Underwater flight in sea turtles and plesiosaurs

Dissection, muscle reconstructions, analog models, and finite element structure analyses inform on flipper twisting and muscle forces in plesiosaurs

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Summary

This dissertation contributes to our understanding of plesiosaur locomotion by providing foreflipper and hindflipper muscle reconstructions and studying aspects of their muscle physiology (functions, forces, muscle length changes) in comparison to recent sea turtles. This was accomplished by a transdisciplinary biomechanical approach combining knowledge and methods from engineering sciences, comparative anatomy, and paleontology.

Plesiosauria belong to a group of extinct reptiles, the Sauropterygia, that adapted to a life in the sea. Plesiosaurs evolved in the Late Triassic and died out at the K/Pg boundary. They are characterized by the increasingly evolving disparity in body form, i.e., either pliosauromorph (large head, short neck) or plesiosauromorph (small head, long neck). Contrastingly, the locomotory apparatus, a fusiform body with a relatively reduced tail and four hydrofoil flippers, experiences little change during over 135 Ma of plesiosaur evolution. So, once the locomotory apparatus of plesiosaurs had evolved, it must have been highly efficient.

In **Chapter 1** flipper osteology and the mode of locomotion of Nothosauria and Plesiosauria are assessed in comparison to recent sea turtles. Plesiosaur locomotion has been disputed for over a century. It has been proposed that plesiosaurs were underwater fliers like penguins and sea turtles, or rowers like e.g., otters, or employing a mixture of both locomotory styles, like sea lions. How the four flippers are coordinated is also still debated. Sea turtles fly underwater. Nonetheless, sea turtles are capable of various rowing motions and even crawling on land. The review concludes that especially joint anatomy and mobilities have largely remained unstudied in all three taxa. Further, osteological evidence mostly corroborates that plesiosaurs were underwater fliers like extant sea turtles while nothosaurs swam partially by tail undulation supported by the foreflippers.

In **Chapter 2** the array of methods (building an analog model of humerus musculature, obtain muscle courses and muscle functions geometrically, pairing up agonistic and antagonistic muscles, finite element structure analysis (FESA) of the humerus) to study underwater flight in plesiosaurs is tested on a recent underwater flying reptile taxon, the sea turtles. This is because for sea turtles muscle attachments and courses can be confirmed by dissection in contrast to the fossil plesiosaurs. To conclude, operating muscle forces during foreflipper up- and downstroke were calculated that show that the downstroke provides more propulsion than

the upstroke. Further, the humerus is mostly loaded by compression due to a complex interplay of agonistic and antagonistic muscles and muscle wrappings. This is confirmed by a close match of the compressive stress distribution with the humerus microstructure.

In **Chapter 3** fore- and hindflipper muscles are reconstructed with the extant phylogenetic bracket for the plesiosaur *Cryptoclidus eurymerus* (IGPB R 324). Additionally, plesiosaur muscle reconstructions are matched with eventually functionally analogous sea turtles, penguins, sea lions, and whales. It turns out that plesiosaurs had complex muscular systems in their fore- and hindflippers that allowed them to twist their flippers along the respective length axis, a feature which has been proven to be crucial for underwater flight by hydrodynamic studies.

In **Chapter 4** *Cryptoclidus* (IGPB R 324) humerus and femur FESA was computed comparable to Chapter 2. Muscle forces support that the downstroke in plesiosaurs contributed more to propulsion than the upstroke. Further, extensors and flexors that originate from humerus and femur have very high muscle forces corroborating the myological flipper length axis twisting mechanism proposed in chapter 3 and proving its importance for plesiosaur locomotion.

In **Chapter 5** a preliminary FESA of a sea turtle femur, that is part of a rowing and not underwater flying appendage, is presented. The highest muscle forces are obtained for femur pro- and retractors. This highlights that with FESA it is possible to determine differences between limb bones that are employed in different locomotory styles.

Chapter 6 concludes with a summary of the results of this dissertation placing muscle functions in the context of sauropsid muscle functions and by comparing results for sea turtle and plesiosaur FESA point by point. There are considerable similarities between both underwater flying reptile taxa but also profound differences which highlight the convergently evolved different locomotory muscuskeletal systems but also how similar selective pressures lead to similar adaptations and morphologies.

Contents

Chapter 1

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The locomotory apparatus and paraxial swimming in fossil and living marine reptiles: comparing Nothosauroidea, Plesiosauria, and Chelonioidea

Anna Krahl

Abstract

Sauropterygia are basal Diapsida of uncertain affinity. Nothosauroidea lived in the Triassic in shallow marine habitats for the very limited period of approximately 15 Ma. Contrastingly, the pelagic and globally dispersed Plesiosauria evolved in the Late Triassic and died out about 135 Ma later, at the end of the Late Cretaceous. The origin of Testudines is highly controversially discussed to this day. Modern sea turtles, the Chelonioidea, populate the oceans since the Cretaceous (~ 100 Ma). Nothosaurs swam with their foreflippers, supported by the swimming tail. As only tetrapods ever, plesiosaurs have evolved four hydrofoil-like flippers. The plesiosaur flipper beat cycle has been debated for nearly two centuries. The different proposed locomotory styles (rowing, rowing-flight, underwater flight) are discussed in this review. A fourth gait, that is employed by *Carettochelys insculpta*, which combines rowing and flying, is introduced. The osteology of the locomotory apparatus of nothosaurs and plesiosaurs is reviewed and compared to that of extant underwater-flying Chelonioidea. In conclusion, underwater flight remains the favored locomotory style for plesiosaurs. Also, the review reveals that nothosaur locomotion has largely remained unstudied. Further, our understanding of joint morphologies and mobilities of the foreflipper in nothosaurs, plesiosaurs, and even recent sea turtles, and of the hindflipper in plesiosaurs, is very limited. It is crucial to the discussion of locomotion, to find out, if certain limb cycles were even possible, as evidence seems to point to the improbability of a rowing motion, and humerus and femur long axis rotation in plesiosaurs.

Keywords:

Nothosauroidea, Plesiosauria, Chelonioidea, mode of locomotion, rowing, underwater flight

1. Evolution of Nothosauroidea and Plesiosauria (Eosauropterygia) and Chelonioidea

1.1 Phylogeny, ecology, and distribution of Nothosauroidea and Plesiosauria

Sauropterygia were amongst the first fossil reptiles subjected to paleontological research (Beche and Conybeare 1821; Owen 1840; Meyer 1847-1855). Since then, researchers studied not only their morphology and phylogeny, but also different aspects of their biology (Taylor 1989; Cruickshank et al. 1991; Storrs 1993; Buchy et al. 2006; Araújo and Polcyn 2013; Foffa et al. 2014a; Klein et al. 2016; Neenan et al. 2017; O'Keefe et al. 2017; Wintrich et al. 2017b; Nagesan et al. 2018; Troelsen et al. 2019). Yet many questions remain to be answered.

Sauropterygia cover a spectrum of gradual adaptations from a shallow marine benthic (Rieppel 1995) to a pelagic lifestyle (Rieppel 2000; Wintrich et al. 2017a). These are accompanied by fundamental restructuring of the locomotory apparatus and thus the mode of locomotion. Paraxial locomotion evolved three times convergently in Sauropterygia, i.e., in Placodontia, Nothosauroidea, and Plesiosauroidea. The following text will focus on evaluating what we know about the locomotion of two of them, namely Nothosauroidea and Plesiosauria, by comparing them to a possible recent functional analogue, the Chelonioidea.

Sauropterygia are marine Diapsida, which split into basal taxa (Placodontia, Pachypleurosauria, Nothosauroidea, and Pistosauroidea) and derived crown-group taxa (Plesiosauria). The affinities of Sauropterygia remain unresolved (Fig. 1 a-b). However, depending on the author, they are either basal Lepidosauromorpha (Rieppel and Reisz 1999) (Fig. 1 c), basal Archosauromorpha (Merck 1997) (Fig. 1 b), or the sister group to Archosauromorpha and Lepidosauromorpha (Neenan et al. 2013, appears to be the latest one)

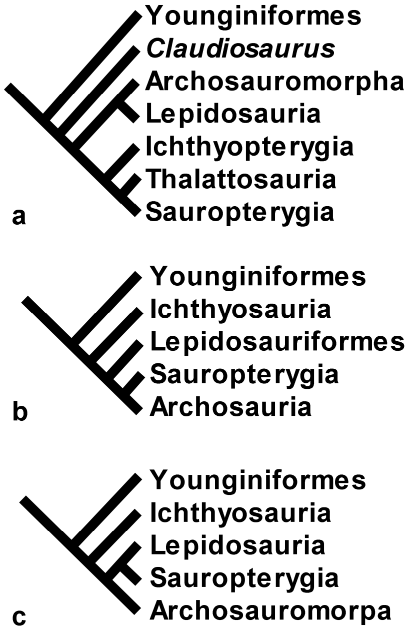

Fig.1 Hypotheses of relationships of Sauropterygia. a Sauropterygia is the sistergroup of Thalattosauria, after Neenan et al. (2013); b Sauropterygia is the sistergroup of Archosauria, after Merck (1997); c Sauropterygia is the sistergroup of Lepidosauria, after Rieppel and Reisz (1999)

(Fig. 1a). Nothosauroidea (or colloquially termed nothosaurs, include the genera *Simosaurus* sp., *Germanosaurus* sp., *Nothosaurus* sp., and *Lariosaurus* sp.) are the sister group of Pachypleurosauria (Rieppel 2000; Holmes et al. 2008) (Fig. 2 a-c), whose monophyly has been doubtful since Holmes et al. (2008) work on *Keichousaurus*. However, integration of recent Chinese sauropterygian findings into phylogenies mostly resulted in unstable phylogenetic relationships (Neenan et al. 2015; Cheng et al. 2016) (Fig. 1 b-c).

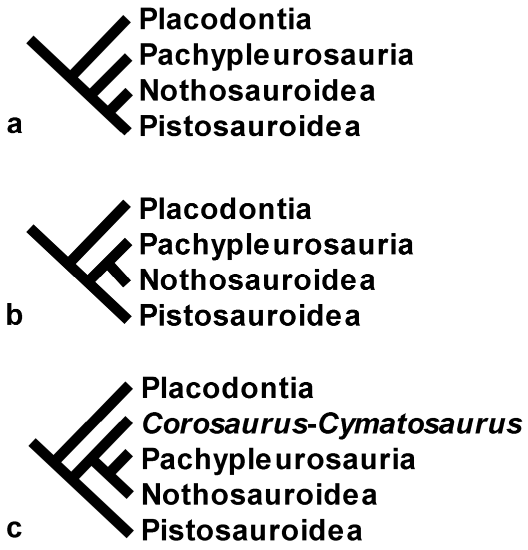

Fig.2 Selection of representative sauropterygian ingroup phylogenies; a showing Placodontia as the most basal sauropterygians, followed by Pachypleurosauria, Nothosauria and Pistosauroidea, after Rieppel (2000); b Shang and Li (2015) differ from a in that Pachypleurosauria and Nothosauria form a clade, after Shang and Li (2015); c Placodontia remain the most basal and Pistosauroidea the most derived sauropterygians, while *Corosaurus-Cymatosaurus* (usually found as basal pistosauroids) are at the base of a clade comprising Pachypleurosauria and Nothosauria as well, after Neenan et al. (2013)

Nothosauroidea existed only for a very limited time period in the Triassic, from the late Olenekian to the early Carnian (about 15 Ma) (Hagdorn and Rieppel 1999; Jiang et al. 2014). Nothosaurs lived in coastal shallow-marine epicontinental habitats (Hagdorn et al. 1991; Hagdorn and Rieppel 1999; Hagdorn and Simon 2005; Rieppel 1999; Neenan et al. 2017) and were faunivorous. Their dentition indicates that they were probably mainly specialized for piscivory (Rieppel 2002; Shang 2007). *Nothosaurus* fossils were found in Europe (Klein et al. 2015; Chaves et al. 2016; Miguel Chaves et al. 2018), China (e.g., Liu et al. 2014; Lin et al. 2017), Tunisia (Rieppel 1997), and Israel (Rieppel et al. 1997).

Basal Sauropterygia remained stratigraphically restricted to the Triassic (Bardet 1994; Hagdorn and Rieppel 1999; Rieppel 1999). Plesiosaurs were long considered to have evolved in the Late Triassic (Bardet 1994; Rieppel 1999; O'Keefe 2001a; Fabbri et al. 2013) but conclusive fossil evidence was lacking until very recently (Wintrich et al. 2017a). These new fossils and new phylogenetic hypotheses (Benson et al. 2012) indicate that plesiosaurs quickly reached a high diversity and global distribution (Bardet 1994; Rieppel 1999; O'Keefe 2001a;

Ketchum and Benson 2010; Bardet et al. 2014). Plesiosaurs died out at the K/Pg boundary (Bardet 1994; Motani 2009; Vincent et al. 2011; Vincent et al. 2013).

In the traditional view, Plesiosauria split into two monophyletic groups: plesiosaurs (long neck and small head) and pliosaurs (short neck and large head) (Williston 1914; Brown 1981; Druckenmiller and Russell 2008; Smith and Dyke 2008). However, modern cladistic analyses prove this dichotomy to be invalid. In contrast, these two plesiosaur types rather represent morphotypes, plesio- and pliosauromorphs, that evolved several times convergently (O'Keefe 2002; O'Keefe and Carrano 2005; Ketchum and Benson 2010; Benson and Druckenmiller 2014). These two extreme morphotypes evolved from basal intermediate Late Triassic and Early Jurassic forms during the Jurassic and Cretaceous. Pliosauromorphs usually have larger hindflippers than foreflippers (O'Keefe 2002; O'Keefe and Carrano 2005) and are generally considered as fast, powerful, and agile predators that chase their prey down (Taylor 1981; Massare 1988; O'Keefe 2001b).

Plesiosauromorphs have larger foreflippers than hindflippers (O'Keefe 2002; O'Keefe and Carrano 2005) and are generally regarded as ambush predators (Taylor 1981; Massare 1988) and efficient, moderately fast long-distance swimmers (O'Keefe 2001b). Plesiosaurs lived in open marine habitats and to a minor extent in brackish, and fluvial habitats (Kear et al. 2006). They were all faunivorous, but showed quite different dietary preferences, as is suggested by their dentition and by fossil gastric contents (Sato and Tanabe 1998; Cicimurri and Everhart 2001; McHenry et al. 2005; O'Keefe et al. 2017). Foffa et al. (2014b) suggested that some pliosauromorphs might also be generalists. Filter feeding has also been recently proposed for an elasmosaur (O'Keefe et al. 2017). It is noteworthy that plesiosaur skeletons are often associated with gastroliths. Whether gastroliths had an influence on the plesiosaur’s buoyancy, or whether they aided in food processing has not been clarified yet (see Wings 2007 for review; Schmeisser and Gillette 2009; O'Gorman et al. 2013; O'Gorman et al. 2014). Jurassic plesiosaurs are mostly known from the Tethys, especially from England and Germany, but also from, e.g., France, Spain, and from North America. Cretaceous plesiosaurs were found on all of today’s continents and were globally distributed (for review, s. Bardet et al. 2014, Fig. 4).

1.2. Phylogeny, ecology, and distribution of recent Chelonioidea

Chelonioidea are basal Cryptodira (Shaffer et al. 1997; Hirayama 1998; Joyce 2007; Werneburg and Sanchez-Villagra 2009; Crawford et al. 2015). Cryptodira and Pleurodira form the clade Testudines (Fig. 3 d). Testudines may have been derived from a terrestrial ancestor (Joyce and Gauthier 2004; Scheyer and Sander 2007; Schoch and Sues 2015) or from a marine one. Turtle origins remain still highly controversial (Hill 2005 and Iwabe et al. 2005 for a brief summary; for more detail e.g., Lyson et al. 2012; Carroll 2013; Wang et al. 2013; Crawford et al. 2015; Schoch and Sues 2015) (Fig. 3 a-d). Interrelationships of Testudines are contentious, too. Especially Trinonychia are characterized by highly variable positions in the cladogram (s. Crawford et al. 2015). Recent Chelonioidea are composed of two families, Dermochelyidae and Cheloniidae. The first family includes only one recent species, namely *Dermochelys coriacea*, and the second comprises all other six extant species. *Dermochelys coriacea* forms the outgroup to Cheloniidae. Either *Chelonia mydas* or *Natator depressus* occur in the basal most position. Successively, *Eretmochelys imbricata* and *Caretta caretta* follow. *Lepidochelys olivacea* and *L. kempii* are the most derived recent Cheloniidae (Naro-Maciel et al. 2008).

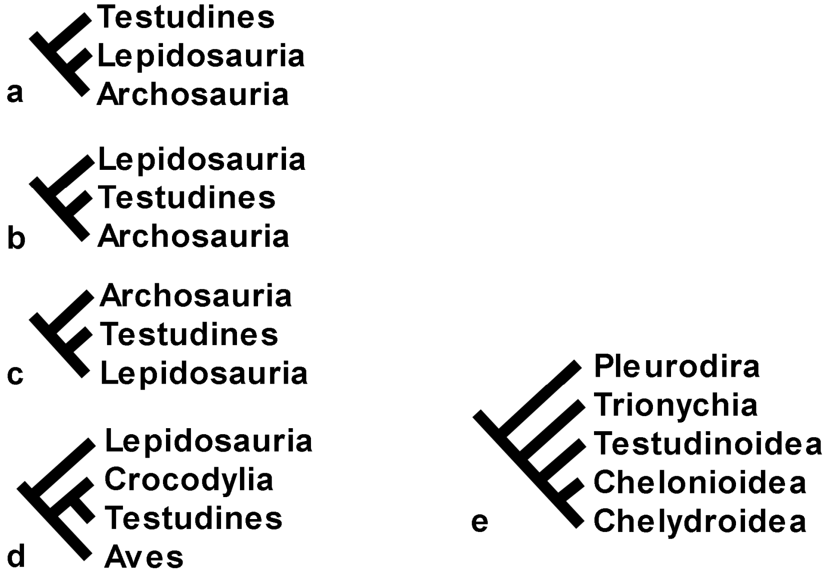

Fig.3 a to d Hypotheses of relationships of Testudines based on Iwabe et al. (2005) a as sistergroup to Lepidosauria and Archosauria; b as sistergroup to Archosauria; c as sistergroup to Lepidosauria, d as sistergroup to Crocodylia; e most recent phylogeny depicting Testudines interrelationships, after Crawford et al. (2015)

Chelonioidea, like Plesiosauria, are a long-lived radiation of secondarily aquatic reptiles (Bardet 1994; Motani 2009; Vincent et al. 2011; Vincent et al. 2013). Similarly to plesiosaurs (see also Bardet 1994; Rieppel 1999; O'Keefe 2001a; O'Keefe and Carrano 2005; Ketchum and Benson 2010; Bardet et al. 2014), Chelonioidea are globally distributed although they are restricted to warmer waters as they are ectotherms. Chelonioidea have inhabited the oceans since the middle Cretaceous (~ 100 Ma) or possibly since the Early Cretaceous (~ 145 Ma) (Evers et al. 2018) to the present day. Presumably the behavior of recent chelonioids resembles that of their fossil ancestors closely (Motani 2009). Juveniles of e.g., *Caretta caretta* hatch on a beach, head in the “frenzy” towards the ocean, and spend their first years in the open ocean. These years are called "lost years" (Carr 1952). Juvenile chelonioids are carried by oceanic currents with sargassum rafts, which serve as shelters and supply them with food. The currents bring them to new habitats. As subadults, they migrate to coastal waters (Frick et al. 2009). When Chelonioidea reach sexual maturity, they migrate hundreds of kilometers across the ocean to return to their birthplace, to mate and nest (Meylan 1982; Limpus et al. 1992). Chelonioids are associated with numerous epibionts (Frick et al. 2003).

The seven recent sympatric species avoid interspecific competition by different ecological and dietary adaptations: *Caretta caretta* is characterized by rather generalized, less unusual behavior than, for example, *Lepidochelys olivacea* and *L. kempii* which crawl all together onto the beach in a very short time frame. This phenomenon is called "arribada" (e.g., Bernardo and Plotkin 2007). *Natator depressus* does not pass through an oceanic juvenile phase (Walker and Parmenter 1990; Bolten 2003). *Dermochelys coriacea* has an increased body core temperature, lives in colder waters, and is the only recent truly pelagic sea turtle (Davenport et al. 2015). *Dermochelys* feeds mostly on jellyfish, *Chelonia mydas* is herbivorous (Hendrickson 1980), and *Eretmochelys* is "spongivorous", i.e., it is specialized on feeding on siliceous sponges (Meylan 1988).

2 Sauropterygian (Nothosauroidea and Plesiosauria) and chelonioid locomotion

2.1 Locomotory apparatus and locomotion of Sauropterygia (Nothosauroidea and Plesiosauria)

2.1.1 Nothosauroidea

2.1.1.1 Osteology

Nothosaurs have a long, laterally compressed swimming tail. The trunk region shows several characteristics for secondary stiffening, e.g., the densely packed gastralia and the ventrally strongly developed shoulder girdle (Carroll and Gaskill 1985). Dorsal elements of the nothosaur pectoral and pelvic girdle (scapula, ilium) are relatively reduced in size in comparison to the ventrally lying bones (clavicula, coracoid, pubis, ischium) (Kuhn-Schnyder 1987).

Humeri have an anteriorly straight shaft, like pachypleurosaurs as well. The proximal and distal ends of the nothosaur humerus are angulated posteriorly (Bickelmann and Sander 2008; Klein 2010). The midshaft cross section is triangular (Bickelmann and Sander 2008; Klein 2010; Hugi 2011; Krahl et al. 2013; Klein et al. 2016). The ventral side of the humeri shaft is roughly flat. The humerus is thicker anteriorly than posteriorly (Bickelmann and

Sander 2008; Klein 2010). The overall strongly derived morphology of the nothosaur humeri was likely not exclusively determined by humerus function, but possibly by sexual dimorphism (Renesto 1993; Bickelmann and Sander 2008; Klein 2010) as in pachypleurosaurs (Sander 1989; Cheng et al. 2004; Motani et al. 2015; Griebeler and Klein 2019).

Radius and ulna are short and especially the ulna is dorsoventrally flattened (Kuhn-Schnyder 1987; Storrs 1993; Rieppel 1998; Bickelmann and Sander 2008). In nothosaurs, carpus and tarsus are often poorly ossified. Metacarpal I and V have migrated proximally into the row of the distal carpals (Kuhn-Schnyder 1987). Kuhn-Schnyder (1987) suggests that metacarpal V could have been spread to extend the web of the hand. Some nothosaur taxa display hyperphalangy (Storrs 1993; Rieppel 1998). Overall the foreflippers are round or paddle-shaped and probably had webbed digits (Storrs 1993).

2.1.1.2 Joints

The glenoid articulation of nothosaurs has not been closely studied so far in terms of degrees of freedom. Yet, Storrs (1993) suggests that the rather oval (long axis oriented in dorsoventral direction) humeral articulation surface seems to exclude long axis rotation of the humerus. Further, he suggested that nothosaurs show secondarily stiffened foreflippers (Storrs 1993), e.g., a stiffened elbow joint (Kuhn-Schnyder 1987). In general, nothosaur foreflipper mobility has not been investigated in detail.

2.1.1.3 Mode of locomotion

In nothosaurs the laterally compressed, long swimming tail probably served as main propulsive organ with which they swam by lateral undulation. Nonetheless, authors agree with Carroll and Gaskill (1985) that the foreflippers played an important role in propulsion since they are strongly morphologically (Carroll and Gaskill 1985; Kuhn-Schnyder 1987; Sues 1987; Storrs 1993) and histologically derived (Krahl et al. 2013; Klein et al. 2016). As opposed to foreflipper morphology, nothosaur hindflipper morphology is plesiomorphic, and it thus is assumed that hindflippers were employed in maneuvering (Storrs 1993). This hypothesis was corroborated by Krahl et al. (2013) and Klein et al. (2016) by studying *Nothosaurus* long bones histologically. They showed that humeri, unlike femora, show some remarkable microanatomical specializations. In addition, the foreflippers show adjustments to torsional forces, suggesting a complex movement cycle, possibly underwater flight (Krahl et al. 2013; Klein et al. 2016). Further evidence for this hypothesis is provided by nothosaur trace fossils described by Zhang et al. (2014).

2.1.2 Plesiosauria

2.1.2.1 Osteology

The locomotory apparatus of Plesiosauria is morphologically highly derived over that of the more basal sauropterygians, e.g., nothosaurs. Plesiosaurs have a greatly shortened tail (Taylor 1989; Wintrich et al. 2017a), with possibly a tail fin (for review Smith 2013) and a greatly shortened trunk. The latter is secondarily stiffened by densely packed gastralia and much enlarged plate-like girdle elements (scapula, coracoid, pubis, ischium), similar to a turtle's plastron (Sues 1987; Taylor 1989). The dorsal portion of the scapula as well as the ilium are much reduced in size (Frey and Riess 1982; Tarsitano and Riess 1982; Godfrey 1984).

Dorsally, plesiosaur humeri and femora have a trochanter-like structure which is called tuberosity in the former and trochanter in the latter (Andrews 1910). The proximal heads of both bones are round in cross section. Distally both bones are increasingly dorsoventrally flattened and expanded (Andrews 1910). How humeri and femora expand distally may vary across taxa: Sometimes the anterior side is rather straight and the posterior side is expanded and curved posteriorly (Druckenmiller and Russell 2008; Schumacher and Martin 2015; Delsett et al. 2016; Sachs et al. 2016), sometimes the anterior and posterior side are expanded and curved anteriorly and posteriorly (Hawkins 1840; Andrews 1910; Großmann 2006; Araújo et al. 2015; Frey et al. 2017). The degree of expansion may also vary (Hawkins 1840; Andrews 1910; Großmann 2006; Druckenmiller and Russell 2008; Araújo et al. 2015; Schumacher and Martin 2015; Delsett et al. 2016; Sachs et al. 2016; Frey et al. 2017). Further, it is possible that either femur and humerus have approximately the same shape or that they may differ (Hawkins 1840; Großmann 2006; Schumacher and Martin 2015; Sachs et al. 2016).

Radius, ulna, tibia, and fibula are shortened and may diverge from the hourglass long bone shape they have in Eosauropterygia (Rieppel 2000) becoming more rounded, disc-like (Andrews 1910; O'Keefe 2002; Großmann 2006; Sato et al. 2006; Druckenmiller and Russell 2008; Schumacher and Martin 2015; Sachs et al. 2016; Frey et al. 2017). Often, accessory ossicles are present at the level of the zeugopodium or carpus and tarsus on that side of humerus or femur which is flared (Andrews 1910; Sato and Storrs 2000; Großmann 2006; Sato et al. 2006; Smith 2007; Druckenmiller and Russell 2008; Schumacher and Martin 2015;

Sachs et al. 2016; Frey et al. 2017). The Vth metacarpal and metatarsal have moved into the row of distal carpals/tarsals (Robinson 1975). The digits show hyperphalangy. Joint surfaces of the successive digits do not lie in the same plane. The middle digit is the longest. They become successively shorter in digit II and IV and then in I and V (Caldwell 1997, compare to e.g., Hawkins 1840; Andrews 1910; Großmann 2006; Druckenmiller and Russell 2008; Araújo et al. 2015; Schumacher and Martin 2015; Delsett et al. 2016; Sachs et al. 2016; Frey et al. 2017). All four plesiosaur limbs are transformed into hydrofoil-like flippers (Robinson 1975, 1977; Wintrich et al. 2017a). The flipper profiles are possibly asymmetrical (Robinson 1975; Caldwell 1997) as those of recent underwater fliers, i.e., sea turtles and penguins (Fish 2004).

2.1.2.2 Joints

The proximal articular surfaces of humeri and femora are very incongruent with the glenoid and acetabular articulation surfaces. The glenoid is formed by scapula and coracoid and is oval in shape. Its long axis lies in horizontal direction. The acetabulum is formed by all three hip bones (Druckenmiller and Russell 2008). It is oval in shape, but its anteroposterior axis is longer and its dorsoventral axis is shorter than in the glenoid. Posterodorsally the ilium contributes to the acetabulum and expands it (personal observations on *Cryptoclidus eurymerus* (IGPB R 324). Humerus and femur epiphyseal surfaces are pierced by vascular canals (Liebe and Hurum 2012; Fleischle et al. 2018) and show a roughened surface (personal observation). At mid-shaft, humerus and femur are oval in transverse cross section (Krahl et al. 2013; Wintrich et al. 2017a). By comparison to *Dermochelys* (Rhodin et al. (1981) Fig. 1 c, p. 245 and Snover and Rhodin 2008 Fig. 2.3, p. 24) it is thinkable, that plesiosaur humeri and femora were comparably capped by thick, vascularized cartilage caps that were non-parallel to the underlying bone (compare to Rhodin et al. (1981), Fig. 1 b, p. 245 and Snover and Rhodin 2008, Fig. 2.5, p. 24 and Fig. 2.6, p. 25). The elbow and carpal joints are stiffened (Storrs 1993).

2.1.2.3 Mode of locomotion

2.1.2.3.1 Proposed modes of locomotion

Plesiosaurs are unique among recent and fossil tetrapods in that they evolved four very similarly shaped flippers. Plesiosaurs have long been regarded as rowers or paddlers (Fig. 4 a). In both cases, drag-based propulsion is used. By performing a rowing or paddling movement, the flipper is maximally spread and pushes against the water to propel the body forward. The recovery stroke is carried out with as little water resistance as possible (Williston 1914; Tarlo 1958). Recently, this hypothesis was reactivated again based on muscle reconstructions (Araújo and Correia 2015; Araújo et al. 2015). Rowing appears to be useful in complex habitats, in which a lot of maneuvering, acceleration, and deceleration is necessary (Walker and Westneat 2000; Fish et al. 2003).

Godfrey (1984), Lingham-Soliar (2000), and Liu et al. (2015) suggested a further hypothesis, i.e., that plesiosaurs employed the so-called "rowing-flight" of sea lions (Otariinae) (English 1976b; Feldkamp 1987) (Fig. 4 b). This locomotory mode is a combination of underwater flight and rowing elements, i.e., a combination of lift-based and drag-based propulsion. Initially the sea lion draws its foreflippers downwards (ventrally), resulting in lift and propulsion. When the maximum ventral flipper excursion is reached, the sea lion pulls its foreflippers suddenly backwards in a lateral rowing motion. When the body sinks slightly downwards, the foreflippers are passively rotated into the initial position (English 1976b; Feldkamp 1987). Liu et al. (2015) computationally modelled plesiosaur locomotion and find support for a rowing-flight stroke under certain circumstances, i.e., if maximum flipper excursions are presumed.

A third swimming hypothesis was proposed by (Robinson 1975, 1977), the underwater flight. In contrast to rowing, in underwater flight the flipper is always moved through the water at an angle smaller than 90° (Davenport et al. 1984; Walker and Westneat 2002). Because of the arched flipper profile, a net overpressure results on the under side of the profile and an underpressure on the upper side of the profile and the flipper is “sucked” forward (Baudinette and Gill 1985; Fish 1996; Walker and Westneat 2000). This type of locomotion is well suitable for long-distance swimmers travelling at moderate speeds (Walker and Westneat 2000).

Requiring additional discussion is the so-called "four wing problem". This is based on the unique situation that plesiosaurs have four uniformly shaped hydrofoil flippers (Halstead 1989). The question is how the four flippers were coordinated and how the hindflippers avoid the vortex wakes of the foreflippers. Frey and Riess (1982) and Tarsitano and Riess (1982) advocate that the fore- and hindflippers were moved alternatingly, thus a continuous propulsion is ensured. That way, the hindflippers are prevented from entering the vortex wakes of the foreflipper. The recovery stroke was then supposed to have occurred passively (Frey and Riess 1982; Tarsitano and Riess 1982). Lingham-Soliar (2000) and

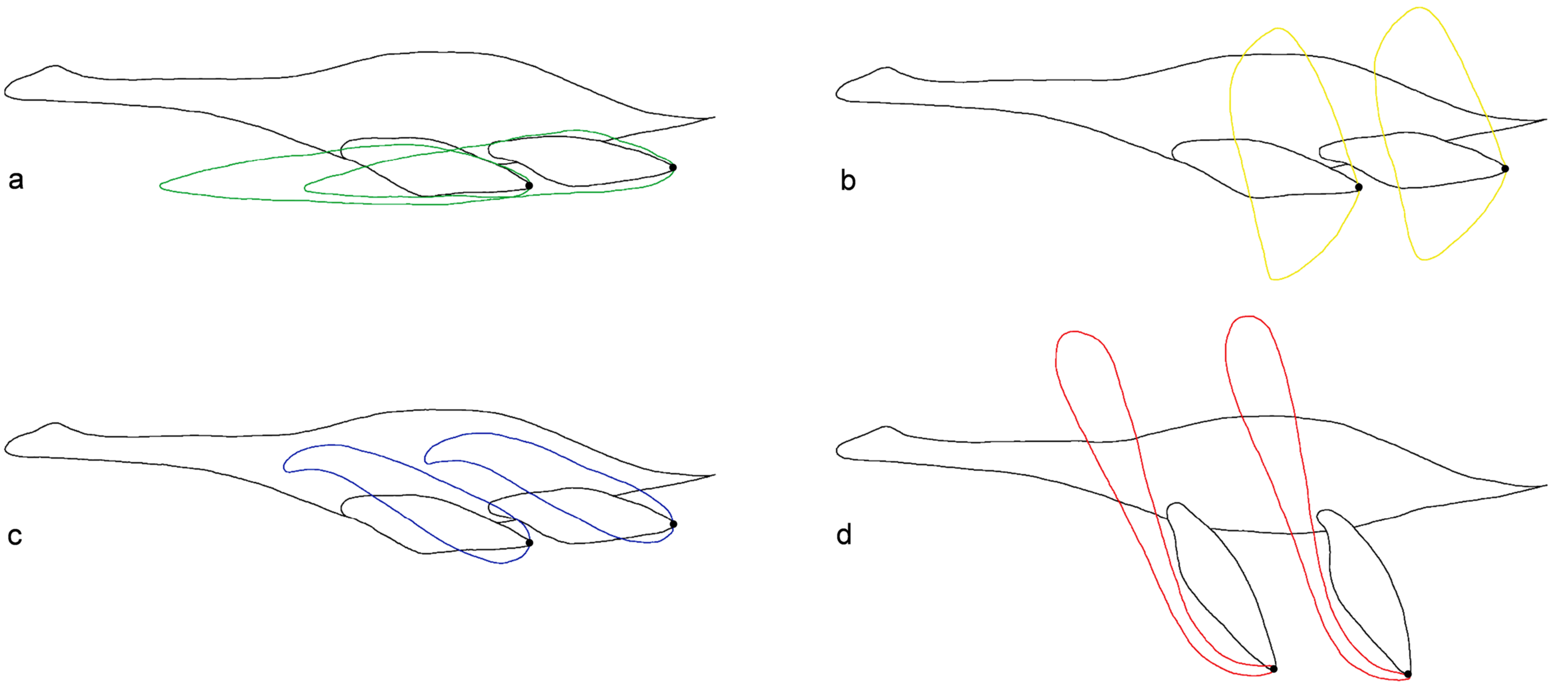

Fig.4 Schematic drawing of a plesiosaur, based on the mounted *Cryptoclidus eurymerus* (IGPB R 324) skeleton on display at Goldfuß Museum, University of Bonn, Germany. Not to scale. Flipper tip excursion of one motion cycle of different groups was projected onto the plesiosaur model. a rowing in the freshwater turtle *Trachemys scripta*, after Rivera et al. (2013); b "rowing-flight" in the sea lion *Zalophus californianus*, after Feldkamp (1987); c "synchronous rowing" in the pig-nosed turtle *Carettochelys insculpta*, after Rivera et al. (2013); d underwater flight in the sea turtle *Caretta caretta*, after Rivera et al. (2013)

Carpenter et al. (2010) endorsed the alternative hypothesis that all four flippers were moved synchronously. The plesiosaur would have moved simultaneously up- and forward, thus avoiding the danger of plunging into the vortex wakes. Long et al. (2006) carried out experiments with a swimming robot and suggested that plesiosaurs had a repertoire of different gaits, asynchronous, synchronous, and semi-synchronous. These were used when needed, and they might have varied between taxa (Long et al. 2006). Based on assumptions of a variety of fore- and hindflipper motion ranges, Liu et al. (2015) show with computer simulations that the three proposed gaits are possible (Liu et al. 2015). This does not appear unlikely, because plio- and plesiosauromorph plesiosaurs have different hunting and dietary strategies (see above).

2.1.2.3.2 Pros and cons for different modes of locomotion

In particular the stiffness of the trunk analogous to chelonioids and the long necks of the plesiosauromorph plesiosaurs, imply the necessity of evolving a paraxial mode of swimming (Storrs 1993; Lingham-Soliar 2000) but which one was employed by plesiosaurs is still controversially discussed. The enlargement of the ventral pectoral and pelvic girdle elements anterior and posterior to glenoid and acetabulum (Watson 1924; Tarlo 1958; Godfrey 1984) accompanied by the reduction of the dorsal bony elements (scapular blade and ilium) were used as arguments for rowing or a rowing element in plesiosaur locomotion (Frey and Riess 1982; Tarsitano and Riess 1982; Godfrey 1984). This is because it seems to imply relative hypertrophy of especially the locomotor muscles used in protraction and retraction originating on the coracoid and the pubis (and to a minor extent on the ventral side of the scapula and the ischium). At the same time, this would indicate a reduction of musculature dorsal to the glenoid/acetabulum that is necessary for humeral and femoral elevation (Frey and Riess 1982; Tarsitano and Riess 1982; Godfrey 1984; Araújo and Correia 2015).

Godfrey (1984) argues that the pectoral girdle in recent underwater fliers is a strong dorsoventral support structure that suspends the forelimb to the rib cage and vertebral column and that hampers the limb‘s displacement during a flipper beat cycle. Contrastingly, in plesiosaurs neither the scapula nor the ilium is tightly connected to the vertebral column. Therefore he concluded, that recent penguins and sea turtles may be poor analogues for plesiosaurs. Instead, he introduced sea lions that employ rowing-flight as functional analogues (Godfrey 1984).

The concept of underwater flight in plesiosaurs (Fig. 4 d) is based on the form of glenoid and acetabulum which allows mostly elevation and depression and restricts protraction and retraction (Storrs 1993). Robinson (1975) notes that plesiosaur flippers are hydrofoil-shaped, i.e., they converge distally in a pointed tip, are anteriorly thicker than posteriorly, and have an arched flipper profile (Robinson 1975; Caldwell 1997). These are criteria which are not met by rowing tetrapods which have webbed and blunt-ended paddle-like feet (Robinson 1975). Sea lions and *Carettochelys* do not meet these characteristics, either (English 1976a; English 1977; Rivera et al. 2013). The hydrofoil-shape of plesiosaur flippers seems to be corroborated by the discovery of preserved flipper soft tissue (Dames 1895; Frey et al. 2017). Flipper hydrofoils are usually utilized in underwater flight, as in Chelonioidea (see below) and Spheniscidae (penguins) (Robinson 1975, 1977; Lingham-Soliar 2000; Carpenter et al. 2010; Liu et al. 2015).

2.1.2.3.3 *Carettochelys* mode of locomotion

A recent study by Rivera et al. (2013) shows that the pig-nosed turtle *Carettochelys insculpta*, a freshwater turtle, usually considered as convergent to Chelonioidea, also falls into this spectrum between rowing and underwater flight, like Otariinae. However, the flippers of *Carettochelys* move through a much larger dorsoventral excursion range than in “true” rowing turtles, but the range is significantly smaller than in Chelonioidea. On the other hand, the anteroposterior range of motion of the foreflipper is significantly greater than in sea turtles. Compared to sea lions, the underwater flight phase occupies a much smaller percentage of the locomotory cycle (Rivera et al. 2013). Both Otariinae (Feldkamp 1987) and *Carettochelys* illustrate that the dichotomy of underwater flight vs. rowing might actually be considered as a continuum (Rivera et al. 2013). Therefore, the flipper beat cycle of *Carettochelys* is proposed here for the first time as a possible swimming mode for plesiosaurs in Fig. 4 c.

2.2 Locomotory apparatus and locomotion of Chelonioidea

2.2.1 Osteology

The chelonioid trunk is stiffened by the carapace and plastron. In aquatic (marine) and semi-aquatic (freshwater) turtles, the coracoid is elaborated and the scapula is reduced as compared to tortoises (Walker 1973; Wyneken 1997; Depecker et al. 2006). This results in a flattened, stream-lined body outline which is hydrodynamically optimized for a life in water (Davenport et al. 1984). Thus, in freshwater and marine turtles, the dorsal musculature, which originates at the scapula, is significantly reduced, while the coracoid musculature is hypertrophied (Walker 1973). The humerus of Chelonioidea shows morphological specializations, such as a v-shaped deltopectoral crest and a greatly enlarged medial process (Hirayama 1992).

The humerus is dorsoventrally flattened, and its shaft is rather oval in cross section (Walker 1973; Zug et al. 1986; Hirayama 1994; Wyneken 2001). The actual hydrofoil-like flipper (Walker 1973) with an asymmetrical profile (Fish 2004) is formed by radius, ulna, and the manus (Walker 1973), without a contribution from the humerus. The ulna is shorter than the radius. The latter has been relatively moved to the side of the palm. Chelonioids have a large pisiform, intermedium, and ulnare. Contrastingly, the radiale is small (Walker 1973).

Chelonioid flippers evolved by extension of the metacarpals and phalanges of the three middle digits (Shaffer et al. 1997; Richardson and Chipman 2003). In the course of ontogeny, radius and ulna are tightly linked by connective tissue. Likewise, the digits are increasingly encased by connective tissue. Additionally, the foreflipper is covered by tough and scaly skin. Overall, this leads to a secondarily stiffened semi-rigid hydrofoil-like flipper. Contrastingly, the small, round hindflippers are not particularly stiffened or elongated (Walker 1973; Wyneken 1997). They may provide additional propulsion and are otherwise used for maneuvering (Walker 1973; Davenport et al. 1984; Wyneken 1997).

2.2.2 Joints

The glenoid cavity of chelonioids is oval. Its long axis diverges by ~40° from the horizontal which results in an anterodorsal-posteroventral direction (compare to Wyneken 2001: Fig. 99, p.51, bottom right; personal observation). The likewise oval humeral head fits relatively well into the glenoid, it only appears to be slightly larger than the cavity (Walker 1973; Zug et al. 1986; Wyneken 2001), personal observation), i.e., the contact surface of humerus and glenoid is smaller than the whole humeral head. The shoulder joint of sea turtles allows humeral depression and elevation to a greater degree than protraction and retraction and does not allow no rotation (Walker 1971; Davenport et al. 1984; Pace et al. 2001; Rivera et al. 2011). The mobile elbow functions in extension and flexion (Rivera et al. 2011). Flipper rotation appears to take place by rotation of the carpus against radius and/or ulna. The digits have only limited mobility (personal observation).

2.2.3 Mode of locomotion

In chelonioid underwater flight, the foreflippers beat cyclically, approximating the form of a narrow skewed "O" from anterodorsal to posteroventral (Davenport et al. 1984; Rivera et al. 2011; Rivera et al. 2013) (Fig. 4). The hypothesis of Walker (1971), who described the flipper beat cycle as an oblique figure eight was not confirmed by subsequent authors (Davenport et al. 1984; Rivera et al. 2011; Rivera et al. 2013). Walker's (1971) description greatly influenced the work of several authors working on plesiosaur locomotion (see, e.g., Robinson 1975).

At the beginning of the downstroke, chelonioids rotate the leading edge of the foreflipper anteroventrally by rotating the carpus and manus, while during the upstroke it is rotated anterodorsally (Walker 1971). The foreflippers are thereby moved through the water at an angle of 40-70° from the horizontal (Davenport et al. 1984). Testudines that row pull the flippers horizontally through the water (Davenport et al. 1984; Pace et al. 2001; Rivera and Blob 2010; Rivera et al. 2013). While propulsion in underwater flight is generated by both, upstroke as well as downstroke, the downstroke of Chelonioidea is observed to be more powerful than the upstroke (Walker 1971; Davenport et al. 1984; Wyneken 1997). This is in contrast to penguin underwater flight, in which up- and downstroke are equally efficient (Clark and Bemis 1979).

3. Discussion

Nothosaurs inhabited shallow epicontinental seas (Hagdorn et al. 1991; Hagdorn and Rieppel 1999; Rieppel 1999; Hagdorn and Simon 2005), sea turtles mostly inhabit the warmer oceans, and plesiosaurs were globally distributed. This was suggested to be due to the development of endothermy in plesiosaurs in contrast to ectothermy in sea turtles and nothosaurs (Krahl et al. 2013; Klein et al. 2016; Wintrich et al. 2017a; Fleischle et al. 2018).

Nothosaurs have a swimming tail which contributed to locomotion (Carroll and Gaskill 1985). In sea turtles the tail is much reduced, paralleled by the loss of the m. caudofemoralis portion originating from it (Walker 1973). In plesiosaurs the tail is much reduced, too. Although a tail fin may be present (Smith 2013), the tail probably contributed mostly to streamlining (compare to Frey et al. 2017).

The reduction of dorsal bones and the expansion of ventral bones of the nothosaur and plesiosaur pectoral and pelvic girdle (Godfrey 1984; Kuhn-Schnyder 1987) is paralleled by aquatic turtles (independent of whether they live in freshwater or salt water) (Walker 1973; Wyneken 1997; Depecker et al. 2006). Therefore, this trend is independent of the locomotory mode employed, too but instead probably connected with the reduction of the impact of gravitation on the body by buoyancy in water due to a shift from life on land to water (Depecker et al. 2006). This means that the similar trend observed in Sauropterygia probably delineates convergently the transition from life on land to a life in water, but that it does not allow inferences on their locomotory style.

Furthermore, the reduction of the dorsal bony elements and the expansion of the ventral bony elements in plesiosaurs appears to have been driven to an extreme in comparison to the state found in turtles. As pachypleurosaurs and plesiosaurs have been proven to be life-bearing (Cheng et al. 2004; O'Keefe and Chiappe 2011; Griebeler and Klein 2019), therefore by inference with the extant phylogenetic bracket, nothosaurs may have been giving birth to life young as well. This could indicate that Sauropterygia were completely independent from the terrestrial environment, unlike aquatic turtles, and were therefore completely freed from supporting their bodies on land. That could be the reason why sauropterygians, and especially plesiosaurs, were able to reduce the dorsal projections of the pectoral and pelvic girdle more extremely and why a simultaneous partially extreme enlargement of the ventrally lying bones was possible in comparison to turtles.

Nothosaur and plesiosaur flippers show increasingly hyperphalangy (for nothosaurs e.g., Storrs 1993; Rieppel 1998, for plesiosaurs e.g., Caldwell 1997, compare to e.g., Hawkins 1840; Andrews 1910; Großmann 2006; Druckenmiller and Russell 2008; Schumacher and Martin 2015; Delsett et al. 2016; Sachs et al. 2016; Frey et al. 2017). Unlike Chelonioidea, whose flippers are mainly formed by elongation of individual phalanges of especially the three middle digits (Walker 1973). Sea turtle and plesiosaur foreflippers taper to the flipper tip, i.e., digit III (in plesiosaurs also the hindflippers) (Walker 1973; Robinson 1975). Sea turtles have an asymmetrical or cambered profile which is a key characteristic for underwater flying tetrapods (Fish 2004). Plesiosaurs might have had asymmetrical flipper profiles as well (Robinson 1975; Caldwell 1997). Contrastingly, nothosaur hands are shorter and more paddle-like (Storrs 1993) and less comparable to sea turtle and plesiosaur flippers. This underscores that plesiosaur fore- and hindflippers are overall convergently comparable to the hydrofoil-like foreflippers of sea turtles, but the underlying bony adaptations of both vary greatly.

The variably posteriorly expanded plesiosaur humeri and femora morphology and the possibly associated accessory ossicle formation (e.g., Andrews 1910; Sato and Storrs 2000; Großmann 2006; Sato et al. 2006; Smith 2007; Druckenmiller and Russell 2008; Schumacher and Martin 2015; Sachs et al. 2016; Frey et al. 2017) would need thorough investigations on whether this represents a phylogenetic, a stratigraphic, or an ecological signal. It should also be checked, if the different observed patterns eventually correlate with the flipper geometries determined by measuring aspect rations by O'Keefe (2001b).

The glenoid and acetabulum of plesiosaurs greatly resemble the ellipsoid glenoids of sea turtles. Although, their long axes are differently oriented (horizontally) in plesiosaurs (personal observation, Storrs 1993) than in Chelonioidea (anterodorsally-posteroventrally) (Walker 1973; Wyneken 2001, personal observation). It remains speculative what plesiosaur humeral and femoral heads looked like because they were probably, convergently to *Dermochelys coriacea*, (Rhodin et al. 1981; Snover and Rhodin 2008) covered by thick vascularized cartilage caps and their articulation surfaces were not parallel to the underlying bone. Sea turtles are able to elevate/depress or protract/retract the humerus, long axis rotation is inhibited (Walker 1971; Davenport et al. 1984; Pace et al. 2001; Rivera et al. 2011). Considering the similarity between the chelonioid glenoid and the plesiosaur glenoid and acetabulum this leads to the surprising conclusion that plesiosaurs were probably unable to rotate their humeri and femora as extremely (~ 90°) as suggested by authors discussing either style of locomotion for plesiosaurs (compare to Watson 1924; Tarlo 1958; Robinson 1975; Godfrey 1984; Lingham-Soliar 2000; Carpenter et al. 2010; Liu et al. 2015). A humerus or femur rotation by approximately 90° would presuppose some kind of a ball-and-socket joint that plesiosaurs certainly did not have. This leads to interesting implications: The plesiosaur glenoids/acetabula may have diverged to some degree from the sea turtle type and actually allowed some degree of humeral/femoral rotation. Alternatively, it may have been greatly underestimated and understudied how much flipper twisting along the flipper chord length (suggested briefly by Robinson 1975; Liu et al. 2015; Witzel et al. 2015) contributes to plesiosaur locomotion. During e.g., the downstroke, the flipper leading edge is twisted downwards along the flipper length axis and the trailing edge is twisted upwards. So the most extreme points in the flipper, the terminal phalanges of digit I and V, may even align in a vertical line (Krahl and Witzel (chapter 3)). A combination of both, humeral/femoral rotation and flipper twisting, may actually have been possible. It is difficult to compare the nothosaur glenoid to either turtles or plesiosaurs because it has not been described in detail. Further, thorough investigations of joint surfaces, ranges of motion of sauropterygian limb joints could yield new insights into the evolution of paraxial swimming in Sauropterygia.

Sea turtles have a functional elbow joint. Possibly the wrist joint, or an intracarpal joint, allows rotation but this has not been studied in detail to my knowledge. The distal flipper is much stiffened (Walker 1973). The nothosaur elbow is believed to be immobile (Kuhn-Schnyder 1987). The arrangement of radius, ulna, and the carpals suggest that lower arm rotation was possible in nothosaurs, as well as mobility in the carpometacarpal and the intraphalangeal joint (personal observation). In the fore- and hindflipper of plesiosaurs, only the glenoid and acetabulum were functional joints (Storrs 1993). This needs further research, because at least the carpometacarpal/tarsometatarsal and intraphalangeal joints appear to be mobile to some degree (personal observation). Additionally, if the glenoid and acetabulum largely restricted long axis rotation, flipper twisting would be inevitably needed for locomotion. Therefore, the issue of mobility within plesiosaur flippers would need profound investigation, taking into account the existing morphological differences between taxa. Nevertheless, the mobility of the foreflipper joints of sea turtles also remains understudied. In nothosaurs, this issue has remained basically untouched. Yet, foreflipper (in plesiosaurs also hindflipper) joint mobility in all three taxa would be crucial for our understanding of paraxial locomotion in secondary aquatic tetrapods.

This article also suggested the locomotor style of *Carettochelys* (Rivera et al. 2013) as a possible locomotory style for plesiosaurs. Many of the osteological characteristics arguing against rowing in plesiosaurs might also argue against this type of locomotion. Yet, the flipper tip excursion path seems to fit more adequately the plesiosaur hindflipper movements that Liu et al. (2015) inferred from computer simulations (compare Fig. 4c to Liu et al. 2015, Fig. 4A and B, p. 8) than the flipper tip excursion path described by Feldkamp (1987) for sea lions. Many osteological clues lead to the conclusion that plesiosaurs were not adapted for rowing as mode of locomotion but instead were more suited for underwater flight. Underwater flight is employed by long distance travelers (Walker and Westneat 2000). However, it remains a possibility that nothosaurs and plesiosaurs were able to modify their locomotory style to rowing or a rowing and flight combination for changes of direction or for surfacing for breathing like sea turtles (Wyneken 1997).

4. Conclusions

While nothosaurs partially relied on tail propulsion, plesiosaurs and sea turtles rely on paraxial locomotion. The reduction of the dorsal bracing system and simultaneous increase in coracoid size in nothosaurs and plesiosaurs, often used as argument pro rowing, is convergent to the secondary adaptation of turtles to salt and freshwater. In turtles this suit of adaptations does not reflect the change in locomotion from the terrestrial to the aquatic habitat but instead the diminishing of the impact of gravity on the body by buoyancy. Nothosaurs and plesiosaurs are not comparable to sea turtles in that the former evolved their flippers by hyperphalangy and the latter by phalangeal elongation. Superficially sea turtles and plesiosaurs are comparable because both have cambered hydrofoil flippers unlike nothosaurs that evolved more paddle-like flippers. A comparison of the plesiosaur glenoid and acetabulum to the glenoid of chelonioids shows, that plesiosaurs were probably unable to rotate their flippers by approximately 90° as depicted in the reconstructions of plesiosaur swimming modes so far. Studying the joints (glenoid, acetabulum, carpometacarpal, tarsometatarsal, and interphalangeal) of plesiosaurs and nothosaurs in comparison to recent taxa could shed light on degrees of freedom and actual motion range which would be necessary to paint a realistic picture of plesiosaur and nothosaur locomotion on an osteological basis, including flipper rotation and flipper twisting. The mode of locomotion employed by *Carettochelys insculpta*, that combines lift-based and drag-based components, is discussed for the first time as an option for plesiosaurs. Yet, many osteological clues point to underwater flight as the mode of locomotion for plesiosaurs. While plesiosaur locomotion has been subject to a number of studies. Nothosaur locomotion has remained largely unstudied.

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Chapter 2

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Humerus osteology, myology, and finite element structure analysis of Cheloniidae

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Running title: Humerus myology and FESA of Cheloniidae

Abstract

Adaptation of osteology and myology lead to formation of hydrofoil foreflippers in Cheloniidae (all recent sea turtles except *Dermochelys coriacea*) which are used mainly for underwater flight. Recent research shows the biomechanical advantages of a complex system of agonistic and antagonistic tension chords that reduce bending stress in bones. Finite element structure analysis (FESA) of a cheloniid humerus is used to provide a better understanding of morphology and microanatomy and to link these with the main flipper function, underwater flight. Dissection of a *Caretta caretta* gave insights into lines of action, i.e., the course that a muscle takes between its origin and insertion, of foreflipper musculature. Lines of action were determined by spanning physical threads on a skeleton of *Chelonia mydas*. The right humerus of this skeleton was micro-CT scanned. Based on the scans, a finite element (FE) model was built and muscle force vectors were entered. Muscle forces were iteratively approximated until a uniform compressive stress distribution was attained. Two load cases, downstroke and upstroke, were computed. We found that muscle wrappings (m. coracobrachialis magnus and brevis, several extensors, humeral head of m. triceps) are crucial in addition to axial loading to obtain homogenous compressive loading in all bone cross sections. Detailed knowledge on muscle disposition leads to a compressive stress distribution in the FE model which corresponds with the bone microstructure. The FE analysis of the cheloniid humerus shows that bone may be loaded mainly by compression if the bending moments are minimized.

keywords: Cheloniidae, humerus, muscle forces, dissection, micro-CT, lines of action, FESA

1. Introduction

1.1 Foreflipper osteology and myology of Cheloniidae

In comparison to other Testudines, Cheloniidae display numerous osteological and myological adaptations especially in the pectoral girdle (Walker, 1973; Wyneken, 1997; Depecker et al., 2006; Walker, 1971) and foreflippers (Renous, 1995; Wyneken, 1997; Walker and Westneat, 2000; Rivera et al., 2011) which form hydrofoils (Davenport et al., 1984). Some locomotory muscle origins spread onto the carapace and plastron, i.e., the musculus (m.) latissimus dorsi/teres major, m. pectoralis, and m. deltoideus clavicularis (Walker, 1973; Wyneken, 2001). The coracoid of Cheloniidae is relatively enlarged and shows large attachment areas for the m. biceps complex (i.e., m. brachialis inferior, m. biceps profundus, m. biceps superficialis) and m. coracobrachialis brevis (Walker, 1973; Depecker et al., 2006). The scapula is reduced in size, and the origin sites of m. latissimus dorsi/teres major, m. deltoideus scapularis, and m. subscapularis are relatively smaller (Walker, 1973) than in other turtles. Humeri of sea turtles, like long bones of other Tetrapoda, show in proximodistal section that they are hourglass-shaped which reflects cones of endochondral bone surrounded by a mantle of periosteal bone (Francillon-Vieillot et al., 1990). The v-shaped lateral process provides insertion area for m. pectoralis and m. supracoracoideus (Walker, 1973; Hirayama, 1994; Wyneken, 2001) (Fig. 1). The greatly expanded proximal medial process on the sea turtle humerus hosts attachment surfaces for the hypertrophied m. coracobrachialis magnus and m. subscapularis (Fig. 1). The ulna lies relatively dorsal and posterior to the markedly longer radius. The ulnare and intermedium are much larger than the radiale in turn. Connective tissue ontogenetically conjoins radius and ulna. The pisiform is enlarged. The flipper blade evolved by elongation of the phalanges of digit II, III, and IV (Walker, 1973; Wyneken, 2001). In sea turtles some extensors and flexors, especially in the manus, were reduced, but the remaining ones are well developed (Walker, 1973). Fusion of muscles, extensive formation of aponeuroses, and connective tissue partially fused to the dermis are responsible for the development of a semi-rigid flipper during postnatal ontogeny (Walker, 1973; Wyneken, 2001; Abdala et al., 2008).

Adult Chelonioidea usually swim by underwater flight. In this mode of locomotion, the humerus is mainly moved through the vertical plane and subordinately through the horizontal plane (Walker, 1971; Davenport et al., 1984; Pace et al., 2001; Rivera et al., 2011; Rivera et al., 2013). During the downstroke, the humerus is depressed and retracted, the elbow flexed (Davenport et al., 1984; Rivera et al., 2011) and the anterior flipper edge is rotated downward at the wrist joint. During the upstroke, the humerus is elevated and protracted, the elbow extended (Davenport et al., 1984; Rivera et al., 2011), and the anterior flipper edge is rotated upward at the wrist joint. Thus, the flipper tip describes the path of a skewed slim “O” in anterodorsal-posteroventral direction during underwater flight (Davenport et al., 1984; Rivera et al., 2011).

1.2 Finite element structure analysis

Homogenization of stresses in bone can lead to evolutionary beneficial lightweight structures (Klenner et al., 2015). Such a loading regime is established by agonistically and antagonistically acting tension chords which can be either passive (ligaments) or active (muscles; Witzel and Preuschoft, 2005; Rayfield, 2007; Sverdlova and Witzel, 2010; Curtis et al., 2011; Witzel et al., 2011; Klenner et al., 2015; Felsenthal and Zelzer, 2017). Because muscle forces are constantly changing during the flipper beat cycle of sea turtles, two load cases (Witzel and Preuschoft, 2005), i.e., the upstroke and downstroke of the foreflipper, were analyzed. The resulting functional loading is calculated by superposition of the loading conditions of all load cases (Carter et al., 1989). Functional loading of long bones leads to the development of bone curvature (Lanyon, 1980) which minimizes bending (Milne, 2016; McCabe et al., 2017). Long-term bending strains are reduced by bone remodeling (Lanyon, 1980). Computational simulations of the development of a human phalanx under axial compression and torsion correctly predicted its outer and inner bony structure (Lipphaus and Witzel, 2018). Muscle forces were calculated for a human femur model by minimization but not complete elimination of bending strain (Lutz et al., 2016). The model of Lutz et al. (2016) was validated by a finite element (FE) model, electromyography (EMG), and hip reaction force calculations which were computed and compared to data obtained from in vivo experiments by Bergmann et al. (2001).

Nonetheless, in vivo strains in vertebrate long bones indicate a more complex loading regime which includes bending, torsion, and axial compression (Blob and Biewener, 1999; Butcher et al., 2008; Sheffield et al., 2011; Young and Blob, 2015; Main and Biewener, 2004; Biewener and Dial, 1995; Carrano, 1998; Lieberman et al., 2004; Main and Biewener, 2007; Butcher and Blob, 2008; Young et al., 2017). Long bones of vertebrates, including Testudines, are either loaded by bending alternatingly or to a relatively large extend by compressive stresses and to a significantly lower degree by tensile stresses (Biewener and Dial, 1995; Blob and Biewener, 1999; Lieberman et al., 2004; Main and Biewener, 2004; Butcher and Blob, 2008; Butcher et al., 2008; Sheffield et al., 2011). However, if the recorded load cases were superposed, their superposition would show a more homogenous stress distribution and predominantly compressive stresses as the generally lower tensile stresses would be cancelled out. In turtles that walk on land, high torsional loads were found in the long bones (Butcher and Blob, 2008; Butcher et al., 2008). Considerable torsional loads were reported for archosaurs (Biewener and Dial, 1995; Carrano, 1998; Blob and Biewener, 1999; Main and Biewener, 2007), lepidosaurs (Blob and Biewener, 1999; Sheffield et al., 2011), but less so in mammals (e.g., Main and Biewener, 2004). The shift from the terrestrial to the aquatic habitat in Testudines is accompanied by a significant reduction of torsional loading. This could be the reason for the evolution of limb bone shapes in highly aquatic turtles species that differ from the common tubular form observed in terrestrial Tetrapoda, which are well adapted for shear strains (Young and Blob, 2015; Blob et al., 2016; Young et al., 2017).

The aim of this study is to conduct finite element structure analysis (FESA) on a sea turtle humerus for two load cases based on the criterion of bending minimization. The analysis was supported by dissection of sea turtle humerus musculature. Muscle functions were determined and agonistic and antagonistic muscles were grouped. Muscle forces were calculated for the foreflipper down- and upstroke. The results support observations that during underwater flight of sea turtles, the foreflipper downstroke contributes more to propulsion than the upstroke. FESA of this cheloniid humerus supports the importance of bending minimization for lightweight bony structures (Witzel and Preuschoft, 2005; Sverdlova and Witzel, 2010; Curtis et al., 2011; Witzel et al., 2011; Klenner et al., 2015).

2. Material & Methods

2.1 Dissection of *Caretta caretta* humerus musculature

At the Stazione Zoologica Anton Dohrn of Naples (SZN), Italy, in the dedicated marine turtle research center, a subadult Mediterranean female *Caretta caretta* was dissected. Its carapace length as measured over the curve was 66.6 cm and a body mass of 33.38 kg. The turtle had been caught accidentally by a bottom-trawler and was brought to the SZN for rescue. However, the turtle died within 24 hrs of its capture and was then frozen for later autopsy. The specimen was in good health as suggested by thick fat pads found during dissection. The main focus of the dissection of the *Caretta* specimen was the locomotory musculature of the foreflipper, especially those muscles that insert into, originate from, or span the humerus. Identification of these muscles was based on Walker (1973) and Wyneken (2001). Flexors and extensors were mainly identified by comparison with Walker (1973) (Fig. 17 A and B, p. 51). Myological terminology is based on Walker (1973). For positional terms, we follow Romer (1976) in the usage of anterior vs. posterior, ventral vs. dorsal, and proximal vs. distal, although these orientations do not necessarily correlate with humerus orientation during the movement cycle (see Davenport et al., 1984; Rivera et al., 2011 and Rivera et al., 2013 for description of the flipper beat cycle).

2.2 Lines of action

The cheloniid specimen used for derivation of lines of action (LOA) is a *Chelonia mydas* (ZFMK 70222) from the Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (Fig. 2). It had a curved carapace length of 107.7 cm. Lines of action are the connection between origin and insertion of a muscle in a straight line. They were obtained for each muscle inserting into, originating from, or spanning the humerus by clamping threads with tape onto the pectoral limb of ZFMK 70222. For muscles that originate or insert on large areas, usually the extreme points for attaching the threads were chosen, e.g., for m. pectoralis (Fig. 2). Two-bellied muscles were represented by two threads to show their main directions, although only the resultant vector was entered in the FE models. LOA were recorded in photographs. Photos of LOA were edited in Photoshop CS4. These photos provided the basis for sketches of the humerus and all its attaching muscles in form of LOA drawings. These were then implemented in to the FE model (Figs. 2 A, C, E; 4 A, E).

The plastron of ZFMK 70222 was removed because carapace and plastron largely covered the studied area. However, it was still not possible to photograph muscle attachments in standardized views because the carapace covers the pectoral girdle as well as the proximal half of the humerus in dorsal view. Therefore, views were chosen in a way that all muscles were visible from at least two different points of view and that as many muscles as possible were visible.

From the geometrical arrangement of LOA, muscle functions and agonistic and antagonistic relationships were deduced (Tab. 1, Tab. 2). The terminology used below follows Rivera et al. (2011) who use protraction vs. retraction and elevation vs. depression to describe the movement directions of the *Caretta caretta* humerus. This terminology suits the concept of underwater flight best.

Muscle functions were derived for FESA solely by their geometrical arrangement. Muscle functions derived from electromyography (m. latissimus dorsi/teres major, m. triceps, m. pectoralis, m. coracobrachialis, m. deltoideus) (Tab. 1) by (Rivera et al., 2011) did not influence the functional assessment at this point. However, discrepancies between the two methodically different data sets will be discussed in the relevant section.

2.3 FE model generation and FESA load cases

The micro-CT scans were done at the Division of Paleontology at the Institute of Geosciences of the University of Bonn with a v|tome|x S240 scanner manufactured by GE phoenix|x-ray (Wunstorf, Germany). A total of 600 images with an exposure time of 667 ms and an average of four were recorded for the scan. Voxel size was 236.4 µm, the voltage was set to 80 mV and the current was set to 80 µA. The image stacks in z direction for the volume model were generated by the software VG Studio Max from the rotational X-ray images.

The image stack of humerus cross sections in z direction generated from the micro-CT scans were imported into Simpleware ScanIP 5.1. By selecting a grey scale interval that includes cortex and spongiosa, but not their surroundings, the bony structure was segmented out in all images of the stack and used to generate the FE model of the bone (Fig. 4 A, E). Next, the volumetric model was meshed and then exported to ANSYS 16.0 (ANSYS Inc., Canonsberg, PA, USA). Then, the volumetric model was scaled to the dimensions measured on the actual humerus, since micro-CT images are virtually composed slices. The FE model of the humerus was modelled using the element type "solid 185", which is tetrahedral and has eight nodes. The articulation surfaces of the humeral head were constrained by bearings, i.e., the humeral head was immobilized. The FE model consists of 374768 tetrahedral elements and 84172 nodes. Cortical bone as well as spongy bone were modelled with a Poisson’s ratio of 0.3 each (Preuschoft and Witzel, 2005; Witzel and Preuschoft, 2005). Via greyscale selection, Young’s moduli was assigned to different microstructures. The material properties of spongiosa and cortex do not suddenly change. Their transition is gradually from lower to higher Young’s moduli from the center towards the periphery of the bone. Therefore, the bone cortex was subdivided into areas with two different Young’s moduli of 17500 MPa and 8000 MPa. The spongy bone was modelled with a Young’s modulus of 410 MPa. Values for Young’s moduli are based on Sverdlova and Witzel (2010).

Myologic characteristics, i.e., origin, insertion, LOA, muscle wrapping (Fig. 3 C), were transferred into LOA drawings of the humerus in anterior, posterior, dorsal, and ventral views and then entered as force vectors into the FE model (Fig. 4 A, E). Vector origins in the FE model represent insertions and origins of muscles on humerus (Fig. 1), vector directions are equal to the LOA (Fig. 2) of the respective muscles, and vector sizes illustrate muscle force (Tab. 3). Some muscles with relatively large attachment areas on the humerus, i. e., m. subscapularis, humeral head of m. triceps brachii, m. brachialis inferior, and m. coracobrachialis magnus, although they are represented by one LOA, were subdivided into several compartments. This means, that these muscles are not represented by one vector yielding the total force of the respective muscle, but by several smaller vectors that sum up to its total muscle force. These subdivisions were undertaken to obtain a more homogenous compressive stress distribution. Two-joint muscles, i.e., m. triceps brachii and m. biceps brachii, span the humerus as they originate from the pectoral girdle and insert into the radius or the ulna. Muscle forces of m. triceps brachii and m. biceps brachii influence the humerus FESA only indirectly. These muscles are represented by the resultant vectors acting on the distal humerus. They add to the counterforce which is applied on the humeral epicondyles by radius and ulna. The counterforce resulted from the axial components of the force vectors and the propulsive force. Although hydrodynamic forces have been calculated by computational fluid dynamics (CFD), complex movement and muscle activation make it impossible to define an average joint force. Therefore, the area of the joint was measured in the computational model to be 1657 mm^2. Values of average physiological loads of cartilage are 1-2 MPa (Ateshian and Hung, 2006; Harris et al. 2011). The resulting counterforce was calculated using the joint area and an average contact pressure of 1.5 MPa. Vectors of muscles wrapping around bone are represented by split-up vectors with different directions. This is necessary because ANSYS is not able to simulate stresses generated by curved lines. Therefore, the muscle wrapping is broken down into several smaller (straight) vectors to trace the curved muscle. Muscle wrappings aid in bone compression but also in moment rejection.

As the loading regime changes during a limb cycle, two load cases (Fig. 4 B and F, C and G) (Witzel and Preuschoft, 2005), down- and upstroke, i.e., humeral elevation and depression, were computed. We defined the following flipper position for down- and upstroke: the flipper trailing edge is angled at 90° to the cheloniid body length axis (through the midline) (compare to Rivera et al., 2011 Fig. 1A) and where it is at the same height of the glenoid in lateral view (corresponding approximately to Davenport et al., 1984 Fig. 7, p. 455, interval three and twelve). The long axis of the humerus is approximately angled at 45° to the body length axis (as derived from Rivera et al., 2011 Fig. 1, p. 3316).

Computing FESA of the two load cases is only possible if muscles are considered as pairs of agonists and antagonists (Tab. 2) (Jenkins and Goslow, 1983; Sverdlova and Witzel, 2010; Witzel et al., 2011). During the downstroke, the agonists power depression and retraction of the humerus and flexion of the flipper at the elbow at high force levels. The opposing antagonists keep this movement controllable by exerting lower levels of force. Humeral elevators and protractors and elbow extensors become the agonistic muscles that enable the flipper upstroke which has a high force output at this part of the cycle. The antagonists, i.e., the agonists from the downstroke, are now working at lower force levels and help to control the movements. At no point in the flipper beat cycle do all muscles work with maximum force at the same time. During normal swimming behaviour, maximum muscle forces are likely not reached. High muscle forces are expected for the agonists of the downstroke and upstroke, while considerably lower muscle forces are expected for the antagonists. Muscle forces were determined in iterative steps (Tab. 3).

Humerus maximum muscle forces for the dissected *Caretta caretta* specimen were approximated. This was done by measuring muscle architectural details, presuming all muscles would be parallel-fibred, and calculating the cross sectional areas of each muscle by employing the established formula for deriving muscle forces from the physiological cross sectional areas (Alexander and Vernon, 1975; Gans, 1982; Sacks and Roy, 1982; Powell et al., 1984; Anapol and Barry, 1996; Narici et al., 1992; Azizi et al., 2008). Then maximum muscle forces were calculated following e.g., Medler (2002) and (Gröning et al., 2013). Nevertheless, these approximated muscle forces provided us only with relative maximum force levels. This is because the FE model was built from a *Chelonia mydas* humerus of unknown ontogenetic stage (beyond early juvenile), and interspecific and intraspecific muscle (force) scaling relationships have not been established for extant sea turtle taxa.

