Summary

The research presented in this PhD thesis focuses on two contrasting paleogeographical and paleoenvironmental settings of different ages. As such, this thesis is not structured around a single, case study-specific research problem. Instead, it asks: In which ways can isotope geochemistry support, test, and expand on the findings of more 'traditional' paleontology? In the reconstruction of ancient habitats and the behavior of their inhabitants, how can geochemical tools best be embedded? Special consideration is given to the the question of diagenesis, the post-mortem and post-depositional chemical alteration that is a constant threat to the preservation of the original isotopic composition of fossil material. How should we test for and mitigate the effects of diagenetic alteration?

The first part centers on the type area of the Maastrichtian Stage, which includes the southern part of the Dutch Limburg province as well as the neighboring provinces of Limburg and Liège in Belgium. Its soft carbonate deposits, which have long been excavated to produce building stone and cement, were laid down in a shallow subtropical sea that covered this area at the end of the Cretaceous period (Felder, 1994; Herngreen and Wong, 2007; Vonhof et al., 2011). A variety of vertebrate fossils have been recovered from these highly fossiliferous sediments: abundant shark and ray teeth, remains of turtles, mosasaurs, plesiosaurs, elasmosaurs and crocodiles, and rare finds of terrestrial taxa such as hadrosaurid dinosaurs (Dortangs et al., 2002; Jagt, 2003; Mulder, 2003; Schulp et al., 2016).

In Chapter 2, we inventory *Allopleuron hofmanni* specimens in public collections, and here provide an overview of our taphonomic and paleopathological findings. A preservation and collection bias has resulted in an overrepresentation of the large, robust skeletal elements of the skull, carapace and pectoral girdle. Tooth marks present on 6-12% of carapace specimens do not occur on other parts of the skeleton, and mostly seem to be inflicted post-mortem by scavengers. Shallow semi-circular lesions occur on 30% of carapace specimens and are likely barnacle attachment sites. Most abnormalities in carapace morphology occur in the posterior portion, with 21% of suprapygal elements affected. All reconstructed carapace lengths are >90 cm, suggesting that the collections almost exclusively yield adult individuals. We hypothesize spatial niche partitioning between adults and younger individuals, whereby the home range of the latter group is located outside of the Maastrichtian type area.

In Chapter 3, we present the isotope compositions of structural carbonate ($\delta^{13}C$ and $\delta^{18}O_{sc}$) and phosphate ($\delta^{18}O_p$) in the teeth of ten late Maastrichtian and early Paleocene neoselachian (shark and ray) species, as well as carapace bone of *A. hofmanni*. A lack of correlation between neoselachian $\delta^{18}O_p$ and $\delta^{18}O_{sc}$ values, and offset with modern shark

$\delta^{18}O_{sc}$ values suggests diagenetic alteration of structural carbonate oxygen. Neoselachian $\delta^{18}O_p$ values (16.9 to 25.0‰) are comparable to extant shark $\delta^{18}O_p$ values. Based on the median value of 22.3‰ for these samples we calculate a paleoseawater temperature of 19.7°C, which is in good agreement with expected temperatures for this region in the Maastrichtian. The total range in $\delta^{18}O_p$ values is interpreted to reflect both temperature variation and spatial variation in seawater $\delta^{18}O_w$. There is an offset between dentin and enamel $\delta^{13}C$ values in the fossil neosalachian teeth, similar to the offset found in modern shark teeth. Overall more enriched $\delta^{13}C$ values for the Maastrichtian-Paleocene dataset suggest relatively high $\delta^{13}C$ values at the base of the food chain. Carbon isotope values of *A. hofmanni* bone cannot exclude the possibility that this species engaged in frequent long-duration dives, but in light of realistic diet $\delta^{13}C$ values it is deemed more likely that the $\delta^{13}C$ bone values in this marine turtle were not significantly affected respired CO_2 accumulation during long dives. A carnivorous diet and a herbivorous (seagrass) diet for *A. hofmanni* are both feasible possibilities given the measured $\delta^{13}C$ values, but the latter option would require relatively low seagrass $\delta^{13}C$ values compared to that of extant species.

