower by 3-4 Celsius degrees. This by extension meant that aridity was increased, with seasonality being more pronounced, resulting in the fragmentation of the rainforest by savanna vegetation (Van den Bergh et al. 1996). Furthermore, the eustatic sea - level was lowered by 125m, increasing physical erosion and causing river channels incision. Around the Middle Pleistocene (0.78 - 0.12 ma), the sea level started to rise and fall more drastically, with the minimum sea level reaching 170m below where it presently stands, decreasing the distance between Java and the mainland (Van Gorsel, 2020). Most likely faunal immigrations took place during these conditions. During the Late Pleistocene, Java was connected with Sumatra and Borneo and the mainland, via a land corridor that allowed for overland migration of tropical rainforest taxa (Moores, 1997; Van den Bergh et al. 1996).

1.2.1. THE SANGIRAN AND TRINIL AREAS

Since most of the *A. lydekkeri* and *D. santeng* specimens studied in this thesis came from excavation sites in the Sangiran dome (254 specimens, both species combined) and Trinil main bone bed (H.K., short for Hauptknochenschicht) (61, both species combined), its necessary to include in this thesis a basic description and the general geology and stratigraphy of these particular areas. There are also 150 studied specimens of unspecified origin in the Dubois collection, which most likely belong to either one of these sites, based on similarity in fossilization and field notes in the Dubois archive (Naturalis Biodiversity Center, Leiden, The Netherlands).

Hertler and Rizal in their Excursion guide (2005) to the Pleistocene hominid sites in Central and East Java, geologically describe Sangiran as a dome-shaped anticline located in East Java. Its axis is trending in a general N-S direction and is separated by several rivers, the biggest being Kali Cemoro. These rivers erode the topography to the point where today, the center of the dome is below the level of the surrounding terrain. The deposition of Sangiran started in the Early Pleistocene and is still ongoing. The oldest sequences lie in the center of the anticline and belong to the Kalibeng Formation, which is represented here by blue-gray marine marl and clay. The upper sequences are the Sangiran formation, consisting of black clays, about 30-40m thick. These lower beds locally contain several gastropods and pelecypods and a rich ostracod fauna, indicating a brackish water depositional environment, while the mollusk and *Balanus* fauna of the upward beds is a clear indicator of beach deposits and tidal zones respectively. On top of these beds, lay unconformably volcanic deposits of Lower Pleistocene and on top of those, sandy layers with marine mollusks are found, representing a marine ingression. After that, there are limnic black clay sediments with numerous *Melania* fossils. From then on the depositions become increasingly sand-like, and end in a sand-conglomeratic layer of a calcareous breccia, containing cross-bedded sandstones and is extremely rich in vertebrate fossil remains typical for the *Homo erectus*-*Stegodon* fauna. Unconformably overlaying these deposits, are volcanic elements that indicate nothing less of an increase in volcanic activity (Hertler and Rizal, 2005).

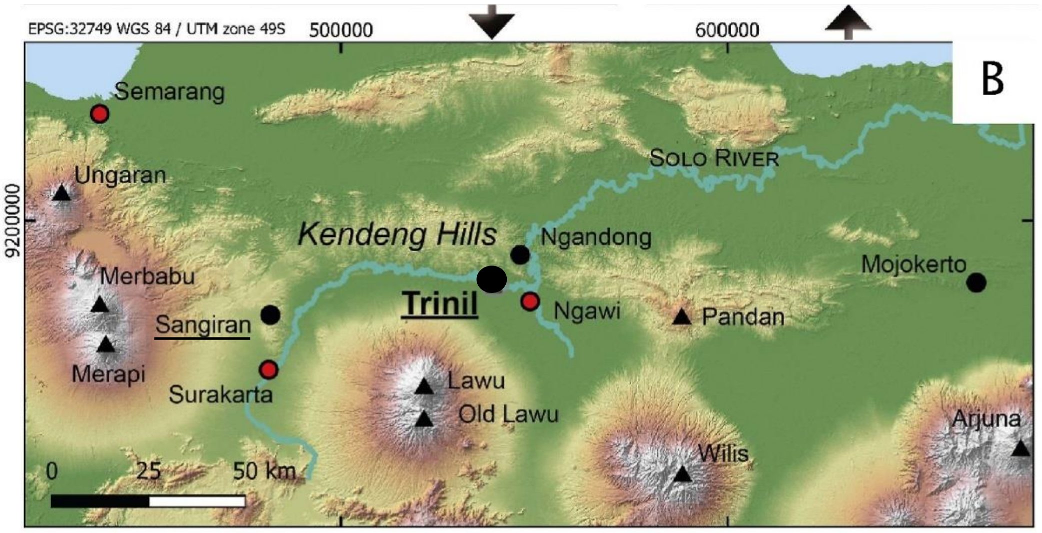

Fig. 1.2. Topography of Central-East Java showing the relative locations of fossil-bearing sites (black circles) like Trinil and Sangiran along with volcanoes (triangles) and major cities (red dots). Image taken and edited from Hilgen et al., 2023.

The same authors (Hertler and Rizal, 2005), describe the stratigraphic sequence of the Trinil area, that is located in Eastern Java as well, from older to younger is as follows: Kalibeng Formation, Pucangan Formation, Kabuh Formation, and Notopuro formation, all of which are unconformably overlain by terrace materials, which date to Late Pleistocene. The Kabuh formation is described by Duyfies (1933) as consisting of andesitic and tuff sandstones, often cross-bedded. A bed of Lapilli (LB) between the Pucangan and Kabuh formations contains a lot of vertebrate remains and its called “Hauptknochenschicht or HK”, meaning “main fossiliferous layer”. It’s the one that contains most of the Middle Pleistocene *Homo erectus* - *Stegodon* fauna specimens found in Trinil. The river Bengawan Solo meanders through the valley, cutting through these formations. The Trinil H.K. layer was excavated by Dubois in the years between 1891-1905 and by Selenka in 1907-1908. Terrestrial vertebrate species comprise about 90% of the HK fossil finds, with deer, large bovids and *Stegodon* fossils constituting the majority (Hertler, 2005; Huffman et al., 2022).

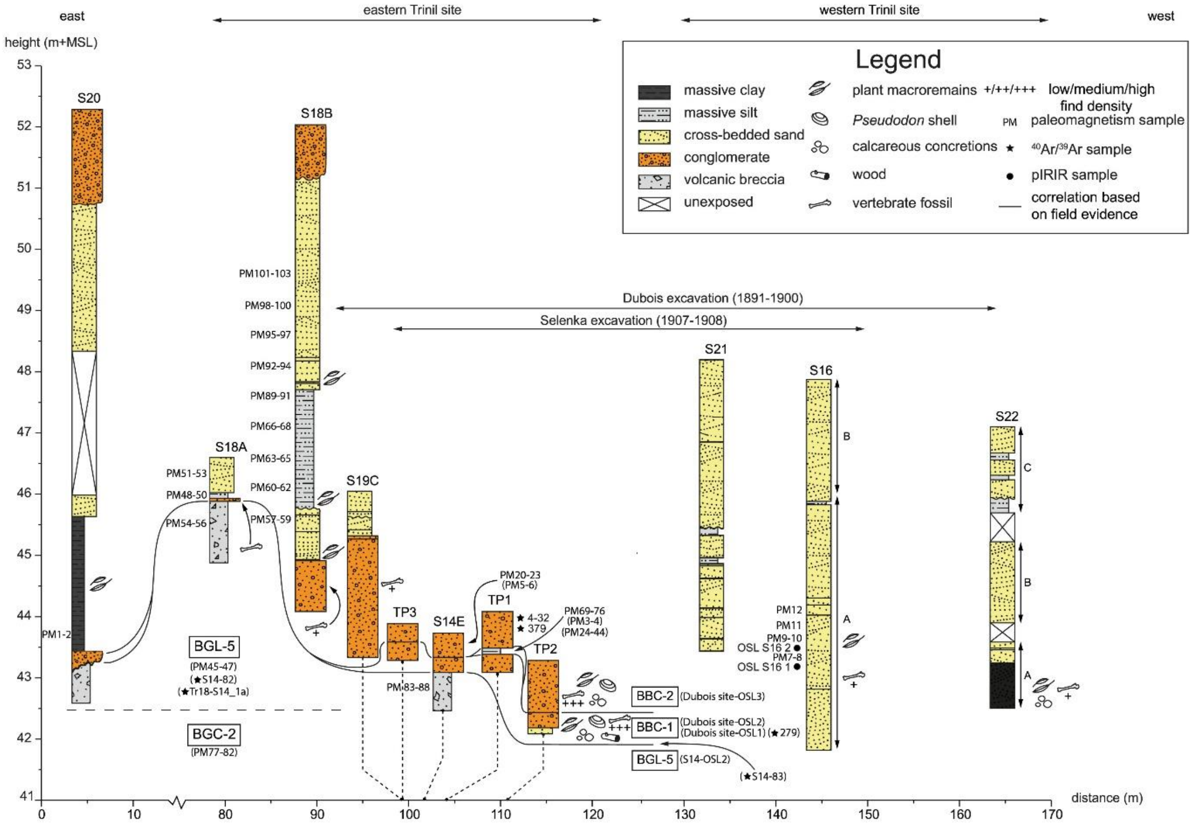

Fig. 1.3. Lithostratigraphy of the Trinil area. BGC-2 = Batu Gajah Clay 2, BGL-5 = Batu Gajah Lahar 5, BBC-1 = Bone Bearing Channel 1, BBC-2 = Bone Bearing Channel-2, T2 = Terrace 2. (L. Hilgen et al., 2023)

1.3 THE DUBOIS COLLECTION

The Dubois Collection was assembled by Eugène Dubois when Indonesia was a colony of the Netherlands and part of the Dutch East Indies. The first Dutch ship arrived at the Indonesian Archipelago in the 16th century and the Dutch controlled the indigenous populations as a colonial power, up until the end of the Second World War when the declaration of independence of Indonesia was a fact in 1945. The collection that was assembled by Dubois is one of the most well-known paleontological collections with ample published material (e.g., de Vos and Sondaar, 1994; Hooijer and Kurtén, 1984; Vos, 1999, 1984, 1983). Its importance is primarily associated with the first *Homo erectus* fossil remains (a molar, a skullcap, and a femur) that were ever found, the role these played in our understanding of human evolution, and the development of paleoanthropology as a research field (Shipman and Storm, 2002). Eugeène Dubois was born in 1858, a year before Charles Darwin published his groundbreaking *Origin of Species*. Between 1877 and 1884, Dubois studied medicine at the University of Amsterdam. Nevertheless, his passion for natural history dictated him to give up his position at the university and leave for the Netherlands East Indies in 1887 in search of what he called the “missing link” in human evolution. He unwaveringly believed that the cradle of humanity was in the tropics, following the suggestions of Darwin, who in his *Descent of Man* (Darwin, 1871) had argued that humanity originated in Africa, Haeckel who in his *Evolution of Man: A Popular Exposition of the Principal Points of Human Ontogeny and Phylogeny* (Haeckel, 1897) suggested that humans are closely related to orangutangs and based on Lydekker, who in 1879 described a primate fossil from the Siwalik Hills of British India.

As a result, Dubois joined the Dutch East Indies army and in May 1888 began to scout for caves suited for paleontological excavations. The colonial government enabled him to carry out excavations first in Sumatra and then in Java and even assigned him two members of the army engineering corps, along with a number of forced laborers. The findings were not satisfactory though until November 1890, when he found a human mandible fragment in Kedung Brubus, in Java (Dubois, 1891). Excavations in Trinil a year later were an even bigger success, with a large amount of fossils unearthed and among the rich faunal material, a hominin molar and a skullcap were found (Dubois, 1892a). A year later Dubois’ army sergeant found a hominin femur, southeast of Trinil (Dubois, 1893). Dubois attributed all these hominid fossils to a new species, *Pithecanthropus erectus* and he considered the three Trinil fossils (the skullcap, the femur and the molars) to even belong to the same individual (Dubois, 1894a, 1896a). The genus *Pithecanthropus* was later synonymized with the genus *Homo*, but Dubois's excavations and research were pivotal in the discussion surrounding the origin of humanity and human evolution and sparked a heated debate in the scientific community (de Vos, 2003).

The Dubois fossil finds of Java count more than 20.000 vertebrate specimens from different sites (mainly Trinil, Sangiran and Kedung Brubus) and helped uncover the biostratigraphy of Java, with Von Koenigswald's division of the Pleistocene of Java from 1933 to 1956 being used as a standard for more than forty years. Hooijer described the fossil faunas in great detail and published his results in subsequent papers from 1946 up until 1962, a taxonomical work that helped study faunal compositions of all localities. In the early 80's a joint team of the Utrecht University, the Nationaal Natuurhistorisch Museum of Leiden (now Naturalis) and the Indonesian Geological Research and Development Center interpreted the faunal succession using only fossils from stratigraphically known localities, concluding that the Trinil H.K. fauna was older than the Kedung Brubus fauna (de Vos & Sondaar, 1982). De Vos (1983) studied the fauna from Punung and showed that it is of similar age and composition as the one from the Sumatran caves and revised the faunal succession and biostratigraphy as follows, from old to young: Satir, Ci Saat, Trinil H.K., Kedung Brubus, Ngandong, Punung and Wajak.

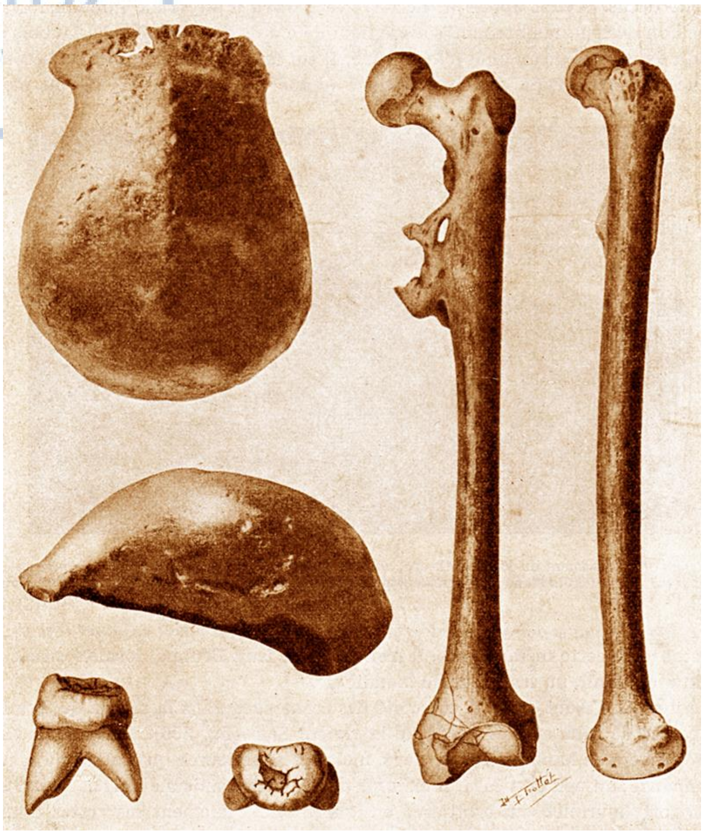

Fig 1.4. Artwork of fossil specimens of Pithecanthropus erectus (now Homo erectus) found in Java during excavations led by Eugene Dubois. A skullcap, a molar, and a thighbone, each seen from two different angles. (www.sciencephoto.com).

The hominid sites of Trinil, Kedung Brubus and Ngandong contain archaic faunal elements belonging to the *Stegodon* - *Homo erectus* faunas. The fauna shows clear affinities with those from the Siwaliks and Burma and reached Java via the Siva - Malayan Route (de Vos, 1996; Sondaar et al., 1996). The Javanese *Stegodon trigonocephalus* (Martin, 1887) is related with the Siwalik *Stegodon ganesha* (Faloner and Cautley, 1846), *Elephas husudrindicus* (Dubois, 1908) with *Elephas hysudricus* (Falconer and Cautley, 1845) and Duboisia *santeng* with the Boselaphini. This fauna became extinct at the end of Middle Pleistocene, at which point a faunal turnover took place and the *Pongo* - *Homo sapiens* fauna migrated into the Indonesian Archipelago (de Vos, 1983). The Punung site represents this latter fauna, which includes *Elephas maximus* (Linnaeus, 1758), *Pongo pygmaeus* (Linnaeus, 1760), *Hylobates syndactylus* (Raffles, 1821) and *Ursus malayanus* (Raffles, 1821), all species still existing in the Indonesian Archipelago, but no longer inhabiting Java. The balanced nature of this later stage fauna implies that the connection with the mainland was more continuous, at which period Homo sapiens migrated and joined the tropical rainforest faunal association (de Vos, 1983).