So in a first run of the model, muscle forces were simply assumed based on relative muscle force levels gained from the *Caretta caretta* dissection, and the compressive stress distribution was computed. Then muscle forces were adjusted in such a way that bending moments in the model were minimized and compressive stresses were maximized, and the FESA was rerun. These steps were repeated until a homogenous compressive stress distribution was obtained for the whole bone volume (Sverdlova and Witzel, 2010; Witzel and Preuschoft, 2005).

3. Results

3.1 Muscle functions and myology of the cheloniid foreflipper based on dissection and lines of action

The threads attached onto the skeleton of ZFMK 70222 revealed the following LOA (Fig. 2) and muscle functions (Tab. 1): m. latissimus dorsi/teres major, m. deltoideus scapularis, and m. subscapularis elevate the humerus, whereas m. deltoideus clavicularis, m. pectoralis, m. supracoracoideus, m. coracobrachialis magnus, and m. coracobrachialis brevis depress it. Humeral protraction is provided by m. latissimus dorsi/teres major, m. deltoideus

muscle	function after Walker (1973)	function after Wyneken (2001)	function after Wyneken (2003)	function after Rivera (2011)	own interpretation
m. latissimus dorsi/m. teres major	humeral abduction, less protraction	humeral abduction, less protraction	humeral abduction, less protraction	elevator and protractor of humerus	elevation, protraction
m. deltoideus clavicularis	humeral abduction and protraction	humeral protraction and abduction	humeral abduction, less protraction	constrains humerus retraction during downstroke	depression, protraction
m. deltoideus scapularis					elevation, protraction
m. subscapularis	humeral abduction, protractor	humeral protractor	humeral protractor	/[1]	elevation, retraction
m. triceps brachii (triceps superficialis)	flexion of antebrachium, humeral protraction and abduction	humeral adduction; flipper twisting along its long axis, antebrachial abduction	humeral adduction	extends elbow	elbow extension, diaphyseal compression
m. pectoralis	humeral retraction and adduction	humeral retraction and adduction	/[1]	humeral depression and retraction	depression, retraction
m. supracoracoideus	humeral retraction and adduction, humeral protraction by anterior fibres	posterior portion: humeral protraction and abduction; anterior portion: humeral adduction and retraction	/[1]	/[1]	posterior portions: depression, retraction anterior portions: depression, protraction
m. coracobrachialis magnus	humeral retraction, less abduction	humeral retraction	/[1]	humeral depression and retraction	depression, retraction
m. coracobrachialis brevis	humeral retraction, adduction	/[1]	/[1]		depression, retraction
m. biceps superficialis	humeral retraction and antebrachial flexion	humeral retraction	controls flipper twist/rotation	/[1]	elbow flexion, diaphyseal compression, retraction
m. biceps profundus		humeral retraction, antebrachial flexion	humeral retraction, antebrachial flexion	/[1]	
m. brachialis inferior		/[1]	/[1]	/[1]	flexion
m. flexor carpi ulnaris	flexes antebrachium and manus	/[1]	/[1]	/[1]	flexes antebrachium and manus and rotates flipper
m. flexor carpi radialis	antebrachial flexor	/[1]	/[1]	/[1]	antebrachial flexor and rotates flipper
m. palmaris longus	flexes antebrachium, manus and digits	/[1]	/[1]	/[1]	flexes antebrachium, manus, and digits
m. tractor radii	antebrachial extensor	/[1]	/[1]	/[1]	antebrachial flexor
m. extensor carpi ulnaris	antebrachial extensor	/[1]	/[1]	/[1]	antebrachial extensor and rotates flipper
m. pronator teres	pronator of lower arm	/[1]	/[1]	/[1]	antebrachial flexor
m. extensor digitorum communis + m. extensor radialis superficialis	extends manus	/[1]	/[1]	/[1]	extends antebrachium and manus and rotates flipper
m. extensor radialis intermedius	antebrachial extensor	/[1]	/[1]	/[1]	antebrachial extensor

Tab. 1: Functions of Cheloniidae humerus musculature

/ = no muscle function deduced by the respective author clavicularis, m. deltoideus scapularis, and the anterior portions of m. supracoracoideus. Contrastingly, retraction is provided by m. subscapularis, m. pectoralis, posterior portions of m. supracoracoideus, m. coracobrachialis magnus, m. coracobrachialis brevis, and the m. biceps complex. The antebrachium is flexed by m. flexor carpi ulnaris, m. flexor carpi radialis, m. palmaris longus, m. tractor radii, m. pronator teres, and the m. biceps complex (Fig. 3 C, D). The manus is flexed by m. flexor carpi ulnaris and m. palmaris longus. The latter flexes the digits, too. Extension of the antebrachium is performed by m. extensor carpi ulnaris, m. extensor radialis superficialis + extensor digitorum communis (both muscles are fused in cheloniids according to Walker (1973)), extensor radialis intermedius, and m. triceps brachii, whereas m. extensor radialis superficialis + extensor digitorum communis also extend the manus. The leading edge of the flipper is rotated downwards by m. flexor carpi radialis and m. extensor carpi ulnaris and possibly also by m. extensor radialis superficialis + extensor digitorum communis (Fig. 3 A, B, E, F). The antagonist for this function is m. flexor carpi ulnaris.

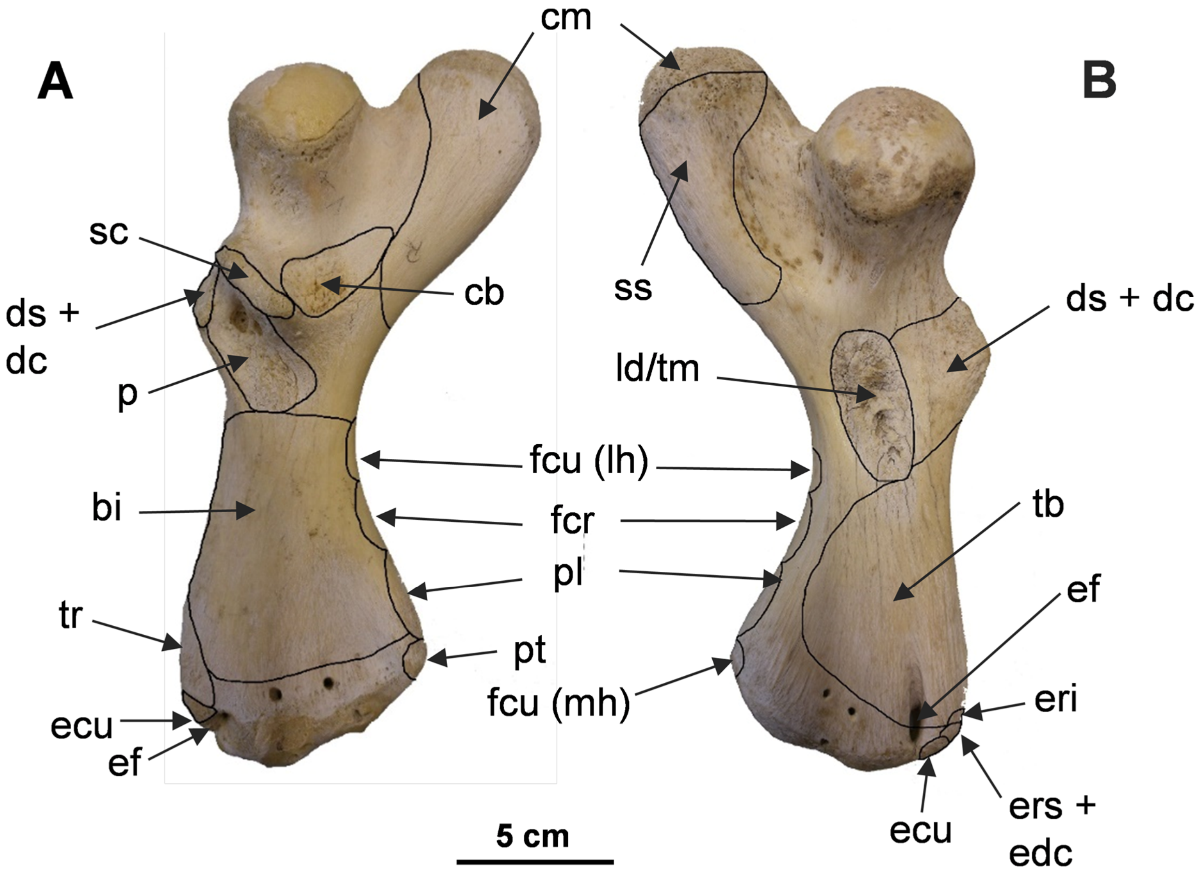

Fig. 1: Muscle attachment areas on (**A**) the ventral and (**B**) the dorsal sea turtle humerus as derived from *Caretta caretta* dissection. Attachment area for eri had to be inferred. Abbreviations: bc, m. biceps complex (i.e., bi, brachialis inferior; bs, biceps superficialis; bp, biceps profundus); cb, m. coracobrachialis brevis; cm, m. coracobrachialis magnus; dc, m.

deltoideus clavicularis; ds, m. deltoideus scapularis; ecu, m. extensor carpi ulnaris; ef, entepicondylar foramen; eri, m. extensor radialis intermedius; ers + edc, m. extensor radialis superficialis + m. extensor digitorum communis; fcr, m. flexor carpi radialis; fcu, m. flexor carpi ulnaris; ld/tm, m. latissimus dorsi/teres major; lh, lateral head; mh, medial head; p, m. pectoralis; pl, palmaris longus; pt, m. pronator teres; sc, m. supracoracoideus; ss, m. subscapularis; tb, m. triceps brachii; tr, m. tractor radii.

A common tendon is shared by m. latissimus dorsi/teres major which inserts into a large scar on the dorsal humerus shaft (Fig. 1). The two deltoid muscles, m. deltoideus scapularis and m. deltoideus clavicularis, converge into a large tendon. The part that m. deltoideus clavicularis contributes to mostly inserts anteriorly into the proximodistally

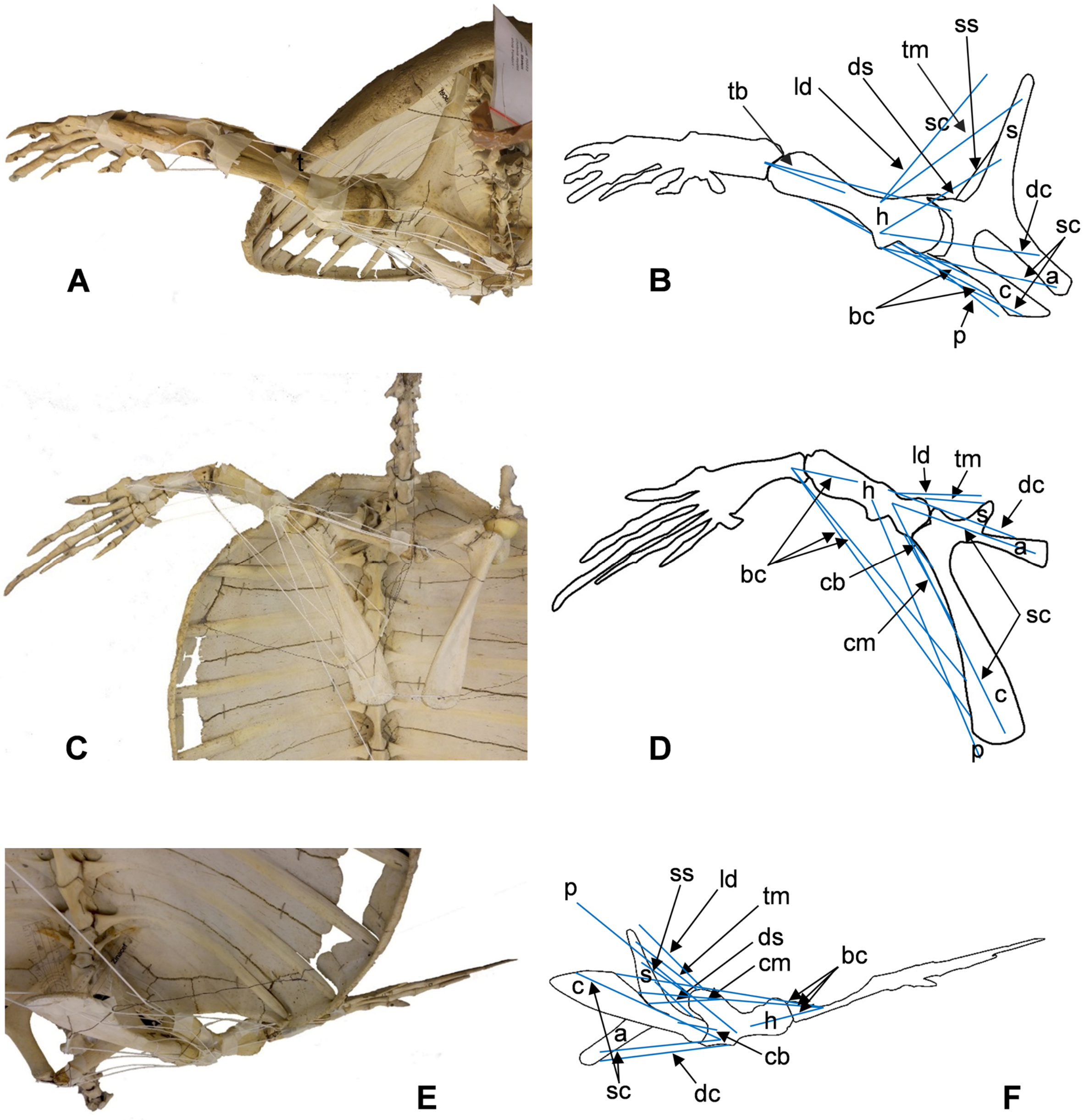

Fig. 2: Lines of action (white threads/blue lines) of proximal humerus musculature of *Chelonia mydas* ZFMK 70222. Plastron removed. Please note how all threads run in a fan shape from their humeral insertions towards the pectoral girdle. (**B**, **D**, **F**) contour drawings of (**A**, **C**, **E**). (**A**, **B**) anterior, (**C**, **D**) ventral, and (**E**, **F**) posteroventral view. Abbreviation: sa, acromion; bc, m. biceps complex (i.e., bi, brachialis inferior; bs, biceps superficialis; bp, biceps profundus); c, coracoid; cb, m. coracobrachialis brevis; cm, m. coracobrachialis magnus; dc, m. deltoideus clavicularis; ds, m. deltoideus scapularis; h, humerus; ld/tm, m. latissimus dorsi; s, scapula; tm, m. teres major; p, m. pectoralis; sc, m. supracoracoideus; ss, m. subscapularis; tb, m. triceps brachii.

extending leg of the v-shaped deltopectoral crest (Fig. 1). The part of the tendon that m. deltoideus scapularis contributes to mostly, attaches dorsally in between the m. deltoideus clavicularis and m. latissimus dorsi/teres major areas onto a smooth, unscarred bone surface. The m. pectoralis tendon inserts into the ventral humerus, distally to the v-shaped deltopectoral crest, at a large and deep muscle scar (Fig. 1). The large common tendon of all four m. supracoracoideus muscle bellies inserts into the ventral leg of the v-shaped deltopectoral crest (Fig. 1). The tendinous part of m. coracobrachialis magnus inserts into the proximal textured part of the medial process which is demarcated by a line. This line demarcates bone covered by periosteum and the fibrocartilaginous insertion. The rest of m. coracobrachialis magnus inserts by fleshy fibres, i.e., by muscle fibres and not by a tendon, into the approximate half of the medial process posteroventrally and extends down to the shaft, leaving no osteological correlates (Fig. 1). The main bulk of m. coracobrachialis brevis inserts by fleshy fibres into the intertubercular fossa distally and above the ventral branch of the v-shaped deltopectoral crest. Yet, this insertion area is associated with a relatively large and deep muscle scar in comparison to muscle size (Fig. 1). Neither flexors nor extensors leave visible osteological correlates on the distal humerus. Musculus coracobrachialis magnus wraps around the medial process. Around the bony saddle, between the humeral head and medial process, m. coracobrachialis brevis is wrapped.

Furthermore, m. triceps brachii, m. extensor carpi ulnaris, m. extensor radialis superficialis + extensor digitorum communis, and m. extensor radialis intermedius are found to wrap around the distal humerus when the elbow is flexed (Figs. 3; 4 A, E). Adjacent to the pisiform, m. flexor carpi ulnaris inserts into the dermis (Fig. 3 D). We were not able to identify m. extensor radialis intermedius and the tendinous scapular head of the m. triceps

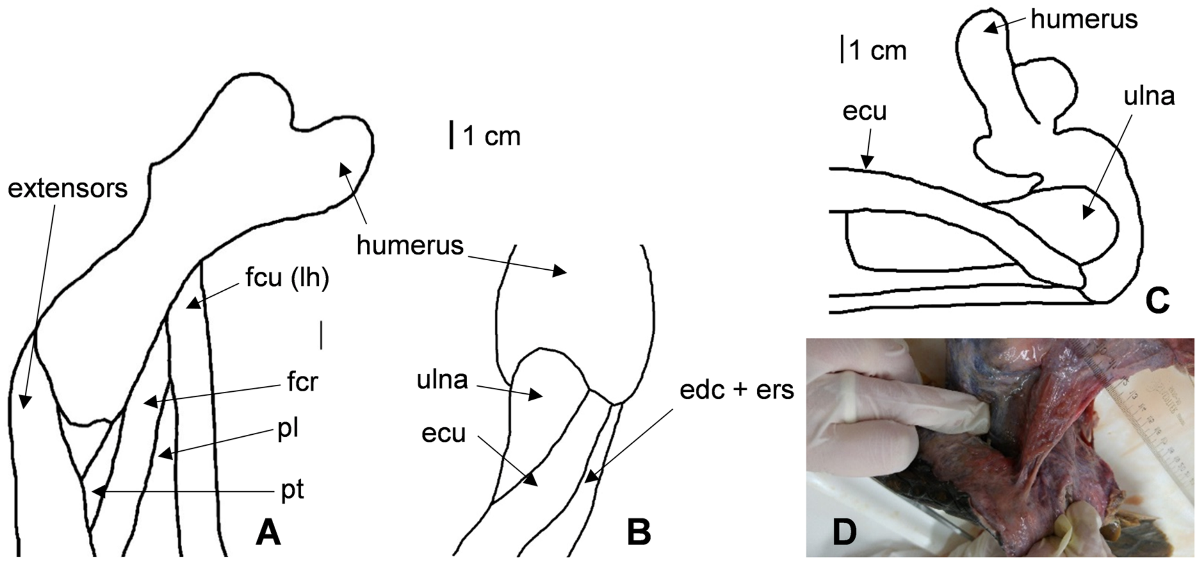

Fig. 3: Dissection of right foreflipper of *Caretta caretta*. (**A**-**C**), tracings from photographs that were taken during dissection. (**A**) dorsal view, ecu and ers + edc are "unwrapped". The straight articulation of humerus and radius/ulna is an artifact of muscle removal (compare to (**B**)). (**B**) ventral view, note the strong bend of the humerus in relation to radius/ulna. (**C**) this position equates to a flipper that is held at approximately body midline. Note how ecu wraps around the radius. The previously removed ers + edc wrapped only slightly around the radius, running toward the distal end of radius/ulna when the flipper is held in a neutral position. (**D**) fcu is inseparable from the dermis at the level of the pisiform. Abbreviations: ecu, m. extensor carpi ulnaris; ers + edc, m. extensor radialis superficialis + m. extensor digitorum communis; fcr, m. flexor carpi radialis; fcu (lh), m. flexor carpi ulnaris lateral head; pl, palmaris longus; pt, m. pronator teres; tr, m. tractor radii.

brachii. Accordingly, we had to rely on literature data for the FE model (Walker, 1973; Wyneken, 2001). The former muscle arises tendinously dorsally to the glenoid from the scapula and inserts in common with the humeral head. The latter originates from the radial epicondyle proximal to m. extensor radialis superficialis + extensor digitorum communis and distal to m. tractor radii, and it inserts dorsally into the radius along its whole length (Walker, 1973). Four muscle bellies of m. supracoracoideus (taking their origin from the coracoid, acromion, plastron and medial scapula, and acromiocoracoid ligament) were found.

3.2 FESA of the *Chelonia mydas* humerus

Initial iterative steps of FESA left the medial process and the radial epicondyle unloaded by compressive stress. Under predictions of FESA, unloaded regions indicate either that there exists no bony material here in the biological structure, or that the model is still flawed. Because the former can be excluded because the FE model was built from micro-CTs of a real bony structure, the latter was considered more likely. The medial process and the distal epicondyles were loaded by compressive stress in subsequent runs, when the muscle wrappings of the m. coracobrachialis magnus and m. coracobrachialis brevis around the medial process and the extensors wrapping around the radial condyle were added. Muscle wrapping imposes compressive force vectors on bony features mentioned above. In contrast to muscles that do not wrap around bony structures, which only impose tensile loading onto their attachment region. Muscle wrappings prove to be crucial for receiving realistic FESA results.

The micro-CT scans of the humerus show the hourglass shape of the compact cortex, being thickest in the center of growth at mid diaphysis and thinning out towards the proximal and distal epiphyses. Underneath the thin cortical joint caps lie cones of spongy bone. The FE model shows moderate to high compressive stress (-3.0 MPa to -13.5 MPa) that corresponds well to the compact cortex (grey areas in the CT scan), whereas low compressive stresses (-1.5 MPa to -3.0 MPa) correspond to spongy bone in the region of the humeral head and the proximal and distal epiphyses (Fig. 4 B-D, F-H). The bridge between the medial process and humeral head displays a thicker covering of compact cortex than the adjacent areas. The FE model shows high compressive stresses, up to -13.5 MPa in this region (Fig. 4 B, C, F, G). The richness in detail with which bone microanatomical features could be redrawn by the FESA validate the accuracy of the musculoskeletal model build for the cheloniid humerus. Differences between the compressive stress distributions of the two load cases indicate subordinate tensile forces (Fig. 4 B, C, F, G).

During the downstroke load case, the agonistic muscles depress and retract the humerus and the flexors flex the flipper at the elbow and rotate the leading edge downward at the wrist joint. While the antagonists with the opposing functions control the movement. During the upstroke load case muscles that are responsible for humeral elevation and protraction, flipper extension at the elbow and flipper leading edge upward rotation at the wrist joint become the agonists. For the first time, muscle forces imposing a compressive stress regime for cheloniid humerus musculature was derived experimentally by FESA. An agonistic muscle operates with about twice the force with which it operates as an antagonistic muscle. For example, when m. coracobrachialis magnus functions as an agonist in flipper depression and retraction during the downstroke, it develops a muscle force of 970 N. Contrastingly, it only operates with half that force, 485 N (Tab. 2, Tab. 3), when it

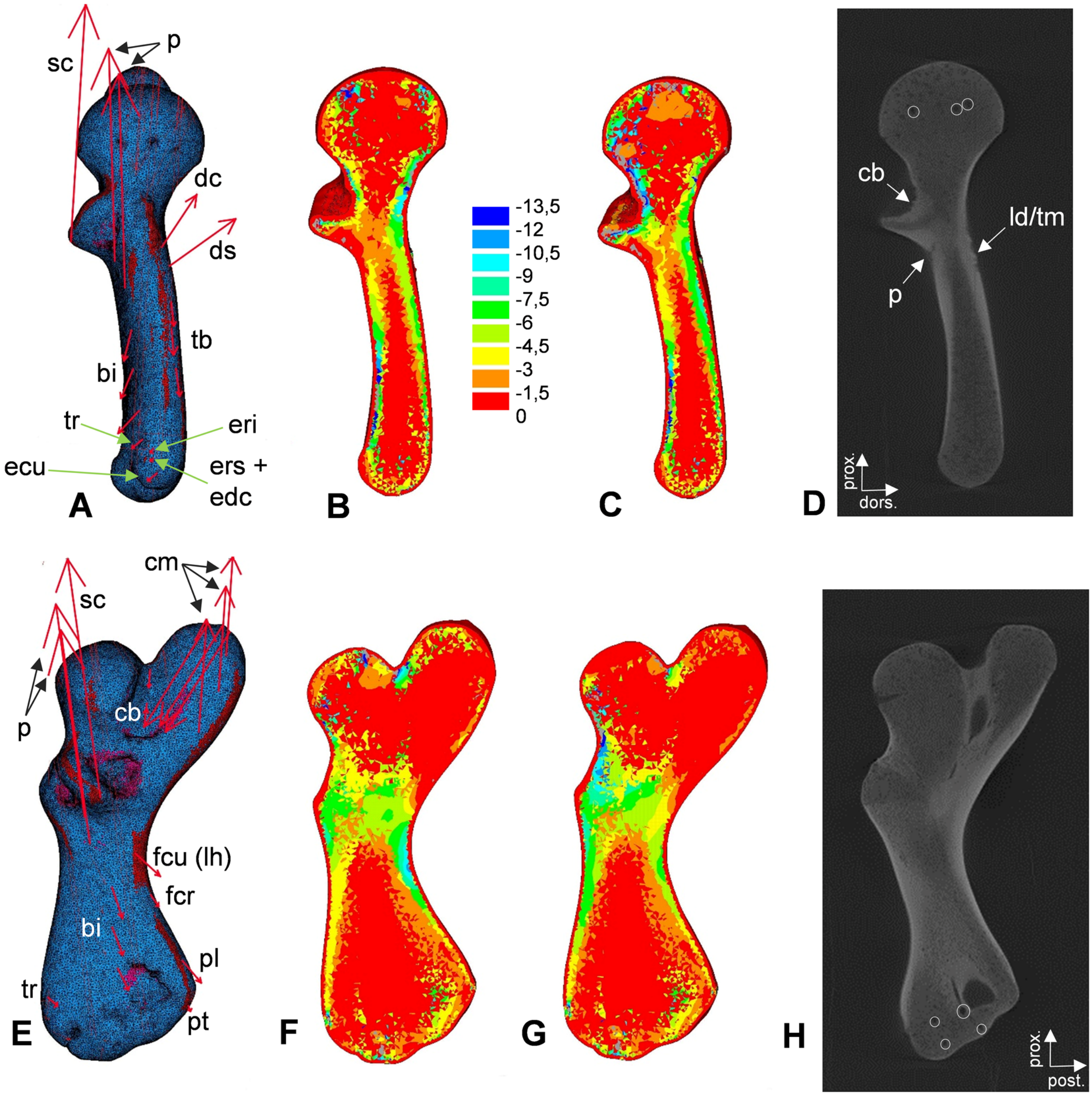

Fig. 4: FESA of the right humerus of *Chelonia mydas* ZFMK 70222. (**A**, **E**) volume model with force vectors entered in (**A**) anterior view and (**E**) ventral view. (**B**, **C**, **F**, **G**) compressive stress distribution; (**B** and **F**) load case downstroke, (**C** and **G**) load case upstroke, (**B** and **C**) in anteroposterior view and (**G** and **F**) in dorsoventral view. (**D**, **H**) micro-CT slices in (**D**) anteroposterior view and (**H**) dorsoventral view. The colour spectrum codes the compressive stress in MPa. Please note how well areas of higher compressive stress (green and blue colour spectrum) and lower compressive stress (yellow to red colour spectrum) (**B**, **C**, **F**, **G**) correspond with areas of compact bone (denser, or lighter appearing areas) and spongy bone (less dense, or darker appearing areas) in the micro-CT slices (**B** and **C**). White circles indicate artifacts from skeleton mounting (drill holes). Abbreviations: bi, brachialis inferior; cb, m. coracobrachialis brevis; cm, m. coracobrachialis magnus; dc, m.

deltoideus clavicularis; ds, m. deltoideus scapularis; ecu, m. extensor carpi ulnaris; eri, m. extensor radialis intermedius; ers + edc, m. extensor radialis superficialis + m. extensor digitorum communis; fcr, m. flexor carpi radialis; fcu (lh), m. flexor carpi ulnaris; ld/tm, m. latissimus dorsi/teres major; p, m. pectoralis; pl, m. palmaris longus; pt, m. pronator teres; sc, m. supracoracoideus; tb, m. triceps brachii; tr, m. tractor radii.

functions as an antagonist. During the downstroke load case, m. pectoralis is the strongest muscle (1210 N) followed closely by m. supracoracoideus (1100 N). The muscle with the highest muscle force during the upstroke is m. subscapularis (873 N). The forces of the muscles inserting into the proximal half of the humerus are substantially higher than those originating from the distal half (Tab. 3), despite the counterforce induced by radius and ulna during swimming which had been added. Forces of those muscles inserting proximally into the humerus range from 91 to 1210 N. Contrastingly, muscle forces of extensors and flexors arising from the distal humerus range from around 11 to 87 N.

Agonists	Antagonists
m. latissimus dorsi/m. teres major (elevation, protraction)	m. pectoralis (depression, retraction), m. supracoracoideus (posterior portions) (depression, retraction)
m. subscapularis (elevation, retraction), m. biceps (retraction)	m. deltoideus clavicularis (depression, protraction), anterior portions of m. supracoracoideus (depression, protraction)
m. deltoideus scapularis ((elevation) protraction)	m. coracobrachialis magnus, m. coracobrachialis brevis ((depression) retraction)
m. triceps (elbow extension and diaphyseal compression)	m. biceps (elbow flexion and diaphyseal compression)
m. triceps humeral head (elbow extension)	m. brachialis inferior (elbow flexion)
m. flexor carpi ulnaris (lateral and medial head) (rotates posterior edge down/anterior edge up)	m. extensor carpi ulnaris and m. flexor carpi radialis (rotate anterior flipper edge down)
m. flexor carpi ulnaris (lateral and medial head) (rotates posterior edge down/anterior edge up)	m. extensor-radialis superficialis + m. extensor digitorum communis (rotate anterior flipper edge down)
m. extensor digitorum communis + m. extensor radialis superficialis (extension of lower arm)	m. palmaris longus (flexion of lower arm and digits)
m. extensor carpi ulnaris (extension of lower arm)	m. flexor carpi radialis (lower arm flexion, rotates flipper leading edge down)
m. extensor radialis intermedius (extension)	m. tractor radii (flexion), m. pronator teres (flexion), m. flexor carpi ulnaris (flexion)

Tab. 2: Agonists and antagonists of the foreflipper of ***Chelonia mydas***.

muscle	**load case downstroke [N]**	**load case upstroke [N]**
m. latissimus dorsi + teres major	129	259
m. deltoideus clavicularis	365	182
m. deltoideus scapularis	91	181
m. subscapularis	437	873
m. triceps	77	77
m. pectoralis	1210	605
m. supracoracoideus	1100	414
m. coracobrachialis magnus	970	485
m. coracobrachialis brevis	22	11
m. biceps	294	294
m. brachialis	291	146
m. tractor radii	52	26
m. extensor radialis superficialis + m. extensor digitorum communis	32	65
m. extensor carpi ulnaris	11	22
m. extensor radialis intermedius	10	20
m. flexor carpi ulnaris (medial part)	22	11
m. flexor carpi ulnaris (lateral part)	87	43
m. palmaris longus	24	49
m. flexor carpi radialis	52	26
m. pronator teres	23	26

Tab. 3: Muscle forces for ***Chelonia mydas*** humerus musculature

4. Discussion

In comparison to *Pseudemys scripta elegans* muscle attachments described by Walker (1973) (Fig. 6, p. 16), muscles inserting into the humerus (m. coracobrachialis magnus, m. coracobrachialis brevis, m. subscapularis, m. deltoideus scapularis, m. deltoideus clavicularis, m. supracoracoideus, m. pectoralis, m. latissimus dorsi/teres major) are relocated distally toward the shaft in *Caretta caretta* (Fig. 1; compare to Walker (1973), Fig. 6, p. 16). The anterior edge of the cheloniid humerus is rather straight, and the extensors (except for m. tractor radii) of Cheloniidae are placed distally, close to the radial capitellum and close to the elbow joint capsule, as seen in *Pseudemys* Walker (1973) (Fig. 1). Posteriorly the humerus of Cheloniidae is markedly curved and distally expanded (Fig. 1). In *Caretta caretta*, the flexor origin areas are shifted proximally by up to half of the humerus length, and they are markedly larger than the extensors (Fig. 1). Possibly, the proximal shift of flexor attachments onto the humeral shaft induces the humerus' posterior curvature and provides a more efficient moment arm. The difference in extensor and flexor size is consistent with the observation by Davenport et al. (1984) that the downstroke contributes more to propulsion than the upstroke.

Interpretations of muscle functions (Tab. 1) mostly corroborate the results of Walker (1973), Wyneken (2001), Wyneken (2003), and Rivera et al. (2011) for the pectoral musculature and those of Walker (1973) for the limb extensors and flexors. Electromyographically derived functions for m. latissimus dorsi/teres major, m. pectoralis, coracobrachialis, and m. triceps brachii by Rivera et al. (2011) were corroborated in this study. For m. deltoideus, Rivera et al. (2011) did not distinguish between the scapular and the clavicular head and did not state which head was implanted with an electrode. M. deltoideus was found to be active as an antagonist to the retractional and depressional function of m. pectoralis during the downstroke (Rivera et al., 2011). This could possibly indicate that the EMG study obtained data for the clavicular head of m. deltoideus, and that more refined EMG data for m. deltoideus scapularis would show the expected activational pattern during humeral protraction and elevation. The largest differences between the results presented here and those of other authors were found in the function of the scapular head of the m. triceps brachii and the coracoidal heads of the m. biceps complex, and in m. coracobrachialis magnus, m. coracobrachialis brevis, m. extensor radialis superficialis + extensor digitorum communis, m. extensor carpi ulnaris, m. flexor carpi radialis, and m. flexor carpi ulnaris. While the coracoidal heads of the m. biceps complex may add to retraction power, the moment arm of m. triceps brachii is inappropriate for an elevational component.

Our finite element modelling showed that it was impossible to load the humeral diaphysis by compression without including muscle forces of the two-joint muscles (m. triceps brachii, m. biceps complex). While the proximal pectoral musculature pulls the humeral head into the glenoid, the distal extensors and flexors likewise pull radius and ulna onto the humeral epiphyses. The two two-joint muscles (m. triceps brachii, m. biceps complex) are the only muscles that compress the region of the humeral diaphysis.

Contrastingly, the proximal epiphysis is functionally loaded by compression by all other pectoral muscles. The distal epiphysis is compressed by the extensors and flexors that originate from the distal humerus.

Thus, dissection showed that m. extensor radialis superficialis + extensor digitorum communis, m. extensor carpi ulnaris, and m. flexor carpi radialis have the additional function of jointly rotating the leading edge of the cheloniid flipper ventrally. These are the muscles that diagonally cross the antebrachium. Musculus flexor carpi ulnaris is the only muscle that appears to have an appropriate lever arm to rotate the leading edge of the flipper dorsally.

The EMG activity patterns obtained for five selected cheloniid muscles by Rivera et al. (2011) document their active contraction during the limb cycle. During the passive stretching of a muscle, a significantly lower activity, the resting potential, should be expected. This appears to contradict our findings that antagonistic muscles are also active and develop muscle forces although, according to the EMG, they should seemingly be inactive. Muscles experience either a stretching-shortening or a shortening-stretching cycle during a movement (Rassier et al., 1999). On the one hand, muscles that experience stretching, passively resist their stretching by intrinsic forces (e.g., Gordon et al., 1966). On the other hand, antagonistic muscles show detectable electric activation, just markedly lower than the agonistic muscles (Aagaard et al., 2000). Therefore, an EMG study that would specifically investigate agonistc and antagonistic muscle activity in sea turtles could corroborate the findings of this study. Strain gauges could give insights into the in-vivo loading regime of cheloniid humeri during underwater flight. Maximum muscle force determination with the help of physiological cross sectional areas of cheloniids that are of similar size as the *Chelonia mydas* in the current study, could corroborate the magnitude of muscle forces calculated by FESA.

Many muscles were found to wrap around bony parts (medial process, bridge between medial process and humeral head, radial epicondyle): m. coracobrachialis magnus, m. coracobrachialis brevis, m. extensor radialis superficialis + extensor digitorum communis, m. extensor carpi ulnaris, m. extensor radialis intermedius, and m. triceps brachii. These muscles prove to be important because without them, it would be impossible to load adjacent bony regions by compressive stresses and they would be solely loaded by tensile stresses (Fig. 4 A, E) (Curtis et al., 2008).

Initial versions of the model resulted in, e.g., highly loaded spongy areas, insufficiently loaded compact cortical regions, and even tensile stresses. After dissection of the *Caretta* specimen and numerous refinements of muscle forces and directions, the FE models (strength of compressive forces) and micro-CTs (degree of bone compactness) (Fig. 4

B-D, F-H) match very well. Although Young's moduli were set manually in advance based on the greyscale values of the micro-CTs, this supports our hypotheses about LOA and muscle forces. For the upstroke, m. subscapularis produces the highest muscle force (792 N), whereas for the downstroke, m. pectoralis produces the highest muscle force (1100 N) (Tab. 3). This corroborates the observation by Davenport et al. (1984) that the downstroke contributes relatively more to propulsion than the upstroke. Future studies deriving muscle forces via physiological cross sectional areas and elaborate EMG studies focussing on agonistic and antagonistic muscle relationships and strain gauges could validate our FESA results and help to establish FESA as a non-invasive method for muscle force determination.

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Chapter 3

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Appendix

Homology of plesiosaur foreflipper and hindflipper myology.

Foreflipper and hindflipper muscle reconstructions of *Cryptoclidus eurymerus* in comparison to functional analogues: Introduction of a myological mechanism for flipper twisting

Anna Krahl and Ulrich Witzel

Keywords

Plesiosauria, muscle reconstructions, underwater flight, flipper twisting, functional analogues

Abstract

Plesiosaurs, diapsid crown-group Sauropterygia, inhabited the oceans from the Late Triassic to the Late Cretaceous. Their most exceptional characteristic are four hydrofoil-like flippers. The question whether plesiosaurs employed their four flippers in underwater flight, rowing flight, or rowing has not been settled yet. Plesiosaur locomotory muscles have been reconstructed in the past, but neither the pelvic muscles nor the distal fore- and hindflipper musculature have been reconstructed entirely. All plesiosaur locomotory muscles were reconstructed in order to find out whether it is possible to obtain muscles that are necessary for underwater flight including those that enable flipper twisting, which has been proven by hydrodynamic studies to be necessary for efficient underwater flight. So, *Cryptoclidus eurymerus* fore- and hindflipper muscles and ligaments were reconstructed with the extant phylogenetic bracket (Testudines, Crocodylia, and Lepidosauria) and correlated with osteological features. Muscle functions were geometrically derived. Additionally, plesiosaur joint morphology, osteology, and myology are examined in contrast to potentially functionally analogous Chelonioidea, Spheniscidae, Otariinae, and Cetacea. Extensor and flexor origin areas on the plesiosaur humerus, which show usually no osteological correlates in sauropsids, were probed osteohistologically to find out whether they provide evidence for muscle attachment. 52 plesiosaur fore- and hindflipper muscles were reconstructed. Amongst these are flipper depressors, elevators, retractors, protractors, and rotators which are necessary for a fore- and hindflipper downstroke and upstroke, the two sequences that represent an underwater flight flipper beat cycle. Additionally, other muscles were capable to twist fore- and hindflippers along their length axis during down- and upstroke accordingly. A combination of these muscles and intermetacarpal/intermetatarsal and metacarpodigital/metatarsodigital ligament systems that passively engage the successive digits could have accomplished fore-and hindflipper length axis twisting in plesiosaurs that is

essential for underwater flight. Furthermore, muscles that could possibly actively adjust the flipper profiles for efficient underwater flight were found, too.

1 Introduction

1.1 Plesiosaur locomotory and muscuskeletal system

Plesiosauria are secondary aquatic tetrapods which form the crown-group of Sauropterygia and are found within Diapsida. Sauropterygia are either placed on the basal archosauromorph (Merck, 1997) or lepidosauromorph lineage (Rieppel & Reisz, 1999), or forming the sister-group to both (Neenan, Klein & Scheyer, 2013). In the Late Triassic plesiosaurs arise (Wintrich et al., 2017) and go extinct at the K/Pg boundary (Bardet, 1994; Motani, 2009; Vincent et al., 2011; Vincent et al., 2013). The most unique character of plesiosaurs are their four very similarly shaped flippers. They taper to the flipper tip and form a hydrofoil (Robinson, 1975, 1977) with an asymmetrical flipper profile (Robinson, 1975; Caldwell, 1997). All other extinct and extant secondary aquatic tetrapods that have evolved hydrofoil-shaped flippers (Chelonioidea, Spheniscidae, Otariinae, Cetacea), solely evolved one pair of flippers, namely the foreflippers (Walker, 1973; Feldkamp, 1987; Fish & Battle, 1995; Fish, 2004; Cooper et al., 2007b). Plesiosaur locomotion, whether they fly underwater, row, or employ a combination of both styles, has remained debated for over two centuries until today (Krahl dissertation (chapter 1) for review). Krahl (chapter 1) suggests that flipper twisting along the flipper length axis is largely understudied in plesiosaurs, in comparison to their locomotory style. Flipper twisting is a crucial component of underwater flight (Witzel, Krahl & Sander, 2015). It has been briefly addressed by Robinson (1975) and Liu et al. (2015) and hydrodynamically tested by (Witzel, Krahl & Sander, 2015).

The shoulder and hip joint are mobile in plesiosaurs. The plesiosaur glenoid is oval in shape with its long axis lying anteroposteriorly (Robinson, 1975). The acetabulum is also oval in shape but unlike the glenoid it is dorsoventrally more depressed and lengthened anteroposteriorly. Posteriorly to posterodorsally the ilium contributes to the acetabulum which is formed by pubis and ischium to a greater extend (Andrews, 1910). The articular surfaces of the proximal humerus and femur are round, so both shoulder and hip joint are not congruent. The elbow/knee and wrist/ankle joints are relatively stiffened and possibly allow some minor degree of mobility. The interphalangeal joints are mobile and maybe even more mobile towards the flipper tip than towards metacarpals/metatarsals (Robinson, 1975).

The scapula and the greatly enlarged coracoid of *Cryptoclidus eurymerus* are two plate-like bones that lie ventrally anteriorly to the closely arranged gastralia. Both bones contact their opposite side in the ventral body mid-line slightly v-shaped. The dorsal expansion of the scapula is very short. Anterior to the scapula some dermal, possibly clavicular or interclavicular, remains may be found. The pectoral girdle mirrors the shoulder girdle: The pubis is greatly expanded, pubis and ischium are ventrally positioned plate-like bones that meet slightly angulated in the body midline with their counterpart from the other body side. The ilium is very small and unfused with neither pubis nor ischium or sacrum. Humerus and femur have an oval mid-shaft cross-section. Proximally the shaft is rounded and ends in a roughly pitted articular surface. Dorsally both bones have a tuberosity/trochanter that slants mildly posteriorly. Distally, humerus and femur of *Cryptoclidus* expand hammer-shaped (humerus more than femur). Radius/ulna and tibia/fibula are dorsoventrally depressed and much shortened in comparison to Eosauropterygia. Carpals and tarsals are well ossified as well as the metacarpals and phalanges. Andrews (1910) describes incipient accessory ossicles in the carpus and tarsus, which are not present in specimen IGPB R 324 on which this study is based. All five digits of fore- and hindflipper are hyperphalangic. In both, fore- and hindflipper, digit I and V are the shortest, II and IV are successively longer, and digit III is the longest (Andrews, 1910).

Ligaments (scapulohumeral, scapulosternal, and mesocleidosternal) in the shoulder girdle have been reconstructed by Araújo & Correia (2015). A puboischial, iliopubic, and ilioischial ligament have been reconstructed for the plesiosaur pelvic girdle by Robinson (1975).

Plesiosaur muscles have been reconstructed by Watson (1924), Tarlo (1958), Robinson (1975), Lingham-Soliar (2000), Carpenter et al. (2010), and Araújo & Correia (2015). It is not clearly stated on which taxa the plesiosaur muscle reconstructions are based on by Watson (1924), Tarlo (1958), Robinson (1975), and Lingham-Soliar (2000). Carpenter et al. (2010) and Araújo & Correia (2015) based plesiosaur myology on the extant phylogenetic bracket (EPB), the former on lepidosaurs (tuatara) and turtles and the latter on lepidosaurs, crocodilians, and turtles. Araújo & Correia (2015), Tarlo (1958), and Watson (1924) reconstructed muscles of the pectoral girdle and Robinson (1975), Lingham-Soliar (2000), and Carpenter et al. (2010) also reconstructed muscles of the pelvic girdle.

P, scs, sc, cb, cl, ds, and ld which originate from the pectoral girdle and insert into the humerus in sauropsids were reconstructed by all six above mentioned studies. Dc was not reconstructed by Tarlo (1958). Scapulohumeralis anterior was not reconstructed by Araújo & Correia (2015) and Carpenter et al. (2010). Shp was not reconstructed by Tarlo (1958), Watson (1924), and Robinson (1975). Tb and bb were only considered by Robinson (1975) and Araújo & Correia (2015) and only the latter by Carpenter et al. (2010). An attempt at reconstructing distal plesiosaur humerus and flipper musculature has been made exclusively by Robinson (1975) who reconstructed a highly reduced foreflipper (fcr, fcu, and long flexors) which appears almost cetacean-like (compare to Cooper et al., 2007b).

Cfb, cfl, pe, pi, and ife have been reconstructed by Robinson (1975), Lingham-Soliar (2000), and Carpenter et al. (2010). It, ifi, and pit have been reconstructed by Robinson (1975) and Lingham-Soliar (2000). Only Robinson (1975) has reconstructed f, a, i, af, and reconstructed plesiosaur hindflipper musculature (peroneus, and ta+plantar aponeurosis). Pti, fti, and fte are present in Sauropsida (Romer, 1923; Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011) but have not been reconstructed by any of the authors. No muscles that originate from the distal femur or hindflipper have been reconstructed.

While Watson (1924), Tarlo (1958), Robinson (1975) assigned functions to every muscle they reconstructed for plesiosaurs, Lingham-Soliar (2000) only assigned functions to p, cb, cl, and sc, and Carpenter et al. (2010) deduced functions for most reconstructed muscles except for dc, ds, and bb. Araújo & Correia (2015) reconstructed ld but assigned no function to it. They also suggest that p is reduced in plesiosaurs and therefore did not assign any muscle functions to it. Hindflipper muscle functions were given by Carpenter et al. (2010) and Robinson (1975) for all muscles they reconstructed.

1.2 Functional analogues locomotory and muscuskeletal system

It is impossible to find a recent (or extinct) functional analogue to the plesiosaur hindflipper, as Plesiosauria are the only tetrapods that have ever evolved four hydrofoil-shaped hindflippers. Recent highly aquatic groups either evolved flukes like cetaceans (Fish, 1996; Woodward, Winn & Fish, 2006) or webbed paddle feet for rowing, steering, and walking on land (Walker, 1971; Pinshow, Fedak & Schmidt-Nielsen, 1977; Clark & Bemis, 1979; Davenport, Munks & Oxford, 1984; Feldkamp, 1987; Wyneken, 1997; Berta, Sumich & Kovacs, 2005). Therefore, the best this study can do is provide possible functional analogues for the plesiosaur foreflipper. Then, based on the very similar morphology of the pectoral and pelvic limb, it is presumed, that similar conditions that are found for the foreflipper must also hold true for the hindflipper.

1.2.1 Chelonioidea

Chelonioidea have evolved many adaptations in comparison to other turtles due to their secondary aquatic lifestyle. Sea turtles are underwater fliers (Walker, 1971; Davenport, Munks & Oxford, 1984; Wyneken, 1997; Rivera, Wyneken & Blob, 2011; Rivera, Rivera &

Blob, 2013) and have a hydrofoil-like foreflipper (Walker, 1973) with an asymmetrical profile (Fish, 2004). The hindflippers show aquatic adaptations, but are flat, rounded, and webbed paddles (Walker, 1971; Davenport, Munks & Oxford, 1984) that aid in swimming in ontogenetically young turtles, in maneuvering, and in terrestrial locomotion (Walker, 1971; Davenport, Munks & Oxford, 1984; Wyneken, 1997). The glenoid is oval and concave and its long axis is oriented anterodorsally-posteroventrally. It deviates by approximately 40° from the horizontal (compare to Wyneken, 2001 Fig. 99, p. 51, bottom right; personal observation). The convex humeral head is oval with its long axis oriented in anterodorsal-posteroventral direction (Walker, 1973; Zug, Wynn & Ruckdeschel, 1986; Wyneken, 2001; personal observation). Sea turtles have a functional elbow joint (Rivera, Wyneken & Blob, 2011). Flipper rotation appears to take place by rotation of the carpus against radius and/or ulna (personal observation).

The pectoral girdle of sea turtles (Walker, 1973; Wyneken, 1997; Depecker et al., 2006) and the limb are highly derived (Renous, 1995; Wyneken, 1997; Walker & Westneat, 2002; Rivera, Wyneken & Blob, 2011). The scapula of chelonioids has become relatively smaller, while the coracoid has become relatively bigger in size (Walker, 1973; Depecker et al., 2006). Accordingly, the shell is dorsoventrally more depressed and more rounded (Depecker et al., 2006; Benson, et al., 2011). The humerus is dorsoventrally depressed, the medial process much enlarged, and the deltopectoral crest is v-shaped (Walker, 1973; Hirayama, 1994; Wyneken, 2001). Articular cartilage of the humeral head of *Dermochelys coriacea* is vascularized, much thicker than the usual hyaline cartilage, and not parallel to the underlying bony surface. The bone surface underneath the cartilage cap is perforated by the blood vessels and rugose (Rhodin, Ogden & Conlogue, 1981; Snover & Rhodin, 2008). The distinctly longer radius has moved relatively ventrally to the shorter and stouter ulna. During ontogeny, connective tissue fuses increasingly both bones (Walker, 1973; Wyneken, 2001). In comparison to the big intermedium and ulnare, the radiale is small. The pisiform of Chelonioidea is large. The elongated phalanges of the three middle digits contribute to the formation of the hydrofoil-like flipper (Walker, 1973).

Origins of p, ld, and dc have spread onto plastron and carapace in turtles (Walker, 1973; Wyneken, 2001). Along with the changes in size of scapula and coracoid in cheloniids, the muscle origin areas of m. teres major, m. deltoideus scapularis, and m. subscapularis on the scapula have been reduced in size as well, while those of bb and m. coracobrachialis magnus on the coracoid have hypertrophied (Walker, 1973; Depecker et al., 2006). M. coracobrachialis magnus (synonym to cl here) and m. subscapularis (synonym to scs here) insert into the enlarged medial process (Walker, 1973; Wyneken, 2001; Krahl et al. (chapter 2)). P and sc attach ventrally to the deltopectoral crest. The two deltoid muscle bellies insert by a common tendon into the deltopectoral crest dorsally (Walker, 1973; Wyneken, 2001; Krahl et al. (chapter 2)). The scapular head of the triceps is small or possibly also reduced in sea turtles (Walker, 1973). Extensors and flexors of the cheloniid flipper are partially reduced, especially those muscles, that allow interdigital movement (Walker, 1973). Further, muscles that arise from the distal humerus, or distal to this, show fusion with other muscles and/or form thin aponeuroses (Walker, 1973; Wyneken, 2001; Abdala, Manzano & Herrel, 2008), and muscles or tendinous tissue may fuse with the dermis (Walker, 1973; Wyneken, 2001; Abdala, Manzano & Herrel, 2008; Krahl et al. (chapter 2)). Fcu fused with the dermis adjacently to the pisiform). All of these instances lead to the ontogenetic formation of a secondarily stiffened chelonioid foreflipper (Walker, 1973; Wyneken, 2001; Abdala, Manzano & Herrel, 2008).

1.2.2 Spheniscidae

Penguins are underwater flyers (Neu, 1931; Clark & Bemis, 1979). As penguins are birds, they employ a bird wing with an acrocoracohumeral ligament. This ligament is part of a specialized mechanism that is crucial to bird flight and exclusive to Aves (Baier, Gatesy & Jenkins, 2007). Penguin limb bones are not pneumatized, in contrast to limb bones of other birds (Meister, 1962; Ksepka et al., 2015). Penguins are reported to have a ball-and-socket glenoid joint. The shoulder joint allows three degrees of freedom. The elbow joint allows only little extension and flexion. More distal joints of the penguin foreflipper show even less movement (Louw, 1992).

The penguin foreflipper is hydrofoil-like, it has asymmetrical profiles and tapers to the tip like in sea turtles (Fish, 2004). Compared to birds (Alcids and Pelecanoididae) that are capable of aerial and aquatic flight at the same time (Clark & Bemis, 1979), penguins have smaller, dorsoventrally depressed wings, a more massive skeleton, a relatively larger body size (Schreiweis, 1982; Elliott et al., 2013), and an accessory sesamoid in the elbow region (Schreiweis, 1982; Louw, 1992). All flipper bones are greatly enlarged and dorsoventrally flattened. The penguin flipper is formed by an enlarged digit II and III. Digit I is reduced or mostly fused. The other two digits are completely reduced. Penguin foreflipper bones partially fuse with the tough and thick skin that covers it. This leads to a secondary immobilization of flipper joints (Louw, 1992). The hindlimbs are webbed and represent evolved paddles (Shufeldt, 1901). The feet are used for maneuvering as a control surface and for stabilization in water (Clark & Bemis, 1979) and for waddeling and tobogganing the body over snow and ice during long terrestrial journeys (Pinshow, Fedak & Schmidt-Nielsen, 1977).

Penguin flipper osteology transformations were accompanied by modifications of the musculature. Muscles spanning the shoulder joint are generally well developed (Schreiweis, 1982; Louw, 1992). Most of the flipper rotation is accomplished by shoulder musculature inserting proximally into the humerus (Neu, 1931). The main muscles enabling flight in penguins (and other birds) are sc and p. In penguins, the former has been increased in size and has obtained a size comparable to that of p (Schreiweis, 1982; Watanuki et al., 2006) which results in a strengthened upstroke (Schreiweis, 1982). The tb (scapulotriceps and humerotriceps, each is two-headed) is a strongly developed muscle, unlike bb which has been completely reduced, as well as other muscles associated with the loss of elbow rotation in penguin flippers (Schreiweis, 1982). A reduction of extensors and flexors takes place, while muscles for elevating the wing are hypertrophied. Distal wing musculature is highly reduced sometimes even just to ligamentous mechanisms (Schreiweis, 1982; Louw, 1992).

1.2.3 Otariinae

Otariinae evolved a swimming style which is termed rowing flight, in which lift-based elements of true underwater flight and drag-based elements from rowing are combined. The symmetrical hydrofoil-like foreflippers of sea lions show specialized adaptations for this and provide the main propulsion, while the hindlegs act as control surfaces (English, 1976b; Feldkamp, 1987) and aid in terrestrial locomotion (Berta, Sumich & Kovacs, 2005). English (1977) mentions that in Otariinae rotation of the scapulothorarcic region probably contributes to locomotion (see also Gordon, 1983). The shoulder joint of sea lions is a highly mobile ball-and-socket joint that allows humeral depression/elevation, retraction/protraction, and rotation along its long axis (English, 1977). The elbow joint is a relatively complex combination of joints that are formed by humerus-ulna and radius-ulna. The former allows flexion and extension of the lower arm and the latter allows a reduced degree of supination and pronation of the distal flipper in comparison to fissiped Carnivora. There are three joint surfaces in the carpus of Otariinae (antebrachiocarpal, midcarpal, and carpometacarpal joint). An increased range of motion in the carpal joints on the side of digit I and V was described by English (1976a).

The scapula is a roughly triangular mediolaterally flattened bone in Otariinae, which, in contrast to Cheloniidae and Spheniscidae, is expanding mainly dorsoventrally and mainly anterodorsally to dorsally of the glenoid (English, 1977). The humerus of sea lions is morphologically well differentiated and bulky with an enlarged prominent deltopectoral crest and an enlarged medial epicondyle in comparison to the smaller lateral epicondyle (English, 1977). Bones of the lower arm of Otariinae are dorsoventrally depressed (English, 1976a). The olecranon process is much enlarged in comparison to fissiped Carnivora. The radius is round and slim proximally and expands dorsoventrally depressed distally (English, 1977). The bones that lie more anteriorly, on the radial side, in the distal flipper are larger than those that lie more posteriorly and the digits become successively smaller posteriorly (English, 1976a). Accordingly, the associated limb muscles are relatively larger or smaller, too. Radius, ulna, and the carpal bones are curved backwards. Each terminal bony phalanx is lengthened by cartilage rods. The skeleton is wrapped into dense connective tissue, convergent to sea turtle and cetacean flippers and is covered by blubber and skin (English, 1976a).

Generally, pectoral muscles are well developed as well as extensors and flexors of the distal flipper. Ld, p and deltoideus (not separated into two heads and bellies) insert into the deltopectoral crest as in other tetrapods. P and ld are relatively hypertrophied in comparison to fissiped carnivors. P is also unique as it is reported to contribute to the fascia of the forearm and to fuse with the flipper dermis. Bb and tb are well developed and play an important role in elbow straightening. Associated with the increase in size of the medial epicondyle of the humerus, the flexors that originate from it are also relatively increased in size (English, 1977). In comparison to fissiped carnivores, the much markedly enlarged fcu (whether it is synonymous to the fcu I describe for Sauropsida in this study was not established, as this is beyond the scope) of Otariinae is specialized. It crosses the lower arm from proximoposterior to anterodistal inserting into metacarpal II-IV, a fascia, the anterior side of digit I, and attaches to the dermis of the palm. Otariinae have well developed muscles for spreading the digits apart and realigning them (English, 1976a).

1.2.4 Cetacea

Cetaceans have evolved lift-producing (Miklosovic et al., 2004; Weber et al., 2009; Weber et al., 2014) hydrofoil-like flippers (Fish & Battle, 1995; Cooper et al., 2007b) with a symmetrical profile (Fish & Battle, 1995; Fish, 2004). Unlike Chelonioidea, Spheniscidae, and Otariinae, Cetacea propel themselves by caudal oscillation of the fluke (Fish, 1996; Woodward, Winn & Fish, 2006) while the foreflippers act in maneuvering (Fish, 2002; Woodward, Winn & Fish, 2006).

The ovoid-shaped glenoid is shallow and the humeral head is approximately round. The shoulder joint is not congruent as the articulation surface of the proximal humeral head is much larger as that of the glenoid. A fibrocartilaginous rim seems to aid in attaining joint congruence (Carte & Macalister, 1868). The elbow joint is stiffened (Cooper et al., 2007b). Carpus and interphalangeal joints are often cartilaginous, and not functional anymore. Many Cetacea display hyperphalangy to a minor degree (Cooper et al., 2007a). Nevertheless, there is considerable taxonomic variation in joint stiffening and muscle reduction of the flipper (Cooper et al., 2007b). Cetacean flippers are covered in connective tissue, blubber, and tough skin to exclude displacement of the digits (Cooper et al., 2007a).

Cetacean humeri are bulky but shortened. Radius and ulna are relatively long and dorsoventrally depressed, as is the rest of the flipper (Carte & Macalister, 1868). Three flipper forms were delineated for Cetacea: lengthened and tapering (Fish & Battle, 1995; Sanchez & Berta, 2010), expansive and tapering, and expansive and blunt (Sanchez and Berta, 2009).

Overall, Cetacea display a well muscled shoulder joint, while the extensors and flexors of antebrachium and manus are extremely reduced (Howell, 1930; Strickler, 1978; Cooper et al., 2007b). The flipper is mainly moved by muscles acting over the shoulder joint and to a large extend by m. subscapularis and m. deltoideus (s. e.g., Carte & Macalister, 1868; Schulte & Smith, 1918; Cooper et al., 2007b). In many taxa flexor carpi ulnaris is present. It reaches from the olecranon of the ulna to the pisiform on the posterior edge of the flipper. Flexor and extensor digitorum communis are usually present (Cooper et al., 2007b). They insert into all digits, except for digit I, which is markedly reduced or even lost (e.g., Schulte & Smith, 1918; Cooper et al., 2007b). This could indicate, as noted by Cooper et al. (2007b), that at least some cetaceans are able to at least to some extend control the angle of attack by manipulating the anterior and posterior flipper edge. However, delphinid flipper bones are merely covered in proximodistally parallel-fibred connective tissue (Cooper et al., 2007b).

1.3 Bone histology of entheses

Most studies of entheses, attachments of tendons and ligaments on bone, and their osteological and microanatomical correlates emanate from medical examinations. Therefore, most research concentrated on humans (Knese & Biermann, 1958; Benjamin & Ralphs, 1998; Hems & Tillmann, 2000) and other mammals for comparative reasons (Johnson, 1983; Gao & Messner, 1996; Al-Qtaitat, Shore & Aaron, 2010; Thomopoulos, Genin & Galatz, 2010). Muscles may attach fleshy (directly) or via tendons (indirectly) to bone. There are two types of entheses: fibrocartilaginous and fibrous entheses. Fibrocartilaginous entheses are zonated quadrinominally: 1) a layer of bone with mineralized extrinsic fibres, covered by 2) a layer of calcified cartilage with mineralized extrinsic fibres, followed by 3) a zone of fibrocartilage, which passes over into 4) the tendon. Fibrous entheses are subdivided into periosteally mediated and unmediated. In the former, tendon fibres attach to the periosteum but few fibres also pass through it and anchor the periosteum into the bone. In the latter, tendon fibres pass the periosteum unaffected and insert the tendon into the bone (Benjamin et al., 2006). Fibrocartilaginous entheses are located in the epiphyseal regions whereas fibrous entheses are mostly found in the diaphyseal regions. The amount of extrinsic fibres present seems to be directly related to the amount of mechanical stress exerted (Jones & Boyde, 1974; Kawamoto, 1992; Hieronymus, 2006).

Research on histology and microanatomy of entheses in reptiles is a very recent trend sparked by evolutionary biologists and paleontologist (Suzuki, Murakami & Minoura, 2002; Hieronymus, 2006; Suzuki & Hayashi, 2008, 2010; Petermann & Sander, 2013; Sanchez et al., 2013). While medical and biomechanical examinations aim at a better understanding of entheses for better therapy of muscle tendon and ligament failures in humans (Liu et al., 1995; Hansen, Masouros & Amis, 2006; Yang & Temenoff, 2009). Paleontologists and evolutionary biologist aim at a better understanding of entheses of extant reptiles and mammals to provide a comparative basis for muscle reconstructions in extinct taxa (Hieronymus, 2006; Shaw, 2010; Petermann & Sander, 2013; Sanchez et al., 2013).

Bone histology of plesiosaurs investigates life history and how their secondarily aquatic adaptation is expressed by bone microanatomy (Houssaye, Sander & Klein, 2016; Wintrich et al., 2017). Further histology corroborates that plesiosaurs were presumably endothermic (Fleischle, Wintrich & Sander, 2018). Entheses of plesiosaurs have not been studied yet. We chose to sample the humerus anteriorly and posteriorly where it suddenly expands towards the distal end, to substantiate the idea that these are the sites where extensors and flexors presumably arise from.

The aim of this study is to examine whether it is possible to reconstruct locomotory muscles for a plesiosaur which were able to perform an underwater flight flipper beat cycle, including flipper length axis twisting, which has been found to be crucial for underwater flight by hydrodynamical studies. To do so *Cryptoclidus* (IGPB R 324) fore- and hindflipper muscles were reconstructed with the EPB and assigned to osteological correlates. The locomotory apparatus of plesiosaurs is compared to those of functional analogues (Chelonioidea, Spheniscidae, Otariinae, and Cetacea). Muscle functions are obtained geometrically. Further, humeral extensor and flexor origins, that leave no osteological correlates on the bone surface, were sampled histologically to see whether histology yields prove of their presence. This resulted in 52 plesiosaur fore- and hindflipper muscles. Humeral and femoral depressors, elevators, retractors, protractors, and rotators were obtained that were able to power underwater flight. Further, muscles were found that twist the fore- and hindflipper along its length axis. A few muscles were found to be possibly responsible for actively inducing asymmetry and therefore cambered flipper profiles, which would have increased the efficiency of underwater flying plesiosaurs.

2. Material and Methods

2.1 Extant phylogenetic bracket

Muscles were reconstructed for the plesiosaur *Cryptoclidus eurymerus* (IGPB R 324) exhibited at the Goldfuß Museum, Section Paleontology, Institute of Geosciences, Rheinische Friedrich-Wilhelms-Universität Bonn, Germany. They were reconstructed with the extant phylogenetic bracket (EPB) (Bryant & Seymour, 1990; Bryant & Russel, 1992; Wittmer, 1995). To bracket Plesiosauria Lepidosauria, Archosauria (i.e., Crocodylia), and Testudines were chosen.

Pectoral and pelvic limb myology of lepidosaurs relies mostly on Russell & Bauer (2008) who present each locomotory muscle for *Iguana*, but extensively review lepidosaur myological research and homologies including *Sphenodon*. *Sphenodon* musculature was sometimes considered in the following study, as it sometimes represents a possibly more plesiomorphic state in comparison to *Iguana*. Thus, if EPB turned out to be little informative, *Sphenodon* was considered as well. In case of doubt or additional questions on lepidosaur forelimb musculature Zaaf et al. (1999) (on two gekkotans), Anzai et al. (2014) (on various *Anolis* species), Jenkins & Goslow (1983) (on *Varanus exanthematicus*) were considered. Additional information on lepidosaur hindlimb myology was drawn from Snyder (1954) who studied hindlimb musculature of Iguanidae and Agamidae.

Crocodilian forelimb myology is based on Meers (2003) who sampled various crocodilian taxa (*Alligator mississippiensis*, *Crocodylus siamensis*, *C. acutus*, *Osteolaemus tetraspis*, and *Gavialis gangeticus*) and also compared them. Suzuki & Hayashi (2010) were also consulted for crocodilian muscle attachments on the pectoral girdle, humerus, and radius and ulna. They sampled *Caiman crocodilus* and *Crocodylus siamensis* and *C. niloticus*. Crocodilian hindlimb myology is largely based on Suzuki et al. (2011) who studied *Caiman crocodilus fuscus*, *Crocodylus siamensis*, and *C. porosus*. Supplementary and comparative information on pelvic muscles inserting into the femur or spanning it were taken from Otero, Gallina & Herrera (2010) (on *Caiman latirostris*), Romer (1923) (*Alligator mississippiensis*), and Gatesy (1997) (*Alligator mississippiensis*).

Turtle forelimb and hindlimb myology is based on Walker (1973) who primarily describes fore- and hindlimb myology of *Pseudemys scripta elegans*, but he compares them to other turtles he dissected including terrestrial, semi-aquatic, and marine ones. Further, Walker (1973) also extensively reviews turtle myological literature and included muscle homologies. Abdala, Manzano & Herrel (2008) who studied lower arm and hand muscles of several terrestrial and semi-aquatic Testudines were additionally considered.

In comparison to other turtles, which have rather straight and only slightly distally expanding humeri, sea turtle humeri are anteriorly straight and posteriorly curved and expanded (Walker, 1973; Wyneken, 2001; Krahl et al. (chapter 2)). Extensors originate anteriorly from the radial epicondyle just proximal to the joint capsule in cheloniids and other turtles alike (Walker, 1973; Krahl et al. (chapter 2)). On the posterior side, flexors usually arise in turtles in the same fashion as the extensors anteriorly. In Cheloniidae the origin areas have migrated proximally up to approximately half the shaft length (Walker, 1973; Krahl et al. (chapter 2)). One of the most apparent features of *Cryptoclidus* fore- and hindflippers is the hammer shape of its humeri and femora, which is more pronounced in the former than in the latter (Andrews, 1910). In comparison to the sea turtle humeri, it was decided to place the origins of extensors and flexors on the humerus (ecr, ecu, edc, fcu, fcr, pte, fdl) and femur (edl, fdl, ge, and gi) of *Cryptoclidus* rather proximal onto the curved and expanding epicondyles from approximately half the shaft length on further distally.

Hindlimb myology of Testudines was also based on Zug (1971) who nicely depicts and describes variability to the pictured musculature of *Pseudemys* by Walker (1973) who despite describing variability of muscle attachments, did not figure them.

For help with forelimb myological homologies across Sauropsida Remes (2007) was consulted. Generally, muscle homology was established by topology, if it was not deducible from literature mentioned above.

Further, for plesiosaur foreflipper muscle reconstructions it was considered that the overall spatial arrangement of sauropsid pectoral myology is quite generic on a large scale: In lateral view of a sauropsid, superficially lying p fans out from the humerus ventrally to posteroventrally. Ld, also lying superficially, fans out from the humerus dorsally and caudodorsally. Sauropsids also have in common, that the ds muscle belly runs rather dorsally above the humerus, while the dc portion runs anteriorly (Walker, 1973; Jenkins & Goslow, 1983; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010; personal observation of *Caretta caretta* dissection). If ld is dissected off a lepidosaur, sc and scs become visible (that take an anterior to anterodorsal course Jenkins & Goslow, 1983; Russell & Bauer, 2008). This is similar in crocodilians and turtles, except that the latter lack shp (Walker, 1973; Meers, 2003; Suzuki & Hayashi, 2010; personal observation). If p is dissected off in ventral view, the deltoids and sc can always be found anteriorly. Variable across sauropsids appears to be the deeper musculature that follows from anterior to posterior: in crocodilians bb, cb, and scs (Meers, 2003; Suzuki & Hayashi, 2010), in lepidosaurs cb, bb, and cl (Jenkins & Goslow, 1983), and in turtles cb, cl, and bb, also visible in turtles is the sc due to its peculiar origin on the ventral coracoid (Walker, 1973; personal observation).

Despite variable origins and insertions of extensors and flexors that are on the ent- and ectepicondyle of the humerus, their course is the same. Across Sauropsida sl and ecr, edc, and ecu fan out over the lower arm from anterior to posterior (digit I to digit V) (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). Similarly, the flexors originating from the humerus also fan out over the lower arm. From digit I to digit V these are fcr, fdlf, fcu. Pte lies deep to fcr and fdlf in lepidosaurs and turtles (Walker, 1973; Russell & Bauer, 2008). Crocodilians pose the exception, as such that fcr is reduced and pte is situated in its place.

Further criteria were used to improve muscle reconstructions: consideration of three dimensional arrangement of musculature that certain muscles are always found in a similar (s. above) spatial arrangement even if origin or insertion areas may vary (e.g., ld is always lying superficial to other locomotory muscles and never in a deeper layer). The limb skeletons were examined for osteological correlates and muscles were ascribed to them. Histological sections were produced to find evidence for muscles that were reconstructed based on the EPB but show no osteological correlates exemplaric.

Araújo & Correia (2015) proposed three possible hypotheses for how the plesiosaur pectoral girdle could have evolved from that of basal Eosauropterygia. They find that one of them is the most plausible one, i.e., that the coracoids have been displaced posteriorly (Araújo & Correia, 2015). To establish homology between the pelvic girdle of Plesiosauria and extant Sauropsida, on which the EPB is based on, the authors follow Araújo & Correia‘s (2015) conclusion.

Bone orientational terminology for Sauropsida was aimed to match the result, the locomotory musculature of plesiosaurs and leans on Romer (1976): Regions of the vertebral column are described with cranial and caudal. Otherwise, orientations in the pectoral and pelvic limb are given with dorsal and ventral, anterior and posterior, and proximal and distal. The exception pose the dorsal projection of the scapula and the ilium, which are described with dorsal vs. ventral, medial vs lateral, and anterior vs. posterior.

