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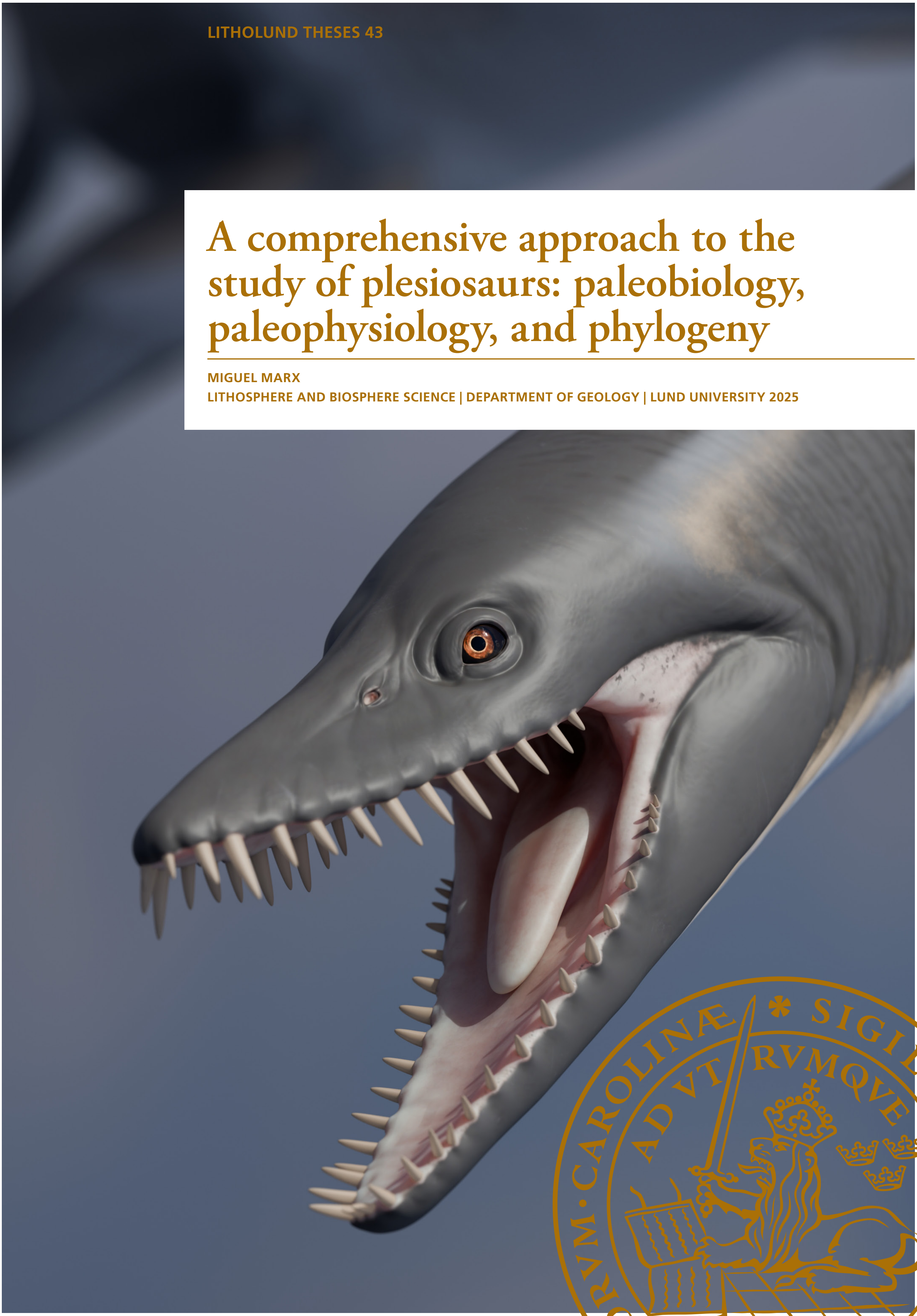
MIGUEL MARX

LITHOSPHERE AND BIOSPHERE SCIENCE | DEPARTMENT OF GEOLOGY | LUND UNIVERSITY 2025



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A comprehensive approach to the study of plesiosaurs: paleobiology, paleophysiology, and phylogeny

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Lithosphere and Biosphere Science
Department of Geology

DOCTORAL DISSERTATION

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Cover image of *Elasmosaurus platyurus* by Oak, with permission

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Title: A comprehensive approach to the study of plesiosaurs: paleobiology, paleophysiology, and phylogeny

Abstract:

Plesiosaurs are charismatic marine reptiles of the Mesozoic Era. Life-like reconstructions of long-necked forms are typically ‘shrink-wrapped’ with a narrow, snake-like neck and a sea turtle-like body; a depiction that has changed little since the initial discovery of plesiosaurs over 200 years ago. Despite their long geological history and importance in founding paleontology as a scientific discipline, minimal attention has hitherto been paid to the paleobiology of plesiosaurs—the behaviors and adaptations these animals evolved to become one of the most successful lineages of marine tetrapods in Earth`s history. The objective of this thesis entails the study of these ancient reptiles using a suite of approaches to provide a better understanding of the life, appearance, and relationships of plesiosaurs.

The exceptionally preserved specimens from the world-renowned Posidonia Shale (Posidonienschiefer Formation) in Germany formed the primary source of information for the majority of the papers included in this thesis. Among these, are MH 7 (*Plesiopterys wildi*), which represents an essentially complete and articulated skeleton with fossilized soft tissues in the tail region and along the trailing edge of one flipper. In Paper I, I conclude that this plesiosaur had a mosaic of smooth, scaleless skin, and scales on different parts of the body. Furthermore, the remarkable preservation allowed a description of the integument, including keratinocytes and melanophore pigment cells. Assessment of the osteology of this new *P. wildi* fossil provided novel insights into the skeletal anatomy of this taxon and an updated diagnosis for the species, but also new inferences on the evolution and paleobiogeography of long-necked (plesiosauroid) plesiosaurians during the Early Jurassic (Paper II).

Another important species is *Seeleyosaurus guilelmiimperatoris*, which is represented by the holotype (MB.R.1992) and a second individual (SMNS 12039). Historically, this plesiosaur has been instrumental in providing a more complete concept of the external appearance of long-necked forms, as the holotype is a complete skeleton with preserved soft tissues in the right front flipper and distal tail region—leading Wilhelm Dames to publish the earliest scientific reconstruction of a plesiosaur based on soft-tissue remains in 1895. The osteology, phylogeny, and preserved tissues are the focus of Paper III, where I, along with my coauthors, found *S. guilelmiimperatoris* to be a derived Microcleidid plesiosaurian, diagnosable by a set of morphological characters that include one autapomorphy. *Seeleyosaurus guilelmiimperatoris* also formed the basis of Paper IV, as this plesiosaur exhibits a neural spine arrangement in the dorsal vertebral series that appears to be virtually identical to that of many modern-day cetaceans equipped with a fleshy dorsal fin. Morphometric analysis of *Seeleyosaurus* and other Posidonia Shale plesiosaurs identified three individuals with a shift in the orientation of the dorsal neural spines from recumbent to procumbent. In Paper IV, I conclude that this directional change likely represents an osteological correlate for a dorsal fin.

Paper V deals with the hydro- and thermodynamic capabilites of long-necked plesiosaurs using computational fluid dynamics (CFD) simulations. Our CFD analyses demonstrate that a thicker neck, insulated with peripheral blubber, would have benefitted these ancient reptiles, especially individuals living in cold ocean waters near the poles. Additionally, a thicker neck did not create a negative effect on the overall drag. Thus, I conclude that plesiosaurs likely possessed an insulating peripheral layer of blubber to protect against the thermal conductivity of water, which in turn creates a more of a torpedo-shaped body form—a profile typical for many marine tetrapods today.

Paper VI comprises a review of plesiosaur finds from the Cretaceous of Angola, which have provided new insights into plesiosaur paleobiology and evolution. These discoveries include the bones of aristonectine elasmosaurids that exhibit an external morphology that is immature, yet their histology is like that of skeletally mature individuals, indicating ontogenetic paedomorphism. Further inferences on the evolution of paedomorphic traits and adaptations for life in a pelagic environment are presented in the skeletal anatomy of *Cardiocorax mukulu*. A femur of the first known polycotylid plesiosaurian from sub-Saharan Africa is also described, along with aristonectine basioccipitals that provide insights into plesiosaur biodiversity. A review of the taphonomy of the ‘Bench 19 Bonebed’ in Bentiaba reveals that plesiosaur skeletal elements often show bitemarks inflicted by sharks but not mosasaurs, which were otherwise abundant conteporaries of plesiosaurs along the coast of what is today Angola.

Collectively, this thesis shows that plesiosaurs lost the scalation on their body (apart from the flippers), and presumably evolved a dorsal fin and blubber as adaptations for pelagic life. These results thus provide a noteworthy update of their apperance from shrink-wrapped creatures to animals that were well-adapated to thrive in the oceans. Additional findings from Angola provide a rare window into the evolution and diversity of plesiosaurs at the end of the Mesozoic.

Key words: adaptations, Angola, blubber, dorsal fin, pelagic, phylogeny, scales, skin, thermodynamics

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I, the undersigned, being the copyright owner of the abstract of the above-mentioned dissertation, hereby grant to all reference sources permission to publish and disseminate the abstract of the above-mentioned dissertation.

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I dedicate this work to my parents, Jacinta and Kurtis Marx, who with their love and unwavering support have made this dream possible.

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List of papers

This thesis includes six papers. Papers I, II, and III have been published and are reprinted here with permission. Paper IV is an unpublished manuscript. Paper V will be published as a conference paper, and Paper VI is unpublished but in-press and printed with permission.

Paper I:

Marx, M., Sjövall, P., Kear, B. P., Jarenmark, M., Eriksson, M. E., Sachs, S., Nilkens, K., Op De Beeck, M., and Lindgren, J. (2025). Skin, scales, and cells in a Jurassic plesiosaur. *Current Biology*, *35*(5), 1113–1120. DOI: 10.1016/j.cub.2025.01.001.

Paper II:

Marx, M., Sachs, S., Kear, B. P., Eriksson, M. E., Nilkens, K., and Lindgren, J. (2025). A new specimen of *Plesiopterys wildi* reveals the diversification of cryptoclidian precursors and possible endemism within European Early Jurassic plesiosaur assemblages. *PeerJ*, *13*, e18960. DOI: 10.7717/peerj.18960

Paper III:

Sachs, S., Madzia, D., Marx, M., Roberts, A. J., Hampe, O., and Kear, B. P. (2025). The osteology, taxonomy, and phylogenetic placement of *Seeleyosaurus guilelmiimperatoris* (Plesiosauroidea, Microcleididae) from the Lower Jurassic Posidonia Shale of Germany. *The Anatomical Record*, *308*(9), 2283–2346. DOI: 10.1002/ar.25620

Paper IV:

Marx, M., Eriksson, M. E., and Lindgren, J. Putative osteological correlates for a dorsal fin in plesiosaurs. (manuscript)

Paper V:

Marx, M., Szász, R. Z., and Lindgren, J. (2025). CFD modelling of the thermo- and hydrodynamic capabilities of long-necked plesiosaurs (Reptilia, Sauropterygia). Proc. Conference on Modelling Fluid Flow (CMFF'25), Budapest, Hungary, 1–8.

Paper VI:

Marx, M., Araújo, R., Nsungani, P. C., and Polcyn, M. J. Plesiosaurs of Angola. In: J. O'Gorman and N. Bardet (eds.) *Gondwanan Plesiosaurs*. (in press)

Acknowledgements

My PhD journey (in addition to my time in Sweden) has been the adventure of a lifetime, and I am indebted to a long list of people who have made this experience possible and filled it with wonderful memories. I am recalling now as I write this the euphoria I felt when I was accepted to this PhD program four years ago in my small studio apartment in Dallas, Texas, realizing I would be living in Sweden studying my favorite group of prehistoric beasts, the plesiosaurs.

My PhD supervisor, Johan Lindgren, has been a role model for me during my time at Lund University. He is a real scientist who critically thinks about every step in the scientific process and certainly *does not* cut corners. His mentorship has made me a better scientist, and I am grateful for his time and patience with me. I am also very grateful to my co-supervisor, Mats Eriksson, who has been a friend, colleague, and fellow concertgoer at metal music festivals. Thanks again Mats for the advice on pensions (we all know it is never too early to start setting up a smart pension plan!).

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I would like to thank my other co-supervisors for their tremendous help and mentorship during my time as a PhD student. Benjamin Kear is a master writer, and I learned how to better structure my writing for high-impact journals from him. Sven Sachs, being a world-renowned plesiosaur expert, helped significantly as a mentor and with the identification of MH 7 as *Plesiopterys wildi* (RIP *Posidoniasaurus* gen. nov.) and was wonderful company as we spent days studying plesiosaurs in Berlin. Robert Szász, your patience has no bounds; thank you for teaching me the basics of computational fluid dynamics (CFD), how to set up CFD cases and the theory behind it all, as we ventured into the unknown trying to model a complex animal using some basic assumptions. I would like to thank Martin Jarenmark for being super helpful and patient with my basic understanding of chemistry and for making lab work possible. I also thank Peter Sjövall for his tremendous help with the study of plesiosaur soft tissues at RISE in Borås—you are a true ToF-SIMS wizard!

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Finally, my dear family has supported my obsession with paleontology, and I am forever grateful for their love. Kurt and Mom, thanks for having my dreams come true! ♥

Introduction

Vertebrate paleontology can trace its beginnings as a scientific discipline back to the late 18th and early 19th centuries with discoveries of ancient marine reptiles, including plesiosaurs, the topic of this thesis (De la Beche and Conybeare, 1821; Conybeare, 1824; Taylor, 1997). The first complete plesiosaur to be studied, *Plesiosaurus dolichodeirus*, revealed a body plan to these early scientists that was clearly distinct from all other known reptiles: a skull with sharp needle-like teeth attached to a long neck, a round body with two pairs of flippers, and a tail at the end. The genus, *Plesiosaurus*, from which the group name Plesiosauria derives, means 'near lizards' (Conybeare, 1824) and was meant to denote their position as being between the fish-like ichthyosaurus and reptiles like crocodiles and lizards in the Great Chain of Being—a hierarchy of life before the concept of evolution was applied (Taylor, 1997). The body plan coupled with the apparent lack of modern analogues have long rendered plesiosaurs as oddities, with much of their biology being poorly understood. In this same vein, our basic idea of what these animals would have looked like when alive remains a mystery.

The conventional life reconstruction of a plesiosaur follows the tradition of 'shrink-wrapping', which entails simply following the contour of the skeleton to demarcate the boundaries of the body (McDermott, 2020). Portrayals of plesiosaurs thus illustrate these animals generally as "a snake drawn through the shell of a turtle"—a quote possibly attributable to William Buckland (Williston, 1914). This creates a depiction where the neck is exceedingly narrow (Figure 1; Noè et al. 2017, figures 1–3; Sander, 2023, figure 1). This Loch Ness monster-like design has become pervasive throughout both scientific and popular depictions of these animals.

However, this illustration of a plesiosaur faces several practical and obvious issues that suggest shrink-wrapping is certainly underestimating the volume of soft tissue these animals would have had in life. Firstly, a narrow, unprotected neck would leave the long-necked plesiosaurs exceedingly vulnerable to predatory attacks (Troelsen et al., 2019). Moreover, a lack of insulating peripheral tissue, such as blubber, would be detrimental to their survival in cool to freezing environments. Sedimentological and wood growth-band evidence from the Early Cretaceous of Australia indicates that freshwater plesiosaurs inhabited rivers that froze during the winter months (Kear, 2003, 2004, 2006; Kear et al., 2006). Based on analyses of oxygen isotopes, Late Cretaceous plesiosaurs likewise inhabited cold, high latitude ocean waters in the Western Interior Seaway (5º C at ~60ºN paleolatitude) (Petersen et al., 2016) and in Antarctica (7º C at 64ºS) (Leuzinger et al., 2023). Furthermore, a study employing 3D models of long-necked plesiosaurs and simulations of these animals swimming against a flow stream concluded that a narrow neck would have increased drag compared to a thicker one (Troelsen et al., 2019). A thick neck, allowing for a seamless transition to the rest of the body, in turn provides a fusiform/torpedo-shaped body, convergent with those of other secondarily marine amniotes (Fish, 2023).

Another feature that is missing in plesiosaur depictions, but otherwise nearly ubiquitous in marine animals, is a dorsal fin (Lingham-Soliar, 2005; Renesto et al., 2020). Plesiosaurs have an evolutionary history of over 140 million years (Sander, 2023), and their pelagic lifestyle likely necessitated a dorsal fin of some kind to control roll, which is present not only in modern whales, but also in other extinct marine reptiles like ichthyosaurs and perhaps also mosasaurs (Konishi et al., 2023).