1.4 BIOZONES OF JAVA

As mentioned above, the first studies on the biostratigraphy of Java were made by von Koeningswald (1934) and were later revised by de Vos (1982) and van den Bergh (2001). The faunal succession is as follows, from old to young: Satir fauna (Early Pleistocene stage), Ci Saat, Trinil H.K., Kedung Brubus and Ngandong faunas (Middle Pleistocene stage) followed by Punung and Wajak faunas (Late Pleistocene stage) and finally the modern fauna (Holocene). The transitions between these stages are gradual because the occurrences of extinctions, new arrivals and speciation are not simultaneous. The first group is the only one that is truly unbalanced and endemic, while the penultimate fauna is balanced and non-endemic, typical of tropical rainforests, with modern humans. The group of interest for the purpose of this thesis though, is the Middle Pleistocene one, which shows clear affinities with that of the Siwaliks (India - Pakistan), but with some level of endemism.

The *Stegodon* - *Homo erectus* faunal stage is attributed to the Ci Saat, Trinil H.K., Kedung Brubus, Ngandong and similar sites, and it ranges between 1.5 Ma to 128 ka (Van Den Bergh et al., 2001). The fauna arrived on Java via filter dispersal through the Siva - Malayan route, but not all faunal elements from the Siwaliks reached Java, nor did they arrive at a single event. This faunal stage included *Stegodon trigonocephalus*, *Elephas hysudrindicus*, *Rhinoceros unicornis kendengidicus* (Linnaeus 1758), *Homo erectus*, *Axis lydekkeri* and *Duboisia santeng*. This is also the stage where some of the first carnivores arrive in Java, namely *Megacyon merriami* (von Koenigswald, 1940) (or *Xenocyon* or even *Cuon* as it was originally referred to), *Mececyon trinilensis* (Stremme, 1911) and *Pachycrocuta brevirostris* (Gervais, 1850), forming a threat to both *Axis lydekkeri* and *Duboisia santeng* while *Panthera tigris* (Linnaeus, 1758) had already been on the scene by that time (van der Geer et al., 2018). *Homo erectus* is present in Java, from about 1.5 Ma and went extinct around 117 ka (Indriati et al., 2011; Yan Rizal et al., 2020; L. Hilgen et al., 2023). This means that the Ngandong faunal stage marks the last occurrence of *Homo erectus*, although the fossil finds of this later stage (Ngandong Man), are distinct from the previous ones (Huffman and Zaim, 2023).

At the end of this Middle Pleistocene faunal stage, a faunal turnover took place, with completely new species migrating to Java via the Sino-Malayan route coming from the region of southern China. This fauna is known as the *Pongo-Homo sapiens* faunal stage and its typical of a tropical mainland (Indian elephant, pig-tailed macaque, Malay tapir, wild water buffalo etc.) and all its species are still inhabiting the Indonesian Archipelago (de Vos, 1983). It is still debatable whether *Homo erectus* went extinct before *Homo sapiens* inhabited the island of Java. Different methods by two different research teams (Indriati et al., 2011; Yan Rizal et al., 2020) give an estimate of 143 ka and 108-117 ka minimum age respectively for the *Homo erectus* of Ngandong. This leaves all possibilities open, since the Punung fauna, represented most notably by *Homo sapiens* remains has an age between 126 and 81 ka.

2. LIFE HISTORY THEORY

2.1 LIFE HISTORY DATA

Life history is a term that quantifies key events in an organism’s life such as survival, growth and reproduction rate, as well as size in an effort to explain ecological and evolutionary processes (Oli and Coulson, 2016). Those quantities are called life history traits and the most notable ones are body size, growth rate, age at first reproduction, maximum life span, number of offspring, age at maturity and adult body size. These traits affect population dynamics and thus play a key role in ecology and evolution. Life history theory provides possible explanations for biodiversity and the means by which natural selection operates. (Alonzo and Kindsvater, 2008; Oli and Coulson, 2016). Life history theory is an extension of r/K selection theory in ecology, which is a dated notion, but it still provides some general understanding of how life history traits accumulate. The theory predicts that in an unstable environment, species adapt by developing rapid body growth, early sexual maturity, a large number of offspring, and a short lifespan. These strategies are called “r-selected” and are in contrast with “K-selection” strategies, which occur in stable environments - such as islands - and include populations that are maintained near their carrying capacity (Pianka, 1993). In short, their strategies are translated to the opposite life history traits which include slow body growth, late sexual maturity, small number of offspring and long lifespan. Still, r/K selection theory is hard to generalize, much like the Island Rule, since both were based on different species - usually fossil ones - from single islands (Hayashi et al., 2020).

Natural selection favors individuals who display the greatest fitness or genes in a specific environmental scenario, by means of heredity and random factors. Having said that though, this would result in a single super-organism that would transcend the constraints of nature and would never age, produce an infinite number of offspring, and be born into adulthood (Alonzo and Kindsvater, 2008). Therefore, life history tradeoffs restrict phenotypic models and genotypes of organisms and maximize their fitness for specific circumstances. Life history traits are a result of an organism’s phylogenetic constraints as well as environmental variation after all. An example of such a trade-off is that of offspring size vs offspring number. Mammals for instance reduce offspring number and increase parental care to ensure a low juvenile mortality while fish opt into an increase of the number of juveniles while at the same time reducing their size and putting in minimum parental care, in hopes that some of their offspring will be able to make it into adulthood (Alonzo and Kindsvater, 2008).

The Pleistocene glaciation and deglaciation periods are ideal for studying life-history-related trade-offs in mammals. The rapid ecological changes, typical of these periods can lead to extensive extinctions, speciations and colonizations of new, unpopulated places that were unreachable before (e.g., islands). Resource availability would fluctuate between abundance and limitations and so there are two possible natural selection mechanisms for maximum efficiency: maintenance versus novelty. Maintenance phenotypes survive with increasingly less resources and trade novelty for imitation of older individuals that have proven to have greater survivability. The end result is that the final phenotype becomes less and less able to adapt to environmental changes which eventually leads to its extinction. Novelty phenotypes on the other hand appear during luxury conditions and must be able of great innovation in order to disperse and adapt to new conditions. In the life history traits language, that usually translates as a shorter life expectancy, high mortality rates and a younger age of maturity, while on the other hand maintenance types have higher adult survivability, older age of maturity and a slower life in general (Geist, 1998).

When studying life history traits of animal species the most important study unit is the population or, in the case of fossil species, the metapopulation. While studying a fossil assemblage, the individuals often do not belong to a single population, from a specific place and time, but rather they form a metapopulation, comprised of animals from different time periods (Klein and Cruz-Uribe, 1984). This gives paleontologists the advantage of studying the life history of a fossil species over an extended period of time, minimizing fluctuations a single population could have thanks to environmental changes and many other reasons. Life history research is dependent upon the knowledge of the age of all individuals because that way we can reach conclusions about mortality, survivability, reproduction rate, slow or fast life, etc. This is reflected in a life table, which in its most basic form consists of three columns: age, survivorship, and fecundity (Caughley, 1966). In the context of metapopulations though, the age of the specimen becomes by default the age of death and so life tables of fossil species comprise from age (x), mortality (dx) and survivability (lx) (Caughley, 1966; Oli and Coulson, 2016). Mortality profiles in ungulates get affected by age and sex-related differences in survival tactics, presence or absence of predators, and vegetation density and distribution (Klein and Cruz-Uribe, 1984).

Thus, in fossil populations, the age profile is always a mortality profile (dx) if there are attritional factors involved in the death of the individuals. Accidents, predation, old age, and other routine factors are considered attritional and have their biggest effect on very young and very old individuals, and as such the mortality profile ends up being U-shaped. On the other hand, if a fossil population died thanks to a catastrophic event such as a flood or a volcanic eruption, then the age profile represents the original living structure of a population, in other words, the survivorship (lx), and the profile is L-shaped (Klein and Cruz-Uribe, 1984). From the above one can assume that by studying the shape of the profile alone, we can conclude whether a mortality profile is catastrophic or attritional for species of which, the females only have maximal one offspring per year. In catastrophic L-shaped profiles, most individuals are prime adults, while in attritional U-shaped mortality profiles, most of the individuals are either juveniles or old. There are exceptions of course, or cases , where one can not differentiate between the two, nature, is not obliged to follow man-made rules after all (Caughley, 1966; Gaillard et al., 1998; Klein and Cruz-Uribe, 1983; Kubo et al., 2011; Stiner, 1991).

It is generally the norm for juveniles to be underrepresented in the fossil record because their teeth and bones are more fragile and can't withstand the same weathering as the adult ones, especially so when carnivores are present and acting in an area. In their study, Klein and Cruz-Uribe (1983) mention that lions prey mainly on very young zebras, buffalos and chamois and that they devour the animals “too quickly and completely”. Even so, it is expected in populations of mainland herbivores that are being targeted by carnivores, to have two peaks in the age profiles, one for the very young and one for the very old, since these age groups are the prime focus of hunters because they are easy to catch (van der Geer et al., 2014). By contrast, when there is human hunting activity on an ungulate population, there is an excess of mortality on middle age classes because younger individuals don't provide as much food quantity and also, they are poor trophies, thus producing a more catastrophic-looking profile. This is also why human activity drove many species to extinction, as reproductively active age classes are responsible for the birth rates of a population, and with them gone, the numbers are in decline (Stiner, 1991).

In attritional profiles, the second peak might not be visible due to sampling errors. Migrating or wandering animals tend to assemble themselves into age or sex-related groups, thus potentially resulting in a biased sample. Knowing about such possible biases in advance can reduce the sampling error of the collector, but with fossil species, accurately predicting this is not possible. Also, sampling errors may come from the collectors themselves since in many cases they were not specialized scientists, but I will expand more on that later.

2.2 THE ISLAND RULE

Apart from predator and prey dynamics, life tables and life history traits are affected by resource limitations. Such conditions can be observed in energy-poor islands even today and that was likely also the case during Pleistocene deglaciation periods where places that use to be connected with the mainland during the glaciers, got isolated with the rising sea levels as the temperatures rose (Geist, 1998; van der Geer et al., 2021). This was the case with many islands of the Mediterranean Sea but also with Java in Indonesia, which is the focus of the present study. Large mammals are generally characterized by high metabolic and growth rates, which are a problem when paired with a limited supply of resources. Yet the fossil record provides us with abundant cases that prove that large mammals were actually dominant faunal elements of many islands, with deer, elephants, hippos and bovids being the most predominant ones. Insular mammals share some special life history characteristics thanks to their endemic nature, with size variation being the most obvious one. Insularity in ungulates leads primarily to dwarfism and sometimes to gigantism and the hypothesis that aims to explain and possibly predict these body size alterations is called the Island Rule (Foster, 1964; Valen, 1973).

Palkovacs (2003) explains that size shifts in vertebrates have usually been explained by either the scope of low interspecific competition, lack of predation or resource limitation. The most questionable explanation of the three is that of limited competition leading to vacant niches in an island. It assumes that increasing or decreasing body size generates an expansion of niche breadth but fails to foresee how factors such as food acquisition methods, feeding structure morphology and dietary changes can affect the adaptability of mammals. On the other hand, forces of predation are indeed lower on islands than on the mainland, because, for one, predators usually lack the colonizing ability of other animals and two there rarely is prey abundance on islands. The argument this hypothesis makes is that without hunting pressure, prey populations attain optimal body size since there is no selection pressures for survival but rather only for food acquisition and niche expansion. As discussed above, predation is usually apparent in mortality patterns in younger and older age classes, but as seen in van der Geer et al. (2014), along with a great many others, mortality profiles show an abundance of juvenile individuals. And yes the argument can be made for Java, that it had some large predators like tigers, dogs and hyenas but that wasn't the case at all in the Pleistocene Cretan ecosystem. Recent studies have shown that mortality in herbivores most predominantly has to do with accidents, starvation and harsh weather conditions, especially so in islands (Koike and Ohtaishi, 1987; Kubo et al., 2011; Minami et al., 2009; van der Geer et al., 2014). There have been minimum differences in the mortality profiles observed in mainland and island ungulate populations and even between domesticated and wild ones. So while yes, the absence of predators alleviates some of the pressure, it's hardly enough to trigger such extreme body size alterations.

And so all but one option remains, that of resource limitation. It is hard to both dismiss and confirm this hypothesis because for one, it can explain very well why large herbivores reduce their size to island dwarves and that is because body size decrease is an efficient way to reduce individual energy needs. However, as with the competition hypothesis, dietary and feeding behaviour changes affect an organism's access to resources way more than body size ever could. That is where life history theory comes in to explain the island rule and provide a framework in which many elements and trade-offs in an organism's life accumulate and result in the morphologies we come across in the fossil record. Limited resource availability and lack of predation alter an organism's life history traits and such changes result in differences in body size. Low extrinsic mortality and limited resources trigger both a genetic response and a phenotypically plastic response, meaning adjustments occur between certain hereditary and environmental limits (Palkovacs, 2003). Adaptive plasticity resists the evolution of natural selection by making it reliant on the random nature of genes, except under extreme conditions, such as the ones we're investigating. In this case, resource and space limitation tip the scales of body size alteration in a different direction than low extrinsic mortality does. This model predicts that when the first category predominates, body size decreases while if the absence of predators affects populations more, then body size increases (Geist, 1998; Köhler and Moyà-Solà, 2009). Therefore, organisms opt into what is more efficient. In Java for example, because there are active predators and resource limitation, endemic ungulates *Duboisia* and *Axis* opted to smaller body size, while in Crete, because both conditions existed (resource limitation and low predation) *Candiacervus* most likely developed into different ecomorphs, both large and small, to explore all the available niches (Besou et al., 2022).

As a final note on the matter of the Island Rule, I would like to mention the research by Raia and Meiri (2006), in which they performed a series of statistical tests to determine what affects body size more and arrived at the conclusion that, in ungulates, primarily competition, but also predation are the main suspects that cause dwarfing. They dismiss island size, isolation and size of the mainland ancestor from being major determinants of body size evolution, as they note several cases of different islands being colonized repeatedly by the same species, and yet size variation still follows the competition/predation hypotheses regardless of the phylogenetic load or the size of said island. Still, I think there is a case to be made about how an island's geology, overall size, and isolation affect its richness in resources and the number of competitors. What is of paramount importance, is to recognize that the conditions (amount of resources, competitors, predators) mammals face when arriving on an island is what is going to affect their body size and in turn their level of endemism. Ultimately though, the reason that body size variation is important is because it affects many aspects of an organism's life history traits. Reduction of size in large mammals on islands is generally associated with a slower growth rate, later sexual maturity, and an extension of maximum lifespan.

2.3 IMMIGRATION PATTERNS

In biogeography, there are three types of barriers for large-sized animals to overcome. The first one is physical, geological barriers such as extensive mountain chains, seas or arid desserts. Another type is the climatic barrier that limits the distribution of a species. Very low temperatures for example can prove to be fatal for many animals that are not adapted to this sort of climate. At the same time, the very nature of the habitat might prove to be a barrier for a certain type of species, small volcanic islands (like Krakatoa) for example are such a case for a great many big animals. Finally, there can also be biological barriers that prevent organisms from advancing any further away from their place of origin, such as parasites, predators or even food competitors (Renema, 2007).

Sheer chance plays an often undervalued role in the distribution of animals and that also applies to island biodiversity. For example, animals that accidentally reached an island by rafting or blown by strong winds. Where the impact of chance actually occurs though, is when we consider the timing of an animal's arrival and how this tips the scales of the ecosystem for other organisms that were there before or those who will arrive in the future. Whatever the mechanism of immigration, when animals are confined to a reduced space such as an island, they tend to develop certain characteristics, whether they are based on the "island rule" or not, in order to adapt and eventually evolve into endemic species. In this case the barrier is not necessarily physical, but the animals own physiology which has adapted to a very specific range of environmental conditions (Renema, 2007).

By means of extensive research in islands globally, several dispersal methods of big animals have been specified: The first and easiest one to imagine is dispersal by a land corridor. Such was the case with the *Gomphotherium* land bridge that connected Eurasia to the Arabian Plate between approximately 19 Mya and 15 Mya, thus allowing the interchanging of African and Eurasian taxa (Harzhauser et al., 2007; Rögl, 1999). Other possible dispersal methods include filter dispersal in which spread is probable for some organisms but improbable for others and the pendelum route that is easily crossed on both ways for some mammals but presents an insurmountable barrier to others. Great example of this was the Siva - Malayan route connecting Java with the mainland during the glacial periods, where some mammals could cross and inhabit Java, while others couldn’t. These selective dispersals could be either because of climatic, ecological and physiological barriers or thanks to the seasonality of the route. Lastly, sweepstake dispersal is improbable for most organisms and utterly impossible for others but weirdly it is something that happens more often than someone would expect (Vos et al., 2007).