2.2 Bone histological sampling

Sample sections were taken where extensors and flexors of the humerus are reconstructed. Sections 1 and 2 were cut perpendicular to the bone surface and section 3 and 4 were cut perpendicular to the articulation surfaces of the humerus with radius and ulna. Samples were sectioned in the laboratory of Olaf Dülfer at the Division of Paleontology of the Steinmann-Institut for Geology, Mineralogy, and Paleontology, University of Bonn. They were taken after standard petrographic sampling methods (see e.g., Klein & Sander (2007): The bones were cut with a diamond-studded rock saw and ground in a dispersion of water and grinding powder (SiC 600 and afterwards SiC 800) to create a smooth surface. Then, samples are glued with Araldite 2020 onto object plates and are ground with SiC 600 and 800 down to a thickness of around 70 µm. Next, samples were covered with a cover slip with Verifix 700, which is a UV glue. Micrographs were taken with a Leica DFC420® compound microscope on which a digital camera is fastened with which they were also studied. The pictures are processed with Imagic Imageaccess. Bone histological terminology follows generally (Francillon-Vieillot et al., 1990).

2.3 Muscle function deduction of muscles originating from the pectoral and the pelvic girdle

Different functions were assigned to muscles that extend from the glenoid/acetabulum cranially or anteriorly and caudally and posteriorly. It is likely that the former plays a role in protraction and the latter in retraction. Also, muscles that originate dorsally to the glenoid/acetabulum or on the dorsal pectoral or pelvic girdle have an elevational function, contrary to muscles that originate ventrally to the glenoid/acetabulum which act as depressors. Rotators have the ability to rotate humerus or femur or distal bony elements and therefore the whole flipper by approximately 19° (Witzel, Krahl & Sander, 2015). They rotate either by rotating the flipper leading edge downward or the posterior edge upward or by rotating the leading edge upward or the posterior edge downward. Hence, muscles that rotate effectively the flipper leading edge downward originate posterior to glenoid/acetabulum from ventral coracoid/ischium or originate anterior or cranially to glenoid /acetabulum from the dorsal pectoral or pelvic girdle or dorsally to this from the vertebral column. For an upward rotation of the flipper leading edge the opposite is true. In the following text the terms anterior and posterior portion of a certain pectoral muscle will be used, because in the pectoral girdle anterior and posterior portions of a muscle do not necessarily correspond to an origin from scapula or coracoid (Tab. 1). For pelvic musculature they will be termed pubic or ischial portion, as they do seem to correspond well with the bony elements (Tab. 2).

In the following text muscle functions as the authors themselves interpreted them are discussed, not secondary interpretations of other authors as e.g., done by Carpenter et al. (2010). Watson (1924) poses the exception, as he writes that every muscle that originates ventral to the glenoid has probably a depressional function, but does not list them. Therefore, we deduced that these are: cb, p, the deltoids, scapulohumeralis anterior, and sc (which was depicted as depressor by Watson (1924) himself). Further adductor/abductor is used by following authors (Robinson, 1975; Lingham-Soliar, 2000; Carpenter et al., 2010; Araújo & Correia, 2015) for muscles that move the plesiosaur flippers ventrally below the body midline or dorsally above the body midline. Instead, depression and elevation are used in this study because it highlights the concept of underwater flight, as used by e.g., Rivera, Wyneken & Blob (2011) and Rivera, Rivera & Blob (2013), Krahl et al. (chapter 2) for sea turtle underwater flight.

2.4 Abbreviations

a, Musculus ambiens; abdV, Musculus abductor digiti V; addV, Musculus adductor digiti quinti; adm, Musculus adductor digiti minimi; af, Musculus adductor femoris; apb, Musculus abductor pollicis brevis; b, Musculus brachialis; bb, Musculus biceps brachii; cb, Musculus coracobrachialis brevis; cfb, Musculus caudifemoralis brevis; cfl, Musculus caudifemoralis longus; cl, Musculus coracobrachialis longus; dc, Musculus deltoideus clavicularis; ds, Musculus deltoideus scapularis; ecu, Musculus extensor carpi ulnaris; edb, Musculus extensores digitores breves; edbp, Musculi extensores digitores breves profundi; edbs, Musculi extensores digitores breves superficialis; edc, Musculus extensor digitorum communis; edl, Musculus extensor digitorum longus; ehp, Musculus extensor hallucis proprius; f, Musculus femorotibialis; fcr, Musculus flexor carpi radialis; fcu, Musculus flexor carpi ulnaris; fdb, Musculus flexores digitores breves; fdlf, Musculus flexor digitorum longus (foreflipper); fdlh, Musculus flexor digitorum longus (hindflipper); fdls, Musculi flexores digitorum superficialis; fh, Musculus flexor hallucis; fte, Musculus flexor tibialis externus; fti, Musculus flexor tibialis internus; gi and ge, Musculus gastrocnemius internus and Musculus gastrocnemius externus; i, Musculus ischiotrochantericus; ife, Musculus iliofemoralis; ifi, Musculus iliofibularis; it, Musculus iliotibialis; ld, Musculus latissimus dorsi; p, Musculus pectoralis; pb and pl, Musculus peroneus brevis and Musculus peroneus longus; pe, Musculus puboischiofemoralis externus; pi, Musculus puboischiofemoralis internus; pit, Musculus puboischiotibialis; pte, Musculus pronator teres; pti, Musculus pubotibialis; pp, Musculus pronator profundus; sc, Musculus supracoracoideus; scs, Musculus subcoracoscapularis; shp, Musculus scapulohumeralis posterior; sl and ecr, Musculus supinator longus and Musculus extensor carpi radialis; sm, Musculus supinator manus; ta, Musculus tibialis anterior; tb, Musculus triceps brachii.

3. Results

3.1 Muscle reconstructions

3.1.1 Foreflipper musculature

3.1.1.1 Ligaments of the pectoral girdle and limb

Araújo & Correia (2015) reconstruct a scapulohumeral ligament in the plesiosaur pectoral girdle with which this study agrees. The scapulosternal ligament they reconstructed takes a ventral course in their reconstructions, although it is reported to take a course dorsal to the shoulder girdle in extant lepidosaurs (compare to Russell & Bauer, 2008 Fig. 1.8, p. 97, or Fig. 1.25 p. 237). The current study refrains from reconstructing a scapulosternal ligament for plesiosaurs, because during its course it would mostly lie on or wrap around the surface of the dorsal pectoral girdle, therefore it is presumed to have become superfluous. A mesocleidosternal ligament was found to be absent in plesiosaurs by Araújo & Correia (2015) and will not be reconstructed here either.

An extensor retinaculum, a ligament which ties the extensors at about the hight of the dorsal wrist was reported for lepidosaurs (Russell & Bauer, 2008, p. 263, Fig. 1.27). It is a derivative of the subdermal fascia. The extensor retinaculum was neither reported for crocodylians (Meers, 2003), nor for Testudines (Walker, 1973). The figures by Russell & Bauer (2008) suggest an attachment at a relatively similar position as the flexor retinaculum on the ventral wrist, from radiale to ulnare. Although this ligament is weakly supported by the EPB, it would be tempting to reconstruct it for plesiosaurs because it might bear interesting implications for flipper twisting (s. chapter 4.3.1) and would be mirroring the plesiosaur hindflipper.

A ventral annular ligament or flexor retinaculum is present in crocodilians (Meers, 2003), in turtles (Abdala, Manzano & Herrel, 2008), and in lepidosaurs (Russell & Bauer, 2008 for *Iguana*, Abdala, Manzano & Herrel, 2008 for *Liolaemus*) it attaches to the radiale and the pisiform in lepidosaurs and it is connected with the aponeurosis from which mm. flexores digiti breves originate (Abdala & Moro, 2006). The reconstruction of a ventral flexor retinaculum is well supported by the EPB and was therefore also reconstructed for

Cryptoclidus eurymerus (IGPB R 324). A similar arrangement of ligaments (intermetacarpal ligaments and metacarpodigital ligaments) that connect successive metacarpals and metacarpals with phalanx I of bordering digits as described in the lepidosaur carpus and metacarpus (Russell & Bauer, 2008 Fig. 113, p. 119) is reconstructed for plesiosaurs because this may be functionally relevant (s. chapter 4.3.1).

3.1.1.2 Pectoral muscles

Dorsal group

Musculus latissimus dorsi (ld)

-latissimus dorsi (Walker, 1973; Zaaf et al., 1999; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010; Anzai et al., 2014)

-teres major (Walker, 1973; Meers, 2003; Suzuki & Hayashi, 2010)

Teres major is considered a derived portion of latissimus dorsi (Remes, 2007). It was treated together with latissimus dorsi, because of its closely associated insertion tendons (Walker, 1973; Meers, 2003; personal observation of *Caretta caretta* dissection). It is not reported by Russell & Bauer (2008), Zaaf et al. (1999), and Anzai et al. (2014). It lies beneath ld therefore a similar yet more narrow function as the ld (unlike e.g. in cb, cl, ds, and dc, which are geometrically differently organized).

Ld originates from the neural spines of the vertebral column by an aponeurosis in crocodiles and lepidosaurs (Meers, 2003; Russell & Bauer, 2008). In crocodiles the origin area extends from approximately the first dorsal vertebra caudally to the sixth rib (Meers, 2003). In lepidosaurs the aponeurosis of origin of the ld begins with the first cervical vertebra. The number of vertebrae involved in the origin area of this muscle varies across taxa from three to four in chameleons to 12 in e.g., *Sphenodon* and *Iguana* (Russell & Bauer, 2008). Turtles pose the exception, in which the muscle origin is on the dorsal scapula and has spread laterally onto the carapace reaching the posterior border of the first peripheral plate (Walker, 1973). Crocodiles and lepidosaurs suggest that ld may arise from at least 1st to 6th dorsal vertebra in plesiosaurs (Meers, 2003; Russell & Bauer, 2008), but it might as well have extended further caudally along the vertebral column up to at least the 12th dorsal vertebra based on the EPB.

The ld attachment in lepidosaurs, crocodiles, and turtles is on the proximal dorsal humerus (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). In

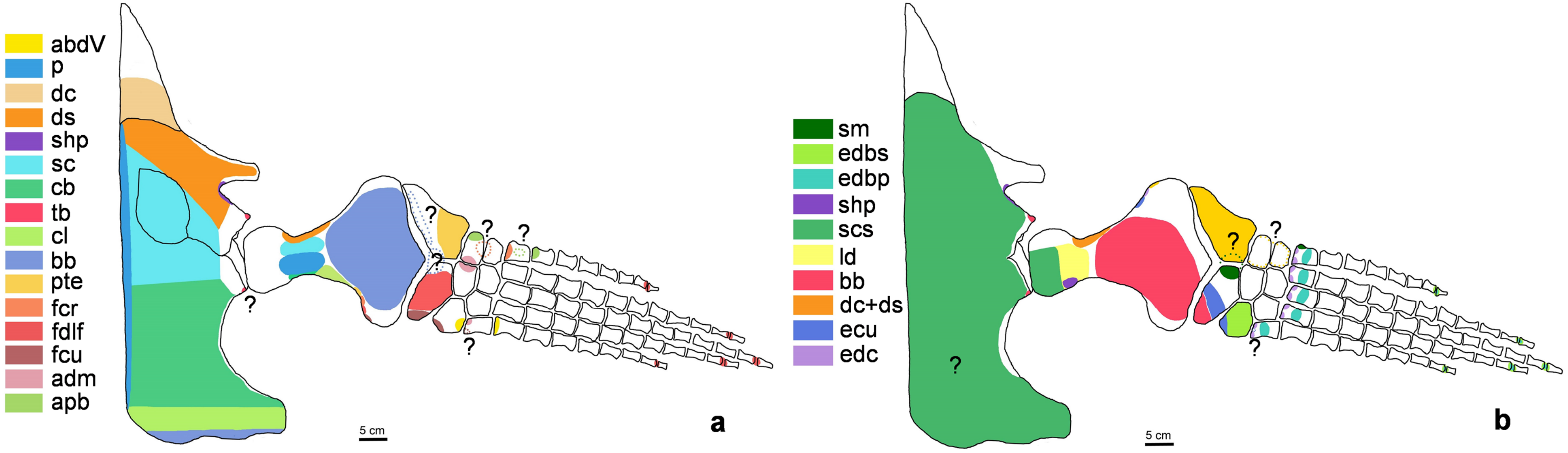

Fig. 1: *Cryptoclidus eurymerus* (IGPB R 324) foreflipper muscle reconstructions in a) ventral and b) dorsal view. Abbreviations: abdV, Musculus abductor digiti V; Musculus adductor digiti minimi; apb, Musculus abductor pollicis brevis; bb, Musculus biceps brachii; cb, Musculus coracobrachialis brevis; cl, Musculus coracobrachialis longus; dc, Musculus deltoideus clavicularis; ds, Musculus deltoideus scapularis; ecu, Musculus extensor carpi ulnaris; edbp, Musculi extensores digitores breves profundi; edbs, Musculi extensores digitores breves superficialis; edc, Musculus extensor digitorum communis; fcr, Musculus flexor carpi radialis; fcu, Musculus flexor carpi ulnaris; fdlf, Musculus flexor digitorum longus (foreflipper); ld, Musculus latissimus dorsi; p, Musculus pectoralis; pte, Musculus pronator teres; sc, Musculus supracoracoideus; scs, Musculus subcoracoscapularis; shp, Musculus scapulohumeralis posterior; sm, Musculus supinator manus; tb, Musculus triceps brachii.

crocodiles and some lepidosaurs it it placed anteriorly to shp (Zaaf et al., 1999; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). It is positioned on the humerus posteriorly to the deltoid insertions, distally to the scs insertion and distally bordered by the humeral tb head in all three taxa (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). Therefore, ld insertion was reconstructed on the anterodorsal tuberosity of the plesiosaur humerus (as supported by all three taxa) associated with part of the very rugose and deeply striated muscle scar on the tuberosity. Ld attachment site is distally to scs (as in all three EPB taxa) and anterior to shp (as in crocodiles and lepidosaurs).

Musculus subcoracoscapularis (scs)

-subcoracoscapularis (Russell & Bauer, 2008)

-subscapularis (Walker, 1973; Meers, 2003; Suzuki & Hayashi, 2010)

Term coined for most plesiomorphic (origin areas on coracoid and on scapula) taxon employed in this study, Lepidosauria, is given priority over the probably derived states in crocodilians (Meers, 2003; Suzuki & Hayashi, 2010) and Testudines (Walker, 1973), which show only a scapular portion.

Scs has its origin area in crocodiles and turtles only on the scapula but in the former on the medial side (Meers, 2003; Suzuki & Hayashi, 2010) and in the latter rather from the lateral scapular blade (Walker, 1973). In lepidosaurs it takes its origin on most of the medial and dorsal scapulocoracoid and spreads partially around the scapula onto its posterolateral side (Russell & Bauer, 2008; Anzai et al., 2014). A scapula portion of the scs is well supported for plesiosaurs by all three taxa, while a coracoid portion is only supported by lepidosaurs. Yet, a large coracoid portion would be possible, if one considers that in lepidosaurs and turtles the dorsal coracoid is well covered by muscles (in crocodilians merely to a lesser degree).

Scs inserts posterodorsally into the proximal humerus in lepidosaurs (lesser tubercle), crocodiles (medial protuberance), and turtles (medial process) (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). In turtles it is bordered anterodistally by the ld insertion and posteriorly by the cl insertion (Walker, 1973). In lepidosaurs and crocodilians it is the most posterior insertion of a pectoral muscle on the humerus (Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). In all three taxa it inserts proximally to the ld insertion on the humerus (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). According to the EPB, the scs attachment was reconstructed on the posterodorsal proximal plesiosaur humerus as in all three taxa, relatively closer to the glenoid than the ld insertion. It was correlated with part of the large, rugose, and deeply striated muscle scar on the dorsal tuberosity of the plesiosaur humerus.

Musculus scapulohumeralis posterior (shp)
-scapulohumeralis posterior (Zaaf et al., 1999; Russell & Bauer, 2008)
-scapulohumeralis caudalis (Meers, 2003; Suzuki & Hayashi, 2010)
Decided to choose the term shp because the term is used in the lepidosaur articles this work is based on, simply paying tribute to lepidosaurs showing the more plesiomorphic condition than Crocodylia (in which the anterior part is reduced). Has not been observed in Testudines (Walker, 1973).

This muscle's origin surface is located posteriorly on the lower half of the scapula in crocodiles and some lepidosaurs (*Sphenodon* (Russell & Bauer, 2008), *Varanus* (Jenkins & Goslow, 1983)) and reaches around onto the medial and lateral surface of the scapula (Jenkins & Goslow, 1983; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). Towards the glenoid it borders a tb origin in crocodiles and lepidosaurs (Jenkins & Goslow, 1983; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). Medially it flanks scs in crocodiles (Meers, 2003; Suzuki & Hayashi, 2010). On the lateral lepidosaur scapula it is paralleled anteriorly by ds (Jenkins & Goslow, 1983). Accordingly, this muscle arises in plesiosaurs from the posterior edge of the scapula and from the lower part of the small scapular blade, spreading around onto the dorsal and ventral surface. Dorsally it is bordered by scs as in crocodiles and ventrally by ds as in lepidosaurs.

Shp inserts differently in lepidosaurs and crocodiles. In the former it attaches to the lesser tubercle of the humerus posterodorsally (Jenkins & Goslow, 1983; Russell & Bauer, 2008) and in the latter its insertion area is large and on the proximodorsal humerus (Meers, 2003; Suzuki & Hayashi, 2010). In crocodiles and lepidosaurs alike, it inserts more distally than scs and posterior and at about the same level as the ld and posterior to ds (Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). Due to the distinctively reduced size of the origin area of shp in plesiosaurs, a comparatively small attachment site was on the proximodorsal humerus, posteriorly on the humeral tuberosity of the plesiosaur humerus. It was, like scs and ld, associated with the heavily striated, rugose large muscle scar on the humeral tuberosity.

Musculus deltoideus clavicularis (dc)

-deltoideus clavicularis (Walker, 1973; Meers, 2003; Suzuki & Hayashi, 2010)
-clavodeltoideus (Zaaf et al., 1999; Russell & Bauer, 2008; Anzai et al., 2014)
I stick to deltoideus clavicularis as it seems to be the term used in recent works on more taxa in Sauropsida (Walker, 1973; Meers, 2003; Suzuki & Hayashi, 2010).

Dc arises from the ventral, dorsal, and medial clavicula in lepidosaurs (Russell & Bauer 2008), from the dorsal acromion in Testudines (Walker, 1973) and due to loss of the clavicula in crocodiles from the anterolateral scapula (Meers, 2003; Suzuki & Hayashi, 2010). In lepidosaurs and turtles this is the most anterior muscle origin area of a locomotor muscle visible on the ventral pectoral girdle (Walker, 1973; Wyneken, 2001; Russell & Bauer, 2008). Thus, in plesiosaurs this muscle origin area was on the very reduced clavicular remains ventrally and posteriorly. Anteriorly to it attaches visceral arch musculature which will not be further discussed in this paper as it is beyond the scope of this work (Russell & Bauer, 2008).

In lepidosaurs and Testudines dc and ds join into a common tendon and attach to the humerus as described below (s. ds) (Walker, 1973; Russell & Bauer, 2008). Only in Crocodylia the insertion tendons of dc and ds are well separated (Meers, 2003) and dc inserts anteriorly into the deltopectoral crest (Meers, 2003; Suzuki & Hayashi, 2010). For description of its insertion in plesiosaurs please view the section on ds insertion below.

Musculus deltoideus scapularis (ds)

-scapulodeltoideus (Zaaf et al., 1999; Russell & Bauer, 2008; Anzai et al., 2014)
-deltoideus scapularis (Walker, 1973; Meers, 2003; Suzuki & Hayashi, 2010)
I stick to deltoideus scapularis as it seems to be the term used in recent works on more taxa in Sauropsida (Walker, 1973; Meers, 2003; Suzuki & Hayashi, 2010)

Ds originates from the ventral anterolateral scapula in Testudines (Walker, 1973), lepidosaurs (Russell & Bauer, 2008), and crocodiles (Meers, 2003; Suzuki & Hayashi, 2010) and from the suprascapula adjacently in lepidosaurs (Russell & Bauer, 2008) and in crocodiles (Meers, 2003; Suzuki & Hayashi, 2010). Thus, ds was found to take its origin on the anteroventral and lateral plesiosaur scapula (supported by all three taxa) extending posteriorly towards the scapular glenoid portion. Its attachment site, and that of dc, on the pectoral girdle is demarcated posteriorly by a ridge that expands from the body midline anteriorly posterolaterally to the glenoid.

In crocodiles only, the insertion tendon of ds is separated from that of dc. It attaches to the anterodorsal deltopectoral crest of the humerus proximal to the dc insertion (Meers, 2003; Suzuki & Hayashi, 2010). Opposed to that ds inserts via a shared tendon with dc into the deltopectoral crest in Testudines (Walker, 1973) and Lepidosaurs (Russell & Bauer, 2008). Therefore, the insertion of both deltoid muscle bellies by a common tendon, as suggested by turtles and lepidosaurs was reconstructed on the anterior plesiosaur humerus shaft adjacently to all other pectoral girdle musculature. It is partially associated with the anteroventral rugose muscle scar at approximately humeral mid-shaft.

Musculus triceps brachii (tb)

-triceps complex: subdivision into scapular head, coracoid head, lateral humeral head, and medial humeral head (Russell & Bauer, 2008)
-triceps (Zaaf et al., 1999)
-triceps brachii (subdivision into: triceps longus lateralis (Meers, 2003; Suzuki & Hayashi, 2010), triceps longus caudalis (Meers, 2003) – longus medialis (Suzuki & Hayashi, 2010), triceps brevis cranialis, triceps brevis intermedius, triceps brevis caudalis (Meers, 2003; Suzuki & Hayashi, 2010)
-triceps brachii: humeral head and scapular head (Walker, 1973)
We agree with Remes (2007) (see also for discussion on homology of this muscle) and call this muscle accordingly. It is also the most commonly used name in the zoological studies on which this study is based on.

An origin area on the scapula dorsally, just above the glenoid is shared by all three taxa (Walker, 1973; Jenkins & Goslow, 1983; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). Lepidosaurs may have a second tb head which arises from the sternoscapular ligament (Jenkins & Goslow, 1983; Russell & Bauer, 2008), and crocodiles have a second and third tendinous tb origin on the posterolateral scapula and the posteromedial coracoid just below the glenoid (Meers, 2003; Suzuki & Hayashi, 2010). In lepidosaurs the two heads are involved in a complex sling mechanism that spans the insertion tendon of ld. They are probably involved in reducing anteroposterior humeral movement (Jenkins & Goslow, 1983; Russell & Bauer, 2008). The tb head from the coracoid is lost in chameleons and therefore the sling mechanism is reduced (see Russell & Bauer, 2008 for review). Russell & Bauer (2008) suggest that this might be due to a loss of the restricting mechanism in chameleons. We think, it could also be connected to a loss in lateral undulation, as not only chameleons have only the tb which arises from a region just dorsally of the glenoid, but also Testudines (Walker, 1973; Russell & Bauer, 2008). In crocodiles the two additional tb tendons join into a common tendon distally (Meers, 2003; Suzuki & Hayashi, 2010). According to the EPB, two possibilities are equally probable to reconstruct for plesiosaurs: If taking crocodiles and *Iguana iguana* into consideration, an origin posterior and anterior to the glenoid is possible as the scapular blade has been displaced cranially relative to the glenoid and the coracoid relatively posteriorly (please view Araújo & Correia, 2015 for discussion of homology of the sauropterygian pectoral girdle). If taking Testudines and chameleons into account, which are both possibly better functional analogues, only the scapular origin of the tb remains. Also, a restrictive anteroposterior function may be obsolete in plesiosaurs, as the glenoid shape seems to restrict anteroposterior motion of the humerus already.

origin on humerus:

In recent sauropsids, several portions of the humeral head are often recognized (medial and lateral head in lepidosaurs (Zaaf et al., 1999; Russell & Bauer, 2008) and triceps brevis cranialis, t. b. intermedius, and t. b. caudalis in crocodiles (Meers, 2003; Suzuki & Hayashi, 2010). In this study it is impossible to find evidence for muscle portions, so it was reconstructed undivided. In all three taxa it arises from a large origin area situated on the dorsal humerus distal to the insertions of the proximal pectoral musculature and proximal to or reaching distally the most proximal origins of the brachial and antebrachial extensors (Walker, 1973; Zaaf et al., 1999; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). In crocodiles the tb origin on the humerus spreads around the humeral shaft anteriorly and posteriorly, thus the antagonistic bb on the ventral humerus is markedly smaller (Meers, 2003; Suzuki & Hayashi, 2010). Therefore, the humeral tb origin was on the dorsal plesiosaur humerus (as in turtles, lepidosaurs, and crocodilians) distal to the proximal pectoral musculature adjacent to the extensor origins. It can be correlated with the tendentially fan-shaped striated and rugose dorsal distal surface of the plesiosaur humerus.

The insertion area of tb is posterodorsally on the olecranon of the ulna via a common tendon in lepidosaurs (Zaaf et al., 1999; Russell & Bauer, 2008; Anzai et al., 2014), turtles (Walker, 1973), and crocodiles (Meers, 2003; Suzuki & Hayashi, 2010). According to all three taxa, the tb insertion in plesiosaurs is on the posterodorsal edge of the ulna and adjacent bony areas due to the lack of an olecranon in plesiosaurs.

Ventral group

Musculus pectoralis (p)

No synonyms employed in articles used in this study (Walker, 1973; Zaaf et al., 1999; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010; Anzai et al., 2014; for a list of synonyms see Discussion in Remes, 2007). Subdivisions are common (see Remes, 2007 for review)

P is a large fan-shaped muscle, often subdivided into various portions, which arises ventrally from the middle axis of the body in tetrapods and often spreads posteriorly onto adjacent bony or cartilagous elements. In lepidosaurs and crocodiles alike, it originates from the sternal elements (Zaaf et al., 1999; Meers, 2003; Russell & Bauer, 2008; Anzai et al., 2014). Additionally, it arises from the lepidosaur interclavicula (Zaaf et al., 1999; Russell & Bauer, 2008; Anzai et al., 2014) and from the crocodilian thoracal ribs (Meers, 2003). As there is no interclavicula or sternum in turtles, p has spread onto the plastron. The attachment surface is situated posterior to the ligamentous articulation of the acromion to the plastron and extends posteriorly and curves in an arc laterally (Walker, 1973; personal observation). As the p origin often spreads onto different skeletal elements in various tetrapod groups to keep its relative position in the body (s. chapter 2.1), it was reconstructed in *Cryptoclidus* (IGPB R 324) along the midline of the scapula and coracoid along the ventral crest that each element of both side forms at the body midline, superficial to sc and cb. Substantiated by the EPB, it is possible that it might have spread onto adjacent gastralia caudally as in crocodilians.

The attachment site of p via a large tendon is in crocodiles, lepidosaurs, and turtles on the deltopectoral crest and relatively posterodistally to the attachment site of sc and anteriorly to coracobrachialis insertions (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). Therefore, supported by all three taxa, the muscle insertion of p was on the posteroventral proximal plesiosaur humerus associated with part of the rugose muscle scar on the ventral humerus.

Musculus supracoracoideus (sc)

-supracoracoideus (Walker, 1973; Russell & Bauer, 2008)
-supracoracoideus + coracobrachialis brevis dorsalis (Meers, 2003; Suzuki & Hayashi, 2010)
-subdivision into supracoracoideus longus, intermedius, brevis in crocodilians (Meers, 2003; Suzuki & Hayashi, 2010)

The term is well accepted across sauropsid taxa (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010) therefore this paper concurs with it.

The sc originates in Crocodylia from the anteroventral and anterodorsal coracoid, and the anterolateral and anteromedial scapula (Meers, 2003; Suzuki & Hayashi, 2010). In Testudines it arises from the ventral side of the coracoid and scapula (Walker, 1973) and in lepidosaurs usually from the anteroventral coracoid (Russell & Bauer, 2008) while a scapular origin poses the exception (Russell & Bauer, 2008). The sc origin lies in lepidosaurs and crocodiles anteriorly to cb and cl (Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). The pectoral girdle of turtles appears to show here a highly derived condition. Therefore, sc origin site was on the posterior portion of the scapula in plesiosaurs (supported by lepidosaurs and crocodilians) behind the ridge that demarcates the posterior border of ds. Sc also arises from the anterior portion of the coracoid (as in lepidosaurs and crocodilians) posteriorly bordered by a bulging rounded ridge that runs from the posteroventral glenoid medially towards the body midline. It is also presumed that it covers the coracoid foramen (Araújo & Correia, 2015), as it is known to cover two fenestrae in the lepidosaur shoulder girdle (Russell & Bauer, 2008). In none of the three groups used for EPB (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010), sc origin area contacts the glenoid, so in the plesiosaur muscle reconstruction it does not either.

This muscle inserts anteroventrally proximally into the proximal border of the deltopectoral crest on the humerus in Lepidosauria (Russell & Bauer, 2008) and Crocodylia (Meers, 2003; Suzuki & Hayashi, 2010). Contrastingly, in Testudines the insertion is positioned proximally to the deltopectoral crest but anteriorly extending slightly dorsally and more ventrally (Walker, 1973). In turtles and lepidosaurs the insertion is proximal to the deltoid insertion (Walker, 1973; Russell & Bauer, 2008) in crocodiles the proximal extension of the deltoids reaches the same level as the sc insertion (Meers, 2003; Suzuki & Hayashi, 2010). It is positioned anteriorly to the cb and cl insertions (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010) and proximal to the p insertion (lepidosaurs, turtles) or at the same level as the p (Russell & Bauer, 2008). According to the EPB, the sc insertion is on the anterior to anteroventral proximal plesiosaur humerus, anteriorly to the p, cl and cb insertions (as in all three EPB taxa) but at about the same level as the deltoid insertion (as in crocodiles). This is due to a relative displacement of the sc insertion further distally determined by its correlation with part of the ventral rugose muscle scar on the plesiosaur humerus.

Musculus coracobrachialis brevis (cb)

-coracobrachialis brevis (Walker, 1973; Russell & Bauer, 2008)
-coracobrachialis (Zaaf et al., 1999)
-coracobrachialis brevis ventralis (Meers, 2003; Suzuki & Hayashi, 2010)
Nomenclature by Russell & Bauer (2008) was chosen because it describes the geometry of cb and cl well.

Cb takes its large origin on the anteroventral coracoid posterior to the sc and reaches far back to meet the cl origin posteriorly in Crocodylia (Meers, 2003; Suzuki & Hayashi, 2010) and lepidosaurs (Russell & Bauer, 2008). Opposing, in Testudines it attaches to the proximal part of the posterolateral rim of the coracoid posterior to the glenoid (Walker, 1973). In plesiosaurs, the origin area of cb was on the ventral coracoid surface as in Crocodylia and lepidosaurs posterior to sc, anterior to cl, covering about 4/5 of it presuming that the state found in the turtle pectoral girdle is highly derived due to its position inside the rib cage and the shell (Nagashima et al., 2012). Cb origin is placed posteriorly behind a broad bulging ridge that expands from the posteroventral glenoid to the body midline.

Cb attaches posteroventrally to the humeral head and extends proximodistally in lepidosaurs (Zaaf et al., 1999; Russell & Bauer, 2008) and into the ventral intertrochanteric fossa in Crocodylia and Testudines (Walker, 1973; Meers, 2003; Suzuki & Hayashi, 2010). P and sc insertions are positioned anteriorly to it in all three taxa (Walker, 1973; Meers, 2003; Suzuki & Hayashi, 2010; Abdala et al., 2014). In turtles and crocodiles, b insertion lies distal to it (Walker, 1973; Meers, 2003; Suzuki & Hayashi, 2010) while it borders the b proximoposteriorly in lepidosaurs (Russell & Bauer, 2008). The EPB suggest that an insertion similar to the state seen in crocodiles and turtles is favorable in plesiosaurs, proximal to b insertion on the ventral humerus. Therefore, the insertion of cb was correlated with the rough rugosities on the ventral to posteroventral plesiosaur humerus proximal to cl insertion.

Musculus coracobrachialis longus (cl)

-coracobrachialis longus (Zaaf et al., 1999; Russell & Bauer, 2008; Anzai et al., 2014)
-coracobrachialis magnus (Walker, 1973)
Name was chosen for the same reason as discussed for cb. This muscle is not reported in Crocodylia.

In lepidosaurs cl originates from the ventral posterior coracoid, posteriorly to cb (Jenkins & Goslow, 1983; Russell & Bauer, 2008) and in Testudines covers most of the dorsal coracoid (Walker, 1973). The state of the pectoral girdle of the turtles is here considered to be the highly derived state, in comparison to Lepidosauria, due to its placement inside the shell and the rib cage (Nagashima et al., 2012). Accordingly, for *Cryptoclidus* (IGPB R 324) the origin area of the cl was on the posterior coracoid as reported for lepidosaurs and along with the other parts of this muscle, cb, which also derives from the lateral side of the pectoral girdle in crocodiles (Meers, 2003; Suzuki & Hayashi, 2010) and lepidosaurs (Russell & Bauer, 2008).

In lepidosaurs, the insertion of cl is situated posteroventrally on the humerus, distal to the cb insertion, and extends far distally, reaching almost the epicondyle in lepidosaurs (Russell & Bauer, 2008). It attaches posteroventrally into the turtle humerus and proximally into the medial process, posterior to the coracobrachialis insertion (Walker, 1973). In plesiosaurs, the attachment of cl was on the posteroventral and distal humerus shaft, similarly to lepidosaurs (Russell & Bauer, 2008). This is due to the observation of a rugose muscle scar that expands relatively far distally along the posterior shaft of the plesiosaur humerus.

Musculus biceps brachii (bb)

-biceps (Zaaf et al., 1999)
-biceps brachii (Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010; Anzai et al., 2014)
-biceps brachii, subdivisions into biceps profundus and biceps superficialis (Walker, 1973)

Since bb is the most common term for this muscle, it will be used in the following study, because it is the one which most authors could agree on (Remes, 2007).

Bb originates from the posterior coracoid in lepidosaurs posterior to cl and cb (Russell & Bauer, 2008) and from the posterolateral coracoid in Testudines. In turtles it lies posterior to cb. It is bordered ventrally by sc and dorsally by cl (Walker, 1973). Contrastingly, it arises in crocodiles from the anterior coracoid placed between suparcoracoideus anteriorly and cb posteriorly. The bb origin area was on the posterior plesiosaur coracoid supported by lepidosaurs and partially Testudines (Meers, 2003; Suzuki & Hayashi, 2010). The crocodilian condition is thought to be the derived one here by the author because they have become secondarily aquatic and are able to sprawl, but also to employ a “high walk” (Reilly & Elias, 1998).

Musculus brachialis (b)

-brachialis anticus (Russell & Bauer, 2008; Anzai et al., 2014)
-brachialis inferior (Walker, 1973; Meers, 2003)
-brachialis (Zaaf et al., 1999; Suzuki & Hayashi, 2010)
The term brachialis will be employed in this work according to suggestion of Remes (2007).

In lepidosaurs and turtles b covers most of the ventral humerus shaft. Proximally it is flanked by shoulder musculature and distally it extends to and partially proximally borders the extensors and flexors of the antebrachium and brachium which originate from the ect- and entepicondyle (Walker, 1973; Zaaf et al., 1999; Russell & Bauer, 2008; Anzai et al., 2014). In crocodiles this muscle is distinctly smaller than the antagonistic tb, which reaches around the humeral shaft anteriorly and posteriorly onto the ventral side and displaced the b origin somewhat anteriorly (Meers, 2003; Suzuki & Hayashi, 2010). Thus, the attachment surface of b was placed on the ventral surface of the plesiosaur humerus distally to the shoulder musculature, like all three taxa suggest, bordering extensors and flexors. The very “veiny” or tendentially fan-shaped striated and slightly rugose surface in this area suggests an association with a muscular covering. A similar arrangement, where the flexors spread proximally onto the humeral shaft was observed in *Caretta caretta* (Cheloniidae) by dissection in comparison to non-marine turtles by Walker (1973).

Bb and b insert by a common tendon which attaches to either radius or radius and ulna. In turtles they insert into the posterior radius and anterior ulna at about mid-length on shaft (Walker, 1973). Zaaf et al. (1999) and Russell & Bauer (2008) report that in geckos and *Iguana iguana* the common tendon attaches to the posterior radius and anterior ulna, too but more proximally and may even be associated with the elbow joint capsule (Russell & Bauer, 2008). Contrastingly, in crocodiles (Meers, 2003; Suzuki & Hayashi, 2010) and in various *Anolis* species (Anzai et al., 2014) the insertion tendon only attaches to the proximal radius. Therefore, the insertion of the common bb and b tendon could be reconstructed on the proximal posterior radius and anterior proximal ulna, a placement on their shafts is impossible due to the derived bone shapes radius and ulna have in plesiosaurs. An attachment solely on the radius is just as well supported by the EPB.

3.1.1.3 Antebrachial muscles

Dorsal group

Musculus extensor carpi ulnaris (ecu)

-extensor carpi ulnaris (Walker, 1973; Russell & Bauer, 2008)
-extensor ulnaris (Suzuki & Hayashi, 2010)
-flexor ulnaris (Meers, 2003)
Here we go along with the homology established by Suzuki & Hayashi (2010) and not with Remes (2007) for flexor ulnaris of Meers (2003)

Ecu originates tendinously from the ectepicondyle of the humerus in lepidosaurs, crocodiles, and turtles (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010) In lepidosaurs the origin area is situated dorsally (Russell & Bauer, 2008), in crocodiles anterodorsally (Meers, 2003; Suzuki & Hayashi, 2010), and in turtles anteroventrally (Walker, 1973). Additionally, it also arises in lepidosaurs from the olecranon of the ulna dorsally (Russell & Bauer, 2008). In turtles ecu origin lies slightly posterodistally to that of sl and ecr. In turtles ecu origin lies in between the origins of sl and ecr proximally and edc (Walker, 1973). In crocodilians ecu is situated anterodorsally just above the joint capsule (Meers, 2003; Suzuki & Hayashi, 2010). In lepidosaurs ecu is the most distal extensor (Russell & Bauer, 2008). Therefore, the attachment area of ecu was on the anterodorsal ectepicondyle of the plesiosaur humerus as crocodiles and lepidosaurs suggest. Ecu origin was reconstructed to be the most proximal extensor origin on the plesiosaur humerus so that it meets the criteria discussed above about the overall arrangement in all Sauropsida of the extensors originating from the humerus.

The ecu insertion is variable across the EPB. In turtles and crocodiles it inserts into a large area of the shaft of the ulna (Walker, 1973; Meers, 2003; Suzuki & Hayashi, 2010). In crocodiles the attachment area lies anterodorsally (Meers, 2003; Suzuki & Hayashi, 2010), while it covers most of the dorsal surface of the turtle ulna (Walker, 1973). Ecu inserts into the dorsal pisiform in lepidosaurs and turtles as well (Walker, 1973; Russell & Bauer, 2008). In lepidosaurs a second muscle belly inserts into the shaft of metacarpal V posteriorly (Russell & Bauer, 2008). In turtles, lepidosaurs, and crocodiles ecu insertion is bordered proximoposteriorly by tb insertion (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). The sm origin lies anteriorly to it in turtles and lepidosaurs (Walker, 1973; Russell & Bauer, 2008). This results in a relatively large muscle insertion area for ecu in plesiosaurs. An attachment on the ulna (according to crocodiles and turtles) and pisiform (according to turtles and lepidosaurs) or adjacent areas is probable. There is no designated pisiform in the plesiosaur flipper, but accessory ossicles are regularly found in a similar relative position of the carpus in plesiosaurs. These accessory ossicles may well have been involved in ecu insertion area. It is also possible, but only supported by *Iguana iguana* that ecu inserted into metacarpal V.

Musculus extensor digitorum communis (edc)
-extensor digitorum longus (Russell & Bauer, 2008)
-extensor digitorum communis (Walker, 1973; Suzuki & Hayashi, 2010)
-extensor carpi ulnaris (Meers, 2003)
For homology of extensor carpi ulnaris (Meers, 2003) we follow the homology statement established by Suzuki & Hayashi (2010). This study goes along with extensor digitorum communis because it is most commonly used across taxa and literature employed for this study.

Edc arises from the ectepicondyle dorsally in turtles and lepidosaurs (Walker, 1973; Abdala, Manzano & Herrel, 2008; Russell & Bauer, 2008) and anteriorly in crocodiles (Meers, 2003; Suzuki & Hayashi, 2010). In lepidosaurs its origin is closely associated with the capsule of the elbow joint and with the origin of ecr. In turtles edc is the most distal extensor (Walker, 1973). It arises from a similar position from the humerus as in crocodilians (Meers, 2003; Suzuki & Hayashi, 2010). In lepidosaurs this muscle arises in between sl and ecr proximally and ecu distally (Russell & Bauer, 2008). The EPB suggests that edc arises from the ectepicondyle of the plesiosaur humerus anterodorsally in between the origin of ecu proximally and sl and ecr distally (s. chapter 2.1).

The most elaborated insertion pattern of edc is seen in turtles where the muscle belly gives way distally to a tendon, which splits up into four motor tendons that take course in between the digits where each of them splits up again into two tendons which finally insert by the following pattern into the metacarpals: posterodistally on the dorsal metacarpal I, antero- and posterodistally onto metacarpal II, III, IV and anterodistally onto metacarpal V (Walker, 1973; Abdala, Manzano & Herrel, 2008). In *Iguana iguana* edc gives way to three tendons which attach to metacarpals II, III, and IV proximally and posterodorsally. Additional tendons and attachments on metacarpal I and V are observed in *Sphenodon punctatum* for the former and in chameleons for the latter (see Russell & Bauer, 2008 for review). For Crocodylia a single attachment on proximodorsal metacarpal II is described, except for *C. acutus* where edc inserts into the extensor fascia at the level of digit I (Meers, 2003). It appears that the state of edc as represented by turtles poses the plesiomorphic condition and that it was reduced partially in above mentioned lepidosaurs and crocodilians. Thus, insertions of the edc were reconstructed proximally and posterodorsally on metacarpal I, anterodorsally and posterodorsally on metacarpal II, III, and IV and anterodorsally onto metacarpal V as presumed to be plesiomorphic for Sauropsida similarly as seen in Testudines.

Musculus supinator longus and Musculus extensor carpi radialis (sl and ecr)
-supinator + extensor carpi radialis (Russell & Bauer, 2008)
-tractor radii (Walker, 1973; Meers, 2003; Suzuki & Hayashi, 2010) (s. Remes, 2007)
-extensor carpi radialis superficialis (Walker, 1973)
-extensor carpi radialis intermedius (Walker, 1973)
-extensor carpi radialis profundus (Walker, 1973)
-supinator (Meers, 2003)
-brachioradialis (Suzuki & Hayashi, 2010)
-supinator (Suzuki & Hayashi, 2010)
-abductor radialis (Meers, 2003)
-extensor carpi radialis longus (Meers, 2003; Suzuki & Hayashi, 2010)

It was decided to go along with the simplifying terminology of Russell & Bauer (2008), because it is impossible to reconstruct this muscle for a fossil in such detail as in e.g., turtles in which it has three subportions.

This muscle arises from the humeral ectepicondyle anteriorly in turtles (Walker, 1973) and lepidosaurs (Russell & Bauer, 2008), slightly anteroventrally in crocodiles (Meers, 2003; Suzuki & Hayashi, 2010). Sl and ecr originates from the humerus as most proximal extensor in turtles and lepidosaurs (Walker, 1973; Russell & Bauer, 2008). Therefore, the origin area of sl and ecr was found to be on the ectepicondyle of the plesiosaur humerus as suggested by all three taxa. Its origin is the most distal one of the three extensors that arise from the plesiosaur humerus to achieve the general organisation described for extensors arising from the humerus (s. chapter 2.1).

Sl and ecr inserts into the dorsal and anterior radius in lepidosaurs, turtles, and crocodiles (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). In lepidosaurs it also extends onto the radiale (Russell & Bauer, 2008). Hence, the attachment surface for this muscle was on the dorsal and anterior plesiosaur radius, possibly extending onto the radiale, because no other muscles occupy the space.

Musculus supinator manus (sm)

-supinator manus (Walker, 1973; Russell & Bauer, 2008)

-extensor carpi radialis brevis pars radialis and pars ulnaris (Meers, 2003; Suzuki & Hayashi, 2010).

Sm is used as described by Remes (2007).

Sm arises from the anterodorsal edge of the ulna in turtles, lepidosaurs, and crocodiles anterior to ecu insertion (Walker, 1973; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). The origin area extends onto the proximal intermedium in Testudines (Walker, 1973) while in crocodiles it also originates from the posterodorsal and distal dorsal radius (Meers, 2003; Suzuki & Hayashi, 2010). Thus, sm origin area was on the anterodorsal plesiosaur ulna as in all three EPB taxa and on the adjacent carpal element proximally and anteriorly as observed in turtles and crocodilians.

Sm inserts in turtles and lepidosaurs alike into the proximal anterodorsal metacarpal I (Walker, 1973; Russell & Bauer, 2008) and to the radiale in crocodiles (Meers, 2003). Hence, the insertion area for sm was reconstructed to be on the proximal and anterodorsal metacarpal I in plesiosaurs. Its insertion was correlated with the anterior prominence on metacarpal I.

Ventral group

Musculus pronator teres (pte)

No synonyms in literature used in this study (Walker, 1973; Meers, 2003; Abdala, Manzano & Herrel, 2008; Russell & Bauer, 2008; Suzuki & Hayashi, 2010).

Pte originates in turtles, lepidosaurs, and crocodiles from the humeral entepicondyle posteroventrally (Walker, 1973; Meers, 2003; Abdala, Manzano & Herrel, 2008; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). In crocodiles and lepidosaurs its origin area is the most proximal of the flexors originating on the humerus distally followed by fcr (Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). In Testudines it is distally and ventrally situated, but at the same level as fcu origin area and proximally bordered by fdlf (Walker, 1973). Hence, pte was reconstructed to arise in plesiosaurs from the posteroventral surface of the humerus where it fans out and bends caudally. It was placed as the most proximal flexor arising from the plesiosaur humerus as in lepidosaurs and crocodiles, distally bordered by fcr.

In all three taxa it inserts into the ventral radius, in turtles distally (Walker, 1973; Abdala, Manzano & Herrel, 2008) in lepidosaurs anteroventrally and for approximately half its distal length (Russell & Bauer, 2008) and in crocodiles it covers most of the ventral shaft (Meers, 2003). Accordingly, the insertion area of pte was reconstructed to be on the lower half of the plesiosaur radius.

Musculus flexor carpi ulnaris (fcu)
-epitrochleoanconeus (Russell & Bauer, 2008)
-flexor carpi ulnaris (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010)
Epitrochleoanconeus is a portion of flexor carpi ulnaris according to Remes (2007). Flexor carpi ulnaris was chosen, as it is used by all authors on which this work is based on and the detailed differentiation into several muscle bellies was not undertaken.

Fcu arises from the entepicondyle of the humerus posteroventrally in all three taxa used for the EPB (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). It is the most distal flexor that originates from the posterodorsal turtle humerus, at the same level as the pte origin area posteroventrally (Walker, 1973). In crocodylians and lepidosaurs, fcu arises as the most distal flexor from the humerus, proximally bordered by fdlf (Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). Thus, fcu was reconstructed to arise as the distalmost flexor from the plesiosaur humerus, proximally bordered by fdlf as well.

Fcu inserts ventrally into the pisiform in turtles, crocodiles, and lepidosaurs (Walker, 1973; Meers, 2003; Russell & Bauer, 2008). In lepidosaurs it also attaches to metacarpal V (Russell & Bauer, 2008) and in turtles and lepidosaurs also onto the posteroventral ulna (Walker, 1973; Russell & Bauer, 2008), anteriorly bordered by the ulnar origin area of fdlf as in crocodiles, lepidosaurs, and turtles (Walker, 1973; Meers, 2003; Russell & Bauer, 2008). As this muscle insertion may spread onto adjacent bony elements, it was reconstructed in plesiosaurs on the posterodistal ulna as supported by turtles and on the forming accessory ossicle (s. Andrews, 1910, forming on proximoposterior ulnare) which is in a similar position as the pisiform is in crocodiles, turtles, and lepidosaurs. An insertion into metacarpal V could be favorable for flipper twisting in plesiosaurs.

Musculus flexor digitorum longus (fdlf)

-flexor digitorum longus (Meers, 2003; Russell & Bauer, 2008)

-palmaris longus of turtles (Walker, 1973) is homologous to humeral head/s of crocodylians and lepidosaurs (Meers, 2003; Russell & Bauer, 2008)

The term fdlf is chosen because of its wide acceptance across taxa and literature studied in this project.

Fdlf has two bellies, one of which arises posteroventrally from the entepicondyle of the humerus and the other one ventrally from the ulna (Walker, 1973; Meers, 2003; Russell & Bauer, 2008). The ulnar origin in crocodilians is confined to the distal ulna, but additionally a carpal muscle belly arises from the ulnar side (Meers, 2003). In crocodiles and lepidosaurs fdlf arises from the humerus proximal to fcu (Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010), but distally to fcr in lepidosaurs (Russell & Bauer, 2008) and to pte in crocodiles (Meers, 2003; Suzuki & Hayashi, 2010). In turtles it originates distally to fcr but proximally to fcu and pte (Walker, 1973). Thus, the humeral head of fdlf was reconstructed to arise from the ventral ulnar epicondyle in plesiosaurs, as supported by lepidosaurs, crocodiles, and turtles but bordered by fcr proximally and by fcu distally as seen in lepidosaurs. The ulnar head arises in plesiosaurs from an extensive origin ventrally as in turtles and lepidosaurs.

In turtles and lepidosaurs the common tendon of the two muscle bellies of fdlf add to a flexor aponeurosis, the flexor plate (Walker, 1973; Russell & Bauer, 2008). Contrastingly, in crocodiles the tendon splits into three smaller tendons (Meers, 2003). In lepidosaurs and turtles alike, the five tendons insert into the terminal phalanx of digit I-V (Walker, 1973; Russell & Bauer, 2008), merely in crocodiles the three tendon slips insert into the penultimate phalanges of digit I-III (Meers, 2003). Thus, in plesiosaurs it seems likely that as in turtles and lepidosaurs the common tendon of fdlf contributes to a flexor plate which sends five tendons to the terminal phalanx of digit I-V.

Musculus flexor carpi radialis (fcr)

No synonyms known for taxa and literature studied in this work (Walker, 1973; Russell & Bauer, 2008). This muscle is reduced in crocodilians (Meers, 2003; Remes, 2007)

Fcr originates posteroventrally from the entepicondyle of the humerus of turtles and lepidosaurs (Walker, 1973; Russell & Bauer, 2008). At its origin, this muscle is associated in lepidosaurs with pte, which arises proximal to it (Russell & Bauer, 2008). In turtles, fcr is the most proximal flexor arising from the humerus (Walker, 1973). Distally to fcr arises fdlf in lepidosaurs and turtles (Walker, 1973; Russell & Bauer, 2008). Hence, fcr origin area was on the entepicondyle of the plesiosaur humerus distal to pte origin and proximal to fdlf origin.

In Testudines fcr attaches to the anterodistal radiale-centrale and adjacently to the proximal distal carpal (Walker, 1973). Contrastingly, in lepidosaurs fcr inserts into proximal metacarpal I (Russell & Bauer, 2008). Therefore, both states are equally likely to reconstruct for the plesiosaur foreflipper. Although an insertion to metacarpal I could be favorable for flipper twisting in plesiosaurs.

3.1.1.4 Manual muscles

Dorsal group

Musculi extensores digitores breves superficialis (edbs)

-extensores digitores breves superficialis (Russell & Bauer, 2008)
-extensores digitorum breves (Walker, 1973)
-extensor digitorum superficialis and extensor pollicis superficialis et indicus proprius (Meers, 2003)

The authors decided to choose extensores digitores breves superficiales and extensores digitores breves profundi after Russell & Bauer (2008) as it clarifies, that this muscle group consists of a superficial and a deeper muscle layer.

Edbs arise in turtles and lepidosaurs dorsally from the ulnare (Walker, 1973; Russell & Bauer, 2008) and from the distal ulna in turtles (Walker, 1973). In crocodiles, muscles to digit I, II, and III originate from the radiale, the muscle for digit IV from both, radiale and ulnare, and the muscle for digit V originates from ulnare and distal most ulna (Meers, 2003). So, EPB suggests to reconstruct the origin area of this muscle on the plesiosaur ulnare as seen in turtles and lepidosaurs. Although, an origin on ulna, radiale, and intermedium is also possible because no muscles originate or insert here otherwise, except for ecu which inserts into the ulnare.

All five tendons insert into the proximal dorsal terminal phalanges of digit I-V in crocodiles and lepidosaurs (Meers, 2003; Russell & Bauer, 2008) and into the penultimate phalanges in turtles (Walker, 1973). Additionally, extensor pollicis superficialis et indicus proprius attach to the first phalanx of digit I and II. Accordingly in plesiosaurs, the tendon insertions were proximodorsally on the terminal phalanx of each digit.

Musculi extensores digitores breves profundi (edbp)
-extensores digitores breves profundi (Russell & Bauer, 2008)
-interossei dorsales (Walker, 1973)
-dorsometacarpalis (Abdala, Manzano & Herrel, 2008)
-extensor digitorum profundi (Meers, 2003)
Please view explanation for extensores digitores breves superficiales above.

In lepidosaurs and turtles edbp originate from the proximal dorsal metacarpals (Walker, 1973; Abdala, Manzano & Herrel, 2008; Russell & Bauer, 2008) and in turtles from bordering areas of the adjacent distal carpal I-V distally as well (Walker, 1973; Abdala, Manzano & Herrel, 2008). Origin areas of these muscles in crocodiles are quite complex: Extensor digiti III has three muscle bellies, while the other four only have one muscle belly. Extensor digiti I arises from the proximal anterodorsal metacarpal I and extensor digiti II from the proximal posterodorsal metacarpal I. Extensor digiti III originates from ulnare and radial distal carpal, and metacarpal II. Extensor digiti IV arises from proximal dorsal metacarpal III. Extensor digiti V from distal carpal to metacarpal V. Involvement of origin areas with the ligaments of the carpus are common (Meers, 2003). So an origin area on the metacarpals would be supported by turtles and lepidosaurs (Walker, 1973; Abdala, Manzano & Herrel, 2008; Russell & Bauer, 2008), while an origin on adjacent carpal elements would be supported by turtles and crocodiles (Walker, 1973; Meers, 2003). An origin on the metacarpals was reconstructed for plesiosaurs, but the origin areas might have been spread over the adjacent distal carpal elements, as they appear to be free of muscles yet. The one or the other reconstruction would not change the muscles function, so both options are equally well supported.

In crocodilians and lepidosaurs, edbp attach to the terminal phalanges in all five digits (Meers, 2003; Russell & Bauer, 2008) except for the fifth digit in crocodiles (Meers, 2003). How they attach in turtles is differently reported by Walker (1973), who states an attachment on the penultimate phalanx (Walker, 1973) and Abdala, Manzano & Herrel (2008) who report insertions on the terminal phalanges. Hence, the insertions of edbp were reconstructed on the unguals of digit I-V in plesiosaurs. Both layers of mm. extensores digitorum breves (superficialis and profundi) were reconstructed as they are necessary for digital extension and because they are well supported by the EPB. Yet, it is likely that both portions are fused or undifferentiated as observed in chelonioids due to a reduction of digital mobility (Walker, 1973).

Ventral group

Musculi flexores digitorum superficialis (fdls)

-flexores digitores breves (Russell & Bauer, 2008)
-flexor brevis superficialis (Walker, 1973; Abdala, Manzano & Herrel, 2008)
-flexor digitorum brevis superficialis I-IV (Meers, 2003)
This study agrees on the established homology by Remes (2007).

Fdls originate from the annular ligament in lepidosaurs (Russell & Bauer, 2008) and the flexor retinaculum (which appears to be homologous to the annular ligament in lepidosaurs) in turtles according to Abdala, Manzano & Herrel (2008). Walker (1973) describes it as originating from the flexor plate in turtles which would be similar to the situation described for Crocodylia (Meers, 2003). In plesiosaurs, if fdls is differentiated from the fdlf, it arises from a tendinous structure and not from a bony area.

The insertions of this muscle are highly variable across Sauropsida. In turtles (Walker, 1973), crocodilians (Meers, 2003), and lepidosaurs (Russell & Bauer, 2008) it may insert into digit I-IV and in turtles and lepidosaurs also to digit V). In crocodylians in attaches anteriorly and posteriorly to phalanx I in digit I, III, and IV, and to phalanx II in digit II (Meers, 2003). In turtles, mm. flexores digitorum superficialis insertion may be into phalanx I, the paenultimate phalanx, or the tendon sheath of each digit. Additionally, the portion to digit I or digit V may be lost, or in Cheloniidae all but the portion to digit V are reduced (Walker, 1973). In lepidosaurs the portion to digit I inserts into proximal phalanx I, the ones to digit II-V insert into phalanx II. The tendon to digit III shows an additional insertion into phalanx III and the tendons to digit IV and V additionally insert into the penultimate phalanges (Russell & Bauer, 2008). For plesiosaurs an insertion into the paenultimate phalanx paralleling fdlf displayed by turtles and partially by lepidosaurs appears to be likely (and possibly plesiosmorphic in diapsids), whereas the other proposed states appear to be reductional states of fdls.

Musculus abductor digiti V (abdV)

-abductor digiti quinti (Russell & Bauer, 2008)
-abductor digiti minimi (Walker, 1973)
-abductor digitorum V (Abdala, Manzano & Herrel, 2008)
-abductor metacarpi V (Meers, 2003)

The term abductor digiti V by Remes (2007) will be followed due to reasons discussed in Remes (2007).

AbdV originates ventrally from the pisiform in crocodilians (Meers, 2003). In turtles its origin is situated on the 5th distal carpal according to Walker (1973) and from the pisiform as reported by Abdala, Manzano & Herrel (2008). Contrastingly, in lepidosaurs it arises from the tendon of fcu and the annular ligament (Russell & Bauer, 2008). Thus, the origin area of this muscle was on the accessory ossicle adjacent to ulnare, respectively the adjacent ulnare (compare to Andrews, 1910, Fig. C, p. 182) in the plesiosaur foreflipper, which are in a similar position as the pisiform in extant sauropsids.

AbdV inserts ventrally into phalanx I of digit V in lepidosaurs and turtles (Abdala, Manzano & Herrel, 2008; Russell & Bauer, 2008) but proximoposteriorly in turtles (Walker, 1973) and ventrally in lepidosaurs (Russell & Bauer, 2008). In crocodiles only, its insertion area is situated along the shaft of metacarpal V (Meers, 2003). AbdV inserted into the first phalanx of digit V proximally in plesiosaurs.

Musculus abductor pollicis brevis (apb)
-abductor metacarpi I (Meers, 2003)
-abductor pollicis brevis (Walker, 1973; Abdala, Manzano & Herrel, 2008)
-anteriormost belly of interossei ventrales to digit I (Russell & Bauer, 2008)
The established name by Remes (2007), abductor pollicis brevis, will be followed here as well.

In Testudines apb arises from the distal carpal adjacent to digit I (Walker, 1973) or from the distal radius (Abdala, Manzano & Herrel, 2008). In crocodilians it originates from the radiale anterodistally (Meers, 2003) and in lepidosaurs from a ligament at the level of the radiale and from distal carpal IV (Russell & Bauer, 2008). Accordingly, apb origin surface was on the plesiosaur radiale as reported for crocodiles and lepidosaurs.

Apb inserts into phalanx I of digit I anteroproximally in turtles and lepidosaurs (Walker, 1973; Russell & Bauer, 2008) and distally into metacarpal I in lepidosaurs, too (Russell & Bauer, 2008). In Crocodylia, it only attaches to metacarpal I anteroproximally (Meers, 2003). The insertion site of apb was on phalanx I of digit I of the plesiosaur foreflipper as reported for turtles and lepidosaurs because this may be of advantage for flipper twisting, although an attachment on metacarpal I is equally possible.

Musculus adductor digiti minimi (adm)

-adductor digiti minimi (Walker, 1973)

-flexor digiti quinti pars superficialis and profundus (Meers, 2003)

-(no actual name given) mesial lumbricales branch from metacarpal I to digit V (Russell & Bauer, 2008)

The term adductor digiti minimi will be used in the following text, to underline its different function to abdV.

In lepidosaurs it originates from anteroproximal metacarpal I (Russell & Bauer, 2008), in turtles from distal carpal I and II (Walker, 1973; Abdala, Manzano & Herrel, 2008), and in crocodiles from the posterodistal radiale (Meers, 2003). The origin of adm was on the plesiosaur radiale as in crocodiles. This way it is ensured that this muscle takes a course similar to that observed across sauropsids from anteroproximal to posterodistal (Walker, 1973; Meers, 2003; Russell & Bauer, 2008).

Adm inserts anteroproximally into metacarpal V in lepidosaurs (Russell & Bauer, 2008), turtles (Walker, 1973; Abdala, Manzano & Herrel, 2008), and crocodiles (Meers, 2003). Additionally, in crocodilians it also attaches to phalanx 3 of digit V (Meers, 2003). The insertion of adm was found to be into metacarpal V of the plesiosaur as suggested by all three taxa from the EPB, with a possible insertion into phalanx III as in crocodilians.

3.1.2 Hindflipper musculature

3.1.2.1 Homology statement

Further, for the pelvic girdle of Plesiosauria homology has yet to be established. The authors presume that anterior and posterior sides of the ischium and pubis correspond to the same sides as in extant Sauropsida. In extant sauropsids ischium and pubis somewhat inclined dorsoventrally. For plesiosaurs it is presumed that the acetabulum has been relatively moved ventrally while the suture of the opposing sides of pubis and ischium in the body mid-line has been shifted dorsally. This way pubis and ischium have become two almost flat-lying bones on the plesiosaur belly. From the lateral side to the body mid-line, pubis and ischium slant slightly v-shaped (Andrews, 1910). The lateral concavity anterior to the acetabulum on the pubis may be convergent to the lateral process in turtles (Walker, 1973) or the pubic tubercle in lepidosaurs (Russell & Bauer, 2008). A lateral process (called like that in turtles (Walker, 1973) or an ischiadic tuberosity (called like that in lepidosaurs (Russell & Bauer, 2008) is not present in the plesiosaur ischium.

3.1.2.2 Ligaments of the pelvic girdle and limb

The presence of ligaments in the pelvic girdle varies considerably in Sauropsida: Testudines only have a puboischiadic ligament that connects the posterior ischial symphyseal region with its lateral process and with the lateral process of the pubis (Walker, 1973) which is similarly described for lepidosaurs by Russell & Bauer (2008). Contrastingly, this ligament is reduced in crocodilians (Romer, 1923). Lepidosaurs in general and crocodilians have an ilioischiadic ligament, which connects the lateral process of the ischium with the posterior ilium, and an iliopubic ligament, that spans from the anterior ilium to the lateral process of the pubis (Romer, 1923; Russell & Bauer, 2008). Yet, *Sphenodon* does not have an ilioischiadic ligament (Russell & Bauer, 2008). Therefore, EPB would allow to reconstruct all three ligaments relatively well supported for plesiosaurs. Although, a puboischiadic ligament seems unlikely for plesiosaurs: First of all, in plesiosaurs there does not seem to be a distinctive lateral ischial process/ischiadic tuberosity or lateral pubic process that provide the attachment surfaces for this ligament in turtles and lepidosaurs (Walker, 1973; Russell & Bauer, 2008). Second, the crocodilian ischium and pubis which lacks this ligament also does not show these processes. Third, if one connects the questionable areas in the plesiosaur pelvic girdle by a thought line, it basically lies in the plane of ischium and pubis. Therefore, an ilioischiadic ligament is not reconstructed for plesiosaurs. An iliopubic and ilioischiadic ligament are possible in plesiosaurs, although the course of an iliopubic ligament would be quite close to the glenoid and the pubis eventually leaving not enough room for the large pi portions that originate from the dorsal pelvic girdle and insert into the proximal femur to pass ventrally to it (chapter 3.1.2.1). Suitable osteological correlates, that appear to be present in those taxa having these ligaments are lacking in plesiosaurs which speaks against their reconstruction in plesiosaurs. Therefore, none of the three ligaments was reconstructed for the plesiosaur pelvic girdle as the plesiosaur pelvic girdle does not seem to show the morphologies correlated with their presence, although EPB would support all three of them.

In the forelimb, crocodilians have a flexor retinaculum which is associated with the tibiocalcaneal tendon (Suzuki et al., 2011). Similar structures, associated with the gastrocnemius heads are visible in lepidosaurs (compare to Russell & Bauer, 2008 Fig. 1.43, p. 347) and turtles (compare to e.g., Walker, 1973 Fig. 25, p. 71). Accordingly, a similar ligament was reconstructed for plesiosaurs. An extensor retinaculum/annular ligament that extends between pl and ta is known from lepidosaurs and crocodilians (Russell & Bauer, 2008; Suzuki et al., 2011) but not from turtles (Walker, 1973). Therefore, this ligament was reconstructed for plesiosaurs as well. A comparable set of ligaments, intermetacarpal and metacarpodigital ligaments, as could be reconstructed for the plesiosaur carpus and metacarpus (Russell & Bauer, 2008; s. chapter 3.1.1.1) would be tempting to reconstruct for the plesiosaur hindflipper as well, because it could contribute to the flipper twisting mechanism in plesiosaurs (s. chapter 4.3.2).

3.1.2.3 Muscles of the pelvis

Dorsal group

Musculus iliotibialis (it)

-iliotibialis (Snyder, 1954; Zug, 1971; Walker, 1973; Suzuki et al., 2011)
-iliotibiales (Otero, Gallina & Herrera, 2010)
-ilio-tibialis (Romer, 1923; Gatesy, 1997)

It was chosen, because its usage is the most common amongst the chosen literature for plesiosaur muscle reconstructions.

It originates across Sauropsida broadly similarly, i.e., from the dorsal rim of the lateral ilium (Snyder, 1954; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). In crocodilians it arises by three heads from the approximately first two thirds of the dorsal ilium (Romer, 1923; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). In lepidosaurs it originates anteriorly fleshy and posteriorly aponeurotically from the lateral ilium (Russell & Bauer, 2008) dorsally to the origin areas of ifi and ife (Snyder, 1954; Russell & Bauer, 2008). In crocodilians and lepidosaurs it arises cranially/anteriorly to fte and dorsal to ife (Romer, 1923; Snyder, 1954; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). Walker (1973) reports that in Testudines it arises from the posterodorsal rim of the lateral ilium and tendinously from its anterior border (Walker, 1973) dorsally or partially from the same level as the ife origin (Zug, 1971; Walker, 1973). This is supported partially by observations of Zug (1971) who observed this bifurcated origin for it as well. Yet, Zug (1971) reports that it is origin is more variable than this though, i.e., some taxa were studied that only have either one or the other origin area. The biggest consensus for plesiosaurs is found, if it arises from the anterodorsal lateral ilium, anteriorly to fte and dorsally to ife as across supported by all three taxa. A posterior origin as in lepidosaurs and some turtle taxa is nonetheless possible.

Its insertion is very uniform across Sauropsida. Across the EPB it contributes to a common tendon with f and a and attaches to the proximodorsal tibia (Otero, Gallina & Herrera, 2010; Suzuki et al., 2011) or the cneminal crest (Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008). Hence, the concerted insertion area of it, a, and f was on the proximodorsal tibia because a cneminal crest is lacking in plesiosaurs.

Musculus femorotibialis (f)

-femorotibialis (Snyder, 1954; Zug, 1971; Walker, 1973; Suzuki et al., 2011)
-femorotibiales (Otero, Gallina & Herrera, 2010)
-femoro-tibialis (Romer, 1923; Gatesy, 1997)
Femorotibialis was chosen, because it is the most commonly used name in the literature on which this study is based on.

F originates in Testudines, crocodilians, and lepidosaurs from the femoral shaft dorsally, but reaches around it anteriorly and posteriorly onto the ventral side of the femur (Romer, 1923; Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). In crocodilians two subportions are discerned (externus and internus) (Romer, 1923; Otero, Gallina & Herrera, 2010) and in turtles three (vastus internus, medialis, and externus) (Walker, 1973). In sauropsids, f origin area is situated on the femur distally to those insertions of the pelvic musculature that insert into the femur, except for af, which may ventrally separate the overlapping origin area of f across the EPB (Romer, 1923; Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). Therefore, for plesiosaurs an origin area on the dorsal femoral shaft that reaches around it anteriorly and posteriorly onto its ventral side is well supported by crocodilians, turtles, and lepidosaurs. The origin site was associated with the fan-shaped striations and rugosities on the distal dorsal plesiosaur femur.

F shares a common tendon of insertion with it and a across the EPB (Romer, 1923; Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011) (for details on insertion see chapter on it).

Musculus ambiens (a)

No synonyms reported in the literature on which this study is based (Romer, 1923; Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011).

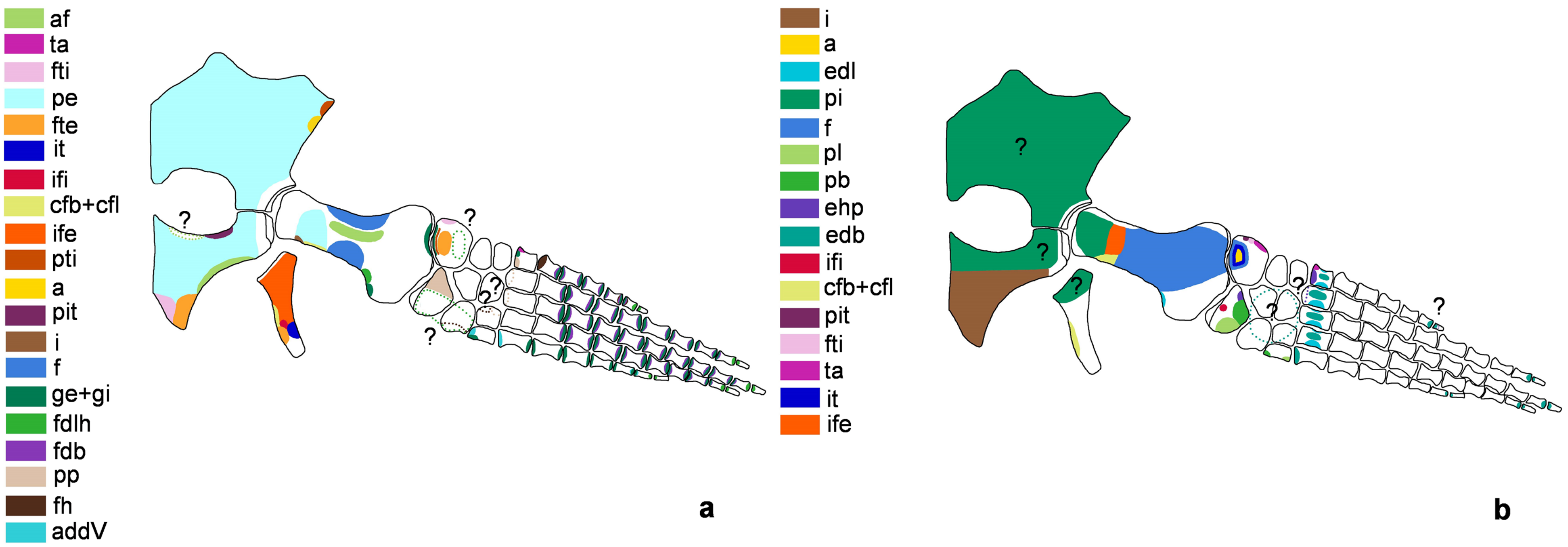

Fig. 2: *Cryptoclidus eurymerus* (IGPB R 324) hindflipper muscle reconstructions in a) ventral and b) dorsal view. Abbreviations: a, Musculus ambiens; addV, Musculus adductor digiti quinti; af, Musculus adductor femoris; cfb, Musculus caudifemoralis brevis; cfl, Musculus caudifemoralis longus; edb, Musculus extensores digitores breves; edl, Musculus extensor digitorum longus; ehp, Musculus extensor hallucis proprius; f, Musculus femorotibialis; fdb, Musculus flexores digitores breves; fdlh, Musculus flexor digitorum longus (hindflipper); fh, Musculus flexor hallucis; fte, Musculus flexor tibialis externus; fti, Musculus flexor tibialis internus; gi and ge, Musculus gastrocnemius internus and Musculus gastrocnemius externus; i, Musculus ischiotrochantericus; ife, Musculus iliofemoralis; ifi, Musculus iliofibularis; it, Musculus iliotibialis; pb and pl, Musculus peroneus brevis and Musculus peroneus longus; pe, Musculus puboischiofemoralis externus; pi, Musculus puboischiofemoralis internus; pit, Musculus puboischiotibialis; pti, Musculus pubotibialis; pp, Musculus pronator profundus; ta, Musculus tibialis anterior.