The dearth of information regarding basic aspects of the biology of plesiosaurs is a consequence of the few preserved body outlines and fossilized tissues in the plesiosaur fossil record. Accordingly, our knowledge on the skin morphology and biology of plesiosaurs is limited. Reptiles tend to reduce or lose their scalation as they transition from land to sea (Lindgren et al., 2009, 2018; 2025). The integument (skin) of plesiosaurs is often assumed to have been scaleless (Sander, 2023). However, the most complete plesiosaur fossil to preserve soft-tissue remains (*Mauriciosaurus fernandezi*) was interpreted to have scales (Frey et al., 2017). A juvenile plesiosaur from the Posidonia Shale (Lower Jurassic of Germany) was also hypothesized to have had scales covering parts of the body (Vincent et al., 2017). Conversely, smooth and scaleless skin was described in *Attenborosaurus conybeari* (see Sollas, 1881). Thus, there are conflicting interpretations as to how the integument would have appeared on plesiosaurs. Contemporaries of the plesiosaurs

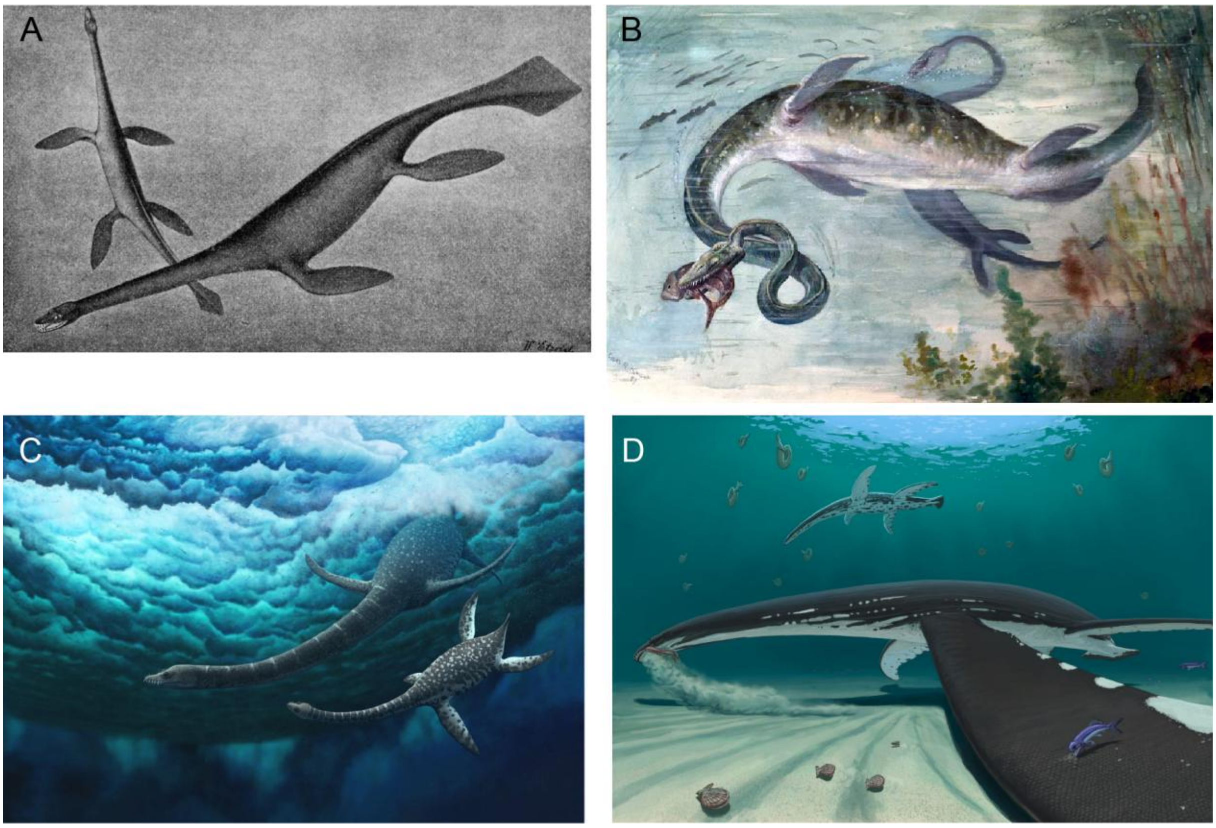

Figure 1. Collage of plesiosaur life reconstructions. **A.** *Seeleyosaurus guilelmiimperatoris* with a tail fin inferred from preserved soft-tissues in MB.R.1992 (Dames, 1895, page 79). **B.** Reconstruction of *Elasmosaurus platyurus* by Charles R. Knight (1897) (Wikimedia Commons). **C.** *Jucha squalea* in cold ocean water with ice cover as envisioned by Andrey Atuchin (2020); used with permission. **D.** *Plesiopterys wildi* by Joschua Knüppe with added tissue around the neck (2025).

(such as the ichthyosaurs), on the other hand, are represented by numerous specimens with preserved soft tissues, and even complete body outlines that allow for unprecedented insights into their paleobiology (Lindgren et al., 2010, 2018; 2025; Eriksson et al., 2022).

Taken together, I hypothesize that long-necked plesiosaurs would have benefitted from having a considerably thicker neck (insulated by peripheral blubber) than what is conventionally assumed. Furthermore, at least some plesiosaurs may have evolved a dorsal fin, as such an extremity necessitates control of roll for virtually all marine amniotes and fish (Lingham-Soliar, 2005; Fish, 2023). I further hypothesize that plesiosaurs lost their scalation after invading the oceans, just like other Mesozoic marine reptiles.

But how do we test these hypotheses? Without a complete body outline of a long-necked plesiosaur to directly study, I needed to consider alternative approaches. Consequently, in this thesis, I utilized a variety of methods to reconstruct the appearance, adaptations, paleobiology, and paleophysiology of plesiosaurs. Along the way, additional information regarding plesiosaur anatomy and phylogeny was elucidated.

Thesis objectives

My thesis project used a combination of approaches to discern the appearance and adaptations plesiosaurs acquired for life in the oceans. Fossils from the Posidonia Shale (Toarcian-aged sediments in southern Germany) constituted most of the material used in this work, as specimens from this rock unit are essentially complete and occasionally preserved with associated soft tissues. Additional fossil material included elasmosaurid and polycotylid remains from Bentiaba, Angola (collected by Projecto PaleoAngola) and cetacean skeletons used for morphometric studies. The holotype of the elasmosaurid, *Albertonectes vanderveldei* (TMP 2007.011.0001; Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada

), was employed to construct the meshes for testing the hydro- and thermodynamic capabilities of a long-necked plesiosaur using computational fluid dynamics (CFD) simulations.

The first component of my thesis focused on the recovery and characterization of endogenous soft parts and biomolecules. A newly prepared plesiosaur from the Posidonia Shale (MH 7; Urwelt-Museum Hauff, Holzmaden, Germany) was found to include preserved soft-tissue remains, which were studied using infrared (IR) microspectroscopy, time-of-flight secondary ion mass spectrometry (ToF-SIMS), electron microscopy coupled with elemental analysis (SEM, EDX, and EBSD), and light microscopy. MH 7, along with other exquisitely preserved plesiosaur skeletons from the Posidonia Shale, were also the subject of osteological descriptions and phylogenetic analyses, which collectively illuminate the evolutionary history of plesiosaurs during the Early Jurassic.

Another component of my thesis entails the use of morphometric data to identify potential osteological correlates for soft tissue structures, as has been previously done by Lindgren et al. (2007, 2011). The angle of inclination of the neural spines in the trunk region of plesiosaurs and extant cetaceans was quantified and compared to identify possible correlates for the presence of a fleshy dorsal fin. Modern dolphins and porpoises for this study were accessed from the world's largest collection of whale bones; i.e., the Smithsonian's Museum Support Center, and The Zoology collection at Lund University. In addition to neural spine inclination, other details that could be relevant to the presence of dorsal fin in plesiosaurs (orientation of the limbs, and body size) were also investigated.

The CFD portion of this thesis forms the third component and includes numerical simulations of the hydro- and thermodynamic capabilities of long-necked plesiosaurs. To achieve this, two meshes of the long-necked elasmosaurid, *Albertonectes vanderveldei*, were constructed: one mesh representing a classic shrink-wrapped version (i.e., without blubber), and a second mesh representing a version equipped with an insulating peripheral layer of blubber. Hypothetic metabolic rates (ranging from ectothermic to endothermic) were applied as the heat-generating mechanism in the plesiosaur models, allowing me to test how well the two replicas retained heat under different assumptions of their physiology. These geometries were also subjected to flow simulations to test potential effects on drag. The model that is both hydrodynamically efficient and capable of 'surviving' in cool waters, as some plesiosaurs evidently were capable of (Kear, 2006; Leuzinger et al., 2023), was hypothesized to be the most realistic representation for the life appearance of these long-necked reptiles.

The final component of this thesis includes a review of the plesiosaur fossil record of Angola, and highlights important new findings that have expanded our understanding of plesiosaur paleobiology and phylogeny. This includes comments on paedomorphic features of the skull of *Cardiocorax mukulu*, and the convergent morphology of the semi-circular canals with modern pelagic marine reptiles. Bite marks on the bones of plesiosaurs indicate that their remains were scavenged by sharks, with no record yet of a mosasaur bite mark. Thus, despite sharing the same environment with macropredaceous mosasaurs, plesiosaurs seemingly were not often scavenged upon or hunted by mosasaurs at the Bench 19 locality. Further, the first record of Polycotylidae in sub-Saharan Africa, represented by a single femur, is also described in this work.

Thus, the aims of my Ph.D. project were to discern the adaptations acquired by plesiosaurs for efficient life in the marine realm using a broad range of methodologies, including approaches used in molecular biology, morphometrics, and computational fluid dynamics. Addressing the following questions were central to the aims of my project:

1. What can fossilized remains inform us about plesiosaur paleobiology and how they adapted to life in the oceans?

2. Can endogenous soft tissues and residual biomolecules from plesiosaur fossils be identified and characterized, and, if so, what if anything, can they say about plesiosaur biology?

3. Can osteological and morphometric data be used to infer the presence of a fleshy dorsal fin in plesiosaurs?

4. How much blubber would a plesiosaur need to maintain a stable body temperature in cool to near-freezing waters?

5. How does added blubber affect the hydrodynamics of the plesiosaur body?

6. What do new plesiosaur fossils reveal about the evolutionary relationships within Plesiosauria?

Plesiosauria

To get a better overview of what exactly a plesiosaur is and why they are significant, I have included an overview of their evolutionary history, with comments on their paleobiology and ecology. This review will also set the context for this Ph.D. thesis and how the enclosed papers fill some gaps in our current knowledge regarding these marine reptiles.

Plesiosauria (to which all plesiosaurs belong) is a clade of reptiles that were fully adapted for an aquatic lifestyle. They are characterized by paraxial swimming, which was achieved with two pairs of limbs modified into hydrofoil flippers, and an elongated neck composed of numerous (37–76) vertebrae (Kubo et al., 2012; Otero et al., 2018; Wang et al., 2022; Sander, 2023). Plesiosauria is part of a larger group of marine reptiles called Sauropterygia. The precise evolutionary origin of Sauropterygia remains debated; some studies indicate an ancestry based within Archosauria (which includes, e.g., crocodiles, birds, and dinosaurs) (Hu et al., 2024), while others have this group being more closely related to turtles and Lepidosauromorpha (that is, snakes, lizards, and the *Tuatara*) (Liu et al., 2011), or neither of the aforementioned groups (Scheyer et al., 2017; Sues, 2019, figure 2.6). We can, however, say that Plesiosauria is included within Diapsida (reptiles with two pairs of openings in the back of their skull; Sues, 2019; Liu et al., 2023) and they were a remarkably successful group. Plesiosaurs evolved sometime during the Triassic and thrived in the Mesozoic oceans and rivers up until the end-Cretaceous mass extinction event (the K/Pg event) that also killed the last non-avian dinosaurs (Wintrich et al., 2017).

Plesiosauria has traditionally been dichotomized into two camps: the large-headed and short-necked 'pliosauromorphs' and small-headed and long-necked 'plesiosauromorphs' (Andrews, 1910; Welles, 1952; Persson, 1963; Cruickshank, 1994; O'Keefe, 2002), although recent phylogenetic analyses have demonstrated that the pliosauromorph body plan evolved independently at least three times in Plesiosauria (O'Keefe, 2002; Benson and Druckenmiller, 2014): once in Pliosauridae, and Rhomaleosauridae during the Jurassic, and again in Polycotylidae during the Cretaceous (O'Keefe, 2002; Benson and Druckenmiller, 2014; Fischer et al., 2017). Although, there is almost a continuum between the two morphotypes, with some species falling between these two body forms (e.g., *Plesiosaurus*) (O'Keefe, 2002).

The two main hypotheses for how the three major groups within Plesiosauria (Plesiosauroidea, Pliosauridae, and Rhomaleosauridae) are related to one another follow either a monophyletic Neoplesiosauria (Plesiosauroidea + Pliosauridae) with Rhomaleosauridae branching outside this clade (Ketchum and Benson, 2010), or Plesiosauroidea being the sister taxon of Pliosauroidea (Pliosauridae + Rhomaleosauridae) (Benson and Druckenmiller, 2014). For now, whether Rhomaleosauridae forms a monophyletic clade with Pliosauridae remains unresolved, although Marx et al. (2025a; supplementary info) (Paper II) recently recovered the Rhomaleosauridae as being the outgroup of Plesiosauroidea and Pliosauridae in the equal weight parsimony analysis (Fig. 2).

The stratigraphically oldest plesiosaur is *Rhaeticosaurus mertensi* from Rhaetian marine mudstones of Germany (Wintrich et al., 2017). Interestingly, this species was returned within a phylogenetic analysis by Wintrich et al. (2017) as a relatively derived pliosauroid. What this means is that, even though it is the oldest plesiosaur found to date, it was quite 'advanced' by plesiosaur standards given its age. Certainly, and consequently, the earliest plesiosaurs have yet to be discovered.

Soon after the Triassic, plesiosaurs experienced a significant radiation (Benson et al., 2012). Fortunately, the fossil record for plesiosaurs during the Early Jurassic is good, especially in Europe (Tutin and Butler, 2017). Long-necked forms (plesiosauromorphs) diversified into mostly small to moderate-sized animals (e.g., Microcleididae) that were piscivorous (fish eating) and teuthophagous (cephalopod eating), in addition to preying upon benthic organisms (Marx et al., 2025b). The pliosaurids during the Early Jurassic were also not massive in size, rather, the rhomaleosaurids were the largest among the plesiosaurs, with some species reaching about seven meters in length (Smith and Dyke, 2008). Beautifully preserved and articulated plesiosaur skeletons from this early radiation have been found in Germany, France, Luxembourg, and England (Bardet et al., 1999; Groβmann, 2007; Vincent et al., 2017; Marx et al., 2025a; Sachs et al., 2025).

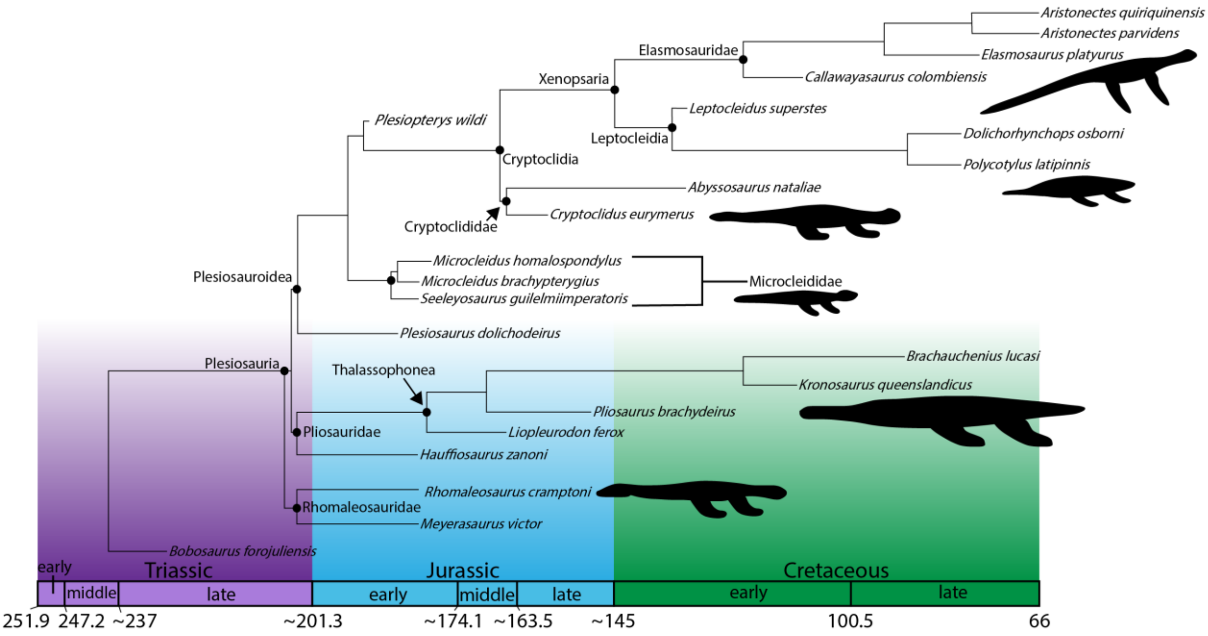

Figure 2. Timescale of the Mesozoic Era with major plesiosaur clades included. Clade locations and names are based on fig. 3 in Benson and Druckenmiller (2014) and phylogenetic analyses in Marx et al. (2025a; Paper II). Plesiosauria originated sometime in the Triassic, along with the major clades, Plesiosauroidea, Pliosauridae, and Rhomaleosauridae. A major radiation ensued in the Early Jurassic, with a turnover event transitioning from the Late Jurassic into the Cretaceous. Three lineages of plesiosaurs survived into the Cretaceous (Thalassophonea, Cryptoclididae, and Xenopsaria). At the end of the Cretaceous, only the clade Elasmosauridae remained. Species names are represented in the timescale by their approximate age in the fossil record. Ages for the timescale are based on the most recent version of the geologic timescale by The Geological Society of America (v. 6.0) (Walker and Geissman, 2022). Silhouettes represent the typical body shapes of various clades (starting from the top and moving downward: *Elasmosaurus platyurus*, *Polycotylus latipinnis*, *Cryptoclidus eurymerus*, *Seeleyosaurus guilelmiimperatoris*, *Kronosaurus queenslandicus*, and *Rhomaleosaurus cramptoni*.