Most insular species that evolved giant or dwarf body mass form part of unbalanced faunas, which are a typical indicator of sweepstake dispersal. Unbalanced faunas pinpoint that an area has rather high isolation, meaning it is difficult to reach by most taxa and has been isolated for a long time. Taking into account faunal elements of the fossil record alone, it is to be expected that islands that maintain a certain degree of faunal exchanges with the mainland would have a more balanced character and therefore the palaeoenvironment would not most likely be characterized as insular (Vos et al., 2007). What all these insular faunas have in common are mammal species with the ability to swim and traverse great distances by sea (van der Geer et al., 2010). Hippos have a semi-aquatic lifestyle, proboscideans are great swimmers and gain buoyancy thanks to gasses in their digestive tracts, something that also stands true for deer. On the other hand, smaller mammals may reach isolated islands by rafting on floating debris and driftwood (Dermitzakis, 1990). This also explains the apparent absence of carnivores and perissodactyls in islands, since they don’t have the ability to swim for long distances. With the passage of time and with the condition that the mammal remains in isolation long enough, speciation may occur and in some instances, even species radiation. Species radiation, or cladogenesis, is the rapid increase of the population of a species that is characterized by great morphological diversity, a mechanism that is often reflected in adaptations to different ecological contexts. In addition, it is a common observation in some of the bigger islands the occupation of different niches with different microclimate within the same island, by organisms that are phylogenetically close but share some adaptation differences, that they evolved in order to take advantage of said niche (van der Geer et al., 2010; Geist, 1998; van der Geer et al., 2014).

3. Systematic Paleontology

3.1 Order: Artiodactyla (Owen, 1848)

Artiodactyla or Even - Toed Ungulates form one of the most diverse and successful groups of mammals, playing a key role in the ecosystems of the Cainozoic, especially in the Neogene and Quaternary. They are called even-toed, because, for the most part, they have either two of four toes such as pigs, sheep, goats, deer, giraffes, hippos, camels, llamas, antelopes etc. (Foss, 2007). They have been extensively under the microscope of scientists regarding their evolution, morphology, ecology, and behavior, mainly because of their early role in humanity's survival, their economic value, and their impact on culture.

Traditionally, based on morphological traits, artiodactyls have been regarded as of a single origin and were usually divided into three suborders: Ruminantia, Tylopoda and Suiformes (Simpson, 1945). However, as DNA research progressed and molecular studies took over morphology-based phylogenetic analyses, a lot of previously solid ideas were challenged and ultimately changed. Artiodactyls provide an excellent opportunity to study incoherencies between morphological and molecular approaches in phylogeny, such as the relationship between major families of artiodactyls and the phylogeny of the Bovidae family (Foss, 2007; Wang and Yang, 2013).

In the last 50 years, whales have been added to the order Artiodactyla, based on molecular studies by Boyden and Gemeroy (1950), Irwin and Arnason (1994), Graur and Higgins (1994), and Gatesy et al. (1996) to name a few, who found that whales are closely related to extant hippopotamids, thus changing the name from Artiodactyla to Cetartiodactyla to include Cetacea. Paleontological research is what gave a further boost to this idea however, with the discovery that whale fossils have paraxonic feet (meaning they're bearing weight evenly on two parallel axes within the foot, typically the third and fourth digits) and double a pulley astragalus, both considered to be characters unique to the artiodactyls (Gingerich et al., 2001; Theodor, 2001; Thewissen et al., 2001). This realization opened up a heated debate but also a window of opportunity to combine morphological data from fossils and molecular ones from extant species to try and achieve a reanalysis of both artiodactyl and cetacean systematics resulting in the following tree.

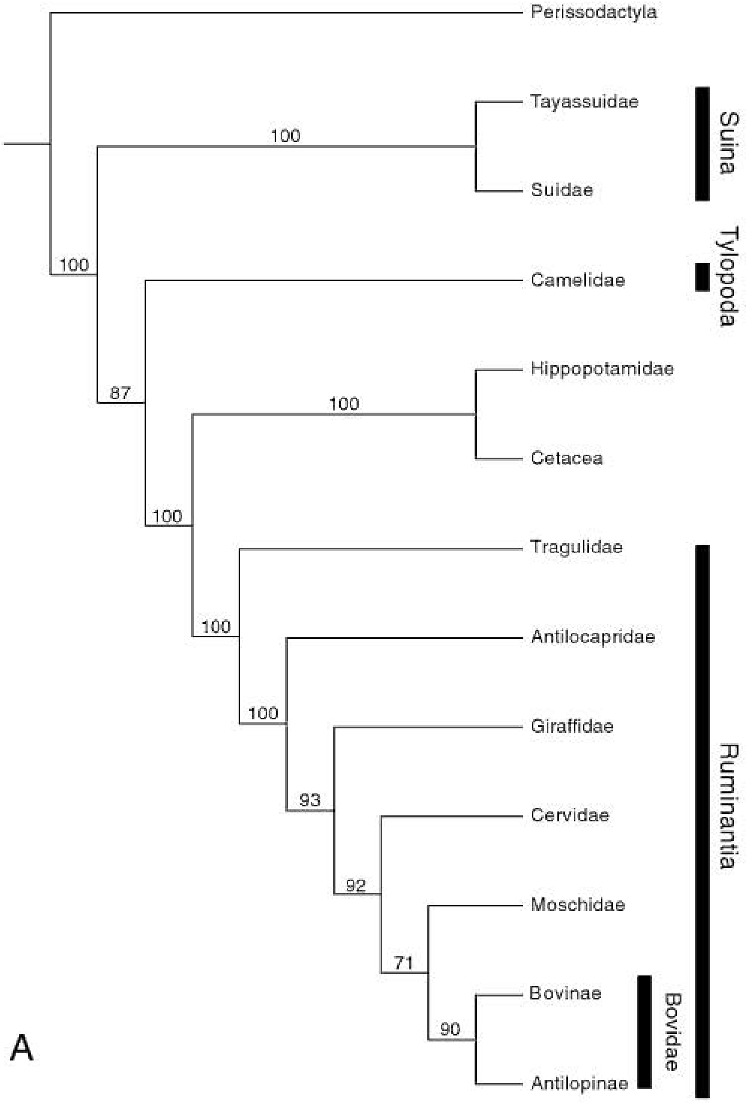

Fig. 3.1. A super-tree, combining morphological and molecular data, showing the phylogeny of the families within the order Artiodactyla. Seven ruminant families form one large group, while whales and hippos team up together and finally camels belong in a group of their own, Tylopoda, contrary to common belief, that would group them with the rest of ruminants (Foss, 2007).

The state of the super-order Cetartiodactyla (Montgerald et al., 1970) today does not appear to be so bright, with very few people agreeing to the necessity of it. Prothero et al. (2021) state that Cetacea is not the sister - taxon of Artiodactyla but is rather nested deep inside the order as a sister taxon of Hippopotamidae, hence the change in nomenclature is unnecessary. They further argue that not only is the term Cetartiodactyla a junior synonym of Artiodactyla (Asher and Helgen, 2010), but it also diminishes our understanding of the phylogenetic relationships of artiodactyls and cetaceans, as hippos and whales share a common ancestor within the paraphyletic group Anthracotheria (Irwin et al., 1994; Gatesy et al., 1996; Waddell et al., 1999). As of today, the order Artiodactyla consists of the following families: Cetacea, Hippopotamidae, Antilocapridae, Moschidae, Tragulidae, Bovidae, Cervidae, Giraffidae, Suidae, Tayassuidae and Camelidae. The exact topology of the families however remains highly controversial still. Mitochondrial genome analysis performed by Wang and Yang, (2013), supports the idea that Artiodactyla is not monophyletic, with Cetacea being a sister clade to Hippopotamidae, henceforth being grouped under the sub-order Whippomorpha (Waddell et al. 1999). They also suggest, in accordance with other research, that Tragulidae is relative to Pecora families and that Moschidae is the sister group to bovids, but that is still debatable as only recently have the Moschidae been recognized as a completely different group, as they were traditionally considered cervids.

3.2 Suborder: Ruminants

The suborder Ruminantia consists of six families: Tragulidae, Giraffidae, Antilocapridae, Moschidae, Cervidae and Bovidae, all of them terrestrial, herbivorous mammals. They are native to all the continents of the world, except Australia and Antarctica, since the past 50 million years. Ruminant species have an incredible size variation, with the smallest extant species being *Tragulus javanicus* (20-35 cm shoulder height) and the tallest being *Giraffa camelopardalis*, reaching up to 5.8 meters. The main reason why phylogenetic relationships between Ruminantia families are problematic is that there were periods of vast and rapid radiation during the Oligocene, Miocene and Pliocene and as such, some morphological traits developed several times in parallel, resulting in difficulties in recognizing true ancestry (Gentry, 1992). Fernández and Vrba (2005) tried to, at least partially, solve this issue by creating a “supertree” with both morphological and molecular data from both extant and fossil taxa.

Ruminants and Tylopoda developed complex stomachs that permit rumination independently, and although there are similarities in dentition, like selenodont teeth and a large diastema between the labial and cheek teeth, ruminants are distinguished by the horny pad that replaces the incisors of the maxilla and the lower incisiform canine. Moreover, ruminants possess fused navicular and cuboid bones of the tarsus and fused magnum and trapezoid bones of the carpus. Therefore, these are the diagnostic features of all ruminants, including of their hypothetical common ancestor (Fernández and Vrba, 2005; Foss, 2007; Hassanin and Douzery, 2003). The fossil record indicates that ruminant traits first appeared during Middle-Late Eocene, while by molecular estimations, the Tragulina - Pecora split happened somewhere around the same time (44-46 mya) (Hassanin and Douzery, 2003).

Pecora (Flower, 1883) is an infraorder within Ruminantia, the sister group of Tragulina (Flower, 1883), of which Tragulidae is the sole surviving family. Almost all Pecora are characterized by cranial appendages, that although not homologous, have been used to unite some families: Permanent, unbranched, horns in Bovidae, antlers that are branched and shed for Cervidae, deciduous and branched horns in Antilocapridae, with the exceptions of Hydropotes and Moschus and skin-covered cones for Giraffidae (Fernández and Vrba, 2005; Foss, 2007; Hassanin and Douzery, 2003). Tragulidae is the only family of Ruminants that is distinct from other Pecora, a divergence that is supported by both molecular and morphological data. Molecular analyses also support the monophyly of Pecora and all the subsequent families, while morphology helps recognize the general interfamily relationships, although a definitive solution has not yet been found (Hassanin and Douzery, 2003). Molecular estimations by the same authors indicate that the Pecora evolutionary radiation occurred some time at Early Oligocene, just after the Grande Coupure (Stehlin, 1909), with the characters that defined them appearing in the Early Miocene.

Subfamilies and tribes within the Cervidae and Bovidae began to split between 25 and 13 Mya, with Fernández and Vrba (2005), counting five main episodes in their cladogenesis. The first major chapter in their radiation occurred sometime around 25-22 mya, which gave birth to Bovinae, Antilopinae, and Aepycerotinae probably in response to rapid climatic change during the Oligocene - Miocene transition. The second increased radiation (20-17 mya) was associated with a cooling episode in Early Miocene, giving rise to most of the cervid and bovid subfamilies we encounter today. Subsequently, the third one occurred between 14-13 mya, with the split of Reducinae and Peleinae and that of Caprinae and Cervinae, coinciding with a global cooling again. A fourth event is recognized by the diversification of Capreolinae and finally, at 2.5 mya an intergenetic cladogenesis is detected, which coincides with the start of Plio-Pleistocene glacial cycles.

3.3 Family: Cervidae

Cervidae (deer) is the second most diverse group of ruminants and are distributed in America, Europe and Asia, inhabiting a broad variety of different environments. Notwithstanding the plethora of studies concerning the systematics of deer, the relationship between the different species and the rich fossil record, researchers still have only reached a partial consensus, as many question marks still remain (Foss, 2007; Geist, 1998).

All cervids share a number of cranial anatomical characteristics such as pre-orbital vacuity, two lacrimal foramina and a lacrimal fossa. The pre-orbital vacuity varies in size and form, while the lacrimal fossa can be deep and round. Antler morphology is unique for each species and is often used in phylogeny, but at the same time has high variability both intraspecifically and ontogenetically. Finally, the most important dental characters used in classification are derived from lower premolars and upper molars. Upper canines, when present, are a primitive characteristic seen in Miocene cervids and are fully functional in muntjacs today, while the upper incisors and first premolars are absent in all Cervids (Veitschegger and Sánchez-Villagra, 2016).

The Cervidae are divided into three sub-families by Groves and Grubb (1987), the Hydropotinae (Chinese water deer), the Odocoileinae (New World Deer) and the Cervinae (Old World Deer). This diversification was based on the reduction of the lateral metacarpals: Odocoileinae have preserved the distal ends, while Cervinae have retained the proximal ends. As such, the two groups are called telemetacarpals and plesiometacarpals respectively. Cervinae also share a special cranial character, which was described by Bouvrain et al (1989) and involves the postglenoid foramen which is in its entirety within the squamosal. These phylogenetic splits have also been supported by molecular studies.

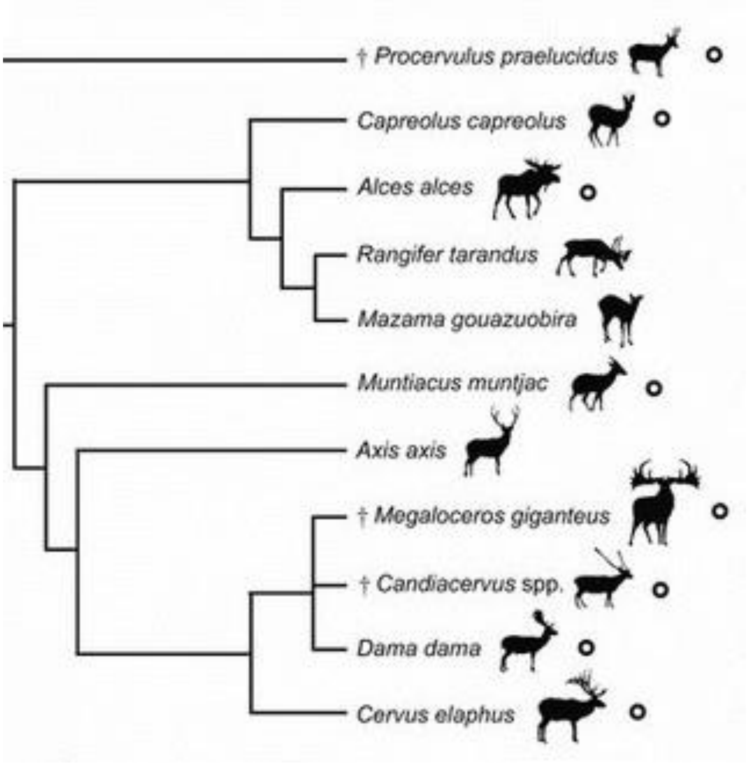

Fig. 3.2. Phylogenetic tree, showing the taxonomy of extinct and extant species within the Cervidae tribe, based on morphological data as well as on growth rates of teeth and long bones (Kolb et. al, 2015).

3.4 Family: Bovidae

Bovidae is a family that includes 137 extant and more than 300 fossil species. The majority of living taxa are native to Africa, but they are also present in Europe, Asia and North America. They are one of the most diversified families of mammals and that makes their family member's relationships difficult to describe. Gatesy et al. (1992) combined molecular and morphological data to prove the monophyly of the clade, with the most unambiguous morphological character being the presence of bony horns, covered by keratinous sheaths. Typically, Bovidae are divided into two sub-families: Bovinae, which is further divided into three tribes, Bovini, Tragelaphini and Boselaphini, and Antilopinae - Aegodontia which is a clade that includes all bovids that are not Bovinae and which is further divided into six tribes (Bibi et al., 2009).

Bovids differ from their closest relatives, the giraffids and cervids, among other things, by the possession of permanent horns, that derive from frontal bone, unlike deer, which posses annually shed antlers that derive from periosteum and are covered with skin. Bovid horns consist of three parts: the horn core, the bony core that originates from the frontal bone, the pedicle, which is part of the frontal bone and is fused with the horn core, and finally the horn sheath (Foss, 2007). Another very important character in the systematics of bovids is dentition. Bovinae tend to have a lesser degree of hyspodonty, little enamel complication, basal pillars, and sharp cusps both on premolars and molars. There are several ungulate groups that developed hyspodonty (equids, rhinocerotids, oreodonts, camelids, antilocaprids and bovids) and in most cases, hyspodonty correlates with grazing (Bibi, 2006).

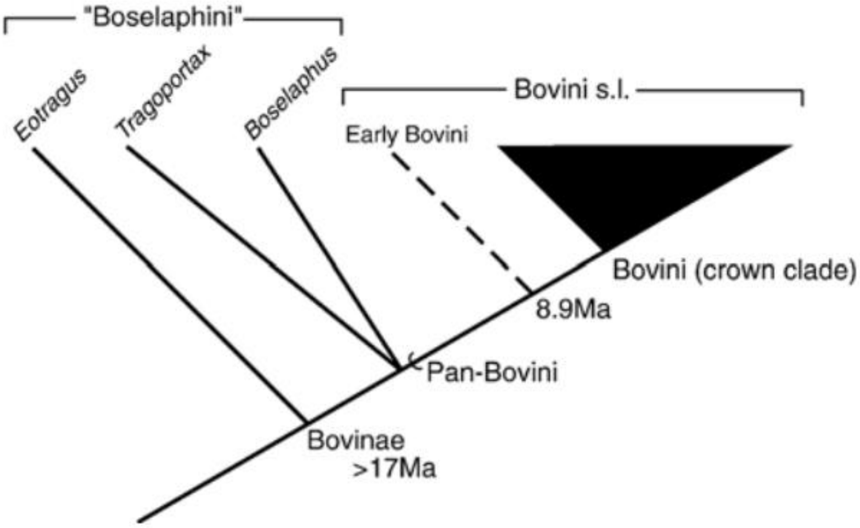

Fig. 3.3. A cladogram showing possible relationships between early bovines and Boselaphini. Pan-Bovini here are considered the stem bovines, ancestors to the crown clade. *Duboisia santeng* is closely related to the genus Boselaphus (Bibi, 2006).