In a superficial, geometrical way, a originates from the pelvis relatively similar across crocodilians, turtles, and lepidosaurs namely anteroventrally to the acetabulum, but in detail they vary (Romer, 1923; Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). From the puboischiadic ligament anteriorly and/or the lateral pubic process posteriorly originates the a in Testudines (Zug, 1971; Walker, 1973). Crocodilians have two tendinous a origin areas, with *Caiman latirostris* posing the exception having one head arising from a region anterior to the acetabulum (Otero, Gallina & Herrera, 2010). In the other crocodilians, two a origin tendons arise from the suture between pubis and ischium anteroventral to acetabulum and from pubic peduncle on the dorsal side ventrally to the acetabulum (Romer, 1923; Suzuki et al., 2011). In lepidosaurs, two a tendons arise laterally from the pelvic girdle just ventrally and anteriorly to the acetabulum, they soon converge and are followed by the muscle belly which soon merges towards the knee into a tendon which joins the patellar tendon. Ventrally it adds to the joint capsule (Russell & Bauer, 2008). In turtles, crocodilians, and lepidosaurs it is flanked by the pe origin area (Romer, 1923; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Suzuki et al., 2011), in the former also by the pi origin area (Zug, 1971; Walker, 1973). The most common origin area for a in plesiosaurs seems to be the origin area on the pubic tubercle anterior to the acetabulum as reported for all three extant taxa. Here, it would also be bordered by pe as reported for all three sauropsid taxa. This arrangement would be most closely to the turtle condition and would be somewhat similar to and mirror the bb arrangement of the pectoral limb. An attachment on the area ventrally to the acetabulum where pubis and ischium meet would be possible for plesiosaurs and also well supported by crocodilians and lepidosaurs.

A inserts together with it and f in sauropsids as described above (Romer, 1923; Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011) (for details see above it insertion).

Musculus iliofibularis (ifi)

-iliofibularis (Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011)

-ilio-fibularis (Romer, 1923; Gatesy, 1997)

Ifi was chosen, because its usage is the most common amongst the chosen literature for plesiosaur muscle reconstructions.

Ifi originates from the posterolateral ilium in crocodilians, lepidosaurs, and turtles (Romer, 1923; Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). Its exact origin area is slightly variable across all three taxa, but it is situated generally posterior to ife origin and not on the dorsal border of the ilium and ventrally to it and fte origin (Romer, 1923; Snyder, 1954; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011), except for various turtles as reported by Zug (1971). Therefore, it is reasonable to reconstruct the origin area of ifi on the posterior plesiosaur ilium ventrally to it and fte.

Across crocodilians, turtles, and lepidosaurs ifi inserts into the proximal third of the dorsal fibula proximal to the origins of pb and pl (Romer, 1923; Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). It may be displaced distally at approximately half the fibula length in turtles (s. Walker, 1973). Accordingly, the insertion area of ifi was on the dorsal fibula relatively proximally and proximal to pb and pl origin site in plesiosaurs.

Musculus iliofemoralis (ife)

-iliofemoralis (Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011)
-ilio-femoralis (Romer, 1923; Gatesy, 1997)
Ife was chosen, because it is most commonly used in the literature on which this study is based on.

Ife origin area lies on the lateral ilium dorsal to the acetabulum deep to it in crocodilians, turtles, and lepidosaurs (Romer, 1923; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). In turtles it additionally arises from the last one to two dorsal vertebrae, from the first sacral vertebra, and from bordering areas on the carapace (Zug, 1971; Walker, 1973). In lepidosaurs ife also arises from a ventral septal origin it shares with pit (Russell & Bauer, 2008). Hence, ife origin area can be confidently placed on the lateral plesiosaur ilium, as supported by all three taxa, below the it origin area and above the acetabulum. A spreading onto the adjacent vertebral column as described in turtles is possible.

In Testudines ife inserts dorsally into trochanter major (Zug, 1971; Walker, 1973). In lepidosaurs its insertion area is a comparatively large surface that covers much of the proximal and ventral femur and wraps around the posterior femur onto its posterodorsal side (Snyder, 1954; Russell & Bauer, 2008). In crocodilians it inserts posteriorly along the femoral shaft (Romer, 1923; Gatesy, 1997; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). Therefore, a dorsal insertion of ife on the proximal plesiosaur femur is well supported for plesiosaurs by the EPB. Although a posterior insertion would be equally well supported, the former is preferred, as it matches well with part of the rugose and deeply striated muscle scar on the dorsal femoral trochanter.

Musculus puboischiofemoralis internus (pi)

-puboischiofemoralis internus (Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011)
-pubo-ischio-femoralis internus (Romer, 1923; Gatesy, 1997)
Puboischiofemoralis internus was chosen, because its usage is the most common amongst the chosen literature for plesiosaur muscle reconstructions.

Pi has three heads in lepidosaurs (pi 1-3) (Russell & Bauer, 2008) and two heads in crocodilians (pi I and pi 2) and turtles (Walker, 1973; Otero, Gallina & Herrera, 2010), although a single-headed state was described by Zug (1971) for Testudines, too. In crocodilians pi I has its origin area situated on the medial ilium and ischium posteriorly at their symphyseal region below the sacral rib facets on the ilium (Romer, 1923; Suzuki et al., 2011). Pi 2 arises ventrally from up to seven lumbar vertebrae and their transverse processes (Romer, 1923; Gatesy, 1997; Otero, Gallina & Herrera, 2010). The posterodorsal portion of turtles arises from the medial median ilium and ventrally from the first or second sacral and the first two caudal vertebra and ribs (Zug, 1971; Walker, 1973). The anteroventral head arises from the epipubic cartilage and the pubis dorsally (also from the thyroid fenestra). (Zug, 1971; Walker, 1973). In lepidosaurs Russell and Bauer (2008) describe three portions of this muscle (pi 1-3, from posterior to anterior). Pi 3 arises from most of the dorsal pubis extending posteriorly to the thyroid fenestra. Pi 1 arises from the symphysis of the ischia and posteriorly to the thyroid fenestra almost up to the ilium. Pi 2 arises in between pi 1 and 3 (Russell & Bauer, 2008). Four origin areas for pi in plesiosaurs can be discerned that appear to be equally possible according to EPB: An origin on the medial ilium and from the vertebral column as in crocodilians and turtles is thinkable. The second option allows to reconstruct pi onto the sacrum as well as have it being spread onto the first caudal or the last dorsal vertebrae. An origin on most of the dorsal plesiosaur pubis is possible to reconstruct as in turtles and lepidosaurs, as well as an origin on the anterior ischium as in crocodilians and lepidosaurs.

Pi inserts in crocodilians and often in lepidosaurs into separate insertion areas on the femur anterodorsally to dorsally and posterodorsally (Romer, 1923; Snyder, 1954; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). In turtles pi attaches to the dorsal to anterodorsal femur distally onto trochanter minor (Zug, 1971; Walker, 1973). In all three taxa it inserts proximally to f and distally to pe into the femur (Romer, 1923; Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Suzuki et al., 2011). Accordingly, a pi insertion site on the anterodorsal proximal plesiosaur femur, proximal to f origin and distal to pe insertion, would be well supported. Its attachment site was correlated with part of the large heavily striated and rugose muscle scar on the dorsal trochanter of the plesiosaur femur.

Ventral group

Musculus puboischiotibialis (pit)

-puboischiotibialis (Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011)

-pubo-ischio-tibialis (Romer, 1923; Gatesy, 1997)

Pit was chosen, because it is the most commonly used term amongst the literature used for this study.

On the anterolateral ischium of crocodilians is the pit origin area situated (Romer, 1923; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). Contrastingly, in turtles and lepidosaurs alike, it arises from the puboischiadic ligament (Snyder, 1954; Walker, 1973; Russell & Bauer, 2008). In crocodilians and turtles pit is a small muscle (Romer, 1923; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). Zug (1971) was not able to find it in its myological studies of turtles. In lepidosaurs, pit is a large fan-shaped muscle (Snyder, 1954; Walker, 1973; Russell & Bauer, 2008). Although the turtle and lepidosaur state would be preferable to the crocodilian state regarding the EPB, the latter was reconstructed for plesiosaurs, as it is presumed, that the puboischiadic ligament is absent in plesiosaurs (s. chapter 3.1.2.2).

Pit inserts into the tibia anterodorsally distal to the patellar tendon formed by a, f, and it in lepidosaurs and crocodilians (Snyder, 1954; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). In turtles it attaches anteroventrally to the tibia (Walker, 1973). Accordingly, pit insertion was on the anterodorsal plesiosaur tibia distal to the patellar tendon insertion as in crocodilians and lepidosaurs.

Musculus pubotibialis (pti)

No synonyms in the literature on which this muscle reconstruction is based on (Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008). Pti is not reported in crocodilians (Romer, 1923; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011)

In Testudines and lepidosaurs it originates from the puboischiadic ligament (Zug, 1971; Walker, 1973; Russell & Bauer, 2008) anterior and superficial to pit (Walker, 1973; Russell & Bauer, 2008). A second pti head is known in lepidosaurs to arise ventrally from the pubis anteroventrally to a from the processus lateralis of the pubis (Snyder, 1954; Russell & Bauer, 2008). The best supported hypothesis would be that pti originated from the puboischiadic ligament, but due to the rearrangement of the pelvic girdle, there seems to be good proof, that this ligament did not exist in plesiosaurs (s. chapter 3.1.2.2). So, one must presume that pti spread onto the adjacent pubis (pubic tubercle) in plesiosaurs, similar to what has been described for lepidosaurs.

Pti attaches ventrally and proximally to the tibia, proximally to the attachment sites of fte and fti in turtles and lepidosaurs (Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008). Hence, an insertion on the proximoventral plesiosaur tibia, proximally to the insertion area of fte and fti, is well supported.

Musculus flexor tibialis internus (fti)

No synonyms in the literature on which this study is based on (Romer, 1923; Snyder, 1954; Zug, 1971; Walker, 1973; Gatesy, 1997; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011).

In turtles one or two origins for fti are known (Zug, 1971; Walker, 1973). Two or three fti heads are described in lepidosaurs (Snyder, 1954; Russell & Bauer, 2008). For crocodilians three to four heads are observed (Romer, 1923; Gatesy, 1997; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). All three taxa share a ventrally situated fti origin on the posterior ischium (fti1 and fti3 in crocodilians) (Romer, 1923; Zug, 1971; Walker, 1973; Gatesy, 1997; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). In turtles this head also originates from the posterior puboischiadic ligament (Zug, 1971; Walker, 1973) and in lepidosaurs also from ilioischiadic ligament and the perineal region (Snyder, 1954; Russell & Bauer, 2008). Crocodilians, lepidosaurs, and turtles have a dorsally arising component of fti (Romer, 1923; Zug, 1971; Walker, 1973; Gatesy, 1997; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). In crocodilians, an iliac origin of fti (fti2 and 4) is present (Romer, 1923; Gatesy, 1997; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). In lepidosaurs this head originates from an intermuscular septum it shares with fte and from the ilioischiadic ligament (Russell & Bauer, 2008). In turtles, there may be an iliac origin and/or on the vertebral column, i.e., from one sacral and one to two or three caudal vertebrae (Zug, 1971; Walker, 1973). So in plesiosaurs a ventral origin area of fti on the posteroventral ischium is well supported by all three taxa. A second fti from a dorsal origin area was reconstructed for plesiosaurs. As all three states provided by the EPB are equally likely and no preferred hypothesis was implied, therefore *Sphenodon* was considered additionally. In *Sphenodon* the ilioischiadic ligament is reduced as is presumably also the case in plesiosaurs (s. chapter 3.1.2.2). In *Sphenodon* fti originates from the vertebral column (from the first six caudal vertebrae's transverse processes (reviewed in Russell and Bauer 2008) as in turtles. Hence, the second origin area of fti in plesiosaurs was reconstructed to be on the first two to six caudals and possibly also on the sacrum.

In turtles two muscle bellies converge into a common tendon which inserts proximoventrally to anteriorly into the tibia, distally to pit and pti insertion (Zug, 1971; Walker, 1973). In lepidosaurs and crocodilians the insertions of this muscle are highly complex, a complexity which cannot be reconstructed in detail for extinct plesiosaurs. In a simplified way, fti portions insert tendinously partially together with pit and partially by themselves into the proximal tibia (Gatesy, 1997; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011) posterodorsally in lepidosaurs (Russell & Bauer, 2008) and anterodorsally in crocodilians in common with FTE (Gatesy, 1997; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). An additional tendon inserts into the gastrocnemius in lepidosaurs and crocodilians (Gatesy, 1997; Russell & Bauer, 2008; Suzuki et al., 2011). In plesiosaurs, the fti insertion was placed in common with the pit insertion on the proximal anterior tibia as in crocodilians and lepidosaurs. An additional tendon to the m. gastrocnemius would be equally well supported by these two taxa.

Musculus flexor tibialis externus (fte)

-flexor tibialis externus

No synonyms in the literature on which this muscle reconstruction is based on (Romer, 1923; Snyder, 1954; Zug, 1971; Walker, 1973; Gatesy, 1997; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011).

Fte is single-headed in lepidosaurs and crocodilians (Romer, 1923; Snyder, 1954; Gatesy, 1997; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011) and may be double-headed in turtles (Zug, 1971; Walker, 1973). Laterally on the dorsal ilium border (Romer, 1923; Gatesy, 1997; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011), posterior to it and ifi, fte origin area is situated in crocodilians (Romer, 1923; Gatesy, 1997; Suzuki et al., 2011). In lepidosaurs it arises from the ilioischiadic ligament, partially closely associated with the posterior portion of fti (Russell & Bauer, 2008). In *Sphenodon* though, where the ilioischiadic ligament was reduced, fte also arises from the caudal vertebral column (Russell & Bauer, 2008). Contrastingly, in Testudines fte may have one or two heads which take their origin on the lateral posterodorsal ilium (Zug, 1971; Walker, 1973) or from adjacent 2nd sacral rib or from 1st to 5th caudal vertebrae (Zug, 1971) and posterodorsally from ischium (Zug, 1971; Walker, 1973) or puboischiadic ligament (Zug, 1971). Therefore, fte origin site was reconstructed on the plesiosaur vertebral column as reported from turtles and *Sphenodon* and from the lateral ilium as in crocodilians and turtles.

In lepidosaurs, turtles, and crocodilians fte attaches by a bifurcated tendon to the tibia, and via a common tendon with fti, it converges with gi (Romer, 1923; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). In turtles, a single tendon attachment on the posteroproximal tibia is possible (Zug, 1971). In crocodilians and turtles fte inserts into the proximoventral tibia (Romer, 1923; Zug, 1971; Walker, 1973; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011) and in lepidosaurs into the posteroventral tibia proximally (Snyder, 1954; Russell & Bauer, 2008). Hence, an insertion of fte on the proximal tibia as in crocodilians, turtles, and lepidosaurs and posteroventrally as in crocodilians and turtles was reconstructed for plesiosaurs. In plesiosaurs, an additional tendon inserts into the gi as in lepidosaurs, turtles, and crocodilians.

Musculus caudifemoralis brevis (cfb)

-caudofemoralis brevis (Gatesy, 1997; Otero, Gallina & Herrera, 2010)
-caudifemoralis brevis (Snyder, 1954; Russell & Bauer, 2008; Suzuki et al., 2011)
-caudi-iliofemoralis (Zug, 1971; Walker, 1973)
-coccygeo-femoralis brevis (Romer, 1923)

This study chose to go along with m. caudifemoralis brevis, as this name seems to find more acceptance across taxa and amongst the authors describing myology of recent sauropsids.

Cfb originates in crocodilians from the ventral posterolateral ilium (Romer, 1923) and either from the first caudal vertebra (Gatesy, 1997; Otero, Gallina & Herrera, 2010) or also from the last sacral vertebra (Gatesy, 1997). In turtles, the origin of cfb seems to be more variable. It involves the posteromedial ilium, the sacral vertebrae, and may spread onto up to two dorsal vertebrae and onto up to four caudal vertebrae (Zug, 1971; Walker, 1973). In lepidosaurs it originates from the first postsacrals and does not involve the ilium as origin surface (Snyder, 1954; Russell & Bauer, 2008). For plesiosaurs supported would be a cfb origin on the first caudals by all three taxa and one from the posterior ilium and the sacrum by turtles and crocodilians. Thus, these options were reconstructed for plesiosaurs.

Across all three taxa, cfb attaches posteroventrally to the femur (Romer, 1923; Zug, 1971; Walker, 1973; Gatesy, 1997; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). In turtles it attaches to trochanter major (Zug, 1971; Walker, 1973), in lepidosaurs to the femoral trochanter (Snyder, 1954; Russell & Bauer, 2008), and in crocodilians to the fourth trochanter (Romer, 1923; Gatesy, 1997; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). In lepidosaurs and crocodilians it attaches distally to the pe insertion (Romer, 1923; Snyder, 1954; Russell & Bauer, 2008; Suzuki et al., 2011) and in turtles it attaches adjacently to it (Walker, 1973). Hence, the insertion area of cfb was on a much rugose scar posteriorly on the plesiosaur femur as supported by all three taxa, but adjacently to pe insertion as in turtles.

Musculus caudifemoralis longus (cfl)

-caudofemoralis longus (Gatesy, 1997; Otero, Gallina & Herrera, 2010)
-coccygeo-femoralis longus (Romer, 1923)
-caudifemoralis longus (Snyder, 1954; Russell & Bauer, 2008; Suzuki et al., 2011)
This study chose to go along with caudifemoralis longus, as this name seems to find more acceptance across taxa and amongst the authors describing myology of recent sauropsids.

Cfl is absent in turtles, probably along with the the strongly reduced turtle tail (Walker, 1973). In crocodilians and lepidosaurs cfl is a large muscle mass that arises caudally to and partially along with cfb from the centra, ventral transverse processes, and the lateral haemal arches (Gatesy, 1997; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010) from 14 caudal vertebrae in lepidosaurs (Russell & Bauer, 2008) and from up to 13 (Otero, Gallina & Herrera, 2010) or 15 (Romer, 1923; Gatesy, 1997) caudal vertebrae in crocodilians. So, in plesiosaurs cfl may have originated from the centra, lateral haemal arches, and ventral transverse processes as in crocodilians and lepidosaurs for at least up to 13 caudal vertebrae or even further caudally.

Cfl inserts via a long tendon together with cfb in the femur in crocodilians and lepidosaurs (Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010). Part of the tendons runs further distally to insert ventrally into the knee joint in lepidosaurs (Russell & Bauer, 2008). In crocodilians the insertion of cfl is complex: it splits up and one part attaches to the ventral and proximal fibula, another part converges with a tendon of ifi and with the tendon of ge (Otero, Gallina & Herrera, 2010). An insertion in common with the cfb on the femur is likely in plesiosaurs. The insertion of the tendon into either the ventral knee joint as in lepidosaurs, or in the complex crocodilian way are both equally likely for plesiosaurs.

Musculus ischiotrochantericus (i)

-ischiotrochantericus (Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011)
-ichio-trochantericus (Romer, 1923; Gatesy, 1997)
Ischiotrochantericus was chosen, because its usage is the most common amongst the chosen literature for plesiosaur muscle reconstructions.

I origin area is situated in turtles, lepidosaurs, and crocodilians on the dorsal ischium (Romer, 1923; Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). In the former, it occupies the first ~ 2/3 of the ischium, the ventralmost region of the medial ilium and the membrane covering the thyroid fenestra (Walker, 1973) and in the latter two the posterior ~ third to half of the ischium (Romer, 1923; Snyder, 1954; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). In lepidosaurs, crocodilians, and turtles the origin area of i lies posterior to pi (ischial head) (Romer, 1923; Snyder, 1954; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). In turtles i arises anterior to fte (Zug, 1971; Walker, 1973). In plesiosaurs, i seems to have been arising from the medial ischium as in all three taxa and from approximately the posterior half of the ischium, posterior to pi as lepidosaurs and crocodilians.

I inserts proximally posteroventrally into the lepidosaur femur (Snyder, 1954; Russell & Bauer, 2008), posteroventrally or ventrally into the intertrochanteric fossa in turtles (Zug, 1971; Walker, 1973) and posteriorly to lightly posteroventrally in crocodilians (Romer, 1923; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). It inserts into the femur in all three taxa as one of the most proximal pelvic muscles (Romer, 1923; Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). I insertion area was reconstructed on the proximal posteroventral plesiosaur femur as in lepidosaurs and in turtles, and approximately as in crocodilians. It was associated with part of the posteroventral rugose muscle scar on the plesiosaur femur, therefore the insertion site was displaced further distally as reported for extant sauropsids.

Musculus adductor femoris (af)
-adductor femoris (Zug, 1971; Walker, 1973)
-adductor femoris 1 and adductor femoris 2 (Romer, 1923; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011)
Af was chosen, because its usage is the most common amongst the chosen literature for plesiosaur muscle reconstructions.

In crocodilians af is two headed. One belly originates from the anterolateral and the other one from the posterolateral ischium. In between stretches the origin area of the pe3. The former reaches up to the pit origin towards the acetabulum and the latter is bordered towards the body midline by fti1 (Romer, 1923; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). In turtles and lepidosaurs af takes its origin on the puboischiadic ligament (Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008). In lepidosaurs it arises superficial to pit and posterior to pti (Russell & Bauer, 2008). In turtles its attachment also spreads onto adjacent areas of the lateral process of the ischium. The best supported origin area for af in plesiosaurs would be, due to the absence of the puboischiadic ligament, on the posterolateral ischium.

Af inserts rather anteroventrally along and into the femoral shaft in lepidosaurs and turtles (Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008) and rather posteroventrally on the distal half in crocodilians (Romer, 1923; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). Across all three extant taxa, this muscle inserts into the femur in between the origin areas of f which overlap the femoral shaft anteriorly and posteriorly and reach onto the ventral side. Therefore, af was confidently reconstructed onto the ventral femoral shaft in between f overlapping origins and distal to the pe insertion on the plesiosaur femur. It can be correlated with parts of the striated plesiosaur femur shaft surface.

Musculus puboischiofemoralis externus (pe)

-puboischiofemoralis externus (Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011)

-pubo-ischio-femoralis externus (Romer, 1923; Gatesy, 1997)

Puboischiofemoralis externus was chosen, because it is most common in the literature on which this work is based on.

Pe arises in crocodilians, lepidosaurs, and turtles from the ventral pubis and ischium (Romer, 1923; Zug, 1971; Walker, 1973; Gatesy, 1997; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011) and only in crocodilians also from the anterodorsal pubis (Romer, 1923; Gatesy, 1997; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). In turtles an anterior (pubis) and posterior portion (from thyroid fenestra and ischium) are reported (Zug, 1971; Walker, 1973). Pe1, 2, and 3 are described for crocodilians: 1 from anterodorsal pubis, 2 from anteroventral pubis, and 3 from lateral ischium bordered anteriorly by af 1 origin and posteriorly by af 2 and fti1 (Romer, 1923; Gatesy, 1997; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). In lepidosaurs there are two portions of pe described as well as in turtles, but they are subdivided into a1, a2, a3, and b. a1 and a2 originate from most of the pubis, a3 from posterior thyroid fenestra and ischium and b from posterior and medial ischium. In plesiosaurs pe origin area was on the ventral pubis and ischium as in all three extant taxa described. Probably, it also originates from the membrane covering the thyroid fenestra.

Pe inserts in turtles and lepidosaurs anteriorly dorsally and ventrally (Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008) into the trochanter minor of the femur in the former (Zug, 1971; Walker, 1973) and the femoral trochanter in the latter. In lepidosaurs the subportions are divisible at their insertions as well (Snyder, 1954; Russell & Bauer, 2008). In crocodilians pe portions insert in common into trochanter major anteroventrally (Romer, 1923; Gatesy, 1997; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). Pe insertion area was on the anteroventral proximal plesiosaur femur as observed in turtles, crocodilians, and lepidosaurs, although a large muscle scar on the proximoventral plesiosaur femur suggests that it inserted unspecified ventrally.

3.1.2.4 Muscles of the crus

Dorsal group

Musculus extensor digitorum longus (edl)

-extensor digitorum communis + extensor hallucis longus (Walker, 1973)

-extensor digitorum communis (Zug, 1971)

-extensor digitorum longus (Snyder, 1954; Russell & Bauer, 2008; Suzuki et al., 2011)

Extensor digitorum longus is more accepted across taxa and literature on which this study is based, so this name was chose for better understanding.

Edl arises from the fibular epicondyle dorsally, just proximal to the joint capsule (Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Suzuki et al., 2011). Accordingly, this muscle's origin was reconstructed on the fibular epicondyle of the plesiosaur femur (s. chapter 2.1 for explanation).

In lepidosaurs it attaches to metacarpal II and III (Snyder, 1954; Russell & Bauer, 2008), in crocodilians additionally to metacarpal IV (Suzuki et al., 2011), and in turtles additionally to that to metacarpal I (Walker, 1973). In turtles and lepidosaurs it inserts into the posterodorsal shaft of the metacarpals (Snyder, 1954; Walker, 1973; Russell & Bauer, 2008), while in crocodilians it attaches dorsally to them (Suzuki et al., 2011). In Testudines there is also an anterodorsal insertion on metacarpal IV. In turtles edl may become fascial, especially the slips to metatarsal I-III and in sea turtles this muscle is reduced to a facia (Walker, 1973). Hence, the best supported insertion of this muscle by EPB (lepidosaurs, turtles, and crocodilians) would be posterodorsally on metatarsal II and III. However, due to the different arrangement of the plesiosaur pes and probable loss of individual toe movement it appears to make sense to place their insertions on the dorsal metatarsals. Additionally, we reconstructed this muscle onto metacarpals I-IV as in turtles because we presume it is more likely, that slips of a muscle get reduced, than that they suddenly differentiate from another muscle mass, although both states do appear naturally.

Musculus peroneus brevis and Musculus peroneus longus (pb and pl)

-peroneus anterior and M. peroneus posterior (Zug, 1971; Walker, 1973)

-peroneus brevis and peroneus longus (Snyder, 1954; Russell & Bauer, 2008; Suzuki et al., 2011)

Pb and pl was given priority as it finds the most acceptance across the literature on which this study is based on.

Pl arises from the distal dorsal and posterior half of the fibula in turtles (Walker, 1973; Suzuki et al., 2011) and in crocodilians it spreads further onto the ventral side than in turtles and reaches further proximal, too (Suzuki et al., 2011). In lepidosaurs its origin area is situated on the fibular epicondyle of the femur (Russell & Bauer, 2008). Pb originates from a small area on the posterodorsal distal fibula in Testudines and crocodilians (Walker, 1973; Suzuki et al., 2011). In lepidosaurs pb origin covers most of the femoral shaft except for a thin area extending proximodistally (Russell & Bauer, 2008). In all three taxa, pb and pl arise distally to the insertion ifi on the fibula. The EPB (crocodilians and turtles) suggest a pl origin on the posterodorsal distal half of the fibula and a pb origin on the posterodorsal distal fibula in plesiosaurs, distally to the attachment of ifi on the fibula.

In crocodilians and turtles pl and pb insert into dorsal metatarsal V (Walker, 1973; Suzuki et al., 2011). The former proximoposteriorly in crocodilians (Suzuki et al., 2011) and distoposteriorly in turtles and lepidosaurs (Walker, 1973; Russell & Bauer, 2008). The latter posterodistally in crocodilians (Suzuki et al., 2011) and proximoposteriorly in turtles (Walker, 1973; Russell & Bauer, 2008). Accordingly, pb and pl insertion areas were on the dorsal metatarsal V in plesiosaurs. The former on the proximoposterior tubercle and the latter on the distoposterior tubercle of metatarsal V.

Musculus tibialis anterior (ta)

No synonyms in the studies on which theses muscle reconstructions are based on (Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Suzuki et al., 2011).

Ta arises from the tibia across the EPB. Ta arises from the distal 2/3 of the anterior tibia in turtles (Walker, 1973). In crocodilians this muscle arises from the dorsal tibia relatively proximally (Suzuki et al., 2011). In lepidosaurs it arises from most of the dorsal tibial shaft (Russell & Bauer, 2008). In all three taxa it arises relatively distal to the insertion of the patellar tendon (Walker, 1973; Russell & Bauer, 2008; Suzuki et al., 2011). This means that the EPB helps to devise that ta arises from the tibia, preferably distal to the patellar tendon insertion and probably dorsally to anterodorsally.

In turtles and lepidosaurs it attaches to metatarsal I proximally and anteriorly and it spreads onto the ventral and dorsal side (Walker, 1973; Russell & Bauer, 2008). In crocodilians ta inserts into proximal dorsal metatarsal I and II (Suzuki et al., 2011). In plesiosaurs, ta insertion area was on the proximal anterior metatarsal I as in lepidosaurs and turtles.

Ventral group

Musculus gastrocnemius internus and Musculus gastrocnemius internus (gi and ge)

-gastrocnemius internal/tibial and femoral/external head (Walker, 1973)
-gastrocnemius and anterior and posterior head (Zug, 1971)
-gastrocnemius extra lateral, lateral, and medial head (Suzuki et al., 2011)
-femorotibial and femoral gastrocnemius (Russell & Bauer, 2008)
-fibular and tibial gastrocnemius (Snyder, 1954)
-gastrocnemius externus and gastrocnemius internus (Otero et al. 2011)

Internal/tibial head of gastrocnemius in Testudines (Walker, 1973) equals the medial head in crocodilians (Suzuki et al., 2011) and the femorotibial/tibial one of lepidosaurs (Snyder, 1954; Russell & Bauer, 2008). External/femoral gastrocnemius head of gastrocnemius (Walker, 1973) is the same as the lateral and extralateral portion of gastrocnemius in crocodilians (Suzuki et al., 2011) and these are the same as the femoral/fibular head in lepidosaurs (Snyder, 1954; Russell & Bauer, 2008). Further the lateral portion after Suzuki et al. (2011) equals gastrocnemius externus (Otero, Gallina & Herrera, 2010) and the medial portion (Suzuki et al., 2011) is homologous to gastrocnemius internus (Otero, Gallina & Herrera, 2010). It was decided to go along with the terminology of turtles and Otero, Gallina & Herrera (2010) for crocodilians because a detachment from the various origins of gastrocnemius and to focus on its general position in the hindlimb helps to identify the muscular head more clearly.

Gastrocnemius comprises two large heads by which it arises in turtles, crocodilians, and lepidosaurs (Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). Ge arises distally from the fibular epicondyle of the femur (Walker, 1973; Russell & Bauer, 2008; Suzuki et al., 2011) posteriorly in crocodilians and turtles (Walker, 1973; Suzuki et al., 2011) and ventrally in lepidosaurs (Russell & Bauer, 2008). In lepidosaurs it is also closely associated with the ventral knee joint capsule and there appears to be a connection with ifi. In crocodilians an extralateral subportion of this muscle is present (Suzuki et al., 2011). Gi head arises from the tibia in crocodilians, lepidosaurs, and turtles (Walker, 1973; Russell & Bauer, 2008; Suzuki et al., 2011). In turtles it arises by two subportions from the anterodorsal and anteroventral and the ventral tibia (Walker, 1973). In crocodilians it arises from the anterior and proximal tibia (Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). In lepidosaurs it arises from the anterior and anteroventral tibia, but it is also associated with the ventral knee joint capsule and the meniscus and partially arises from the tibial femoral epicondyle (Russell & Bauer, 2008). For some turtles a spreading of the origin area onto the distal femur is reported, too (Walker, 1973). So for plesiosaurs it is possible to reconstruct ge from the fibular epicondyle of the femur as was found across EPB. There are two options to reconstruct gi in plesiosaurs: Either exclusively from the tibia as found in crocodilians and some turtles, or from the tibial epicondyle of the femur and the tibia, associated with the joint capsule as in lepidosaurs and some turtles.

In turtles, crocodilians, and lepidosaurs the gastrocnemial heads converge and become aponeurotic at approximately ankle level (Walker, 1973; Russell & Bauer, 2008; Suzuki et al., 2011) and form the plantar aponeurosis and are associated the flexor retinaculum inserting into the tubercle of metatarsal V posteroventrally and into the tubercle of metatarsal I anteroventrally (Walker, 1973; Suzuki et al., 2011). Further, it inserts into digits I-IV in common with fdb (Walker, 1973; Suzuki et al., 2011). Russell & Bauer (2008) show how very complex the insertion of the gastrocnemii is in lepidosaurs. This amount of detail is impossible to reconstruct for a fossil animal therefore this will only be treated in a relatively superficial way in this text. Gastrocnemius has basically three partially amongst each other attached, partially independently acting layered subportions. It inserts into metatarsal V and anteriorly onto the astragalocalcaneum. Additionally, it either sends out own motor tendons or is associated with fdb to all 5 digits. The gastrocnemius layers are associated amongst each other tendinously, but also with pl and pb and with fte (Russell & Bauer, 2008). For plesiosaurs one learns from it: The insertion of the different bellies of gastrocnemius seems to be very complex across sauropsids. They all have in common that at approximately ankle level the separated muscle bellies become associated with each other and form tendinous structures (aponeuroses, tendons) which attach to metatarsal V posteroventrally and with the anterior crus either at the astragalocalcaneum or possibly with metatarsal I in turtles. Further, gastrocnemius is closely associated with fdb and inserts partially alone, partially in common with it into digit I to V in lepidosaurs and to digits I-IV in crocodilians and turtles which, due to the loss of digit V in crocodilians it is equally likely that gastrocnemius attaches to digit I-IV or I to V.

Musculus flexor digitorum longus (fdlh)

-flexor digitorum longus (Russell & Bauer, 2008)
-flexor digitorum longus and musculi lumbricales (Snyder, 1954; Zug, 1971; Walker, 1973)
-flexor digitorum longus + flexor hallucis longus serving digit I + flexor digiti II-IV (Suzuki et al., 2011)

Although other names experience more acceptance across taxa and literature on which this study is based on, fdlh was given priority just to pay tribute to simplification of the terminology.

In turtles fdlh originates from the posteroventral fibular epicondyle proximal to the ge origin (Zug, 1971; Walker, 1973), while in crocodilians adjacently to it but more ventrally (Suzuki et al., 2011), and in lepidosaurs distal to it (Snyder, 1954; Russell & Bauer, 2008). Fdlh also arises from the fibula. In turtles this origin area is situated along the ventral shaft (Walker, 1973). In lepidosaurs it arises relatively proximal from the anterior fibula (Russell & Bauer, 2008) and in crocodilians from the ventral proximal tibia and fibula (Suzuki et al., 2011). A tibial origin is also reported by Zug (1971) (for *Trionyx*). Fdlh forms a flexor plate (Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Suzuki et al., 2011). In lepidosaurs, the fibular origin gives rise to two muscle bellies. Lepidosaurs have additional contributions to fdlh from the astragalocalcaneum anteroventrally, metatarsocalcaneal posteroventrally from metatarsal V and from distal calcaneum, and aponeurotically arising fdlh heads (Russell & Bauer, 2008). Additionally, in crocodilians there are heads from metatarsals II-IV (Suzuki et al., 2011). From the flexor plate arise muscles, often termed lumbricals, in crocodilians, turtles, and lepidosaurs (Walker, 1973; Russell & Bauer, 2008; Suzuki et al., 2011). An fdlh origin area on the posteroventral fibular epicondyle of the plesiosaur femur would be equally supported by EPB to be proximal or distal to the ge origin. A ventral fibular origin of fdlh is also well supported by all three taxa of the EPB. A tibial origin would only be supported by crocodilians and some turtle taxa. From the flexor plate in all three taxa lumbricals originate so this might as well have been the case in plesiosaurs.

Fdlh inserts into the terminal phalanges of digit I-IV in most turtle taxa (Zug, 1971; Walker, 1973), but in some, e.g. Cheloniidae also onto the terminal phalanx of digit V (Walker, 1973). The internal insertion patterns are difficult but generally speaking, all of the heads of fdlh in lepidosaurs contribute to tendons that insert into the terminal phalanges of digits I-V according to Snyder (1954) and to the terminal phalanges of digits I-IV in *Iguana* and crocodilians (Russell & Bauer, 2008; Suzuki et al., 2011). The “lumbricals” that arise from the flexor plate insert into the terminal phalanges of digit II, III, and IV in turtles (Walker, 1973), to III and IV in lepidosaurs (Russell & Bauer, 2008), and to digit I-IV in crocodilians but in digit I at midlength of the shaft of phalanx I posteroventrally, in digit II and III at proximoposterior phalanx I, and anteriorly on midshaft length on the proximal phalanx in digit IV (Suzuki et al., 2011). A “lumbrical” insertion on digit III and IV is best supported for plesiosaurs by all three taxa, but one on digit II (crocodilians) or digit V (turtles) is possible. It seems likely that the lumbricals are either highly aponeurotic in plesiosaurs or that they do not differentiate much or that they are relatively reduced.

Musculus pronator profundus (pp)

No synonyms in the literature on which this study is based on (Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Suzuki et al., 2011).

Pp originates from the fibula in turtles and lepidosaurs (Walker, 1973; Russell & Bauer, 2008). In lepidosaurs, its origin area is situated on the ventral and anterior fibula extending across most of the distal shaft, in Testudines it extends proximodistally along the ventral fibula (Walker, 1973; Russell & Bauer, 2008). In crocodilians, it originates from the posterior tibia and the anterior fibula (Suzuki et al., 2011). In all three taxa it arises anteriorly to the origin of the fibular head of fdlh (Walker, 1973; Russell & Bauer, 2008; Suzuki et al., 2011). Best supported by EPB would be an origin area for pp on the anterior plesiosaur fibula, anterior to the fibular origin site of fdlh. Due to the closely associated tibia and fibula and to the lack of a shaft in both in *Cryptoclidus* (IGPB R 324) this seems highly unlikely. It could possibly be reconstructed on the ventral fibula as in turtles or additionally on the ventral tibia as in crocodilians.

In turtles it inserts into proximoposterior metatarsal I, posterodistal distal tarsal I, and anterodistal distal tarsal II. In lepidosaurs it inserts ventrally into posterior metatarsal I, II, III and proximoventrally on distal tarsal IV (Russell & Bauer, 2008). In crocodilians it attaches to metatarsal I posteriorly and metatarsal II anteriorly (Suzuki et al., 2011). A pp insertion in plesiosaurs would be best supported (by all three taxa) on the ventral metatarsal I and in crocodilians and turtles this is also proximally. An attachment on metatarsal II also seems likely and an attachment on metatarsal III would only be weakly supported.

3.1.2.5 Muscles of the pes

Dorsal group

Musculi extensores digitores breves (edb)

-extensores digitores breves (Russell & Bauer, 2008)
- extensor digitorum II, III, IV and ext. hallucis brevis (Suzuki et al., 2011)
-extensores digitorum breves and abductor hallucis (Walker, 1973)
-extensores digitores breves and interossei dorsales (Zug, 1971)
-extensor digitorum brevis (Snyder, 1954)

Extensores digitores breves by Russell & Bauer (2008) was chosen as it seems to be generally accepted across taxa and as it simplifies terminology in comparison to other options.

In turtles edb originates dorsally from anteroproximal metatarsal I and the bordering anterodistal distal tarsal, and distal tarsal III and IV (Walker, 1973). In crocodilians edb originates from dorsal shafts of metatarsal I-IV. Edb I-III also arises from the distal dorsal tibia and edb IV also from calcaneum posterodorsally (Suzuki et al., 2011). In lepidosaurs origin of edb is complex as they often arise from various associated ligaments of the crus. In this depth, it is impossible to reconstruct plesiosaur muscles, therefore these will be ignored in the following description. Generally, one can say that muscle bellies of edb arise adjacently to the digits from the tarsus. The heads serving digit I and II originate from proximal dorsal metatarsal I and III. The latter has a second origin area on distal dorsal metatarsal II. The edb to digit III, IV, and V have an astragalocalcaneal origin. The edb portion of digit III has two additional muscle bellies which originate from distal metatarsal II anteriorly and distal dorsal metatarsal IV. Digit IV head of edb also arises from metatarsal IV and from the tibiofibular ligament. Digit V comprises three muscle heads from astragalocalcaneum, from metatarsal V, and from a fascia overlying part of the astragalocalcaneum (Russell & Bauer, 2008). An origin of edb in plesiosaurs on the metatarsals is well supported by crocodilians and lepidosaurs and only partially by turtles. An origin on the astragalocalcaneum in lepidosaurs and calcaneum in crocodilians would suggest a posterior tarsal origin of edb in plesiosaurs. In crocodilians and lepidosaurs its proximalmost origin involves the tibia/fibula which would both be equally possible to reconstruct for *Cryptoclidus* (IGPB R 324) as well.

In all three taxa edb inserts into the ungual phalanx of digit I-IV (Walker, 1973; Russell & Bauer, 2008; Suzuki et al., 2011). In turtles it is reported that edb attaches to the connective tissue of the joint capsules of the penultimate and terminal phalanx, i.e., in turtles edb also attaches to the distal dorsal penultimate phalanx of digit I-IV. Additionally, there is a muscle inserting into the terminal phalanx of digit V in Fig. 30 (Walker, 1973) but it is designated as being part of the peroneus anterior, so it is possible that this could be synonymous with edb V tendon (Walker, 1973). Contrastingly, crocodilians only have four toes, the fifth is reduced (Suzuki et al., 2011). Accessory edb tendons that attach to other phalanges than the ungual ones are found in lepidosaurs in digit II-V and in crocodilians in digit I-IV (Russell & Bauer, 2008; Suzuki et al., 2011). An insertion on the ungual phalanges of digit I-IV can be confidently reconstructed for plesiosaurs as it is supported by crocodilians, turtles, and lepidosaurs. An insertion on the ungual phalanx of digit V can be presumed based on lepidosaur myology. The loss of digit V in crocodilians does not support this nor does it contradict. In turtles, the insertion of the muscle slip on digit V may be misidentified or missed out or the slip is lost and another muscle emulates its function.

Ventral group

Musculi flexores digitores breves (fdb)

-flexor digitorum communis sublimis (Zug, 1971; Walker, 1973)
-flexores digitores breves (Russell & Bauer, 2008)
-flexor digitorum brevis profundus and superficialis (Suzuki et al., 2011)
Flexores digitores breves by Russell & Bauer (2008) was given priority as it reflects better that it is the counterpart to extensores digitores breves.

This muscle originates from the flexor plate of fdlh in turtles and crocodilians (Zug, 1971; Walker, 1973; Suzuki et al., 2011) and from the aponeurosis of the deep ge and from the plantar tubercle of metatarsal V in lepidosaurs (Russell & Bauer, 2008). Therefore, if plesiosaurs developed the deeper layers of the fdlh then they are of an aponeurotic origin and much reduced, or fused with the overlying muscle. In crocodilians fdb arises from the ventral proximal, anterior, and posterior calcaneum, the posterior edge of metatarsal V (Suzuki et al., 2011).

Tendons bifurcate and insert anteroventrally and posteroventrally into phalanx I of digit I-IV in Testudines. This muscle is absent in sea turtles (Walker, 1973). In lepidosaurs it inserts into proximal phalanx I of digit I, onto proximal and posterior phalanx I, proximal phalanx II of digit II, proximal phalanx I on digit III (Snyder, 1954). In crocodilians they insert ventrally and proximally into all phalanges of digit I-IV and also into the ungual phalanges (Suzuki et al., 2011). So if this muscle is not reduced in plesiosaurs, then it inserts into digits I-IV as supported by crocodilians, turtles, and lepidosaurs. Into which exact phalanges fdb inserts is difficult to reconstruct, as there appears to be no consensus across EPB so all options mentioned above are equally likely.

Musculus extensor hallucis proprius (ehp)

-extensor hallucis proprius (Zug, 1971; Walker, 1973)
-adductor hallucis dorsalis (Suzuki et al., 2011)
-adductor et extensor hallucis indicus (Russell & Bauer, 2008)
Ehp was given priority, as it is the most accepted term across that literature on which this study is based on.

Ehp has its origin area on the distal dorsal fibula in turtles, crocodilians, and lepidosaurs, distal and adjacently to pb and pl origins (Walker, 1973; Russell & Bauer, 2008; Suzuki et al., 2011). Additionally, in lepidosaurs it arises from the astragalocalcaneum (Russell & Bauer, 2008). Hence, ehp origin was on the distal dorsal fibula as suggested by all three taxa in plesiosaurs.

In turtles ehp inserts distoposteriorly into metacarpal I, proximoposterior into phalanx I, and anterodistal into phalanx I which is also the penultimate phalanx in *Pseudemys* (Walker, 1973). In crocodilians it inserts into anteroproximal metatarsal I (Suzuki et al., 2011). In lepidosaurs it inserts by a bifurcated tendon into metatarsal I anteriorly and posteriorly and into metatarsal II (Russell & Bauer, 2008). Therefore, an insertion on metatarsal I in plesiosaurs is well supported by the EPB. An attachment on metatarsal II or to the penultimate phalanx is possible of which only the latter could have interesting implications for plesiosaur flipper twisting.

Musculus adductor digiti quinti (addV)

This muscle is only described for lepidosaurs by Russell & Bauer (2008), neither for turtles (Walker, 1973), nor for crocodylians (Suzuki et al., 2011). There are no synonyms (Russell & Bauer, 2008)

In lepidosaurs, addV arises by two heads from the tubercle of metatarsal V anteroventrally and proximally from it (Russell & Bauer, 2008). It attaches to proximoventral phalanx I and to the penultimate phalanx of digit V (Russell & Bauer, 2008). In turtles this muscle is not described, and in crocodilians, the authors presume it is lost due to the loss of digit V in crocodilians. Therefore, this muscle was reconstructed for plesiosaurs as it was found in lepidosaurs.

Musculus flexor hallucis (fh)

-flexor hallucis (Russell & Bauer, 2008)

-flexor hallucis brevis superficialis and flexor hallucis brevis profundus (Suzuki et al., 2011)

The term fh by Russell & Bauer (2008) was given priority as it was decided to summarize the subportions of this muscle which would be expressed by the term employed by Suzuki et al. (2011).

The two muscle bellies of fh arise from the posteroventral calcaneum in crocodilians (Suzuki et al., 2011). In lepidosaurs this muscle originates from the anterior surface of distal tarsal IV (Russell & Bauer, 2008). So for plesiosaurs, both origin areas are equally possible, i.e., on the fibulare or the adjacent distal tarsal element.

In crocodilians it inserts along the anteroventral shaft of metatarsal I and into posteroventral and proximal phalanx I of digit I (Suzuki et al., 2011) and in lepidosaurs into the metatarsophalangeal joint of digit I (Russell & Bauer, 2008). In plesiosaurs it may insert into proximoventral phalanx I of digit I as in lepidosaurs and crocodilians.

3.2 Muscle functions

3.2.1 Foreflipper

Several of the reconstructed pectoral muscles turn out to be humeral protractors. These are dc, ds, and the respectively anterior portions of sc, p, scs, and eventually the most cranial portion of ld. Cb, cl, bb, and the posterior portions of sc, p, scs, ld act as humeral retractors. Ds, scs (elevation via deflection on the tuberosity), tb, and ld (deflection on tuberosity) elevate the humerus. Shp may have a minor elevational function. Depressors of the humerus are cb, cl, dc, bb, p, and sc. Pectoral muscles that are able to rotate the humerus and hence the leading edge of the flipper downward are dc, shp, bb, p (posterior portion), scs (anterior portion), and tb. Humeral rotators that enable an upwards rotation of the flipper leading edge are ds, cb, cl, p (anterior portion), scs (posterior portion), and ld (Tab. 1).

Ecu crosses the carpus diagonally from anteroproximal to posterodistal. It displaces the ulna slightly relatively dorsally to the humerus. Alternatively, although weaker supported by the EPB, it could allow flexion of metacarpal V on the adjacent distal carpal. Edc is aponeurotic as in other sauropsids and it extends the metacarpals on the adjacent distal carpal elements. Sl and ecr might relocate the radius slightly dorsally relative to the humerus. It is also possible, although weaker supported by EPB, that an insertion on the radiale would allow displacement of the whole radial side of the carpus. Sm abducts metacarpal I on the adjacent distal carpal element and it possibly allows extension to a minor degree. Edbp and edbs allow the extension of each digit (Tab. 1).

Pte crosses the carpus diagonally from posteroproximal to anterodistal and shifts the radius slightly relatively ventral to the humerus. Fcu displaces the ulnar side of the carpus relatively slightly ventrally in relation to the humerus. A weaker supported additional insertion on metacarpal V would allow the plesiosaur to flex metacarpal V on the adjacent distal carpal. Fdlf (and fdls) forms an aponeurosis with five tendons that allow the flexion of all digits. Fc flexes metacarpal I on the distal carpal element. An insertion on the radial side of the carpus so that the whole side could be displaced ventrally is possible. AbdV abducts and slightly flexes digit V. Apb could either abduct or flex digit I on the metacarpophalangeal joint or flex metacarpal I on the adjacent distal carpal. Adm adducts and flexes digit V on the metacarpophalangeal joint (Tab. 1).

3.2.2 Hindflipper

Muscles that enable an elevation of the femur are pi, it, ife, ifi, cfb, cfl, fte (portion from ilium), and fti (portion to vertebral column). Pe, af, i, pi, fte (portion from ischium), and fti (ischial portion) power femoral depression. Pe (pubic portion), pi (pubic portion; to vertebral column if croc state); a, pti aid in femoral protraction. Pe (ischial portion, but only if femur protracted, minor function), pi (ischial and iliac portion only minorly and only if femur protracted), af (lateroposterior ischial portion; i, ifi (minorly), it, ife, cfb, cfl, fte, and fti retract the plesiosaur femur and flipper (Tab. 2).

Responsible for the downward rotation of the flipper leading edge are i, cfb, cfl, pi (pubis portion), Pe (ischium portion), ifi: clockwise rotation (as long as fibula below origin), pit, both fti portions, both fte portions, a (if femur elevated), and pti (if femur elevated). Ife, pi (ischium and ilium portion), pe (pubis portion), it, a (if femur depressed), ifi (as long as fibula above origin), and pti (if femur depressed) may rotate the flipper leading edge upward (Tab. 2). Pl and pb may extend metatarsal V on adjacent tarsal element and slightly abduct metatarsal V. F, as well as a and it, may contribute to a slight dorsal displacement of the tibia on the distal femur. Ta may abduct metatarsal I relatively anteriorly on the adjacent distal tarsal. Edl extends digits I-IV (on tarsometatarsal joints). Ehp may aid in extension or

muscle	**function after Watson 1924**	**function after Tarlo 1957**	**function after Robinson 1975**	**function after Lingham-Soliar 2000**	**function after Carpenter et al. 2010**	**function after Araújo and Correia 2015**	**function after this study**
m. latissimus dorsi (+ teres major)	retractor, rotator (anterior edge up)	stabilizer	elevator, eventually retractor, rotator (anterior edge down)	/	main elevator rotator, protractor	/	eventually anteriormost portion protraction, posterior portion retraction, elevation; rotation (leading edge upwards)
m. subcoracoscapularis	posterior portion: retractor, rotator (anterior edge up); anterior portion: protractor and rotator (anterior edge down)	protractor, rotator (anterior edge down)	elevator, rotator (anterior edge up)	/	pulls humerus into glenoid (stabilizer), eventually elevator	stabilization	anterior portion protraction, posterior portion retraction, both elevation, anterior portion rotation (leading edge downwards); posterior portion rotation (leading edge upwards)
m. scapulohumeralis posterior	-	-	-	/	protraction, rotation (anterior edge down)	glenohumeral joint stabilizer	eventually minor elevation, rotation (leading edge downwards)
m. deltoideus clavicularis	protractor, rotator (into the horizontal)	rotator, protractor	rotation (anterior edge down), protractor	/	/	protractor	protraction, depression, rotation (leading edge downwards)
m. deltoideus scapularis			rotation (anterior edge up) or abduction	/	/	stabilizer	protraction, elevation, rotation (leading edge upwards)
m. triceps brachii	-	-	adjustment of flipper trim, rotator (anterior edge up)	-	-	/	elevation, rotation (leading edge downwards)
m. pectoralis	retractor, depressor, rotator (anterior side down)	prevents anterior flipper movement	depressor, rotator (anterior side down)	depressor	main depressor, rotator (anterior side down)	-	anterior portion protraction, posterior portion retraction, both depression, posterior portion rotation (leading edge downwards); anterior portion rotation (leading edge upwards)
m. supracoracoideus	retractor, rotator (anterior edge down), depressor	/	rotator (anterior edge down)	rotator	rotator (anterior edge up)	retractor or glenohumeral joint stabilizer	anterior portion protraction, posterior portion retraction, both depression
m. coracobrachialis brevis	retractor, depressor		depressor	rotator (direction	depressor, eventually	mainly retractor	retraction, depression, rotation (leading edge upwards)

m. coracobrachialis longus		„adducted backwards…“ (p.199, line 4)		not specified)	retraction during down stroke		retraction, depression, rotation (leading edge upwards)
m. biceps brachii + brachialis	-	-	adjustment of flipper trim	-	/	/	retraction, depression, rotation (leading edge downwards)
m. extensor carpi ulnaris	-	-	-	-	-	-	displaces ulna dorsally/ although weakly supported by EPB an insertion to metacarpal V would allow extension of metacarpal V on the adjacent distal carpal
m. extensor digitorum communis	-	-	-	-	-	-	extends metacarpals on distal carpals
m. supinator longus and extensor carpi radialis	-	-	-	-	-	-	displaces radius slightly dorsally/ weakly supported insertion that expands onto the radiale would allow to displace the whole radial side of the carpus slightly
m. supinator manus	-	-	-	-	-	-	abducts metacarpal I on adjacent distal carpal + minor extension
m. pronator teres	-	-	-	-	-	-	displaces radius ventrally
m. flexor carpi ulnaris	influences flipper trim	-	-	-	-	-	displaces ulnar side of carpus ventrally/badly supported possibly additional insertion to metacarpal V would allow to flex metacarpal V on the distal carpal element
m. flexor digitorum longus (and flexores digitorum superficialis)	-	-	-	-	-	-	flexion of each digit
m. flexor carpi radialis	influences flipper trim	-	-	-	-	-	flexes metacarpal I on adjacent distal carpal element/ equally well supported would be an insertion to the radial side of the carpus allowing to displace the radial side of the carpus slightly ventrally

mm. extensores digitorum superficialis and profundi	-						extension of each digit
m. abductor digiti V	-						abducts and slightly flexes digit V
m. abductor pollicis brevis	-						abducts and flexes digit I on metacarpophalangeal joint/might also insert to metacarpal I and would then allow flexion of it on the adjacent distal carpal element
m. adductor digiti minimi	-						adducts and flexes digit V on metacarpophalangeal joint

Tab. 1: *Cryptoclidus eurymerus* (IGPB R 324) foreflipper muscle functions in comparison to literature

adduction of metatarsal I (on tarsometatarsal joint) depending on how it is reconstructed. Edb extend the phalanges of digit I-V (Tab. 2). Ge and gi is a flexor of all 5 digits in all phalangeal joints. It also acts on metatarsal I and V. Fdlh flexes the phalanges of all 5 digits and fdb are the flexors of digits I-IV lying deep to the former and addV is the flexor of digit V and fh flexes digit I. Pp is responsible for flexion of tarsometatarsal joints of digit I, and eventually digit II and III (Tab. 2).

3.3 Bone histology of plesiosaur humerus extensor and flexor origin areas

General plesiosaur bone histology (bone matrix, vascularization etc.), including this specimen (IGPB R 324), was already described by Wintrich et al. (2017) and will not be repeated here. The focus of this work is the observation of fibres in the cortical bone. The authors refrain from calling the fibres Sharpey's fibres, which would certainly indicate soft tissue attachments (i.e., muscle, ligament/joint capsule insertions, dermis) (Francillon-*Vieillot* et al., 1990) because they usually anchor deeper into the bone and do look differently, especially longer, than the here observed fibres (compare to Petermann & Sander, 2013 Fig. 6, p. 426).

The origin sites of extensors and flexors generally do not leave osteological correlates on the bone surface (e.g., Meers, 2003; Petermann & Sander, 2013; Krahl et al. (chapter 2)), therefore the authors tried to substantiate the reconstructed plesiosaur extensors and flexors in this region by histology. Fibres oriented in various angles are present only in very limited regions just beneath the bone surface and do not reach deep into the cortical bone, as Sharpey's fibres generally would (compare to Petermann & Sander, 2013, Fig. 6, p. 426). Sections are sorted from anterior to posterior and from proximal to distal.

Section 1 only shows fibres in two restricted areas anterodorsally and anteroventrally. Anterodorsally, fibres of two directions are visible, some fibres leave the bone steeply inclined in rather dorsoventral to dorsodistal or slightly diverging orientation, other fibres beneath the bone surface (Fig. 3 e). Anteroventrally, two fibre directions can be observed, but unlike to the situation on the anterodorsal side, both do not intermingle, instead each one occurs in a separate area. More proximally, fibres leave the bone surface angulated in anteroventral and proximal direction. More distally, fibres appear as dots in the section, i.e, they run parallel beneath the bone surface on the anteroventral side in proximoposterior-anterodistal direction (Fig. 3 c).

muscle	**function after Robinson (1975)**	**function after Carpenter et al. (2010)**	**function, this study**
m. iliotibialis	adjusting flipper trim and rotate anterior flipper edge up	-	elevation, retraction, rotates anterior edge up, slight dorsal displacement of tibia on distal femur
m. femorotibialis			slight dorsal displacement of tibia on distal femur
m. ambiens			protraction, (if femur depressed, similar to delt. clav. rotates anterior edge up; if elevated then rotates anterior edge down), slight dorsal displacement of tibia on distal femur
m. iliofibularis	adjusting flipper trim posteriorly	-	elevation, rotates anterior edge down, retraction, rotates anterior edge up (as long as fibula above origin)
m. iliofemoralis	elevation	rotates anterior edge up	elevation, retraction, rotates anterior edge up
m. puboischiofemoralis internus	elevator	elevation	four possible muscle bellies: elevation -from pubis: elevation, rotates anterior edge down, protraction -from ischium: elevation, rotates anterior edge up, minorly retraction -from ilium: elevation, rotates anterior edge up, minorly retraction -from vertebral column: elevation, protraction
m. puboischiotibialis	adjusts flipper trim	-	depression, rotates anterior edge down
m. pubotibialis	-	-	protraction, (if femur depressed, similar to delt. clav. rotates anterior edge up; if elevated then rotate anterior edge down)
m. flexor tibialis internus	-	-	from ischium: retraction, depression, rotates anterior edge down from ilium/sacral vertebrae/transverse processes of caudal vert.: retraction, rotates anterior edge down, elevation

m. flexor tibialis externus	-	-	from ilium: rotates anterior edge down, retraction, elevation from ischium: rotates anterior edge down, retraction, depression
m. caudifemoralis brevis and m. caudifemoralis longus	elevation, rotates anterior flipper edge down	rotates anterior flipper edge down	c. b.: elevation, retraction, rotates anterior edge down c. l.: retraction, elevation, rotates anterior edge down
m. ischiotrochantericus	rotate anterior flipper edge down, elevation, retraction	-	retraction, depression, rotation of anterior edge down
m. adductor femoris	depressor, rotation anterior flipper edge down”	-	from anterior ischium: depression from lateroposterior ischium: adduction, retraction
m. puboischiofemoralis externus	depressor	depressor	from pubis: depression, protraction, rotates anterior edge up from ischium: depression, retraction, rotates anterior edge down
m. extensor digitorum longus	-	-	extension of digits I-IV (on tarsometatarsal joints)
m. peroneus longus and m. peroneus brevis	adjusts flipper trim	-	extends tarsometatarsal joint of digit V, abduct metatarsal V
m. tibialis anterior	adjusts flipper trim	-	abduct metatarsal I
m. gastrocnemius internus and m. gastrocnemius externus	-	-	flexors of all 5 digits in all phalangeal joints, also acting on metatarsal I and V
m. flexor digitorum longus	-	-	long flexors of all 5 digits
m. pronator profundus	-	-	flexion of carpometacarpal joints of digit I (eventually digit II and III)
mm. extensores digitores breves	-	-	extension of all phalangeal joints in all V digits

mm. flexores digitores breves	-	-	flexors of digits I-IV
m. extensor hallucis proprius	-	-	extension of extends or adducts metatarsal I (on tarso-metatarsal joint)
m. adductor digiti quinti	-	-	flexor of digit V
m. flexor hallucis	-	-	flexor of digit I

Tab. 2: *Cryptoclidus eurymerus* (IGPB R 324) hindflipper muscle functions in comparison to literature

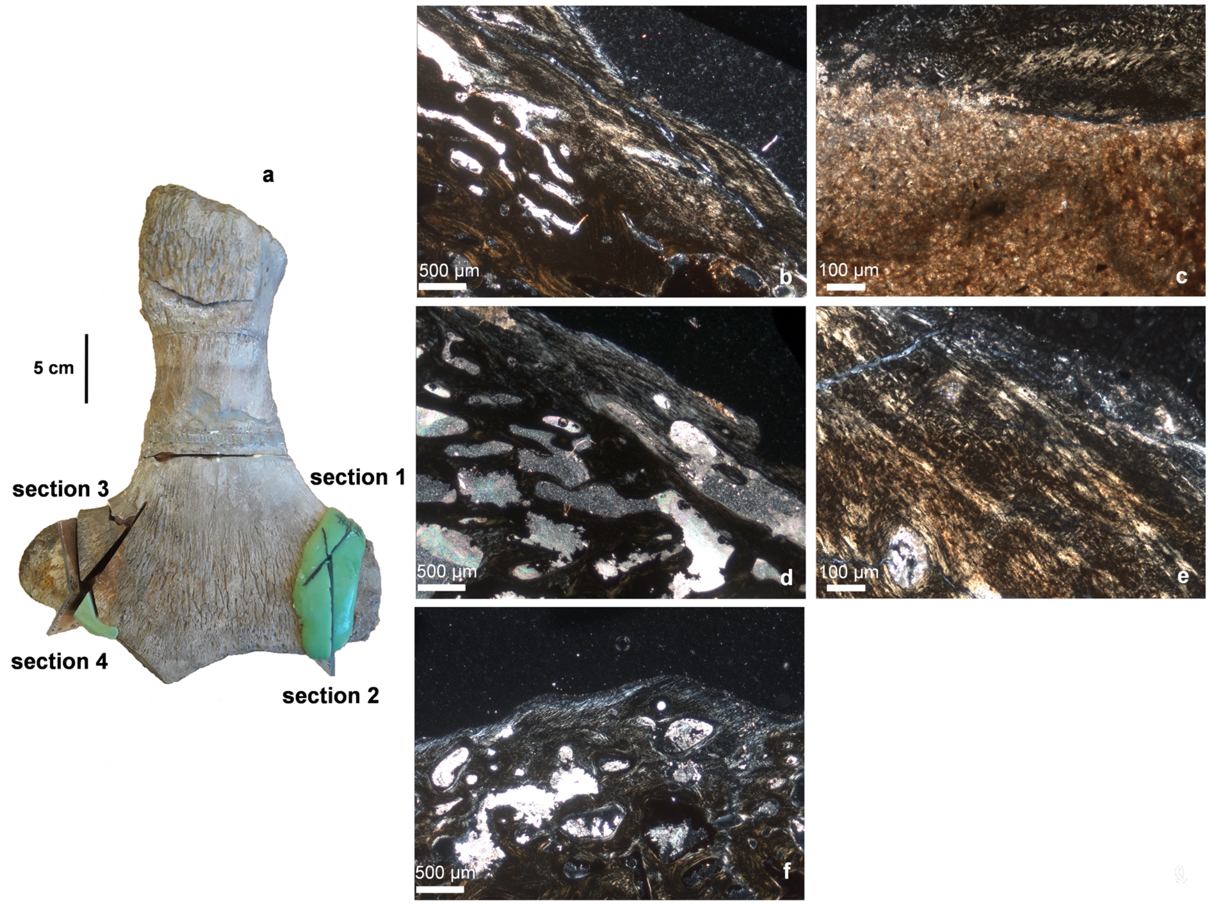

Fig. 3: Histological thin sectioning of *Cryptoclidus eurymerus* (IGPB R 324) humerus extensor and flexor origin sites. a) *Cryptoclidus* humerus in dorsal view. Sites of section 1 to 4 are marked (modified, picture by P. M. Sander). b) micrograph representative of dorsal side of section 2 and ventral side of section 4, bone surface on top right corner, moderately inclined fibres cross the humeral cortex. c) section 1, bone surface on top, cortex of anteroventral humerus shows two small areas of two different fibre orientations that are separated from each other; more proximal fibres are angulated and more distal fibres are parallel to the bone surface and perpendicular to the section plane. d) representative of ventral section 2, ventral section 3, and dorsal section 4, bone surface on top right corner, fibres are nearly bone surface parallel. e) section 1, bone surface on top right corner, cortex of anterodorsal humerus shows fibres oriented in two different directions: parallel to bone surface and perpendicular to the section plane and steeply inclined fibres. f) section 3, bone surface on top, steeply inclined fibres cross the cortex on the posterodorsal humerus margin.

Fibres, bone matrix, and vascularization just below the bone surface in section 2 are oriented rather parallel to the bone surface on the ventral side of the humerus running overall in proximodistal direction of the humerus (Fig. 3 d). On the dorsal side of the humerus, fibres are anchored proximally and pass the bone surface under a very low angle a little further distally (Fig. 3 b).

In section 3 the fibres just below the bone surface are oriented on the ventral humeral side rather parallel to the bone surface under a small angle being anchored proximally and piercing the bone surface distally (Fig. 3 b). On the dorsal side, the fibres are more steeply inclined. They are anchored proximally and pass and leave the bone in distal direction (Fig. 3 f).

A similar situation as in section 2 was found in section 4. Fibres, matrix, and vascularization in the outermost layer of the dorsal humerus side run rather parallel or only very slightly angulated to the bone surface, overall in proximodistal direction of the humerus (Fig. 3 d). Contrastingly to the more proximal posterior section 3, fibres of section 4 are slightly more angulated on the ventral side. They are anchored proximally and pierce the bone surface distally (Fig. 3 b).

4. Discussion

4.1 Reconstructed muscle attachment sites

4.1.1 Foreflipper

4.1.1.1 Origins on pectoral girdle or vertebral column

Cb and cl origin area covers most of the coracoid posterior to sc and anterior to bb origin meeting in the body midline as demonstrated by Araújo & Correia (2015) and Robinson (1975), too. Watson‘s (1924) and Tarlo‘s (1958) reconstructions are relatively similar to this study’s results with minor differences. Both authors show an origin area that expands not as far anteriorly on the coracoid, but instead cover it to its posteroventral rim. The results presented here and those of Araújo & Correia (2015) show that this is impossible, as the posteroventral portion of the coracoid provides attachment surface for the bb. The overall position of cb and cl is comparable to the reconstructions by Lingham-Soliar (2000) and Carpenter et al. (2010), yet they differ profoundly from the results presented in this study. The former provided an attachment area situated centered on each coracoid. The latter depicts an attachment surface on the ventral and lateral coracoid.

The authors agree on the overall position of sc origin anterior to cb and cl origins and posterior to dc/ds on the ventral pectoral girdle with Watson (1924), Tarlo (1958), Robinson (1975), Lingham-Soliar (2000), and Araújo & Correia (2015). Carpenter et al. (2010) reconstructed an origin area exclusively on the posterior clavicula which is contrary to what has been reported for the EPB that would only support an origin on scapula and coracoid

(Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). We reconstructed it to cover the coracoid foramen (sensu Araújo & Correia, 2015) like Robinson (1975). Further, the sc origin surface reaches posteriorly adjacently up to the cb origin area as in Araújo & Correia‘s (2015) reconstructions. That sc originates exclusively from the coracoid as demonstrated by Araújo & Correia (2015), Tarlo (1958), and Lingham-Soliar (2000) could not be corroborated, instead it expands onto the scapula adjacently to the ds.

Dc is the most anterior locomotory muscle that arises from the pectoral girdle and ds originates from the scapular prong. This is agreed on in all plesiosaur muscle reconstructions (Watson, 1924; Tarlo, 1958; Robinson, 1975; Lingham-Soliar, 2000; Carpenter et al., 2010; Araújo & Correia, 2015). The results of this study approve the overall origin area of both muscles as reconstructed by Araújo & Correia (2015) from the ventral scapula, the clavicular remains, and the lateral scapular blade. Differences emerge if the distribution of the origins of both portions is looked at. Araújo & Correia (2015) figure a large dc that arises from the ventral scapula as well as from the clavicular remains, while ds arises only from the lateral scapula. Our results disagree, as this study found a larger scapularis portion originating from the ventral and lateral scapula and a small clavicularis portion arising merely from the clavicular remains. Araújo & Correia (2015) argue, that in crocodilians the clavicula is reduced and the dc has instead spread onto the scapula (Meers, 2003; Suzuki & Hayashi, 2010) and therefore possibly the same happened in plesiosaurs. This is though just as possible as to presume, that because the clavicula and the scapular prong become relatively smaller in plesiosaurs in comparison to other Sauropterygia the associated muscles become smaller in size, too, as the current study does. However, both mechanisms, muscle migrations onto other skeletal elements (e.g., dc in crocodilians (Meers, 2003; Suzuki & Hayashi, 2010)), as well as relative reduction/increase in size e.g. (muscles on cheloniid scapula become relatively reduced over those of other turtles while those of the coracoid become relatively enlarged (Walker, 1973; Depecker et al., 2006) are observed in extant taxa. Either way, functionally there would possibly be no or only little difference for the animal, as the lines of actions would not change majorly. Araújo & Correia‘s (2015) and our results are in stark contrast to ds and dc reconstructions by Watson (1924), Tarlo (1958), Robinson (1975), Lingham-Soliar (2000), and Carpenter et al. (2010) who solely reconstructed them onto various small patches on the ventral and lateral scapula.

Shp attaches to the posterior scapular blade and to the portion of the scapula bending towards the glenoid. This is similar to the origin area figures by Araújo & Correia (2015). Lingham-Soliar (2000) placed it anteroventrally below the glenoid, which is not supported by

EPB, i.e., crocodilians (Meers, 2003; Suzuki & Hayashi, 2010) and lepidosaurs (Jenkins & Goslow, 1983; Russell & Bauer, 2008).

We agree with Araújo & Correia (2015) on the origin of the bb being on the posteroventral coracoid posterior to cl. Carpenter et al. (2010) picture a small origin area on the ventral scapula, which is neither supported by lepidosaurs nor by turtles which they used for the EPB. The results of Robinson (1975) are contradictory to results presented here in which the long bb head from the pectoral girdle is reduced or moved into a position close to the glenoid. Further, b arises in Sauropsida across the EPB from the dorsal humeral shaft (Walker, 1973; Zaaf et al., 1999; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010; Anzai et al., 2014), while Robinson (1975) reconstructed it onto the anterior humeral shaft.