By the Middle Jurassic, the classic large-bodied pliosaurids with massive heads had evolved; this group called the Thalassophonea, meaning 'sea slayer' (Benson and Druckenmiller, 2014), would occupy the upper trophic levels as megapredators (Sachs et al., 2023). The rise of thalassophonean plesiosaurs coincided with the decline of the Rhomaleosauridae (Sachs et al., 2023). This decline in the Rhomaleosauridae, along with other early Jurassic plesiosaurs (Microcleididae) however appears to be part of a turnover event between the Early and Middle Jurassic that had a global effect on marine reptiles (Fischer et al., 2021). The cause for this turnover can possibly be attributed to cooling during the Aalenian and Bajocian which possibly lead to belemnite extinctions, in turn affecting the bottom-up ecology of Mesozoic ecosystems (Dera et al., 2016; Neige et al., 2021; Fischer et al., 2021).

By the Late Jurassic, truly massive pliosaurids were present, reaching lengths of 10 meters or more (Martill et al., 2023). Also during this time, a derived group of plesiosauroids, the Cryptoclidia, were flourishing (Benson and Druckenmiller, 2014). This group includes the family, Cryptoclididae, long-necked plesiosauroids that are represented by fossils spanning the Boreal region to the Southern hemisphere (Andrews, 1910; Gasparini et al., 2002; Otero et al., 2020; Roberts et al., 2020). Cryptoclidids have been the subject of quantitative approaches that have revealed underwater flying (like that of modern penguins and sea turtles) to be the most likely mode of swimming employed by plesiosaurs (Krahl et al., 2022), and a unique feeding ecology as generalists that consumed soft-bodied prey and small shelled invertebrates—a category referred to as the 'trap guild' (Chatterjee and Small, 1989; Foffa et al., 2024). Cryptoclidia was successful during the Jurassic and managed to survive the Jurassic/Cretaceous turnover event, which otherwise negatively impacted plesiosaur diversity at the beginning of the Cretaceous (Benson and Druckenmiller, 2014).

In the Cretaceous, Cryptoclidia gave rise to a derived group, Xenopsaria ('strange angler';

Benson and Druckenmiller, 2014) that comprises some remarkable plesiosaurs. These include the iconic elasmosaurids, which are characterized by their exceedingly long necks with over 50 neck vertebrae (Welles, 1962; Kubo et al., 2012; Otero, 2016), and Leptoclidia with short-necked forms evolving during the mid-Cretaceous (Fischer et al., 2018). The thalassophoneans also survived the Jurassic turnover event and continued to evolve into large species during the Early Cretaceous, such as *Kronosaurus queenslandicus* from Australia (Kear, 2003), and *Sachicasaurus vitae* (Páramo-Fonseca et al., 2018) from Colombia. There is a notable case of predator–prey interaction, that demonstrates that these large pliosaurids were preying on smaller, long-necked plesiosaurs with a bitten skull of the elasmosaurid, *Eromangasaurus australis* that was likely inflicted by a *K. queenslandicus* (Thulborn and Turner, 1993). In addition to other large marine reptiles, pliosaurids were also hunting fish (Foffa et al., 2014). Some pliosaurid plesiosaurs would also evolve a longirostrine skull associated with a fish-based diet, which is nearly identical to that of the distantly related polycotylids (Fischer et al., 2017).

The pliosaurids would go extinct in the early part of the Late Cretaceous (Benson et al., 2013). The elasmosaurids and leptoclidians, however, persisted well into the latest Cretaceous, with a cosmopolitan fossil record (Otero et al., 2015; O'Gorman, 2020). The derived leptoclidians, Polycotylidae, evolved into a diversity of species in the Late Cretaceous, some of which were convergent with elasmosaurids in having elongated necks (Fischer et al., 2018; Persons et al., 2022). A remarkable fossil of the polycotylid, *Polycotylus latippinus*, even preserves a fossilized fetus, providing evidence that plesiosaurs likely gave live birth like modern-day, warm-blooded animals (O'Keefe and Chiappe, 2011).

Within Elasmosauridae, there were some specialized forms, called aristonectines, which comprised the largest long-necked plesiosaurs known, reaching 13.5 tons in weight (O'Gorman et al., 2019). These aristonectines are typified by extremely short cervicals, and broad skulls filled with numerous small needle-like teeth that were procumbent, and thus were pointed outward (O'Keefe et al., 2017; O'Gorman, 2020, O'Gorman et al., 2023). Their small teeth and broad skulls have led to the hypothesis that these plesiosaurs may have been filter-feeders (O'Keefe et al., 2017). The skull architecture of elasmosaurids was otherwise conservative in morphology over the course of 30 million years (Marx et al., in press; Paper VI).

Elasmosaurid fossils can be found in abundance in Maastrichtian (latest Cretaceous) strata, indicating that these plesiosaurs were thriving immediately before the K/Pg extinction event (Gasparini, 1979; Otero et al., 2015; Strganac et al., 2015). Polycotylids, while diverse and speciose during the Late Cretaceous, appear to go extinct before the end of the Maastrichtian (Otero et al., 2015; Fischer et al., 2018).

Plesiosaurs have an extensive fossil record in marine depositional environments; however, they were clearly also inhabiting freshwater environments (Bunker et al., 2022). Examples include fluviolacustrine deposits from the Middle Jurassic of China (Gao et al., 2019), the high latitude rivers of Early Cretaceous Australia that would even freeze over in the winter months (Kear, 2006), and the Late Cretaceous fluvial paleochannel deposits in Canada (Campbell et al., 2021). Thus, plesiosaurs were clearly highly adaptive to diverse environments and climates (see Paper V).

It is peculiar that throughout the history of the Plesiosauria, an elongate neck remained a consistent feature of their body plan; it even evolved independently multiple times in various lineages (Fischer et al., 2018; Persons et al., 2022). A wide range of hypotheses have been proposed to explain the function of this long neck (Noè et al., 2017). Based on these, it appears likely that the neck conferred advantages during prey acquisition (Noè et al., 2017; Troelsen et al., 2019).

Despite their success, plesiosaurs became extinct at the end of the Cretaceous, leaving behind a rich fossil record on every continent. Understanding their rise and fall is important to deciphering the effects of both small and large-scale extinctions on ocean biodiversity and ecology. Further research and discoveries will be imperative to reconstruct ancient environments and ecosystems that were subjected to climate change, varying sea levels, the rifting of continents, and fluctuations in ocean chemistry; all of which provide pertinent information for how future alterations to the Earth system will affect the biosphere.

The case for revised life reconstructions of plesiosaurs: lessons from extant marine amniotes

The Leatherback turtle (*Dermochelys coriacea*): a reasonable modern analog for plesiosaurs?

To infer what adaptations an extinct group of reptiles might have possessed, it is imperative to start with comparisons to modern animals. Organisms that are only distantly related but share similar lifestyles and environmental constraints can evolve similar adaptations (Gabora, 2013). For plesiosaurs, *Dermochelys coriacea* (the Leatherback turtle) may be our best modern analog based on its size, physiology, and lifestyle. Like plesiosaurs, *Dermochelys* is a large-bodied marine reptile (average size: 250–450 kg), with the largest individuals reaching nearly a ton in body weight (Paladino et al., 1990). Adult *Dermochelys* also inhabit cold ocean waters in the high latitude regions of the Atlantic and Pacific for feeding, and thus experience similar environmental conditions as some plesiosaurs did (James and Herman, 2001; Witt et al., 2007; Fossette et al., 2012; Benson et al., 2020). The adaptations of these large turtles for surviving in cold ocean waters will be explored in this section to draw inferences on the evolutionary adaptations plesiosaurs might have acquired.

Larger animals can sustain a high temperature gradient between the core body and skin surface, and therefore conserve heat energy better than smaller animals (which rely on a high metabolism and insulating integumentary structures to maintain body heat (Paladino et al., 1990)). Consequently, *D. coriacea* capitalizes on this thermal inertia to retain heat generated by its metabolism (Paladino et al., 1990; Wallace and Jones, 2008; Davenport et al., 2009).

As an additional adaptation, *D. coriacea* benefits from having a thick insulating layer of blubber that covers its body, including the head and neck (Davenport et al., 2009, fig. 3). The Leatherback turtle also has blubber surrounding the esophagus as a means to protect itself from its jellyfish prey, which has the same temperature as the surrounding seawater (Davenport et al., 2009). Blubber is a specialized fibro-adipose tissue that is present in both mammals and reptiles to survive in cold environments (Strandberg et al., 2008; Davenport et al., 2009; Lindgren et al., 2018). This combination of features (insulation and thermal inertia) in the presumably ectothermic (although see Bostrom et al., 2010 who argue for endothermy in the Leatherback turtle) *D. coriacea* led Paladino et al. (1990) to classify this turtle as a ‘gigantotherm’.

Other adaptations that the Leatherback turtle employs to adjust its body temperature come in the form of behavior (Paladino et al., 1990; James et al., 2005; Bostrom and Jones, 2007; Bostrom et al., 2010; Lindgren et al., 2014). In addition to blubber, it likely capitalized on adaptive melanism to absorb heat while basking at the sea surface (James et al., 2005; Lindgren et al., 2014). Melanism refers to an increase in dark colors through the presence of the pigment eumelanin (Osinga et al., 2010), a common biochrome in animals that is used for a broad range of functions, including visual signaling, participation in the immune system, photoprotection, and thermoregulation (Burkhart and Burkhart, 2005; Lindgren et al., 2014, 2018; McNamara et al., 2021). In the case of the Leatherback turtle, the dorsal half of the body is very dark in color, which would allow for the effective absorption of solar radiation and conversion of harmful UV-light into heat, thereby warming the body (James et al., 2005; Clusella et al., 2007; Clusella et al., 2009; Lindgren et al., 2014). Indeed, adult Leatherback turtles have been observed when basking at the surface to warm their bodies (James et al., 2005). More broadly, melanism likely is a widespread phenomenon among marine reptiles, including the extinct ichthyosaurs and mosasaurs, and the extant semi-aquatic marine iguana (*Amblyrhynchus cristatus*), with thermoregulatory functions likely being one of the main drivers behind this convergence (Bartholomew, 1966; Lindgren et al., 2014, 2018).

Leatherbacks can also temporarily increase their core body temperature in cold water via vigorous swimming (Bostrom and Jones, 2007). Conversely, they show decreased swimming activity in warm waters to avoid overheating (Paladino et al., 1990; Bostrom et al., 2010). Leatherback turtles also modify the blood flow to tissues near the skin to cool themselves in tropical waters or when nesting, thereby reducing the temperature gradient between the body core and surrounding water or air (Paladino et al., 1990). These turtles also adjust the depth at which they are swimming to change their body temperature; in cold conditions, they swim near the surface where warmer water is present, while in warm environments, the Leatherback turtle can dive to deeper, cooler water depths (Bostrom and Jones, 2007; Bostrom et al., 2010). An additional adaptation for life in cold water includes an arteriovenous plexus that warms the limb musculature of this turtle (Davenport et al., 2015). The metabolic activity of food digestion and nutrient absorption can also be an important source of heat gain for leatherbacks (Secor, 2009).

It is currently contended if Leatherbacks have elevated resting metabolic rates relative to other reptiles (Paladino et al., 1990; Lutcavage et al., 1990; Wallace et al., 2005; Wallace and Jones, 2008). It is worth pointing out though, that the growth rates of *Dermochelys* are noticeably higher than those of other sea turtles (Zug and Parham, 1996; Avens et al., 2020). In fact, leatherbacks may be the fastest growing non-avian reptile in the world (Davenport et al., 2009). Their bones are also highly vascularized, which is a typical trait of animals with an elevated metabolism (Rhodin, 1985; Zug and Parham, 1996; Fleischle et al., 2018).

Various studies have interpreted plesiosaurs as endotherms based on histology, and geochemical studies of their fossils (Bernard et al., 2010; Wintrich et al., 2017; Fleischle et al., 2018; Wiemman et al., 2022). Note, however, that Séon et al. (2025) recently interpreted plesiosaurs as poikilothermic endotherms (capable of temporarily raising their metabolism to that of a warm-blooded animal) rather than true endotherms based on a new data set of stable oxygen isotopes from plesiosaur tooth and bone bioapatite. Conversely, Fleischle et al. (2018) reported metabolic rates of plesiosaurs as being as high as in modern-day birds, which have the highest metabolic rates of any living group of animals. To reach this conclusion, Fleischle et al. (2018) quantified bone growth and metabolic rates in a phylogenetic context, using phylogenetic eigenvector maps (PEM) with primary osteon density in sauropterygians and extant taxa as the predictor variable. The PEM for both metabolic rate and bone apposition in sauropterygians were comparable to those of extant birds and mammals. Additionally, the resting metabolic and bone apposition rates in Sauropterygia generally increased through time toward more derived taxa. These results imply that the origins of high metabolism and fast growth rates can be found in the early history of Sauropterygia or perhaps even earlier.

Based on comparisons with the extant Leatherback turtle, I infer that plesiosaurs likely had an insulating layer of blubber that encapsulated the head, neck, and body. A peripheral blubber layer, especially around the neck, would provide a hydrodynamic and fusiform shape reminiscent of other marine amniotes (Fig. 3). Plesiosaurs might have benefited from blubber surrounding the esophagus as well, since the diet of many forms comprised primarily fish and invertebrates (Massare et al., 1987; Cicimurri and Everhart, 2001; Groβmann, 2006; Foffa et al., 2024), which presumably had nearly the same temperature as the surrounding water (Stevens and Sutterlin, 1976; Yalçinkaya et al., 2019).

A thicker neck is hydrodynamically more advantageous than a narrower one (Troelsen et al., 2019). A blubber-lined neck would also provide enhanced protection against predation, which would otherwise expose critical arteries to attacks from sharks, mosasaurs, and pliosaurids. Interestingly, bite marks are relatively rare in plesiosaur neck vertebrae, but exceedingly common in the limbs (Araújo et al., 2015a; Troelsen et al., 2019). From other functional points of view, blubber acts as energy storage, holds elastic properties, and resists compression (Strandberg et al., 2008; Lindgren et al., 2018; Grear et al., 2018). I also find it likely that plesiosaurs were counter-shaded, with a dark back, like the Leatherback turtle, which would have provided means for both crypsis and thermoregulation (Lindgren et al., 2018).

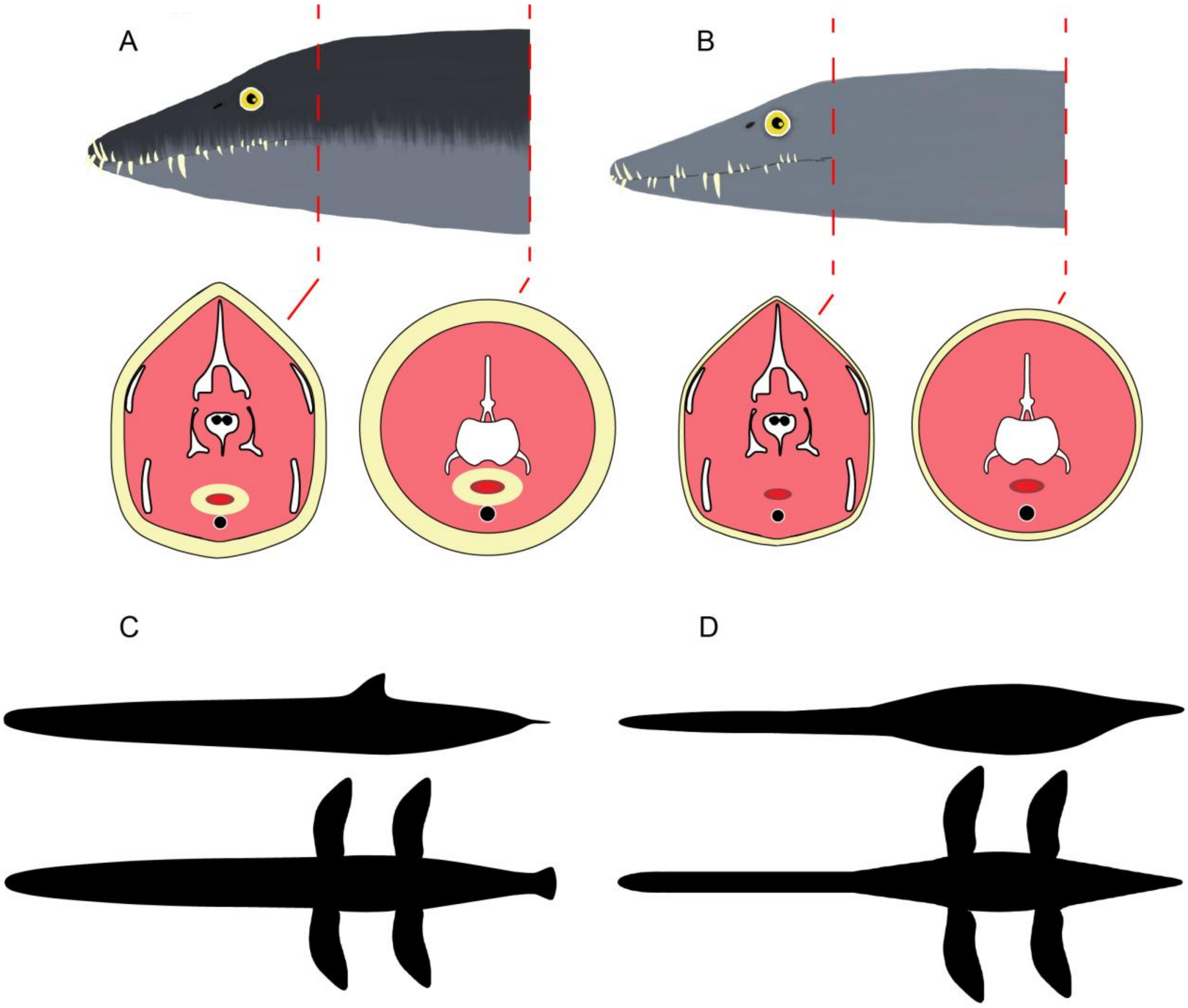

Figure 3. **A.** Plesiosaur with a thick layer of blubber (yellow-colored tissue in the cross-sections) for insulation encapsulating the skull and neck like *Dermochelys coriacea*. **B.** Traditional plesiosaur reconstruction with almost no blubber. **C.** Body contour of a plesiosaur in lateral and dorsal view with blubber surrounding the body, a dorsal fin for stabilization, and a tail fin. **D.** Body contour of a 'traditional' plesiosaur reconstruction in lateral and dorsal views. Skull cross-section illustrations inspired by Carpenter (1997); figure 5.