3.5 *Axis lydekkeri*

Order: Artiodactyla, Owen, 1848
Family: Cervidae, Goldfuss, 1820
Subfamily: Cervinae, Goldfuss, 1820
Tribe: Cervini, Batsch, 1788
Genus: *Axis*, Smith, 1827
Species: *Axis lydekkeri*, Stremme, 1911

The species is based on an antler described by Martin (1886), the type specimen is from an ontogenetically young individual and is stored in Naturalis Biodiversity Center, Leiden, the Netherlands. The antler of *Axis lydekkeri* is lyre-shaped and it consists of a burr, a short base, a smooth beam, and two brow tines of which the second one points inside (Zaim et al., 2003). Tropical Asia was probably the center of the Cervini deer radiation (Geist, 1998), although their systematics remains controversial. Deer have been a part of both mainland and island Pleistocene faunas, west of Wallace's line and their fossils have been found in deposits from Borneo, Sumatra, Malaysia, Palawan, Luzon and of course, Java (Gruwier et al., 2015). Martin (1884, 1886) described several Javanese fossils and recognized that these mammal remains probably came from an Indian faunal association which had in turn been described by Murchison (1868), and thus an ancestor of *Axis lydekkeri* probably reached Java via the Siva - Malayan Route by filter dispersal. Lydekker's deer uniquely shaped antler makes it difficult to recognize it's Siwalik ancestor (van der Geer et al., 2021), but Dubois was the first to recognize its relation with the genus *Axis* of the chital (*Axis axis*) and the Indian hog deer (*Axis (Hyelaphus) porcinus*). Finally, *Axis lydekkeri* belongs to the Ci Saat, Trinil H.K. and Kedung Brubus biozones which span from the Early to Middle Pleistocene (1.5 ma - 128 ka).

Axis lydekkeri is generally smaller than *Axis axis* but is similar in size to *Axis (Hyelaphus) porcinus* and based on skull morphology and craniometrics, it is indeed closer to the subgenus *Hyelaphus* (Meaard and Groves, 2004). Berkhout et al. (2021), translated the excavation reports of Selenka and Blanckehorn carried out in Trinil in 1911 and among other things, they mention some allometry measurements such as that the ratio of occipital bone width to parietal length of *Axis lydekkeri* is 1.44, while the distance between the frontal foramina is 1.70, both fairly similar to the measurement results for *Axis axis* (1.41 and 1.69 respectively), so there is little doubt that it belongs in the *Axis* genus. Furthermore, the results of a geometric morphometric analysis on the upper molars performed by Gruwier et al., (2015), showed that the fossil *Axis lydekkeri* grouped together with the two extant species of the *Hyelaphus* subgenus (*A. kuhlii* and *A. porcinus*) in the PCA, in agreement with the results of Meijaard and Groves, (2004) so it most likely should be placed under that subgenus and not under *Axis*. If Lydekker's deer was anything like it's living relative, the Indian Hog deer, then it should prefer grass - jungles with moderate size bushes, while it shouldn't form large groups or herds, since Hog deer are not sociable by nature and seldom do they form pairs of even two or three animals, even in mating season (Lydekker, 1898). Synonyms of *Axis lydekkeri* include : *Cervus lydekkeri* (Martin, 1888, Vogel von Falkenstein, 1910), *Cervus liriocerus* (Dubois, 1907, 1908) and *Cervus (Axis) lydekkeri* (Stremme, 1911; Stehlin, 1925; von Koenigswald, 1933, 1934).

There are hundreds of mandibles, jaw fragments and isolated molars of *Axis lydekkeri* in the Dubois collection and most of them come from Sangiran and Trinil H.K. There are several similarities between the mandibles of *Axis axis* and *Axis lydekkeri*. In both, the horizontal part of the ramus is slightly curved but in *Axis lydekkeri*, the ventral groove is not as clearly shaped as in *Axis axis*. There is an alveolar socket for the canine and behind it, one mental foramen. The condylar process is crosswise elongated, and the coronoid process is curved caudally (Kumawat et al., 2014). The lower dentition of *A. lydekkeri*, is fairly similar to that of its extant *Axis* relatives. The enamel of mandibular molars is very rough, and the prism is prominent. There is also a considerable size difference between mandible premolars and molars, with the former of course being the smaller, while m3 is the tallest tooth in the toothrow. The size range of the third, lower, isolated molar is as follows: For crown height, I measured a total of 22 mm for some unworn molars, while the most worn-down tooth had a crown height of 11 mm. As for tooth length, the variations in size was less apparent, with the longest tooth being 21mm and the shortest one being 16mm and finally, for breadth, the numbers ranged between 10 and 7mm. First and second-isolated molars cannot be differentiated so they are not taken into account here.

Fig. 3.4. Right mandible (p2 - m3) of *Axis lydekkeri*, specimen No.1957 from the Dubois collection. The origin of the specimen is Trinil, Java and the age of the individual estimated by the QCHM is 6 RDY (red deer years). Based on the first molar, the age estimation is 1 year, while age estimations from m2 and m3 are 4.9 and 12.1 respectively, so an average of 6 years is calculated in this way. The scale is 10cm for reference.

3.6 *Duboisia santeng*

Order: Artiodactyla, Owen, 1848
Family: Bovidae, Gray, 1821
Subfamily: Bovinae, Gray, 1821
Tribe: Boselaphini, Knottnerus-Meyer, 1907
Genus: *Duboisia*, Stremme, 1911
Species: *Duboisia santeng*, Dubois, 1891

Dubois' antelope is a small boselaphine with short and keeled horn cones that characterizes the Trinil H.K. and Kedung Brubus faunal units (0.9 - 0.7 Ma) (Van Den Bergh et al., 2001). Most of the chosen specimens from the collection originate from the Sangiran dome and Trinil HK. *D. santeng* is related to the living boselaphines of India, namely *Boselaphus tragocamelus* and *Tetracerus quadricornis*. Hooijer (1958) was the first to recognize the occurrence of the genus outside of Java, however, due to the absence of conclusive fossil evidence of *Duboisia* on South-East Asia, the questions of when the animal colonized Java and its exact relationship with extant relatives remained unanswered for decades. Nishioka and Vidthayanon (2018) found evidence that the genus existed outside of Java and described cranial remains from Thailand, pointing out morphological affinities between the two forms, the continental *D. aff. santeng* and the endemic *D. santeng*, but since they are not sure whether the specimen belongs to the upper geological layer (Early Pleistocene) or the lower unit (dated to Miocene), the matter of the exact timing of *Duboisia's* arrival in Java remains unresolved still. The estimation is that the first appearance of *Duboisia* in the Southeast Asian continent occurred sometime at the beginning of the early Pleistocene (Wibowo, 2020). Whatever the case may be, since mainly cranial morphology and horn cores shape are diagnostic for the genus, the fact remains that *Duboisia* is characterized by a squared braincase, weak temporal crests and keeled horn cores that are also compressed anteroposteriorly. In the Dubois collection at Naturalis, (Leiden, Netherlands) there are many specimens of mandibles and maxillary bones, along with a great many isolated teeth and jaw fragments. Because in this research, all the data were acquired by either mandibles or lower molars, I will limit the description to the mandible and dental elements.

Mandibles of *Duboisia santeng* resemble those of *Boselaphus tragocamelus* in the long part of the ramus and the height difference of the mental foramen to the second premolar. Unfortunately, the condylar and coronoid processes are missing from the studied specimens. The angle of the ramus seems sharp and it's base becomes much narrower behind the molars. The mandible of *Duboisia* differs though, thanks to the rapid increase in height from p2 to m3 (Hooijer, 1958). Isolated molars have been described by Stremme (1911, p. 120) who was the first to draw similarities in morphology between *Duboisia* and *Boselaphus*, namely the similarity in hyspodonty, the smoothness of enamel and the shape of the premolars. *Duboisia* lower molars mostly lack basal pillars and are more hypsodont than those of *Boselaphus*, which is to be expected since an increase in hyspodonty is a feature of island endemics (van der Geer, 2014). The enamel foldings of the premolars are sharp and pronounced, with two anterior and two posterior wings both in the third and the fourth premolars. Maximum and minimum crown height for isolated third molars of Duboisia, out of the 79 specimens studied, are 30mm (unworn) and 11mm (extremely worn) respectively while for most individuals (50 specimens), crown height is ≥20mm. The length of the third molar ranges from 14 to 26mm and breadth starts from 8mm and goes up to 12mm. The size variation in crown height is mainly due to different wear stages (not all of them age related) while for the molar length difference, the main reason is probably sexual dimorphism.

Fig. 3.5. Right mandible (p2-m3) of *Duboisia santeng*, specimen No. 2068d from the Dubois collection. The origin of the specimen is Trinil, Java and the average age of the individual as calculated by the QCHM is 1.7 GY (goat years). Based on the m1, the age estimation is 0.8 years, while based on m2 and m3 the age is estimated as 1.4 and 3 years respectively. The scale is 10 cm.

Rozzi et. al. (2013) performed mesowear and DASTA analysis (Dental Areal Surface Texture Analysis) in order to determine the feeding habits and paleohabitat preference of *Duboisia* and contrary to expectation, they found a typical signature of a forest dweller, with a predominantly browsing feeding habits. This is not as surprising though, because interglacial Java was covered by mangrove forests and a more open forest formation, while as time moved more towards Middle Pleistocene, the environment changed to a more seasonal type of forests, fragmented by grasslands. They also confirmed that the endemic *D. santeng* had some unique characteristics in post-cranial bones and underwent size reduction as a result of insular process which resulted in it becoming (at least partially) a forest dweller. Wibowo (2020) modelled the paleohabitat of *Duboisia* by combining mathematical functions (geographically explicit suitability scores) with occurrence data and environmental factors and arrived at the conclusion that the east Java environment of today is comparable of that in Pleistocene, while central Java was dominated by savannah. In present times, only one bovid species remains in Java, *Bos javanicus* (d’Alton, 1823), which can be found both in west Java forests and in east Java savannah so a similar situation can be expected of *D. santeng*.

4. Material and methods

4.1 Studied Specimens

In the present study, fossil material of *Axis lydekkeri* and *Duboisia santeng* was examined, from the historical Dubois Collection. The material is housed at Naturalis Biodiversity Center, in Leiden, Netherlands and was kindly provided by Natasja den Ouden (fossil curator) and dr. Alexandra van der Geer, after the approval of the head of the VEDE (Vertebrate Evolution, Development and Ecology) department, dr. Martin Rücklin. A total of 72 mandibles of *Duboisia santeng* were used to calculate age estimations, with the addition of 108 isolated molars, to statistically strengthen the dataset. As for the deer, the dataset numbers 204 mandible specimens and 94 isolated molars, almost all of which are suitable for producing age estimations. The complete list of fossil material, along with the measurements taken, the age estimations produced and the mortality rates and survivability curves, are presented in the appendix.

4.2 Age Estimations of Ruminants - Tooth Eruption and Wear

In order to create a composite life table, and mortality profiles and calculate the survivability of animals, each specimen needs to be aged using the same methodology. Zooarcheologists rely on various methods to procure these age estimations, such as bone fusion sequences, tooth eruption stages or cementum annuli counts. For mammals, teeth are overabundant in the fossil record thanks to their resilience in the taphonomic processes making them a prime target for such research by palaeontologists and archaeologists alike. One method in particular that is most frequently applied, especially in ungulates, is the tooth wear age estimation because it is efficient and precise enough to create reliable life tables, non-destructive and easy to apply. This method works best with adult and older individuals, while age estimations based on the stage of the eruption of the dentition are reserved for juvenile and sub-adult individuals. Aging based on tooth eruption sequences requires the knowledge of the order of each deciduous and permanent tooth eruption time. These sequences are specific to each genus, species or even population (Hillson, 2005). For fossil species in particular, it can be inferred by studying the eruption pattern of their closest extant relatives (Kohut, 2022; Twiss, 2008). Here, I restrict the analysis to the lower dentition, as is commonly the case in ruminant tooth wear age estimation studies. In addition, I added isolated lower molars in order to increase the sample size and therefore strengthen the results statistically.

Dental wear is mainly related to the type of food and matter an animal chews over the span of its lifetime and thus the number of years the individual has lived is only indirectly related (Hillson, 2005; Kohut, 2022). In ruminants, such as bovids and cervids for example, chewing and re-chewing vegetation has as a result the contact of the maxillary and the mandibular, occlusal surfaces of molars and premolars. The enamel then is worn out, exposing the dentine underneath it, which can go on, until the tooth is worn out to the root or is completely lost (Hillson, 2005; Twiss, 2008). Of course, the eruption time of each tooth plays a crucial part when calculating tooth wear age estimations and that is because the first molar erupts and comes into wear much earlier than the third molar and so most of the time, the former will show a much older age estimation than the latter. What is more, tooth wear variation is not only related to the animal's diet, whether it is a grazer (prefers eating grass), a browser (prefers leaves) or a mixed feeder, but also to the individual's age and that's because the dentition of a younger animal has a faster wear rate, since the teeth still have sharper cusp tips. This means that the relationship between wear rate and age is not linear (Klein and Cruz-Uribe, 1984). Furthermore, especially in ruminants, differences regarding sex can also be observed, because males are physically larger and thus have a faster rate of wear because they need to feed more often. Also, individuals can develop chewing side preferences, thus affecting the outcome of the estimation (Kohut, 2022; Twiss, 2008). On a final note, there have been reported cases of osteophagia in ruminants, where the individuals are seen to chew on bones or antlers to balance the calcium-phosphorus ratio, which causes extreme cases of dental wear (see further on).

4.3 The Quadratic Crown Height Method

The crown height age estimation method relies on mathematical models to estimate individual age based on teeth (Gifford-Gonzalez, 1991; Klein and Cruz-Uribe, 1983). Spinage (1973) was the first researcher to make a correlation between an animal's age and the crown height of its molars. Later, more researchers expanded upon this idea (Steele, 2006; Pike-Tay et al., 2000; Gifford-Gonzalez, 1991; Davis, 1983; Klein & Cruz-Uribe, 1983; Levine, 1982; Klein et al., 1981, 1983) and thus the Quadratic Crown Height Method was created (QCHM), which is being adjusted even today. The most important variable for the QCHM is of course the crown height (CH) which is measured from the enamel-cementum junction to the top of the mesial cusp, on the buccal side of a tooth (buccal crest. Other notable variables include Age_{pel} ,which stands for potential ecological longevity or put simply, the maximum expected lifespan of the animal. Age_e is the age at which the molar comes into wear (age of eruption) and finally, CH_o is the height of the molar crown before the occlusal wear starts to take place, in other words, the highest molar crown measurement of the specific dataset. The formula produced by Klein et al., 1981, 1983 and which was used in this research is as follows:

$$Age = Age_{pel} - 2\left(Age_{pel} - Age_e\right)\left(\frac{CH}{CH_0}\right) + \left(Age_{pel} + Age_e\right)\left(\frac{CH^2}{CH_0^2}\right) .$$

Fig. 4.1. First or second isolated lower molar specimen of *Duboisia santeng* showing how the crown height measurement is taken. The measurement is the same for *A. lydekkeri*.

When the focus of a study is extinct species, as is the case in this research, potential ecological longevity and ages of eruption of molars are calculated in correlation with living relatives, for which such data are easily accessible and are well known. As such, the age estimations produced by the QCHM are calculated for *Axis lydekkeri* in red deer (*Cervus elaphus*) years, while for *Duboisia santeng* in goat (*Capra hircus*) years. The constants of the formula are then formed in this case as follows: For *Axis lydekkeri* the age of eruption of the first molar is 0.5 years (6 months), of the second molar is 0.9 years (almost 11 months), and of the third molar is 1.5 years (18 months), while the potential ecological longevity used in the formula is 16 years. For *Duboisia santeng* on the other hand, Age_pel is 18 years, while the Age_e for the first molar is 0.25 years (3 months), for the second molar is 1 year, and for the third is 2 years. Furthermore, it needs to be noted that to successfully analyze crown height measurements there are a couple of assumptions that need to be fulfilled: Firstly, individual variation within a population (or meta-population) that stems from dietary and chewing habits and from sexual dimorphism should not significantly affect eruption sequences and wear patterns. Secondly, within the (meta-) population the rate of wear of a specific tooth type should be relatively consistent in all individuals of all age classes (Twiss, 2008).