Scs was reconstructed to arise from most of the dorsal scapula and coracoid which corroborates the results of Robinson (1975). It is difficult to determine whether or not Araújo & Correia (2015) reconstruct the coracoidal portion, too, as they do not express it clearly in the text, but in Fig. 5 13, 14, p. 11 it does look like it. In the text of Araújo & Correia (2015) it does not become clear, whether they also reconstruct a coracoidal portion of this muscle, but in Fig. 5 13, 14, p. 11 (it does look like it). Watson (1924) and Tarlo (1958) figure small and separated portions from the dorsal coracoid at about half its anteroposterior length and from the scapula. Origin areas of scs by Carpenter et al. (2010) are very different as they reconstructed small origins on the scapula and on the clavicular remains. The latter of which is not supported by EPB (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010; Anzai et al., 2014), instead a coracoidal portion is possible (Russell & Bauer, 2008; Anzai et al., 2014). Lingham-Soliar (2000) did not reconstruct any musculature onto the dorsal pectoral girdle and moved scs onto the ventrolateral scapula which cannot be substantiated at all by the EPB whatsoever (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). Carpenter et al. (2010) did not reconstruct locomotor muscles onto large parts of the pectoral girdle while they covered especially the dorsal pelvic girdle heavily by musculature.

P reconstructed in this study is comparable to that of Robinson (1975). It arises from the ventral keel in the body midline and mostly superficial to sc, cb, cl, and bb. Both sides intermingle in the body midline. Generally, these reconstructions are similar to those presented by *Carpenter* et al. (2010), but they only reconstructed an origin on the coracoid midline suture and not from the scapula. Instead they picture an origin on the gastralia which may have been true for plesiosaurs (s. chapter muscle reconstructions p). Lingham-Soliar

(2000) depicts a rather small p that arises only from the anterior part of the coracoid suture. Tarlo (1958) mentions a strong p but only reconstructs its insertion on the humerus and not its origin area, but derived from the drawing (Fig. 4, p.157) it takes a course towards the gastralia, but this remains speculative on my behalf. Watson (1924) describes an origin of p exclusively on the gastralia. Araújo & Correia (2015) completely reduce the p in plesiosaurs, based on the premise, that it arises in crocs and lepidosaurs mostly from the interclavicula and the sternum. As both are either absent or very small in plesiosaurs, Araújo & Correia (2015) argue that there would be no support for a p and EPB would not support a spreading of p onto other bony elements. Yet, Araújo & Correia (2015) consider turtles for nearly every other muscle they reconstruct, but not for the reconstruction of p. In turtles, p origin has spread onto the plastron and it is also the largest locomotory muscle of the forelimb (Walker, 1973; Wyneken, 2001). Additionally, there is no extant sauropsid which has a reduced p to the knowledge of the authors. Therefore, the argument a p origin migration onto adjacent bony elements is impossible becomes invalid. It is rather likely, that p migrated from the interclavicula onto the scapula and the coracoid keeping its overall spatial position constantly in sauropterygian evolution, as seems to be the case in other Sauropsida (s. chapter 2.1). This could have been possible e.g., if the coracoid foramen between the two sides of the pectoral girdle would have been covered by a membrane similar to the obturator foramen in the pubis of turtles where big muscles originate from (Walker, 1973).

Generally, the results presented here corroborate the results of Araújo & Correia (2015) who reconstructed the ld origin from the first to fourth thoracic respectively the seventh dorsal vertebra accordingly. There is evidence though for lepidosaurs that it may spread even further caudally on the vertebral column up to the 12th dorsal vertebra which could be considered for plesiosaurs as well. Carpenter et al. (2010) picture a large ld (Fig. 17 C, p. 22) but do not give details on where it originates from, although generally it appears to look similar to the results of this study. Robinson (1975) does not give details on where exactly the origin is situated, so it remains obscure for comparison, too. Tarlo (1958) and Watson (1924) reconstruct only the insertion of ld on the humerus but not its origin.

Tb arises from the coracoid just posterior to the glenoid by Robinson (1975). This is similar to the results of this study. Further, Robinson (1975) reconstructed a humeral head from a small portion of the posterior humeral shaft which is unsupported by EPB (Walker, 1973; Zaaf et al., 1999; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). The tb reconstructions of Araújo & Correia (2015) appear to be inconsistent. They reconstructed four heads. In the text body they write that two arise from the humerus and two from the pectoral girdle. In Fig. 12, p. 21 it looks as if only one portion arises from the humerus and three portions from the shoulder girdle (Araújo & Correia, 2015). Additionally, in extant sauropsids the origin area of the humeral head (which may be subdivided into portions (Zaaf et al., 1999; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010)) of the tb covers most of the dorsal surface of the shaft distal to the proximally inserting locomotory muscles from the pectoral girdle (Walker, 1973; Meers, 2003; Suzuki & Hayashi, 2010). This is not pictured by Araújo & Correia (2015), contrarily they reconstructed a relatively proximal attachment surface. Further they picture a tb head taking a course ventrally along the humerus. This is not the case in extant Sauropsida where this muscle runs on the dorsal side of the humerus (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010).

Robinson (1975) is the only other author who reconstructed musculature for the fore- and hindflipper. On a very broad scale we agree on the origin of fcu. Fcr arises from the ulnar epicondyle as well according to the EPB but was figured to arise from the radial epicondyle by Robinson (1975). The palmar aponeurosis figured by Robinson (1975) may represent the fdlf that arises by two heads from the entepicondyle and the ulna in lepidosaurs, crocodilians, and turtles (Walker, 1973; Meers, 2003; Russell & Bauer, 2008). It is presumed that Robinson (1975) pictured the ventral flipper in Fig. 20 C, p. 321 as the flexors run on the ventral side of the limb (Walker, 1973; Meers, 2003; Russell & Bauer, 2008). A dorsal flipper side was not reconstructed, although by no means the dorsal and the ventral side are the same in Sauropsida (Walker, 1973; Meers, 2003; Russell & Bauer, 2008).

4.1.1.2 Insertions on humerus, radius, or ulna

In terms of muscle insertion areas on the humerus the results presented here mostly contradict those of Watson (1924), Tarlo (1958), and Robinson (1975). The insertion of the ds and dc into the anterior humerus shaft are amongst the only ones we can agree on. The scs insertion on the tuberosity shown by Robinson (1975) concurs with the result presented here although it shares the tuberosity with the attachment area of the ld in contrast to Robinson (1975).

It is quite difficult to interpret Lingham-Soliar‘s (2000) muscle insertions on the humerus because neither he describes them exhaustively nor are his figures very much detailed, as they happen to be rather schematic. Important features like e.g., the dorsal tuberosity are not shown (Lingham-Soliar, 2000). The sc insertion, ventrally anteriorly to the p insertion, is in accordance with the results of the current study. Overall, we agree on the insertions of shp. Subsequently, posteriorly to sc, are the attachment areas of cb and cl. Cl was not reconstructed to insert into the rugosities on the posterior humeral shaft though as suggested by the current study. Lingham-Soliar (2000) depicts the deltoids to attach to the tuberosity on the anterodorsal plesiosaur humerus which contradicts the results presented here, as they seem to insert into the rugosities on the anterior humeral shaft. Lingham-Soliar‘s (2000) reconstruction of the insertions of ld and scs are in disagreement with the current study‘s results, as he shows ld to insert more proximally into the dorsal tuberosity on the plesiosaur humerus than scs which is the opposite to what was reconstructed in the current study. Overall, study of osteological correlates on the humerus suggest in comparison to the reconstructions of Lingham-Soliar (2000) that the muscle attachments he pictured should be shifted more distally. This study’s results are (roughly) in accordance with the reconstructed insertion areas of ld, scs, and coracobrachialis (s. list of synonymies) by Carpenter et al. (2010) with rather minor differences, as e.g., coracobrachialis insertion area is not as small but instead expands further distally covering the rugosity on the posterior shaft. We disagree on the insertions of the ventral musculature. As there are also proximoposterior rugosities, it appears impossible to reconstruct p and sc only onto the anteroventral osteological corelates as Carpenter et al. (2010) did, but instead sc inserts anteroventrally and p posteroventrally.

Araújo & Correia (2015) show that the deltoids insert anteroventrally and then sc insertion covers the rest of the large area of strong rugosities on the proximoventral plesiosaur humerus. Unlike Araújo & Correia (2015), in the current study a large p was reconstructed which inserts posteroventrally into the proximal humerus. Therefore, sc inserts anteroventrally and the deltoids accordingly anteriorly into the humeral shaft. We agree with the insertion of ld figured by Araújo & Correia (2015) but not with the shp insertion which inserts in extant sauropsids either similarly to how Araújo & Correia (2015) reconstructed it or similar to what was presented in the result section of the study, namely into the posterodorsal humerus. As both options are equally well supported, both Araújo & Correia (2015) and the hypothesis presented here are equally possible. Araújo & Correia (2015) describe that ld, as well as scs attach to the dorsal tuberosity of the plesiosaur humerus and they depict them in their fleshed out figures (Fig. 5, p. 11; Fig. 11, p. 20) in a very similar area. In the figure, which shows muscle insertion areas on the humerus, scs is missing (Fig. 4, p. 10). Therefore, it is impossible to compare the results concerning this muscle.

According to Robinson (1975), flexor carpi radialis inserts into metacarpal I and fcu into metacarpal V. The former was reconstructed like that, too in this study, but the latter inserts into the ulna and ulnare as is more likely according to the EPB, although lepidosaurs do support an insertion into metacarpal V (Russell & Bauer, 2008). An insertion of the long flexor tendons on the terminal phalanges is well supported for Sauropsida (Walker, 1973; Meers, 2003; Russell & Bauer, 2008).

4.1.2 Hindflipper

4.1.2.1 Origins on pelvic girdle or vertebral column

The origin area of i on the posterodorsal ischium by Robinson (1975) could be corroborated. According to Robinson (1975), it originates from an iliopubic ligament, which was not reconstructed in the current study. Instead, it arises from the dorsal ilium but unlike to Lingham-Soliar (2000) not from the posterior but from the anterior ilium. F originates from the dorsal femur and the origin area wraps around it anteriorly and posteriorly that they almost meet ventrally. Robinson (1975) shows an attachment surface only on the anterior femur which could not be corroborated in the current study. Robinson (1975) shows and origin area for the a on the pubis anteriorly to the acetabulum, but we found it to arise from an area that resembles the area of the pubic tubercle in extant sauropsids. Ifi arises from the ilium but ventrally to it and fte on the posterodorsal ilium unlike what is shown by Lingham-Soliar (2000) and Robinson (1975) who reconstructed its origin on the posterior ilium. Pit was reconstructed by Lingham-Soliar (2000) and Robinson (1975) but its origin surface was not reconstructed in detail and is not properly discernable. Af origin is not clearly described by Robinson (1975) and therefore cannot be properly compared. Carpenter et al. (2010) and Robinson (1975) reconstruct only a caudofemoralis portion from the tail and none from the ilium. Lingham-Soliar (2000) who figures a portion of this muscle from the tail but also a portion from what seems to be the ischium, which is not found to be supported by the EPB (Romer, 1923; Snyder, 1954; Walker, 1973; Gatesy, 1997; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). In terms of pe origin areas this study corroborates the reconstructions by Carpenter et al. (2010) and mostly those of Robinson (1975). Unlike Robinson (1975) the current results do not cover the anterior rim of the ischium ventrally which might yield muscle origins for pti and af. This could indicate that pe did not cover the obturator foramen. Lingham-Soliar (2000) did reconstruct two muscle portions but only very small ones which were not found to be corroborated. Pi origin area of Robinson (1975) could be confirmed. Generally, the reconstructions of Carpenter et al. (2010) are in accordance with the current results, but it does not spread onto the dorsal ischium as shown by Carpenter et al. (2010) as here i arises. As for the pe, Lingham-Soliar (2000) reconstructed only two very small muscle bellies for pi which is unsupported by EPB (Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). It, fte, and ifi arise dorsally to ife from the ilium in contrast to the depictions of Carpenter et al. (2010), Robinson (1975), and Lingham-Soliar (2000).

Robinson (1975) is the only other author who reconstructed a dorsal plesiosaur hindflipper including ta, peroneus, and a plantar aponeurosis. The first two arise from the femoral epicondyles according to Robinson (1975), which cannot be substantiated with help of the EPB as in extant sauropsids they actually arise from the tibia and fibula (Walker, 1973; Russell & Bauer, 2008; Suzuki et al., 2011).

4.1.2.2 Insertions on femur, tibia, or fibula

The results of this study agree with the insertion of it, a, and f via a common tendon into the proximal and dorsal tibia (Robinson, 1975). Further, the insertion of i was corroborated (Robinson, 1975) as well as the insertion of ifi on the fibula as reconstructed by Robinson (1975), Lingham-Soliar (2000). Pit is reconstructed by Lingham-Soliar (2000) and Robinson (1975) but the insertion was not reconstructed in detail and is therefore not properly discernable. Robinson (1975) reconstructed an attachment of af on the proximal femoral head which is unsupported by the EPB, which suggest a large insertion along the femur shaft as in other Sauropsida (Romer, 1923; Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). Muscle insertion of cfb and cfl by Lingham-Soliar (2000), Carpenter et al. (2010), Robinson (1975) on the posteroventral femur are in accordance with this study, but it attaches much more proximal than in Robinson‘s (1975) muscle reconstructions. Additionally, these muscles are known in crocodilians and lepidosaurs to send a motor tendon to attach further distally to the lower leg which was reconstructed for the plesiosaur, too for the first time. The attachment of pe on the proximal dorsal femur by Robinson (1975), Carpenter et al. (2010), and Lingham-Soliar (2000) could be verified. The femoral pi insertion by Robinson (1975) and Carpenter et al. (2010) could be substantiated while it is not well deducible from the Lingham-Soliar (2000) figures. Attachment surface of ife is in support of the reconstructions of Carpenter et al. (2010). It is in disagreement with Robinson (1975) who reconstructed it on the posterior proximal femur unlike us and Carpenter et al. (2010) who reconstructed it dorsally on the femoral tuberosity distal to pi.

This study corroborates the results of Robinson (1975) that ta inserts into metatarsal I and peroneus into metatarsal V (Robinson, 1975). The long flexor tendons attach to the ungual phalanges of digit I-V which is well supported by the EPB (Walker, 1973; Walker, 1998; Meers, 2003; Russell & Bauer, 2008).

4.2 Muscle functions

4.2.1 Foreflipper

As differentiated as we have ascribed functions to p, especially with a possible minor anterior portion (aiding in protraction, upward rotation of the humerus) depending on the relative position in relation to the glenoid, no other author has described it. Therefore, the functions going along with this portion have never been suggested before. Functional interpretations for this muscle vary greatly. Araújo & Correia (2015) found p to be almost entirely reduced and without function. Tarlo (1958) describes it as a muscle which prevents anterior flipper movement. None of which are in accordance with the results presented here, namely that the large posterior portion acts as humeral depressor (Watson, 1924; Robinson, 1975; Lingham-Soliar, 2000; Carpenter et al., 2010), retractor (Watson, 1924; Carpenter et al., 2010), and rotator that turns the humerus anteriorly downward (Watson, 1924; Robinson, 1975; Carpenter et al., 2010; Tab. 1).

Only Watson (1924) has assigned different functions to the different portions of scs, too. Hereby he described the anterior portion to rotate the limb anteriorly downward (also Tarlo, 1958; Watson, 1924) and protract (also Tarlo, 1958; Watson, 1924) it and the posterior portion is involved in limb retraction (Watson, 1924) and upward movement of the flipper leading edge (Watson, 1924; Robinson, 1975) which could be corroborated. Scs was also found to elevate the humerus as also suggested by Robinson (1975) and Carpenter et al. (2010). It could not be confirmed, that it is a joint stabilizer restricting humeral movement (Carpenter et al., 2010; Araújo & Correia, 2015; Tab. 1).

Cb and cl are conflated, as they pose two heads of one muscle, that have the same functions. They retract (Watson, 1924; Carpenter et al., 2010; Araújo & Correia, 2015) and depress the humerus (Watson, 1924; Robinson, 1975; Carpenter et al., 2010) and rotate the flipper leading edge upward. Tarlo (1958) expresses his ideas equivocal „…adducted backwards…“ (p. 199, line 4, Tarlo, 1958). The term adduction is usually used as an equivalent to humeral elevation, but the backwards movement would be retraction. Further Lingham-Soliar (2000) suggest cb and cl rotate the humerus without further details on how (Tab. 1).

Discrimination into an anterior and posterior portion of sc is exclusive to this study. Hence, the possibility that an anterior sc muscle portion may aid in humerus protraction, too.

That it is a humeral depressor is supported by Watson (1924) and that the posterior portion (new in this study) also retracts the humerus meets agreement by Araújo & Correia (2015) and Watson (1924). No support was found for sc being a joint stabilizer (Araújo & Correia, 2015) or a humerus rotator (Watson, 1924; Robinson, 1975; Lingham-Soliar, 2000). Carpenter et al. (2010) suggest that sc rotates the humerus anteriorly upwards which could not be corroborated (Tab. 1).

Shp aids in downward rotation of the flipper leading edge and might have a protractional and elevational function. The first two muscle functions have also been suggested by Carpenter et al. (2010). This interpretation disagrees with shp being a stabilizer of the shoulder joint, as proposed by Araújo & Correia (2015). Dc was found to protract (Araújo & Correia, 2015) and rotate the anterior humerus side downwards (Robinson 1975) and depress it. Watson (1924) and Tarlo (1957) do not differentiate into the two muscular heads. Watson (1924) describes them to rotate the humerus into the horizontal. Tarlo (1957) describes them as upward rotators and protractors. Ds shares with the dc head a protractional function as this study found out. It also aides in humeral elevation and rotates the flipper leading edge upward as suggested by Robinson (1975). It could not be endorsed as a stabilizer of the glenoid, as suggested by Araújo & Correia (2015) (Tab. 1).

Ld was subdivided anew into a small posterior and large posterior portion. Although it originates in extant Sauropsida from the vertebral column, only Carpenter et al. (2010) and Robinson (1975) discuss this and the deriving elevational function as an option. This study approves that ld is also a humeral retractor (Watson, 1924) and rotates the anterior humerus side upwards (Watson, 1924; Carpenter et al., 2010). Robinson (1975) considers that ld may be a retractor and rotator, in which case it would be an anterior downward rotator of the humerus. Carpenter et al. (2010) also discuss a protractional component by ld which is in accordance with this study. No support was found for Tarlo‘s (1958) theory that this muscle is a joint stabilizer (Tab. 1).

Bb may retract and depress the flipper and it may aid in downward rotation of its leading edge. Neither of these are discussed by Robinson (1975) who interprets it to adjust the flipper trim, or by Araújo & Correia (2015) who propose no function for it. Tb influences the flipper trim and is an upward rotator of the humerus according to Robinson (1975). Araújo & Correia (2015) interpret it as a joint stabilizer i.e., it restricts the humeral movement. None of the above-mentioned functions can be confirmed, instead tb is found to be a humeral elevator and downward rotator of the flipper. Fcr and fcu are there to influence the flipper trim according to Robinson (1975). This study finds, that the first muscle flexes metacarpal I on the contiguous distal carpal. The second muscle aids in flipper twisting by displacing the ulnar side of the carpus relatively ventrally in relation to the humerus (Tab. 1).

4.2.2 Hindflipper

Pe is merely described to be a strong femoral depressor by Robinson (1975) and Carpenter et al. (2010) with which this study agrees. Yet, especially the acknowledgement of a pubic and an ischial portion lead to considerably more femoral movements in which this muscle aids. Pi is interpreted as a strong femoral elevator (Robinson, 1975; Carpenter et al., 2010) which could be supported by this study. A division into possible muscle portions originating from the pubis, the vertebral column, the ischium, and the ilium led to several other functions this muscle may have contributed to. This study confirmed the interpretation by Robinson (1975) that i retracts and elevates the femur and rotates the flipper leading edge downward. Corroborated was that af is a femoral depressor. Not found was a rotational function as suggested by Robinson (1975). Muscle reconstructions presented in this study allowed it to be a femoral retractor. Elevation of the femur (Robinson, 1975) and upward rotation of flipper leading edge (Carpenter et al., 2010) were confirmed to be movements the ife participates in. Additionally, it was found to be a retractor, too. Cfb and cfl rotate the flipper leading edge downward (Robinson, 1975; Carpenter et al., 2010), aid in elevation (Robinson, 1975) and also retraction. Pit, ifi, it, a, f, peroneus, ta have only been reconstructed by Robinson (1975) so far. She interpreted all of them to be flipper trim adjusters and a, it, and f that insert via a common tendon were additionally interpreted to be upward rotators of the flipper leading edge (Robinson, 1975). This study does not agree with this, but instead found that these muscles take part in all parts of hindflipper movement during up- and downstroke and flipper twisting and have very diverse functions (s. chapter 3.2.2; Tab. 2).

4.3 Limb cycle and myological mechanism for flipper twisting

4.3.1 Foreflipper

At the beginning of the downstroke the flipper leading edge is rotated downwards by rotating humerus with the help of the humeral rotators (bb, scs (anterior portion), dc) which originate from the pectoral girdle or the vertebral column. Downwards rotation can also be initiated by an upward rotation of the flipper trailing edge (shp, p, and tb). Then, the humerus is depressed and retracted accompanied by flipper twisting along the flipper length axis by slightly displacing the carpus ventrally on the flipper leading edge and dorsally on the flipper trailing edge and flexion of digit I while the following digits are decreasingly depressed towards digit V. On the ventral foreflipper pte and fcr run diagonally across the carpus from proximoposteriorly to disteroanteriorly. The former could slightly displace the radius ventrally against the humerus in concert with b and the latter might flex metacarpal I on the adjacent distal carpal or displace the radial side of the carpus slightly ventrally. Both could slightly compress and bulge the carpus. Apb acts in concert with them and flexes digit I. At the same time the posterior side of the carpus and manus might have experienced an upward twisting by muscles that are reconstructed on the dorsal side of the plesiosaur flipper. The humeral tb head and ecu could have displaced ulna and ulnare slightly dorsally to the humerus, ecu might have alternatively extended metacarpal V on the adjacent distal carpal in a concerted action with an individually acting edbs and edbp slip to digit V (Tab. 1).

The foreflipper upstroke begins with an upwards rotation of the flipper leading edge and a simultaneous downwards rotation of the flipper trailing edge (ds and ld rotate the humerus anteriorly upward, while cb, cl, p (anterior portion), ld, and scs (posterior portion) rotate the humerus posteriorly downward). Then, humeral elevators and protractors draw the flipper back by drawing the humerus into the starting position for the downstroke. At the same time the flipper is being twisted along the flipper length axis but in the opposing direction as described above for the downstroke. Twisting upwards of the anterior carpus and manus is enabled by muscles on the dorsal side of the plesiosaur foreflipper. Sm and ecr displaces the radius slightly dorsally to the humerus or even the whole radial side of the carpus while sm extends metacarpal I on distal carpal, while an individually movable edbs and edbp slip to digit I extends the first finger. It is well possible that the two latter may also be involved in a very moderate hand-cupping, which could be opposed by adm on the palm. Muscles on the ventral foreflipper side twist the flipper leading edge relatively downwards in a concerted action. Fcu displaces ulna and ulnare slightly downwards relatively to the humerus or possibly flexes metacarpal V on the adjacent distal carpal and abdV which might have initiated the flexion of digit V. Sm dorsally and adm could induce dorsal, respectively ventral cupping of the plesiosaur carpus. The ligaments (extensor and flexor retinaculum and the intermetacarpal and metacarpodigital ligaments) could contribute passively to flipper twisting. If flipper twisting would be initialized by flexion or extension of e.g., digit I, the ligamentous system of the hand would passively induce digit II, III, IV, and V to successively follow the movement of digit I (Tab. 1).

4.3.2 Hindflipper

The downstroke is initialized by the femoral rotators. Pit, both fti portions, both fte portions, a (if femur elevated), pi (pubis portion), pe (ischium portion), and pti (if femur elevated) rotate the femur anteriorly downward and i, cfb, cfl, ifi rotate it posteriorly upward. Femoral depressors and retractors move the flipper downwards and backwards through the water. At the same time the hindflipper is twisted in a similar fashion as the foreflipper. The leading edge is twisted increasingly downwards along the flipper length axis and the trailing edge upward. Downwards twisting of the hindflipper is managed by muscles that are situated on the ventral tarsus and pes. Pp and ta flex metatarsal I on distal tarsal I and fh flexes digit I independently from the other digits. Which muscle could displace the tibia relatively ventral to the femur remains, in convergence with humerus and radius, speculative? It could be done by fte, fti, or pti. It is likely that a contraction of the ge could also induce flipper twisting. Muscles situated on the dorsal plesiosaur tarsus and pes aid in curling the flipper trailing edge upwards during downstroke. Pb and pl extend metatarsal V on the distal tarsal. An edb slip running to digit V may be individually controllable and responsible for extension of digit V. It is possible that ifi that takes its origin from the ilium, has an additional function, namely to displace the fibula slightly dorsally to the femur (Tab. 2).

At the lowest point of the limb cycle, the flipper is rotated in the opposite direction by approximately 19° (Witzel, Krahl & Sander, 2015) by muscles that either rotate the anterior femur upward or the posterior femur downward (it, a (if femur depressed) pti (if femur depressed) ifi (as long as fibula above origin), Pi (ischium and ilium portion), pe (pubis portion), and ife) or those that insert further distally into the tarsus. Then, femoral elevators and protractors return the flipper into its initial position. Simultaneously, the hindflipper is twisted (flipper leading edge curled upward and flipper trailing edge curled downward). Flipper twisting may be initiated by f (a and it) which might displace the tibia slightly dorsally to the femur. Ehp extends metatarsal I on distal tarsal in concert with slip to digit I of edb which extends the first toe. At the same time, the ventral tarsus and pes muscles aid in twisting. It is difficult to determine how it is induced on the ventral plesiosaur hindflipper, but it is likely that a contraction of the gi head could initialize it. Further addV would aid by independently flexing digit V. In addition, a ventrally lying fh and pp could possibly induce ventral cupping of the tarsus of the hindflipper. Their respective dorsally situated counterpart could be ehp. Extensor and flexor retinaculum and the intermetacarpal and metacarpodigital ligaments that could possibly be reconstructed for plesiosaurs could contribute passively to flipper twisting as described above for the plesiosaur foreflipper (s. chapter 4.3.1; Tab. 2).

Especially in the hindlimb, complex patterns of tendons interconnecting seemingly independent muscles are known: cfl tendon which is associated with ifi and ge in crocodilians (Otero, Gallina & Herrera, 2010) inserts into ge, fte and fti are tendinously associated and insert into gi (Romer, 1923; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011), or even the gi and ge themselves are a highly complex layered partially independent, partially dependently acting muscles (Snyder, 1954; Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki et al., 2011). It appears that the functional implications of these interconnections in recent Sauropsida are not studied in depth, therefore it is impossible to interpret their hypothetical functions in too much detail for fossil taxa (Tab. 2).

4.4 Bone histology of plesiosaur humerus extensor and flexor origin areas

The very localized appearing fibres in section 1 are difficult to interpret. The two different fibre orientations could indicate two different muscle attachments (Petermann & Sander, 2013), if these fibres represent actual Sharpey’s fibres (Fig. 3 e). Fibre directions on the anterodorsal side in section 1 could quite well be correlated with the extensor origins whose muscle fibres fan over the whole breadth of the dorsal plesiosaur hand. Puzzling though is, that the histology of this fibre mesh resembles the fibre mesh described by Scheyer & Sander (2004) for ankylosaur (nodosaur) osteoderms. This raises the question of whether it would actually be possible, if the plesiosaur humerus could fuse with the dermis. Louw (1992) reported that in penguins the skin may actually fuse with foreflipper bones but there was no detailed information available on this. Therefore, this would need further investigation by penguin flipper preparation and histological (soft and bony tissue) sampling in order to address the question whether the same could have actually happened in plesiosaur flippers.

The correlation of fibres on the anteroventral plesiosaur humerus in section 1 (Fig. 3 c) proves to be difficult to interpret: The steeply inclined fibres, if they are associated with a muscle, would mean that a muscle originating from the pectoral girdle would be inserting this far distally into the humerus. The only muscle insertion that could in any way be associated with these fibres would be the deltoideus insertions. Although, this would be an absolutely unique and unlikely state because in any extant sauropsids this muscle insertion is always associated with the, in the proximal half of the humerus situated, deltopectoral crest (Walker, 1973; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). If an attachment of the dermis on the humerus would actually be possible, as discussed above, it could be speculated that fibres of this direction could actually anchor scales that cover the flipper (Frey et al., 2017). Even more difficult to interpret are the fibres running in posteroproximal to anterodistal direction on the anteroventral side of the humerus, as there should be no muscles running in this direction according to the muscle reconstructions presented here. On the anterior epicondyle of the *Cryptoclidus* (IGPB R 324) humerus, there is a groove suggesting that it articulated in this area with maybe a cartilaginous supernumery or a cartilaginous extension of the radius. It is possible that the fibres that take the course described above, parallel to the bone surface, actually represent fibres that anchor connective tissue that covers the elbow joint. This would also be in agreement with the conclusions from sections 2, 3, and 4, where rather bone surface parallel fibres were also interpreted as possible soft tissue attachments of the elbow joint. So it seems likely that the two different fibre directions on the anterodorsal plesiosaur humerus may document the insertions of two differently oriented muscles. Contrastingly, on the anteroventral side of the humerus the two differently oriented fibres may be possibly indicating a muscle insertion on or an attachment of dermis on the bone and the attachment of the joint capsule.

The observed fibre directions in section 2 could correlate quite well with b origin ventrally. The observations suit the dorsal humeral tb head less well, as the corresponding fibres would be expected to be oriented anteroproximal to posterodistal. The shortness of the fibres possibly indicates, that they were sectioned angulated to their long axis. Further, especially in this distal region of the humerus, the observed fibres could represent attachments of the tough connective tissue that connects humerus, radius, and ulna and covers the interosseous space of the the dysfunctional elbow joint in plesiosaurs (compare cetacean humerus in Fig. 1, p. 1124, Cooper et al., 2007b; Fig. 3 b, d).

The ventrally observed fibres in section 3, as they appear in the distal part of the section, may be associated with the connective tissue covering the elbow. The dorsally situated steeply inclined fibres seem to rather speak for attachment of a muscle or a tendon as reported by Petermann & Sander (2013) (Fig. 3 f). The flexors take their course along the ventral side of the humerus, so they cannot be the fibres‘ cause. Dorsally in this region the humeral tb head may originate, but its fibre orientation should be expected to be rather more in anteroproximal-posterodistal direction. This could possibly indicate that either the fibres were not cut optimally to catch them in their full length or that the insertion of the tb tendon needs to be shifted more towards the anterior ulna (Fig. 3 d).

In section 4, which is overall very similar as section 2, fibre directions would rather match with the dorsal origin of the humeral tb head, while the ventrally situated fibres do match the possible b fibre directions (rather posteroproximal to anterodistal) on the humeral ventral side well. Comparable to section 2, the observed fibres in section 4 might as well be fibres of connective tissue that covers the dysfunctional elbow joint (Fig. 3 b, d).

4.5 Plesiosaur joint morphology, osteology, and myology in comparison to that of convergently evolved functional analogues (Chelonioidea, Spheniscidae, Otariinae, Cetacea)

4.5.1 Joint morphology

English (1977) and Gordon (1983) mention that scapular rotation may add to the locomotion cycle in Otariinae. Schmidt, Mehlhorn & Fischer (2016) and Baier & Gatesy (2013) report that scapular rotation contributes to tortoise and alligator locomotion. Furthermore, Mayerl, Brainerd & Blob (2016) show that pelvic rotation adds to locomotion in turtles, too, if it remains unfused with the sacrum and the carapace. These observations seem to imply, that the contribution of the ligamentously and muscularly suspended pectoral and pelvic girdles to locomotion is severely understudied with eventual consequences for the reconstruction of locomotory styles in fossil taxa and including plesiosaurs.

Otariinae, Cetacea, and Spheniscidae have ball-and-socket shoulder joints (Carte & Macalister, 1868; English, 1977; Louw, 1992). Contrastingly, Chelonioidea have an oval-shaped ellipsoid glenoid and humeral head (Wyneken, 2001; personal observation). The long axis of this joint is sloping anterodorsally-posteroventrally. The plesiosaur glenoid surface resembles the sea turtles‘ glenoid but its long axis is oriented horizontally. The oval acetabular articulation surface is longer and narrower than the glenoid. Counter-intuitively this could actually mean that the hindlimb is more restricted in its anteroposterior range of motion, because the glenoid of sea turtles shows, that this joint type restricts mobility more in the direction of the long axis than in direction of the short axis. The articulation surfaces of the plesiosaur humeral and femoral head are more puzzling though. The heads of both bones have roughly round potential articulation surfaces that are very rough and pitted resembling closely the state found in the *Dermochelys coriacea* humerus (Rhodin, Ogden & Conlogue, 1981; Snover & Rhodin, 2008). As the authors show, the unusual thick vascularized cartilage cap is by no means parallel to the underlying bone and the actual cartilaginous articulation surface has a much diverging form being slightly larger than the ellipsoidal glenoid surface (Rhodin, Ogden & Conlogue, 1981; Snover & Rhodin, 2008). Therefore, it is probable that the proximal hyaline cartilage caps of plesiosaur humeri and femora were not parallel to the underlying bony articulation surfaces, too, leaving room for speculation. Ball-and-socket joints have three degrees of freedom. The ellipsoidal joint of sea turtles restrains the humerus from long axis rotation and restricts movement in the direction of the long axis of the glenoid which translates to pro- and retraction. This joint type allows a great range of motion in the direction of the short glenoid axis resulting in humeral elevation and depression (Rivera, Wyneken & Blob, 2011; Rivera, Rivera & Blob, 2013). If plesiosaurs had similar ellipsoidal joints like sea turtles, this would strongly hint at flying as their mode of locomotion. Although, even if we consider shoulder and pelvic girdle rotation in plesiosaurs, this does not fully explain how humerus and femur are able to rotate about their long axis for about 19° (Witzel, Krahl & Sander, 2015) which hydrodynamic studies have proven to be necessary for plesiosaur underwater flight. So the plesiosaur glenoid and acetabulum would need to deviate to some degree from the shape of the sea turtle shoulder joint.

Otariinae and Chelonioidea have a mobile elbow joint (English, 1976a; Rivera, Wyneken & Blob, 2011). The penguin joint is largely immobile (Louw, 1992). The cetacean elbow joint is not functional anymore (Cooper et al., 2007b). The immobile elbow joint of plesiosaurs resembles rather broadly the Cetacean like state (compare to Cooper et al., 2007a). The immobile elbow joint does not necessarily object underwater flight. In sea turtles the mobile elbow joint seems to be constraint by phylogeny. Due to the presence of the armor, two mobile joints are necessary to place the hand on the ground or to hold a flipper to the side of the body. In Otariinae a mobile elbow joint appears to be necessary for the rowing movement and the recovery stroke (English, 1977).

In penguins, whales, and probably also in sea turtles the carpal region seems to be stiffened which is also the case in in plesiosaurs (Walker, 1973; Louw, 1992; Cooper et al., 2007a). English (1976a) suggests considerable mobility in the carpus of Otariinae which is possibly necessary for digital spreading during the rowing portion of the flipper beat cycle. To be fair, the intercarpal, carpometacarpal flexibility has actually not been studied in such detail for either of the other three recent taxa or in plesiosaurs, so there actually might be a considerably higher degree of mobility in all four taxa than accounted for at the moment.

A certain degree of interphalangeal movement can be presumed for sea turtles, cetaceans, and otariids simply due to the observation, that all flippers bow proximodistad to different degrees during flipper beating (e.g., Edel & Winn, 1978; Davenport, Munks & Oxford, 1984; Feldkamp, 1987; Lucas et al., 2014). The amount of interphalangeal movement in the taxa convergent to plesiosaurs has not been studied yet. The joint surfaces of plesiosaur phalanges in the fore- and hindflipper suggest that there is some movement possible, to how much this would sum up in total, would be something to also test in the future.

4.5.2 Osteology

The bony elements of the girdle regions of Chelonioidea, Spheniscidae, Otariinae, and Cetacea (e.g., Carte & Macalister, 1868; Walker, 1973; English, 1977; Louw, 1992; Wyneken, 2001; Depecker et al., 2006) diverge from the adaptations found in plesiosaurs. None of the above have scapula, coracoid, pubis, and ischium arranged ventrally as such large bony plates as the plesiosaurs have (e.g., Andrews, 1910). Although, in sea turtles the plastron (and carapace) serves as origin area for locomotory muscles, e.g., the enormous p originates from about two thirds of the plastron (Walker, 1973; Wyneken, 2001; personal observation). In mammals and birds, the sternum appears to have evolved as the convergent bony structure (Schreiweis, 1982; Louw, 1992; Berta, Sumich & Kovacs, 2005). The big difference is though that in plesiosaurs dorsoventrally directed bony structures are markedly reduced which does not seem to be the case in penguins, whales, sea lions, and fur seals (English, 1977; Godfrey, 1984; Louw, 1992; Berta, Sumich & Kovacs, 2005). Highly aquatic turtles (fresh water and marine) do seem to show a similar trend as plesiosaurs: The approximately dorsoventrally directed scapula is reduced in sized, while the approximately anteroposteriorly directed coracoid is much enlarged. Additionally, it can be ruled out, that the reason for this development is the style of locomotion, because rowing turtles show the same trend as underwater flying turtles (Depecker et al., 2006; Benson, et al., 2011). One can speculate, that the strong dorsoventrally directed bony components in the pectoral and pelvic girdles of sea turtles and Otariinae derive from a trade-off between a highly specialized aquatic lifestyle and the ability for terrestrial locomotion. Yet, this theory fails to explain the large dorsoventrally directed structure of the pectoral girdle in penguins, even though the penguin wing is freed from the constraint of terrestrial locomotion (e.g., Shufeldt, 1901; Pinshow, Fedak & Schmidt-Nielsen, 1977). Cetaceans also do show a considerably large dorsoventrally directed scapula. The difference between plesiosaurs and the above discussed taxa may be that locomotory muscles might have spread onto the vertebral column (ife, cfb, fti, fte), their function is emulated by other muscles, or they are indeed heavily reduced in size and functionally only minorly important. Humeri of sea turtles, whales, and penguins have approximately oval mid-shaft cross sections like humeri and femora of plesiosaurs (Zug, Wynn & Ruckdeschel, 1986; Krahl, Klein & Sander, 2013; Nakajima, Hirayama & Endo, 2014; Houssaye et al., 2015; Ksepka et al., 2015; Wintrich et al., 2017). Humeri and femora of plesiosaurs are morphologically less elaborated than those of Spheniscidae, Chelonioidea and Otariinae (Andrews, 1910; Walker, 1973; English, 1977; Zug, Wynn & Ruckdeschel, 1986; Louw, 1992; Hirayama, 1994). The rest of the flipper is dorsoventrally flattened in all five taxa (Andrews, 1910; Walker, 1973; Robinson, 1975; Feldkamp, 1987; Louw, 1992; Fish & Battle, 1995; Fish, 2004; Cooper et al., 2007b). Radius/ulna and tibia/fibula, are markedly reduced in size in plesiosaurs (Andrews, 1910). Contrastingly, penguins, Otariinae, sea turtles, and whales have a significantly longer radius/ulna (Andrews, 1910; Walker, 1973; English, 1977; Louw, 1992; Cooper et al., 2007b). Plesiosaur fore- and hindflippers show considerable hyperphalangy (Andrews, 1910). The flippers of the functional analogues mostly evolved by elongation of phalanges involving comparatively little hyperphalangy (Walker, 1973; English, 1976a; Louw, 1992; Cooper et al., 2007a). As suggested by Cooper et al. (2007a) the joint spaces between elongated phalanges are bigger than in between the hyperphalangic joints of plesiosaurs. This means that the former probably extend/flex at a larger angle than the latter in each joint. This would allow plesiosaurs, who have proportionately more joints with a smaller range of motion, to control the anterodistal bending of the flipper and the flipper twisting along the flipper length axis more smoothly than the functionally analogous tetrapods (Cooper et al., 2007a).

4.5.3 Myology

Locomotory muscles spanning the shoulder joint of the here considered tetrapods generally do not appear to experience reduction in the land-water transition, independent of the locomotory mode they employ (Walker, 1973; English, 1977; Schreiweis, 1982; Wyneken, 2001; Cooper et al., 2007b). The set of muscles they have is determined by their phylogeny. So depending on whether plesiosaurs are on the archosaur or on the lepidosaur lineage they either could have a scapulohumeralis anterior, shp, or a second fte head. A reduction takes place in the two-joint muscles that span the glenoid and the elbow, bb and tb: in penguins and whales bb is fully reduced (Schreiweis, 1982; Cooper et al., 2007b). In sea turtles tb is either much reduced or entirely reduced depending on the species (Walker, 1973). Sea lions and fur seals have both muscles well developed (English, 1977). Although this tends to suggest, that one of them might get reduced during readaptation to the aquatic realm, based on the EPB both muscles were reconstructed for plesiosaurs.

Due to the lack of adequate functional analogues to the plesiosaur hindflipper a comparison to extant taxa is hampered. All muscles inserting into the proximal plesiosaur femur are well corroborated by EPB and can be confidently reconstructed comparable to the plesiosaur foreflipper. The sauropsid hindlimb has more two-joint muscles than the forelimb (fte, fti, ifi, it, a, pti, pit, and in a way cfl). Supported by lepidosaurs, crocodilians, and turtles are fte, fti, ifi, it, a, cfl, and pit, while pti is well but weaker supported by EPB (turtles, lepidosaurs). The iliac heads of ifi and it might have been much reduced as suggested by the small ilium size in plesiosaurs.

Cetacea have extremely reduced flexors and extensors of the lower arm and hand in comparison to Chelonioidea, Spheniscidae, and Otariinae who have partially well developed flexor and extensor groups (Walker, 1973; English, 1976a; Schreiweis, 1982; Louw, 1992; Cooper et al., 2007b). The foreflipper of the former is a control surface (Fish, 1996, 2002; Woodward, Winn & Fish, 2006), while the foreflippers of the latter three are the main propulsive organs (Neu, 1931; Walker, 1971; Clark & Bemis, 1979; Davenport, Munks & Oxford, 1984; Feldkamp, 1987; Wyneken, 1997; Rivera, Wyneken & Blob, 2011; Rivera, Rivera & Blob, 2013). Therefore, plesiosaurs, as they also rely on their flippers as the main power generating organs, must have distinctively more extensors and flexors as Cetacea, too, as the results of the plesiosaur muscle reconstructions show.

Fcu is hypertrophied in sea turtles and Otariinae and present in Spheniscidae and Cetacea (Walker, 1973; English, 1976a; Schreiweis, 1982; Louw, 1992; Cooper et al., 2007b). It is possible that it rotates the flipper leading edge up in both former taxa and therefore needed to be relatively stronger than in a terrestrial environment due to the higher viscosity of water in comparison to air.

Extensors and flexors are generally reduced in sea turtles, penguins, and cetaceans (Walker, 1973; Schreiweis, 1982; Louw, 1992; Cooper et al., 2007b) in comparison to their terrestrial predecessors. During the ontogeny of sea turtles, extensors and flexors show an increase in fascia development and in connective tissue (Walker, 1973; Wyneken, 2001; Abdala, Manzano & Herrel, 2008). Muscle fusion with dermis is reported for sea turtles, penguins, and otariines (Walker, 1973; English, 1976a; Louw, 1992; Wyneken, 2001; Abdala, Manzano & Herrel, 2008). In penguins, skin even fuses to bone (Louw, 1992). Muscles that enable Otariinae to spread their digits, probably for the rowing motion during the flipper beat cycle, are lacking in penguins, sea turtles, and cetaceans (Walker, 1973; English, 1976a; Schreiweis, 1982; Cooper et al., 2007b) and accordingly probably in plesiosaurs as well.

For plesiosaurs a considerable amount of extensors and flexors were reconstructed for the foreflipper (ecu, edc, sl + ecr, sm, pte, fcu, fdlf, fcr, edbp and edbs, fdls, abdV, apb, adm) and hindflipper (edl, pb and pl, ta, gi and ge, fdlh, pp, edb, fdb, ehp, addV, fh). These were reconstructed to fulfil certain requirements, i.e., they must enable flipper twisting, as well as it is e.g., necessary that all five digits of the fore- and hindflipper must have been moveable, as none of them seems to have been in the course of reduction. Therefore, while extensors and flexors of both forelimb and hindlimb are generally well supported by the EPB, addV and fh of the hindflipper are only supported by lepidosaurs, yet they were reconstructed for the above-mentioned reasons. Muscles that are responsible for digital spreading were not reconstructed for plesiosaurs comparable to above discussed functional analogues. By no means this high number of foreflipper and hindflipper extensors and flexors in plesiosaurs necessitates that all of them must have had highly developed big muscle bellies. Especially the layered digital flexors and extensors of hand and foot may have become aponeurotic, or did not fully differentiate, or partially fused as observed in extant functional analogues.

5. Conclusions

Homology amongst the three extant taxa, as well as amongst plesiosaur muscle reconstructions was established. In total 52 locomotory muscles, 26 foreflipper muscles (12 pectoral, 8 antebrachial, and 6 manual muscles) and 26 hindflipper muscles (15 pelvic, 6 crural muscles, and 5 muscles of the pes), were reconstructed with the EPB (based on crocodilians, turtles, lepidosaurs) for *Cryptoclidus* (IGPB R 324). Ligaments in the pectoral and pelvic girdle appear unlikely due to lacking osteological evidence and their hypothetical courses. Flexor and extensor retinacula and intermetacarpal/intermetatarsal and metacarpodigital/metatarsodigital ligaments appear likely due to mechanical reasons although they are not necessarily well supported by EPB.

Muscle origin sites on the pectoral and pelvic girdle and insertion sites on the humerus and femur of *Cryptoclidus* (IGPB R 324) are compared to other plesiosaur myology studies. Foreflipper muscle origins are very similar to the reconstructions by (Araújo and Correia 2015). Otherwise the reconstructions provided in this study differ partially profoundly from literature. This is partially due to the choice of extant taxa on which the reconstructions rely, partially due to incomplete muscle reconstructions provided by all other authors so far, and partially due to that Robinson (1975) interpreted humerus and femur articulation differently.

Geometrically obtained muscle functions are compared to the interpretations of other authors. Differences are given by differences in muscle reconstructions. Additionally, the strictly geometrically deduced muscle functions gained in the current study show, that muscles may have had up to three functions that contribute complexly to locomotion. Furthermore, especially large muscles may have been compartementalized (e.g., p, scs), i.e., part of the muscle lies anteriorly/cranially and posteriorly/caudally to glenoid or acetabulum. Therefore, their functions eventually added up to six, which were possibly recruited during different sequences of the flipper beat cycle.

A plesiosaur flipper beat cycle could have looked like this: The humerus and femur were slightly rotated downwards (~19°) and were strongly depressed and little retracted during the downstroke. Additionally, flipper length axis twisting is induced by muscles that twist the flipper leading edges downward and the trailing edges upward. The successive digits follow the actively induced twisting of the first digit passively because of the intermetacarpal/intermetatarsal and metacarpodigital/metatarsodigital ligaments. Then, the propodials are rotated upwards by ~38 ° during the fore- and hindflipper upstroke and are strongly elevated and little protracted. At the same time the flippers are twisted into the opposite direction, i.e., the leading edge is turned upward and the trailing edge myologically. Active flipper profile manipulation may have been possible which would have led to an asymmetry of the fore- and hindflipper profiles which in turn would have provided an increased efficiency over a symmetrical profile.

Eventual extensor and flexor origin areas above the epicondyles on the anterior and posterior *Cryptoclidus* (IGPB R 324) humerus were sampled histologically. Fibres of various angles are found to be incorporated into the cortex localized. Some of them may correlate with muscle origins, but others may rather anchor soft tissue associated with the elbow joint or fusion of dermis to bone. Histology of muscle attachments in plesiosaurs would need further research in the future.

The foreflipper apparatus of Chelonioidea, Spheniscidae, Otariinae, and Cetacea was examined in contrast to that of plesiosaur fore- and hindflippers. Pectoral and pelvic girdle swinging, still understudied in the functional analogues, contributes to their locomotion. Pectoral and pelvic girdle swinging in plesiosaurs could contribute to plesiosaur fore- and hindflipper length axis rotation reducing the contribution by actual humerus and femur length axis rotation. The plesiosaur glenoid and acetabulum are best comparable to the ellipsoid glenoid of sea turtles which inhibits humeral long axis rotation in cheloniids (Rivera, Wyneken & Blob, 2011). How the hyaline cartilage caps of the plesiosaur humeral and femoral heads looked like remains speculative because they were likely non-parallel to the bone surface. The plesiosaur elbow and knee may be best compared to the immobile elbow joint of Cetacea. Carpal and carpometacarpal mobility has only thoroughly been studied in sea lions so far (English, 1976), so functional analogues as well as plesiosaurs would need further studies.

In plesiosaurs the scapula blade and the ilium have become very small, while coracoid and pubis alike have been expanded much. A trend which is convergent to the evolution of the chelonioid pectoral girdle. Accordingly, the locomotory muscles that originate from the respective bony element hypertrophied or were either reduced or shifted their origin onto other surrounding bones. Therefore, we reconstructed all pectoral and pelvic locomotory muscles for *Cryptoclidus* (IGPB R 324) that are present and well supported by EPB while we carefully reconstructed more distally arising fore- and hindflipper muscles, well aware that these are the muscles that experienced possibly reduction and an increase in aponeurosis formation.

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Appendix

App. 1: Homology of plesiosaur foreflipper and hindflipper myology

Foreflipper

Musculus pectoralis

pectoralis (Watson, 1924; Tarlo, 1958; Robinson, 1975; Lingham-Soliar, 2000; Carpenter et al., 2010; Araújo & Correia, 2015)

Musculus subcoracoscapularis

subcoracoscapularis (Lingham-Soliar, 2000; Araújo & Correia, 2015)
subscapularis and subcoracoideus (Watson, 1924; Tarlo, 1958)
subscapularis, subcoracoideus, subcoracoscapularis (Robinson, 1975)
subscapularis and subclavicularis (Carpenter et al., 2010) (termed by position, but not really explained how Carpenter et al. (2010) came to this conclusion)

Musculus supracoracoideus

supracoracoideus (Watson, 1924; Tarlo, 1958; Robinson, 1975; Lingham-Soliar, 2000; Araújo & Correia, 2015)
supraclavicularis (Carpenter et al., 2010) (termed by Carpenter et al. (2010) by position but did not describe detailed how they came to the conclusion, so we presume it is supposed to be the supracoracoideus that has just been shifted anteriorly

Musculus coracobrachialis longus

coracobrachialis longus (Lingham-Soliar, 2000; Araújo & Correia, 2015)
coracobrachialia (Tarlo, 1958)
coraco-brachialis longus (Watson, 1924)
coracobrachialis (Carpenter et al., 2010), it is not possible to determine whether the coracobrachialis of Carpenter et al. (2010) is supposed to represent both muscular heads or only one subportion, but since it is separated into two heads in extant lepidosaurs and turtles (Walker, 1973; Russell & Bauer, 2008) on which their study is based, we presume that they imply by „coracobrachialis“ both, coracobrachialis brevis and longus.

Musculus coracobrachialis brevis

coracobrachialis brevis (*Lingham-Soliar*, 2000; *Araújo & Correia*, 2015)

coracobrachialis (Robinson, 1975; Carpenter et al., 2010)
coracobrachialia (Tarlo, 1958)
coraco-brachialis brevis (Watson, 1924)
coracobrachialis (Carpenter et al., 2010) (s. coracobrachialis longus)

Musculus scapulohumeralis anterior

scapulohumeralis anterior (Tarlo, 1958; Robinson, 1975; Lingham-Soliar, 2000)
scapulo-humeralis anterior (Watson, 1924)
scapulohumeralis (Carpenter et al., 2010) cannot surely be determined if they mean scapulohumeralis anterior or posterior, as they base their reconstructions on lepidosaurs, but also on *Sphenodon*, which has both muscles, but the position in which it is reconstructed hint to a scapulohumeralis anterior, but the homology remains doubtful

Musculus scapulohumeralis posterior

scapulohumeralis posterior (Lingham-Soliar, 2000)
scapulohumeralis (Araújo & Correia, 2015) as they synonymized it with the respective muscles in crocodilians and lepidosaurs

Musculus deltoideus clavicularis

deltoideus clavicularis (Carpenter et al., 2010)
deltoides clavicularis (Robinson, 1975; Lingham-Soliar, 2000)
clavodeltoideus (Araújo & Correia, 2015)
deltoid (Watson, 1924), as this muscle was reconstructed to take its origin from the clavicula and the scapula, it is probable that Watson (1924) means both, deltoideus scapularis and deltoideus clavicularis with this term, which is substantiated by Fig. 5, p. 896 in which a humeral „Del Sc“ and „Del Cl“ are marked, but the authors could not find a legend to these abbreviations in Watson (1924).

Musculus deltoideus scapularis

deltoideus scapularis (Carpenter et al., 2010), abbreviation of this muscle listed in Fig.17, p. 22 but not pictured, but instead the deltoideus clavicularis is shown to arise probably from the scapular prong, which is rather the origin surface for the deltoideus scapularis
scapulodeltoideus (Araújo & Correia, 2015)
deltoides scapularis (Robinson, 1975; Lingham-Soliar, 2000)

scapular deltoid (Tarlo, 1958)

deltoid (Watson, 1924), please view comment on this in „deltoideus clavicularis“ section

Musculus latissimus dorsi

latissimus dorsi (Watson, 1924; Tarlo, 1958; Robinson, 1975; Lingham-Soliar, 2000; Carpenter et al., 2010; Araújo & Correia, 2015)

teres major (Carpenter et al., 2010)

Musculus triceps brachii

triceps (Robinson, 1975)

triceps brachii (Araújo & Correia, 2015)

Musculus biceps brachii

biceps (Robinson, 1975; Carpenter et al., 2010)

biceps brachii (Araújo & Correia, 2015)

Musculus brachialis

brachialis (Robinson, 1975)

Musculus flexor carpi ulnaris

flexor carpi ulnaris (Robinson, 1975)

Musculus flexor carpi radialis

flexor carpi radialis (Robinson, 1975)

Hindflipper

Musculus iliotibialis

iliotibialis (Robinson, 1975; Lingham-Soliar, 2000)

Musculus femorotibialis

femorotibialis (Robinson, 1975)

Musculus ambiens

ambiens (Robinson, 1975)

Musculus ischiotrochantericus

ischiotrochantericus (Robinson, 1975)

Musculus iliofibularis

iliofibularis (Robinson, 1975; Lingham-Soliar, 2000)

Musculus puboischiotibialis

puboischiotibialis (Robinson, 1975; Lingham-Soliar, 2000)

Musculus adductor femoris

adductores (Robinson, 1975)

„Primitively the adductor arises midventrally from the puboischiadic ligament…“ (Robinson, 1975). In lepidosaurs adductor femoris originates from the puboischiadic ligament (Snyder, 1954) and this seems to fit well name-wise as well as in terms of described insertion area on the femur. In turtles fti, pubtib, pubischtib originate from the aforementioned ligament, but they span the femur (Walker, 1973), so adductores cannot be one of them. Crocodilians have no puboischiadic ligament, so they provide no further information here.

Musculus caudifemoralis brevis

caudifemoralis brevis (Robinson, 1975)

caudofemoralis (Carpenter et al., 2010), not clearly deducible whether or not it represents both muscular heads of caudifemoralis or simply brevis. Fig. 18 A and 14 D rather suggest that they only refer to caudifemoralis brevis, although in lepidosaurs c. brevis and longus is present and only in turtles there is only one head, c. brevis

caudifemoralis (Lingham-Soliar, 2000) (seems to be synonymous to both portions, (s. Fig. 10 D) because two muscle bellies are shown of which one runs posterior/caudal to the tail)

Musculus caudifemoralis longus

caudifemoralis longus (Robinson, 1975)

caudifemoralis (Lingham-Soliar, 2000)

Musculus puboischiofemoralis externus

puboischiofemoralis externus (Robinson, 1975; Lingham-Soliar, 2000; Carpenter et al., 2010)
ischiofemoralis externus (Carpenter et al., 2010), difficult to determine which muscle this is supposed to be in turtles and lepidosaurs, but given its origin area on the pelvic girdle it seems to be reasonable to presume that this is an ischial head of puboischiofemoralis externus (compare to Snyder (1954), Walker (1973), Russell & Bauer (2008)) as it is also shown to insert together with the PIFE into the femur (compare Fig. 17 F, Carpenter et al. (2010))

Musculus puboischiofemoralis internus

puboischiofemoralis internus (Robinson, 1975; Lingham-Soliar, 2000; Carpenter et al., 2010)
pubofemoralis internus (Lingham-Soliar, 2000)
ischiofemoralis internus (Carpenter et al., 2010), it is difficult to determine which muscle this is supposed to be as the authors do not describe how they have come to the conclusion. Given its position on the pelvic girdle, this muscle could be an ischial head of puboischiofemoralis internus, which would only be supported by lepidosaurs (and not turtles, as their EPB is based on these two taxa). A separated insertion into the femur for Pifi (as shown in Fig. 17 E, Carpenter et al. (2010)) is supported by Russell & Bauer (2008), although Snyder (1954) depicts a common insertion as shown for turtles, too (Walker, 1973).
Supported by turtles and lepidosaurs would be ischiotrochantericus, which would also be in agreement with Fig. 17 E by Carpenter et al. (2010), in which this muscle is shown to insert independently from PIFI. Yet, its anterior position on the ischium is only supported by turtles, not by lepidosaurs, in which pifi arises from this position. So both muscles are thinkable to be synonymous to ischiofemoralis internus defined by their origin areas. The part of the name „internus“ might hint, that it is supposed to be a portion of PIFI though.

Musculus iliofemoralis

iliofemoralis (Robinson, 1975; Lingham-Soliar, 2000; Carpenter et al., 2010)

Musculus peroneus brevis and Musculus peroneus longus

peronaeus longus (Robinson, 1975)

Musculus tibialis anterior

tibialis anticus (Robinson, 1975)

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Chapter 4

In preparation:

Krahl, A.; Witzel, U.; Lipphaus, A.; Sander, P. M. *Cryptoclidus eurymerus* humerus and femur FESA inform on plesiosaur muscle forces and flipper twisting.

Author contributions:

AK, UW, and PMS designed the research. AK and PMS wrote the paper. AK provided data. UW, AK, and AL built the analog plesiosaur fore- and hindflipper model. AL, AK, and UW contributed to FESA.

Cryptoclidus eurymerus humerus and femur FESA inform on plesiosaur muscle forces and flipper twisting

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Keywords: plesiosaur, finite element analysis, underwater flight, flipper twisting

Abstract

Plesiosauria (Sauropterygia) are secondarily marine Diapsida. They are the only tetrapods that evolved hydrofoil fore- and hindflippers. Once this locomotory specialization had evolved, it remained essentially unchanged for 135 Ma. It is still contentious whether plesiosaurs flew underwater, rowed, or employed a mixture of both styles. Long bones of Tetrapoda experience torsion, bending, and compression during locomotion. Load case superposition indicates that bones are loaded primarily by compression. Thus, it is possible to use finite element analyses as a test environment for hypotheses of muscle lines of action (LOA), if the objective is to receive a homogenous compressive stress distribution and to optimize for bending minimization. To study locomotion in plesiosaurs, a *Cryptoclidus eurymerus* (Middle Jurassic Oxford Clay of the UK) humerus and femur were analyzed with FE methods according to this concept. Based on muscle reconstructions that had been undertaken earlier, LOA were deduced experimentally for all humerus and femur muscles of *Cryptoclidus*. These were acquired by spanning threads into a cast of a fore- and hindflipper of a mounted skeleton. LOA and muscle attachments were conveyed to a meshed volumetric model of the humerus and femur that were created from micro-CT scans. By computing the compressive stress distribution for two load cases, down- and upstroke, for each bone, muscle forces were approximated by stochastic iteration. After the reconstruction of a flipper twisting mechanism driven by muscles and the addition of those extensors and flexors in the finite element models that originate from humerus and femur and contribute to flipper twisting, a homogenous compressive stress distribution was obtained. Humeral and femoral elevators and depressors, powering underwater flight and not rowing, were found to have the highest muscle forces. Extensors and flexors exert high muscle forces in comparison to Cheloniidae. This corroborates a myological flipper twisting mechanism in plesiosaurs complementing hydrodynamic studies that showed that flipper twisting is crucial for plesiosaur underwater flight.

1. Introduction

1.1 Plesiosaur muscuskeletal apparatus and locomotion

1.1.1 *Cryptoclidus eurymerus* osteology

Plesiosauria are secondarily aquatic Tetrapoda that roamed the marine realm from the Late Triassic (Wintrich et al., 2017) until the K/Pg mass extinction (Bardet, 1994; Motani, 2009; Vincent et al., 2011; Vincent et al., 2013; Bardet et al., 2014). Plesiosauria form the most derived group of Sauropterygia. The origin of Sauropterygia remains obscure. They could have evolved from basal archosauromorphs (Merck, 1997) or lepidosauromorphs (Rieppel & Reisz, 1999), or they may be the sister taxon to archosauromorphs and lepidosauromorphs (Neenan, Klein & Scheyer, 2013). The most striking and unique key innovation of plesiosaurs is that they have evolved four similarly looking wing-like flippers by the Late Triassic (Wintrich et al., 2017). All four flippers are dorsoventrally flattened, have greatly foreshortened zeugopodium (< 1/3 of autopodium length), and form a hydrofoil (Robinson, 1975, 1977). They possibly had an asymmetrical profile (Robinson, 1975; Caldwell, 1997) like the flippers of recent underwater-flying Spheniscidae and Chelonioidea. Unlike plesiosaurs, Spheniscidae, Chelonioidea, Cetacea, and Otariinae have only evolved hydrofoil-like foreflippers (Walker, 1973; Schreiweis, 1982; Feldkamp, 1987; Fish & Battle, 1995; Fish, 2004; Cooper et al., 2007; Elliott et al., 2013). Sea turtle, penguin, and sea lion hindflippers evolved into paddles (Shufeldt, 1901; Walker, 1971b; Davenport, Munks & Oxford, 1984) and are employed in steering and terrestrial and aquatic locomotion (Walker, 1971b; Pinshow, Fedak & Schmidt-Nielsen, 1977; Clark & Bemis, 1979; Davenport, Munks & Oxford, 1984; Feldkamp, 1987; Wyneken, 1997). Whale hindlimbs are almost entirely reduced. Scapula, coracoid, pubis, and ischium of plesiosaurs lie ventrally and meet the element from the other side in the body midline in a slightly v-shaped configuration. Coracoid and pubis are much expanded. The dorsal expansion of the scapula and the dorsally directed ilium are much reduced (Andrews, 1910). Gastralia lie in between the pectoral and the pelvic girdle and stiffen the trunk region (Sues, 1987; Taylor, 1989). Humeri and femora of *Cryptoclidus eurymerus* have a round proximal end, an oval midshaft cross section, and the epicondyles are expanded and hammer-shaped (Andrews, 1910; personal observation on IPB R324, a *Cryptoclidus eurymerus* exhibit (Oxford Clay, Middle Jurassic, UK) at the Goldfuß Museum, Rheinische Friedrich-Wilhelms-Universität Bonn).

The distal expansion of the humerus of *Cryptoclidus* is larger than that of the femur and rather untypical for most plesiosaurs (compare to e.g., Großmann, 2006, Sachs, Hornung & Kear, 2016). Radius/ulna, and tibia/fibula are much shortened and rather disc-like in appearance (Andrews, 1910). Metacarpal V and metatarsal V have been moved proximally into the rows of carpals and tarsals (Robinson, 1975). Fore- and hindflippers are hyperphalangic (Andrews, 1910).

1.1.2 Plesiosaur muscle reconstructions

Plesiosaur muscles have been reconstructed by Watson (1924), Tarlo (1958), Robinson (1975), Lingham-Soliar (2000), Carpenter et al. (2010), Araújo & Correia (2015), and by Krahl and Witzel (dissertation, chapter 3). Carpenter et al. (2010) Araújo & Correia (2015), and Krahl and Witzel (chapter 3) relied on the extant phylogenetic bracket (EPB), a method that emerged in the 1990s which provides reliable inferences for soft tissue anatomy of fossils (Bryant & Russel, 1992; Wittmer, 1995). Older studies (Watson, 1924; Tarlo, 1958; Robinson, 1975; Lingham-Soliar, 2000) did not employ the EPB and did not clearly state which extant taxa they relied on for their muscle reconstructions. Muscles that originate on the pectoral girdle and insert into the humerus or span it have been reconstructed by Watson (1924), Tarlo (1958), Robinson (1975), Lingham-Soliar (2000), Carpenter et al. (2010), Araújo & Correia (2015), and by Krahl and Witzel (chapter 3). Locomotor muscles which arise from the pelvic girdle, traverse the femur, and attach to the femur have been partially reconstructed by Robinson (1975), Lingham-Soliar (2000), and Carpenter et al. (2010) and completely by Krahl and Witzel (chapter 3). Muscles which arise distally from the humerus and femur have been partially reconstructed by Robinson (1975) and entirely by Krahl and Witzel (chapter 3). Robinson (1975) seems to have reconstructed the ventral side of the foreflipper and the dorsal side of the hindflipper although thus is not clearly stated (Robinson, 1975; Krahl and Witzel (chapter 3)). The possible implication is that the dorsal and ventral fore- and hindflipper sides could look the same in plesiosaurs is unsubstantiated by the EPB, as dorsal and ventral fore- and hindlimb musculature of extant Sauropsida is not symmetrical (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki et al., 2011). The distal plesiosaur fore- and hindflipper musculature reconstructed by Robinson (1975) looks very similar to the cetacean foreflipper musculature in terms of how extremely reduced it is (Cooper et al., 2007). This whale-like state appears unlikely for plesiosaurs, as cetacean foreflippers are merely control surfaces and not hydrofoils (Fish, 2002; Woodward, Winn & Fish, 2006) while the main propulsive organ of whales is a large muscular swimming tail with a fluke (Fish, 1996; Woodward, Winn & Fish, 2006). Contrastingly, plesiosaurs actively swam with their fore- and hindflippers (Krahl chapter 1). Krahl and Witzel (chapter 3) are the first who reconstructed the entire locomotor musculature of a plesiosaur fore- and hindflipper.

They reconstructed a complex array of muscles for fore- and hindflipper of plesiosaurs which enables the plesiosaur to twist both its flipper pairs along the flipper length and maybe even actively control the flipper profile, as hydrodynamic computations of plesiosaurs by Witzel, Krahl & Sander (2015) suggest.

1.1.3 Plesiosaur locomotion

The locomotory style of plesiosaurs has been an ongoing debate since over one century (Williston, 1914; Watson, 1924; Tarlo, 1958; Robinson, 1975, 1977; Feldkamp, 1987; Lingham-Soliar, 2000; Carpenter et al., 2010; Araújo et al., 2015; Araújo & Correia, 2015; Liu et al., 2015; Krahl and Witzel (chapter 3)). It has been suggested that plesiosaurs row like ducks or otters (Williston, 1914; Watson, 1924; Tarlo, 1958; Araújo et al., 2015; Araújo & Correia, 2015), fly underwater like sea turtles and penguins (Robinson, 1975, 1977; Lingham-Soliar, 2000; Carpenter et al., 2010; Liu et al., 2015; Krahl and Witzel (chapter 3)), or use rowing-flight like sea lions (Feldkamp, 1987; Liu et al., 2015). The main difference between the different locomotory styles results from the underlying hydrodynamics: In rowing, water drag is used to push the body forward while in underwater flight, lift produced by the onflowing water travelling around a cambered flipper profile is used (e.g., Baudinette & Gill, 1985; Fish, 1996; Walker & Westneat, 2000). The rowing-flight of sea lions relies on both hydrodynamic mechanisms, drag-based and lift-based, at different phases of the limb cycle (Feldkamp, 1987). It was also proposed that the foreflipper pairs employ a different mode of locomotion (Tarlo, 1958; Lingham-Soliar, 2000; Liu et al., 2015).

A flipper used in rowing is mostly moved in anteroposterior direction with little dorsoventral motion (Pace, Blob & Westneat, 2001; Rivera, Rivera & Blob, 2011; Rivera, Rivera & Blob, 2013). The anteroposterior expansion and the dorsoventral reduction of the bony elements of the plesiosaur pectoral and pelvic girdle, as well as the accompanying reduction or hypertrophy of locomotory muscles have been interpreted as being in favor for protraction and retraction of the flipper, i.e., a rowing motion (Watson, 1924; Tarlo, 1958; Godfrey, 1984).

Contrastingly, during underwater flight, the flipper is beaten mainly in dorsoventral direction with a minor anteroposterior component. The flipper downstroke of Chelonioidea and Spheniscidae is characterized by major depression and minor retraction of the flipper. The upstroke is performed by humeral elevation and protraction. The flipper tip describes a skewed “O” in anterodorsal-posteroventral direction (Clark & Bemis, 1979; Davenport, Munks & Oxford, 1984; Rivera, Wyneken & Blob, 2011; Rivera, Rivera & Blob, 2013). As

Robinson (1975) noted, the hydrofoil-shaped flippers of plesiosaurs, tapering towards the tip, superficially comparable to that of penguins and sea turtles, imply that they were used for underwater flight and not for rowing. Also, the glenoid and acetabular shape of plesiosaurs restrict movement in anteroposterior direction more than in dorsoventral direction (Krahl (chapter 1)).

During rowing flight, the downstroke is lift-generating and similar to the downstroke of the underwater fliers. At the point of maximum flipper depression, the flipper is turned around like a paddle and pushes against the water during its retraction and elevation. During the recovery stroke, the flipper is brought back anteriorly and dorsally, possibly also producing propulsion by lift (Feldkamp, 1987). Godfrey (1984) found that in recent underwater fliers, the shoulder girdles are characterized by a strong bony support expanding in the dorsoventral direction, which is not present in plesiosaurs. Therefore, he noted that there is more similarity between sea lions and plesiosaurs than with recent “true” underwater fliers (Godfrey, 1984).

Besides the locomotory style, it is still being discussed how the four flippers were moved in relation to each other, i.e., fore- and hindflipper synchronously, asynchronously, or out of phase. This debate is based on the so called four-wing problem which addresses how plesiosaurs avoided placing their hindflippers into the vortices shed by their foreflippers which would mean a considerable performance decrease of the hindflippers (Frey & Riess, 1982; Tarsitano & Riess, 1982; Lingham-Soliar, 2000; Carpenter et al., 2010; Muscutt et al., 2017).

1.2 Muscle physiology

During a limb motion cycle, muscles may follow either a shortening-stretch cycle or a stretch-shortening cycle. During the former, the muscle is shortened while its force output increases. Then, the muscle is stretched and the force output decreases. During the latter, the muscle is stretched at the beginning while its force output increases. When the muscle contracts, its force output drops (Rassier, MacIntosh & Herzog, 1999). Muscle force production depends on muscle architecture. Muscle architecture includes muscle length and tendon (if present) length, lines of action, muscle mass, specific density of muscle, intrinsic muscle strength, fascicle length, and pennation angles (Alexander & Vernon, 1975; Gans, 1982; Sacks & Roy, 1982; Powell et al., 1984; Narici, Landoni & Minetti, 1992; Anapol & Barry, 1996; Kummer, 2005; Azizi, Brainerd & Roberts, 2008). Parallel-fibred muscles have on average longer fascicles, a larger volume, and can contract faster (which depends on the fibre type composition) than pennate muscles. However, more muscle fibres can be arranged adjacently to each other in a pennate muscle than in a parallel-fibred muscle of the same size. Thus, a pennate muscle can exert a higher force than a same-sized parallel-fibred muscle, although the pennate muscle has shorter fibres. This is so because the exerted maximum muscle force does not only depend on the fibre length but also on the physiological cross sectional area (PCSA), i.e., the sum of fibre cross sections (Gans, 1982; Burkholder et al., 1994; Allen et al., 2010; Huq, Wall & Taylor, 2015).