A dorsal fin?

While an adult *Dermochelys* may be our best modern analog for a plesiosaur generally (given that both are reptiles), we must still recognize that their anatomy, and indeed sea turtle anatomy in general, is notably different from that of plesiosaurs. These differences pertain not only to volume, length/size ratios, and neck length, but perhaps most notably to the carapace and plastron that encapsulates the body of leatherbacks. Plesiosaurs are free from a shell-like structure and thus comparisons also to other marine amniotes are warranted. In both extant and extinct marine amniotes, a dorsal fin is a near-ubiquitous adaptation to control for roll when swimming (Lingham-Soliar, 2005; Renesto et al. 2020), although it should be noted that some species lack this feature, including the Beluga whale (*Delphinapterus leucas*), Northern right whale dolphin (*Lissodelphis borealis*), and Indo-Pacific finless porpoise (*Neophocaena phocaenoides*). Currently, there is no preserved residue or tissue from a dorsal fin in any plesiosaur fossil. However, there may be osteological correlates that we can examine to infer the presence of such a fleshy structure.

In mosasaurs, the presence of a fleshy dorsal tail fin lobe was first hypothesized based on, e.g., the caudal neural spines shifting from recumbent to procumbent and then back to recumbent again (Lindgren et al., 2007). This arrangement is shared by ichthyosaurs with soft-tissue remains in the tail that associate a relationship between the inflection of the neural spines with the presence of a dorsal soft-tissue caudal lobe (Nicholls and Manabe, 1999; Lindgren et al., 2007, 2011). As another example, structural support for the caudal fluke can be more notably exemplified by the directional change of the haemal arches of sharks, which go from being recumbent to more vertically oriented in the area for the lower lobe of the tail fluke (Lindgren et al., 2007, fig. 5B). The functional interpretation for the change in the angle of the neural spines is to evenly distribute the neural spines in the area with the greatest curvature, thus providing stable support that works against the water pressure when the tail oscillates from side to side (Lindgren et al., 2007, 2011). The presence of a dorsal caudal fin lobe in mosasaurs was later confirmed by a preserved soft-tissue outline of a hypocercal tail in an exceptional specimen from Jordan (Lindgren et al. 2013).

The dorsal vertebrae of some complete plesiosaur skeletons from the Posidonia Shale exhibit a similar arrangement where the neural spines change from being oriented in a recumbent manner to procumbent in the torso (Fig. 4). This, in turn, may be indirect evidence for a dorsal fin. In a recent study, Konishi et al. (2023) inferred the presence of a dorsal fin in the mosasaur *Megapterygius wakayamaensis* based on a change in the orientation of the dorsal neural spines, similar to many cetaceans with a dorsal fin. Morphometric data collected for this project have been used to identify possible osteological correlates for a soft-tissue dorsal fin also in plesiosaurs (Paper IV).

In modern-day cetaceans, the neural spines show a clear inflection directly toward the area of the dorsal fin (Fig. 5). However, the fan-shaped orientation of the neural spines in dolphins has been attributed to increased stiffness in the anterior trunk region and regionalization of the body into segments that confer enhanced or limited flexibility (Buchholtz and Schur, 2004). As of yet, there is no extensive study that identifies an osteological correlate for a dorsal fin in marine reptiles. Gatesy et al. (2013) assert that in extinct cetaceans there are no known osteological correlates for a dorsal fin.

All of this shows a clear gap in our knowledge; the work of Konishi et al. (2023) is the only study that has ever attempted to establish some relationship between the osteology and presence of a soft-tissue dorsal fin in a marine reptile. Konishi et al. (2023) however do not conduct a systematic study linking the shift in the dorsal neural spines as a correlate for a dorsal fin. A far more extensive study incorporating a larger sample of cetaceans, at the very minimum, would be needed to more confidently assign a relationship between the presence of a dorsal fin and osteology, and this is where Paper V is relevant.

The caudal fin

The tail is an often-overlooked component of the locomotory apparatus in plesiosaurs (Sennikov, 2019). This is likely due to the predominant hypothesis of limb-propelled locomotion in this group of secondarily aquatic reptiles using two pairs of hydrofoil-like flippers to produce lift in the forward direction through stroke movements, much in the same way as sea turtles and penguins do today (Robinson, 1975; Carpenter et al., 2010; Liu et al., 2015; Muscutt et al., 2017). However, recent studies of the tail morphology in plesiosaurs suggest that the tail was likely used as a rudder and therefore an integral part of swimming (Smith, 2013; Sennikov et al., 2019). What follows is a brief review of plesiosaur tail fin structures, functional morphology of the caudal vertebrae, and comparisons with modern analogs.

There is one exceptionally well-preserved plesiosaur, the holotype of *Seeleyosaurus guilelmiimperatoris* (MB.R.1992; Museum für Naturkunde Berlin, Berlin, Germany) from the Jurassic Posidonia Shale of Germany that includes soft-tissue residues in the posterior end of the tail, and which appears to take on the shape of a partial caudal fin (Fig. 6; see also Dames, 1895). The exact orientation of this fin (sagittal or horizontal) remains up for debate (Sennikov, 2019). Whereas the primitive condition of reptile locomotion involves lateral movements of the axial skeleton, the axial skeleton in mammals bends along the sagittal plane (Jones et al., 2021). As a consequence, reptilian tail fins (in mosasaurs, ichthyosaurs, and metriorhynchid

Figure 4. Photograph of the holotype (MB.R.1992) of *Seeleyosaurus guilelmiimperatoris* from the Toarcian Posidonia Shale of Holzmaden, Germany, with arrows indicating the direction of the neural spines in the dorsal region. In the center of the trunk, there is a noticeable change in the inclination of the neural spines. This arrangement is similar to the inflection point of the neural spines in dolphins underneath the dorsal fin, and kink in the tails in mosasaurs and ichthyosaurs (Nicholls and Manabe, 1999; Lindgren et al., 2007; Lindgren et al., 2013) where a dorsal fleshy lobe is located. This inflection in *S. guilelmiimperatoris* thus represents indirect evidence for the presence of a dorsal fin. Photograph by Benjamin Kear. Scale bar is 50 cm.

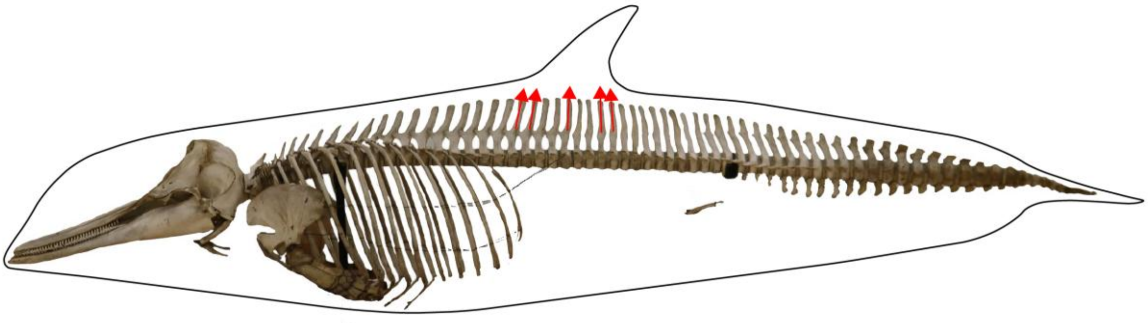

Figure 5. Lateral view of the skeleton of a Common short-beaked dolphin skeleton (*Delphinus delphis*). Red arrows in the torso region indicate the shift in the direction of the neural spines towards the dorsal fin.

crocodyliforms) tend to be vertically oriented and those of mammals horizontal (Lindgren et al., 2013). Thus, the most parsimonious prediction for fin orientation in plesiosaurs would also be vertical. However, the morphology of the vertebrae is integral to the degree of intervertebral flexibility (in addition to tissues, like cartilage and ligaments: Cobley et al., 2013). The distal-most caudal centra of ichthyosaurs and mosasaurs are mediolaterally compressed (Buchholtz, 2001; Lindgren et al., 2007) to enhance lateral undulations. Conversely, in dolphins, the distal caudal centra are dorsoventrally compressed to allow dorsoventral movements of the horizontal tail fluke (Buchholtz, 2001, fig. 4).

Length, width, and height dimensions measured from the centra of *S. guilelmiimperatoris* indicate that the distal caudal vertebrae would likely have been preferentially displaced in the vertical plane (Fig. 7). While the length and height of the caudal centra are sub-equal in *S. guilelmiimperatoris*, width is clearly the greatest dimension at the distal end of the caudal series. The greater width

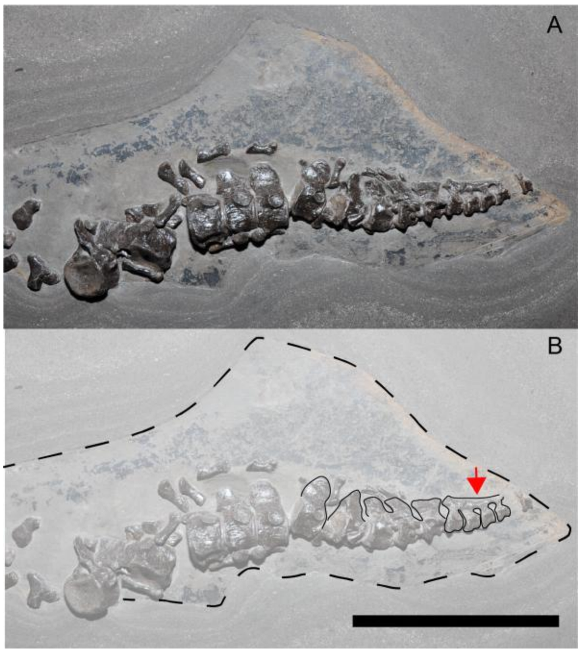

Figure 6. **A.** Photograph of the distal end of the tail in *Seeleyosaurus guillelmiimperatoris* (MB.R.1992). **B.** Distal end of tail with dashed outline indicating the extension of the soft-tissue residue; however, this extent is artificial, as the specimen has been cut out of its original rock slab and then inserted into a new one. The red arrow indicates the pygostyle-like unit of bone. Photograph by Benjamin Kear. Scale bar is 10 cm.

relative to the length and height is morphologically like that of cetaceans that use the tail for displacement dorsoventrally. This inference in combination with the partial soft-tissue caudal 'fin' structure preserved in MB.R.1992 (Marx et al., 2025b; Sachs et al., 2025) suggests that the orientation of the tail fin in *S. guilelmiimperatoris* would have preferentially been horizontal. The wide distal tail vertebrae are distinct from the laterally compressed fluke vertebrae of ichthyosaurs, like *Opthalmosaurus icenicus* (Buchholtz, 2001), and mosasaurs (e.g., *Plotosaurus bennisoni*; Lindgren et al., 2007).

Interpretations regarding the orientation of the plesiosaur caudal fin varies. In the case of *Rhomeleosaurus zetlandicus* (YORYM G503), in the anterior and middle caudal vertebrae, nearly all the centra are wider than high until the distal-most caudal vertebrae which are compressed and therefore (H > W); the 'node' vertebrae at the transition between the middle and distal caudal vertebrae are shortened and may have given the distal end of the tail in *R. zetlandicus* a slight downward turn (Smith, 2013). Similar wedge-shaped vertebrae that may have inflected the tail ventrally occurs also in *Macroplata tenuiceps* (Ketchum and Smith, 2010). Wilhelm (2010) interpreted the tails of cryptoclidid plesiosaurs as supporting a vertical tail fin based on the anterior inclination of the neural spines in the posterior caudal vertebrae, along with an enlarged neural spine in a *Cryptoclidus* (R8575) that Wilhelm (2010) interpreted as supporting a vertical tail fin. Conversely, the caudal vertebrae of aristonectine elasmosaurids have been interpreted as support for horizontal tail fins, based on several characteristics of the caudal vertebrae (Otero et al., 2018). These traits include: dorsoventrally compressed caudal centra (W > H > L), in combination with short neural spines with a broad attachment area for ligaments, broad and dorsoventrally compressed caudal ribs with distal facets for the attachment of cartilage, and unfused chevrons with spacing that likely allowed for improved displacement in the vertical plane (Otero et al., 2018).

Seeleyosaurus shows another anatomical feature worth noting at the distal end of the tail: a pygostyle-like unit of bone (Fig. 6). Pygostyles are a series of fused caudal vertebrae at the end of the tail, characteristic of Aves (birds) but also present in some non-avian theropod dinosaurs (Barsbold et al., 2000; Xing et al., 2016; Rashid et al., 2018). Some pterosaurs may also have possessed a pygostyle (Bennet et al., 1987).

The pygostyle is unique in that no other Mesozoic marine reptile (aside from Aves) has this feature. The pygostyle-like unit preserved in *S. guilelmiimperatoris* is shared with penguins, animals that use the tail as a rudder rather than as a means for propulsion (Hui, 1985; Felice and O'Conner, 2014). In addition to *S. guilelmiimperatoris*, a pygostyle-like segment has also been observed in the tails of other plesiosaurs: *Albertonectes vanderveldei*, *Rhomaleosaurus zetlandicus*, *Brancasaurus brancai*, *Cryptoclidus oxoniensis*, and *Umoonasauus demoscyllus* (Wegner, 1914; Kear et al., 2006; Wilhelm, 2010; Smith, 2013; Kubo et al., 2012; Sachs et al., 2016).

The lack of a pygostyle-like structure reported in other plesiosaurs may be due to incomplete skeletons, or the ontogenetic stage of the individual. In modern birds, the pygostyle is not fully developed until late in life (Rashid et al., 2018). Similarly, the formation of a pygostyle-like unit may be a late-stage ontogenetic character in plesiosaurs (Sachs et al., 2025).

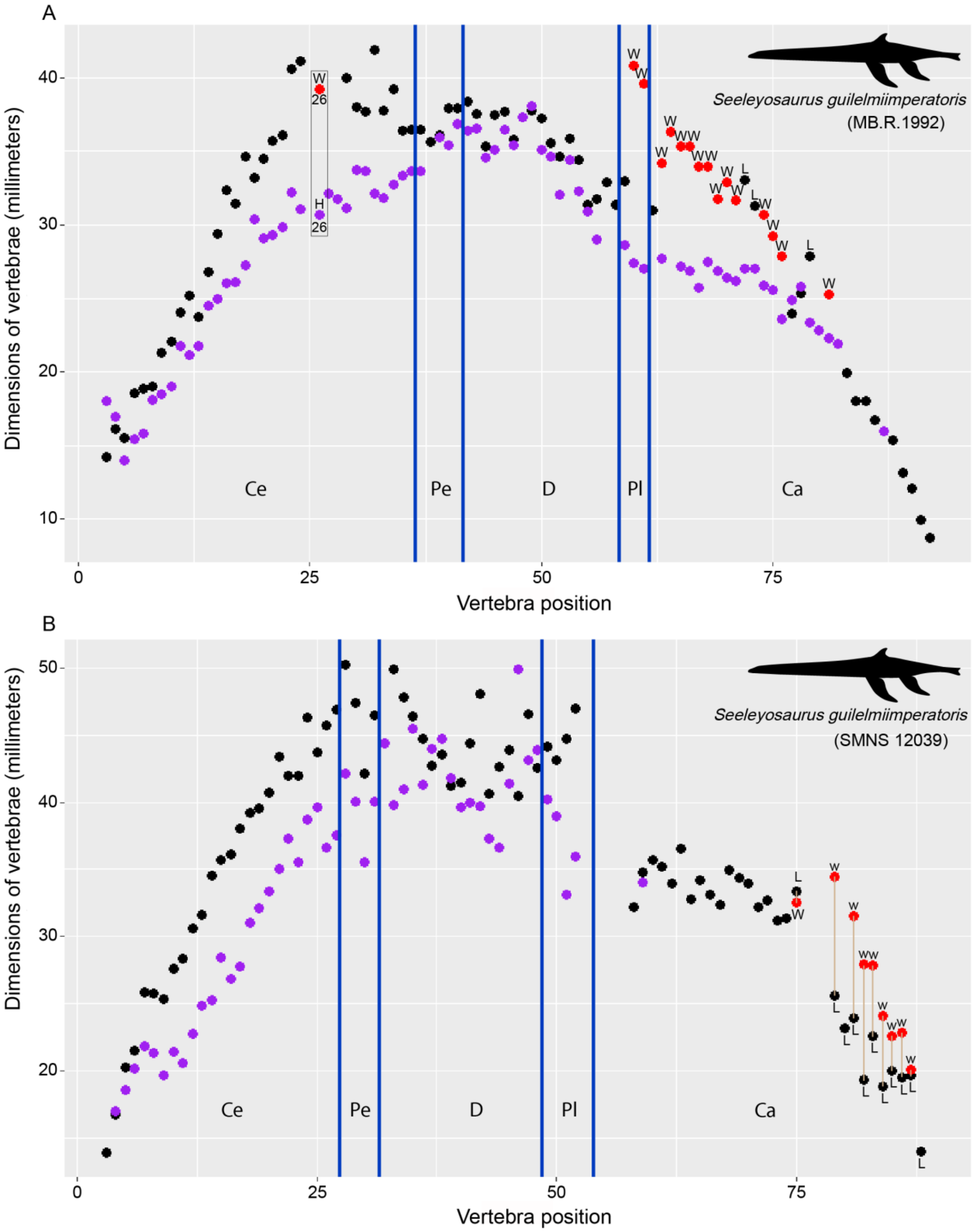

Figure 7. Scatterplots of centra dimensions from *Seeleyosaurus guilelmiimperatoris*: **A**. MB.R.1992, and **B**. SMNS 12039. Length (L) dimension = black, width (W) dimension = red, and height (H) dimension = purple. Abbreviations for regions of the axial skeleton: Ca, caudal (tail); Ce, cervical (neck); D, dorsal (middle torso region); Pe, pectoral (anterior torso region); Pl, pelvic (posterior torso region).