Both in the case of isolated teeth and of those still incorporated in the mandible, the crown height was measured from the distal-most cusp of the molar but for the third molar, the second cusp. Several researchers (Kohut, 2022; Ruscillo, 2015; Morrison and Whitridge 1997) suggest taking the average of all crown height measurements of the tooth's cusps, but in this research, this was deemed unnecessary. For the isolated molars, the measurement is a bit different since the tooth is out of the socket and instead, crown height is measured from the enamel-dentine junction where the crown and root meet to the tip of the buccal crests. Also, because it is not possible to reliably differentiate between the first and second molars in isolation, it is useful to sometimes use the formula two times and produce two age estimations, one assuming that the molar is the first and another one assuming that it's the second and then take the average of the two age estimations. The difference in the estimations produced stems solely from the age of eruption. For *Axis*, this difference was considered irrelevant because in *Cervus elaphus*, the second molar erupts only about five months later than the first and this only affects the outcome marginally. In the case of *Duboisia* though, things are different, because here there is a substantial time gap between the two ages of eruption in goats (9 months) and so the final age estimation for each specimen was calculated as the average of two estimates. Finally, for teeth still incorporated in the mandible, an age estimation was calculated for each molar present and then an average was produced as a final estimate of the specimen/individual.

Age estimation based on the stages of eruption method is more straightforward, since deciduous teeth erupt from anterior to posterior. Incisors are followed by canines (if at all present) and then premolars. Also, deciduous teeth often grow larger the later the eruption is so, for example, the last deciduous premolar (dp4) can grow to be as large as the first molar in adults (m1), which is the next tooth to erupt (Hillson, 2005). In addition, in families such as Cervidae and Bovidae, dp4 can appear to be similar to m3, a process called molarization. In this research, the categorization between juvenile individuals and sub-adult ones was based on the presence or absence of deciduous dentition. If a deciduous premolar was present in the mandible, the individual was deemed juvenile and one year of age at the most, even if the first molar had fully erupted. On the other hand, if the first two molars had erupted but the third molar was still in the process of eruption, then the specimen was categorized as sub-adult and ascribed to the age of roughly one year and a half. There needn't be a more precise categorization on the basis of months, not only due to the age estimations of the QCHM being in years (either *Cervus elaphus* or *Capra hircus* years), but also because in the mortality profiles, all the individuals in the first two years of their life are binned into a single category.

5. Results and Discussion

5.1 Problems and Errors of the QCHM

Regarding the age estimations of the quadratic crown height method, there are a couple of issues that need to be addressed. First of all, the age estimations are counted in *Cervus elaphus* and *Capra hircus* years instead of actual individual years, which creates by default on its own a systematic error in the estimations. This is unavoidable because we can never know for sure the potential ecological longevity of an extinct animal and for that very reason, a living relative must be used as a reference point. The ideal scenario would be to choose the closest living relatives of the focal extinct animals for reference, assuming that there are no or only a few taxonomic issues with their phylogeny. In our case, that would probably be *Axis porcinus* for Lydekker's deer and *Boselaphus tragocamelus* for Dubois' antelope. The problem with this approach is that it would create all manners of confusion in the scientific community since very few people know how long is, for example, the lifespan of a nilgai, since it is insufficiently studied. Thus, for standardization and allowing for taxon-wide comparisons among fossil taxa, reference points are crucial. I here use RDY (Red Deer Years) for the extinct deer and GY (Goat Years) for the extinct bovid. In that sense, this source of error in the estimations is then unavoidable.

The most alarming observation to be made here is that the QCHM produces various age estimations for the same specimen. For example, out of the 21 mandibles of *Duboisia santeng* with both m2 and m3 still included, only for 9 of them did the m3 estimate an age older than the one produced by m2. Logically, the expectation would be for the m2 to produce younger age estimations since it erupts much earlier than the m3. The counterargument here is that the second molar is worn down more rapidly than the third, because it is used more in chewing. Interestingly, in only 7 out of the 24 mandibles of *Duboisia* with both m1 and m2 still preserved, did m1 give the older age estimation. This means that m2 produces the older age estimation with a relative consistency. This was clearly the case with the deer as well, with 40 out of the 59 mandibles with both molars present, the m3 produced a younger age estimation than the m2 did for the same specimen. Comparing the first and the second molar age estimations of the same specimen, m2 proved again to give the older age in 57 mandibles out of a total of 81. This leads us to conclude at least two things: That crown height plays a far more important role for the formula than the age of eruption and as such the worn crown height - unworn crown height ratio is the most powerful component of the QCHM formula. The other one is that m2 produces repeatedly the older age estimation, an observation that puts in question results being supported solely by age estimations of isolated first and second molars.

There are also some tendencies in the age estimations of the QCHM that are known to occur regarding the species of the animal and the age of the individual (Gifford-Gonzalez, 1991; Klein and Cruz-Uribe, 1983; Ruscillo, 2015; Steele and Weaver, 2012). More specifically the formula may need adjustments and modifications, especially so for bovids and third molars (Gaastra, 2016). This is also the case in this research, where the QCHM both underestimates and overestimates the age of the specimens. In short, the more unworn the tooth is, the more the formula underestimates the age while conversely, the more worn out the molar is, the more the formula overestimates the individual’s age. This observation enforces the idea of using an average based on each molar of the mandible as a final age estimation even more because it reduces the error caused by differences in age of eruption, rate of wear, and the formula in and of itself. Steele and Weaver (2012) update the formula and change the exponent of QCHM for each molariform tooth using Power Law Curve Fit. For *Duboisia* and *Axis*, these changes didn’t produce any positive results, since they either gave negative results or an extreme overabundance of young, sub-adult individuals. There also exists the LCHM (Linear Crown Height Method) produced by Duco (1968, 1988, 2000) in which the crown height measurement is taken on the lingual side of the tooth from the bifurcation of the roots to the highest point of the anterior cusp. The LCHM is more suited for isolated teeth of younger individuals specifically, as it doesn’t produce reliable results (or no results at all) for middle-aged and older individuals and thus this formula wasn’t opted for in this research either. Instead, the classic QCHM was preferred, even though it’s more likely than not to have severely overestimated the age of older individuals.

Overestimating the age might not be a real issue, because a prolongation of maximum lifespan is to be expected with island dwellers. Specifically for ruminants, higher crown height is directly related to an increase in the potential ecological longevity. This is supported by the findings of Jordana et al. (2012) regarding the extremely hypsodont insular bovid *Myotragus balearicus* of Late Pleistocene-Holocene Mallorca (Spain). Tooth wear is a main reason of death in herbivores, because older individuals lose the ability to chew properly or even eat at all and therefore die of malnutrition or starvation. It is thus not unexpected that an increase in tooth height has been shown to be related with life-history traits such as reproductive ability and longevity in *Myotragus*. This is also in line with the life history theory that under low extrinsic mortality and limited resource availability (as is the case in almost every insular environment), populations switch epigenetically from novelty to efficiency and opt into a maintenance phenotype to minimize costs (Geist, 1998).

5.2 *Axis lydekkeri* mortality profiles and mortality curve

Results from the age estimations are grouped in cohorts as follows: Group I: ages 0-2 years, Group II: ages 3-5 years, Group III: ages 6-8 years, Group IV: ages 9-10 years, Group V: ages 11-13 years, Group VI: ages 14-16 years and Group VII: ages older than 16 years. These groupings differentiate between young, adult, mature and extremely old individuals because the QCHM cannot accurately predict ages for the very young and the old and consistently either underestimates or overestimates their age. These groupings thus help reduce the error in the estimations and render the method reliable enough to procure life history data for extinct species. The five age groups from young (ages 0-2 years) to senile (over 16 years of age) are represented on the x-axis while the number of individuals is given on the y-axis. The mortality curve was based on mortality data from mandibles and isolated third molars and was expressed as a graph, with the y-axis being the log of the supposed number of individuals that died at a certain age cohort, versus age as a percentage of potential ecological longevity in the x-axis.

Mortality profiles were calculated using age estimations based on mandibles and isolated molars. In total, five mortality profiles were reconstructed in order to test for possible discrepancies: for mandibles only, for isolated first and/or second molars, for isolated third molars, for mandibles and the first/second isolated molars combined and lastly for mandibles and the third isolated molars combined. The mortality profile made solely by mandibles is based on a total of 195 individuals and is clearly U-shaped (Fig. 5.1). More than 70 specimens belong to the youngest age group (Group I) and more than 30 specimens to the oldest age group (Group VII). *Axis lydekkeri* shows high death rates in the first two years, after which mortality drops significantly for years three to five and continues to decrease up until ten years, after which point it remains more or less constant, before increasing again for ages over sixteen. Within the first age group, 15 mandibles belong to juvenile or sub-adult individuals, while the rest were classified as adults based on tooth eruption pattern, yet still produced a young age estimation based on crown height. A similar issue might apply to the oldest age group. Juvenile mortality is generally high in mortality profiles of megaherbivores, as it is here. This might indicate that predation plays a more modest role in deer juvenile mortality than previously thought and that other factors such as malnutrition, diseases and accidents are sufficient to explain an increase like that in their mortality. Potentially, if it would have been possible to divide specimens within this age group into more precise age cohorts, the final peak might have been flattened to some extend. The reason to not do that, is that at the current state of knowledge, the potential ecological longevity of *Axis lydekkeri* is not known. *Cervus elaphus* can live up to 25 years in captivity and 20 years in the wild (Senseman, 2002.), while *Axis porcinus's* maximum lifespan for both conditions is 20 years

(Michelin, 2002). Therefore, theoretically Lydekker's deer may have lived up to 30 years, based on the age estimations produced by the QCHM, but a more precise method of ageing (other than the QCHM) is needed to test this assumption. For now, I thus follow a conservative approach based on red deer, with a single group for the old plus extremely old individuals combined.

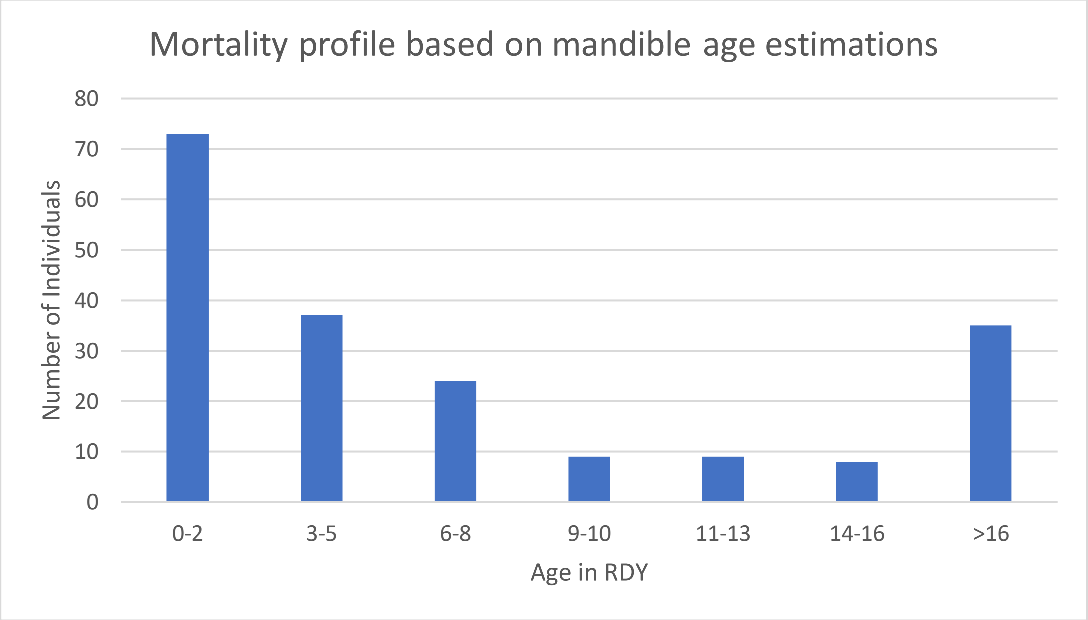

Fig. 5.1. Mortality profile of *Axis lydekkeri* showing a U-shaped pattern, typical for attritional mortality, with two peaks dominating, one for both for the first and the last age groups. On the x-axis are the age groups counted in red deer years.

The mortality profile based on isolated third molars has an attritional signature as well, with more than 50 of the total of 65 specimens falling in the two youngest age groups (Fig. 5.2). What is particularly interesting here is the absence of a second peak. There is only one individual in the last age group. There are two explanations for this. First is that the QCHM fails to produce reliable age estimations for older individuals based on isolated 3rd molars or, second, that there was an error in the sampling (undersampling of isolated senile third molars). In my opinion, the latter explanation is more likely, judging by the historical background of the excavation. Dubois acquired untrained workers for his excavation in Java, back in the 1890s. That meant that unskilled locals probably wouldn't have been able to recognize worn-down third molars or they simply didn't care enough to pick them up, since there was an abundance of specimens anyway. This, however, does not explain why this does not apply to the bovid third molars (see below).

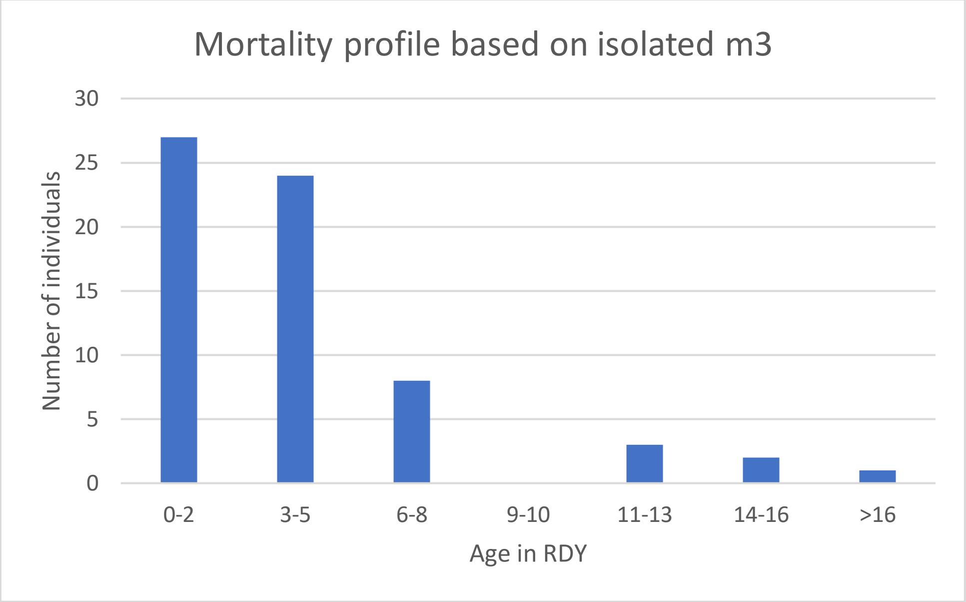

Fig. 5.2. Mortality profile of *A. lydekkeri* based on age estimations of isolated third molars alone.

Regardless of the type of isolated molar, the final mortality profiles combining both data from mandibles and isolated teeth (Fig. 5.3), show a clear U-shaped pattern, typical for attritional, mortality profiles with a high amount of deaths for the younger individuals and a second peak for individuals that exceed the sixteen years of age. The resulting curves bear some similarity with the mortality profiles of the dwarf deer of Pleistocene Crete (*Candiacervus ropalophorus* and *Candiacervus* sp. II) of localities Gerani 4 and Liko of Crete, Greece calculated by van der Geer et al. (2014) and also with those of sika deer (*Cervus nippon*) of the Kinkazan Island of Japan, calculated by Minami et al., (2009), while one can also draw similarities between the survivorship curve produced here and the one by Hayashi et al., (2020) concerning extant *Cervus nippon* of Hokkaido mainland. The main difference between mortality patterns between island faunas as presented in Hayashi et al., (2020), Minami et al., (2009), van der Geer et al., (2014) and the present one, and the mainland ungulate populations of Elandsfontein in the Cape province of South Africa as presented by Klein and Cruz-Uribe, (1983), is that there is no second peak in the mainland ungulate populations. Meaning, that while there is a large amount of juvenile mortality in all these ungulate populations, even if the younger age classes are underrepresented, in the South African ones, there is a clear pattern of the number of older individuals decreasing progressively. Keeping in mind that all the above profiles are considered attritional some cautionary conclusions can be drawn in regard to life history traits of endemic deer species.