Also, muscle length of a parallel-fibred, fast contracting muscle (or one close to it) varies substantially and is traded off for a high metabolic intake and a relatively low force production. Contrastingly, strongly pennated muscles exert relatively high forces at markedly lower metabolic costs but are much slower contracting and have poor fibre contraction control (Biewener & Roberts, 2000).

Pennate muscles may develop relatively high forces while their muscle lengths behave almost isometrically (e.g., turkey (musculus (m.) gastrocnemius) (Roberts et al., 1997) or wallaby (m. gastrocnemius, m. plantaris) (Biewener, Konieczynski & Baudinette, 1998). Contrastingly, the fan-shaped m. pectoralis, which has a very high initial power output, shows a very great muscle length change of 30-40% for *Columba liva* (Biewener, Corning & Tobalske, 1998; Biewener & Roberts, 2000) or approximately 30% for *Anas platyrhynchos* (Williamson, Dial & Biewener, 2001). Generally, muscle length change of vertebrate striated muscle may span up to +/- 25% (contraction and stretching in relation to resting length (=0%)) before its capability to generate force drops markedly (Biewener & Roberts, 2000).

1.3 Finite element structure analysis

As strain gauge measurements demonstrate, long bones of Tetrapoda are functionally loaded fluctuatingly by torsion, compression, and bending (Biewener & Dial, 1995; Carrano, 1998; Blob & Biewener, 1999; Lieberman, Polk & Demes, 2004; Main & Biewener, 2004, 2007; Butcher et al., 2008; Butcher & Blob, 2008; Sheffield et al., 2011; Young & Blob, 2015; Young et al., 2017). They are mostly loaded by bending in alternating directions or primarily by compression and subordinately by tension (Biewener & Dial, 1995; Blob & Biewener, 1999; Lieberman, Polk & Demes, 2004; Main & Biewener, 2004; Butcher et al., 2008; Butcher & Blob, 2008; Sheffield et al., 2011). High torsional loads are imposed on terrestrial tetrapod long bones (Biewener & Dial, 1995; Carrano, 1998; Blob & Biewener, 1999; Main & Biewener, 2004, 2007; Butcher et al., 2008; Butcher & Blob, 2008; Sheffield et al., 2011).

To reflect such changing loading conditions, a number of loadcases can be analyzed with finite element structure analysis (FESA; Witzel & Preuschoft, 2005) and then be superimposed on each other (Carter, Orr & Fyhrie, 1989). By reducing the bending moment (Klenner et al., 2015; Lutz et al., 2016; Milne, 2016; McCabe et al., 2017; Lipphaus & Witzel, 2018), biological lightweight structures may evolve (Klenner et al., 2015). FESA is used in different disciplines encompassing engineering sciences and biomechanics (Rayfield, 2007). FESA allows analysis of mechanical stresses and strains in technical and biological structures in 2-D or 3-D (Rayfield, 2007; Witzel et al., 2011) and may add to our understanding of the function of bony elements (Witzel et al., 2011). Compressive loads are applied to the bone via tension chords. Tension chords are either muscles (active tension chord) or ligaments (passive tension chords), and they act in pairs of agonists and antagonists (Witzel & Preuschoft, 2005; Sverdlova & Witzel, 2010; Curtis et al., 2011; Witzel et al., 2011; Klenner et al., 2015; Felsenthal & Zelzer, 2017). A movement is powered by the agonist while the antagonist opposes it to fulfill a controlled movement (Sverdlova & Witzel, 2010). If the same movement is inverted, the agonist becomes the antagonist and vice versa. Thus, agonists and antagonists load a bony structure constantly by compressive stress, although the agonist is exerting proportionally a higher force than the antagonist.

The aim of this study was to test plesiosaur muscle reconstructions with FESA. So the muscle reconstructions obtained with the EPB, i.e., based on comparative anatomical studies, were cross-checked with the mechanically imposed demands on muscles. We evaluated how muscle physiological details, such as muscle length changes can contribute to muscle reconstructions of fossils and whether FESA of the plesiosaur humerus and femur can inform on plesiosaur locomotion. The results complement earlier hydrodynamic studies that implied that plesiosaurs must have used flipper twisting for efficient underwater flight (Witzel, Krahl & Sander, 2015) and corroborate the myological flipper twisting mechanism reconstructed by Krahl and Witzel (chapter 3).

2. Material and Methods

2.1 Analog model of lines of action

Lines of action (LOA) represent the direct connection in a straight line between a muscle's origin and insertion (Krahl et al. (chapter 2)). They were experimentally attained in an analog model (Fig. 1) with the help of casts of the pectoral (Fig. 2, 3) and pelvic girdle and limbs (Fig. 4, 5) of the *Cryptoclidus eurymerus* specimen (IGPB R 324) on exhibition in the Goldfuß Museum, Division of Paleontology, Institute of Geosciences, Rheinische Friedrich-

Wilhelms-Universität Bonn. The casts of the pectoral and pelvic girdle were mounted on a wooden frame and fixed with screws. In place of the vertebral column, which also serves as origin of locomotory muscles, wooden bars were screwed. The anatomical positioning of the casts and the vertebral column are based on the mounting of IGPB R 324. Thick styrofoam was used to replace the missing cartilage capping in the shoulder and hip joint. The fore- and hindflipper were hung into the construction and the respective joint with the help of the muscle lines of action. Supportively, the flippers were fixed by additional ropes in the chosen flipper positions (Fig. 1).

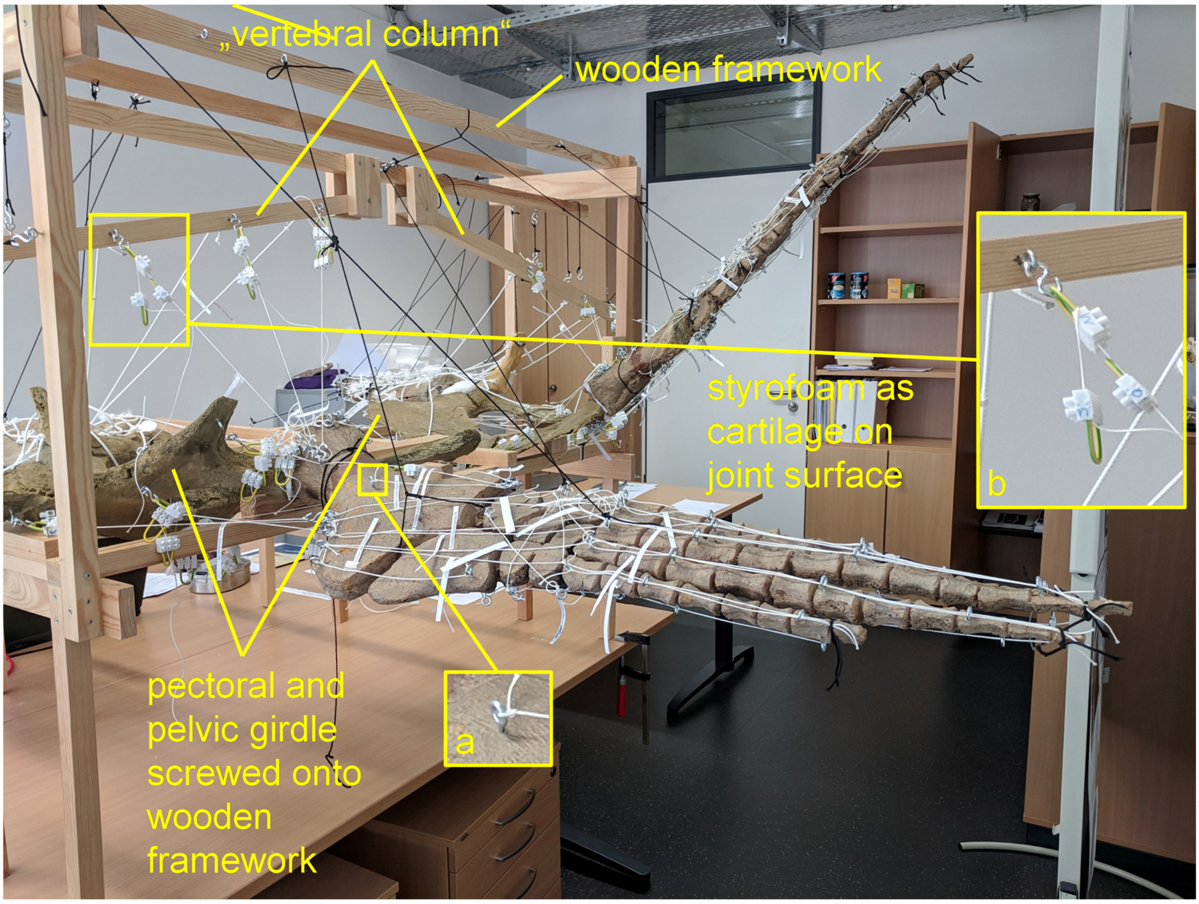

Fig. 1: Analog model demonstrating LOA of *Cryptoclidus eurymerus* (IGPB R 324) fore- and hindflipper. Pectoral and pelvic girdle were fixed on a wooden frame. Thick styrofoam was placed into the glenoid and acetabulum joint cavity. Black threads helped to fix the flippers in their respective position. White threads represent LOA: a) screw eye pins were screwed into muscle attachment surfaces. Three electrical terminal strips were attached to one end. With hooks attached to each end of the thread, LOA were hung into the screw eye pins.

To physically model the lines of action, non-elastic thread was used. Screw eye pins were screwed into the cast at the muscle origin and insertion surfaces. Muscle attachments of all locomotory muscles of the fore- and hindflipper that span either glenoid or acetabulum (12 on foreflipper, 14 on hindflipper) were adopted from Krahl and Witzel (chapter 3). Each thread was strung through three electrical terminal strips. Next, hooks were tied to both ends of the threads, which were then hooked into the screw eyes representing muscle origins and insertions (Fig. 1). If a muscle attachment surface is small, the screw eye pin was screwed approximately in the middle of it. Contrastingly, muscles with large attachment areas were subdivided into several subportions to better encompass the varying fiber insertion angles and directions and to obtain more evenly distributed compressive stresses in the FE models. Correspondingly, the total muscle force of a muscle was subdivided, too, and fractions of the total muscle force were assigned to the subportions. Usually, the most anterior and posterior points in the body midline were chosen for placement of the screw eye pins (e.g., m. subcoracoscapularis, m. coracobrachialis brevis, m. pectoralis). In the case of, e.g., m. latissimus dorsi, a position in between the cranialmost and caudalmost origin was chosen. This is done in order to represent those portions that are supported the best by EPB (cranial and middle portion) but also to cover the less well supported portion (caudal) (Krahl and Witzel (chapter 3)).

These subportions do not necessarily represent actual partitions of the reconstructed muscles, although some muscles may have likely been compartementalized, e.g., m. pectoralis, m. latissimus dorsi, m. puboischiofemoralis internus, and m. puboischiofemoralis externus. Muscles with two or more heads (i.e., m. deltoideus scapularis, m. deltoideus clavicularis, m. coracobrachialis brevis, m. coracobrachialis longus, m. triceps brachii, m. caudifemoralis brevis (ilium and vertebral column), m. flexor tibialis internus, m. flexor tibialis externus, m. puboischiofemoralis internus, and m. puboischiofemoralis externus were assigned two (or more) threads. The resultant vector of the various subportions of those muscles that have a large origin area went into the FE models. Agonistically and antagonistically acting muscles that insert into, originate from, or span the humerus (Tab. 2) and femur (Tab. 3) were devised from the mount. Pictures were taken for documentation from cranial/anterior (Fig. 2 a-f; Fig. 4 a-f), caudal/posterior (Fig. 3 a-f; Fig. 5 a-f), ventral (Fig. 2 g, h; Fig. 4 g, h) and dorsal (Fig. 3 g, h; Fig 5 g, h). Limb cycle movement terminology follows Rivera, Wyneken & Blob (2011) and Krahl and Witzel (chapter 3) who used humeral and femoral depression, elevation, protraction, and retraction, which reflect the requirements for underwater flight well.

2.2 Changes in muscle length

Three positions in the fore- and hindflipper beat cycle were chosen to measure the total muscle length change for muscles that originate on the pectoral and pelvic girdle or the vertebrae and insert into or span the humerus and femur. These positions are the maximum dorsal excursion of the fore-/hindflipper during the upstroke (~ +50° to the horizontal) (Fig. 2 a, b; Fig. 3 a, b; Fig. 4 a, b; Fig. 5 a, b), maximum ventral excursion of the fore-/hindflipper during the downstroke (~ -50°) (Fig. 2 e, f; Fig. 3 e, f; Fig. 4 e, f; Fig. 5 e, f), and the neutral position (0°) (Fig. 2 c, d; Fig. 3 c, d; Fig. 4 c, d; Fig. 5 c, d). Based on the orientation of glenoid and acetabulum, the tip of the foreflipper points slightly forward, the hindflipper tip points slightly backward. Protraction and retraction were not considered because, based on the osteology, they contribute minorly to the flipper beat cycle. Also, in this study we examined basically whether or not total muscle length changes may add value for muscle reconstructions of extinct vertebrates.

Flipper range of motion has been determined before by Carpenter et al. (2010) and Liu et al. (2015) for various plesiosaur species, but the results depend greatly on how much cartilage is presumed to have been capping the humerus and femur and the glenoid and acetabulum, as indicated by Liu et al. (2015), and on the species (which differ in size of the dorsal tuberosity/trochanter). The authors presumed that the humeral and femoral head of *Cryptoclidus* (IGPB R 324) were capped by thick vascularized cartilage comparable to that described for *Dermochelys coriacea* (Rhodin, Ogden & Conlogue, 1981; Snover & Rhodin, 2008). This is based on the observation that the proximal bone surfaces of both, the humerus and femur of *Cryptoclidus* (IGPB R 324), are pierced by large vascular canals and are very similar looking to the proximal humeral head of *Dermochelys* (Rhodin, Ogden & Conlogue, 1981; Snover & Rhodin, 2008) (Krahl (chapter 1)).

The authors refrained from calling the neutral flipper position the resting position of the flipper because it is probably impossible to determine the flipper resting position for an extinct species. Furthermore, in the muscle physiological literature, the term „resting length“ usually refers to individual sarcomeres (Rassier, MacIntosh & Herzog, 1999) or fascicles of a muscle (Biewener & Roberts, 2000). Moreover, not to know the exact flipper resting length influences the exact value of muscle stretching and contraction but not the end result of total length change of a muscle which was calculated in this study (s. below). This is because the absolute values of muscle stretching and contraction are measured in relation to the neutral position but the total muscle length change is the difference between maximum muscle stretching and contraction.

All three positions of the fore- and hindflipper were successively fixed with ropes suspended from the wooden frame holding the casts. For each of the three states, the optimal length of each muscle was fixed with the help of the terminal strips. Afterwards, each muscle was removed and all three muscle lengths, i.e., maximum excursion during downstroke, neutral position, and maximum excursion during downstroke were measured with a measuring tape in cm. Length changes between maximum excursion at downstroke and the neutral position as well as between maximum excursion at upstroke and the neutral position were expressed first in cm and then in %, by setting resting length as 100%. Next, muscle stretching, muscle contraction, and the difference between both, the total length change of muscle, were calculated in % (Tab. 1). Bar graphs for total muscle length changes in % were plotted with Microsoft Excel (Fig. 6 b). Some muscle length changes were recorded as 0 cm because the actual changes in length could not be measured because they were smaller than the width of the terminal strips. In one case, i.e., m. deltoideus scapularis, it was found that the total muscle length change with an insertion on the lateral scapula blade was unphysiologic (see chapter 3.3.1.1.), another origin area (from the ventrolateral scapula) was tested and shown to give physiologically plausibel results that were then measured for all three positions.

2.3 FESA and muscle force determination by computation

The right humerus and left femur of IGPB R 324 were scanned with the micro-CT scanner at the author's institution with an industrial high-resolution computed tomography (µCT) scanner (model phoenix v|tome|x s 240, produced by General Electric Phoenix X-ray, Wunstorf, Germany). The scans were processed with the dedicated software datos|x and the program VGStudio MAX (Volume Graphics) to obtain image stacks in the z direction.

The image stack was loaded into Simpleware ScanIP 5.1 (Krahl et al. (chapter 2)) for further processing. For each image, the bone tissue was selected and segmented out with the help of grey scale intervals and a 3D mesh model was generated. Next, the model was imported into ANSYS 16.0 (ANSYS Inc., Canonsberg, PA, USA). The measured dimensions of the humerus and femur of IGPB R 324 were used to scale the respective volumetric model. Next, proximal articular cartilage, respectively the glenoid/acetabular articulation surface, were modelled. The FE models were created with the element type SOLID92. The humerus

Musculus	number coding for muscle (portion) in respective diagram	maximum ventral excursion [cm]	neutral position [cm]	maximum dorsal excursion [cm]	muscle length change (- = shortening, + = lengthening) from neutral position to maximum ventral excursion [cm]	muscle length change (- = shortening, + = lengthening) from neutral position to maximum ventral excursion [%]	muscle length change (- = shortening, + = lengthening) from neutral position to maximum dorsal excursion [cm]	muscle length change (- = shortening, + = lengthening) from neutral position to maximum dorsal excursion [%]	muscle stretching = muscle neutral position (=100%) + muscle lengthening [%]	muscle contraction = muscle neutral position (=100%) - shortening of muscle [%]	total length change of muscle [%] (= muscle stretching - muscle contraction)
m. deltoideus scapularis	1	22,2	13,6	9,8	8,6	63,24	-3,8	-7,63	163,24	92, 37	70,87
m. deltoideus scapularis corrected	2	22,6	22,6	22,6	0	0	0	0	100	100	0
m. deltoideus clavicularis	3	36,5	36,5	36,5	0	0	0	0	100	100	0
m. latissimus dorsi (anterior)	4	42,7	34,9	29,8	7,8	22,35	-5,1	-14,61	122,35	85,39	36,96
m. latissimus dorsi (in between)	5	43,9	37,6	32,6	6,3	16,76	-5	-13,3	116,76	86,7	30,06
m. latissimus dorsi (posterior)	6	52,7	47,9	42,2	4,8	10,02	-5,7	-11,9	110,02	88,1	21,92
m. subcoracoscapularis (anterior portion)	7	32,8	29,3	24,3	3,5	11,95	-5	-17,06	111,95	82,94	29,01
m. subcoracoscapularis (posterior portion)	8	36,3	33,2	33,2	3,1	9,34	0	0	109,34	100	9,34
m. scapulohumeralis anterior	9	30,9	29,5	27,4	1,4	4,75	-2,1	-7,12	104,75	92,88	11,87

m. scapulohumeralis posterior	10	24,9	22,7	19,4	2,2	9,69	-3,3	-14,54	109,69	85,46	24,23
m. coracobrachialis brevis (anterior)	11	29,3	36,7	40,5	-7,4	-20,16	3,8	10,35	110,35	79,84	30,51
m. coracobrachialis brevis (posterior)	12	43,8	43,8	45,5	0	0	1,7	3,88	103,88	100	3,88
m. coracobrachialis longus	13	43,1	52	53,9	-8,9	-17,12	1,9	3,65	103,65	82,88	20,77
m. pectoralis (anterior)	14	29,9	30,4	35,6	-0,5	-1,64	5,2	17,11	117, 11	98,36	18,75
m. pectoralis (posterior)	15	27,4	33,1	39,2	-5,7	-17,22	6,1	18,43	118,43	82,78	35,65
m. supracoracoideus	16	24,5	31,7	31,7	-7,2	-22,71	0	0	100	77,29	22,71
m. biceps brachii	17	56,7	67,8	72,4	-11,1	-16,37	4,6	6,78	106,78	83,63	23,15
m. triceps brachii (anterior)	18	36,8	36,8	36,8	0	0	0	0	100	100	0
m. triceps brachii (posterior)	19	31,2	31,2	31,2	0	0	0	0	100	100	0

Musculus	number coding for muscle (portion) in respective diagram	maximum ventral excursion [cm]	neutral position [cm]	maximum dorsal excursion [cm]	muscle length change (- = shortening, + = lengthening) from neutral position to maximum ventral	muscle length change (- = shortening, + = lengthening) from neutral position to maximum ventral excursion [%]	muscle length change (- = shortening, + = lengthening) from neutral position to maximum dorsal excursion [cm]	muscle length change (- = shortening, + = lengthening) from neutral position to maximum dorsal excursion [%]	muscle stretching = muscle neutral position (=100%) + muscle lengthening [%]	muscle contraction = muscle neutral position (=100%) - shortening of muscle [%]	total length change of muscle [%] (= muscle stretching - muscle contraction)

					excursion [cm]						
m. caudofemoralis longus	1	61,3	63,5	64,6	-2,2	-3,46	1,1	6,15	106,15	96,54	9,61
m. caudofemoralis brevis (ilium)	2	17,9	17,9	17,9	0	0	0	0	100	100	0
m. caudofemoralis brevis (vc)	3	37,6	36,9	33,6	0,7	1,9	-3,3	-8,94	101,9	96,7	5,2
m. flexor tibialis internus (vc)	4	63,7	58,4	52,3	5,3	9,8	-6,1	-10,45	109,8	93,9	15,9
m. flexor tibialis internus (ischium)	5	43,1	47,1	49,2	-4	-8,49	2,1	4,46	104,46	91,51	12,95
m. flexor tibialis externus (ischium)	6	42,8	47,5	49,4	-4,7	-9,89	1,9	4	104	90,11	13,89
m. flexor tibialis externus (ilium)	7	42,6	37,2	31,9	5,4	14,52	-5,3	-14,25	114,52	85,75	28,77
m. iliofibularis	8	33,1	29	25,3	4,1	14,13	-3,7	-12,76	114,13	87,24	26,89
m. ambiens	9	29,3	29,3	31,7	0	0	2,4	8,19	108,19	100	8,19
m. puboischiotibialis	10	38,3	42,3	45,8	-4	-9,46	3,5	8,27	108,27	90,54	17,73
m. pubotibialis	11	33,4	33,4	33,4	0	0	0	0	100	100	0
m. iliofemoralis	12	18,3	14,2	13,6	4,1	28,87	-0,6	-4,23	128,87	95,77	33,1
m. ischiotrochantericus	13	21,5	21,5	23,7	0	0	2,2	10,23	110,23	100	10,32
m. iliotibialis	14	40,1	26,6	26,6	7,3	27,44	0	0	127,44	100	27,44
m. adductor femoris (anterior)	15	30,4	32,8	36,2	-2,4	-7,31	3,4	6,71	106,71	92,69	14,02
m. adductor femoris (lateroposterior)	16	26,6	30	32,9	-3,4	-11,33	2,9	9,67	109,67	88,67	21

m. puboischiofemoralis internus (pubis)	17	36,8	32,3	30,3	4,5	14,85	-2	-6,19	114,85	93,81	21,04
m. puboischiofemoralis internus (ischium)	18	29,4	27,2	23,3	2,2	8,09	-3,9	-14,34	108,09	85,66	22,43
m. puboischiofemoralis internus (ilium)	19	10,4	9,5	9,5	0,9	9,47	0	0	109,47	100	9,47
m. puboischiofemoralis internus (vertebral column)	20	39,6	32,1	28,1	7,5	23,36	-4	-12,46	123,36	87,54	35,82
m. puboischiofemoralis externus (pubis)	21	39,1	42,5	45,7	-3,4	-8	3,2	7,5	107,5	92	15,5
m. puboischiofemoralis externus (ischium)	22	22,9	27,6	29,4	-4,7	-17,03	1,8	6,52	106,52	82,97	23,55

Tab. 1: Changes in length of *Cryptoclidus eurymerus* (IGPB R 324) humerus and femur muscles.

model consists of 92665 elements and the femur model of 75784 elements. In the humerus, the cartilaginous articular structure is formed by 19927 elements and by 15472 elements in the femur. Bearings were placed on all nodes of the proximal surface of the cartilage models for a different research project which will not be addressed further in the current study. In both FE models, bone was modelled with a Young's modulus of 12000 Mpa and cartilage with a Young's modulus of 5 Mpa.

LOA and attachment angles were figured in sketches of humerus (Fig. 7 a) and femur (Fig, 7 e) in anterior, posterior, dorsal, and ventral view that were implemented in the FE models as vectors (Fig. 7 b, f). Two- or more headed muscle bellies were entered in the FE model in form of the resultant vector. Two-joint muscles add to the counterforce. Radius and ulna/tibia and fibula exert the counterforce on the epicondyles of the humerus and femur. Two-joint muscles of the foreflipper are the m. triceps brachii and the m. biceps brachii. Two-joint muscles of the hindflipper are the m. ambiens, m. pubotibialis, m. flexor tibialis externus, m. flexor tibialis internus, m. iliotibialis, m. iliofibularis, and m. puboischiotibialis. As it is impossible to perform curved vectors in ANSYS 16.0., muscle wrappings were modelled by dividing their lines of action into several smaller straight vectors.

The force transmission on the distal articular surfaces of humerus and femur due to muscular activity was first applied in one point. This resulted in very high localized stress peaks. Therefore, force transmission was split up into several application points scattered over the distal articulation surfaces to receive a more realistic simulation of the load transmission via a surface.

Forces of each humerus and femur muscle were approximated stochastically. The distribution of compressive stress was computed for both long bones (Fig. 7, c, d, g, h). Then, another run was prepared by maximizing compressive stresses and minimizing bending moments. These steps were repeated until a homogenous compressive stress distribution was obtained. This way, muscle forces were iteratively approximated (Tab. 3 and Tab. 4) (Witzel & Preuschoft, 2005; Sverdlova & Witzel, 2010).

2.4 Load case generation

Two load cases, downstroke and upstroke, were chosen to be computed to reflect the constantly varying loading regime of humerus and femur during the flipper beat cycle. For both load cases, a position was chosen in which the humerus is held horizontally at the level of the glenoid pointing laterally and slightly anteriorly, as indicated by the analog model. Similarly, the femur was positioned horizontally at the level of the acetabulum. Its flipper tip points mostly laterally but is also slightly angulated posteriorly. During the downstroke, the humerus and femur were rotated anteriorly downward along their long axis by approximately 19° (Witzel, Krahl & Sander, 2015). During the upstroke, the humerus and femur were rotated back and about 19° posteriorly downward around their long axis (Witzel, Krahl & Sander, 2015).

For the implementation of load cases, it is crucial to identify and consider which muscles act as agonists and antagonists (Witzel & Preuschoft, 2005). Muscle functions for identification of agonists and antagonists (Tab. 2 and Tab. 3) are taken from Krahl and Witzel (chapter 3). The downstroke load case is powered mainly by the humeral and femoral depressors, but also by retractors and those muscles enabling a slight downward rotation of the flipper leading edges. Flexors arising from the humerus and femur are active during the downstroke, flexing the digits and contributing to the twisting of the foreflipper and hindflipper along the flipper lengths. The upstroke load case is powered largely by humeral and femoral elevators. Humeral and femoral protraction and rotation of the flipper leading edge upward add to the upstroke as well. The extensors which originate from the distal humerus and femur aid in flipper twisting and extension of the digits during the upstroke (Krahl and Witzel (chapter 3)).

3. Results

3.1 Mechanically controlled plesiosaur muscle reconstructions

3.1.1 Humerus musculature

Humerus muscles that were reconstructed on a biological basis (Krahl and Witzel (chapter 3)) are counterchecked for their functionality on a mechanical basis. Musculus deltoideus scapularis was reconstructed on the anteroventral scapula posterior to m. deltoideus clavicularis and anteriorly to m. supracoracoideus and on the lateral median scapular blade. Here we can confidently reject an origin from the blade, as a total muscle length change of 70% suggests extreme muscle shortening that it is physiologically impossible (s. chapter 3.3.2) (Fig. 6 a; Tab. 1).

Myological reconstruction suggests an m. biceps brachii origin on the posterior ventral coracoid. Musculus biceps brachii and m. brachialis could either insert via a shared tendon into the proximal radius or into the posteroproximal radius and the anteroproximal ulna. Further, m. triceps brachii originates anteriorly to anterodorsally from the bony ridge surrounding the glenoid on the scapula and from the coracoid just posterior to the glenoid and inserts (well substantiated by the EPB) into the posterodorsal ulna. The posterodorsal ulnar insertion of m. triceps brachii is unquestionable based on the EPB, and the posterior origin of m. biceps brachii is quite well supported as well. In contrast, origin areas of m. triceps brachii are debatable as well as the insertion area of m. biceps brachii and m. brachialis. This lead to interesting mechanical assumptions: our FESA was much improved when the m. biceps brachii/m. brachialis insertion was placed on the proximal and ventral radius and when the m. triceps brachii origin anterior to anterodorsally to the glenoid facet was more pronounced by a higher muscle force. An origin of the m. triceps brachii from the coracoid provides only a little to no lever arm and was therefore possibly reduced or lost.

Myological reconstruction suggests the insertions of m. coracobrachialis brevis and m. coracobrachialis longus due to the presence of osteological correlates on the posterior to posteroventral humeral shaft as observed in lepidosaurs (Russell & Bauer, 2008). This decision is not well supported by the EPB which would rather suggest an insertion ventrally into the intertrochanteric fossa as seen in turtles and crocodilians (Walker, 1973; Meers, 2003; Suzuki & Hayashi, 2010). A shift of their humeral insertions further distally along the shaft, is mechanically favorable as it increases the lever arms and took place comparably in Cheloniidae (Walker, 1973; Krahl et al. (chapter 2)).

Musculus scapulohumeralis anterior was not reconstructed based on myology because this muscle is only present in lepidosaurs and therefore weakly supported by EPB. However, we formulate a description and a reconstruction of this muscle below, because it adds a needed proximal rotatory component to the humeral locomotory musculature. Musculus scapulohumeralis anterior has no synonyms and is only reported for Lepidosauria (Russell & Bauer, 2008). Musculus scapulohumeralis anterior has two portions which originate from the anterior ventrolateral scapula and from the posterolateral scapula, dorsal to the glenoid (in *Varanus exanthematicus*, *Iguana iguana*; Jenkins & Goslow, 1983; Russell & Bauer, 2008). For plesiosaurs, it is reconstructed to originate on the anterior edge of the lateral scapula, on the base of the scapular blade and on the posterior edge of the scapular blade. The lines of action support the latter origin because the former would result in a wrapping of m. scapulohumeralis anterior around the lateral scapular blade and around the musculature that suspends the pectoral girdle from the trunk, which seems rather unlikely. Yet, the origin on the posterior scapular blade would also only be able to support a very small muscle belly because the scapular blade is very much reduced in comparison to archosaurs, lepidosaurs, and turtles in general (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). This means m. scapulohumeralis anterior is expected to contribute with a relatively low muscle force to propulsion.

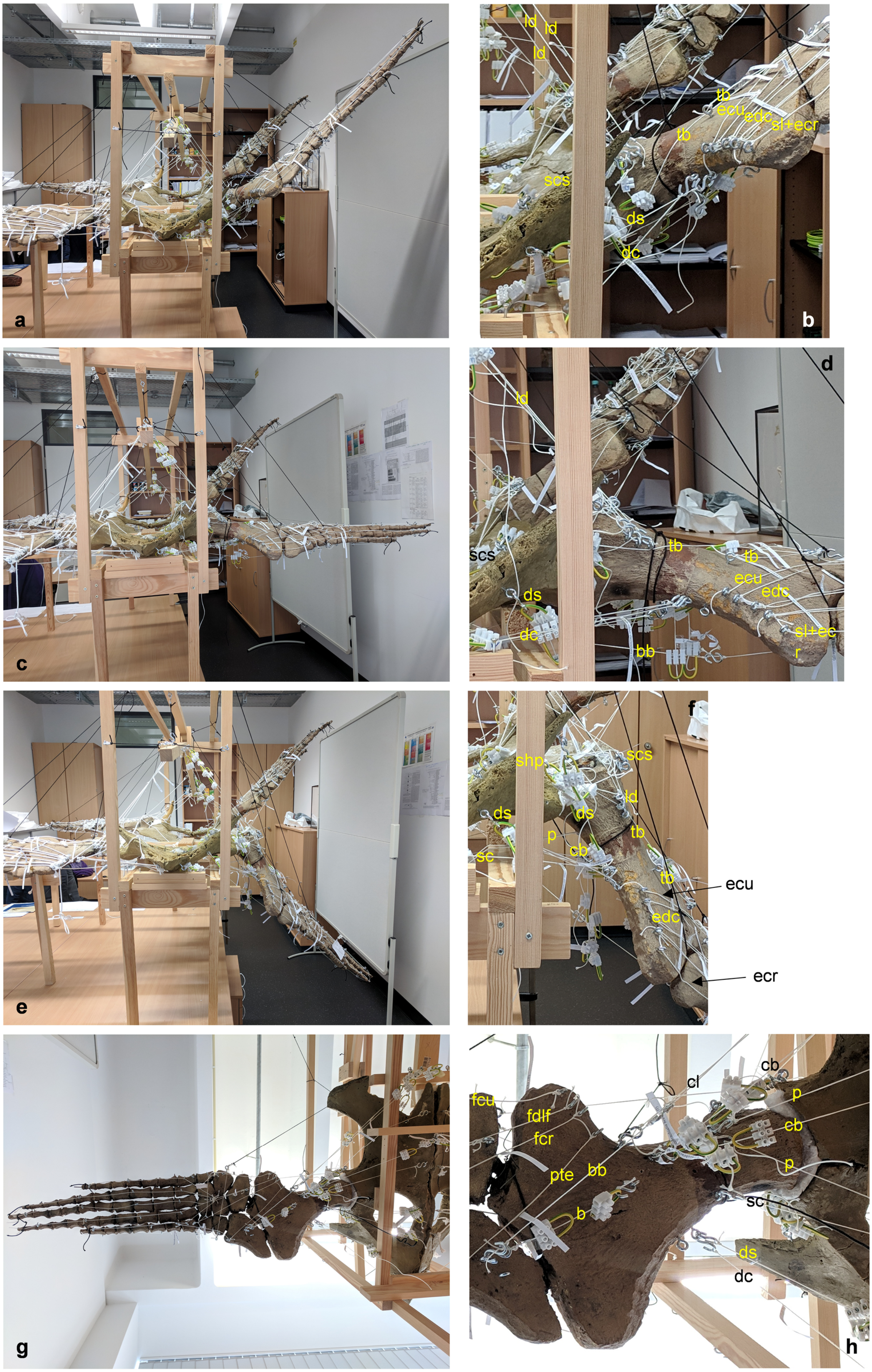
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Fig. 2: LOA of *Cryptoclidus eurymerus* (IGPB R 324) foreflipper in anterior and ventral view. Pictures on the left (a, c, e, g) show an overview over all flipper muscles. Pictures on the right focus on the humerus muscles. a) and b) during maximum dorsal excursion in anterior view. c) and d) in the neutral position in anterior view. e) and f) during maximum ventral excursion in anterior view. g) and h) ventral view of the neutral foreflipper position. Abbreviations: b, Musculus brachialis; bb, Musculus biceps brachii; cb, Musculus coracobrachialis brevis; cl, Musculus coracobrachialis longus; dc, Musculus deltoideus clavicularis; ds, Musculus deltoideus scapularis; ecu, Musculus extensor carpi ulnaris; edc, Musculus extensor digitorum communis; fcr, Musculus flexor carpi radialis; fcu, Musculus flexor carpi ulnaris; fdlf, Musculus flexor digitorum longus (foreflipper); ld, Musculus latissimus dorsi; p, Musculus pectoralis; pte, Musculus pronator teres; sc, Musculus supracoracoideus; scs, Musculus subcoracoscapularis; shp, Musculus scapulohumeralis posterior; sl and ecr, Musculus supinator longus and Musculus extensor carpi radialis; tb, Musculus triceps brachii.

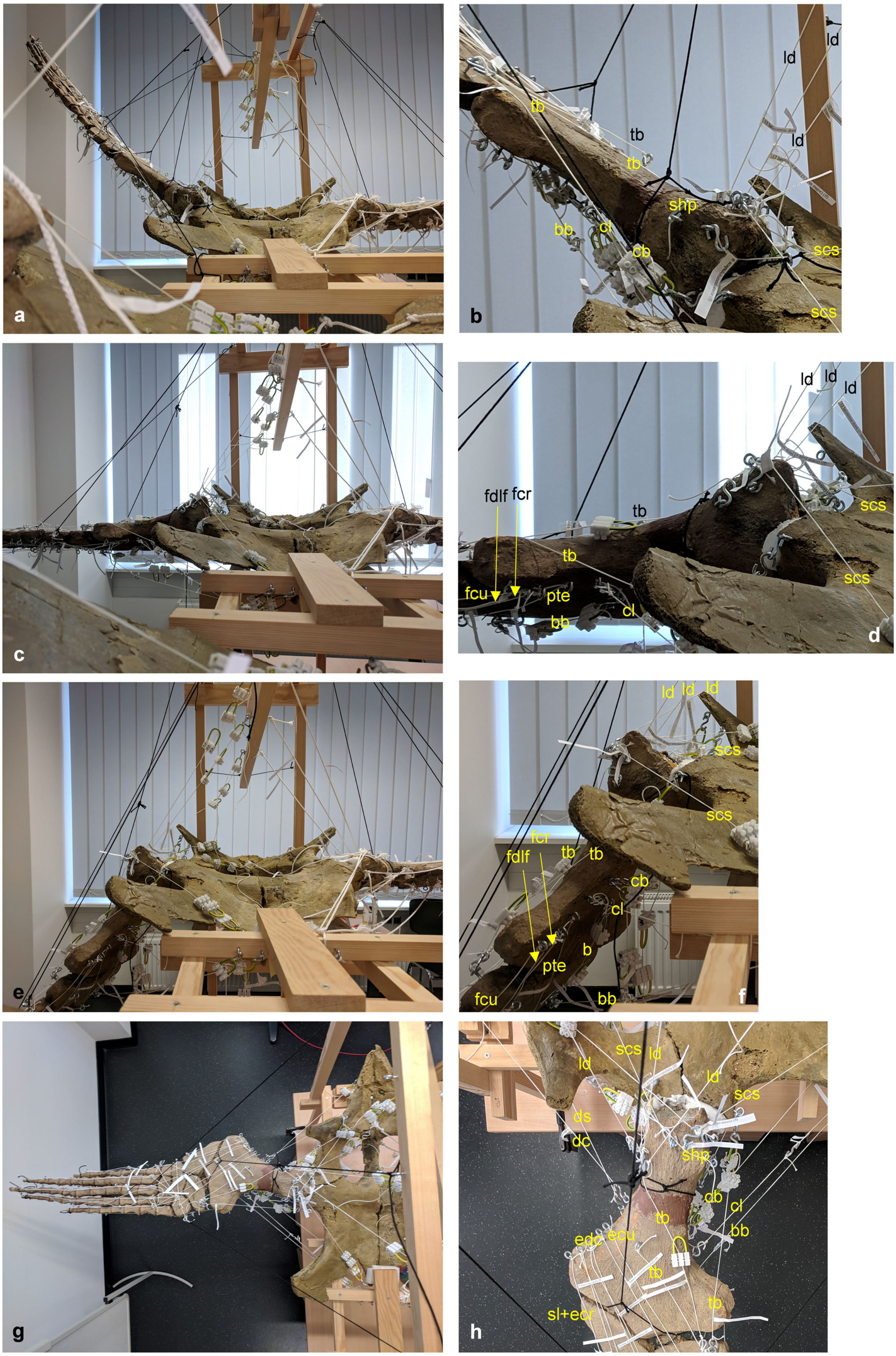
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Fig. 3: LOA of *Cryptoclidus eurymerus* (IGPB R 324) foreflipper in posterior and dorsal view. Pictures on the left (a, c, e, g) show an overview over all flipper muscles. Pictures on the right focus on the humerus muscles. a) and b) during maximum dorsal excursion in posterior view. c) and d) in the neutral position in posterior view. e) and f) during maximum ventral excursion in posterior view. g) and h) dorsal view of the neutral foreflipper position. Abbreviations: b, Musculus brachialis; bb, Musculus biceps brachii; cb, Musculus coracobrachialis brevis; cl, Musculus coracobrachialis longus; dc, Musculus deltoideus clavicularis; ds, Musculus deltoideus scapularis; ecu, Musculus extensor carpi ulnaris; edc, Musculus extensor digitorum communis; fcr, Musculus flexor carpi radialis; fcu, Musculus flexor carpi ulnaris; fdlf, Musculus flexor digitorum longus (foreflipper); ld, Musculus latissimus dorsi; pte, Musculus pronator teres; scs, Musculus subcoracoscapularis; shp, Musculus scapulohumeralis posterior; sl and ecr, Musculus supinator longus and Musculus extensor carpi radialis; tb, Musculus triceps brachii.

Musculus scapulohumeralis anterior inserts proximally and posterodorsally into the lepidosaur humerus, relatively proximally to the latissimus dorsi (Jenkins & Goslow, 1983; Russell & Bauer, 2008). Thus, a possible m. scapulohumeralis anterior insertion could be found proximally and posterodorsally, rather proximal to the m. latissimus dorsi insertion on the dorsal tuberosity of the *C. eurymerus* humerus associated with the strong rugosities on the dorsal humeral tuberosity.

3.1.2 Femur musculature

Femur muscle reconstructions followed biological principles and are counterchecked in the following chapter for their functionality. An m. ambiens origin site on the pubic tubercle is well supported by the EPB. An origin ventrally below the acetabulum would also be well substantiated by the EPB. From a mechanical point of view, the former has a much better lever arm than the latter, due to the rearrangement of pubis and ischium into almost ventrally flat lying plates. Therefore the m. ambiens origin site below the acetabulum can be rejected.

The m. iliofemoralis origin was reconstructed on the lateral ilium. Krahl and Witzel (chapter 3) also discuss a weakly supported option by EPB (only supported by turtles) that m. iliofemoralis origin area may have spread onto the vertebral column (Zug, 1971; Walker, 1973). An origin on the vertebral column would improve the lever arm of this muscle. Further, when the femur is depressed, m. iliofemoralis parallels and wraps around the dorsal trochanter of the femur and therefore exerts compressive stress onto it. The ilium is much reduced in size, comparable to the scapula blade. This would either indicate a much reduced ife or support its origin site shift onto the vertebral column which in turn would not limit its size in such a way.

Four origin areas are equally possible for m. puboischiofemoralis internus according to EPB: a large origin area on most of the dorsal pubis, a smaller origin on the anterodorsal ischium, a small origin area on the medial and ventral ilium, and an origin on the vertebral column. LOA of m. puboischiofemoralis internus show that they wrap around the dorsal trochanter of the plesiosaur femur. This means that m. puboischiofemoralis internus contributes substantially to femoral elevation. A large pubic portion and the ischiadic and vertebral column portion paralleling the dorsal trochanter can be substantiated from a mechanical standpoint. An iliac origin seems to be rather unlikely because it would wrap around the femoral trochanter and than around the anterior ilium. Then due to the reduction of the ilium, this portion can only be small. Further, total muscle shortening length shows this muscle has a bad performance. All of this indicates that an iliac origin of m. puboischiofemoralis internus is at least mechanically unlikely. The reconstructed iliac origin has a rather bad lever arm and shows no muscle shortening while the one from the vertebral column with a greater lever arm would be certainly favorable from a mechanical point of view.

M. gastrocnemius internus originating from the tibial epicondyle is equally well supported as an origin on the distal tibial epicondyle and the proximal tibia by EPB. FESA shows clearly that an origin similar to that of m. gastrocnemius externus, rather proximally on the tibial epicondyle at the point where the femur flairs anterodistally and posterodistally should be favored because otherwise it would be problematic to load the expanded femoral epicondyle by compressive stress in the FESA (chapter 3.3.1.2).

3.2 Agonists and antagonists

3.2.1 Humerus musculature

Musculus coracobrachialis brevis, m. coracobrachialis longus, m. biceps brachii, the large posterior portions of m. pectoralis, m. subcoracoscapularis, m. supracoracoideus, and m. latissimus dorsi are humeral retractors. They oppose the humeral protractors which are m. deltoideus clavicularis, m. deltoideus scapularis, and the small anterior portions of m. supracoracoideus, m. subcoracoscapularis, and m. latissimus dorsi. Musculus deltoideus


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Fig. 4: LOA of *Cryptoclidus eurymerus* (IGPB R 324) hindflipper in anterior and ventral view. Pictures on the left (a, c, e, g) show an overview over all flipper muscles. Pictures on the right focus on the femur muscles. a) and b) during maximum dorsal excursion in anterior view. c) and d) in the neutral position in anterior view. e) and f) during maximum ventral excursion in anterior view. g) and h) ventral view of the neutral hindflipper position. Abbreviations: a, Musculus ambiens; af, Musculus adductor femoris; cfb, Musculus caudifemoralis brevis; cfl, Musculus caudifemoralis longus; edl, Musculus extensor digitorum longus; f, Musculus femorotibialis; fdlh, Musculus flexor digitorum longus (hindflipper); fte, Musculus flexor tibialis externus; fti, Musculus flexor tibialis internus; gi and ge, Musculus gastrocnemius internus and Musculus gastrocnemius externus; i, Musculus ischiotrochantericus; ife, Musculus iliofemoralis; ifi, Musculus iliofibularis; it, Musculus iliotibialis; pe, Musculus puboischiofemoralis externus; pi, Musculus puboischiofemoralis internus; pit, Musculus puboischiotibialis; pti, Musculus pubotibialis.

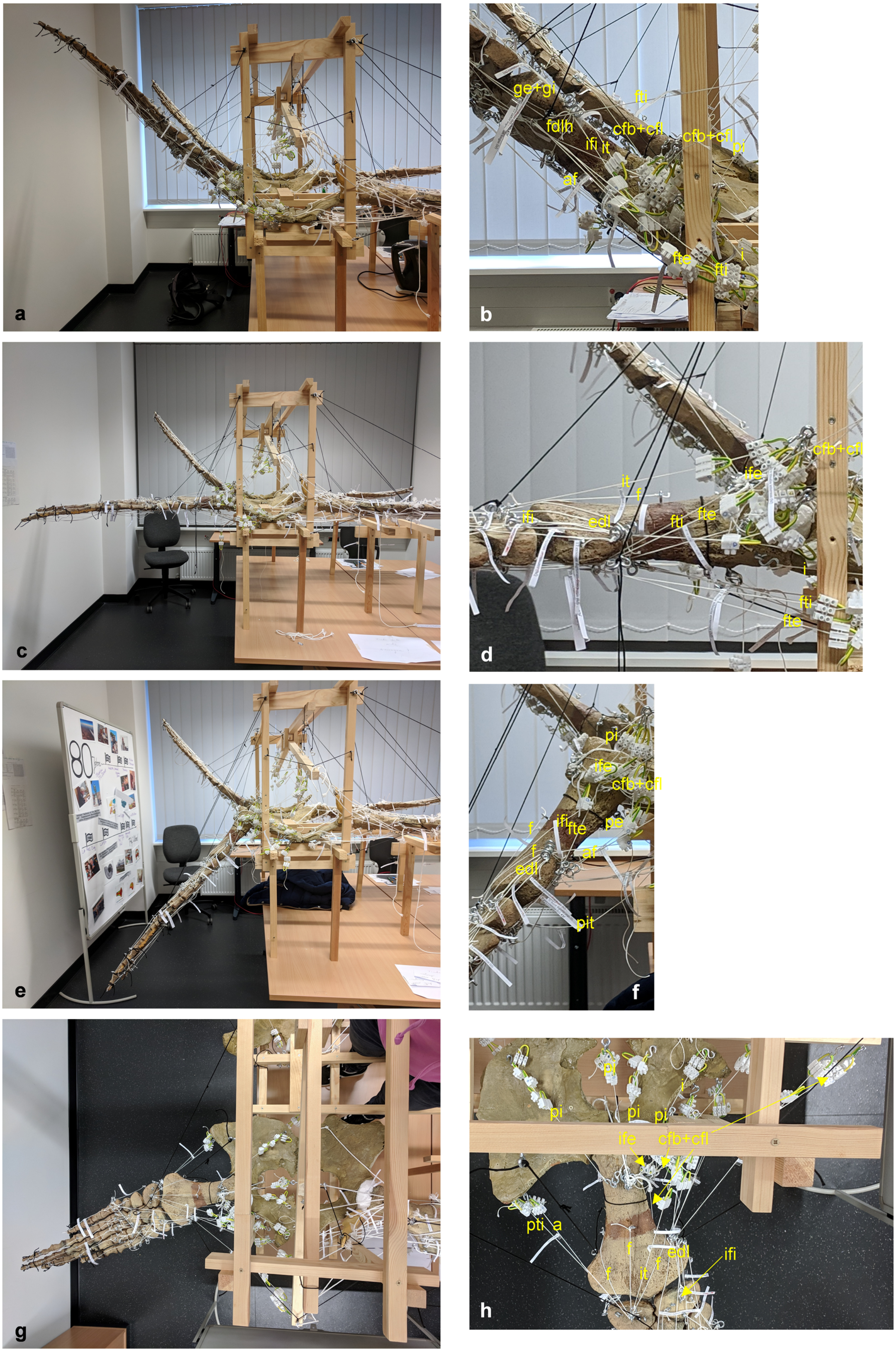
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Fig. 5: LOA of *Cryptoclidus eurymerus* (IGPB R 324) hindflipper in posterior and dorsal view. Pictures on the left (a, c, e, g) show an overview over all flipper muscles. Pictures on the right focus on the femur muscles. a) and b) during maximum dorsal excursion in posterior view. c) and d) in the neutral position in posterior view. e) and f) during maximum ventral excursion in posterior view. g) and h) dorsal view of the neutral hindflipper position. Abbreviations: a, Musculus ambiens; af, Musculus adductor femoris; cfb, Musculus caudifemoralis brevis; cfl, Musculus caudifemoralis longus; edl, Musculus extensor digitorum longus; f, Musculus femorotibialis; fte, Musculus flexor tibialis externus; fti, Musculus flexor tibialis internus; i, Musculus ischiotrochantericus; ife, Musculus iliofemoralis; ifi, Musculus iliofibularis; it, Musculus iliotibialis; pe, Musculus puboischiofemoralis externus; pi, Musculus puboischiofemoralis internus; pit, Musculus puboischiotibialis; pti, Musculus pubotibialis.

scapularis, m. subcoracoscapularis, m. latissimus dorsi and possibly to a very minor degree m. triceps brachii, m. scapulohumeralis anterior, and m. scapulohumeralis posterior power elevation of the humerus. The humeral depressors m. supracoracoideus, m. coracobrachialis brevis, m. coracobrachialis longus, m. deltoideus clavicularis, m. biceps brachii, and m. pectoralis act antagonistic to them. M. triceps brachii, the smaller anterior portion of m. subcoracoscapularis, the large posterior portion of m. pectoralis, m. biceps brachii, m. scapulohumeralis anterior, m. scapulohumeralis posterior, and m. deltoideus clavicularis contribute to downward rotation of the foreflipper leading edge. Functionally antagonistic are m. deltoideus scapularis, m. coracobrachialis brevis, m. corabcobrachialis longus, the larger posterior portion of m. subcoracoscapularis, and m. latissimus dorsi (Tab. 2).

agonists	**antagonists**
anterior portion of m. latissimus dorsi (eventually m. scapulohumeralis posterior and m. scapulohumeralis anterior) (elevation, protraction)	posterior portion m. pectoralis (depression and retraction)
posterior portion of m. latissimus dorsi (elevation, retraction)	anterior portion of m. pectoralis (protraction, depression)
m. subcoracoscapularis (anterior portion), m. deltoideus scapularis (both elevation, protraction)	m. coracobrachialis longus, m. coracobrachialis brevis, m. biceps, posterior

	portion of m. supracoracoideus (all retraction, depression)
m. subcoracoscapularis (posterior portion) (elevation, retraction)	anterior portion of m. supracoracoideus, m. deltoideus clavicularis (all depression, protraction)
m. latissimus dorsi, anterior portion of m. pectoralis, posterior portion of m. subcoracoscapularis, m. deltoideus scapularis, m. coracobrachialis brevis, m. coracobrachialis longus (rotation (leading edge upwards)	m. scapulohumeralis anterior, m. scapulohumeralis posterior, anterior portion of m. subcoracoscapularis, m. deltoideus clavicularis, posterior portion of m. pectoralis, m. biceps brachii, m. triceps brachii (leading edge downwards)
m. biceps (retraction, depression)	m. triceps (elevation, protraction)
m. extensor digitorum communis (extension metacarpals)	m. flexor digitorum longus (flexes digit I-V)
humeral triceps head (offsets ulna slightly dorsally), m. extensor carpi ulnaris (offsets ulna dorsally, or eventually extends metacarpal V)	m. flexor carpi ulnaris (displaces ulnar side of carpus ventrally, eventually flexes metacarpal V)
m. supinator longus and extensor carpi radialis (offsets radius or eventually the radial carpal side dorsally)	m. flexor carpi radialis (flexes metacarpal 1 or offsets the radial carpal side ventrally), m. pronator teres (offsets radius ventrally), m. brachialis (offsets radius slightly ventrally)

Tab. 2: Agonistic and antagonistic humerus muscles of *Cryptoclidus eurymerus* (IGPB R 324)

Further sub-groupings of agonistic and antagonistic muscles are possible: The small anterior portion of m. latissimus dorsi (weak elevation and protraction) opposes the large posterior m. pectoralis portion (strong retraction and depression) in function. The small anteriorly lying m. pectoralis portion (protractor and depressor) and the large posterior m. latissimus dorsi portion (strong elevator and retractor) act as agonist and antagonist. Musculus subcoracoscapularis and m. deltoideus scapularis which elevate and protract the humerus find their functional antagonists in m. coracobrachialis brevis, m. coracobrachialis longus, m. biceps brachii, and the posterior portion of the m. supracoracoideus which depress and retract it. The large posterior portion of m. subcoracoscapularis acts as humeral elevator and retractor and the anterior portion of m. supracoracoideus and m. deltoideus clavicularis operate oppositional to them as humeral depressors and protractors (Tab. 2).

Muscles that originate from the humerus aid in flipper twisting (Krahl and Witzel (chapter 3)): Musculus flexor carpi ulnaris may offset the ulnar side of carpus relatively to the humerus ventrally (or flex metacarpal V) while m. extensor carpi ulnaris and humeral m. triceps brachii could both offset the ulna in the opposite direction and the former could possibly extend metacarpal V. Musculus flexor carpi radialis can either flex metacarpal I or offset the radial side of the plesiosaur carpus ventrally. Musculus brachialis, and m. pronator teres also contribute to the latter function. These are antagonistically matched by antagonistic m. supinator longus + m. extensor carpi radialis. M. flexor digitorum longus (flexion of digit I to V) is opposed by m. extensor digitorum communis and the digital extensors (extension of digits) (Tab. 2).

3.2.2 Femur musculature

Elevators of the hindflipper are m. puboischiofemoralis internus, m. iliotibialis, m. iliofemoralis, m. iliofibularis, m. caudifemoralis brevis, m. caudifemoralis longus, m. flexor tibialis externus (portion from ilium), m. flexor tibialis internus (portion from vertebral column). Musculus puboischiofemoralis externus, m. adductor femoris, m. ischiotrochantericus, m. puboischiotibialis, m. flexor tibialis externus (portion from ischium), and m. flexor tibialis internus (ischial portion) act as femoral depressors. Protractors are m. puboischiofemoralis externus (pubic portion), m. puboischiofemoralis internus (portion from pubis and from vertebral column), m. ambiens, and m. pubotibialis. Retractors of the hindflipper are m. puboischiofemoralis externus (ischial portion), m. puboischiofemoralis internus (ischial and iliac portion), m. adductor femoris, m. ischiotrochantericus, m. iliofemoralis, m. iliotibialis, m. iliofemoralis, m. caudifemoralis brevis, m. caudifemoralis longus, m. flexor tibialis externus, and m. flexor tibialis internus. Downward rotation of the flipper leading edge during the downstroke is enabled by the agonists, m. puboischiofemoralis internus (pubis portion), m. puboischiofemoralis externus (ischium portion), m. caudifemoralis brevis, m. caudifemoralis longus, m. ambiens (if femur elevated), m. ischiotrochantericus, m. iliofibularis (as long as fibula below origin), m. puboischiotibialis, m. pubotibialis (if femur elevated), m. flexor tibialis internus, and m. flexor tibialis externus. The agonists are opposed by the antagonistically acting m. iliotibialis, m. ambiens (if femur depressed), m. pubotibialis (if femur depressed), m. iliofemoralis, m. puboischiofemoralis internus (ischial and iliac portion small), and m. puboischiofemoralis externus (pubis portion large) (Tab. 3).

agonists	**antagonists**
m. puboischiofemoralis internus (pubis, vertebral column) (protraction, elevation)	m. puboischiofemoralis externus (ischium), m. adductor femoris, m. flexor tibialis internus (ischium), m. flexor tibialis externus (ischium), m. ischiotrochantericus, m. puboischiotibialis (retraction, depression)
m. puboischiofemoralis externus (pubis, anterior) (protraction, and depression)	m. puboischiofemoralis internus (ischium, ilium), m. caudifemoralis brevis and m. caudifemoralis longus, m. iliofibularis, m. iliotibialis, m. iliofemoralis, m. flexor tibialis externus (ilium), m. flexor tibialis internus (vertebral column) (retraction elevation)
m. ambiens (protraction), m. pubotibialis (protraction)	m. iliofibularis (elevation, retraction)
m. puboischiofemoralis externus (pubis), m. puboischiofemoralis internus (ischium, ilium), iliofemoralis, iliotibialis (rotates flipper leading edge up), m. ambiens and m. pubotibialis (rotates flipper leading edge up, if tibia below origin area)	m. puboischiofemoralis externus (ischium), m. puboischiofemoralis internus (pubis), m. adductor femoris, m. ischiotrochantericus, m. flexor tibialis internus, m. caudifemoralis brevis, m. caudifemoralis longus, m. flexor tibialis externus, puboischiotibialis, m. iliofibularis (rotates flipper leading edge down), m. ambiens and m. pubotibialis (rotates flipper leading edge down, if tibia above origin area)
m. extensor digitorum longus (digital extensor), femorotibialis (offsets tibia dorsally)	m. gastrocnemius internus + m. gastrocnemius externus, m. flexor digitorum longus (digital flexors)

Tab. 3: Agonistic and antagonistic femur muscles of *Cryptoclidus eurymerus* (IGPB R 324)

Further, the muscles can be assigned to the following subgroups: The m. puboischiofemoralis internus originating from the dorsal pubis and vertebral column is opposed by muscles originating from the ventral ischium (m. puboischiofemoralis externus (ischial portion), m. adductor femoralis, and the ischial portions of m. flexor tibialis internus and m. flexor tibialis externus). The pubic portion of m. puboischiofemoralis externus, m. ambiens, and m. pubotibialis that arise from the ventral pubis have muscles from the ilium and posterior vertebral column as antagonists (m. flexor tibialis internus and m. flexor tibialis externus, m. iliofibularis, m. iliotibialis, m. iliofemoralis, m. puboischiofemoralis internus (ischial portion)). Musculus ambiens and m. pubotibialis have m. iliofibularis as antagonist. Musculus femorotibialis and m. extensor digitorum longus arise mostly dorsally from the femur. Musculus gastrocnemius externus, m. gastrocnemius internus, and m. flexor digitorum longus arise ventrally from the femur. Musculus gastrocnemius externus and m. gastrocnemius internus, and flexor digitorum longus (flexion of digits) seem to oppose m. extensor digitorum longus (extension of digits) and m. femorotibialis (Tab. 3).

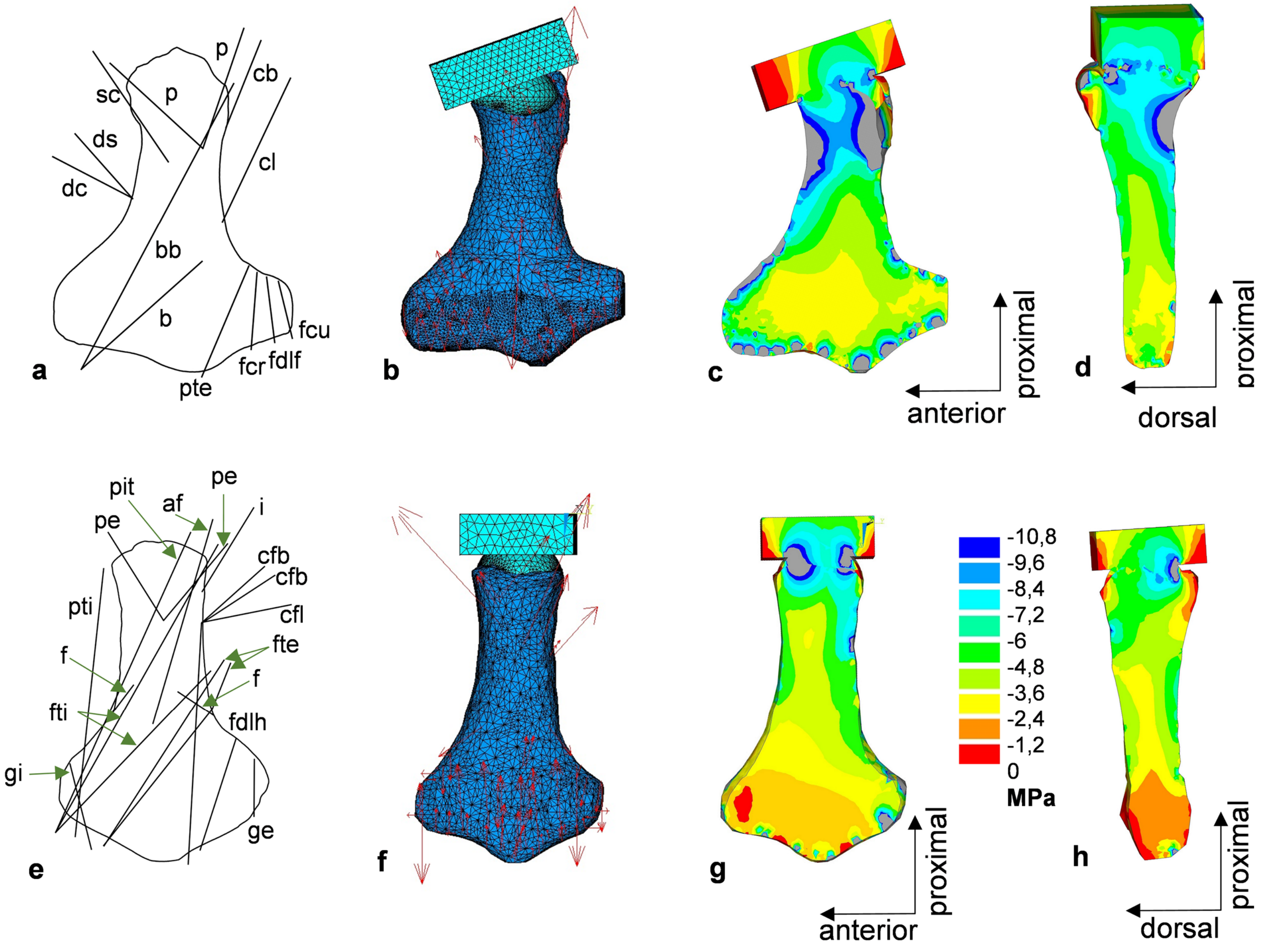
3.3 Muscle physiology and FESA

3.3.1 Muscle forces and FESA

3.3.1.1 Humerus

The compressive stress distribution and the muscle forces were computed for loadcase downstroke and upstroke of the humerus FE model. In initial FESA runs, the dorsal tuberosity of the humerus was left unloaded. Augmenting the FESA with the muscle wrapping of m. latissimus dorsi and m. subcoracoscapularis around the dorsal tuberosity revealed by LOA observations aided in loading this process with compressive stress. In addition, extensors and flexors that wrap around the anterior and posterior distal curved expansions (ectepicondylar and entepicondylar processes) of the humerus allowed to load them by compressive stress. Muscles that wrap around bone impose compressive stress onto it. Contrastingly, muscles that do not wrap around bone impose solely localized tensile loads onto the bone.

In the FESA results for the humerus (Fig. 7 c, d), red, orange, and yellow correspond with low compressive stress (0 to -3,6 MPa). The dorsal tuberosity of the humerus, as well as large parts of its distal expansions, are loaded by low compressive stress. This corresponds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dorsal
proximal

Fig. 7: FESA of *Cryptoclidus eurymerus* (IGPB R 324) humerus and femur. **a)-d)** humerus, **e)-h)** femur. **a)**, **e)** contour drawings of humerus and femur and lines of action of the respective muscles in ventral view which were derived by spanning threads into the flipper skeleton of *Cryptoclidus*. **b) f)** meshed volumetric FE models with force vectors in ventral view which were transferred from the contour drawings (a, e). FESA superpositions of both load cases (down- and upstroke) in **c)**, **d)** in dorsoventral view and **g)**, **h)** in anteroposterior view. The colour spectrum codes the compressive stress in MPa. Please note how regions of lower compressive stress match with regions of spongy bone and regions of higher compressive stress match with cortical bone. Abbreviations: af, Musculus adductor femoris; b, Musculus brachialis; bb, Musculus biceps brachii; cb, Musculus coracobrachialis brevis; cfb, Musculus caudifemoralis brevis; cfl, Musculus caudifemoralis longus; cl, Musculus coracobrachialis longus; dc, Musculus deltoideus clavicularis; ds, Musculus deltoideus scapularis; f, Musculus femorotibialis; fcr, Musculus flexor carpi radialis; fcu, Musculus flexor carpi ulnaris; fdlf, Musculus flexor digitorum longus (foreflipper); fdlh, Musculus flexor digitorum longus (hindflipper); fte, Musculus flexor tibialis externus; fti, Musculus flexor tibialis internus; gi and ge, Musculus gastrocnemius internus and Musculus gastrocnemius externus; i, Musculus ischiotrochantericus; p, Musculus pectoralis; pe, Musculus puboischiofemoralis externus; pit, Musculus puboischiotibialis; pte, Musculus pronator teres; pti, Musculus pubotibialis; sc, Musculus supracoracoideus.

well with the observation that the distal humerus is mostly composed of spongy bone that is covered only by a thin layer of cortical bone (compare to Krahl and Witzel (chapter 3)). The green colour spectrum correlates with moderate compressive stress (-3,6 to -7,2 MPa). Large areas of the cortical and spongy bone, especially in the region of the humerus shaft, but also in smaller regions of the distal expansions are compressed moderately (Fig. 7 c, d). Turquoise to blue colours conform to high compressive stress (-7,2 to -10,8 MPa). High compressive stress partially corresponds to the outermost cortical layer. Especially the proximal region of the head and the proximal shaft are loaded by high compressive stress (Fig. 7 c, d).

On the distal articulation surface of the humerus, high stress peaks occur very narrowly localized (Fig. 7 c). These are artifacts which are due to the application of the counterforce. The counterforce was applied scattered over the large distal articulation surface, instead of applying it to one point, to receive a more realistic force induction. Nevertheless, this is a trade off between realistic conditions and technical software possibilities.

Muscle	Muscle force [N]
M. supracoracoideus	6000
M. coracobrachialis brevis	4800
M. coracobrachialis longus	3600
M. deltoideus clavicularis	1500
M. deltoideus scapularis	1649
M. scapulohumeralis anterior	2400
M. scapulohumeralis posterior	1920
M. biceps brachii	1200
M. brachialis	324
M. triceps brachii	2566
M. triceps humeral head	275
M. pectoralis	9600
M. subcoracoscapularis	4422
M. latissimus dorsi	3918
M. extensor carpi ulnaris	1000
M. extensor digitorum communis	6000
M. extensor carpi radialis	1000
M. pronator teres	640
M. flexor carpi ulnaris	3000
M. flexor digitorum longus	1500
M. flexor carpi radialis	10500

Tab. 4: Muscle forces of *Cryptoclidus eurymerus* (IGPB R 324) humerus by superposition of FESA load cases

During the downstroke, m. pectoralis is the muscle that develops the highest muscle force (9600 N) among the muscles that span the glenoid. Surprisingly, during the upstroke, m. pectoralis still develops a higher force (5267 N) than either one of the main humerus elevators, i.e., m. latissimus dorsi and m. subcoracoscapularis. Nonetheless, both develop high muscle forces, m. subcoracoscapularis (4422 N) and m. latissimus dorsi (3918 N), to sustain the upstroke together. Generally, it becomes apparent, that greater muscle forces are produced by retractors and depressors of the humerus than by its elevators and protractors. Furthermore, extensors and flexors develop partially extremely high muscle forces, with m. flexor carpi radialis producing 8460 N during the downstroke and m. extensor digitorum communis producing 6000 N during the upstroke (Tab. 4).

3.3.1.2 Femur

For loadcase downstroke and upstroke of the femur FE model, the compressive stress distribution and the muscle forces were computed. In initial FESA runs of the femur, we were unable to load the dorsal trochanter and the distal epiphyses of the femur with compressive stress because the muscles would simply pull away from their origin. Thereby only localized tensile loads were observable in FESAs. Then we again introduced the LOA observations on muscle wrapping, with m. iliofemoralis and m. puboischiofemoralis internus wrapping around the dorsal trochanter and the extensor and flexors wrapping around the distally much expanded femoral epicondyles, and the respective structures were loaded by compressive stress.

Muscle	Muscle force [N]
M. puboischiofemoralis externus	7878
M. puboischiofemoralis internus	7611
M. femorotibialis	1521
M. adductor femoris	2536
M. ischiotrochantericus	984
M. iliofemoralis	253
M. caudifemoralis brevis	506
M. caudifemoralis longus	507
M. extensor digitorum communis	1014
M. gastrocnemius	1176
M. flexor digitorum longus	786

Tab. 5: Muscle forces of *Cryptoclidus eurymerus* (IGPB R 324) femur by superposition of FESA load cases

The colour coding of the compressive stress distribution in the plesiosaur femur (Fig. 7 c, d) is the same as for the humerus (Krahl et al. (chapter 3.3.1)). Low compressive stress correlates mostly with the medullary region in the mid to distal femur and the distal expansions of the femur. Moderate compressive stress occurs mostly in regions where cortical bone is found, especially on the outer femur shaft. The high compressive stress values correspond mostly with areas of the femoral head and part of the cortical bone of the proximal shaft (Fig. 7 g, h). Like in the FESA of the humerus, localized compressive stress peaks on the distal articulation surface of the plesiosaur femur derive from the selective application of the counterforce in several points scattered across the articulation surface (Krahl et al. (chapter 3.3.1)) (Fig. 7 g).

The muscle forces of the many two-joint muscles (m. pubotibialis, m. puboischiotibialis, m. flexor tibialis externus, m. flexor tibialis internus, m. ambiens, m. iliotibialis, m. iliofibularis) in the plesiosaur hindflipper cannot be determined because they influence the femur only indirectly by adding to the counterforce. During the downstroke, pe produces the highest muscle force (7878 N). During the upstroke, m. puboischiofemoralis internus produces up to 7611 N. Extensor and flexor muscle forces are considerably lower in the femur than in the foreflipper. M. gastrocnemius, a flexor, develops a total force of up to 1176 N (Tab. 5).

3.3.2 Changes in muscle length

Muscles that are dorsal to the glenoid and acetabulum extend during the downstroke and contract during the upstroke. Muscles that originate ventrally to glenoid and acetabulum contract when the humerus and femur are depressed during the downstroke and are extended during the upstroke when the humerus and femur are elevated.

Total muscle length changes of the foreflipper vary between 0% and 70,87%. Three muscle (or portions thereof) (m. deltoideus clavicularis, m. triceps brachii (anterior and posterior portion) show no length change, i.e., the length changes were immeasurable with the technique employed here, meaning they are smaller than 1,7 cm (breadth of the terminal strips). Musculus coracobrachialis brevis (posterior portion) shows very little muscle shortening (3,88%). Otherwise, total muscle length changes cover the whole physiological spectrum, from around 9% in the posterior portion of m. subcoracoscapularis to 37% for the anterior portion of m. latissimus dorsi. The only muscle that stands out is ds with a total length change of over 70%. This is clearly not physiological. So a screw eye pin was alternatively screwed into the origin area of the m. deltoideus scapularis that is on the ventral to ventrolateral scapula anterior to the glenoid. The total muscle length change was measured again in all three flipper positions and ranged now within the measuring error, i.e., it ranged well within physiological boundaries (Tab. 1).