In the second half of this thesis I focus on the terrestrial environments of Indonesia in the late Quaternary, between 1.5 million and 2.5 thousand years ago. Specifically I examine the extensive fossil assemblages from Java and Sumatra, which include a wealth of terrestrial mammal remains as well as *Homo erectus* and archaic *Homo sapiens*. Repeated glacial periods lower global sea level, so that the western islands of the Indonesian archipelago periodically become mountain ranges on the exposed continental shelf (Hutchison, 1989), thereby allowing faunal exchange with the Asian mainland. This glacial-interglacial cycle also affects regional climate and vegetation, affecting the relative abundance of rainforests and savannas. With the research presented in this thesis I aim to gain more insight into how this dynamic ecological system responds to glacial-interglacial climate change.

Before the study presented in Chapter 4 of this thesis, stable isotope methods had not yet been extensively applied to the fossil assemblages of Sundaland (the biogeographical region comprising most of the Indonesian Archipelago). Here we use the isotope composition of tooth enamel to investigate the diet and habitat of bovids, cervids, and suids from several Holocene and Pleistocene sites on Java and Sumatra. Our carbon isotope results indicate that individual sites are strongly dominated by either C_3-browsers or C_4-grazers. Herbivores from the Padang Highlands (Sumatra) and Hoekgrot (Java) cave faunas were mainly C_3-browsers, while herbivores from *Homo erectus*-bearing sites Trinil and Sangiran (Java) utilized an almost exclusive C_4 diet. The suids from all sites show a wide range of $\delta^{13}C$ values, corroborating their omnivorous diet. For the dataset as a whole, oxygen and carbon isotope values are positively correlated. This suggests that isotopic enrichment of rainwater and vegetation $\delta^{18}O$ values

coincides with an increase of C_4-grasslands. We interpret this pattern to mainly reflect the environmental contrast between glacial conditions (drier, more C_4 plants) and interglacial conditions (wetter, more C_3 plants). Intermediate herbivore $\delta^{13}C$ values indicating mixed C_3/C_4 feeding are relatively rare, which we believe to reflect the abruptness of the transition between glacial and interglacial precipitation regimes in Sundaland. For seven *Homo erectus* bone samples we were not able to distinguish between diagenetic overprint and original isotope values, underlining the need to apply this isotopic approach to *Homo erectus* tooth enamel instead of bone. Importantly, our present results on herbivore and omnivore faunas provide the isotopic framework that will allow interpretation of such *Homo erectus* enamel isotope data.

To further expand our understanding of the paleobiology and paleoecology of the Sundaland fossil faunas, we analyzed the strontium isotope ($^{87}Sr/^{86}Sr$) compositions of a selection of terrestrial vertebrate bone and enamel from the cave sites of Wajak, Hoekgrot, and Punung, and the *Homo erectus*-bearing sites Trinil and Sangiran. We assess the extent to which the Sr isotope ratios of these faunas reflect the surrounding substrate geology, and whether deviation from this general local signal is linked to dietary preferences. Results show that Hoekgrot and Wajak ungulates ranged predominantly on volcanic substrates rather than the nearby limestone terrain. Punung specimens show considerable influence of geological substrates of marine origin, and imply that the bovids found at this site did not roam far inland. At Trinil and Sangiran, a considerable part of the specimens have much higher Sr isotope ratios than we would expect based on the substrate geology isoscapes, indicating that these animals predominantly ranged in the low-lying, limestone-rich areas to the north of both sites. Comparison of Sr isotope values with carbon isotope data ($\delta^{13}C$) from the same specimens shows that the dominant C_4 signal observed in the Sangiran and Trinil herbivore faunas corresponds with foraging in different landscape settings, and thus likely to be representative of the overall balance between C_4 and C_3 vegetation in these areas during the Early and Middle Pleistocene.