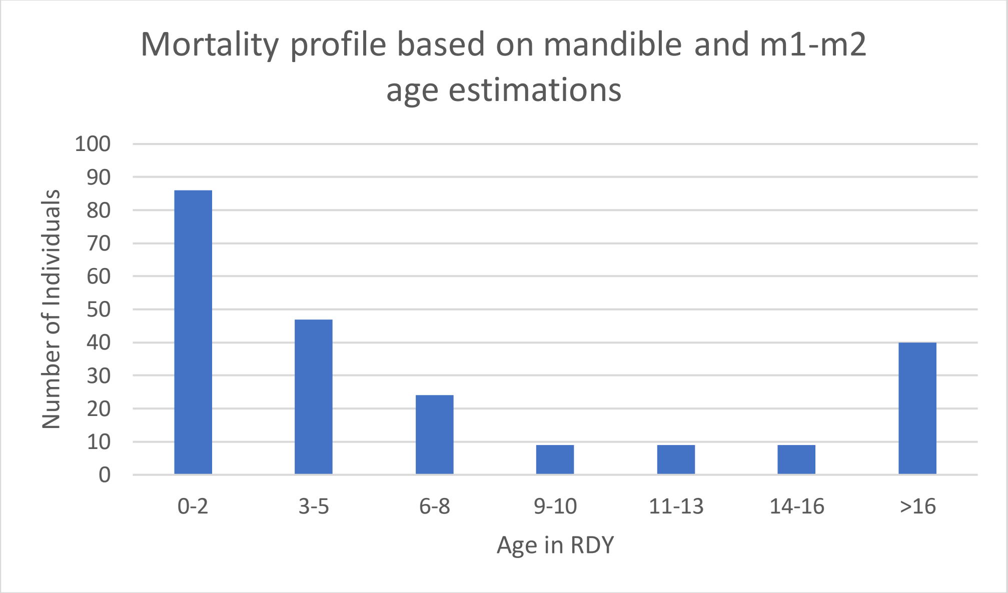

Fig. 5.3. Mortality profile of *A. lydekkeri* based on age estimations from mandible and isolated first and/or second molars combined.

The mortality curve for *Axis lydekkeri* (Fig. 5.5) shows that maximum survivability appears at around 50% and 80% of a deer's maximum lifespan, meaning that there is an advantage in survival for older individuals, which is a clear indicator for a slow life. The survivability curve of *Axis lydekkeri* is similar to the one for mainland *Cervus nippon* of Hokkaido Island (Japan) provided by Hayashi et al. (2020). Hayashi et al. (2020) state that strictly regarding life history traits, the populations of sika deer of Hokkaido (mainland) and Honshu (island) display a more gradual shift towards maintenance strategy, rather than an extreme one; this is because, although the Japanese Archipelago is considered an island in literature, the Japanese mainland deer populations specifically may not be under strong insular influence. This observation may also apply to Pleistocene Java, as although an island, it is large enough to sustain an ample amount of recourses, resulting in large numbers of competitors and predators. So, although endemic, Lydekker's deer seem to share some life history similarities with both its continental (high juvenile mortality) and insular (maximum survivability at 80% of maximum lifespan) counterparts. As a final note, the curve of the mortality of *Axis lydekkeri* appears to be going up instead of decreasing towards its end, because there are some very old age estimations produced by the QCHM, even when excluding the cases of osteophagia (see below).

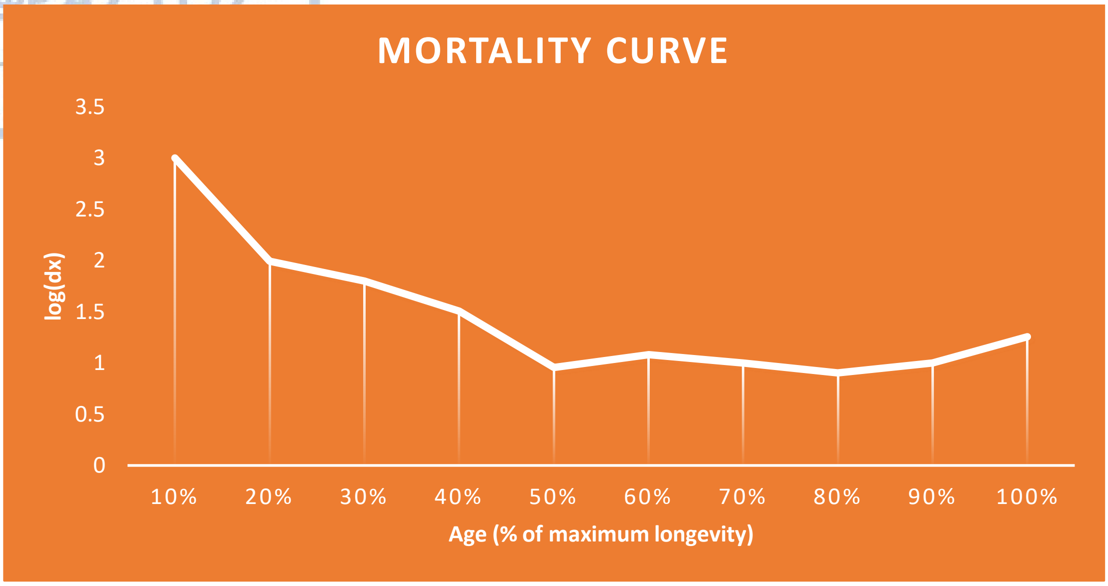

Fig. 5.5. Mortality curve for *Axis lydekkeri* from the Pleistocene of Java that indicates that maximum survivorship occurs around 50 and 80% of potential ecological longevity. The exact maximum lifespan of the deer is not known and some age estimates produced by the QCHM are very high, so that is why the curve seems like rising at 100% of pel (potential ecological longevity).

The results from both the mortality profiles and the mortality curve for *A. lydekkeri* from Java are in good correspondence with the ones produced by Hayashi et al. (2020), Kubo et al. (2011), Minami et al. (2009) and van der Geer et al. (2014) and show an endemic character with a tendency for slow life adaptations and life history traits of a typical maintenance type population albeit not an extreme K-strategy. As stated in Caughley (1966), Klein (1982) and van der Geer et al. (2014) predation can have a major effect in juvenile mortality of ungulates but there are other factors as well. Research has shown that even when there is an absence of predators, juvenile deaths remain increased, despite them being underrepresented, and so the effect of predation on the age profiles of ungulates is negligible at best. Instead, for most of the ungulate fawns, the main causes of death are starvation, accidents, diseases and low neonatal body weight, the last of which can be more pronounced in island dwarf populations, meaning it is difficult to come to any safe conclusion in regards with possible cause of death by studying mortality profiles alone. What can be said though, is that once the individual survives into maturity, it enjoys an extended life span. This suggests that late sexual maturity, high survivability of older, more successful individuals and predominant death rates of juveniles are at least some of the characteristics of endemic, slow life in insular ungulates.

What is also noteworthy, is that the mortality profile produced by the isolated third molars bears a close resemblance to the one produced by Kubo et al. (2011) for the Hokkaido and Izu sika deer populations. In their research, they characterized the profiles as catastrophic but indicated that this, may have been due to the small size of the sample. In the age profile calculated for *Axis lydekkeri*, the near absence of any individual past the age of eight years, could be both a combination of small sample size and sampling error. The method of age estimation used by Kubo et al. (2011) was that of tooth wear rate and regression lines, which, although it perhaps produces more accurate results than the QCHM, it nevertheless suffers from serious underestimations for the young and overestimation for the older individuals, similar to QCHM. The only way to reduce this error, save for statistical methods such as the Power Law Curve Fitting, is to rely age estimations mainly on several teeth of the same mandible. This reduces the error and produces far more reliable estimations and that is why age profiles based solely on isolated molars (especially third ones) suffer from unexplainable patterns and are questionable at best in regards to how reliable they are at producing conclusive life history data.

5.3 *Duboisia santeng* mortality profiles and mortality curve

For *Duboisia santeng*, a total of five mortality profiles were calculated, as in the case of *Axis lydekkeri*: one for age estimations from mandibles, two for the ones produced by the isolated molars and two combining the age estimations from the mandibles and the molars (see Appendix). Statistically, the results are weaker when compared with the ones of *Axis lydekkeri* and that is because the mandible specimens were far fewer. Out of the total of 71 individuals, the majority (51 individuals) belong to the first three age cohorts with 23 being two years old at most (Fig. 5.6). The age group with the lowest mortality is Group V (ages 11-13) while after that, there is a rise in mortality again. The mortality profile is attritional again, but not nearly as U-shaped as the one of *Axis lydekkeri*. The profile could also be described as catastrophic, but that can’t be the case, not only because the fossil specimens are from many different sites of Java, but also because there is a peak in mortality past the age of 14 years. What is interesting to note, is that there is a rise in mortality of prime-age individuals (ages 6-8), which are the main target of *Homo* hunting activity. The expectation would be for both of the profiles to have the same mortality pattern, since they are both endemic ruminants, but this seems not to be the case.

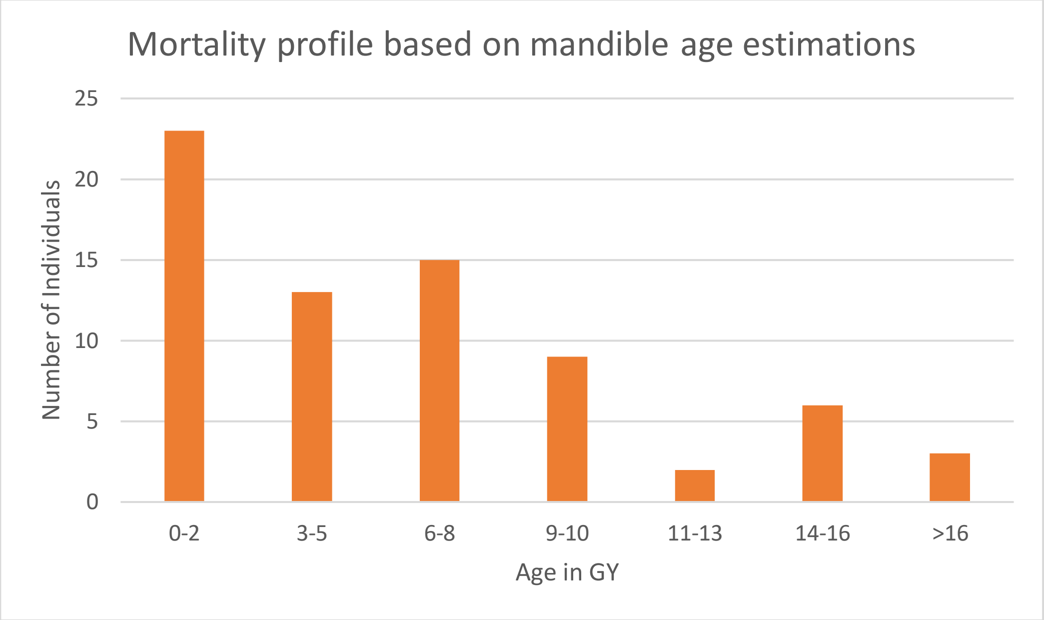

Fig. 5.6. Mortality profile of *Duboisia santeng* from the Pleistocene of Java based solely on mandible molars. Age groups are counted in goat years.

However, there is a slight difference in the mortality profiles calculated by isolated molar age estimations (Fig. 5.7). 43 out of the 79 isolated 3rd molars belong to the first two age groups (ages 0 - 5) while more than half of them (28) gave an age estimation between 3 and 5 years of age. One would expect, as in the case of *Axis lydekkeri*, an abundance of young adult and juvenile individuals, but the over-representation of individuals aged 3-5 years is probably because of the late eruption of m3. Third molars in goats (*Capra hircus*) erupt around 2 years of age and the tooth already comes into wear before it is fully erupted, so the QCHM is expected to produce mostly ages past the second year when the estimation is based on third molars. In addition, as mentioned before, the QCHM doesn't apply as well in small bovids as it does in cervids, plus, the m3 appears not to follow a quadratic rate of age-related wear (Gaastra, 2016; Steele and Weaver, 2012). The mortality profile for *Duboisia* here is U-shaped though, with a rise in mortality for the last age group (past the age of 16), with 13 individuals. Similarly, the mortality profile based on age estimations of the first and second molar (see Appendix), is U-shaped, with a more pronounced mortality for the first and last age cohorts (out of the 29 individuals, 9 of them belong to the first age class, while 5 to the last).

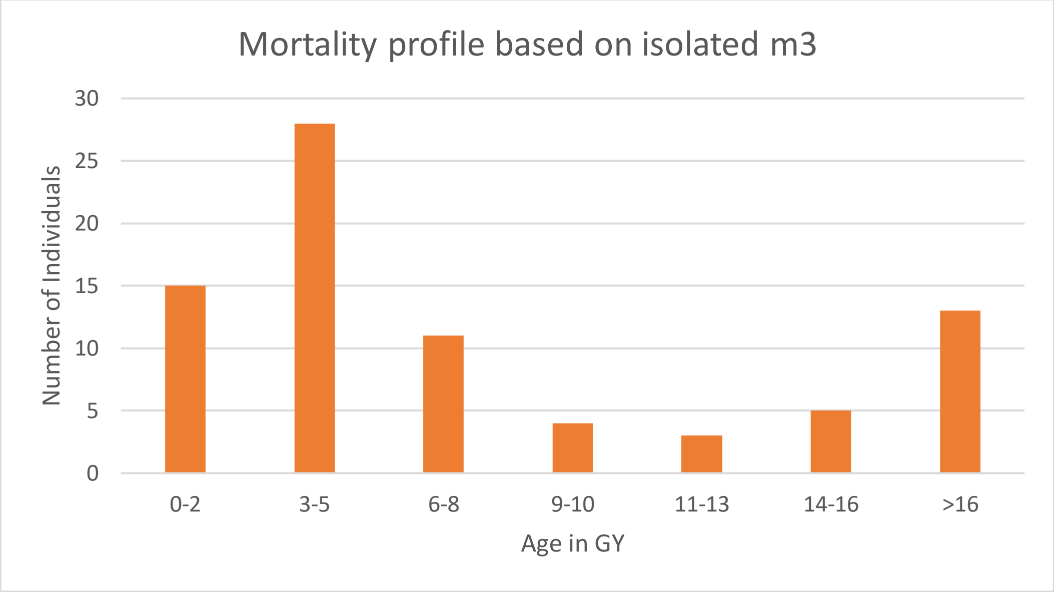

Fig. 5.6. Mortality profile of *D. santeng* based on isolated molars alone showing the spike in 3-5 GY age group.

Despite the reduced reliability of age estimations based on isolated molars, they were necessary here in order to increase the sample size for life history data. The results of the combination of mandible and isolated molars age profiles are mortality profiles with a more pronounced U-shaped pattern (Fig. 5.7). Even so, the profile that's based on mandible and m1-m2 age estimations of *Duboisia*, has some differences compared with the one of *Axis* that are worth noting. First and foremost the mortality rate does not clearly reduce with an increase in age. Mortality is reduced from the first age group to the next but is increased again around ages 6-8 before falling again for ages 9-13 and then rising again for the last two groups. The peculiar part is that there are more deaths in individuals aged 6-8 compared to those aged around 3-5 years and more at age 14-16 compared to those past the age of 16. This could very well be a sampling error or an error of the accuracy of the QCHM estimations for *Duboisia*. However, there are other possible explanations that are worth mentioning.

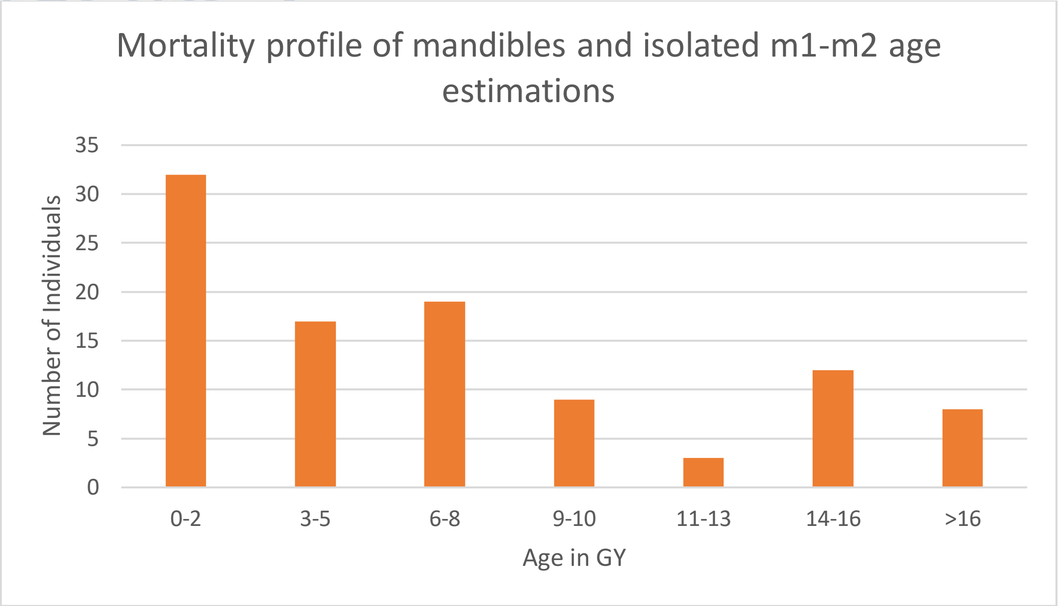

Fig. 5.7. Mortality profile of *D. santeng* based on age estimations of mandible and isolated first and/or second molars combined.