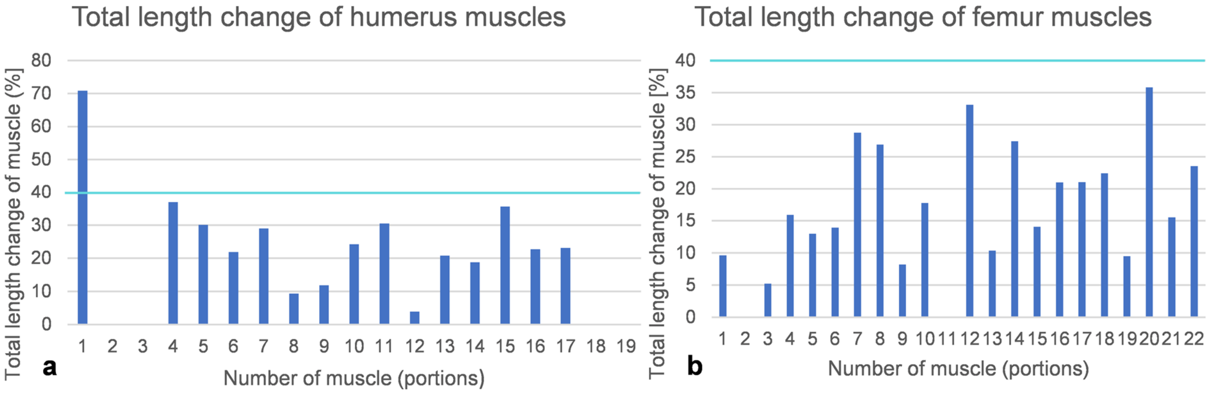

Fig. 6: Total length change of **a)** humerus muscle(s) (portions) and **b)** femur muscle(s) (portions). **a)** and **b)** Locomotory muscles that insert into or originate from humerus and femur cover the whole spectrum of maximum total muscle length change of vertebrate muscle well, ranging from no measurable total length change (of muscles with a complex architecture) to around 40% of total length change of muscle (typical for approximately parallel-fibred muscles; marked by turquoise line) (Biewener, Corning & Tobalske, 1998; Biewener & Roberts, 2000). **N**ote in a) how m. deltoideus scapularis (1), if it originates from the scapula, would show an unphysiological total length change of muscle. If it originates from the ventral scapula (2), total muscle length change drops down into the physiological spectrum and ranges within the measuring error (typical for muscles with a complex internal architecture).

Total muscle length change for the hindflipper ranges from 0% to 35,8%. Musculus caudifemoralis brevis (ilium portion) and m. pubotibialis lack any length change due to methodical reasons (see above). Further, m. caudifemoralis brevis which originates from the vertebral column shows little total muscle length change at 5,2% while the muscle with the largest change (35,82%) in total muscle length is the portion of the m. puboischiofemoralis internus originating at the vertebral column (Tab. 1).

Looking at agonistic and antagonistic muscles, the total length changes of m. pectoralis and m. latissimus dorsi, the two muscles that mainly power down- and upstroke of the foreflipper, are fairly similar: the anterior portion of m. latissimus dorsi (36,96%) and m. pectoralis posterior portion (35,65%) and posterior m. latissimus dorsi portion (21,92%) and m. pectoralis anterior portion (18,75%). Total muscle length changes of agonists and antagonists were expected to be similar due to their opposing functions. Instead it was found that those muscles that show comparable total muscle length changes are rather determined by their geometric arrangement in relation to the glenoid or acetabulum. This means, that a muscle that originates from e.g. the posteroventral ischium (e.g. m. puboischiofemoralis externus (23,55%)) shows a rather similar shortening as one that originates from the anterodorsal pubis (m. puboischiofemoralis internus (21,04%)).

4. Discussion

4.1 Myology

As noted earlier, the muscle reconstructions on which this study is based on were obtained by evaluating comparative anatomical data (i.e., with the EPB) (Krahl and Witzel (chapter 3)). These biologically derived muscle reconstructions are counterchecked on whether they also meet the mechanical criteria to which muscles are subjected. Mostly we find that the reconstructed muscles are in accordance with the mechanical criteria, too. Although some changes of the plesiosaur fore- and hindflipper muscle reconstructions were made due to mechanical reasons (m. biceps brachii, m. deltoideus scapularis, m. gastrocnemius internus), i.e., in terms of receiving a more homogenous compressive stress distribution in FESA of the humerus and femur. We found mechanical evidence of support for some reconstructions made by Krahl and Witzel (chapter 3) which were rather weakly supported by the EPB (i.e., m. subcoracoscapularis from the coracoid, m. coracobrachialis brevis, m. coracobrachialis longus, m. ambiens, m. iliofemoralis, m. puboischiofemoralis).

One muscle, m. scapulohumeralis anterior was reconstructed additionally to Krahl and Witzel (chapter 3), as it could aid in humerus rotation. Convergently to Cheloniidae Krahl et al. (chapter 2), muscles were found that wrap around the humerus as well as the femur in plesiosaurs. The area of origin of m. scapulohumeralis anterior is situated on the anterior scapular blade. In comparison to the reconstruction by Araújo & Correia (2015), it is not as much ventral and more laterally situated. Robinson (1975) and Watson (1924) reconstructed its attachment surface on the medial and ventral scapula which is not supported by the EPB (Jenkins & Goslow, 1983; Russell & Bauer, 2008). Contrastingly, Carpenter et al. (2010) reconstructed a large origin area of m. scapulohumeralis anterior on the lateral scapula. Instead, we reconstructed a large m. deltoideus scapularis in roughly the same area which is better substantiated by the EPB (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). The results presented here disagree with Tarlo (1958) in that the origin of m. scapulohumeralis anterior is on the anteroventral scapula because this is not supported by extant Sauropsida (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). The sketches of the muscle reconstructions by Lingham-Soliar (2000) are solely schematic. It is impossible to determine exact muscle attachments from these drawings. Yet, judging by the geometrical arrangement, his muscle reconstructions resemble our results. M.

scapulohumeralis anterior occurs exclusively in lepidosaurs and neither in turtles nor in crocodilians (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010). It inserts posterodorsally into the humerus in lepidosaurs; therefore, according to the EPB this pattern was transferred to the plesiosaur in this study. None of the previous authors who have reconstructed this muscle, reconstructed its insertion in this place. They either placed it at the anterodorsal humerus (Watson, 1924; Tarlo, 1958; Robinson, 1975) or at the dorsal humerus (Lingham-Soliar, 2000; Carpenter et al., 2010).

M. scapulohumeralis anterior is reconstructed in agreement with Tarlo (1958) and Watson (1924) to potentially protract the humerus subordinately and to rotate it (Watson, 1924; Tarlo, 1958). Watson (1924) and Tarlo (1958) disagree on how protraction and rotation took place. Whereas Watson (1924) proposed the muscle to rotate the humerus anteriorly upwards, Tarlo (1958) infers the opposite. Whereas Tarlo (1958) and Robinson (1975), and the current study agree on the direction of humerus rotation, Robinson (1975) additionally describes sha as a depressor, which contradicts the results of this study. A possible minor elevational function was not described by any previous author.

4.2 Muscle physiology

4.2.1 Total muscle length changes

Total muscle length changes were calculated for glenoid and acetabulum spanning muscles and tested whether they lie within physiological boundaries. The total muscle length change of m. deltoideus scapularis, if it would have originated from the lateral scapula, is not physiological and would not allow the muscle to produce much power (compare Biewener & Roberts, 2000) (Tab. 1; Fig. 6 a). This could indicate, that the muscle reconstruction of m. deltoideus scapularis on the scapula blade by Krahl and Witzel (chapter 3) is wrong, despite being well supported by the EPB, and that its origin could have been restricted to the ventral side of scapula. An origin of m. deltoideus scapularis on the ventral to ventrolateral scapula anterior to the glenoid would result in a length change that is within the physiological limits (Tab. 1). Further, a muscle length change within the measuring error, i.e., a small one, would actually account better for the often non-parallel and rather complex architecture of the deltoid muscle (s. e.g., Krahl et al. (chapter 2), Walker, 1973; Meers, 2003; Russell & Bauer, 2008). A reduction of the m. deltoideus scapularis from the scapular blade would mean that no locomotory muscles attach to the lateral scapular blade in plesiosaurs anymore. Solely muscle attachments that suspend the shoulder girdle remain on the scapular blade. Besides aquatic adaptation (Krahl et al. (chapter 2)), this could be another explanation for why the dorsal scapular projection is so much smaller than in extant Sauropsida (compare to Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Suzuki & Hayashi, 2010) and potential functional analogues (compare to Walker, 1973; English, 1977; Schreiweis, 1982; Louw, 1992; Cooper et al., 2007). Similarly, a relocation or reduction of muscles originating from the ilium (e.g., m. iliofemoralis), could free or mostly free the ilium of locomotory musculature and therefore allow its reduction.

For several muscles (e.g., m. deltoideus clavicularis, the two m. triceps brachii, m. coracobrachialis brevis (posterior portion); m. caudifemoralis brevis (ilium), m. pubotibialis), nearly isometrical conditions were determined for elevation and depression of plesiosaur humerus and femur. If one would additionally consider protraction and retraction and long axis rotation of the humerus, muscle length changes would provide different results in all of these muscles. Possibly, these almost isometrical muscles had a complex muscle architecture (see Biewener & Roberts, 2000 for a review). Additionally, it is possible that m. triceps brachii and m. pubotibialis had long tendons (i.e., a large non-contractive component. Another possibility is that those muscles that lack length changes were actually reduced in plesiosaurs. Some clues might be given by the EPB: M. triceps brachii is much reduced or entirely reduced in Chelonioidea, depending on the species. The coracobrachialis brevis is markedly reduced in size in Testudines (Walker, 1973). Possibly, the m. caudifemoralis brevis origin from the ilium was reduced in plesiosaurs and that m. caudifemoralis brevis arose only from the vertebral column. Musculus pubotibialis is absent in crocodilians (Otero, Gallina & Herrera, 2010; Suzuki et al., 2011).

Muscle length changes of agonistic and antagonistic muscles of the pelvic and pectoral girdle do not correspond well. On the one hand, this might be due to differences in the morphology and geometry of the pectoral and pelvic girdle. On the other hand, the results could also change if flipper protraction and retraction were taken into account. Further, muscle architecture and tendon length were not and most probably cannot be inferred for extinct tetrapods.

4.2.2 Muscle forces

4.2.2.1 Humerus

On average, forces of muscles generated during the downstroke, i.e., by the humeral and femoral depressors and retractors, appear to have higher forces than muscles involved in the upstroke (Tab. 4; Tab 5). This could mean that in plesiosaurs the fore- and hindflipper downstroke was more efficient than the upstroke. Similarly, the foreflipper downstroke in

Cheloniidae is more powerful than the upstroke (Davenport, Munks & Oxford, 1984; Krahl et al. (chapter 2)). However, this difference in efficiency is not found in all underwater fliers because it is not found in, e.g., penguins in which the foreflipper downstroke is as efficient as the upstroke (Clark & Bemis, 1979).

The way they were reconstructed here, the m. scapulohumeralis anterior and posterior appear to be solely humeral rotators because they operate with considerably high muscle forces during the downstroke (Tab. 4). This way, their elevational function is minor. This is surprising because in extant Lepidosauria both muscles are rather small (Jenkins & Goslow, 1983; Russell & Bauer, 2008). Either this implies that their origin and insertion areas were enlarged in Krahl and Witzel (chapter 3) or that m. scapulohumeralis anterior and posterior muscle forces would need testing with further FESA runs. These would show whether one can receive a similarly homogenous compressive stress distribution by reallocating a large portion of the muscle force to muscles with a similar function and LOA, e.g., m. latissimus dorsi, m. subcoracoscapularis, etc. LOAs of m. scapulohumeralis anterior and m. scapulohumeralis posterior which would wrap unusually around the dorsal tuberosity in posterior to anterior direction seem to underpin the hypothetical reallocation of muscle force to another muscle as aforementioned.

A surprising result is that m. pectoralis is the muscle that develops the highest muscle force during the foreflipper upstroke (Tab. 4), too. Although in total humeral elevators and protractors should be presumed to produce a higher power output, otherwise foreflipper elevation and protraction become impossible. Furthermore, the pectoral girdle is suspended from the vertebral column, the rib cage, and the gastralia by muscles and tendons (e.g. (Avery & Tanner, 1964; Walker, 1973). Recent studies have shown that a swinging pectoral and pelvic girdle can contribute substantially to locomotion in extant Otariinae, Testudines, and crocodylians (Walker, 1971a; Baier & Gatesy, 2013; Mayerl, Brainerd & Blob, 2016; Schmidt, Mehlhorn & Fischer, 2016). This indicates, that the importance of the contribution to locomotion of pectoral and pelvic girdle swinging in Tetrapoda is not only underestimated in extant taxa but surely in extinct taxa, too. An actively swinging pectoral and pelvic girdle could contribute to the range of motion of the plesiosaur fore- and hindflippers and to the total force with which the flippers are beaten. Especially in the plesiosaur shoulder region, where there is no bony or cartilaginous connection to the trunk (as opposed to the pelvic region), a strong shoulder musculature and ligaments connecting the pectoral girdle with the vertebral column, the ribs, and the gastralia would be necessary.

On the dorsal foreflipper m. extensor carpi ulnaris develops rather low muscle forces (1000 N) in comparison to m. extensor digitorum communis (6000 N). Musculus flexor carpi radialis and m. flexor digitorum longus are topologically comparably arranged to extensor carpi ulnaris and m. extensor digitorum communis but on the ventral side of the foreflipper. Contrastingly, m. flexor carpi radialis develops extremely high muscle forces (10500) and m. flexor digitorum longus considerably lower muscle forces (1500 N) (Tab. 4). Possibly, redistribution of part of the muscle force of m. flexor carpi radialis to the partially similarly running m. flexor digitorum longus would lead in a further FESA run to a similar homogenous compressive stress distribution. If so, this seems to be preferable over m. flexor digitorum longus being recruited with such a comparably low muscle force. This is because m. flexor digitorum longus flexes the digits during the downstroke while m. flexor carpi radialis only slightly displaces the radius on the distal humerus during flipper long axis twisting.

4.2.2.2 Femur

If one compares the muscle forces of the extensors and flexors of the plesiosaur humerus and femur, it becomes apparent that those of the femur (Tab. 5) are generally lower than those of the humerus (Tab. 4). This may be due to the fact that in the plesiosaur hindflipper, there are considerably more two-joint muscles and fewer as well as less independently operating extensors and flexors than in the foreflipper. The two-joint muscles aid in femur protraction/retraction, elevation/depression, and in knee flexion in extant Sauropsida (Snyder, 1954; Walker, 1973; Otero, Gallina & Herrera, 2010; Anzai et al., 2014), too. As the plesiosaur knee was immobile, these muscles were interpreted by Krahl and Witzel (chapter 3) to be part of the flipper long axis twisting mechanism additionally to their functions as depressors/elevators and protractors/retractors. Therefore, it is possible that the numerous two-joint muscles of the plesiosaur hindflipper partially aided in functions that were served by the much more differentiated extensors and flexors in the foreflipper (Krahl and Witzel (chapter 3)). Muscle forces of the two-joint muscles could not be determined in this study because they only indirectly influence FESA by adding to the counterforce imposed by the tibia and fibula. Therefore, it can be expected that the only extensor and the two flexors of the hindflipper should have in total lower muscle forces than the numerous extensors and flexors of the foreflipper. Finally, femur and humerus differ morphologically by the distal expansion, and possibly the hindflipper contributed less to propulsion than the foreflipper, as proposed by Lingham-Soliar (2000) and Liu et al. (2015).

4.2.2.3 Comparison to Cheloniidae humerus

There are some similarities in muscle forces of certain muscles in *Cryptoclidus eurymerus* (IGPB R 324) and in Cheloniidae: m. pectoralis develops the highest force of all muscles that insert proximally into the humerus (Krahl et al. (chapter 2)). Furthermore, of the main humeral elevators, m. subcoracoscapularis generates higher forces than m. latissimus dorsi in both taxa (Krahl et al. (chapter 2)). Musculus coracobrachialis brevis develops lower force in sea turtles (Krahl et al. (chapter 2)) than in plesiosaurs. Contrastingly, m. coracobrachialis longus develops higher forces in sea turtles (Krahl et al. (chapter 2)) than in plesiosaurs. While m. deltoideus scapularis and m. deltoideus clavicularis contribute in markedly different ways to propulsion in Cheloniidae (Krahl et al. (chapter 2)), they operate with broadly similar forces in plesiosaurs.

Another difference between the forces of humerus muscles of cheloniids (Krahl et al. (chapter 2)) and plesiosaurs is that in the former they vary by an order of magnitude unlike in the latter in which they do not necessarily differ much. These results support a hydrodynamic study of *Cryptoclidus eurymerus* (IGPB R 324) that finds flipper twisting to be crucial for underwater flight in plesiosaurs (Witzel, Krahl & Sander, 2015). Furthermore, these findings corroborate the myological flipper twisting mechanism proposed by Krahl and Witzel (chapter 3). Generally, higher muscle forces in plesiosaurs could be due to scaling effects.

The muscle bellies that produce these enormous muscle forces (up to 9600 N) in the shoulder girdle were large and took much space. Therefore, it is indeed problematic that extensors and flexors proved to have produced similarly large forces because their potential origin surfaces are much smaller than for the glenoid spanning muscles. Different solutions to this paradox may exist. M. flexor digitorum longus, for instance, has a second head arising from the carpus in Sauropsida (Walker, 1973; Meers, 2003; Russell & Bauer, 2008), so it could have been able to develop substantially higher force, than just by the humeral muscle belly. Further, possibly these muscles have a complex architecture that saves space in comparison to the musculature originating from the pectoral girdle. Long tendinous structures could have been a mechanism to conserve energy during cruising (Roberts et al., 1997; Biewener & Roberts, 2000).

Dolphins have a relatively well ossified flipper skeleton, although there are basically no individual muscles identifiable anymore. They merely have layers of parallel fibred connective tissue covering the flipper bones (see Cooper et al., 2007, Fig. 4, p. 1128). This means in reverse that the hydrodynamic forces plus the „muscle“ force these layers of connective tissue can exert are in total enough to induce ossification of the flipper bones.

Similar aponeurotic layerings, maybe also directed in the main directions of flipper twisting could account for a considerable part of the muscle forces calculated with FESA. Also, the connective tissue covering the broad space of the non-functional elbow joint, carpus and manus could passively also conserve energy and thus passively compensate for some of the forces computed.

5. Conclusions

The highly aquatically adapted locomotor apparatus of plesiosaurs experienced little change throughout 135 Ma of plesiosaur evolution. The question of whether plesiosaurs rowed, flew underwater, or employed a combination of both has not been fully answered yet. Here we present a computer model which is in agreement with underwater flight in plesiosaurs based on comparative anatomical and muscle physiological data in accordance with mechanical principles.

For this purpose, a foreflipper and hindflipper cast of IGPB R 324 were mounted on a wooden framework. With the help of screw eye pins, electrical terminal strips, and threads humerus and femur muscle LOA were recreated. Three positions representing maximum dorsal and ventral fore- and hindflipper excursion and a neutral position were fixed with ropes. For each muscle that spans glenoid and acetabulum muscle length was measured in all three positions. Then total muscle length changes over a flipper beat cycle were calculated for all muscles. A *Cryptoclidus* humerus and femur FE model were built from micro-CT scans of IGPB R 324. Then, FESA was conducted for load case downstroke and upstroke for both long bones. Muscle insertion angles were obtained from LOA recreation. Muscle forces were stochastically determined in iterative steps.

We demonstrate that by aiming at a homogenous compressive stress distribution in the humerus and femur of *Cryptoclidus* (IGPB R 324), it is possible to test muscle reconstructions and their associated LOA with FESA. Muscle reconstructions by Krahl and Witzel (chapter 3) were found to be largely corroborated, but they were also amended and corrected due to FESA. As in Cheloniidae, muscles wrapping around bony processes, i.e., the dorsal tuberosity of the plesiosaur humerus and dorsal trochanter of the plesiosaur femur, as well as their epicondyles, proved to be necessary to load the aforementioned structures. Further, measuring the total length changes of all muscles that insert into, originate from, and span humerus and femur of a plesiosaur showed that a m. deltoideus scapularis origin from the lateral scapula is unphysiological. This infers a reduction of this muscle from this part of its origin site which is well supported across Sauropsida (Walker, 1973; Meers, 2003; Russell & Bauer, 2008).

Muscle forces show some correlation with cheloniid humerus musculature but also differences which underlines that underwater flight in both lineages was achieved in convergent ways. High extensor and flexor forces in plesiosaurs corroborate the hypothesis that flipper long axis twisting was essential for plesiosaur underwater flight.

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Chapter 5

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FESA of a *Chelonia mydas* femur reveals muscle functions and forces

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Cheloniidae, finite element analysis, muscle forces, rowing

Abstract

Cheloniidae have hydrofoil foreflippers which power underwater flight. Contrastingly, their round plate-shaped hindflippers are mainly used as control surfaces but may also be employed for rowing and maneuvering. After having analyzed a cheloniid humerus with finite element methods, a femur is analyzed to deduce differences between the two on a functional morphological basis. During locomotion, long bones of Tetrapoda are loaded to different degrees by bending, torsion and compression. By superposing load cases, that represent specific loading situations during a limb cycle, bones turned out to be loaded by compressive stress in total. To learn more about the differences between an appendage employed in underwater flight and rowing, a finite element analysis of a *Chelonia mydas* femur was conducted based on the aforementioned hypothesis. Lines of action were determined for *Chelonia mydas* femur muscles, founded on literature data. They were deduced by spanning threads into the hindflipper skeleton of a *Chelonia mydas* specimen. Muscle attachment sites and their respective lines of action were transferred to a finite element model of a *Chelonia mydas* femur which was built from micro-CT scans. The first stage, where all muscles pull with maximum force to load the finite element model homogenously with compressive stress, was computed from which load cases could be derived in the future. The highest muscle forces are developed by protractors and retractors of the femur, namely the agonistic m. puboischiofemoralis internus (200 N) and the antagonistic m. ischiotrochantericus and m. puboischiofemoralis externus (150 N each). This is in contrast to the sea turtle humerus, in which the muscle that develops the highest force is a humeral depressor. Whether this depicts a general trend in differences between a tetrapod appendage employed in rowing and underwater flight would require more future research.

1. Introduction

1.1 Hindflipper of *Chelonia mydas*

1.1.1 Osteology

In contrast to cheloniid foreflippers, their hindflippers are not as strongly morphologically derived (Walker, 1973; Wyneken, 1997). The hindflippers are webbed, rather rounded, and dorsoventrally flattened. They stick out from underneath the carapace approximately rectangular to the vertebral column (Walker, 1971b; Davenport, Munks & Oxford, 1984). In Cheloniidae, the pubic lateral process is much expanded and the thigh is rotated forwards. The usually vaulted turtle femur is straightened in cheloniiids (Walker, 1973). The femur is shorter than the humerus, unlike to other Testudines (Zangerl, 1953). The femoral head is oval to round and arched dorsally. In highly aquatic turtles, the trochanter major is expanded. Consequently, the intertrochanteric fossa has decreased in size (Walker, 1973). A fusion of trochanter minor and major encloses the intertrochanteric fossa in cheloniids (Zug, 1971). Tibia and fibula are slightly longer than radius and ulna and are little flattened. The knee joint of Cheloniidae possibly allows the shank to be flexed, extended, and rotated to a very limited degree as Haines (1942) described for *Emydoidea blandingii* (Walker, 1973). The so-called hooked element of sea turtles evolved by amalgamation of the fifth distal tarsal and the adjacent metatarsal (Joyce, Werneburg & Lyson, 2013). The first metatarsal is enlarged (Walker, 1973; Wyneken, 2001), too. The digits are therefore placed well apart resulting in a broadened paddle (Wyneken, 2001). Digit I and V have a reduced phalangeal number (two), while the other three fingers have three phalanges. The number of claws is reduced in sea turtles to two, one, or none depending on the species (Walker, 1973).

1.1.2 Myology

Along with an enlargement of the femoral trochanter major, the insertion areas of m. iliofemoralis dorsally, m. caudifemoralis, and m. ischiotrochantericus ventrally are also enlarged. These strongly hypertrophied femur retractors improve the hindflipper rowing abilities (Walker, 1973). Extensive extensor and flexor complexes, m. extensor digitorum communis, m. gastrocnemius, and m. flexor digitorum longus act across the knee and mesotarsal foot joint and extend, flex, and spread the digits (Zug, 1971; Walker, 1973). In comparison to the humerus (Walker, 1973; Krahl dissertation (chapter 2)), less extensors and flexors arise from the distal femur. Yet those that do originate from the femur are more complex and less differentiated than those of the humerus (Walker, 1973).

1.1.3 Locomotion

Hindflippers of adult Cheloniidae may concur in vigorous swimming. The hindflipper kick is synchronized with the foreflipper downstroke. While sea turtle foreflippers are employed in underwater flight, hindflippers are employed in rowing. When the hindflippers are drawn anteriorly, flexors and abductors move the femur and the crus. At the same time, the pes is flexed to provide as little surface as possible to reduce drag. When the hindflipper strokes back, it is extended and adducted at the knee joint and the digits are spread to extend the webbing for propulsion (Wyneken, 2001).

Hindflippers are not employed in routine swimming in non-juvenile Cheloniidae (Davenport, Munks & Oxford, 1984). They are either tucked in close to the body or placed into the onflowing water as control surfaces or (Walker, 1971b; Davenport, Munks & Oxford, 1984), i.e., sea turtle hindflippers mainly act as rudders for maneuvering and changing water depth (Walker, 1971b; Davenport, Munks & Oxford, 1984; Renous, 1995; Wyneken, 1997; Renous, Bels & Davenport, 2000). Cheloniid hindflippers also take part in dogpaddling when surfacing for breathing (Salmon & Wyneken, 1987; Wyneken & Salmon, 1992; Wyneken, 1997; Pereira, Booth & Limpus, 2011) or in terrestrial locomotion (Renous & Bels, 1993; Wyneken, 1997; Renous, Bels & Davenport, 2000).

1.2 Finite element structure analysis

Vastly different study fields encompassing engineering sciences, biology, and paleontology use finite element structure analysis (FESA) (Rayfield, 2007 for review) to study functional loading of biological or technical (volume) models (Rayfield, 2007; Witzel et al., 2011). A dominantly compressive stress regime, in superposition of individual load cases, has been shown to be established in bones (Carter, Orr & Fyhrie, 1989; Witzel & Preuschoft, 2005; Krahl et al. (chapter 2, 4)). Bones are functionally loaded by axial compression by agonistically and antagonistically operating active (i.e., muscles) or passive (i.e., ligaments) tension chords (Witzel & Preuschoft, 2005; Rayfield, 2007; Sverdlova & Witzel, 2010; Curtis et al., 2011; Witzel et al., 2011; Klenner et al., 2015; Felsenthal & Zelzer, 2017).

So far, FESA of the humerus of *Chelonia mydas* (ZFMK 70222) has been computed for a foreflipper downstroke and upstroke during underwater flight (Krahl et al. (chapter 2)). Contrastingly, the hindflipper is employed in rowing and maneuvering. Therefore, we provide a preliminary FESA for the femur of the same *Chelonia mydas* specimen (Fig. 1) to highlight differences in muscle orientations, functions, and forces. Lines of action (LOA) were derived with the help of the skeleton of ZFMK 70222 and by combining literature with osteological correlates on the cheloniid femur (Fig. 2). Muscle functions (Tab. 1) and agonistic and antagonistic muscle pairs (Tab. 2) were determined geometrically. By aiming at a homogenized compressive stress distribution, the first stage of FESA (from which load cases can be derived) was conducted. Computed muscle forces for femur muscles (Tab. 3) seem to show a tendency to differ to humerus muscles by an emphasis of the abductors vs. the depressors.

2. Material and Methods

2.1 Lines of action

Muscle attachments on the femur of *Chelonia mydas* were experimentally derived for the FE model. They are based on Walker's (1973) depiction of femur muscle attachments for *Pseudemys* (Fig. 20, p. 56) and the discussion in the text on differences in locomotor musculature of sea turtles. Additionally, muscle scars on the *Chelonia mydas* femur were studied and correlated hypothetically with the respective muscles attaching to them (Fig. 2). Muscle scars as well as lines of action partially imply divergences to Walker's (1973) muscle attachment depiction of *Pseudemys* and need testing by a dissection in the future. Threads were taped onto the skeleton of a *Chelonia mydas* (ZFMK 70222) from the Zoologisches Forschungsmuseum König, Bonn, Germany to retrieve LOA for all locomotory muscles that insert into, span, or originate from the sea turtle femur. LOA represent the direct connection in a straight line between origin and insertion of a muscle. Geometrical determination of muscle functions was based on these which led to the arrangement of muscles into pairs or groups of agonists and antagonists.

In the case of e.g., m. puboischiofemoralis externus, which has a very large origin area, relatively extreme points were chosen for thread attachment (on the anteroventral pubis and the posteroventral ischium). M. femorotibialis arises from a large area that covers most of the femoral shaft. To receive a better concurrence of the FE model and reality, m. femorotibialis origin was split into several artificial portions that yield only fractions of the total force of this muscle. If a muscle has two heads, it was displayed by two threads (e.g. m. flexor tibialis internus and flexor tibialis externus). Yet, only the muscle‘s resultant vector was transferred into the FE model.

The pelvis of Testudines is encased in the shell. Therefore, the plastron of ZFMK 70222 was mounted off the skeleton. Due to the remaining carapace, it was impossible to take pictures of the hindflipper in strict anterior, dorsal, posterior, and ventral view. Instead, it was made sure that each muscle was photographed from at least two different perspectives. Line drawings were produced of these photos. Then the FE model was tilted in the same position as in the drawing and LOA could be entered into the model. Photographs were edited with Photoshop CS4.

To describe sea turtle femur morphology, anterior/posterior, dorsal/ventral, and proximal/distal are adopted from Romer (1976) for the following text. *Chelonia mydas* hindflipper muscle names are used according to Walker (1973). To describe femur movement the terminology of Walker (1971a) is employed here, i.e., protraction/retraction, adduction/abduction, and long axis rotation.

2.2.Generation of FE model and FESA

The *Chelonia mydas* femur was scanned with a v|tome|x s 240 from General Electric phoenix|x-ray (Wunstorf, Germany), an industrial micro-CT scanner, at the Section Paleontology, Institute of Geosciences, Rheinische Friedrich-Wilhelms-Universität Bonn, Germany. Rotational x-ray images were processed with the software datos|x from which image stacks in x-y, x-z, and y-z direction were generated with VGStudio MAX (Volume Graphics).

The image stack in z direction was exported to Simpleware ScanIP 5.1. Via grey scale selection the bone (spongiosa and cortex) was selected in all images of the z directed image stack. This way bone was segmented out and used to create a volumetric femur model. Next, the 3-d model was meshed which was then imported into ANSYS 16.0 (ANSYS Inc., Canonsberg, PA, USA). The 3-d *Chelonia mydas* femur model was adjusted to the size of the modeled bone.

Element type "Solid92" was used to build the femur FE model from. Bearings to constrain movement of the femoral head were added onto the femoral head. 33268 tetrahedral elements and 48953 nodes make up the cheloniid femur FE-model. A Poisson’s ration of 0,3 was used to model bone, independent of its microstructure (Preuschoft & Witzel, 2005; Witzel & Preuschoft, 2005). Young’s moduli were assigned to regions with different microstructures based on selection of greyscales. Spongy bone increases in density from the centre towards the compact cortical outer layer of the bone. Accordingly, Young’s moduli increase from the bone centre towards the bone surface. So Young’s moduli of 330 MPa and 500 MPa were collated for spongy bone and of 12000 MPa and 17500 MPa for compact cortical bone according to Sverdlova & Witzel (2010).

Muscle attachments on the sea turtle femur and LOA were pictured in drawings of the femur in anterodorsal, anteroventral, posteroventral, posterodorsal. Based on these, force vectors were amended to the model (Fig. 1 a and e). The direction of the vectors in the three-dimensional space is given by the LOA and their origin by their attachments to the femur. Muscle force is expressed by vector size.

Muscles that span the acetabulum, femur, and knee (m. iliofibularis, m. ambiens, m. pubotibialis, m. iliotibialis, m. flexor tibialis internus, m. flexor tibialis externus), i.e., two-joint muscles, do not act on the femur directly but their resultant vectors contribute to the counterforce. Tibia and fibula impose the counterforce onto the distal epicondyles of the femur. The m. femorotibialis has a large origin area that covers most of the dorsal and ventral turtle shaft. Therefore, its force vector was split into several fractions that add up in sum to it again, to cover the large origin surface a little more realistically (Fig. 1 a and e). This also leads to a compressive stress distribution that is more homogenous. It is impossible to create curved lines in ANSYS. So it is necessary to divide force vectors in several smaller straight ones with changing directions to describe a muscle that wraps around bone.

In a first step of FESA it is attempted to receive a respective bone model with a homogenous compressive stress distribution where all moments are balanced (Fig. 1 b, c, f, g). This step does not represent a particular load case, i.e., all muscles pull with maximum muscle force at the same time and load the bone with axial compression. Load cases, that are a snapshot of a specific point during the limb movement cycle, are usually derived from this version. All calculated load cases are superposed again and should, in sum, show a comparable compressive stress distribution in theory (Krahl et al. (chapter 2); Krahl et al. (chapter 4)). The cheloniid femur FESA shows the status quo of the very first step of FESA, where all muscles are active at have a high muscle force output. Based on this model, load cases could be computed. Agonistic and antagonistic muscle groupings, that are necessary for load case generation, are done (Tab. 2).

By iteration muscle forces were approximated (Tab. 3): First, a FESA calculation was computed with presumed muscle forces and the corresponding compressive stress distribution was displayed. Second, the goal was to reduce the bending moment and obtain a more homogenous compressive stress distribution. The muscle forces were adjusted accordingly and a new FESA was calculated. Until the mentioned goal was achieved, these steps were reiterated (Witzel & Preuschoft, 2005; Sverdlova & Witzel, 2010).

3 Results

3.1 Osteological correlates on the *Chelonia mydas* femur

The femur of *Chelonia mydas* shows several osteological correlates (Fig. 2 a, b): The femoral head and the distal epicondyles show a facet margin (depicting the area which is covered by hyaline cartilage in the living turtle). Trochanter minor and trochanter major fuse and form a ridge connecting those two with each other, enclosing the intertrochanteric fossa. Both trochanters display a facet margin, too. These areas have a pitted, unfinished looking surface. Distally to this demarcation line the trochanter minor shows anterodorsally a rugose surface, and anteroventrally a more mildly rugose and pitted surface. Posteriorly to posterodorsally the trochanter major bears a large proximodistally stretching scar. Further, the ventral proximal surface of the femur is fan-shaped striated, as well as the ventral and dorsal surfaces stretching towards the epicondyles distally. Dorsally, on the anterior half of the shaft, from approximately one third of the femur length to approximately half its length, is a large oval muscle scar. Anteriorly it is deeply hollowed while distally, proximally, and posteriorly it merely shows a slightly striated to pitted demarcation.

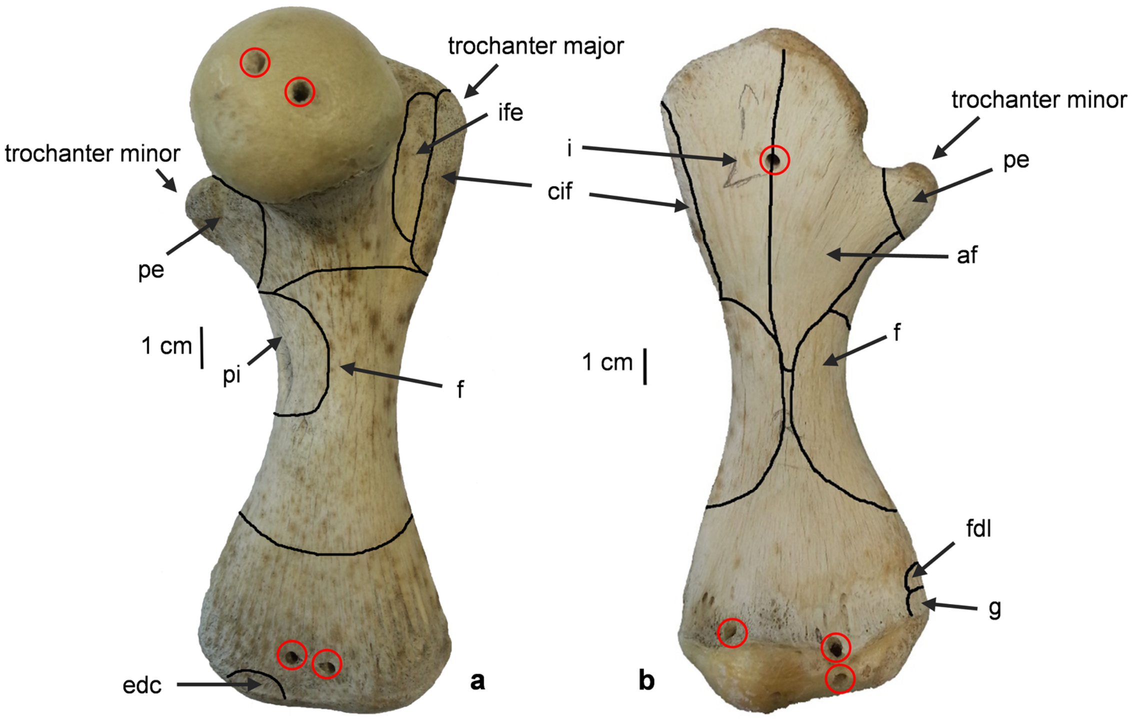

Fig. 2: Muscle attachment areas on *Chelonia mydas* femur. In a) dorsal and b) ventral view based on Walker (1973). Red circles mark drill holes from mounting. Abbreviations: af, m. adductor femoris; cif, m. caudi-iliofemoralis; m. edc, extensor digitorum communis; f, m. femorotibialis; fdl, m. flexor digitorum longus; g, m. gastrocnemius; i, m. ischiotrochantericus; ife, m. iliofemoralis; pe, m. puboischiofemoralis externus; pi, m. puboischiofemoralis internus.

3.2 Muscle attachments on femur and muscle functions

M. puboischiofemoralis internus inserts anterodorsally just distal to the femoral head in *Pseudemys scripta elegans* (Walker, 1973). So for the FE model, the large muscle scar on the anterodorsal femur was correlated with the insertion area of this muscle (Fig. 2 a). In comparison to *Pseudemys* the muscle attachment area of m. puboischiofemoralis internus in *Chelonia mydas* is displaced relatively distally. The anteroventral portion of m. puboischiofemoralis internus is a femoral protractor and rotates the femur along its long axis, namely its anterior side down. Its posterodorsal portion is a protractor and abductor of the femur and rotates it along its long axis with its anterior side down (Tab. 1).

M. iliofemoralis inserts into the femur of *Chelonia mydas* similar as in *Pseudemys* (Walker, 1973), i.e., dorsally along the margin of trochanter major (Fig. 2 a). This muscle is a femoral abductor (Tab. 1).

M. iliofibularis is a two-joint muscle that originates from the ilium, spans the acetabular and the knee joint and inserts into the fibula (Zug, 1971; Walker, 1973). It affects the FE model only indirectly by contributing to the counterforce that the fibula exerts onto the epicondyles of the femur. M. iliofibularis rotates the anterior femur side up and flexes the crus. It possibly abducts the femur, too (Tab. 1).

M. iliotibialis is a two-joint muscle that contributes with m. ambiens and m. femorotibialis to the patellar tendon that wraps around the distal femur end and then attaches to the tibia (Walker, 1973). It adds to the counterforce that acts on the femoral epicondyles. M. iliotibialis is a femoral abductor and possibly retractor. It might as well slightly rotate the femur along its long axis with the anterior side down. It extends the crus (Tab. 1).

M. ambiens, another two-joint muscle, inserts into the patellar tendon which attaches to the tibia together with m. iliotibialis and m. femorotibialis (Zug, 1971; Walker, 1973). It adds to the counterforce as described above. M. ambiens protracts, adducts, and rotates the anterior side if the femur down. It extends the crus, too (Tab. 1).

M. femorotibialis origin is mainly situated on the dorsal femur. It overlaps anteriorly and posteriorly onto its ventral side. In *Pseudemys* it extends proximally far up to the attachment surface of the m. iliofemoralis. This seems to be highly unlikely in *Chelonia mydas*, as the m. puboischiofemoralis internus insertion has been shifted further distally along the dorsal shaft. Therefore, only little less than half of the femoral shaft would be available as dorsal origin area for m. femorotibialis (Fig. 2 a and b). Yet, its origin area could still reach m. iliofemoralis proximally by posteriorly running past m. puboischiofemoralis internus insertion. Ventrally m. femorotibialis origin surface might spread a little more proximal than on the dorsal shaft, but no further than up to the muscle scar of m. puboischiofemoralis internus. M. femorotibialis extends the crus (Tab. 1).

M. extensor digitorum communis originates from just above the knee joint capsule in *Pseudemys* (Walker, 1973). For the FE model built in this study, we adopted this position because the distal shape of the femur of *Chelonia mydas* is very similar to that of *Pseudemys* (Walker, 1973), which suggests that no major changes evolved in the geometrical arrangement of extensor and flexor origin areas of the crus and pes of Cheloniidae in comparison to other turtles (Fig. 2 a). M. extensor digitorum communis wraps around the posterior condyle of the femur and the proximal tibia. M. extensor digitorum communis extends the crus and given its complexity spanning several joints, it should be expected to have other functions functions as well (Zug, 1971; Walker, 1973) (Tab. 1), of which the deduction is beyond the scope of this work.

M. puboischiofemoralis externus appears to insert into the cheloniid femur similarly as in *Pseudemys* (Walker, 1973), namely into trochanter minor and the associated muscle scar (Fig. 2 a and b). Therefore, the facet margin of the trochanter minor delineates fibrocartilage. The anterior portion of m. puboischiofemoralis externus adducts, protracts, and rotates the anterior side of the femur up. Unlike the posterior portion which adducts and retracts the femur (Tab. 1).

M. caudi-iliofemoralis was placed onto the muscle scar on the trochanter major posteriorly (Fig. 2 a and b). This muscle adds to femoral abduction, retraction, and rotates the anterior side of the femur up (Tab. 1).

M. ischiotrochantericus inserts into the intertrochanteric fossa in *Pseudemys*, next to m. caudi-iliofemoralis. In *Chelonia mydas* the insertion area appears to be enlarged. It reaches distally that far, that it comes into contact with the m. femorotibialis origin area (Fig. 2 b) (compare to *Pseudemys* Walker (1973), Fig. 20 A, B, p. 56). This fits well with the observation that the pelvic origin area of m. ischiotrochantericus is greatly expanded anteriorly in cheloniids, too (Walker, 1973). M. ischiotrochantericus retracts and adducts the femur and wraps around the ridge formed by the fused trochanter major and trochanter minor. Additionally, it adds a minor rotational component (anterior femur side up) to locomotion (Tab. 1).

The attachment surface of m. adductor femoris reaches proximally the one of m.

Muscle	**muscle function after Walker (1973)**	**muscle function after Zug (1971)**	**muscle function after Wyneken (2001)**	**own interpretation**
m. puboischiofemoralis internus	femoral protraction and posterodorsal portion additionally femoral abduction	head from pubis: femoral protractor and rotator (anterior side ventrally), posterodorsal belly abducts the femur	protracts and abducts the femur	anteroventral part: femoral protractor, rotation (anterior side down) posterodorsal part: femoral protractor, abductor, rotation (anterior side down)
m. iliofemoralis	femoral protraction and abduction	femoral abductor	/	femoral abductor
m. iliofibularis	flexes crus, and retracts femur	femoral abductor, crus flexor and crus posterior rotation of crus	/	flexes crus, rotates (anterior side up) femur and crus posteriorly, possible femur abductor
m. iliotibialis	femoral abductor and retractor, crus extensor	femoral abductor and extensor of the crus	/	abduction of femur and possibly retraction, knee extensor, possibly a slight rotational component (anterior side down)
m. ambiens	femoral adductor and protractor, crus extensor		protracts and adducts femur, crus extensor	femoral protractor, adduction, knee extensor, possibly slight rotation (anterior side down)
m. femorotibialis	extensor of the crus		/	knee extensor
m. puboischiofemoralis externus	femoral adduction (major function), but probably also femoral protraction and retraction	protracts and rotates femur (counter-clockwise)	adducts femur	anterior portion: femoral adductor, limb protractor rotation (anterior side up) posterior portion: adduction, retraction
m. caudi-iliofemoralis	femoral retractor and abductor	femur abductor and rotator (counter-clockwise)	/	femoral abductor and retractor and rotation (anterior side up)
m. ischiotrochantericus	femoral retraction	femoral retractor and rotator	retracts femur	femoral retraction, adductor due to deflection on trochanters, slight

				rotational component (anterior side up)
m. adductor femoris	adducts and retracts the femur	femoral adductor	adductor of femur	femoral retractor and adductor
m. flexor tibialis internus	retracts femur, flexes crus	femoral abductor and crus flexor	femoral retraction and flexion, influences the posterior flipper shape	anteroventral portion: femoral retractor and knee flexor, adduction posterodorsal portion: femoral retractor and knee flexor, adduction, rotational component (anterior side up)
m. flexor tibialis externus	retracts femur, flexes crus			ventral portion: femoral retraction and knee flexor, adduction dorsal portion: femoral retractor and knee flexor, adduction, rotational component (anterior side up)
m. pubotibialis	flexes the crus and retracts the femur			femoral retractor, knee flexor, adduction
m. extensor digitorum communis	extension of crus, dorsiflexes the mesotarsal joint, extends digit I	extensor of shank, supination of foot	/	extends crus
m. gastrocnemius	flexes crus, pes, toes, abduction of mesotarsal V	foot flexor, the different heads allow rotation in both directions	/	flexes crus
m. flexor digitorum longus	flexes pes and digits I-V	flexor of digits I-IV	/	flexes crus

Tab. 1: Functions of Cheloniidae femur musculature

/= no muscle function deduced by the respective author puboischiofemoralis externus and runs parallel to m. femorotibialis down the shaft (Walker, 1973). This insertion area appears enlarged in *Chelonia mydas*. It covers the whole ventral surface which is formed by the fused trochanter minor and trochanter major that enclose the intertrochanteric fossa. M. adductor femoris adducts and retracts the femur (Tab. 1).

M. flexor tibialis internus is a two-joint muscle that spans the femur. It adds to the counterforce which tibia and fibula impose on the femoral epicondyles. Also, both m. flexor tibialis externus muscle bellies wrap around the proximal ventral femur. The anteroventral portion of m. flexor tibialis internus acts in femoral retraction and adduction and flexes the crus. The posterodorsal portion has the same functions, but also adds to rotating the anterior side of the femur up (Tab. 1).

M. flexor tibialis externus also spans the femur as a two-joint muscle. Its two muscle bellies wrap around the ventral proximal femur. Thereby m. flexor tibialis externus adds to the counterforce in the same way as described above. The ventral portion of the m. flexor tibialis externus retracts and adducts the femur and flexes the crus. Its dorsal portion shows essentially the same functions as the ventral portion and additionally aids in femur rotation (anterior side up) (Tab. 1).

M. pubotibialis is a two-joint muscle which adds to the counterforce imposed by tibia and fibula onto the distal femur. M. pubotibialis retracts and adducts the femur and aids in crus flexion (Tab. 1).

Muscle origins of m. flexor digitorum longus and m. gastrocnemius were placed above the fibular condyle on the posterior side of the femur comparable to *Pseudemys* (Walker, 1973). As the distal cheloniid femur does not show fundamental differences to *Pseudemys* it is presumed, that the muscular arrangement at the origin areas of extensors and flexors is basically the same in both taxa. M. flexor digitorum longus and m. gastrocnemius flex the crus. These two muscles are very complexly arranged in several layers reaching over several joints, so one may presume that they yield various other functions as well of which the deduction is beyond the scope of this work (Tab. 1) (please view Zug, 1971; Walker, 1973), but their deduction was beyond the scope of this work.

3.3 FESA of *Chelonia mydas* femur

FESA and muscle forces were computed for the first step of FESA, i.e., the hypothetical case in which all moments are balanced and all muscles pull at the same time with maximum force. The ventral bony ridge, formed by the fused trochanter minor and major, and the distal epicondyles of the sea turtle femur remain unloaded by compressive stress unless muscles that wrap around these structures are introduced: Both muscle bellies of m. flexor tibialis internus and m. flexor tibialis externus, m. adductor femoris, and m. ischiotrochantericus wrap around the ridge formed by the two fused trochanters on the ventral femur. The knee tendon, that results from m. ambiens, m. femorotibialis, and m. iliotibialis that converge, wraps around the distal femur. Further, m. extensor digitorum communis wraps around the fibular epicondyle. The muscle wrappings load the respective bony structures by compressive stress because the resultant vectors run through the bone.

Agonists	Antagonists
m. iliotibialis, m. femorotibialis, m. ambiens (protraction, knee extension]	m. pubotibialis, m. flexor tibialis internus, m. flexor tibialis externus (retraction, knee flexion)
m. iliotibialis (abduction, protraction, knee extension)	m. pubotibialis, m. flexor tibialis internus, m. flexor tibialis externus (retraction, knee flexion, adduction)
m. ambiens (adduction, protraction, knee extension)	m. ischiotrochantericus (retraction, adduction)
m. iliofemoralis (abduction)	m. iliofibularis (knee flexion, abduction)
m. puboischiofemoralis externus, anterior part (adduction of femur, but limb protraction)	m. caudi-iliofemoralis (abduction, retraction)
m. puboischiofemoralis internus (protraction, abduction) anteroventral portion	m. puboischiofemoralis externus, posterior part (adduction, retraction)
m. puboischiofemoralis internus (protraction, abduction) posterodorsal portion	m. adductor femoris (retraction, adduction)
m. extensor digitorum communis (crus extension)	m. flexor digitorum longus (crus flexion), gastrocnemius (crus flexion)

Tab. 2: Agonistic and antagonistic cheloniid femur muscles

FESA results depict low compressive stress by red, orange, and yellow (0 to -1,5 MPa for compact cortex (Fig. 1 b, f) and 0 to -0,3 MPa for spongy bone (Fig. 1 c, g)). The green colour spectrum stands for medium compressive stress (-1,5 to -3 MPa for compact cortex (Fig. 1 b, f) and -0,3 to -0,6 MPa for spongy bone (Fig. 1 c, g)) and the blue colour complex represents high compressive stress (-3 to -4,5 MPa for compact cortex (Fig. 1 b, f) and -0,6 to -0,9 MPa for spongy bone (Fig. 1 c, g)). Overall the compressive stress distribution delineates

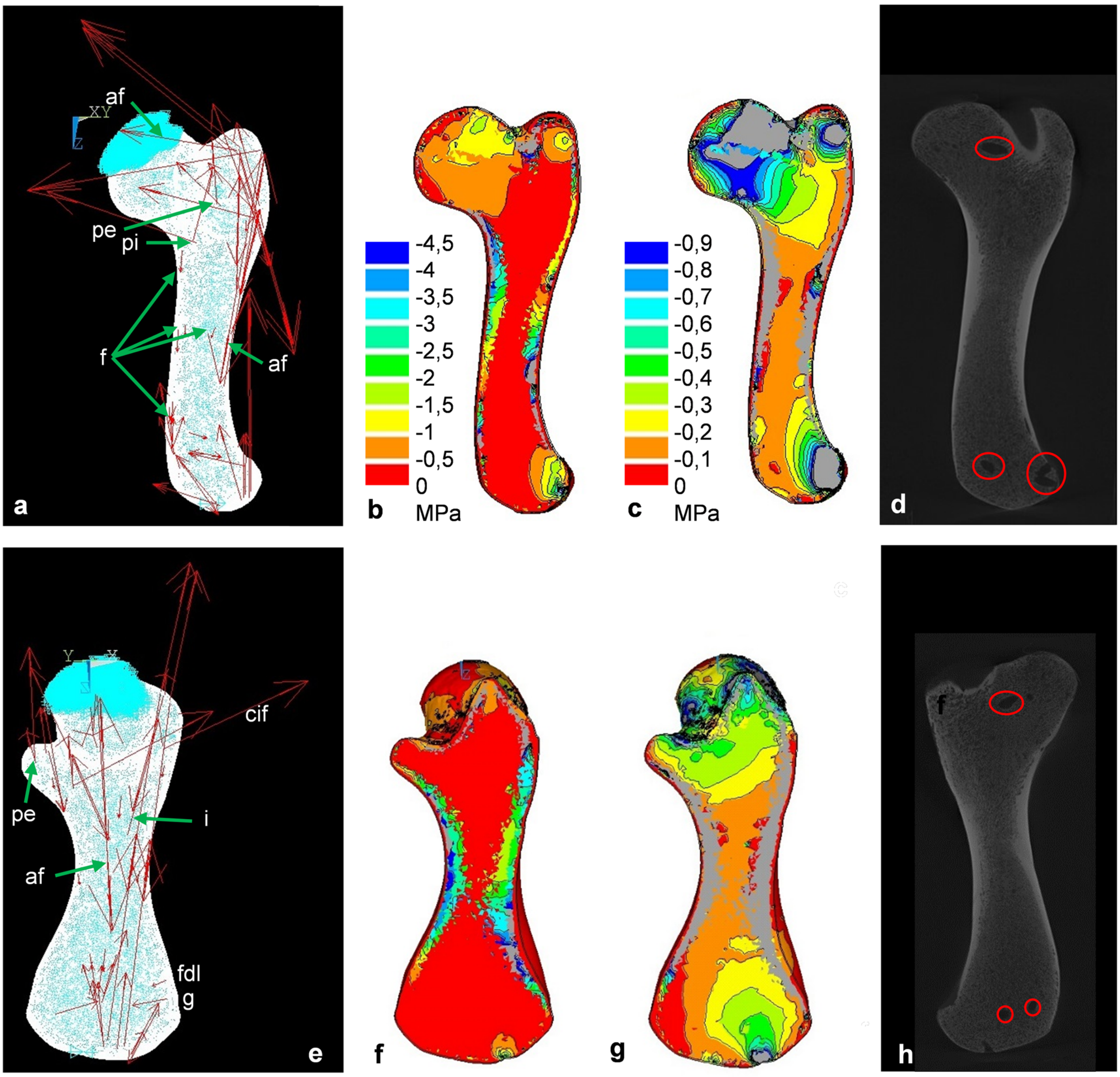

Fig. 1: FESA of *Chelonia mydas* femur. In a) anterior view, b)-d) dorsoventral sections, e) ventral view, f)-h) anteroposterior sections. Meshed FE model and force vectors in a) and e), compressive stress displayed for compact cortex in b) and f) and for spongy bone in c) and g). Selected micro-CT sections in d) and h). Red circles mark drill holes from mounting of the skeleton. Arrows that without annotations in a) and e) lie on the other side, or are resultant vectors from muscle wrapping. Abbreviations: af, m. adductor femoris; cif, m. caudi-iliofemoralis; fdl, m. flexor digitorum longus; g, m. gastrocnemius; i, m. ischiotrochantericus; pe, m. puboischiofemoralis externus; pi, m. puboischiofemoralis internus.

the following microstructure (Fig. 1 d, h): Generally, micro CT scans reveal the typical sandhour glass shape of tetrapod long bones. Compact cortical bone thins out from the centre of growth in the diaphyseal region towards the distal and proximal and epiphyses. Compact cortical bone grades into spongy bone towards the medullary region which is not an open medullary cavity but instead filled entirely with spongy bone. The femoral head, its dorsal neck, the bony ridge, and the ventrally flat surface formed by the fusion of trochanter minor and major are covered solely by a thin compact cortex that quickly grades into relatively dense spongy bone. The connection between the femoral head and the ridge formed by the two fused trochanters shows a thick layering of compact cortex that grades into very dense spongy bone of which the trabeculae seem to be oriented along a trajectory (proximoventral-dorsodistal). Further, compact cortical bone is thicker proximally on the proximodorsal femur shaft than distally on the same side while ventrally the thickest compacta is comparably further distally situated. Not optimal in the FESA results of the *Chelonia mydas* femur is that in dorsoventral section the high compressive stresses appear to be a little too distally on the ventral femur side and in anteroposterior direction they appear to be situated still a bit too distal on the posterior side (Fig. 1 b, f). This would still need to be worked on in the future.

Muscle	**Muscle force [N]**
M. puboischiofemoralis externus	150
M. puboischiofemoralis internus	200
M. femorotibialis	85
M. adductor femoris	60
M. ischiotrochantericus	150
M. iliofemoralis	100
M. caudi-iliofemoralis	75
M. extensor digitorum communis	45
M. gastrocnemius internal/tibial head	30
M. gastrocnemius external/femoral head & M. flexor digitorum longus	45
M. flexor digitorum longus	15

Tab. 3: Cheloniidae femur muscle forces

The highest muscle force is developed by m. puboischiofemoralis internus (200 N) (Tab. 3) which is mainly a protractor, abductor, and a rotator. Further m. puboischiofemoralis externus and m. ischiotrochantericus, which are responsible for femoral adduction, retraction, and rotation antagonistically to m. puboischiofemoralis internus, develop considerable muscle forces (150 N each) (Tab. 3). Muscle forces of two-joint muscles could not be computed with

FESA as they do not attach to the femur. They influence the functional loading of the femur indirectly by pulling tibia and fibula onto the femoral epicondyles and therefore axially compress the femur. The flexors (m. gastrocnemius and m. flexor digitorum longus) that arise from the distal femur appear to develop higher muscle forces in sum than the extensor that arises from the distal femur (m. extensor digitorum communis) (Tab. 3).

4. Discussion

4.1 Cheloniid femur muscle functions

Spanning threads into the hindlimb skeleton of ZFMK 70222 helped to devise muscle functions. LOA confirm that m. puboischiofemoralis internus is a femoral protractor. The posterior portion additionally aids in its abduction (Zug, 1971; Walker, 1973; Wyneken, 2001) and it also acts as a femur rotator (anterior side down) (Zug, 1971) (Tab. 1). M. iliofemoralis is a femoral abductor as described by (Zug, 1971). Its contribution to protraction (Walker, 1973) could not be confirmed (Tab. 1). M. iliofibularis flexes the crus (Zug, 1971; Walker, 1973) and aids in rotation of femur (anterior side up) and crus (Zug, 1971). It might also aid in femoral abduction as described by (Zug, 1971) (Tab. 1). Zug (1971) treated m. iliotibialis, m. femorotibialis, and m. ambiens due to their common insertion into the patellar tendon as one muscle, also termed m. triceps femoris, which assists in femoral abduction and extension of the crus. Zug (1971) did not further discriminate muscle functions for the geometrically very differently arranged muscle bellies. Walker (1973) discussed all three muscle bellies separately despite their common insertion, like we did. M. iliotibialis, m. femorotibialis, and m. ambiens are crus extensors (Walker, 1973). We confirm that m. iliotibialis is a femoral abductor and it may also be a minor retractor (Walker, 1973), but the LOA show, that it may minorly contribute to rotating the anterior side of the femur down. M. ambiens is a femoral adductor and protractor (Walker, 1973) and it was found to additionally rotate the anterior side of the femur down (Tab. 1).

We discriminated m. puboischiofemoralis externus into its two muscle portions (anterior and posterior). Both aid in femur adduction (Walker, 1973; Wyneken, 2001). The anterior portion is a femoral protractor (Zug, 1971; Walker, 1973) and rotator (Zug, 1971). The posterior portion aids in femur retraction (Walker, 1973) (Tab. 1). LOA display that m. caudi-iliofemoralis is a femoral retractor (Walker, 1973), abductor (Zug, 1971; Walker, 1973), and rotator (anterior femur side up), in contrast to Zug (1971) who interprets it as the opposite. Zug (1971) studied terrestrial and semi-aquatic turtles and no Chelonioidea, so the different function could be due to a different geometrical arrangement in chelonioid turtles

(Tab. 1). M. ischiotrochantericus assists in femoral retraction (Zug, 1971; Walker, 1973; Wyneken, 2001), minor rotation (anterior femur side up) (Zug, 1971), and it may add to femoral adduction as it wraps around the fused trochanter major and trochanter minor ventrally that encloses the intertrochanteric fossa (Tab. 1). We confirm that m. adductor femoris aids in femoral adduction (Zug, 1971; Walker, 1973; Wyneken, 2001) and retraction (Walker, 1973) (Tab. 1). Zug (1971) and Wyneken (2001) do not subdivide the m. flexor cruris into its several bellies to ascribe functions to each of them. Walker (1973) depicts the function of the different bellies of the m. flexor cruris (m. flexor tibialis externus, m. flexor tibialis internus, m. pubotibialis), unlike Zug (1971) and Wyneken (2001) who assign functions to this whole muscle complex. We further subdivided m. flexor tibialis externus and m. flexor tibialis internus into their subportions, i.e, ventral and dorsal for the former and anteroventral and posterodorsal for the latter. M. puboischiotibialis is not described here, because it is considered to be reduced in Chelonioidea (Walker, 1973). The authors agree with Wyneken (2001) and Walker (1973) who merely describe it as part of the m. flexor cruris, to aid in retraction and flexion of the crus (Walker, 1973; Wyneken, 2001). The latter function is also depicted by Zug (1971). Zug (1971) finds this muscle complex to be a femoral abductor, while we found m. flexor tibialis internus, m. flexor tibialis externus, and m. pubotibialis to be adductors. LOA also suggest a rotational function of the posterodorsal muscle portion of m. flexor tibialis internus and the dorsal portion of m. flexor tibialis externus (Tab. 1).

M. extensor digitorum communis, m. gastrocnemius, and m. flexor digitorum longus are discussed by Walker (1973) and Zug (1971) as muscles with multiple functions. We did not study their functions in detail, but focused on the effect they have on the knee joint, as this work centers on FESA of the femur. M. extensor digitorum communis extends the crus and M. gastrocnemius and m. flexor digitorum longus flexes it (Tab. 1).

4.2 FESA and muscle forces

Despite that Young’s moduli were assigned in advance to micro-CT based greyscale values, the compressive stress distribution (Fig. 1 b, c, f, g) and the microstructure (Fig. 1 d, h) correspond relatively well. This underscores the experimentally derived LOA and computed muscle forces. Two-joint muscles (m. iliofibularis, m. iliotibialis, m. ambiens, m. flexor tibialis internus, m. flexor tibialis externus, m. pubotibialis) prove to be necessary to load the diaphyseal region of long bones homogenously with compressive stress as Krahl et al. (chapter 2) demonstrated for the cheloniid humerus. Two-joint muscles also prove to aid in keeping the integrity of the femur, while the pectoral muscles bridge the glenoid, flexors and extensors bridge the elbow joint.

Krahl et al. (chapter 2) have shown for the cheloniid humerus, that muscles which wrap around bone are indispensable to load bony processes. We find this corroborated because without muscle wrappings (m. flexor tibialis internus, m. flexor tibialis externus, m. adductor femoris, m. ischiotrochantericus, the knee tendon, and m. extensor digitorum communis) it would be impossible to load the distal epicondyles as well as the ventral ridge enclosing the intertrochanteric fossa of the femur of *Chelonia mydas* functionally by compression. Muscle wrappings are not reported in anatomical descriptions of sea turtles (Zug, 1971; Walker, 1973; Krahl et al. (chapter 2)) posing the exception, possibly because biomechanics are seldom the main focus of such a study. It would be nonetheless helpful if muscle wrappings could be documented in future (comparative) anatomical studies.

A notable difference between the FESA-derived humerus muscle forces and femur muscle forces in Cheloniidae is that the highest forces are attained for humerus depressors (m. pectoralis 1220 N, m. supracoracoideus 1100 N, m. coracobrachialis magnus 970 N) (Krahl et al. (chapter 2)) and for femur pro- and retractors (m. puboischiofemoralis internus 200 N, m. puboischiofemoralis externus and m. ischiotrochantericus 150 N each) (Tab. 3). It has to be taken into account that while there are solely two pectoral two-joint muscles (m. triceps brachii and m. biceps brachii) (Krahl et al. (chapter 2)), there are six pelvic two-joint muscles (m. iliofibularis, m. iliotibialis, m. ambiens, m. flexor tibialis internus, m. flexor tibialis externus, m. pubotibialis) that for which we cannot determine the muscle forces with FESA. Additionally, the functions the pectoral and pelvic two-joint muscles have are presumably more complex than those of muscles that cross only one joint. To confirm the observed trend that in cheloniid hindflipper musculature pro- and retraction are favored unlike to foreflipper musculature, one would have to find a way to determine muscle forces of the respective two-joint muscles. This could be done by electromyographic studies.

The flexors of the sea turtle hindflipper appear to exert higher forces than the extensor. Similar, extensors and flexors of the sea turtle hindflipper should be able to perform more complex movements than those of the foreflipper. This is because extensors and flexors that originate from the humerus are differentiated overall into more separated single muscle bellies as those that originate from the femur which remain complexly intertwined (Walker, 1973). The different degree of muscle differentiation and separation can also also expressed in their quantity, i.e., nine humeral extensors and flexors (Walker, 1973; Krahl et al. (chapter 2)) vs. three femoral extensors and flexors (Walker, 1973). These general differences between forelimb and hindlimb can be observed across Sauropsida (see e.g., Snyder, 1954; Zug, 1971; Walker, 1973; Zaaf et al., 1999; Meers, 2003; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Suzuki & Hayashi, 2010; Suzuki et al., 2011; Allen et al., 2014; Anzai et al., 2014).

To conclude, muscle functions were determined geometrically and are partially in agreement with existing literature. Comparable to cheloniid humerus FESA, muscle wrappings prove to be crucial for loading the ventral ridge of the femur that encloses the intertrochanteric fossa in sea turtles and the epicondyles. Two-joint muscles load the femoral diaphysis. A generally good match of the compressive stress distribution with the microstructure of the femur of *Chelonia mydas* proves how well our FE-model matches the actual loading conditions. Unlike force results of the humerus musculature, which favors humeral depressors, forces of femoral musculature favor femoral pro- and retractors. This is corroborated by the different modes of locomotion in which cheloniid fore- and hindflippers are employed: flying vs. rowing. Future research focussing on determining the muscuskeletal and biomechanical differences between the cheloniid fore- and hindflipper which are employed in underwater flight and rowing could shed further light on how underwater flight evolved. This knowledge could help with understanding convergently evolved underwater flight in other extant and extinct lineages of Tetrapoda.

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Chapter 6

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Krahl, A. Examining underwater flight in plesiosaurs and chelonioids by preparation, muscle reconstructions, building analog models, bone histology, and FE-methods.

Examining underwater flight in plesiosaurs and chelonioids by preparation, muscle reconstructions, building analog models, bone histology, and FE-methods

Anna Krahl

Keywords

marine reptiles, finite element analysis, muscle forces, underwater flight, flipper twisting

Abstract

Sauropterygia, nested within Diapsida, comprises secondarily aquatic marine Placodontia, Pachypleurosauria, Nothosauroidea, Pistosauroidea, and Plesiosauria. Basal Sauropterygia are restricted to the Triassic, plesiosaurs evolved by the Late Triassic and died out in the Late Cretaceous. Underwater flight evolved possibly convergently in Nothosauroidea and Plesiosauria. It has also been discussed that plesiosaurs were rowing, or combining rowing and flying. Nevertheless, the question how plesiosaurs swam has not been settled yet. Due to the probable functional convergence of plesiosaurs and sea turtles and the functional divergence of nothosaurs, based on the evaluation of their locomotor apparatus anatomy, sea turtles were chosen for a closer comparison to plesiosaurs. Turtle origins remain highly disputed. The first Chelonioidea are known from the Early Cretaceous. All recent chelonioid species are underwater flyers. During the limb cycle of a tetrapod compression, torsion, and bending loads are imposed on their long bones. Representative load cases analyzed with FESA and then superposed, reveal that long bones are in sum compressed. This means by trying to receive a homogenous compressive stress distribution in FESA muscle courses for (reconstructed) musculature can be mechanically corroborated. So this approach was employed for FESA of a sea turtle and plesiosaur humerus and femur. By employing the extant phylogenetic bracket, plesiosaur locomotory muscles were reconstructed. Potential humeral extensor and flexor surfaces were sampled histologically. Plesiosaur muscle reconstructions were compared to functional analogues, i.e., Chelonioidea, Spheniscidae, Otariinae, and Cetacea whose foreflipper osteology, joint anatomy, and associated myological specializations were shortly revised. Humerus muscles of *Caretta caretta* were dissected and measurements for physiological cross-sectional area were taken, from which maximum muscle forces were calculated. Lines of action (LOA), threads that connect muscle origins and insertions, were fixed on the fore- and hindflipper skeletons of *Chelonia mydas* and *Cryptoclidus eurymerus*. In the former for muscles that insert into, originate from, or span

humerus and femur and in the latter for all muscles of the fore- and hindflipper. Three positions, maximum and minimum flipper excursion and a neutral position during a hypothetical plesiosaur flipper beat cycle were fixed and the changes in muscle length were measured. Based on LOA muscle functions were derived geometrically and agonistic and antagonistic muscles were grouped together. From micro-CT scans, three dimensional finite element models were built of a humerus and a femur of *Chelonia mydas* and *Cryptoclidus eurymerus*. LOA were entered into the FE-models, and muscle forces were iteratively computed for two load cases, up- and downstroke, by printing out the compressive stress distribution. Except for the sea turtle femur, for which solely a prestage for the load cases was generated. To successfully load the plesiosaur long bones homogenously by compressive stress, muscle reconstructions had to be corrected for mechanical reasons. Muscles that wrap around bony processes were found to be essential for FESA in plesiosaurs and turtles. Also, plesiosaur muscle reconstructions were found to be partially supported by bone histology and corrected and amended by a comparison to the locomotor system of functional analogues. It was also determind whether plesiosaur and sea turtle humerus and femur muscles act within their physiological working range. Generally primary muscle functions of plesiosaurs and Sauropsida are relatively similar. Differences exist especially between the plesiosaur hindflipper and the rowing and steering hindflipper of sea turtles. Further, functions of extensors and flexors arising from humerus, femur, and distally to that differ, which were interpreted to contribute to a flipper long axis twisting mechanism in plesiosaurs. In sea turtle foreflippers and plesiosaur flippers the highest muscle forces are developed by depressors and then by elevators. In the sea turtle hindflipper protractors and retractors are found to be pronounced. Extensor and flexor muscle forces of plesiosaur fore- and hindflipper muscles are much higher than in sea turtles and corroborate a myological flipper twisting mechanism which was also predicted by hydrodynamic research.

1. Introduction

1.1 Nothosaur and plesiosaur osteology, joint morphology, and mode of locomotion

Within the clade Sauropterygia paraxial swimming evolved convergently in Placodontia, Nothosauroidea, and Plesiosauria. The two latter will be looked at in more detail because they possibly performed some kind of underwater flight. Placodontia, Pachypleurosauria, Nothosauroidea, and Pistosauroidea form the secondary aquatic diapsid clade Sauropterygia of which the origins lie either at the base of Lepidosauromorpha, Archosauromorpha or outside as sistergroup to both of them. Relationships within basal Sauropterygia are still currently debated. Plesiosauria represent the most derived clade within Sauropterygia (for review Krahl dissertation (chapter 1.1.1)). Nothosaurs are piscivors that remained restricted to the Triassic (late Olenekian to early Carnian) and Tethys. Plesiosaurs appear in the fossil record for the first time in the Late Triassic, disperse globally, and disappear at the Cretaceous-Paleogene boundary. Plesiosaurs display two morphotypes, i.e., plesiosauromorph (small head and long neck) and pliosauromorph (large head and short neck) correlated with a significant dichotomy in feeding and hunting strategies (for review Krahl (chapter 1.1.1)).