In birds, the pygostyle serves as a scaffold to anchor tail muscles, tail feathers, and the fanning mechanism (Felice and O'Connor, 2014). The shape of the pygostyle in marine birds is attributable to foraging style, with penguins, cormorants, puffins, gannets, and tropicbirds exhibiting convergent evolution toward a straight and elongated pygostyle (Felice and O'Connor, 2014). Felice and O'Connor (2014) found that even among underwater foraging birds, different foraging styles (foot, wing, or plumage propelled diving) could be identified based on pygostyle morphology alone. Thus, the pygostyle is an integral part to marine bird foraging and behavior. For example, the Humboldt penguin (*Spheniscus humboldti*) uses the tail for steering by raising it just before a turn; at the same time the tail is being raised, the beak of the Humboldt penguin also changes direction and aids in the steering motion of the body. The tail, in conjunction with the feet, modulate pitch and yaw in penguins (Clark and Bemis, 1979).

Remarkably, the elongate and cone-shaped ‘pygosytle’-like unit in plesiosaurs (Sachs et al., 2016, 2025) appears to be convergent with the pygostyle in sea birds, which is similarly elongate and narrow (Felice and O’Connor, 2014). However, the plesiosaur tail is long (approximately the same length as the trunk) compared to that of penguins. The long plesiosaur tail could certainly act as an effective rudder, as it is far from the center of mass (Robinson, 1975). A hypothesis for the function of the pygostyle-like unit in plesiosaur tails is its function as a ligament attachment site that allowed for the effective displacement of the tail fin to aid in maneuvering, with the conical shape of the fused caudal vertebrae conferring a mechanical advantage in an aqueous setting as could be the case in aquatic foraging birds (Felice and O’Connor, 2014).

There are no marine mammals with a pygostyle; instead, they (i.e., Sirenia, Cetacea) use the tail as the propulsive organ rather than as a rudder (Fish, 1993). In the Bottlenose dolphin (*Tursiops truncates*), for example, lift-based propulsion is achieved by the tail fin (shaped as a hydrofoil), which is composed internally of several disc-shaped vertebrae that are encompassed by a thick layer of connective tissue (Fish, 1996; Sun et al., 2010). Within the caudal fluke of dolphins, there are collagen fibers that radiate from the body axis (Sun et al., 2010). Similar fiber-like structures have been documented also in *Seeleyosaurus* (MB.R.1992) (Fig. 8A, B).

Among marine mammals, it appears that osteological correlates for a caudal fluke differ between taxa. For example, both the modern Dugong and the White-beaked dolphin exhibit a bilobed caudal fluke, but the morphology of their caudal vertebrae is distinctly different. Whereas the dolphin has disc-shaped caudal vertebrae (Figure. 8E), the Dugong exhibits sequentially widening transverse processes of the caudal vertebrae (Figure 8C). The Manatee has caudal vertebrae at the end of the tail that are more reminiscent of that of the dolphin, rather than the more closely related Dugong (Fig. 8D). Different strategies to support the same soft-tissue structure may have also occurred in plesiosaurs.

Material and Methods

Material

To accomplish the goals of this Ph.D. thesis, plesiosaur skeletons in museum collections from Germany were studied first-hand. These specimens were photographed, with measurement data collected from the skeletons. The newly prepared plesiosaur (MH 7) at Urwelt-Museum Hauff in Holzmaden (Germany) was of particular interest, since this specimen has associated soft-tissue remains that offered rare insights into the integument of plesiosaurs. Fossilized tissues were collected from this specimen and were subjected to biomolecular studies. The osteology of MH 7 was also described, and phylogenetic analyses were run after scoring of morphological character states.

The skeletons of modern marine amniotes were also studied for comparison. Visits to the zoology collection at the Lund University Biological Museum allowed for study of several cetaceans, including: the Harbour porpoise (*Phocoena phocoena*), Killer whale (*Orcinus orca*), and Northern bottlenose whale (*Hyperoodon ampullatus*). Additional cetaceans were examined at the world’s largest storage for whale skeletons: The Smithsonian Museum Support Center in Maryland (USA).

For the CFD chapter, a nearly complete skeleton of the extremely long-necked elasmosaurid, *Albertonectes vanderveldei*, was selected for modeling. The holotype (TMP 2007.011.0001) as figured by Kubo et al. (2012, figures 2 & 3) shows the entire skeleton fully prepared in both left and right lateral views, making this plesiosaur particularly convenient for reconstructions. Additionally, the holotype of *A. vanderveldei* was recovered from southern Alberta, which was part

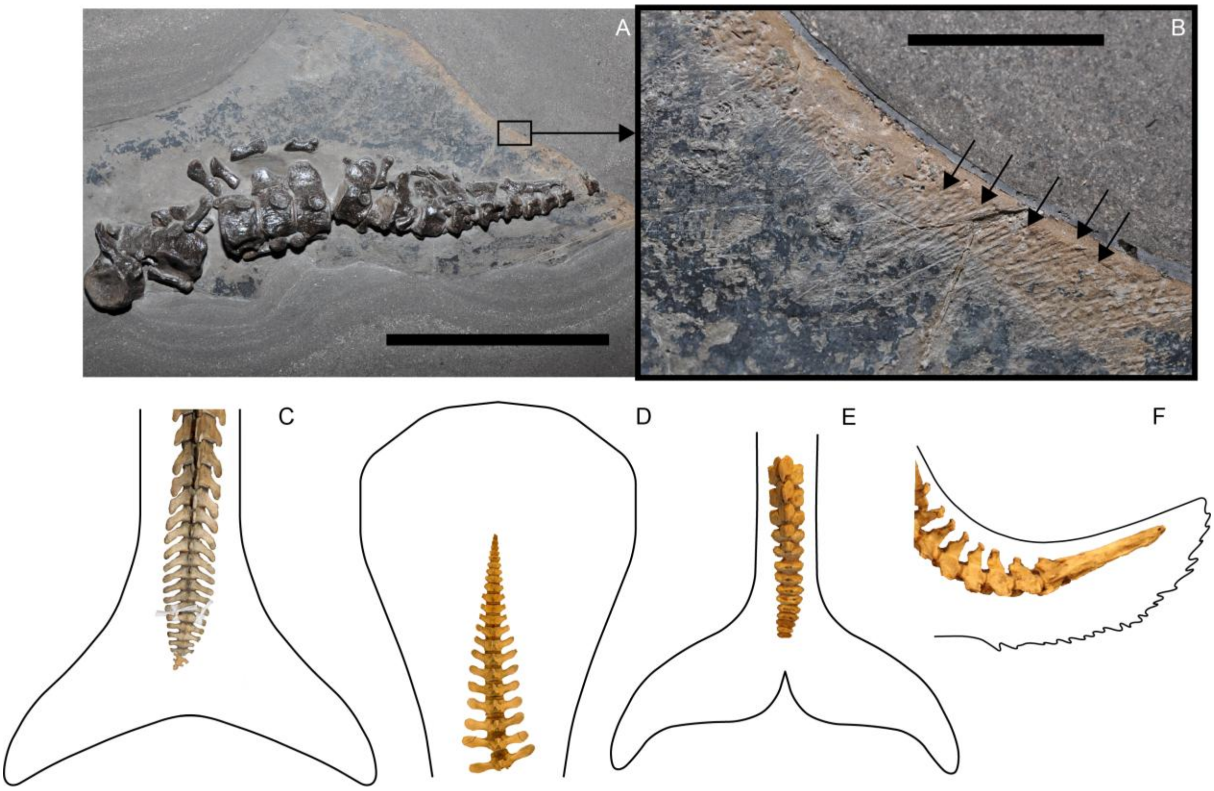

Figure 8. Comparative caudal osteology between *Seeleyosaurus guilelmiimperatoris*, modern marine mammals, and a marine bird. **A.** Distal end of the tail in *S. guilelmiimperatoris* (same specimen as shown in Fig. 4). Scale bar is 10 cm. **B.** Zoomed-in photograph of the margin of the soft-tissue residue with apparent fiberous structures extending to the margin of the residue outline, indicated by black arrows. Scale bar is 1 cm. **C.** Caudal vertebrae of the dugong (*Dugong dugon*) with the outline of the fluke. **D.** Caudal vertebrae of the manatee (*Trichechus*) with the outline of the fluke. **E.** Caudal vertebrae of the White-beaked dolphin (*Lagenorhynchops albirostris*) with the outline of the fluke. **F.** Caudal vertebrae of the Humboldt penguin (*Spheniscus demersus*) with the outline of tail feathers. Photographs of *S. guilelmiimperatoris* by Benjamin Kear.

of the northern portion of the Western Interior Seaway during the Cretaceous, and likely harbored cold water (Petersen et al., 2016). Thus, this taxon, along with its known paleogeographic location and associated paleotemperature estimates made it an ideal subject for the CFD study.

Material examined in the book chapter on Angolan plesiosaurs (Paper VI) was collected over the course of several field seasons by Projecto PaleoAngola going back to 2006. The new specimens described in Paper VI include a femur from the first reported polycotylid in sub-Saharan Africa and two basioccipitals from aristonectine elasmosaurids.

Scanning electron microscopy (SEM), electron backscatter diffraction (EBSD) and energy dispersive X-ray spectroscopy (EDX) (Paper I)

Scanning electron microscopy (SEM) was used to visualize the microstructures and details of tissue samples from MH 7. SEM involves a beam of electrons that when in contact with the surface of the sample produces secondary electrons (Egerton, 2016). These secondary electrons enter a detector and produce images of the sample (Ul-Hamid, 2018). Visible light has a wavelength of 380–760 nm, while the wavelength of an electron beam (0.000004 μm) is much shorter and allows for significantly better resolution (< 1 nm) than conventional light microscopes (Ul-Hamid, 2018).

An SEM works in the following way. Firstly, a beam of electrons is emitted from the source (such as a tungsten filament) and then travels through condenser lenses to narrow the incident beam (also known as the electron probe) toward the specimen using a positive electrical potential (Egerton, 2016; Ul-Hamid, 2018). The electron probe then scans the surface of the sample horizontally (in the x-direction) before shifting perpendicularly (in the y-direction) to start scanning a new line (Egerton, 2016). The electrons from the incoming electron probe bombard the sample surface and free electrons from the sample itself. These freed electrons (secondary electrons) are emitted (Egerton, 2016). The secondary electrons are picked up by a detector that allows for imaging of the topography of the sample by the computer (Egerton, 2016).

Another technique called energy dispersive X-ray spectroscopy (EDX) is used to characterize the elements in a sample. It utilizes the electron beam from an SEM to detect the X-rays emitted from the sample (Mutalib et al., 2017). The electrons from the beam interact with the atoms of elements by removing electrons from the electron surrounding the nucleus. The removal of an electron is followed by its immediate replacement by an electron in an outer electron shell. This action produces an X-ray with a specific energy, allowing for elemental characterization of the sample (Mutalib et al., 2017).

The SEM is equipped with a detector for EBSD and EDX analysis. For EBSD, the sample needs to be polished and tilted at 70º to allow for the beam of electrons to contact the sample at 30º (Griesshaber et al., 2010). The electrons are diffracted from the mineral crystal lattices on the sample. These electrons are collected by a detector to create a picture identifying the crystallographic phase and crystalline orientation of the material (Griesshaber et al., 2010).

Infrared (IR) spectroscopy and time-of-flight secondary ion mass spectrometry (ToF-SIMS) (Paper I)

In addition to electron microscopy, I also used time-of-flight secondary ion mass spectrometry (ToF-SIMS) for molecular analysis of the plesiosaur soft tissues. ToF-SIMS analysis uses primary ions to dislodge secondary ions from a material surface (Thiel and Sjövall, 2015). The primary ion energy is transferred to target atoms via collisions, generating a so-called collision cascade that gives rise to the emission of a variety of atomic and molecular species from the sample surface (Vickerman, 2001). Some of the emitted particles are ionized to form positive or negative ions. These (secondary) ions are accelerated into a time-of-flight detector, where they are analyzed with respect to mass (by monitoring the amount of time it takes for the ions to reach the detector from the moment they are released from the sample) to produce a mass spectrum of the outermost ca 1 nm of the sample surface. Furthermore, spatially resolved mass spectra are acquired by scanning the primary ion beam over the sample surface, allowing for the generation of ion images, showing the spatial distribution of specific secondary ions (representing specific molecular species) over the sample surface, or mass spectra, reflecting the molecular composition, from specific regions of interest (ROIs) (Thiel and Sjövall, 2015). In fossilized tissues, biomolecules can potentially be identified and associated to specific structural features on the fossil surface with this technique (Lindgren et al. 2018).

Another method I employed for paper I is infrared (IR) microspectroscopy for characterization of functional groups in plesiosaur soft tissue remains. IR spectroscopy is a type of vibrational spectroscopy that analyzes the absorption of IR radiation related to the excitation of vibrational modes in the sample molecules (Larkin, 2011). The excitation energies of these vibrational modes are specific for different types of functional groups and the IR absorption spectrum can therefore provide information about the presence of specific functional groups in the sample (Kano et al., 2007). In IR microspectroscopy, IR spectra are acquired separately from an array of points on the sample surface, allowing for imaging of specific vibrational bands (representing specific functional groups) or the extraction of IR spectra from selected ROIs on the sample surface.

Description and phylogeny (Papers II, III, & VI)

A major portion of this PhD thesis relies on osteological descriptions and comparisons with both modern and extinct animals. These appraoches are necessary to understand the taxonomy, evolutionary history, and functional anatomy of ancient taxa. An osteological description of MH 7 was undertaken to accomplish two goals: firstly, to understand whether it is a new species, and secondly, to score morphological characters for a phylogenetic analysis (Paper II).

The skeletons of other Early Jurassic plesiosaurs from Holzmaden were examined and/or described; these include the holotype of *Plesiopterys wildi* (SMNS 16812; Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany), and *Seeleyosaurus guilelmiimperatoris* (holotype MB.R.1992 and the referred specimen, SMNS 12039) (Papers II and III). Comparisons of these specimens to other Early Jurassic plesiosaurs were imperative to constructing updated phylogenies and hypotheses on plesiosaur evolution.

Phylogenetic analyses were conducted using the software, TNT (Goloboff and Morales, 2023). As a basic primer, morphological character states in the skeletons of ancient animals are assessed and scored based on their morphology. These scores are then used to build cladograms (trees); the most parsimonious solution (the tree(s) with the lowest number of character changes) is considered to be the best solution.

Morphometrics (Paper IV)

Measurements of the neural spines and their inclination were measured from plesiosaurs and cetaceans to identify potential osteological correlates for a dorsal fin. The angle of inclination for the neural spines was measured from photographs of the specimens. We use the definition provided by Buchholtz et al. (2005) to define neural spine inclination. We consider anterior inclinations as >90º and posterior inclinations are <90º. Scatterplots were made with Microsoft Excel to plot neural spine orientation along the axial skeleton of examined specimens. In some plots, a trendline was added to more easily visualize the relationship between neural spine orientation and position along the skeleton.

Computational Fluid Dynamics (CFD) (Paper V)

Another critical component of this PhD project pertained to numerical simulations of the hydrodynamic and thermodynamic capabilities of plesiosaurs using computational fluid dynamics (CFD). As a general definition, computational fluid dynamics is the analysis of systems involving fluid flow, heat transfer, and/or other phenomena such as chemical reactions by numerical approximations (Versteeg and Malalasekera, 2007). To begin the setup of a CFD case, the user needs to determine the assumptions related to the physical phenomena of interest (fluid properties, compressible versus incompressible flow, Newtonian versus non-Newtonian fluids, heat transfer type, etc.). Depending on the physics, a set of governing equations are derived which may include partial differential equations (PDEs) governing the conservation of certain physical quantities (e.g., mass, momentum, and energy) and algebraic equations (e.g., describing the temperature dependence of certain fluid properties). The governing equations are solved using numerical methods which involve the conversion of the PDEs into algebraic equations by discretization. For this purpose, the computational domain is divided into discrete cells called control volumes where the conservation equations are directly integrated. Collectively, the sum of all the cells is the computational mesh. There are different approaches to discretization, but for my purposes, we use the finite volume method which, contrary to the finite difference method, can be used on unstructured meshes. We wanted to use unstructured meshes because they can better describe complex geometries and allow more flexible mesh refinements than structured meshes. Once the initial conditions and boundary conditions (such as inlet velocity of the flow, outlet pressure, and slip versus no-slip walls) are set, the governing equations can be solved by appropriate solution methods. Due to the large number of computational cells (often reaching several million), direct solution of the resulting system of algebraic equations is not practical, and thus iterative solution methods are preferred. The iterations are repeated until the residuals have decreased below a user-defined threshold. At the end of our solver step, we are left with the results of the simulation for analysis. Both the discretization and solution is achieved using OpenFOAM (OpenFOAM Foundation Ltd), for post-processing of the results paraview (Ahrens et al., 2005) is used.