There are similarities between this mortality profile and others published by Klein (1982), Klein and Cruz-Uribe (1983) and Koike and Ohtaishi (1987). *Duboisia santeng's* mortality somewhat resembles the attritional one of Cape buffalo from the Middle Stone Age of Klasies River Mouth cave of South Africa as seen in Klein (1982) and originally published by Singer and Wymer (1982). There are also other similarities with other mainland, African mortality rates of ungulates, this time seen in Klein and Cruz-Uribe (1983), namely the Cape buffalo of Akagera, the impala and Burchell's zebra of the same locality, originally published by Spinage (1972) as well as the waterbuck in Queen Elizabeth Park, again by Spinage (1970). What all these profiles have in common is that they represent mortalities of free-ranging herbivores that are predominantly grazers and are preyed upon by predators. The African buffalos, zebras and waterbucks are mostly grazers and opportunistic browsers, while the impala can be both browser and grazer depending on the season. Other mortality profiles that bear some similarity with those of Java's *Duboisia* are those published by Ohtaishi (1987) regarding sika deer from 14 archaeological sites of Prehistoric Japan, showing the influence of human hunting in deer mortality. In all these age profiles though, there is no increase in the older age classes, unlike the one of *Duboisia*. Interestingly enough, it seems that both predation and hunting result in high mortalities in individuals of middle-aged classes.

The mortality curve of *Duboisia* (Fig. 5.8) is quite similar to that of *Axis lydekkeri*, with both species showing maximum survivability at about 60% and 80% of maximum longevity, which again pinpoints to a slower life where older, more experienced individuals have an advantage. The curve can be divided in two parts, the first 40% of maximum lifespan where mortality is high and the rest where mortality is more or less constant. The end tip of the curve is pointing down this time but doesn't quite touch zero and this again is because of the QCHM producing some absurdly old age estimations. *Duboisia santeng's* closest living relative is *Boselaphus tragocamelus* which is one of the largest Asian antelopes and can live up to 21 years, so again a maximum lifespan of 30 - 35 years for Dubois' antelope is within expectations, considering the endemic nature of the animal, its small size and its slow life adaptations.

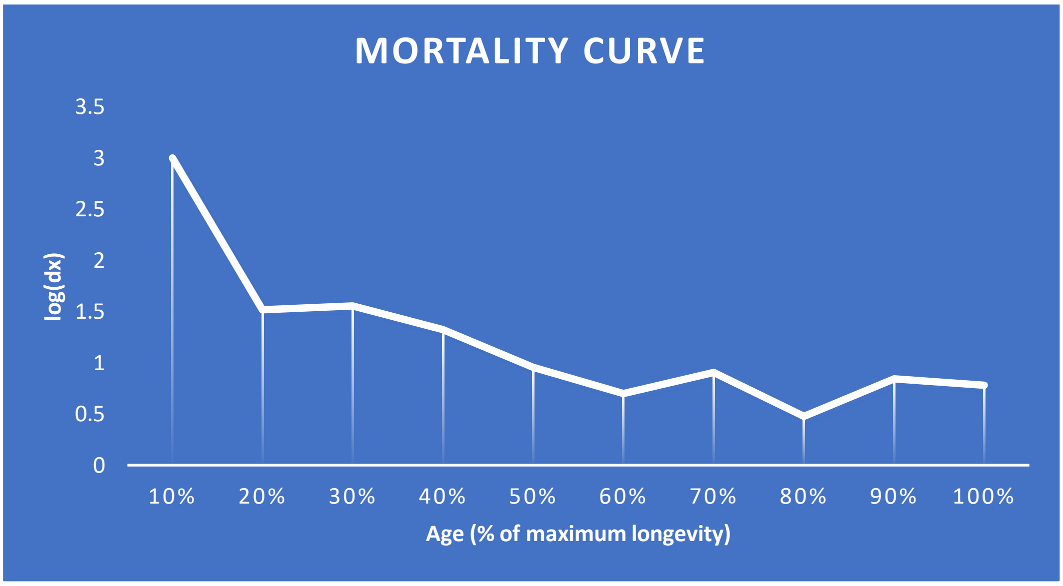

Fig 5.8. Mortality curve for *Duboisia santeng* showing that in the later stages of adult life, maximum survivorship occurs at 60 and 80% of potential ecological longevity. That means that individuals past the first half of their life have better chances of survival than their younger counterparts.

Comparing the profiles of *Axis* and *Duboisia* from the Pleistocene of Java, it appears that there is a signal that the bovid was hunted, unlike the deer, as seen in the high mortality of middle-aged individuals. Bovids usually form larger herds than deer do, normally consisting of at least 10 individuals, while deer usually form smaller groups with family members (Stiner, 1991). Another difference that could play an important part in the differences in mortality patterns is the feeding habits of these animals. Most bovids are grazers, with some of them being mixed feeders, with a clear affinity for open spaces, while deer, although they are considered mixed feeders, often prefer browsing in a more closed environment. This could be an additional reason why *Duboisia* fell victim to predators and hunters more often than *Axis lydekkeri* did. On the contrary though, Rozzi et al. (2013) provided mesowear evidence showing that *Duboisia* was in fact a browser as well, and morphological comparisons of its locomotion showed that it was more suited to be a forest dweller. However, in case different species have the same dietary preference they rarely share the same ecological niches to avoid competition. Therefore, probably Lydekker's deer inhabited a deeper part of the rainforest, while *Duboisia* was found at the edge of the forest canopy, which made it more vulnerable to Java's predators and human hunters.

5.4 Osteophagia Cases

As a final note regarding the observations that can be made solely by looking at the age estimations produced by the QCHM, it is important to mention some irregularities that are less likely related to an error of the method and more to a physiological cause. The age estimations produced for at least two specimens of *Axis* and one for *Duboisia* exceed 50 years which is an exceptional amount even for island dwellers (the maximum should be around 30 years). When examining these specific mandibles, I noticed similarities between these specimens and the ones presented at Cáceres et al. (2013), who examined cases of osteophagia deduced from dental wear patterns rather than bone and antler remains. Osteophagia is the practice where herbivores chew and gnaw on non-food items such as bones and antlers. They place these items in their mouth in a cigar-like manner and the result is an extremely worn-down first and/or second molar (upper as well as lower). This behaviour has been observed in domestic animals such as sheep and goats, but also in wild deer, antelopes and giraffes (Cáceres et al., 2013; Sutcliffe, 1973) and is related to mineral deficiencies in their diet, mainly the phosphorus and calcium ratio, but also hunger and malnutrition (Barrette, 1985). Such deficiencies can be caused by antler growth, for example in male deer, and although the disadvantages of the practise are obvious (infections, injury and lengthy chewing, meaning less time spend on grazing,) the animal still is forced to do it. The dental wear pattern of osteophagia is easily recognized by the extremely worn down first two molars with an almost intact third one. This is also apparent from the age estimations alone, where for example in one specimen of *Duboisia santeng* m1 gave the absurd age estimation of 90 years and m2 that of 69, while m3's age estimation was only 9 years of age. It is to be expected that such behaviour would be more prevalent in a relatively isolated environment, like that of Pleistocene Java, where overpopulation, increased intraspecific competition and perhaps reduced amount of resources would drive some malnourished individuals to the extremes, especially males in mating season and pregnant and lactating females.

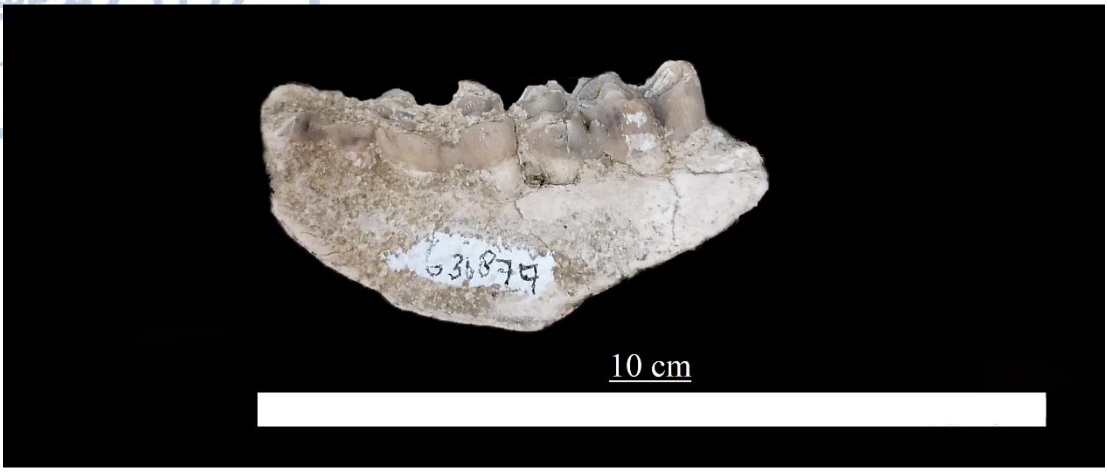

Fig. 5.9. Left mandible fragment (m1-m3), specimen RGM630879, identified as Cervidae gen. indet. sp. indet., but based on morphology and size, it probably belongs to *Axis lydekkeri*. It was collected by Von Koenigswald from Sangiran, Java. Age estimations calculated by the QCHM for this specimen reach the extreme average of 62 RDY and by the crown height measurements of the m1 alone, the estimation of the QCHM goes up to 87 years, while for the m2, the age estimation reaches almost 50 years. These extremely old age estimates are reason enough to count the specimen as a possible osteophagia case. The scale is 10cm.

Fig. 5.10. Left mandible (m1-m3) of *Duboisia santeng*, specimen No. 2036, of the Dubois collection, originating from Kebon Doeren in Java. The ages calculated for this specimen by the QCHM based on the first and second molars are 90 and 69 GY respectively, while m3 produced an age estimation of 9 years. This specimen demonstrates a typical osteophagia case, where the first two molars are extremely worn down, while the third is almost intact, resulting in a steeper slope. The scale is 10cm for reference.

Conclusions

Fossil specimens of the deer *Axis lydekkeri* and the bovid *Duboisia santeng* are a big and important part of the famous Dubois collection. Their remains have been described before but this is the first time that their teeth are being used to infer life history data. Life history studies of endemic species such as these are important to understand life strategies and adaptations of insular mammals and this research contributes to reaching that goal. Statistically, the second lower molar was the one to produce the older age estimations with relative consistency, and the QCHM was found liable for minor errors, which do not significantly affect the outcome of this research. Several teeth produced absurdly high age estimations and some of them are best interpreted as evidence for osteophagia, indicating malnutrition for these individuals. The mortality profiles for both species are clearly attritional, U-shaped, and with a high amount of juvenile mortality, while the mortality curves that were calculated show an increase in survivability as the age, a percentage of potential ecological longevity gets older. The profiles show adaptations for slow life, which is believed to be a characteristic of many endemic species because resource limitation and the absence of predators lead to maintenance life history strategies (Geist, 1998; Köhler and Moyà-Solà, 2009; Minami et al., 2009; van der Geer et al., 2014). However, there were active predators in Java during that time, so that indicates that the presence or absence of predators alone is hardly enough to trigger any evolutionary response in ungulates. Furthermore, there were some differences between the two ruminants' profiles, as *Duboisia's* profile wasn't as clearly attritional and it maintained a rather constant mortality throughout all the age groups. This means that it was likely targeted more by hunters and predators than the deer. This has likely to do with the fact that bovids form bigger groups than deer do, but is also possibly related to the different niches that the deer and the boselaphine occupied. Middle Pleistocene Java was covered by forests fragmented by grasslands and although its proven that both species were forest dwellers, the bovid must have chosen a slightly more open environment than the deer, making it more susceptible to becoming prey. Whatever the case may be, the fact remains that the results of this analysis fit well with others, that show that endemic ungulate populations suffer from high juvenile mortality, while the ones that do manage to survive, enjoy a further extended life span, compared with their continental relatives, regardless of predation, or hunting pressures.

Bibliography

Alonzo, S.H., Kindsvater, H.K., 2008. Life-History Patterns, in: Encyclopedia of Ecology. Elsevier, pp. 2175–2180. https://doi.org/10.1016/B978-008045405-4.00856-9

Asher, R., Helgen, K., 2010. Nomenclature and placental mammal phylogeny. BMC Evolutionary Biology 10, 102. https://doi.org/10.1186/1471-2148-10-102

Barrette, C., 1985. Antler eating and antler growth in wild Axis deer. Mammalia 49, 491-500. https://doi.org/10.1515/mamm.1985.49.4.491

Baumann, P., 1982. Depositional Cycles on Magmatic and Back Arcs: an Example from Western Indonesia. Revue de l'Institut Français du Pétrole 37, 3–17. https://doi.org/10.2516/ogst:1982001

Berkhout, A., Huffman, F., 2021. Translations from the reports on the Selenka and Blackenhorn (1911): Die Pithecanthropous Schichten auf Java: Geologische und Paläeontologische Ergebnisse der Trinil-Expedition (1907 und 1908). 228 pages. https://doi.org/10.13140/RG.2.2.21954.91843

Bibi, F., 2007. Origin, paleoecology, and paleobiogeography of early Bovini. Palaeogeography, Palaeoclimatology, Palaeoecology 248, 60–72. https://doi.org/10.1016/j.palaeo.2006.11.009

Bibi, F., Bukhsianidze, M., Gentry, A.W., Geraads, D., Kostopoulos, D.S., Vrba, E.S., 2009. The Fossil Record and Evolution of Bovidae: State of the Field. Palaeontologia Electronica 12.

Cáceres, I., Esteban-Nadal, M., Bennàsar, M., Marín Monfort, M.D., Pesquero, M.D., Fernández-Jalvo, Y., 2013. Osteophagia and dental wear in herbivores: actualistic data and archaeological evidence. Journal of Archaeological Science 40, 3105–3116. https://doi.org/10.1016/j.jas.2013.04.006

Caughley, G., 1966. Mortality Patterns in Mammals. Ecology 47, 906–918. https://doi.org/10.2307/1935638

Dayan, T., Simberloff, D., 1998. Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. Mammal Review 28, 99–124. https://doi.org/10.1046/j.1365-2907.1998.00029.x

de Vos, D., 1999. The fossil faunas from the Citarum Area, West Java, Indonesia.

de Vos, J., 2003. The Dubois collection: a new look at an old collection. Scripta Geologica, Special Issue 4, 267-285.

de Vos, J., 1984. Reconsideration of Pleistocene cave faunas from South China and their relation to the faunas from Java. Cour. Forsch. Inst. Senckenberg 69, 259–266.

de Vos, J., 1983. The Pongo faunas from Java and Sumatra and their significance for biostratigraphical and paleo-ecological interpretations. Proceedings of the Koninklijke Nederlandse Akadademie van Wetenschappen 86, 417–425.

de Vos, J., Sondaar, P., 1994. Dating hominid sites in Indonesia. Science 266, 1726–1727.

de Vos, J., van den Hoek Ostende, L., Van den Bergh, G., 2007. Patterns in Insular Evolution of Mammals: A Key to Island Palaeogeography, in: Topics in Geobiology. pp. 315–345. https://doi.org/10.1007/978-1-4020-6374-9_10

Fernández, M.H., Vrba, E.S., 2005. A complete estimate of the phylogenetic relationships in Ruminantia: a dated species-level supertree of the extant ruminants. Biological Reviews 80, 269–302. https://doi.org/10.1017/S1464793104006670

Geist, V., 1998. Deer of the World: Their Evolution, Behaviour, and Ecology. Stackpole Books.

Gaastra, J.S., 2016. The Quadratic Crown Height Method and bovidae: Ageing sheep (*Ovis aries*), goats (*Capra hircus*) and cattle (*Bos taurus*). Journal of Archaeological Science: Reports 10, 172–190. https://doi.org/10.1016/j.jasrep.2016.09.022

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13, 58–63. https://doi.org/10.1016/S0169-5347(97)01237-8

Gatesy, J., Hayashi, C., Cronin, M., Arctander, P., 1996. Evidence from Milk Casein Genes that Cetaceans are Close Relatives of Hippopotamid Artiodactyls. Molecular biology and evolution 13, 954–63. https://doi.org/10.1093/oxfordjournals.molbev.a025663

Geist, V., 1998. Deer of the World, 1st edition. ed. Stackpole Books, Mechanicsburg, Pa.