Summary of papers

Paper I: Skin, scales, and cells in a Jurassic plesiosaur

In this publication, the fossilized soft-tissue remains associated with a plesiosaur skeleton (MH 7) from the Lower Jurassic Posidonia Shale of Germany are described in detail using a breadth of analytical techniques. Specimen MH 7 was originally excavated in 1940 by quarry workers, and Dr. Bernard Hauff senior, who also established Urwelt-Museum Hauff in Holzmaden. This plesiosaur skeleton was encased in slabs of shale, some of which were hidden in the Hauff family garden during WWII. MH 7 was planned for exhibition, but another Posidonia Shale plesiosaur (MH 8) was eventually selected. It was not until the COVID-19 pandemic in 2020 that preparation began on MH 7 after Dr. Johan Lindgren had queried Rolf Hauff about potential soft tissues in the museum collection. Preparation revealed fossilized tissue in the tail and flipper regions, a rare occurrence that necessitated investigation.

Samples of the fossilized tissues were retrieved and brought to the fossil laboratory at Lund University (LU). There, they were photographed and demineralized for study at the SOLEIL synchrotron facility near Paris using IR microspectroscopy, the Microscopy Platform at the Biology Department of LU, and RISE (Research Institutes of Sweden, in Borås, Sweden) for chemical characterization and identification of endogenous biomolecules. Demineralized tissue was further studied using polarized light microscopy. Ground sections of the fossilized tissue were also made and compared against histological sections from modern reptiles and subjected to electron backscatter diffraction (EBSD) and electron-dispersive X-ray spectroscopy (EDX). SEM imaging of the tissues before and after demineralization was also carried out, and the results were compared against tissues of both modern and extinct reptiles.

This study identified the tissue in the tail region as being scaleless skin, like that of ichthyosaurs, while the flipper retained the remains of integumentary scales along the trailing edge, thus demonstrating that some plesiosaurs had both smooth and scaled skin in different regions of the body. The scales on the trailing edge of the flipper may also have been keeled, as the scales are eroded along the midline in a straight line that compares favorably with the condition in the fossilized keeled scales of the mosasaur *Plotosaurus bennisoni*. The remarkable preservation further allowed for traces of keratinocytes and corneocytes (with dark residue at their centers presumably denoting the nucleus) to endure fossilization. The smooth skin on the body likely reduced drag while the plesiosaur swam through the water, and the scales enforced a rigid hydrofoil structure and/or provided traction and protection against the bottom substrate when foraging in the mud and sand.

Paper II: A new specimen of *Plesiopterys wildi* reveals the diversification of cryptoclidian precursors and possible endemism within European Early Jurassic plesiosaur assemblages

This publication entails an osteological description of MH 7 (see also Paper I), a taxonomic identification, and phylogenetic analysis of this specimen. The skeleton of MH 7 is articulated aside from the skull, which is scattered throughout the shale matrix at the front end of the animal. This roughly 3-meter-long plesiosaur was a sub-adult individual, made evident by its mixture of juvenile and adult characters: fused neural arches, but unfused cervical and caudal ribs, faceted propodials, and well-developed cornua of the coracoids.

The skull of MH 7 is most similar to that of the holotype of *Plesiopterys wildi* (SMNS 16812). The morphology of the pterygoid is especially informative and shares characters with that of SMNS 16812. This, along with shared characters in the appendicular skeleton and caudal vertebrae allowed for a confident assignment of MH 7 to *P. wildi*.

Plesiopterys wildi was originally established based on a juvenile specimen, which subsequently led to an alternative hypothesis that SMNS 16812 represents a juvenile specimen of another species of plesiosaur from the Posidonia Shale (‘*Hydrorion*’ *brachypterygius*; see Groβmann, 2007). The results of my study (Paper II), however, demonstrate that *P. wildi* is a valid and distinct taxon. Phylogenetic analysis incorporating the new specimen (MH 7) returns *P. wildi* in an intermediate position between more basal forms and derived plesiosaurs that would later dominate the Late Jurassic. Thus, MH 7 was critical in discerning the bridge between ‘primitive’ and more ‘advanced’ plesiosaurs.

The validity of *P. wildi* as a distinct taxon retains a high species diversity for plesiosaurs in the Southwestern German Basin (five distinct species) and its distinct assemblage of plesiosaurs from that of the coeval English Yorkshire Basin during the Toarcian. This disparity supports the hypothesis of plesiosaur endemism during the Early Jurassic, as previously proposed by Groβmann (2007).

Paper III: The osteology, taxonomy, and phylogenetic placement of *Seeleyosaurus guilelmiimperatoris* (Plesiosauria, Microcleididae) from the Lower Jurassic Posidonia Shale of Germany

This paper is a continuation of the description and phylogeny theme centered on Posidonia Shale plesiosaurs. *Seeleyosaurus guilelmiimperatoris* is one of the earliest named plesiosaurs (Dames, 1895), the holotype of which is famous for its preserved soft tissues in the flipper and especially the tail. The focus of this paper was a redescription of the holotype of *S. guilelmiimperatoris* (MB.R.1992) and a second referred specimen (SMNS 12039) with comparisons to other plesiosaurs. We also conducted phylogenetic analyses of Plesiosauria incorporating new and updated character scores for *S. guilelmiimperatoris*.

An osteological description of MB.R.1992 and SMNS 12039 elucidated new diagnostic characters in *S. guilelmiimperatoris*, including one autapomorphy based on the distinct morphology of the posterior cervical, pectoral, and dorsal neural spines. Phylogenetic analyses recovered *Seeleyosaurus* within Microcleididae, as a derived microcleidid, and as the sister taxon of *Microcleidus* spp. Thus, it might be possible to synonymize *Seeleyosaurus* with *Microcleidus*. However, we refrain from doing so until further research on the osteology and taxonomy of *Microcleidus brachypterygius* and other species of *Microcleidus* have been completed, which will clarify diagnostic characters for both Microcleididae and *Microcleidus*. We furthermore conclude that the holotype of *Plesiopterys wildi* (SMNS 16812) is not synonymous with *S. guilelmiimperatoris*.

Seeleyosaurus guilelmiimperatoris has re-emerged as a model for reconstructing the appearance of plesiosaurs. Already by the late 19th century, Dames (1895) used the preserved soft-tissue residues in MB.R.1992 to create one of the earliest scientific life reconstructions of a plesiosaur. The partial tail ‘fin’, preserved as dark residue in MB.R.1992, has been a source of inspiration for multiple paleoartists. The residue in the tail region is black in color, with preserved fiber-like structures like those observed in ichthyosaurs from the Posidonia Shale. Similar ‘fibers’ are also present in the flipper and would have allowed for flexibility of the tail fin and hydrofoil flippers against the turbulent water when swimming.

Paper IV: Putative osteological correlates for a dorsal fin in plesiosaurs

Posidonia Shale plesiosaur fossils were critical for this thesis chapter, as their exquisite preservation allowed for detailed morphological studies of their axial skeleton in search of plausible osteological correlates for a dorsal fin—a control surface structure that is otherwise pervasive in marine animals. A total of thirteen plesiosaurs were studied during collection visits in Germany (Urwelt-Museum Hauff, Museum für Naturkunde Berlin, Institut für Geologie und Paläntologie der Universität Tübingen, and Staatliches Museum für Naturkunde Stuttgart), with four showing complete exposure of the trunk vertebrae. The inclination of the neural spines in the vertebrae in these plesiosaurs was compared against those of modern cetaceans with a dorsal fin. Dorsal fins are necessary structures for stabilizing the body and controlling for roll when swimming (Lingham-Soliar, 2005; Renesto et al. 2020; Konishi et al., 2023). Thus, their presence in plesiosaurs seems necessary based on their aquatic lifestyle.

The orientation of the dorsal neural spines, below where a potential dorsal fin would be, change from being recumbent to procumbent in three of the studied Posidonia Shale plesiosaurs: MB.R.1992, SMNS 12039, and MH 8. This arrangement of the neural spines is remarkably similar to that observed in the torso region of dolphins equipped with a dorsal fin, but dissimilar to that of finless dolphins (e.g., *Lissodelphis borealis*). A first-hand study of twenty cetacean skeletons at the Smithsonian Museum Support Center (Maryland, USA) and the Biological Museum at Lund University revealed a correlation between the shift in orientation of the lumbar neural spines (the vertebrae situated below the dorsal fin in dolphins and porpoises) and the presence of a dorsal fin. Approximately 85% of the cetaceans studied showed a direct correlation between the presence of a dorsal fin and the arrangement of the underlying lumbar neural spines from recumbent to procumbent. By contrast, finless dolphins and porpoises (*Lissodelphis borealis*, *Lissodelphis peronii*, *Delphinapterus leucas*, *Monodon monoceras*, *Neophocoena phocoenoides*, and *Neophocoena asiaorientalis*) all have posteriorly (recumbent) directed lumbar neural spines.

The giant baleen and beaked whales have relatively small dorsal fins located near their tail and do not show a shift in the orientation of the neural spines associated with this structure. Interestingly, the Killer whale (*Orcinus orca*) has the tallest dorsal fin among any living cetacean but notably lacks a shift in neural spine orientation. With this said, however, a general pattern emerges. While the largest whales and dolphins lack osteological correlates for a dorsal fin, there is a clear correlation between neural spine orientation and the presence or absence of a dorsal fin in smaller species of dolphins and porpoises.

The results of this study show the potential utility of the orientation of the dorsal neural spines as an osteological correlate for a dorsal fin in plesiosaurs. The plesiosaur species identified as having a recumbent to procumbent neural spine shift, like that of the small-sized finned dolphins and porpoises, are *Seeleyosaurus guilelimiimperatoris* (MB.R.1992 and SMNS 12039) and *Microcleidus brachypterygius* (MH 8). Both of these taxa are small-bodied (~3 meters in overall length). An additional plesiosaur (*Wapuskanectes betsynichollsae*), assessed from photographs in the published literature (see Henderson, 2024, figs. 5, 6), also demonstrates a comparable dorsal neural spine orientation shift. Thus, the convergence in neural spine arrangement between distant lineages of plesiosaurs, in addition to their similarity to modern cetaceans that are equipped with a dorsal fin, indicates that some plesiosaurs might have evolved a dorsal fin.

Paper V: CFD modelling of the thermo- and hydrodynamic capabilities of long-necked plesiosaurs (Reptilia, Sauropterygia)

Conventional reconstructions of long-necked plesiosaurs assume a narrow, snake-like neck that abruptly transitions to a wide body (so called 'shrink-wrapping'). Comparisons to modern amniotes that inhabit cold ocean waters, like the Leatherback turtle (*Dermochelys coriacea*), indicate that this assumption is at odds with adaptations for a marine lifestyle. The Leatherback, along with modern whales, utilized blubber to insulate themselves from otherwise cold and lethal temperatures (Paladino et al., 1990; Liwanag et al., 2012). To test the effect of an insulating layer of blubber, two virtual geometries of a plesiosaur body were made: one shrink-wrapped without a layer of blubber, and a second one with a blubber layer. The geometries were constructed based on a nearly complete skeleton of the extremely long-necked elasmosaurid, *Albertonectes vanderveldei* (TMP 2007.011.0001). Given the uncertainty around the metabolism of plesiosaurs (Bernard et al., 2010; Flieschel et al., 2017; Wiemann et al., 2022; Séon et al., 2025), a low ectothermic metabolism and endothermic metabolic rate were applied to the modelled plesiosaur bodies, for heat generation. The skin surface of the plesiosaur bodies was defined as 15º C to mimic a cold ocean environment.

The results of this study revealed that blubber is a necessity to protect against heat loss, especially in the neck and head region, as this segment of the body is predisposed to heat loss due to the low volume and high surface area. Conversely, the torso conserved heat the best due to its larger volume to surface area ratio. At a low metabolic rate, both the shrink-wrapped and blubber-coated plesiosaurs experienced body temperatures nearly equal to that of the surrounding water. At a high metabolism, the blubber-coated plesiosaur overheated in the torso and neck region, while the high metabolism applied to the shrink-wrapped (no blubber) plesiosaur produced more survivable body temperatures in the neck region, but overheated in the body. Another simulation included the blubber-coated model and a basic artery along the middle of the body that mimicked blood flow. This artery was efficient in distributing heat throughout the body and keeping the neck warm.

Taken together, long-necked plesiosaurs would have benefited from having a blubber-coated neck, to insulate the vital arteries and brain; a thinner blubber layer around the torso would have counteracted overheating and cooled off this region of the body. Blubber therefore seems to be a necessary tissue to retain heat produced in the bodies, without which the plesiosaur could not survive in cold waters over a prolonged period of time. The thicker neck transitioning to the body of the long-necked plesiosaur would in turn create a more torpedo-like body, somewhat convergent with that of other secondarily marine tetrapods.

Paper VI: Plesiosaurs of Angola

In this paper, a review of plesiosaurs from Angola is provided, along with descriptions of new material that was collected but only studied recently. Vertebrate paleontology in Angola can trace its beginnings back to the early days of exploration in the 18th century (Mateus et al., 2012). Most early Portuguese paleontologists and geologists documented plesiosaur remains along the western coast of Angola but never provided detailed descriptions. Only Antunes (1964) included a general description of plesiosaur vertebrae and teeth. Since Antunes' time, Projecto PaleoAngola has made major advances in geological and paleontological research of Angola.

The first field season for Projecto PaleoAngola began in 2005—since then, much has been discovered about the Cretaceous marine reptiles that invaded the South Atlantic after the rifting of South America from Africa. From the Maastrichtian Bench 19 locality in Bentiaba, a remarkable density of plesiosaur remains has been discovered that is rivaled only by a few places in the world. From here, three individuals of *Cardiocorax mukulu* have been excavated and described along with the remains of aristonectine elasmosaurids.

Cardiocorax mukulu had wide semicircular canals that are morphologically convergent with those of cheloniid sea turtles and likely served as an adaptation for limb-based swimming and a pelagic life (Neenan et al., 2017). Phylogenetic analyses by Marx et al. (2021) placed *C. mukulu* as a basal elasmosaurid. Since then, additional phylogenetic analyses have returned mixed results for the placement of this taxon in Elasmosauridae. The aristonectine elasmosaurids described by Araújo et al. (2015a) are paedomorphic adults, exhibiting an osteologically immature external morphology, but with an internal bone architecture like that of mature adults. The basioccipitals of new aristonectine elasmosaurids are described for the first time as well and indicate that there was likely more than one aristonectine species present at the Bench 19 locality. Furthermore, the first record of Polycotylidae in sub-Saharan Africa is described.

Angola has been a critical country for the study of plesiosaurs. The Bench 19 locality is so dense in plesiosaurs that future discoveries certainly will continue to provide new information on these reptiles just before their extinction at the end of the Maastrichtian. In terms of diversity, this site hosts not only plesiosaur fossils, but also mosasaurs, sea turtles, a plethora of sharks, and pterosaurs (Mateus et al., 2012; Strganac et al., 2015; Fernandes et al., 2022). The accumulation of predators on the coast of Angola was likely supported by fish nourished by deep water upwelling (Handoh et al., 1999; Jacobs et al., 2006, 2009; Polcyn et al., 2014; Strganac et al., 2015). The plesiosaur fossils in the Bench 19 locality are often isolated or disarticulated remains with bite marks from sharks (Araújo et al., 2015a; Strganac et al., 2015). Curiously, any evidence of predator–prey relationships or scavenging actions between mosasaurs and plesiosaurs in the Bench 19 locality has yet to be revealed, despite the abundance of both groups during the same interval of time. We therefore hypothesize that, at least in the Bench 19 locality, plesiosaurs were not actively preyed upon or scavenged by mosasaurs.

Table 1. Author contributions

Contributions	Paper I	Paper II	Paper III	Paper IV	Paper V	Paper VI
Concept and study design	Marx Lindgren Kear Sachs	Marx	Sachs Madzia	Marx Lindgren	Marx Lindgren Szász	Marx Polcyn Araújo
Data collection and analyses						
Sampling/ demineralization	Marx Jarenmark Lindgren Nilkens	N/A	N/A	N/A	N/A	N/A
ToF-SIMS	Sjövall	N/A	N/A	N/A	N/A	N/A
IR-micro-spectroscopy	Op De-Beeck Marx	N/A	N/A	N/A	N/A	N/A
SEM/EBSD/ EDX	Sjövall Marx	N/A	N/A	N/A	N/A	N/A
TLM	Marx	N/A	N/A	N/A	N/A	N/A
Petrographic thin sections	Marx Lindgren	N/A	N/A	N/A	N/A	N/A
Collection visits	Marx Lindgren Sachs Kear	Marx Lindgren Sachs Kear	Sachs Marx Kear	Marx	N/A	N/A
Photography	Marx Nilkens Sjövall Kear	Marx Nilkens	Sachs Kear	Marx	N/A	Marx Araújo
Phylogenetic analyses	N/A	Marx	Madzia	N/A	N/A	N/A
Collection of osteological dimensions	N/A	Marx	Hampe Sachs Marx	Marx	N/A	Marx

Osteological description	N/A	Marx Sachs	Sachs	Marx	N/A	Marx Polcyn Araújo
Geometry design for CFD	N/A	N/A	N/A	N/A	Marx Szász Lindgren	N/A
CFD case setup	N/A	N/A	N/A	N/A	Szász Marx	N/A
Literature review	N/A	N/A	N/A	N/A	N/A	Marx Polcyn Araújo
Data handling						
Data post-processing	Sjövall Marx Op De-Beeck	Marx	Madzia	Marx	Szász Marx	N/A
Data interpretaition	Marx Lindgren Sjövall Op De-Beeck Kear Eriksson	Marx Kear Eriksson Lindgren Sachs	Sachs Madzia	Marx Lindgren Eriksson	Marx Szász Lindgren	Marx Polcyn Araújo
Manuscript preparation						
Writing; original draft	Marx Lindgren Eriksson	Marx	All authors	Marx	All authors	All authors
Writing; review and editing	All authors	All authors	All authors	All authors	All authors	All authors
Figures and tables	Marx Sjövall	Marx	Sachs Madzia Marx	Marx	Szász Marx	Marx Polcyn

Discussion

The results from the enclosed papers show that plesiosaurs converged with other secondarily marine tetrapods by evolving smooth skin on (most of) the body to reduce drag, a dorsal fin to control roll, and blubber to insulate the body from heat loss imposed by the surrounding water. My studies show that plesiosaurs were well-adapted to life in the oceans; a result that can be perceived as a bit ironic considering that these extinct reptiles have such a long fossil record that demonstrates their dominance in marine ecosystems, yet are not usually depicted or understood in a way that makes sense with how we know marine animals (both extant and extinct) look and evolved to live in marine environments. This thesis thus contributes to our understanding of plesiosaur evolution, paleobiology, physiology, and provides a more accurate picture of what these animals might have looked like in life. What follows is a discussion of my in relation to the goals set up in the 'Thesis objectives' section.

Integument structure & taphonomy

In Paper I, smooth (scaleless) skin in the tail region and scales along on the trailing edge of one flipper in *Plesiopterys wildi* (MH 7) are described. The precise shape and size of the scales are difficult to ascertain because the edges appear to be faded and incomplete. Scales along the flipper of MH 7 additionally could have varied in size, as is the case in modern sea turtles (Lee et al., 2014). Comparatively, the possible keels on the scales are somewhat reminiscent of the keeled scales of sharks, which act to reduce turbulent skin friction drag (Lang et al., 2012). However, the scales in MH 7 are notably larger than those of sharks and probably would not have provided this benefit (Palmer and Young, 2015). Perhaps the keeled scales in plesiosaurs could have moderated flow separation, thereby controlling pressure drag, as suggested for keeled mosasaur scales (Gudmundsson, 2014; Palmer and Young, 2015).

However, the scales could have certainly enhanced the rigidity of the hydrofoil (Marx et al., 2025b; Paper I). Alternatively, they could have protected the limbs when the plesiosaur was in contact with the seafloor, hunting for prey that was hiding in the bottom substrate. This interpretation was drawn from two findings: (1) the gastric contents of some Posidonia Shale plesiosaurs contain sand and the shells of mollusks; therefore, we know that plesiosaurs were spending time on the seafloor looking for food (Vincent et al., 2017); and (2) presumed trackways of plesiosaurs on the seabed with dugout areas of sediment made by contact with the flippers (Natali and Leonardi, 2023).

The holotype of *Seeleyosaurus guilelmiimperatoris* (MB.R.1992) also preserves tissues in the flipper and tail regions (Paper III). The preserved tissues in *S. guilelmiimperatoris* have been critical to plesiosaur reconstructions since the time of Dames' 1895 publication. These tissues appear to be only partly phosphatized, with much of the residue appearing as a film of dark matter. In contrast, most of the preserved tissues of MH 7 were more completely phosphatized (see Paper I and Eriksson et al., 2022). The dark-colored film likely represents a layer of melanosomes that coalesced after compaction of the decaying tissues after burial (De La Garza et al., 2023). Ichthyosaurs from the Posidonia Shale often preserve this layer of melanosomes "sandwiched" between thin phosphatized layers (De La Garza et al., 2023). The fiber-like structures in the tail of MB.R.1992 are likely phosphatized connective tissues, which are also seen in some Posidonia Shale ichthyosaurs (Eriksson et al., 2022).

The contrast in preservation between MB.R.1992 and MH 7 likely demonstrates differences in the rate of phosphatization, with the skin in MH 7 being permineralized and encrusted with calcium and phosphate minerals faster than the tissues of MB.R.1992. In MB.R.1992, phosphates likely replaced the network of connective tissues in the tail region, while the rest of the integument was compressed and degraded faster than the phosphate minerals could replace or permineralize the tissues.

Spectrometric and spectroscopic analyses of skin and scale remains from MH 7 did not detect endogenous biomolecules, such as eumelanin. The deterioration and diagenetic transformation of these organic compounds into polycyclic aromatic hydrocarbons. However, eumelanin has been detected in at least one ichthyosaur from the Posidonia Shale (Lindgren et al., 2018) and therefore the search for these precious molecules should be a priority in future research.

The dorsal fin

Paper IV provides osteological correlates to infer the presence of a dorsal fin in plesiosaurs, based on comparisons with extant cetaceans. The shift in the orientation of the neural spines from recumbent to procumbent in dolphins and porpoises broadly correlates with the presence of a dorsal fin, while finless species lack this feature. A similar shift in the neural spine orientation is noticeable also in the microcleidid plesiosaurs *Seeleyosaurus guilelmiimperatoris* (MB.R.1992 and SMNS 12039) and *Microcleidus brachypterygius* (MH 8). This comparable pattern in neural spine orientation between cetaceans and plesiosaurs appears to be a case of convergent evolution in two distantly related lineages of amniotes that independently evolved adaptations for fully marine lifestyles.

In comparing the morphology of the plesiosaur vertebrae with that of cetaceans, it also became clear that body size could be a factor in the expression of this osteological correlate. Small- to medium-sized dolphins and porpoises (e.g., *Tursiops truncatus*, *Lagenorhynchus acutus*, and *Phocoena phocoena*) exhibit a distinct shift in the neural spine orientation. However, in the large Killer whale (*Orcinus orca*) there is no comparable shift in the neural spines despite this species having the largest dorsal fin of any cetacean. Similarly, the studied microcleidids that have a shift in the neural spine arrangement are medium-sized (~3.5 meters in length) (see Papers III and IV). This observation is important because it constrains the size range where this signal is most likely to be expressed. In other words, the shift in the neural spine orientation for a dorsal fin is likely to be observed in small- to medium-sized plesiosaurs and cetaceans.

The number of vertebrae in the lumbar region may also have influence on the expression of this osteological correlate in cetaceans. Those cetaceans with a dorsal fin that lacked a shift in the backbone have a relatively low number of lumbar vertebrae (~10 in *Orcinus orca* and *Kogia sima*, and 6–7 in *Pontoporia blainvillei*). On the other hand, most of the finned dolphins and porpoises have over 12 vertebrae in this region (Paper IV).

Another component to consider with respect to the presence or absence of a dorsal fin in marine amniotes is the orientation of the flippers (Okamura et al., 2021). The main purpose of the dorsal fin is to control roll (Lingham-Soliar, 2005; Renesto et al. 2020; Okamura et al., 2021; Konishi et al., 2023). So, how do finless dolphins and porpoises control for roll when swimming? The answer perhaps lies in the orientation of their flippers (Okamura et al., 2021). For example, the finless Beluga whale (*Delphinapterus leucas*) orients its flippers outward in a straight manner from the body; this positioning prevents the body from rolling. Conversely, dolphins orient their flippers more ventrally (at a larger anhedral) relative to the body, and therefore a dorsal fin is needed to account for this lack of stability (Okamura et al., 2021). The orientation of the limbs in plesiosaurs is normally inferred to be at a slight negative angle relative to the body (Welles, 1943; Liu et al., 2015). Based on the position of where the limbs inserted in the girdles, which is normally depicted at an anhedral angle (Welles, 1943; fig. 11), it is possible that some plesiosaurs would have benefitted from a dorsal fin.

Phylogeny

MH 7 is a subadult and at a more advanced growth stage than the holotype of *Plesiopterys wildi* (SMNS 16812). Using this older individual, I scored morphological characters in the skeleton to conduct phylogenetic analyses, the results of which placed MH 7 as a relatively derived plesiosaur, closely related to Cryptoclidia (plesiosaurs that would dominate the Middle and Late Jurassic). *Plesiopterys wildi* therefore represents a 'missing link' between primitive, Early Jurassic forms and more advanced species from the later part of the Mesozoic.

Previous phylogenetic analyses incorporating *Seeleyosaurus guilelmiimperatoris* recovered this plesiosaur at the base of Microcleididae, as a sister taxon to *Microcleidus* spp. (see Paper III). However, the results of our phylogenetic analyses conversely place *S. guilelmiimperatoris* in a derived position within Microcleididae.

Phylogenetic analyses of Plesiosauria incorporting *Cardiocorax mukulu* have returned mixed results (Araújo et al., 2015b; O'Gorman, 2020; Fischer et al., 2020; Marx et al., 2021;

Armour Smith et al., 2023; O'Gorman et al., 2023). Some of these studies place *C. mukulu* as a basally branching elasmosaurid. This result is congruent with the overall morphology of the skull, which is more similar to non-aristonectine elasmosaurids than aristonectines. Additionally, the cervical centra of *C. mukulu* are only slightly wider than long, as opposed to the highly elongated centra of elasmosaurine elasmosaurids (Otero, 2016), and extremely short and wide centra of aristonectines (O'Gorman, 2020). Therefore, it can be hypothesized that *C. mukulu* represents a basal lineage of elasmosaurids that survived into the latest Cretaceous.

Paleobiogeography

The aspect of paleobiogeography in Paper II is interesting, given how different the plesiosaur assemblage of the Posidonia Shale in south-western Germany is in comparison to other basins of the European Epicontinental Sea that covered much of present-day Europe during the Jurassic (Groβmann, 2007). In the coeval Yorkshire Basin (England), the plesiosaur assemblage is distinct (Benson et al., 2012) and does not share a single species with the Southwestern German Basin (SWGB). This raises the question, how is it possible for there to be distinct and diverse plesiosaur assemblages within the same epicontinental sea? In Paper II, we point to niche partitioning as a possible explanation for this phenomenon.

The most obvious difference in comparing plesiosaurs from the Early Jurassic of England versus Germany is the size of the species. In the English Yorkshire assemblage, the plesiosaurs are noticeably larger and include the massive rhomaleosaurids (6–7 meters in length), *Rhomaleosaurus cramptoni*, and *Rhomaleosaurus zetlandicus* (Smith and Dyke, 2008; Smith, 2013), while the plesiosaurs in the SWGB do not exceed 3.5 meters in length. The rhomaleosaurid, *Meyerasaurus victor*, only reaches 3.35 meters in length (Smith and Vincent, 2010), and *Hauffiosaurus zanoni* (3.4 meters in length, also from the SWGB) (Vincent, 2011) is smaller than its English contemporary *Hauffiosaurus tomistomimus* (~4.2 meters in length) (Benson et al., 2011).

These massive plesiosaurs in the English Basin (with larger skulls and teeth) were presumably consuming larger prey items compared to their smaller contemporaries in Germany. The microcleidid plesiosaurs shared between the basins were likely generalists, preying on fish, cephalopods, and mollusks from the bottom substrate, as previously mentioned. Further research is necessary to test the regionalism hypothesis.

Hydro- and thermodynamic capabilities

The design of long-necked plesiosaurs necessitates a thick blubber coating. This is due to the narrow cylinder shape of the neck, which creates a high surface area to volume ratio. This allows for the escape of heat to the surrounding environment as opposed to a high volume to surface area, which is superior at retaining heat (Paladino et al., 1990.). Taking this into account, a long-necked plesiosaur would benefit from blubber surrounding its neck and head (insulating the brain and protecting vital arteries). Transitioning to the round body, this portion of the plesiosaur has a higher volume to surface area, and in our CFD analyses suffered from high (to extraordinarily high) temperatures. To account for this change, a long-necked plesiosaur could have had less blubber in the torso to cool and offset heat retention. This is likely when also considering the limb, pectoral, and pelvic muscles that would have generated additional heat when swimming.

Thus, our long-necked plesiosaur, with the aforementioned results from our CFD analyses, would optimally have looked almost torpedo-shaped. This, in combination with the results of Paper I and Paper IV, renders a fusiform body plan with smooth skin and perhaps also a dorsal fin to control roll. This reconstruction is far more reminiscent of what one would expect for a marine amniote.

Another finding in Paper V concerns the thermodynamic capabilities of plesiosaurs. Given the uncertainty of the metabolism for these extinct marine reptiles, we assigned two different metabolic rates to the geometry in our CFD simulations: an ectothermic metabolic rate or an endothermic one. In the case of the ectothermic metabolism, the plesiosaur neck and head region were consistently cold in a cool water environment (15° C), while trunk fared slightly better (due to the high volume to surface area), but still remained too cold. Conversely, the plesiosaur with the endothermic (warm-blooded) metabolism sustained more comfortable temperatures in the head and neck region, while the torso was exceedingly hot. Therefore, plesiosaurs would presumably have benefitted from an elevate metabolism (either physiologically or behaviourally induced) to prevent hypothermia but simultaneously would have needed to account for overheating.

Paleoecology

The final paper (Paper VI) entails a review of the plesiosaur fossil record from Angola—a country rich with Mesozoic marine reptiles. The taphonomy of the Bench 19 assemblage reveals that mosasaurs were not actively hunting or scavenging on the remains of plesiosaurs. Rather, sharks were the primary scavengers. This is interesting from an ecological point of view because mosasaurs are the presumed predators of plesiosaurs (Everhart, 2006) with fossil evidence lending support to this relationship in some instances (Everhart, 2004; Einarsson et al., 2010).

The Bench 19 locality was a meeting ground between large megapredatory mosasaurs (e.g., *Mosasaurus* sp. and *Prognathodon kianda*) and small-bodied plesiosaurs (paedomorphic aristonectines). However, despite the shared habitat, the absence of mosasaur bite marks on the collected plesiosaur bones demonstrates that plesiosaurs were likely not the primary prey of mosasaurs, nor were they scavenged by mosasaurs at the Bench 19 locality. Perhaps, the nutrient-rich upwelling that supported schools of fish could explain the preference for fresh and plentiful prey for both mosasaurs and plesiosaurs, with limited competition between these two groups of marine reptiles at the Bench 19 locality.

Conclusions and future outlook

The results from this thesis provide evidence to suggest that plesiosaurs evolved adaptations for a fully marine lifestyle that is convergent with those of other marine amniotes. This includes the loss of scalation on their bodies (while retaining scales on their flippers), a dorsal fin to control roll, and blubber for insulation (indirectly implying the existence of elevated basic metabolic rates). These new inferences change our preconceived ideas of how these animals would have appeared in life. Instead of “a snake threaded through the body of a turtle”, plesiosaurs would have had a more torpedo-like/fusiform body contour, with mostly smooth skin, and even a dorsal fin in some species.

For decades, the ‘odd’ body form of plesiosaurs has been a source of debate among paleontologists, particularly as to how they could have been one of the most successful marine tetrapods in Earth’s history with a body plan that deviates so greatly from the norm (as for example seen in ichthyosaurs, cetaceans, and mosasaurs). It is concluded here that plesiosaurs did not in fact deviate as much from this body plan (although the neck elongation remains a mystery), but rather, evolved and adapted to the same physical constraints imposed by the surrounding water as every other secondarily marine tetrapod.

This thesis further illuminates the evolutionary history of Plesiosauria with phylogenetic analyses conducted on Early Jurassic taxa. Paper II revealed that *Plesiopterys wildi* is an intermediary taxon between basal Early Jurassic plesiosaurs and more derived plesiosaurs, and in Paper III *Seeleyosaurus guilelmiimperatoris* is likely a derived microcleidid and possibly synonymous with the genus, *Microcleidus*.

The last paper in this thesis further augments our understanding of plesiosaur paleobiology based upon plesiosaur fossils that have been found in Angola. The CT-scanned skull of the plesiosaur, *Cardiocorax mukulu* (MGUAN PA278: Museu de Geologia da Universidade Agostinho Neto, Luanda, Angola) has provided insights on the vestibular morphology of elasmosaurids and how it changes in response to adaptations to a pelagic environment, the myology of musculature integral to swimming, and the evolution of elasmosaurid plesiosaurs. Additional aristonectine remains (basioccipitals), the first record of a polycotylid in sub-Saharan Africa, and the taphonomy of the Bench 19 bonebed attest to the diversity of the plesiosaur fossil record during the Late Cretaceous of the South Atlantic and its ecology. All this considered, there remains much left to learn about plesiosaur evolution and paleobiology.

Future research on plesiosaur metabolism and hydrodynamics would benefit from additional CFD simulations incorporating a variety of species, including taxa with shorter necks to test the effect of neck length on body heat conservation and hydrodynamics. A range of water temperatures to test variable environments would provide greater insight into the range of temperatures plesiosaurs had to endure and how they would have responded physiologically. Further, different case setups that more realistically simulate a fluid environment would enhance our CFD study. Specifically, a conjugate heat transfer experiment, which considers heat transfer between a solid and a liquid by including the effects of both conduction and convection. In Paper V, we simply define the outer skin surface of the plesiosaurs as being equal to the water temperature (15° C).

Further research regarding the integument and soft-tissue morphology of plesiosaurs will also be crucial in discerning the appearance of these animals, as MH 7 preserves small patches of skin from the tail and flipper and thus provides limited insight into a single species (*Plesiopterys wildi*). A focused effort on field work from localities that are known to produce specimens with a reasonably high likelihood of soft-tissue preservation, along with careful examination of plesiosaur remains in collections would be a good route to start looking for additional fossilized soft parts. An emphasis on careful preparation and the deliberate search for preserved soft tissues would be essential for future discoveries elucidating the appearance and paleobiology of extinct marine reptiles.

As a final point, basic questions regarding the paleobiology of plesiosaurs still linger. How big were some species of plesiosaurs? How did they swim? What did their diet consist of? What was the purpose of the long neck? How exactly did they go extinct from the K/Pg extinction? These are very basic questions that only a few researchers have attempted to answer. These are also some of the questions I would like to address in the future. There are thousands of plesiosaur fossils in the world and with only a handful of people dedicated to studying these marine reptiles that were vital components of Mesozoic marine ecosystems, clearly there is much left to be discovered.