Gentry, A.W., 1994. The Miocene differentiation of old world Pecora (Mammalia). Historical Biology 7, 115–158. https://doi.org/10.1080/10292389409380449

Gentry, A.W., 1990. Evolution and Dispersal of African Bovidae, in: Bubenik, G.A., Bubenik, A.B. (Eds.), Horns, Pronghorns, and Antlers: Evolution, Morphology, Physiology, and Social Significance. Springer, New York, NY, pp. 195–227. https://doi.org/10.1007/978-1-4613-8966-8_6

Gifford-Gonzalez, D., 1991. Bones are not enough: Analogues, knowledge, and interpretive strategies in zooarchaeology. Journal of Anthropological Archaeology 10, 215–254. https://doi.org/10.1016/0278-4165(91)90014-O

Gilbert, C., Ropiquet, A., Hassanin, A., 2006. Mitochondrial and nuclear phylogenies of Cervidae (Mammalia, Ruminantia): Systematics, morphology, and biogeography. Molecular Phylogenetics and Evolution 40, 101–117. https://doi.org/10.1016/j.ympev.2006.02.017

Gruwier, B., De Vos, J., Kovarovic, K., 2015. Exploration of the taxonomy of some Pleistocene Cervini (Mammalia, Artiodactyla, Cervidae) from Java and Sumatra (Indonesia): a geometric- and linear morphometric approach. Quaternary Science Reviews 119, 35–53. https://doi.org/10.1016/j.quascirev.2015.04.012

Harzhauser, M., Kroh, A., Mandic, O., Piller, W.E., Göhlich, U., Reuter, M., Berning, B., 2007. Biogeographic responses to geodynamics: A key study all around the Oligo–Miocene Tethyan Seaway. Zoologischer Anzeiger - A Journal of Comparative Zoology 246, 241–256. https://doi.org/10.1016/j.jcz.2007.05.001

Hassanin, A., Douzery, E.J.P., 2003. Molecular and Morphological Phylogenies of Ruminantia and the Alternative Position of the Moschidae. Systematic Biology 52, 206–228. https://doi.org/10.1080/10635150390192726

Hatch, J.A., Newsom, S.K., 2010. Life History, in: International Encyclopedia of Education. Elsevier, pp. 430–435. https://doi.org/10.1016/B978-0-08-044894-7.01517-7

Hayashi, S., Kubo, M.O., Sánchez-Villagra, M.R., Taruno, H., Izawa, M., Shiroma, T., Nakano, T., Fujita, M., 2020. Variation and process of life history evolution in insular dwarfism as revealed by a natural experiment (preprint). Evolutionary Biology. https://doi.org/10.1101/2020.12.23.424186

Hilgen L, S., Pop, E., Adhityatama, S., A. Veldkamp, T., W.K. Berghuis, H., Sutisna, I., Yurnaldi, D., Dupont-Nivet, G., Reimann, T., Nowaczyk, N., F. Kuiper, K., Krijgsman, W., B. Vonhof, H., Ekowati, D.R., Alink, G., Ni Luh Gde Dyah Mega Hafsari, Drespriputra, O., Verpoorte, A., Bos, R., Simanjuntak, T., Prasetyo, B., Joordens, J.C.A., 2023. Revised age and stratigraphy of the classic *Homo erectus*-bearing succession at Trinil (Java, Indonesia). Quaternary Science Reviews 301, 107908. https://doi.org/10.1016/j.quascirev.2022.107908

Hillson, S., 2005. Teeth, 2nd ed. Cambridge University Press. https://doi.org/10.1017/CBO9780511614477

Hertler, C., & Rizal, Y., 2005. Excursion guide to the Pleistocene hominid sites in Central and East Java. JWG University Frankfurt–ITB.

Hooijer, D.A., 1958. A. The Pleistocene Vertebrate Fauna of Celebes. Asian Perspectives 2, 71–76.

Hooijer, D.A., 1958. Fossil Bovidae from the Malay Archipelago and the Punjab. Zoologische Verhandelingen 38, 1–112.

Hooijer, D.A., Kurtén, B., 1984. Trinil and Kedungbrubus: the Pithecanthropus-bearing fossil faunas of Java and their relative age. Annales Zoologici Fennici 21, 135–141.

Huffman, O.F., Berkhout, A.W.J., Albers, P.C.H., De Vos, J., Aziz, F., 2022. Geology and discovery record of the Trinil Pithecanthropus erectus site, Java (preprint). Paleontology. https://doi.org/10.1101/2022.03.15.484451

Huffman, O.F., Zaim, J., 2023. Geological age estimate for the Mojokerto child's skull Homo erectus. Comment on Berghuis et al. "The eastern Kendeng Hills (Java, Indonesia) and the hominin-bearing beds of Mojokerto, a re-interpretation" [Quat. Sci. Rev. 295 (2022) 107692]. Quaternary Science Reviews 108058. https://doi.org/10.1016/j.quascirev.2023.108058

Irwin, D.M., Árnason, Ú., 1994. Cytochromeb gene of marine mammals: Phylogeny and evolution. J Mammal Evol 2, 37–55. https://doi.org/10.1007/BF01464349

Jordana, X., Marín-Moratalla, N., DeMiguel, D., Kaiser, T.M., Köhler, M., 2012. Evidence of correlated evolution of hypsodonty and exceptional longevity in endemic insular mammals. Proc. R. Soc. B. 279, 3339–3346. https://doi.org/10.1098/rspb.2012.0689

Keates, S.G., Pasveer, J.M., 2021. Modern Quaternary Research in Southeast Asia, Volume 18: Quaternary Research In Indonesia. CRC Press.

Klein, R., 1982. Patterns of ungulate mortality and ungulate mortality profiles from Langebaanweg (Early Pliocene) and Elandsfontein (Middle Pleistocene), south-western Cape Province, South Africa. Annals of the South African Museum 90, 49–94.

Klein, R.G., Cruz-Uribe, K., 1984. The Analysis of Animal Bones from Archeological Sites, Prehistoric Archeology and Ecology series. University of Chicago Press, Chicago, IL.

Klein, R.G., Cruz-Uribe, K., 1983a. The Computation of Ungulate Age (Mortality) Profiles from Dental Crown Heights. Paleobiology 9, 70–78.

Klein, R.G., Cruz-Uribe, K., 1983b. The Computation of Ungulate Age (Mortality) Profiles from Dental Crown Heights. Paleobiology 9, 70–78.

Köhler, M., Moyà-Solà, S., 2009. Physiological and life history strategies of a fossil large mammal in a resource-limited environment. Proc. Natl. Acad. Sci. U.S.A. 106, 20354–20358. https://doi.org/10.1073/pnas.0813385106

Kohut, G., 2022. Tooth Wear Age Estimation of Ruminants from Archaeological Sites. Pathways 3, 82–105. https://doi.org/10.29173/pathways33

Koike, H., Ohtaishi, N., 1987. Estimation of prehistoric hunting rates based on the age composition of sika deer (Cervus nippon). Journal of Archaeological Science 14, 251–269. https://doi.org/10.1016/0305-4403(87)90014-8

Kolb, C., Scheyer, T.M., Lister, A.M., Azorit, C., de Vos, J., Schlingemann, M.A., Rössner, G.E., Monaghan, N.T., Sánchez-Villagra, M.R., 2015. Growth in fossil and extant deer and implications for body size and life history evolution. BMC Evol Biol 15, 19. https://doi.org/10.1186/s12862-015-0295-3

Kubo, M.O., Fujita, M., Matsu'Ura, S., Kondo, M., Suwa, G., 2011. Mortality profiles of late Pleistocene deer remains of Okinawa Island: evidence from the Hananda-Gama cave and Yamashita-cho cave I sites. AS 119, 183–201. https://doi.org/10.1537/ase.091215

Kumawat, R., Joshi, S., Mathur, R., Choudhary, O.P., 2014. Gross Morphological Studies on Mandible of Indian Spotted Deer (*Axis axis*). The Indian Veterinary Journal.

Lowe, V.P.W., 1967. Teeth as indicators of age with special reference to Red deer (*Cervus elaphus*) of known age from Rhum. Journal of Zoology 152, 137–153. https://doi.org/10.1111/j.1469-7998.1967.tb01881.x

Lydekker, R., 1898. The deer of all lands; a history of the family Cervidæ living and extinct. London, R. Ward, limited.

Meijaard, E., Groves, C.P., 2004. Morphometrical relationships between South-east Asian deer (Cervidae, tribe Cervini): evolutionary and biogeographic implications. Journal of Zoology 263, 179–196. https://doi.org/10.1017/S0952836904005011

Michelin, A., 2023. *Axis porcinus* (hog deer) [WWW Document]. Animal Diversity Web. URL https://animaldiversity.org/accounts/Axis_porcinus/ (accessed 4.16.23).

Minami, M., Ohnishi, N., Higuchi, N., Takatsuki, S., 2009. Early Mortality of Sika Deer, *Cervus nippon* , on Kinkazan Island, Northern Japan. Mammal Study 34, 117–122. https://doi.org/10.3106/041.034.0207

Monson, T.A., Hlusko, L.J., 2018. The Evolution of Dental Eruption Sequence in Artiodactyls. J Mammal Evol 25, 15–26. https://doi.org/10.1007/s10914-016-9362-9

Moores, E.M. (Ed.), 1997. Encyclopedia of European and Asian regional geology, The encyclopedia of earth sciences series. Chapman & Hall, London Weinheim.

Morrison, D., Whitridge, P., 1997. Estimating the Age and Sex of Caribou from Mandibular Measurements. Journal of Archaeological Science 24, 1093–1106. https://doi.org/10.1006/jasc.1996.0189

Nishioka, Y., Vidthayanon, C., 2018. First occurrence of *Duboisia santeng* (Bovidae, Artiodactyla, Mammalia) from Thailand. Foss. Rec. 21, 291–299. https://doi.org/10.5194/fr-21-291-2018

Oli, M.K., Coulson, T., 2016. Life History, What is?, in: Encyclopedia of Evolutionary Biology. Elsevier, pp. 394–399. https://doi.org/10.1016/B978-0-12-800049-6.00083-4

Palkovacs, E.P., 2003. Explaining adaptive shifts in body size on islands: a life history approach. Oikos 103, 37–44. https://doi.org/10.1034/j.1600-0706.2003.12502.x

Philippe, H., Douzery, E., 1994. The pitfalls of molecular phylogeny based on four species, as illustrated by the Cetacea/Artiodactyla relationships. J Mammal Evol 2, 133–152. https://doi.org/10.1007/BF01464365

Pianka, E.R., 2011. Evolutionary Ecology. URL http://www.zo.utexas.edu/courses/bio373/erp-evolecol.html.

Prothero, D., Domning, D., Fordyce, R., Foss, S., Janis, C., Lucas, S., Marriott, K., Métais, G., Naish, D., Padian, K., Rössner, G., Solounias, N., Spaulding, M., Stucky, R., Theodor, J., Uhen, M., 2021. On the Unnecessary and Misleading Taxon “Cetartiodactyla.” Journal of Mammalian Evolution 29. https://doi.org/10.1007/s10914-021-09572-7

Raia, P., Meiri, S., 2006. The island rule in large mammals: Paleontology meets ecology. Evolution 60, 1731–1742. https://doi.org/10.1111/j.0014-3820.2006.tb00516.x

Randi, E., Mucci, N., Claro-Hergueta, F., Bonnet, A., Douzery, E.J.P., 2001. A mitochondrial DNA control region phylogeny of the Cervinae: speciation in *Cervus* and implications for conservation. Animal Conservation 4, 1–11. https://doi.org/10.1017/S1367943001001019

Renema, W. (Ed.), 2007. Biogeography, Time, and Place: Distributions, Barriers, and Islands, Topics In Geobiology. Springer Netherlands, Dordrecht. https://doi.org/10.1007/978-1-4020-6374-9

Rögl, F., 1999. Mediterranean and paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview).

Rozzi, R., Winkler, D.E., De Vos, J., Schulz, E., Palombo, M.R., 2013. The enigmatic bovid *Duboisia santeng* (Dubois, 1891) from the Early–Middle Pleistocene of Java: A multiproxy approach to its paleoecology. Palaeogeography, Palaeoclimatology, Palaeoecology 377, 73–85. https://doi.org/10.1016/j.palaeo.2013.03.012

Ruscillo, D. (Ed.), 2015. Recent Advances in Ageing and Sexing Animal Bones. Oxbow Books. https://doi.org/10.2307/j.ctvh1ds02

Salles, T., Mallard, C., Husson, L., Zahirovic, S., Sarr, A.-C., Sepulchre, P., 2021. Quaternary landscape dynamics boosted species dispersal across Southeast Asia. Commun Earth Environ 2, 240. https://doi.org/10.1038/s43247-021-00311-7

Senseman, R.L., 2023. *Cervus elaphus* (elk) [WWW Document]. Animal Diversity Web. URL https://animaldiversity.org/accounts/Cervus_elaphus/ (accessed 4.16.23).

Shipman, P., Storm, P., 2002. Missing links: Eugène Dubois and the origins of paleoanthropology. Evol. Anthropol. 11, 108–116. https://doi.org/10.1002/evan.10021

Spinage, C.A., 1973. A review of the age determination of mammals by means of teeth, with especial reference to Africa. African J Ecol 11, 165–187. https://doi.org/10.1111/j.1365-2028.1973.tb00081.x

Spinage, C.A., Jolly, G.M., 1974. Age Estimation of Warthog. The Journal of Wildlife Management 38, 229. https://doi.org/10.2307/3800728

Steele, T.E., Weaver, T.D., 2012. Refining the Quadratic Crown Height Method of age estimation: do elk teeth wear quadratically with age? Journal of Archaeological Science 39, 2329–2334. https://doi.org/10.1016/j.jas.2012.02.017

Stiner, M.C. (Ed.), 1991. Human predators and prey mortality, Westview special studies in archaeological research. Westview Press, Boulder.

Storm, P., Nelson, A.J., 1992. The Many Faces of Wadjak Man. Archaeology in Oceania 27, 37–46.

Susilohadi, 1995. Late Tertiary and Quaternary geology of the East Java Basin, Indonesia. University of Wollongong Thesis Collection 1954-2016.

Sutcliffe, A.J., 1973. Similarity of bones and antlers gnawed by deer to human artefacts. Nature 246, 428–430. https://doi.org/10.1038/246428a0

Twiss, K.C., 2008. An assessment of the archaeological applicability of faunal ageing methods based on dental wear. Int. J. Osteoarchaeol. 18, 329–351. https://doi.org/10.1002/oa.940

van den Bergh, G., Vos, J., Sondaar, P., Aziz, F., 1996. Pleistocene zoogeographic evolution of Java (Indonesia) and glacio-eustatic sea level fluctuations: a background for the presence of *Homo*. Indo-Pacific Prehistory Association Bulletin 14, 7–21. https://doi.org/10.7152/bippa.v14i0.11583

van den Bergh, G.D., De Vos, J., Sondaar, P.Y., 2001. The Late Quaternary palaeogeography of mammal evolution in the Indonesian Archipelago. Palaeogeography, Palaeoclimatology, Palaeoecology 171, 385–408. https://doi.org/10.1016/S0031-0182(01)00255-3

van der Geer, A., Lyras, G., Vos, J., 2021. The Island Rule: Dwarfism and Gigantism. Evolution of Island Mammals: Adaptation and Extinction of Placental Mammals on Islands, pp. 477–502. https://doi.org/10.1002/9781119675754.ch23

van der Geer, A., Lyras, G., Vos, J. de, Dermitzakis, M., 2021. Evolution of Island Mammals: Adaptation and Extinction of Placental Mammals on Islands, 2nd edition. ed. Wiley-Blackwell, Hoboken, NJ.

van der Geer, A.A.E., Lyras, G.A., MacPhee, R.D.E., Lomolino, M., Drinia, H., 2014. Mortality in a Predator-free Insular Environment: the Dwarf Deer of Crete. American Museum Novitates 3807, 1–26. https://doi.org/10.1206/3807.1

van der Geer, A.A.E., Lyras, G.A., Volmer, R., 2018. Insular dwarfism in canids on Java (Indonesia) and its implication for the environment of Homo erectus during the Early and earliest Middle Pleistocene. Palaeogeography, Palaeoclimatology, Palaeoecology 507, 168–179. https://doi.org/10.1016/j.palaeo.2018.07.009

Van Gorsel, H., 2020. Bibliography of the Geology of Indonesia and surrounding areas, Ed. 7.1. https://doi.org/10.13140/RG.2.2.19811.58409

Veitschegger, K., Sánchez-Villagra, M., 2016. Tooth Eruption Sequences in Cervids and the Effect of Morphology, Life History, and Phylogeny. Journal of Mammalian Evolution 23. https://doi.org/10.1007/s10914-015-9315-8

Voorhies, M.R., 1969. Taphonomy and Population Dynamics of an Early Pliocene Vertebrate Fauna, Knox County, Nebraska. University of Wyoming, Laramie, WY. https://doi.org/10.2113/gsrocky.8.special_paper_1.1

Waddell, P., Okada, N., Hasegawa, M., 1999. Waddell PJ, Okada N, Hasegawa M. Towards resolving the interordinal relationships of placental mammals. Syst Biol 48: 1-5. Systematic Biology 48. https://doi.org/10.1093/sysbio/48.1.1

Wang, Q., Yang, C., 2013. The Phylogeny of the Cetartiodactyla Based on Complete Mitochondrial Genomes. IJB 5, p30. https://doi.org/10.5539/ijb.v5n3p30

Wibowo, A., 2020. Suitable Habitat Modeling of Prehistoric Antelope-like Bovid *Duboisia santeng* in Java Island in The Early Pleistocene . Earth Sciences. https://doi.org/10.20944/preprints202009.0355.v1

Zaim, Y., de Vos, J., Huffman, O.F., Aziz, F., Kappelman, J., Rizal, Y., 2003. A new antler specimen from the 1936 Perning hominid site, East Jawa, Indonesia, attributable to Axis lydekkeri (MARTIN, 1886). Journal of Mineral Technology, The Faculty of Earth Sciences and Mineral Technology, Institute Technology, Bandung. 10, 1-10