Popular summary

Plesiosaurs were a successful group of marine reptiles that lived in the oceans, while the dinosaurs were on land, during a period of time called the Mesozoic (The Age of Reptiles). Plesiosaurs went extinct along with the last dinosaurs (the birds survived though) at the end of the Cretaceous and they left behind a rich fossil record. The skeletons of some forms reveal a strange body plan unlike that in any other marine animal: a small head with numerous needle-like teeth, a long neck that grades into an oval body with two pairs of flippers, and a short tail. Plesiosaur species with this type of body plan are referred to as plesiosauromorphs. Other plesiosaurs had large and elongate skulls (think of a crocodile) and short necks; these forms are called pliosauromorphs.

Despite all the fossils, relatively little is known about the biology of plesiosaurs, although this has started to change in the last decade or so. To start with, the external appearance of long-necked forms is a mystery. These plesiosaurs are often depicted in a way that puts them at odds with the body plan one would expect in a marine animal. Instead of a hydrodynamic body insulated by blubber, and a dorsal fin, these plesiosaurs are instead rendered in a 'shrink-wrapped' fashion. In other words, plesiosaurs are often too 'skinny' in how we imagine and reconstruct them. This in turn restores them with unnaturally narrow necks that abruptly transition into the rest of the body. A quote often attributed to this traditional reconstruction of a long-necked plesiosaur to describe this appearance is: "a snake drawn through the shell of a turtle".

Under rare and exceptional circumstances, soft-tissue remains, such as body outlines, can reveal what the external appearance of an ancient animal was like. Only one partial body outline of a plesiosaur has ever been found, and this is from a short-necked (pliosauromorph) form. This plesiosaur (*Mauriciosaurus fernandezi*) demonstrates a more streamlined body plan with a wide tail that was likely coated in blubber. However, no body outline of a long-necked plesiosaur has ever been found. Since we lack an exceptional fossil that shows the external appearance of a long-necked form, we must use alternative approaches to discern what they may have looked like, which in turn informs us of the types of adaptations these reptiles evolved to dominate the oceans for millions of years.

To tackle this problem, I used a combination of traditional and more interdisciplinary techniques. While striving to discern the life appearance of long-necked plesiosaurs, I also studied their physiology, early evolution during the Early Jurassic, anatomy, and place in Late Cretaceous marine food webs. In the first paper of this thesis, I used methods that are normally employed in molecular biology to study fossilized soft tissues in a 183-million-year-old plesiosaur (MH 7) from the world famous Posidonia Shale near Holzmaden, Germany. MH 7 represents a rare find as the skeleton is essentially complete and fully articulated. These techniques (infrared microspectroscopy and time-of-flight secondary ion mass spectrometry) analyzed the molecular composition of the plesiosaur tissue to identify organic remains. In addition, I also made thin sections and demineralized (dissolved away the minerals) the tissue to view the remains in extraordinary detail using an electron microscope. The results of this paper demonstrate that plesiosaurs had smooth, scaleless skin in the tail region, while the flippers carried scales on the trailing edge—a mosaic of integumentary structures on the same animal.

Paper II is based on the same plesiosaur as described in Paper I (MH 7), but with the focus on the osteology and evolutionary relationships of this plesiosaur. Careful examination and comparisons of MH 7 with other Jurassic plesiosaurs revealed that the former represents a subadult individual of the species *Plesiopterys wildi*. My study of the bones in MH 7 elucidated new features of the anatomy that helped to identify *P. wildi* as a unique and identifiable species. Phylogenetic analyses (a type of analysis that tests the evolutionary relationships between different species) incorporating this new specimen of *P. wildi* found that it fits between older, and thus more primitive plesiosaurs, and more advanced forms. This new specimen also retains *P. wildi* as a valid species and enforces the high diversity of plesiosaurs species during the Early Jurassic in Germany. Interestingly, the plesiosaurs that swam around the German portion of the sea that once covered Europe are distinct from those that occupied the English portion of the sea. What could be causing this isolation of the two plesiosaur assemblages? I hypothesize that different prey preferences could possibly explain the differences we see in plesiosaur diversity. On the English side, the plesiosaurs are noticeably larger and include some of the biggest plesiosaurs from the Early Jurassic, which occupied a macropredaceous position in their ecosystem (Taylor, 1992). This difference in prey preferences could explain some of the differences we see between the two regions of the European Epicontinental Sea.

Paper III revisits an old friend among plesiosaur researchers, namely the long-necked species *Seeleyosaurus guilelmiimperatoris*. This animal is important in the history of paleontology, as it is one of the oldest plesiosaur species named and studied (by Dames in 1895). The skeletons representing this species were in dire need of a redescription considering more than a century of plesiosaur research (along with improved understandings of their anatomy and evolutionary relationships) had passed when the skeletons of *Seeleyosaurus guilelmiimperatoris* was last studied. The redescription improved our understanding of the anatomy of this plesiosaur species and identified new features in the skeleton to help diagnose *S. guilelmiimperatoris* as a unique species. Among Early Jurassic plesiosaurs, our phylogenetic analysis found *S. guilelmiimperatoris* to be relatively ‘advanced’.

In Paper IV, I took a look at the backbone of exquisitely preserved plesiosaur skeletons with the aim of identifying potential clues to soft-tissue structures on the body; specifically, a dorsal fin (like the ones you see on the top of dolphins and sharks). This required a lot of measurements, as I had this idea that the way the neural spines changed direction in the torso region (from being recumbent to procumbent) in the area where the dorsal fin would have attached was the best clue to infer such a structure in the extinct plesiosaurs. I studied complete skeletons of plesiosaurs in Germany and extant dolphin and porpoise skeletons at Lund University, in addition to the Smithsonian Institution in the U.S., where I could measure the neural spines of these whales to compare with my findings in the plesiosaurs. My findings identify the shift in the neural spines as a potential clue to identify a dorsal fin in some plesiosaurs. Hence, I conclude that some plesiosaurs indeed were equipped with a dorsal fin, and these structures would have benefited these animals in stabilizing their body while swimming.

You can probably now see that we are slowly piecing together a more complete and (hopefully) accurate reconstruction of what a long-necked plesiosaur might have looked like. To continue, in Paper V, I conducted a study to demonstrate that plesiosaurs would have needed blubber (like modern-day whales) to survive in cold ocean waters, which they certainly would have needed to deal with, even during the time of the dinosaurs. In order to do this, I had to go outside of my comfort zone and employ numerical simulations to recreate a plesiosaur immersed in cold water. These computational simulations are typically utilized by engineers or scientists interested in testing, for example, the aerodynamic capabilities of an airplane, or how well a material retains heat. For my purposes, I made virtual 3D models of a long-necked form based on a real specimen from the Late Cretaceous of Canada. For this first model, I just added the tissue representing muscle and skin that would have encased the skeleton in life. This type of reconstruction would be considered partly ‘shrink-wrapped’ because it excludes blubber from the body. I took this shrink-wrapped plesiosaur and created a second model by adding blubber to make it more realistic.

Using these two models (one shrink-wrapped and the second one being coated in blubber), I simulated these two plesiosaurs being submersed in 15º C water (= 59º F for the Americans). The blubber-coated plesiosaur was far better at retaining heat than the shrink-wrapped one. I also varied the amount of heat being generated in the plesiosaur models. I used two heat generating settings: one being closer to an ectothermic reptile and another being like a mammal’s metabolism (endothermic). The ectothermic shrink-wrapped plesiosaur was always cold, whereas the blubber-coated version with an ectothermic metabolism fared better, but still on the cold side.

Conversely, the blubber-coated model was warm in the head and neck region, which is perfect for surviving in cold water! However, the body region was way too hot. Therefore, I hypothesize that blubber and also an elevated metabolism would have benefited long-necked plesiosaurs, with blubber being thinner in the torso to aid in cooling off the large body.

Paper VI entails a review of the incredible plesiosaur fossil record from Angola, along with an overview of the current state of knowledge regarding plesiosaurs from this country. Angola has been critical to our understanding of plesiosaur biology and evolution, with inferences on how plesiosaurs grew and developed being a major contribution to plesiosaur research (Araújo et al. 2015a). In this last chapter, I specifically discuss the plesiosaur, *Cardiocorax mukulu*, and how its morphology provides insights into how plesiosaurs adapted to life in the oceans. The biodiversity of plesiosaurs at the famous ‘Bench 19 bonebed’ is revisited and at least two distinct species of small-bodied aristonectine plesiosaurs were present at this locality during the Cretaceous. Additionally, the first record of a polycotylid plesiosaur is reported based on an isolated femur.

Populärvetenskaplig sammanfattning

Plesiosaurierna (svanödlorna) var en framgångsrik grupp marina reptiler som levde under en tidsperiod som kallas Mesozoikum. De sista medlemmarna försvann tillsammans med de sista dinosaurierna vid slutet av krittiden för ca 66 miljoner år sedan. Skelett från plesiosaurier visar på en kroppsplan som inte liknar någonting man ser hos andra havslevande djur: ett litet huvud med ett stort antal nålliknande tänder, en lång hals som övergår i en oval kropp med två par med simfötter, följda av en kort svans. Former med den här typen av kroppsbyggnad kallas för plesiosauromorfer. Andra plesiosaurier hade stora och långsträckta huvuden och korta halsar, dessa kallas för pliosauromorfer.

Trots mängder med fossil och en vetenskaplig historia som sträcker sig mer än 200 år bakå i tiden vet man relativt lite om svanödlornas biologi. Det är först under det senaste deceniet some detta långsamt börjat att ändra sig. Till att börja med; de långhalsade plesiosauriern (plesiosauroidernas) är ett mysterium. Dessa arter avbildas ofta på ett sätt som inte stämmer överens med den kroppsplan man kan förvänta sig hos havslevande djur. I stället för en hydrodynamisk kropp täckt av späck och med en ryggfena på toppen återges dessa svanödlor normalt på ett sätt där kroppskonturen direkt följer inpå skelettets utformning. Detta ger dem en onaturligt smal hals som övergår i en markant bredare kropp. En beskrivning av denna traditionella bild av långhalsade plesiosaurier är att de ser ut som ”en orm som dragits genom en sköldpaddas skal”, ett begrepp som ursprungligen kan ha myntats av den tyske paleontologen Wilhelm Dames (1843–1898).

Under vissa, mycket speciella, omständigheter kan rester av mjukvävnad (som exempelvis skinn) ge en tydligare bild av hur numera utdöda djur sett ut. Endast en partiell kroppskontur av en plesiosaurie har hittills påträffats, och den tillhör en korthalsad art. Denna pliosauroid (med namnet *Mauriciosaurus fernandezi*) uppvisar en droppformad kropp med en bred svans som sannolikt var täckt av späck. Man har dock hittills inte påträffat något motsvarande fossil av en långhalsad svanödla. Eftersom vi saknar material som direkt visar hur en långhalsad plesiosaurie såg ut måste vi använda oss av alternativa metoder för att kunna närma oss deras utseende, vilket i sin tur ger information om de anpassningar dessa reptiler hade för att kunna dominera livet i haven under miljontals år.

För att tackla denna frågeställning använde jag en kombination av traditionella och tvärvetenskapliga metoder. Samtidigt som jag försökte förstå hur de långhalsade formerna såg ut så studerade jag även deras fysiologi, tidiga evolution (under tidig jura) och plats i de marina näringskedjorna under sen krita. I den första artikeln i denna avhandling använde jag metoder som normalt nyttjas inom molekylärbiologin för att studera resterna av fossil mjukvävnad i en 183 miljoner år gammal plesiosaurie (MH 7) från den världsberömda s.k. ’Posidonia Shale’ nära byn Holzmaden i sydvästra Tyskland. MH 7 är ett sällsynt fynd då skelettet är i det närmaste komplett och artikulerat. De tekniker jag använde avsåg analysera den molekylära sammansättningen av plesiosaurievävnaden i syfte att identifiera ursprungliga organiska rester. Utöver dessa metoder producerade jag även histologiska snitt och demineraliserade (dvs. löste bort mineraler) den fossila vävnaden för att kunna studera vävnaderna i detalj med hjälp av elektronmikroskopi. Resultaten i denna artikel tyder på att åtminstone vissa plesiosaurier hade en slät hud i svansregionen medan fenorna var täckta av fjäll längs bakkanten, dvs. en mosaik av hudstrukturer på samma djur.

Artikel II baseras på samma plesiosaurie som Kapitel I (MH 7), men här med fokus på osteologin och det evolutionära förhållandet mellan denna plesiosaurie och andra kända arter. En noggrann undersökning och jämförelse av MH 7 med andra jurassiska svanödlor visade att fossilet representerar en inte helt fullvuxen individ av arten *Plesiopterys wildi*. Min studie av MH 7:s skelett visar också på anatomiska egenheter som bidrog till att identifikationen av fossilet som en *P. wildi*. En fylogenetisk analys (dvs. en typ av undersökning som testar de evolutionära förhållandena mellan olika arter) som innefattade detta nya exemplar av *P. wildi* visade att arten hör hemma mellan äldre (och därmed mer primitiva) plesiosaurier och mer avancerade former. Det nya fossilet bekräftar även att *P. wildi* är en giltig art och visar på mångfalden av plesiosaurier under tidig jura i det som idag är Tyskland. Intressant nog skiljer sig de plesiosaurier som simmade runt i den tyska delen av det hav som då täckte stora delar av Europa från arter som levde i den engelska delen av havet. Vad kan ha orsakat denna uppdelning? Jag hypotetiserar att preferenser för olika typer av bytesdjur möjligen kan förklara de skillnader vi ser i plesiosauriernas utbredning: på den engelska sidan är djuren märkbart större och inkluderar några av de största formerna vi känner till, vilka hade positionen som makropredatorer i ekosystemen, medan svanödlorna är betydligt mindre i den tyska bassängen och därmed förmodligen mest åt mindre fisk och bläckfisk. Denna skillnad i bytespreferenser kan förklara en del av de skillnader vi ser mellan de två regionerna i det europeiska jurassiska epikontinentalhavet.

I Kapitel III återbesöks en gammal bekant för många plesiosaurieforskare, nämligen typmaterialet till *Seeleyosaurus guilelmiimperatoris*, en långhalsad svanödla som är viktig för plesiosaurieforskningens historia då den är en av de tidigaste arterna som namngavs och studerades i detalj av Dames år 1895. Skeletten som representerar denna art var i stort behov av att beskrivas igen med tanke på årtionden av ny forskning och förbättrad förståelse av djurens anatomi och evolutionära relationer sedan 1800-talet då *S. guilelmiimperatoris* senast undersöktes. Den nya beskrivningen förbättrar vår förståelse av morfologin hos denna plesiosaurie och identifierar nya karaktärer som hjälper till att diagnostisera arten. Vår fylogenetiska analys visade även att *S. guilelmiimperatoris* var en relativt ’avancerad’ form bland de arter som fanns under tidig jura.

I Artikel IV undersöker jag ryggraden hos ett antal välbevarade skelett i jakt på ledtrådar vad det gäller förekomsten av en eventuell ryggfena hos svanödlor. Studien bygger på antagandet att kotutskottens ändrade riktning indirekt skulle kunna indikera förekomsten av en ryggfena hos svanödlor. Jag studerade kompletta skelett av såväl plesiosaurier som moderna delfiner och tumlare, och resultaten tyder på att en övergång från bakåt- till framåtriktade kotutskott hänger samman med förekomsten av en mjukvävnadsfena hos vissa plesiosaurier.

Artikel V behandlar en studie som visar att plesiosaurierna skulle behövt späck (i likhet med dagens valar) för att överleva i kallt havsvatten. För att kunna göra detta var jag tvungen att gå utanför min bekvämlighetszon och använda numeriska simuleringar för att återskapa en plesiosaurie som simmade i kallt vatten. Liknande datorsimuleringar används normalt av ingenjörer eller forskare som är intresserade av att testa exempelvis ett flygplans aerodynamiska förmåga eller hur väl ett material kan behålla värme. Jag byggde virtuella 3D-modeller av en långhalsad svanödla som var baserade på ett verkligt fossilt exemplar från sen krita i Kanada. I den första modellen lade jag bara till vävnad som muskler och hud, men i den andra modellen täckte jag även djuret med späck för att göra den mer realistisk.

Med hjälp av dessa två modeller simulerade jag två plesiosaurier som simmade i 15° C vatten (= 59° F för amerikanerna). Den späcktäckta plesiosaurien var mycket bättre på att behålla värmen jämfört med den utan detta isolerande perifera lager. Jag varierade också mängden värme som producerades i de båda plesiosauriemodellerna. Svanödlan utan späck och som dessutom hade en reptils ämnesomsättning var alltid kall, medan den späcktäckta versionen klarade sig betydligt bättre, även om den fortfarande var för kall för att kunna ha klarat sig i verkligheten.

Omvänt var den späckbelagda modellen med ett däggdjurs ämnesomsättning varm i både huvud- och halsregion, vilket är perfekt för att kunna överleva i kallt havsvatten. Kroppsregionen var dock alldeles för varm för att vara naturlig. Således antar jag att späck och även en förhöjd ämnesomsättning skulle ha gynnat långhalsade plesiosaurier, men att det isolerande lagret var tunnare i bålregionen för att hjälpa till att kyla ner den stora kroppen.

Artikel VI avhandlar en genomgång av de fossil av plesiosaurier som gjorts i Angola och ger dessutom en översikt av vår kunskap om svanödlor från detta land. Angola har varit avgörande för vår förståelse av plesiosauriernas evolution och biologi, och slutsatser om hur plesiosaurier växte och utvecklas har varit ett viktigt bidrag till forskningen om dessa djur. I kapitlet diskuterar jag speciellt arten *Cardiocorax mukulu* och hur dess morfologi ger insikter i hur plesiosaurier anpassade sig till ett liv i haven. Den biologiska mångfalden av svanödlor i det berömda ’Bench 19’ lagret studeras även på nytt och minst två distinkta arter av aristonectina plesiosaurier med liten kropp fanns på denna plats under sen krittid. Dessutom behandlar studien det första fyndet av en polycotylid plesiosaurie från Afrikas krita, nämligen ett isolerat lårben.

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