Nothosaurs were axially undulating swimmers probably supported by foreflipper propulsion of some sort (for review Krahl (chapter 1.2.1.1.3)), as the morphologically derived foreflipper (that probably looked rather like a dorsoventrally flattened paddle, possibly with digital webbing) (for review Krahl (chapter 1.2.1.1.1)) suggests. In nothosaurs, and plesiosaurs even more so, the dorsal scapular projection is reduced in length and the coracoid is enlarged.

Plesiosaurs have a much reduced tail, eventually with a tail fin, in comparison to nothosaurs. A much stiffened and shortened trunk and morphologically highly derived hydrofoil-like fore- and hindflippers, i.e., the flippers are dorsoventrally depressed and they taper to the flipper tip. Plesiosaur fore- and hindflippers are hyperphalangic. Nothosaur and sea turtle foreflippers show significantly less to no indication of hyperphalangy. Flipper morphologies appear to show variability which has been insufficiently studied so far (for review Krahl (chapter 1.2.1.2.1)). The only functional joints in the plesiosaur locomotor apparatus are said to be the shoulder and hip joint. A review shows though that minor movements are possible in the elbow/knee joint, wrist/ankle joint, and intracarpally/intratarsally. Metacarpal/metatarsal and phalangeal joint surfaces suggest quite substantial mobility that would need further studying. Further, the shoulder and hip joint morphology suggest that they were no ball-and-socket joints that would be necessary for three degrees of freedom which have been so far in plesiosaur locomotion descriptions been taken for granted considering the described flipper beat cycles. Although, especially these two joints leave a lot of room for speculation on how the joint surfaces may have actually looked like with cartilage caps (for review Krahl (chapter 1.2.1.2.2)).

Carettochelys insculpta has recently been shown to also fall into the spectrum between rowing and flying. In comparison to Otariinae, the rowing phase of the flipper beat cycle is much more pronounced and the flight phase is significantly shorter. As a potential mode of locomotion for plesiosaurs it was discussed here for the first time (for review Krahl (chapter 1.2.1.2.3.3)). While probably most osteological and joint morphological characters discussed that contradict rowing in plesiosaurs probably also contradict the *Carettochelys* swimming style in plesiosaurs, it correlates well with hindflipper tip excursion paths computed by Liu et al. (2015) (for review Krahl (chapter 1.3 for review)).

Various swimming modes have been suggested to have been employed by plesiosaurs, namely rowing, underwater flight, and rowing flight. Up to today the question has not been settled how plesiosaurs actually swam. Neither the question of how those four wings are coordinated, termed the „four wing problem“. Recent studies, partially made possible due to novel methodological approaches, stirred the debate up anew (Araújo & Correia, 2015; Liu et al., 2015; Muscutt et al., 2017; for review Krahl (chapter 1.2.1.2.3.1)). Pros and cons for one or the other type of locomotion in plesiosaurs were reviewed on an osteological and joint morphological basis (for review Krahl (chapter 1.2.1.2.3.2)).

1.2 Sea turtle osteology, joint morphology, and mode of locomotion

Origins of Testudines are highly debated, as well as interrelationships of turtle clades partially. Chelonioidea phylogeny is fairly settled in comparison to that. Six of the seven recent sea turtles fall into the clade Cheloniidae, with *Dermochelys coriacea*, the seventh sea turtle species, as sister group then forming Chelonioidea. Sea turtles have been shown to be a long-lived radiation that had evolved by the Late Cretaceous. Different diets and modulations of their life cycle and ecology lead to inter- and intraspecific competition avoidance of the recent sympatric sea turtle species (for review Krahl (chapter 1.1.2 for review)).

The turtle armor stiffened the sea turtle trunk. The hydrofoil foreflipper is dorsoventrally flattened and most part of it is formed by elongated metatarsals and phalanges of digits II-IV (for review Krahl (chapter 1.2.2.1)). The glenoid is an ellipsoid joint that inhibits humeral long axis rotation. The elbow joint is a hinge joint that is either being flexed or extended. Flipper rotation appears to be performed by a mobile wrist joint. Digital movement is much reduced in sea turtles (for review Krahl (chapter 1.2.2.2 for review)).

Extant chelonioids fly underwater. The foreflipper tip describes an „O“ that is skewed. The foreflipper is mostly moved dorsoventrally with little anteroposterior movement. The flipper profile is adjusted to the onstreaming water by what is presumably rotation in the wrist joint. The downstroke provides more propulsion than the upstroke (for review Krahl (chapter 1.2.2.3)).

The evaluation of osteology of the locomotor apparatus, joint morphology and mobility, and the mode of locomotion in Nothosauria, Plesiosauria and Chelonioidea showed that although nothosaurs show a higher osteological resemblance to plesiosaurs than sea turtles, sea turtles appear to be the better functional analogue to compare plesiosaurs to in terms of functional questions. This is because in plesiosaurs and sea turtles e.g., the coracoid is enlarged and the scapula reduced (in nothosaurs, too), the trunk is secondarily much stiffened, they have a reduced tail length, and dorsoventrally depressed hydrofoil foreflippers (and in plesiosaurs also hindflippers). Contrarily, nothosaurs show beginning of trunk stiffening, and paddle-like webbed foreflippers (for review Krahl (chapter 1.3)).

2. Lines of action

2.1 State of the art

Lines of action (LOA) connect a muscle`s origin and its insertion by a straight line (Krahl et al. (chapter 2.2.2, 4.2.1, 5.2.1)). Depictions of LOA are usually either drawn onto two dimensional pictures or line drawings (compare to e.g., Reilly & Blob, 2003, Fig. 2, p. 4331) or modelled in 3-d onto a skeletal model built from micro-CTs as for e.g., *Struthio camelus* (Hutchinson et al., 2015). None of the authors I am aware of have spanned threads into actual skeletons to depict the geometrical arrangement of the muscles.

Based on LOA, muscle functions were assigned to musculature inserting into, originating from, or spanning the humerus and femur of *Chelonia mydas* (Krahl et al. (chapter 2.3.1, 5.3.2)) and *Cryptoclidus eurymerus* (IGPB R 324) (Krahl and Witzel (chapter 3.3.2)). Muscle functions were geometrically devised as follows: Depending on whether muscles originate 1) cranially or anteriorly, 2) caudally or posteriorly, 3) dorsal, or 4) ventral to the glenoid or acetabulum their functions differ. 1) These muscles likely contribute to humerus or femur protraction, or in the case of two-joint muscles (e.g., m. ambiens) to limb protraction. Muscles originating like 2) are humerus/femur or forelimb/hindlimb retractors. 3) This type of muscles are elevators in flippers employed in underwater flight (cheloniid foreflipper and plesiosaur foreflipper and hindflipper) or abductors in flippers employed in rowing (cheloniid hindflipper). 4) these muscles aid in depression in flippers that are employed in underwater flight (cheloniid foreflipper and plesiosaur foreflipper and hindflipper) or adduction in flippers that are employed in rowing (cheloniid hindflipper) (Krahl and Witzel (chapter 3.2.3)).

To be more specific, muscles originate cranially/anteriorly and dorsally or ventrally or caudally/posteriorly and dorsally or ventrally to the glenoid or acetabulum. Accordingly, these muscles do not only have one function but at least a second function, i.e., protraction and elevation/abduction, protraction and depression/adduction, retraction and elevation/abduction, and retraction and depression/adduction (Krahl and Witzel (chapter 3.2.3)).

Further, many muscles also have a potential rotational function. Flipper/humerus/femur long axis rotation may take place in two different ways in each direction: Either 1) the flipper trailing edge is rotated upward or 2) the flipper leading edge is rotated downward, or 3) the flipper trailing edge is rotated downward and 4) the flipper leading edge is rotated upward. Muscles that contribute to 1) and 2) take their origin anteriorly/cranially and dorsally or posteriorly/caudally and ventrally relatively to the glenoid/acetabulum. Muscles that aid in 3) and 4) have an origin area that is placed anteriorly/cranially and ventrally or posteriorly/caudally and dorsally relatively to glenoid and acetabulum (Krahl and Witzel (chapter 3.2.3)). Therefore, muscle functions derived from their geometrical position in the three-dimensional space have often led to up to three functions (Krahl and Witzel (chapter 3.3.2); Tab. 1 and Tab. 2 in Krahl and Witzel (chapter 3)).

Abductor and adductor will be used to describe a limb movement towards the dorsal and ventral side for sprawling or rowing appendages (fore- and hindlimbs of crocodilians, lepidosaurs, and turtles (except for the sea turtle foreflipper)) (Krahl et al. (chapter 5.2.1)). For appendages employed in underwater flight, elevation and depression are used (sea turtle foreflipper and plesiosaur fore- and hindflipper) (Krahl et al. (chapter 2.2.2)). Myological terminology for Sauropsida follows the one established by topographical homology in Krahl and Witzel (chapter 3.3.1) for plesiosaurs.

2.2 Summary and comparison of results

2.2.1 Functions of humerus and femur muscles of Cheloniidae and Plesiosauria

Based on data on muscle courses obtained from the dissection of a foreflipper of a *Caretta caretta* specimen (Krahl et al. (chapter 2.2.1)) and based on literature (Walker, 1973). Threads representing the humerus musculature were spanned into the skeleton of a *Chelonia* *mydas* specimen (ZFMK 70222) (Krahl et al. (chapter 2)). Based on literature data (Walker, 1973) alone threads (i.e., LOA) were taped onto the hindflipper of ZFMK 70222 (Krahl et al. (chapter 5)). For the plesiosaur humerus and femur LOA are based on the muscle reconstructions of the entire foreflipper and hindflipper of *Cryptoclidus eurymerus* (IGPB R 324) (Krahl and Witzel (chapter 3.3.1)). The threads that represent the LOA were attached to a cast of IGPB R 324 foreflipper and hindflipper skeleton (Krahl et al. (chapter 4).

According to the principle described above (Krahl (chapter 6.1.1)) muscle functions were assigned to all muscles that insert into, originate from, or span the humerus or the femur of Cheloniidae (Krahl (chapter et al. 2.3.1, 5.3.2); Tab. 1 in Krahl (chapter 1); Tab. 1 in Krahl et al. (chapter 5)) and *Cryptoclidus eurymerus* (IGPB R 324) (Krahl and Witzel (chapter 3.3.2); Tab.1 and 2 in Krahl and Witzel (chapter 3)). For a more convenient comparison of the respective muscle functions two tables were created in which sea turtle and plesiosaur fore- and hindflipper (Tab. 1, 2). Muscle functions were discussed in comparison to the results of published literature so far in each of the four cases (Krahl et al. (chapter 2.4, 5.4.1); Krahl and Witzel (chapter 3.4.2)).

Muscle functions were derived for muscles that span the cheloniid glenoid, LOA (Krahl et al. (chapter 2.3.1)) are mostly in agreement with literature (Krahl et al. (chapter 2.4)). Especially m. triceps brachii and m. biceps brachii functions differ because due to FESA they were found to be necessary for diaphyseal compression. That means, pectoral muscles span the glenoid and insert into the proximal humerus and extensors and flexors of distal humeral origin span the wrist and other joints, but solely m. triceps brachii and m. biceps brachii span the diaphyseal region muscularly. Furthermore, some extensors (m. extensor radialis superficialis + extensor digitorum communis, m. extensor carpi ulnaris) and flexors (m. flexor carpi radialis, and m. flexor carpi ulnaris) were described for the first time as muscles that are capable of rotating the flipper due to their lines of action (Krahl et al. (chapter 2.4); Tab. 1 in Krahl et al. (chapter 2)).

muscle	**Plesiosauria**	**Cheloniidae**
m. latissimus dorsi (+ teres major)	eventually anteriormost portion protraction, posterior portion retraction, elevation; rotation (leading edge upwards)	elevation, protraction
m. subcoracoscapularis	anterior portion protraction, posterior portion retraction, both	elevation, retraction

	elevation, anterior portion rotation (leading edge downwards); posterior portion rotation (leading edge upwards)	
m. scapulohumeralis posterior	eventually minor elevation, rotation (leading edge downwards)	muscle not present
m. deltoideus clavicularis	protraction, depression, rotation (leading edge downwards)	depression, protraction
m. deltoideus scapularis	protraction, elevation, rotation (leading edge upwards)	elevation, protraction
m. triceps brachii	elevation, rotation (leading edge downwards), humeral head displaces ulna slightly dorsally	elbow extension, diaphyseal compression
m. pectoralis	anterior portion protraction, posterior portion retraction, both depression, posterior portion rotation (leading edge downwards); anterior portion rotation (leading edge upwards)	depression, retraction
m. supracoracoideus	anterior portion protraction, posterior portion retraction, both depression	posterior portions: depression, retraction anterior portions: depression, protraction
m. coracobrachialis brevis	retraction, depression, rotation (leading edge upwards)	depression, retraction
m. coracobrachialis longus	retraction, depression, rotation (leading edge upwards)	depression, retraction
m. biceps brachii + brachialis	retraction, depression, rotation (leading edge downwards), brachialis slightly displaces ulna ventrally	elbow flexion, diaphyseal compression, retraction
m. extensor carpi ulnaris	displaces ulna dorsally/ although weakly supported by EPB an insertion to metacarpal V would allow extension of metacarpal V on the adjacent distal carpal	antebrachial extensor and rotates flipper
m. extensor digitorum communis	extends metacarpals on distal carpals	extends antebrachium, manus, and rotates flipper

m. supinator longus and extensor carpi radialis	displaces radius slightly dorsally/ weakly supported insertion that expands onto the radiale would allow to displace the whole radial side of the carpus slightly	antebrachial flexor, antebrachial extensor
m. pronator teres	displaces radius ventrally	antebrachial flexor
m. flexor carpi ulnaris	displaces ulnar side of carpus ventrally/badly supported possibly additional insertion to metacarpal V would allow to flex metacarpal V on the distal carpal element	flexes antebrachium and manus and rotates flipper
m. flexor digitorum longus (and flexores digitorum superficialis)	flexion of each digit	flexes antebrachium, manus and digits
m. flexor carpi radialis	flexes metacarpal I on adjacent distal carpal element/ equally well supported would be an insertion to the radial side of the carpus allowing to displace the radial side of the carpus slightly ventrally	antebrachial flexor and rotates flipper

Tab. 1: Comparison of glenoid-spanning musculature in Cheloniidae and Plesiosauria

Functions of muscles that arise from the cheloniid pelvis and span the acetabulum are in general accordance with the existing literature, but often further functions were amended (Krahl et al. (chapter 5.4.1)). The numerous two joint muscles of the cheloniid hindflipper, namely m. iliofibularis, m. iliotibialis, m. ambiens, m. flexor tibialis internus, m. flexor tibialis externus, and m. pubotibialis are necessary for diaphyseal compression of the sea turtle femur. Functions of the extensor and flexors that arise from the distal cheloniid femur were not studied in detail as they are highly complex (Zug, 1971; Walker, 1973) and would require thorough dissection and studies (Krahl et al. (chapter 5.4.1); Tab. 1 in Krahl et al. (chapter 5)).

muscle	**Plesiosauria**	**Cheloniidae**
m. iliotibialis	elevation, retraction, rotates anterior edge up, slight dorsal displacement of tibia on distal femur	abduction of femur and possibly retraction, knee extensor, possibly a slight rotational component (anterior side down)

m. femorotibialis	slight dorsal displacement of tibia on distal femur	knee extensor
m. ambiens	protraction, (if femur depressed, similar to delt. clav. rotates anterior edge up; if elevated then rotates anterior edge down), slight dorsal displacement of tibia on distal femur	femoral protractor, adduction, knee extensor, possibly slight rotation (anterior side down)
m. iliofibularis	elevation, rotates anterior edge down, retraction, rotates anterior edge up (as long as fibula above origin)	flexes crus, rotates (anterior side up) femur and crus posteriorly, possible femur abductor
m. iliofemoralis	elevation, retraction, rotates anterior edge up	femoral abductor
m. puboischiofemoralis internus	four possible muscle bellies: elevation -from pubis: elevation, rotates anterior edge down, protraction -from ischium: elevation, rotates anterior edge up, minorly retraction -from ilium: elevation, rotates anterior edge up, minorly retraction -from vertebral column: elevation, protraction	anteroventral part: femoral protractor, rotation (anterior side down) posterodorsal part: femoral protractor, abductor, rotation (anterior side down)
m. puboischiotibialis	depression, rotates anterior edge down	
m. pubotibialis	protraction, (if femur depressed, similar to delt. clav. rotates anterior edge up; if elevated then rotates anterior edge down)	femoral retractor, knee flexor, adduction
m. flexor tibialis internus	from ischium: retraction, depression, rotates anterior edge down from ilium/sacral vertebrae/transverse processes of caudal vert.: retraction, rotates anterior edge down, elevation	anteroventral portion: femoral retractor and knee flexor, adduction posterodorsal portion: femoral retractor and knee flexor, adduction, rotational component (anterior side up)
m. flexor tibialis externus	from ilium: rotates anterior edge down, retraction, elevation from ischium: rotates anterior edge down, retraction, depression	ventral portion: femoral retraction and knee flexor, adduction dorsal portion: femoral retractor and knee flexor, adduction, rotational component (anterior side up)

m. caudifemoralis brevis and m. caudifemoralis longus	elevation, retraction, rotates anterior edge down	femoral abductor and retractor and rotation (anterior side up)
m. ischiotrochantericus	retraction, depression, rotation of anterior edge down	femoral retraction, adductor due to deflection on trochanters, slight rotational component (anterior side up)
m. adductor femoris	from anterior ischium: depression from lateroposterior ischium: depression, retraction	femoral retractor and adductor
m. puboischiofemoralis externus	from pubis: depression, protraction, rotates anterior edge up from ischium: depression, retraction, rotates anterior edge down	anterior portion: femoral adductor, limb protractor rotation (anterior side down) posterior portion: adduction, retraction
m. extensor digitorum longus	extension of digits I-IV (on tarsometatarsal joints)	extends crus
m. gastrocnemius internus and m. gastrocnemius externus	flexors of all 5 digits in all phalangeal joints, also acting on metatarsal I and V	flexes crus
m. flexor digitorum longus	long flexors of all 5 digits	flexes crus

Tab. 2: Comparison of acetabulum-spanning musculature in Cheloniidae and Plesiosauria

Functions of muscles that span the glenoid in plesiosaurs are often interpreted with up to three possible functions (Krahl and Witzel (chapter 3.3.2); Tab. 1) which is due to their three-dimensional assessment (Krahl and Witzel (chapter 3.2.3)). This is only rarely the case in the literature so far (e.g. m. pectoralis, m. supracoracoideus by Watson (1924) and m. latissimus dorsi (+ m. teres major) by Robinson (1975) (Tab. 1 in Krahl and Witzel (chapter 3)). A division of muscles into different functional portions was determined by their relative disposition of the glenoid (m. latissimus dorsi (+ m. teres major), m. subcoracoscapularis, m. pectoralis, m. supracoracoideus). Only Watson (1924) reconstructed functional subportions for m. subcoracoscapularis, too (Krahl and Witzel (chapter 3.4.1.1); Tab. 1 in Krahl and Witzel (chapter 3)).

In comparison to the foreflipper, only two authors, Robinson (1975) and Carpenter et al. (2010), have undertaken the challenge of reconstructing plesiosaur hindflipper musculature. In both works, hindflipper musculature has been reconstructed incompletely (Tab. 2 in Krahl and Witzel (chapter 3)). Therefore, the interpretation of muscle functions is very sketchy. Additionally, muscle functions do not appear to have been studied with the same thoroughness as those of the foreflipper. Muscle functions presented here often agree with functions provided by Robinson (1975) and Carpenter et al. (2010) but more possible functions are discussed in addition (Krahl and Witzel (chapter 3.4.2.2); Tab. 2 in Krahl and Witzel (chapter 3)). As in the cheloniid humerus and femur, two-joint muscles were found in the plesiosaur humerus and femur to be necessary for the integrity of the long bones (Krahl and Witzel (chapter 3.4.1)).

Apart from m. flexor carpi radialis, m. flexor carpi ulnaris, m. peroneus, and m. tibialis anterior (by Robinson (1975)), extensors and flexors that originate from the distal humerus and femur or from crus and tarsus have never been reconstructed before nor interpreted for their function (Krahl and Witzel (chapter 3.3.1.1.3, 3.3.1.1.4, 3.3.1.2.4, 3.3.1.2.5, 3.4.2)).

First, newly derived plesiosaur muscle functions will be discussed below in comparison to those sauropsid taxa that were used for the EPB to reconstruct the plesiosaur humerus and femur musculature (Krahl (chapter 6.1.2.2)). The comparison will focus on locomotory pectoral and pelvic musculature that power down- and upstroke (Krahl and Witzel (chapter 3.3.1.1.2, 3.3.1.2.3, 3.3.2); (Tab. 3, 4)). Second, the functions of humerus and femur muscles of *Cryptoclidus eurymerus* (IGPB R 324) (Krahl and Witzel (chapter 3.3.2)) and Cheloniidae (Krahl et al. (chapter 2.3.1, 5.3.2)) will be compared as well as their agonistic/antagonistic relationships (Krahl (chapter 6.1.2.3)).

2.2.2 Plesiosaur muscle functions in comparison to those of Sauropsida

2.2.2.1 Humerus

M. latissimus dorsi/teres major is a humeral elevator/abductor across Sauropsida and plesiosaurs (Walker, 1973; Jenkins & Goslow, 1983; Wyneken, 2001; Meers, 2003; Wyneken, 2003; Russell & Bauer, 2008; Rivera, Wyneken & Blob, 2011; Krahl and Witzel (chapter 3.3.2.1)). While it aids in retraction in crocodilians and lepidosaurs (Meers, 2003; Russell & Bauer, 2008; Anzai et al., 2014), it contrarily aids in protraction in turtles (Walker, 1973; Wyneken, 2001, 2003). In plesiosaurs m. latissimus dorsi/m. teres major could have had both functions (Krahl and Witzel (chapter 3.3.2.1)). In plesiosaurs this muscle is also a humerus rotator, which is only described for crocodilians, too (Meers, 2003; Krahl and Witzel (chapter 3.3.2.1); Tab. 3).

M. subcoracoscapularis comprises in crocodilians and turtles merely a scapular portion (Walker, 1973; Meers, 2003). Contrastingly, lepidosaurs have an additional coracoid portion (Russell & Bauer, 2008). The latter was also reconstructed for plesiosaurs (Krahl and Witzel (chapter 3.3.2.1)). Muscle functions derived from the latter constellation are more diverse than those from the former. M. subcoracoscapularis function in crocodilians and turtles oppose each other: It retracts and adducts the crocodilian humerus and stabilizes the joint (Meers, 2003) and protracts and abducts/elevates the turtle humerus (Walker, 1973). M. subcoracoscapularis functions of lepidosaurs partially diverge from the functions mentioned above. It is a humeral abductor, retractor, rotator, and joint stabilizer. In plesiosaurs m. subcoracoscapularis aids in humerus protraction, retraction, elevation, and humerus long axis rotation in both directions (depends on the portion) (Krahl and Witzel (chapter 3.3.2.1); Tab. 3).

Crocodilians and lepidosaurs have a m. scapulohumeralis posterior. It aids in humerus abduction in both taxa (Jenkins & Goslow, 1983; Meers, 2003). In crocodilians it is also a protractor (Meers, 2003) and in lepidosaurs it is also a rotator (Jenkins & Goslow, 1983; Russell & Bauer, 2008), retractor (Russell & Bauer, 2008), and joint stabilizer (Jenkins & Goslow, 1983). If this muscle is reconstructed in plesiosaurs its muscle course, wrapping around the dorsal tuberosity from posterodorsal to anteroproximal, appears relatively unlikely. It seems to allow mainly humeral rotation with maybe a minor elevational component (Krahl and Witzel (chapter 3.3.2.1); Tab. 3).

In plesiosaurs as well as in lepidosaurs, crocodilians, and probably also turtles m. deltoideus clavicularis aids in protraction (Walker, 1973; Wyneken, 2001; Meers, 2003; Wyneken, 2003; Russell & Bauer, 2008; Anzai et al., 2014; Krahl and Witzel (chapter 3.3.2.1)). This muscle is a rotator in lepidosaurs and plesiosaurs (Russell & Bauer, 2008; Krahl and Witzel (chapter 3.3.2.1)). In lepidosaurs m. deltoideus clavicularis may aid in joint stabilization (Jenkins & Goslow, 1983). In plesiosaurs it contributes to humeral depression. In turtles it was not discriminated between m. deltoideus clavicularis and m. deltoideus scapularis, so both portions are presumed to be abductors (Walker, 1973; Wyneken, 2001, 2003) or maybe joint stabilizer (Rivera, Wyneken & Blob, 2011; Tab. 3).

M. deltoideus scapularis is a humeral abductor in crocodilians (Meers, 2003), lepidosaurs (Jenkins & Goslow, 1983; Russell & Bauer, 2008; Anzai et al., 2014), and also an elevator in plesiosaurs (Krahl and Witzel (chapter 3.3.2.1)). Like in plesiosaurs, in lepidosaurs this muscle also functions in protraction and rotation (Jenkins & Goslow, 1983; Russell & Bauer, 2008; Krahl and Witzel (chapter 3.3.2.1)). In crocodilians this m. deltoideus scapularis appears to be a joint stabilizer (Tab. 3).

Across Sauropsida m. triceps brachii is responsible for elbow extension (Walker, 1973; Jenkins & Goslow, 1983; Meers, 2003; Rivera, Wyneken & Blob, 2011; Anzai et al., 2014). In lepidosaurs it might also have a glenoid stabilizing function (Jenkins & Goslow, 1983). In turtles m. triceps brachii is also discussed as a protractor and abductor/elevator (Walker, 1973) or as an adductor/depressor (Wyneken, 2001, 2003) or as a humeral rotator or as a contributor to flipper twisting (Wyneken, 2003). In plesiosaurs LOA suggest m. triceps brachii to contribute to humeral elevation and rotation and to flipper twisting as well (Krahl and Witzel (chapter 3.3.2.1); Tab. 3).

In all sauropsids m. pectoralis is a humeral adductor/depressor (Walker, 1973; Meers, 2003, 2003; Wyneken, 2003; Rivera, Wyneken & Blob, 2011; Anzai et al., 2014) and retractor (Walker, 1973; Jenkins & Goslow, 1983; Meers, 2003; Wyneken, 2003; Russell & Bauer, 2008; Rivera, Wyneken & Blob, 2011; Anzai et al., 2014) which was also reconstructed for plesiosaurs (Krahl and Witzel (chapter 3.3.2.1)). In plesiosaurs this muscle may also add to humeral protraction and rotation (Krahl and Witzel (chapter 3.3.2.1)) as is also the case in lepidosaurs (Russell & Bauer, 2008). A function as joint stabilizer was proposed for lepidosaurs additionally (Jenkins & Goslow, 1983; Tab. 3).

M. supracoracoideus aids in humeral protraction in crocodilians, turtles, lepidosaurs, and plesiosaurs (Meers, 2003; Wyneken, 2003; Russell & Bauer, 2008; Anzai et al., 2014; Krahl and Witzel (chapter 3.3.2.1)). In turtles and plesiosaurs this muscle also adds to humeral retraction (Walker, 1973; Wyneken, 2003; Krahl and Witzel (chapter 3.3.2.1)). In crocodilians and plesiosaurs m. supracoracoideus is clearly an adductor/depressor, eventually in turtles, too (Wyneken, 2003; Krahl and Witzel (chapter 3.3.2.1)). A function as joint stabilizer (Jenkins & Goslow, 1983) or abductor (Wyneken, 2003; Russell & Bauer, 2008) could not be confirmed for plesiosaurs. In plesiosaurs and lepidosaurs alike m. supracoracoideus acts as humeral rotator (Russell & Bauer, 2008; Krahl and Witzel (chapter 3.3.2.1); Tab. 3).

In Sauropsida (including plesiosaurs) m. coracobrachialis brevis and m. coracobrachialis longus retract and adduct/depress the humerus (Walker, 1973; Meers, 2003; Rivera, Wyneken & Blob, 2011; Krahl and Witzel (chapter 3.3.2.1)). In crocodilians, lepidosaurs, and sea turtles it was suggested that these two muscles also function as joint stabilizers (Walker, 1973; Jenkins & Goslow, 1983; Meers, 2003) which could not be corroborated for plesiosaurs (Krahl and Witzel (chapter 3.3.2.1)). Neither do m. coracobrachialis brevis and m. coracobrachialis longus have a humeral abductional/elevational function as described for turtles by Walker (1973). Only the lepidosaur m. coracobrachialis brevis has a humeral rotator function amongst extant Sauropsida (Russell & Bauer, 2008). In plesiosaurs LOAs strongly suggest, that both, m.

muscle	**function in crocodilians**	**function in Lepidosauria**	**function in Testudines**	**function in Plesiosauria Krahl and Witzel (chapter 3)**
supracoracoideus	protractor, adductor (Meers 2003)	protractor (Anzai et al. 2014; Russell and Bauer 2008); glenoid stabilizer (Jenkins and Goslow, 1983), rotator, abductor (Russell and Bauer 2008)	retractor, adductor (Walker 1973), protractor, abductor, adductor, retractor (anterior portion) (Wyneken 2003)	protractor (anterior portion), retractor (posterior portion), depressor (both)
coracobrachialis brevis	protraction, adductor, flexor at glenoid, joint stabilizer (Meers 2003)	joint stabilizer, retractor (Jenkins and Goslow, 1983), posterior rotator, adductor (only in arboreal lepidosaurs) (Russell and Bauer 2008)	minor retractor, adductor, glenoid stabilizer (Walker 1973)	retractor, depressor, rotator (leading edge upwards)
coracobrachialis longus		adductor (Anzai et al. 2014, Russell and Bauer 2008), retractor (Jenkins and Goslow, 1983, Russell and Bauer 2008)	retractor (Walker 1973, Wyneken, 2001), abductor (Walker 1973, depressor, retractor (Rivera et al. 2011)	retractor, depressor, rotator (leading edge upwards)
deltoideus clavicularis	protractor (Meers 2003)	protractor (Anzai et al. 2014, Russell and Bauer 2008), stabilizer of glenoid (Jenkins and Goslow, 1983); rotator (Russell and Bauer 2008)	abductor, protractor (Walker 1973, Wyneken 2001, Wyneken 2003), constrains humerus retraction during downstroke (Rivera et al. 2011)	protractor, depressor, rotator (leading edge downwards)
deltoideus scapularis	abductor, stabilizer of joint (Meers 2003)	abductor (Anzai et al. 2014, Jenkins and Goslow 1983, Russell and Bauer 2008), rotator, protractor (Jenkins and Goslow 1983, Russell and Bauer 2008)		protractor, elevator, rotator (leading edge upwards)

scapulohumeralis anterior (only Lepidosauria)		abductor (Russell and Bauer 2008, Jenkins and Goslow 1983), protractor (Jenkins and Goslow, 1983)		rotator (leading edge downwards), eventually elevator
scapulohumeralis posterior	abductor, protractor (Meers 2003)	rotator (Russell and Bauer 2008, Jenkins and Goslow 1983), abductor, glenoid stabilizer (Jenkins and Goslow, 1983); retractor (*Anolis*) (Russell and Bauer 2008)		elevator, rotator (leading edge downwards)
biceps brachii	flexor of antebrachium, extensor of humerus at glenoid (Meers 2003)	elbow flexor (Anzai et al. 2014), stabilizer (Jenkins and Goslow, 1983)	retractor, flexor of antebrachium (Walker 1973, Wyneken 2003, Wyneken 2001)	retractor, depressor, rotator (leading edge downwards),
brachialis	flexor of antebrachium (Meers 2003)	elbow flexor (Anzai et al. 2014, Russell and Bauer 2008)	flexor of antebrachium (Walker 1973)	brachialis slightly displaces ulna ventrally
triceps brachii	extensor of antebrachium, flexor of humerus (Meers 2003)	elbow extensor (Anzai et al. 2014, Jenkins and Goslow 1983); stabilizer of elbow joint, extensor at glenohumeral joint (Jenkins and Goslow, 1983)	extensor of antebrachium (Walker 1973, Rivera et al. 2011), protractor, abductor (Walker 1973), adductor (Wyneken, 2001, 2003), rotator, controls flipper twist (scapular head) (Wyneken 2003)	elevator, rotator (leading edge downwards), humeral head displaces ulna slightly dorsally
pectoralis	adductor, retractor (Meers 2003)	retractor (Anzai et al. 2014, Russell and Bauer 2008), adductor (Anzai et al. 2014) rotator, protractor (Russell and Bauer 2008; Jenkins and	retractor, adductor (Walker 1973, Wyneken 2003), depressor, retractor (Rivera et al. 2011)	protractor (anterior portion), retractor (posterior portion), depressor (both), rotator (leading edge

		Goslow, 1983), stabilizer of glenoid, scapulocoracoid retractor (Jenkins and Goslow, 1983)		downwards) (posterior portion); rotator (anterior portion) (leading edge upwards)
subcoracoscapularis	glenoid stabilizer, retractor, adductor (Meers 2003)	abductor (coracoid portion) (Anzai et al. 2014), retractor (scapular portion) (Anzai et al. 2014, Russell and Bauer 2008), rotator (scapular portion), stabilizer of glenoid (coracoid portion) (Russell and Bauer 2008); glenoid stabilizer, rotator, retractor (Jenkins and Goslow, 1983)	abductor, protractor (Walker 1973), flipper protraction (Wyneken 2001)	protractor (anterior portion), retractor (posterior portion), elevator (both), rotator (leading edge downwards) (anterior portion); rotator (leading edge upwards) (posterior portion)
latissimus dorsi/teres major	abductor, rotator, retractor (Meers 2003)	retractor (Anzai et al. 2014, Russell and Bauer 2008) abductor (Jenkins and Goslow, 1983, Russell and Bauer 2008)	protractor (Walker 1973, Wyneken 2001, 2003), abductor (Walker 1973, Wyneken 2001, 2003, Rivera et al. 2011), elevator (Rivera et al. 2011)	protractor (anteriormost portion), retractor (posterior portion), elevator; rotator (leading edge upwards)

Tab. 3: Comparison of functions of glenoid-spanning musculature in Sauropsida and Plesiosauria

coracobrachialis brevis and m. coracobrachialis longus aid in humeral rotation (Krahl and Witzel (chapter 3.3.2.1); Tab. 3).

M. biceps brachii and m. brachialis flex the elbow joint of sauropsids (Walker, 1973; Meers, 2003; Russell & Bauer, 2008; Anzai et al., 2014). In plesiosaurs the elbow joint is not functional, but these muscles may aid in flipper twisting (Krahl and Witzel (chapter 3.3.2.1)). In plesiosaurs m. biceps brachii is also a humeral retractor as in turtles (Walker, 1973; Wyneken, 2001, 2003; Krahl and Witzel (chapter 3.3.2.1)) as well as a humeral adductor/depressor (Krahl and Witzel (chapter 3.3.2.1)). A function as joint stabilizer as described for lepidosaurs (Jenkins and Goslow 1983) cannot be confirmed in plesiosaurs (Tab. 3).

M. scapulohumeralis anterior is only known from lepidosaurs (Russell & Bauer, 2008). It adds to humeral abduction (Jenkins & Goslow, 1983; Russell & Bauer, 2008) and protraction (Jenkins & Goslow, 1983). The former might also be the case in plesiosaurs while the latter was not confirmed. Contrastingly, m. scapulohumeralis anterior may be a humeral rotator (Krahl and Witzel (chapter 3.3.2.1); Tab. 3).

2.2.2.2 Femur

M. iliotibialis aids in knee extension across Sauropsida (Snyder, 1954; Zug, 1971; Walker, 1973; Gatesy, 1997; Reilly & Blob, 2003; Anzai et al., 2014) and in femur abduction in crocodilians (Otero, Gallina & Herrera, 2010) and turtles (Zug, 1971; Walker, 1973) and in its retraction (Walker, 1973). Due to the relative stiffening of the knee joint of plesiosaurs, m. iliotibialis cannot extend the knee, but it does aid in hindflipper twisting (Krahl and Witzel (chapter 3.3.2.2, 3.4.3.2)). The functions of femur abduction/elevation and retraction is shared in plesiosaurs with crocodilians and turtles for the former and with turtles for the latter (Krahl and Witzel (chapter 3.3.2.2); Tab. 4).

M. femorotibialis extends the knee in sauropsids (Snyder, 1954; Zug, 1971; Walker, 1973; Reilly & Blob, 2003; Otero, Gallina & Herrera, 2010; Anzai et al., 2014). In plesiosaurs its role was altered and m. femorotibialis aids in hindflipper twisting (Krahl and Witzel (chapter 3.3.2.2, 3.4.3.2); Tab. 4).

In Sauropsida m. ambiens aids m. femorotibialis and m. iliotibialis in knee extension (Snyder, 1954; Zug, 1971; Walker, 1973; Gatesy, 1997; Reilly & Blob, 2003; Otero, Gallina & Herrera, 2010; Anzai et al., 2014) and therefore in plesiosaurs it contributes to hindflipper twisting (Krahl and Witzel (chapter 3.3.2.2, 3.4.3.2)). In plesiosaurs m. iliotibialis may also add to femur protraction and adduction/depression as reported for turtles as well (Walker, 1973; Krahl and Witzel (chapter 3.3.2.2)). Additionally, in plesiosaurs m. ambiens contributes to femur long axis rotation (Krahl and Witzel (chapter 3.3.2.2); Tab. 4).

M. ischiotrochantericus is a femur retractor in plesiosaurs as it is in lepidosaurs and turtles, too (Zug, 1971; Walker, 1973; Russell & Bauer, 2008; Krahl et al. (chapter 2)). It aids in long axis rotation of the femur in plesiosaurs and across sauropsids (Zug, 1971; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Krahl and Witzel (chapter 3.3.2.2)). M. ischiotrochantericus additionally depresses the plesiosaur femur (Krahl and Witzel (chapter 3.3.2.2)). Contrarily, a function as abductor as found in crocodilians (Otero, Gallina & Herrera, 2010) or a function as joint stabilizer in lepidosaurs (Russell & Bauer, 2008) could not be confirmed in plesiosaurs (Krahl and Witzel (chapter 3.3.2.2); Tab. 4).

M. iliofibularis aids in sauropsids in knee flexion (Snyder, 1954; Zug, 1971; Walker, 1973; Gatesy, 1997; Otero, Gallina & Herrera, 2010; Anzai et al., 2014), i.e., in plesiosaurs in hindflipper twisting (Krahl and Witzel (chapter 3.3.2.2, 3.4.3.2)). Further, this muscle is a femur abductor/elevator in crocodilians (Gatesy, 1997; Otero, Gallina & Herrera, 2010), turtles (Zug, 1971; Walker, 1973), and plesiosaurs (Krahl and Witzel (chapter 3.3.2.2)). M. iliofibularis also has a retractional function in lepidosaurs (Snyder, 1954) and turtles (Walker, 1973), and in plesiosaurs. It may also add to flipper rotation as supported by turtles (Zug, 1971; Krahl and Witzel (chapter 3.3.2.2); Tab. 4).

M. puboischiotibialis is in plesiosaurs as in other Sauropsida an adductor/depressor (Snyder, 1954; Zug, 1971; Walker, 1973; Gatesy, 1997; Hutchinson & Gatesy, 2000; Reilly & Blob, 2003; Otero, Gallina & Herrera, 2010; Krahl and Witzel (chapter 3.3.2.2)). Further, this muscle functions in knee flexion in all Sauropsida (Snyder, 1954; Walker, 1973; Gatesy, 1997; Anzai et al., 2014). In plesiosaurs m. puboischiotibialis may also aid in flipper twisting (Krahl and Witzel (chapter 3.4.3.2)) and rotation (Krahl and Witzel (chapter 3.3.2.2); Tab. 4).

In extant sauropsids m. flexor tibialis internus is always an adductor/depressor of the hindlimb/-flipper (Snyder, 1954; Walker, 1973; Otero, Gallina & Herrera, 2010). In plesiosaurs though, an origin on the ilium or from the vertebral column as in extant turtles would clearly lead to an elevational function of this muscular head (Krahl and Witzel (chapter 3.3.2.2)). M. flexor tibialis internus retracts the sauropsid hindlimb (Snyder, 1954; Walker, 1973; Otero, Gallina & Herrera, 2010) as well as the plesiosaur hindflipper (Krahl and Witzel (chapter 3.3.2.2)). It is also described to flex the knee joint in crocodilians (Otero, Gallina & Herrera, 2010) and in lepidosaurs (Snyder, 1954; Anzai et al., 2014). In plesiosaurs, m. flexor tibialis internus could contribute to hindflipper rotation and twisting (Krahl and Witzel (chapter 3.3.2.2, 3.4.3.2); Tab. 4).

muscle	function in crocodilians	function in Lepidosauria	function in Testudines	function in Plesiosauria Krahl and Witzel (chapter 3)
m. iliotibialis	knee extensor (Gatesy 1997, Reilly and Blob 2003), abductor (Otero et al. 2010)	knee extensor (Snyder 1954, Anzai et al. 2014)	knee extensor, abductor (Zug 1971, Walker 1973), retractor (Walker 1973)	elevator, retractor, rotator (anterior edge up), slight dorsal displacement of tibia on distal femur
m. femorotibialis	knee extensor (Reilly and Blob 2003, Otero et al. 2010)	knee extensor (Snyder 1954, Anzai et al. 2014)	knee extensor (Walker 1973, Zug 1971)	slight dorsal displacement of tibia on distal femur
m. ambiens	knee extensor (Gatesy 1997, Reilly and Blob 2003, Otero et al. 2010)	knee extensor (Snyder 1954, Anzai et al. 2014)	adductor, knee extensor (Walker 1973, Zug 1971), protractor (Walker 1973)	protractor, rotator (if femur depressed, rotates anterior edge up; if elevated then rotates anterior edge down), slight dorsal displacement of tibia on distal femur
m. ischiotrochantericus	abductor, rotator (Otero et al. 2010)	retraction, probably joint stabilization, and long axis rotation of femur (Russell and Bauer 2008)	retractor (Walker 1973, Zug 1971), rotate (Zug 1971)	retractor, depressor, rotator (anterior edge down)
m. iliofibularis	knee flexor, abductor (Gatesy 1997, Otero et al. 2010)	flexor of knee (Snyder 1954, Anzai et al. 2014), retractor (Snyder 1954)	knee flexor, abductor (Zug 1971, Walker 1973), retractor (Walker 1973), crus rotator (Zug 1971)	elevator, rotator (anterior edge down), retractor, rotator (anterior edge up) (as long as fibula above origin)
m. puboischiotibialis	adductor (Gatesy 1997, Hutchinson and Gatesy 2000, Reilly and Blob 2003, Otero et al. 2010), knee flexor (Gatesy 1997)	adductor (Snyder 1954), flexor of knee (Snyder 1954, Anzai et al. 2014)	knee flexor, adductor (Zug 1971, Walker 1973)	depressor, rotator (anterior edge down)
m. flexor tibialis internus	knee flexor, adductor (Otero et al. 2010)	retraction, adductor (Snyder 1954), knee	retractor, adductor (Walker 1973)	from ischium: retractor, depressor, rotator (anterior edge down)

		flexor (Anzai et al. 2014, Snyder 1954)		from ilium/sacral vertebrae/transverse processes of caudal vert.: retractor, rotator (anterior edge down), elevator
m. flexor tibialis externus	knee flexion (Otero et al. 2010), abductor (Gatesy 1997), retractor (Reilly and Blob 2003)	retractor (Snyder 1954) knee flexor (Snyder 1954, Anzai et al. 2014)	abductor, retractor (Walker 1973)	from ilium: rotator (anterior edge down), retractor, elevator from ischium: rotator (anterior edge down), retractor, depressor
m. adductor femoris	adductor (Gatesy 1997, Hutchinson and Gatesy 2000, Reilly and Blob 2003, Otero et al. 2010), retractor (Hutchinson and Gatesy 2000)	adductor (Snyder 1954, Anzai et al. 2014), protraction (Anzai et al. 2014)	adductor, retractor (Zug 1971, Walker 1973)	from anterior ischium: depressor from lateroposterior ischium: depressor, retractor
m. caudifemoralis brevis, m. caudifemoralis longus	retractor (Gatesy 1997, Hutchinson and Gatesy 2000, Otero et al. 2010), rotator (Gatesy 1997, Hutchinson and Gatesy 2000)	retractor (Snyder 1954, Anzai et al. 2014), abductor (Snyder 1954)	abductor, retractor (Zug 1971, Walker 1973)	caudifemoralis brevis: elevator, retractor, rotator (anterior edge down) caudifemoralis longus: retractor, elevator, rotator (anterior edge down)
m. puboischiofemoralis externus	protractor, rotator (Otero et al. 2010), adductor (Gatesy 1997, Reilly and Blob 2003, Otero et al. 2010)	protractor (Snyder 1954), adductor (Anzai et al 2014)	adductor, retraction (Walker 1973), protraction (Zug 1971, Walker 1973), rotator (Zug 1971)	from pubis: depressor, protractor, rotator (anterior edge up) from ischium: depressor, retractor, rotator (anterior edge down)
m. iliofemoralis	abductor (Gatesy 1997, Reilly and Blob 2003, Otero et al. 2010)	abductor (Snyder 1954, Anzai et al. 2014, Russell and Bauer 2008)	abductor, protractor (Zug 1971, Walker 1973)	elevator, retractor, rotator (anterior edge up)

m. puboischiofemoralis internus	protractor (Reilly and Blob 2003, Otero et al. 2010), adductor (Gatesy 1997, Otero et al. 2010)	protractor (Snyder 1954, Anzai et al. 2014), adductor (Snyder 1954)	protractor (Walker 1973), abductor (Zug 1971, Walker 1973), rotator (Zug 1971)	four possible muscle bellies: elevators -from pubis: elevator, rotator (anterior edge down), protractor -from ischium: elevator, rotator (anterior edge up), minorly retractor -from ilium: elevator, rotator (anterior edge up), minorly retractor -from vertebral column: elevator, protractor
m. pubotibialis		flexor of knee (Snyder 1954, Anzai et al. 2014)	/	protractor, rotator (if femur depressed, rotates anterior edge up; if elevated then rotates anterior edge down)

Tab. 4: Comparison of functions of acetabulum-spanning musculature in Sauropsida and Plesiosauria

In Sauropsida and plesiosaurs m. flexor tibialis externus is a hindlimb/-flipper retractor (Snyder, 1954; Walker, 1973; Reilly & Blob, 2003; Krahl and Witzel (chapter 3.3.2.2)). Further, this muscle aids in abduction/elevation in crocodilians, turtles, and plesiosaurs (Walker, 1973; Gatesy, 1997; Krahl and Witzel (chapter 3.3.2.2)). Although, an origin on the ischium in plesiosaurs would lead to a depressional function of m. flexor tibialis externus (Krahl (chapter 3.3.2.2)).

Further, this muscle adds to knee flexion in crocodilians (Otero, Gallina & Herrera, 2010) and lepidosaurs (Snyder, 1954; Anzai et al., 2014). In plesiosaurs it could contribute to hindflipper twisting (Krahl and Witzel (chapter 3.3.2.2, 3.4.3.2); Tab. 4).

In all sauropsids and also in plesiosaurs m. adductor femoris functions as a femoral adductor/depressor (Snyder, 1954; Zug, 1971; Walker, 1973; Gatesy, 1997; Hutchinson & Gatesy, 2000; Reilly & Blob, 2003; Otero, Gallina & Herrera, 2010; Anzai et al., 2014; Krahl and Witzel (chapter 3.3.2.2)). In crocodilians (Hutchinson & Gatesy, 2000), turtles (Zug, 1971; Walker, 1973) and plesiosaurs (Krahl and Witzel (chapter 3.3.2.2)) it appears to have a retractional function. Contrastingly, in lepidosaurs m. adductor femoris aids in femur protraction (Anzai et al., 2014; Tab. 4).

M. caudifemoralis brevis and m. caudifemoralis longus are femur retractors across Sauropsida and in plesiosaurs (Snyder, 1954; Zug, 1971; Walker, 1973; Gatesy, 1997; Hutchinson & Gatesy, 2000; Otero, Gallina & Herrera, 2010; Anzai et al., 2014; Krahl and Witzel (chapter 3.3.2.2)). Further, it was found to be a femoral abductor/elevator in lepidosaurs (Snyder, 1954), turtles (Zug, 1971; Walker, 1973), and plesiosaurs (Krahl and Witzel (chapter 3.3.2.2)). A rotatory function for m. caudifemoralis brevis and m. caudifemoralis longus was described for crocodilians (Gatesy, 1997; Hutchinson & Gatesy, 2000) and plesiosaurs (Krahl and Witzel (chapter 3.3.2.2); Tab. 4).

M. puboischiofemoralis externus protracts (Snyder, 1954; Zug, 1971; Walker, 1973; Otero, Gallina & Herrera, 2010) and adducts/depresses (Walker, 1973; Gatesy, 1997; Reilly & Blob, 2003; Otero, Gallina & Herrera, 2010; Anzai et al., 2014) the femur in Sauropsida as well as in plesiosaurs (Krahl and Witzel (chapter 3.3.2.2)). Additionally, it adds to femur rotation in crocodilians (Otero, Gallina & Herrera, 2010), turtles (Zug, 1971), and plesiosaurs (Krahl and Witzel (chapter 3.3.2.2)). If one discriminates m. puboischiofemoralis externus in turtles and plesiosaurs into its different heads, an additional function as femoral retractor emerges (Walker, 1973; Krahl and Witzel (chapter 3.3.2.2); Tab. 4).

M. iliofemoralis abducts/elevates in plesiosaurs as well as in extant Sauropsida the hindflipper/-limb (Snyder, 1954; Zug, 1971; Walker, 1973; Gatesy, 1997; Reilly & Blob, 2003; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Anzai et al., 2014; Krahl and Witzel (chapter 3.3.2.2); Tab. 4).

In plesiosaurs and extant Sauropsida, m. puboischiofemoralis internus is a protractor (Snyder, 1954; Walker, 1973; Reilly & Blob, 2003; Otero, Gallina & Herrera, 2010; Anzai et al., 2014; Krahl and Witzel (chapter 3.3.2.2)). Further, it adducts the femur in crocodilians and lepidosaurs (Snyder, 1954; Gatesy, 1997; Otero, Gallina & Herrera, 2010). Contrastingly, in turtles and plesiosaurs m. puboischiofemoralis internus appears to be a femoral abductor/elevator (Zug, 1971; Walker, 1973; Krahl and Witzel (chapter 3.3.2.2)). This muscle was discussed to also have a femoral rotational function in turtles as well as in plesiosaurs (Zug, 1971; Krahl and Witzel (chapter 3.3.2.2)). In plesiosaurs m. puboischiofemoralis internus could also have one or two heads that would retract the femur (Krahl and Witzel (chapter 3.3.2.2); Tab. 4).

M. pubotibialis function was not discussed in crocodilian and turtle literature on which this comparison is based on. In lepidosaurs m. pubotibialis is a knee flexor (Snyder, 1954). In plesiosaurs it could be a hindflipper depressor, protractor, and rotator (Krahl and Witzel (chapter 3.3.2.2); Tab. 4).

2.2.2.3 Discussion

Overall, there is considerable similarity between fore- and hindlimb muscle functions in extant Sauropsida and fore- and hindflipper muscle functions in Plesiosauria derived from muscle reconstructions with the EPB, if their main functions are regarded. There are differences due to specializations e.g., origin on dorsal coracoid of m. coracobrachialis magnus in Testudines (Walker, 1973), the loss of m. coracobrachialis longus in crocodilians (Meers, 2003), or the unique situation in lepidosaurs with an origin of m. subcoracoscapularis on scapula and coracoid etc. (Russell & Bauer, 2008).

There are markedly more potential humeral and femoral rotators in plesiosaurs than in extant Sauropsida (Tab. 3, 4). This discrepancy may derive due to different circumstances: a) a different determination method, i.e., by EMG (Jenkins & Goslow, 1983; Gatesy, 1997; Hutchinson & Gatesy, 2000; Reilly & Blob, 2003; Rivera, Wyneken & Blob, 2011). The difficulty here is that the outcome depends on many factors, e.g., on how precisely the electrodes were placed and if they actually reflect the targeted muscle or muscle portion because these may have differing functions functions; b) other studies that probably geometrically (and by dissection) deduced the muscle functions had a different study focus and therefore possibly did not offer muscle functions the same attention as they have had in this thesis (Snyder, 1954; Zug, 1971; Walker, 1973; Wyneken, 2001; Meers, 2003; Wyneken, 2003; Russell & Bauer, 2008; Otero, Gallina & Herrera, 2010; Anzai et al., 2014; Krahl et al. (chapter 2, 5); Krahl and Witzel (chapter 3)); c) that kinematic data and/or osteological observations preclude certain movements. This is the case in cheloniids in which long axis humerus rotation is inhibited (Rivera, Wyneken & Blob, 2011; Rivera, Rivera & Blob, 2013; personal observation; Krahl and Witzel (chapter 3.1.2.1)).

Sometimes sauropsid forelimb muscles are given the function of a „joint stabilizer“ (Jenkins & Goslow, 1983; Meers, 2003; Tab. 3). Jenkins & Goslow (1983) define a joint stabilizer as follows: „Criterion for identifying such muscles is that EMG activity is not accompanied by joint movement (determined cineradiographically) in the direction of the muscle’s line of action, during propulsive phase“ (Jenkins & Goslow, 1983, p. 211). I interpret the „joint stabilizers“ as antagonistic muscles, as also pointed out by Jenkins & Goslow (1983), they are recruited with lower muscle forces during a specific motion than the agonistic muscles. This means, that the antagonist’s actual function is opposing that of the agonists but a movement in the respective direction does not take place, as the force output is lower in the former than in the latter. So they might actually contribute to joint stabilization, but they certainly aid in precise movement control during motions. That it is possible to determine agonistic and antagonistic muscle activity with EMG during a limb cycle was shown by Aagaard et al. (2000) for the human quadriceps and hamstrings.

The two-joint muscles in the sauropsid forelimb, m. triceps brachii and m. biceps brachii, extend and flex the elbow. In plesiosaurs the elbow joint is immobile but instead it was suggested that they contribute to flipper twisting Krahl and Witzel (chapter 3.4.3.1). The two-joint muscles in the sauropsid hindlimb (m. iliotibialis, m. ambiens, m. iliofibularis, m. puboischiotibialis, m. flexor tibialis internus, m. flexor tibialis externus, m. pubotibialis) flex or extend the knee. A function that became obsolete because of the immobilization of the knee joint. Like in the foreflipper, these muscles are interpreted to contribute to hindflipper twisting (Krahl and Witzel (chapter 3.4.3.2)).

2.2.3 Functions of cheloniid and plesiosaur humerus and femur musculature

2.2.3.1 Comparison of cheloniid and plesiosaur humerus muscle functions

Although the muscle functions of cheloniid and plesiosaur humerus muscles represent two independently derived data sets (Cheloniidae: dissection, LOA, FESA (Krahl et al. (chapter 2.2)); Plesiosauria: EPB, LOA, FESA (Krahl and Witzel (chapter 3); Krahl et al. (chapter 4.2))), there is a vast agreement in humerus muscle functions between these two convergent underwater fliers. M. deltoideus clavicularis, m. deltoideus scapularis, m. supracoracoideus, m. coracobrachialis brevis, m. coracobrachialis longus happen to have the same functions in both taxa. Generally similar are the main functions of m. latissimus dorsi, m. subcoracoscapularis, and m. pectoralis in cheloniids and plesiosaurs. Due to a certain range of interpretive freedom of plesiosaur muscle reconstructions based on the EPB, there may have been smaller portions of these muscles cranially/anteriorly to or caudally/posteriorly to the glenoid (unlike to sea turtles). These would have allowed humerus protraction in the case of m. pectoralis and m. subcoracoscapularis and retraction in the case of m. latissimus dorsi/m. teres major (Krahl et al. (chapter 2.3.1); Krahl and Witzel (3.1.2.1, 3.4.2.1)).

Many plesiosaur foreflipper muscles have a potential rotational function, i.e., m. latissimus dorsi/m. teres major), m. subcoracoscapularis, m. scapulohumeralis posterior, m. scapulohumeralis anterior, m. deltoideus clavicularis, m. deltoideus scapularis, m. triceps brachii, m. pectoralis, m. coracobrachialis brevis, m. coracobrachialis longus, m. biceps brachii. Contrastingly, in Cheloniidae this is not the case, because humerus long axis rotation could be precluded due to the kinematic studies of Rivera, Wyneken & Blob (2011) and based on osteological observations of the glenoid shape (Krahl et al. (chapter 2.3.1); Krahl and Witzel (3.1.2.1, 3.4.2.1)).

Differences in extensor and flexor functions are due to a mobile elbow joint in Cheloniidae and an immobile one in plesiosaurs. Furthermore, Cheloniidae are capable to rotate their lower arm and hand unlike plesiosaurs that have an immobile wrist joint (Krahl (chapter 1.2.2.2,; Krahl and Witzel (3.1.2.1)). Sea turtle extensors and flexors contribute to rotation of lower arm and hand and extension and flexion of the phalanges. Contrastingly, plesiosaur extensors and flexors extend and flex the phalanges, too, but otherwise contribute to foreflipper twisting along the middle axis of the flipper length (Krahl et al. (chapter 2.3.1); Krahl and Witzel (3.3.2.1, 3.4.3.1)).

2.2.3.2 Comparison of cheloniid and plesiosaur femur muscle functions

In Plesiosauria and Cheloniidae m. iliotibialis, m. ambiens, m. caudofemoralis brevis and m. caudofemoralis longus, m. ischiotrochantericus, m. adductor femoris, and m. puboischiofemoralis externus appear to have the same functions. This means that divergence in function mainly appears in muscles that either originate dorsally to the acetabulum (m. iliofibularis, m. iliofemoralis, m. puboischiofemoralis internus, m. puboischiotibialis, m. pubotibialis) or that have two muscle bellies of which one originates dorsally and the other one ventrally to the acetabulum (m. flexor tibialis internus and m. flexor tibialis internus). The exception to this pose m. iliotibialis and m. ambiens (Krahl and Witzel (chapter 3.4.2.2); Krahl et al. (5.3.2)). The reason for this may be the fundamental restructuring of the pelvic girdle in plesiosaurs. Here ischium and pelvis meet in the body mid-line in a symphysis and lie slightly v-shaped ventrally in the abdominal region. The ilium is much reduced in size and morphologically little differentiated (Krahl (chapter 1.2.1.2.1); Krahl and Witzel (3.1.1)).

Contrary to the comparison of muscle functions of the convergently evolved hydrofoil foreflippers of Cheloniidae and Plesiosauria (Krahl (chapter 1.2.3.1)), the comparison of plesiosaur hindflipper musculature to any other tetrapod is hampered because plesiosaurs are unique amongst tetrapods in having hydrofoil hindflippers, too. All other secondarily aquatic tetrapods have hindflippers that are paddle- or oar-shaped. As the different flipper shapes imply different hydrodynamics and different flipper beat cycles, it should be expected that muscles could have divergent functions (Krahl and Witzel (chapter 3.1.2)). Contrary to Cheloniidae, the knee and ankle joints are immobile in Plesiosauria (Krahl (chapter 1.2.1.2.2, 1.2.2.2); Krahl and Witzel (3.1.1, 3.1.2.1)). Therefore, muscles that formerly aid in knee extension and flexion in sea turtles, or those that span the ankle joint have lost their functions in plesiosaurs and contribute to hindflipper twisting instead (Krahl and Witzel (chapter 3.4.2.2, 3.4.3.2)).

2.2.3.3 Agonists and antagonist of foreflipper and hindflipper musculature of Cheloniidae and Plesiosauria

Based on muscle functions lists with muscle pairs of agonists and antagonists were assembled (Tab. 3 in Krahl et al. (chapter 2); Krahl et al. (chapter 4.3.2); Tab. 2 and Tab. 3 in Krahl et al. (chapter 4); Tab. 2 in Krahl et al. (chapter 5)). These are crucial for computing FESA load cases. As muscle functions partially differ between the foreflipper and the hindflipper of Plesiosauria and Cheloniidae, the formed pairs of agonistically and antagonistically acting muscles differ, too. All four lists of agonistic and antagonistic muscles have in common that the formed „pairs“ of muscles do not necessarily correspond to two muscles, but may be several muscles that have opposing functions (Tab. 3 in Krahl et al. (chapter 2); Krahl et al. (chapter 4.3.2); Tab. 2 and Tab. 3 in Krahl et al. (chapter 4); Tab. 2 in Krahl et al. (chapter 5)).

Some pairs of muscles form similarly in the foreflippers of both, cheloniids and plesiosaurs (e.g., m. subcoracoscapularis (+ m. biceps brachii) in sea turtles) vs. m. deltoideus clavicularis + the anterior portion(s) of m. supracoracoideus). The main differences between both taxa result on the one hand, from additional potential humerus long axis rotation in plesiosaurs, that was precluded in sea turtles. On the other hand, contrary to Cheloniidae, Plesiosauria have an immobile elbow joint and no rotating wrist joint. Therefore most plesiosaur extensor and flexor functions differ from those of sea turtles and instead contribute to a novel myological mechanism of flipper twisting (Krahl and Witzel (chapter 3.4.2.1); Tab. 3 in Krahl et al. (chapter 2); Krahl et al. (chapter 4.3.2); Tab. 2 in Krahl et al. (chapter 4)).

Conspicuous is, that in the plesiosaur hindflipper, the large pubic portions of m. puboischiofemoralis internus and m. puboischiofemoralis externus are opposed by a large number of muscles of possibly relatively small muscle belly size. Although it should be mentioned, that if muscles like e.g., m. iliofemoralis did spread their origin area onto the vertebral column, they would not have been constrained in size as much as they are by the comparatively small ilium. Nonetheless, this seems to underline the fundamental difference of plesiosaur hindflipper myology to that of the sea turtle hindflipper. Similar to the foreflipper described above, extensor and flexor functions differ in sea turtles and plesiosaurs due to the loss of mobile knee and ankle joints in the latter. Accordingly, femur extensors and flexors of plesiosaurs contribute to flipper twisting (Krahl and Witzel (chapter 3.4.2.2); Krahl et al. (chapter 4.3.2); Tab. 3 in Krahl et al. (chapter 4); Tab. 2 in Krahl et al. (chapter 5)).

3. Finite element structure analysis (FESA)

3.1 State of the art

3.1.1 Loading of vertebrate bone and finite element structure analysis

Bending, torsion, and axial compression fluctuatingly functionally load vertebrate long bones, as in vivo strain gauge measurements indicate (Biewener & Dial, 1995; Carrano, 1998; Blob & Biewener, 1999; Lieberman, Polk & Demes, 2004; Main & Biewener, 2004, 2007; Butcher et al., 2008; Butcher & Blob, 2008; Sheffield et al., 2011; Young & Blob, 2015; Young et al., 2017). Tortoise long bones are subjected to high torsional loads (Butcher et al., 2008; Butcher & Blob, 2008). Significant torsional loading of long bones was found in lepidosaurs (Blob & Biewener, 1999; Sheffield et al., 2011) and archosaurs (Biewener & Dial, 1995; Carrano, 1998; Blob & Biewener, 1999; Main & Biewener, 2007). Mammal bones were found to be loaded less by torsion (e.g., Main & Biewener, 2004). The change in habitat in turtles from terrestrial to aquatic is found to be correlated with a decrease in torsional bone loading. This in turn might free long bones from the mechanical constraint for evolving tubular long bones and allow evolution of differently-shaped humeri and femora (Young & Blob, 2015; Blob et al., 2016; Young et al., 2017) as observed in sea turtle humeri (compare to Zug, Wynn & Ruckdeschel, 1986).

By homogenizing stress in bone, biological lightweigth structures appear to evolve (Klenner et al., 2015). The stress is exerted by tension chords (muscles and ligaments) synergizing as agonists and antagonists (Witzel & Preuschoft, 2005; Rayfield, 2007; Sverdlova & Witzel, 2010; Curtis et al., 2011; Witzel et al., 2011; Klenner et al., 2015; Felsenthal & Zelzer, 2017). As loading conditions change constantly throughout a limb cycle, several load cases that depict various loading stages (Witzel & Preuschoft, 2005) should be analyzed with FE and later be superimposed (Carter, Orr & Fyhrie, 1989). Bone remodeling leads to the development of curvature in bones (Lanyon, 1980) and reduces the bending moment to a minimum (McCabe et al., 2017).

Finite element structure analyses (FESA) have been conducted to learn more about bone loading conditions (Rayfield, 2007 for review) and bone function (Witzel et al., 2011) and are employed by various study fields (Rayfield, 2007 for review). FESA are applied for several different purposes in Biology and Paleontology. Often, they are used to compute bite forces of extant and extinct tetrapods (Sharp, 2015; Snively, Fahlke & Welsh, 2015; Lautenschlager, Witzmann & Werneburg, 2016; Ledogar et al., 2017). FESA also yield insights into feeding behaviour of recent and extinct animals by allowing to test several hypotheses and show whether they are compatible with the skull morphology (e.g., Young et al., 2012; Fortuny, Marcé-Nogué & Konietzko-Meier, 2017; McCurry et al., 2017). So e.g., McCurry et al. (2017) test different feeding behaviours e.g., twisting by comparing FESAs of odontocete and crocodylian skulls with different rostral lengths and different feeding hypotheses are also tested by e.g., Young et al. (2012) for the sauropod dinosaur *Diplodocus* or by Fortuny, Marcé-Nogué & Konietzko-Meier (2017) for extinct fresh water amphibian metoposaurids. Sellers et al. (2017) applied FESA to simulate bite forces of *Alligator mississippiensis* and compare their data to in-vivo measurements to test the robustness of this method (Sellers et al., 2017). Curtis et al. (2008) investigate how muscles wrapping around bones influence FESA of the skull structure of *Macaca fascicularis* and conclude that muscle wrappings do improve FESAs. FESA enables to analyze specific structures, e.g., the zygomatic arch in *Macaca f.* (Curtis et al., 2011) or even bone microstructures such as transverse osteons (Micheli & Witzel, 2011).

A recent trend in especially evolutionary biology is to combine FESA, i.e., the analysis of a possible function of a specific structure, with geometric morphometrics, i.e., the quantification of divergences in shape. The aim is to trace functional and morphological changes in a phylogenetic context, which is demonstrated by Polly et al. (2016) on the example of turtle armors (s. Polly et al., 2016 for review). In turtle biology, FESA are mostly used to study material properties of turtle carapaces to develop bio-inspired materials for technical application (Achrai & Wagner, 2017). So they e.g., simulate predators biting into the turtle carapace (An & Wagner, 2017) on the macro- and on the microanatomical level, by taking different microanatomical layers into account (Balani et al., 2011), or soft tissues (Shelef & Bar-On, 2017), or the contributions of different sutures to the impact absorbing properties of the turtle carapace are investigated (Damiens et al., 2012). Vega & Stayton (2011) demonstrate with FESA that sexual dimorphism expressed in differently-shaped shells in *Chrysemys picta* and *Glyptemys insculpta* effects largely their biology, e.g., different predator escape behaviour. Rivera & Stayton (2011) show, that habitat related differences in shell shape of *Pseudemys concinna* are driven by a trade-off between the degree of hydrodynamic adaptation and shell strength.

To the knowledge of the author, no FESA studies of long bones of Testudines, or more specifically Cheloniidae, and Plesiosauria have been conducted beside those presented in this study (Krahl et al. (chapter 2, 4, and 5)). Volumetric models of a humerus and a femur of *Chelonia mydas* (ZFMK 70222) and *Cryptoclidus eurymerus* (IGPB R 324) were build with Simpleware ScanIP. Material properties were amended in ANSYS and FESAs were computed for two load cases, i.e., up- and downstroke, for the *Chelonia* humerus and *Cryptoclidus* (IGPB R 324) humerus and femur. For the *Chelonia* femur a prestage, from which load cases could be derived, was preliminarily completed.

3.1.2 Physiological cross sectional area and muscle force calculation

Calculation of physiological cross sectional areas (PCSAs) was developed by Alexander & Vernon (1975) and Anapol & Barry (1996). This concept is founded on the assumption that a muscle can exert a force that is equal to the sum of all its muscle fibres. PCSA takes individual, sometimes very complex, muscle architecture into account and recognizes that anatomical muscle cross sections are not necessarily identical with their physiological cross sections (except for parallel-fibred muscles). Muscle architecture comprises several values that need to be measured, i.e., length of a muscle, lines of action (i.e., three dimensional geometric orientation of a muscle connecting origin and insertion in a straight line), muscle mass, specific density, intrinsic muscle strength, fibre/fascicle length, and pennation angle (Alexander & Vernon, 1975; Gans, 1982; Sacks & Roy, 1982; Powell et al., 1984; Narici, Landoni & Minetti, 1992; Anapol & Barry, 1996; Kummer, 2005; Azizi, Brainerd & Roberts, 2008).

Parallel-fibred muscles have on average longer fascicles and can contract faster than pennate muscles. However, more muscle fibres can be arranged adjacently to each other in a pennate muscle than in a parallel-fibred muscle of the same size. Thus, a pennate muscle can exert a higher force than a same-sized parallel-fibred muscle although the pennate muscle has shorter fibres. This is so because the exerted maximum muscle force does not only depend on fibre length but also on the physiological cross sectional area, i.e., the sum of fibre cross sections. Parallel-fibred muscles have larger lever arms and faster muscle contraction velocities than pennate muscles, but pennate muscles are relatively stronger and save space and weight. Strong, parallel-fibred muscles have large volumes (Gans, 1982; Burkholder et al., 1994; Allen et al., 2010; Huq, Wall & Taylor, 2015).

Many articles use PCSAs for muscle force calculations that focus on skull musculature. Thus PCSAs, and the derived muscle forces, aid in either understanding mastication processes or bite force analyses during phases of the mastication process. These studies concentrate mostly on mammals (e.g., Antón, 2000; Ross et al., 2005; Taylor & Vinyard, 2009; Davis et al., 2010; Shi et al., 2012; Watson et al., 2014). Yet to a minor degree, there are also studies on feeding biomechanics of various reptiles, including turtles (e.g., Vincent et al., 2007; Curtis et al., 2010; Pfaller, Gignac & Erickson, 2011; Pfannes-Varow, 2011; Erickson et al., 2012) or on bite forces of extinct animals (view e.g., Bates & Falkingham, 2012; Snively, Fahlke & Welsh, 2015). PCSAs are also used to gain knowledge of ontogenetic scaling effects e.g., Vincent et al. (2007) connected these with changes in the diet of *Nerodia fasciata*, a water snake. Allen et al. (2010) could connect them with changes in locomotory capabilities of alligators. Pfaller, Gignac & Erickson (2011) observed ontogenetic changes in jaw muscles of a semi-aquatic turtle which promote durophagy. Otherwise PCSA and muscle forces may also give information on locomotory adaptations e.g., on bipedalism in ratites (Smith et al., 2006; Lamas, Main & Hutchinson, 2014), on quadrupedal locomotion in mammals (Payne et al., 2005; Gosnell et al., 2011; Huq, Wall & Taylor, 2015), alligators (Allen et al., 2010), various lizards (Sheffield et al., 2011; Anzai et al., 2014; Bergmann & Hare-Drubka, 2015), and on terrestrial locomotion of a semi-aquatic turtle (Butcher & Blob, 2008).

Assessment of *Caretta caretta* humerus musculature followed standard techniques (see e.g., (Anapol & Barry, 1996; Narici et al., 1996; Allen et al., 2010; Gröning et al., 2013). The pennation angles, i.e., the angles of insertion of all fascicles, were mostly presumed to be zero, otherwise they were measured with a goniometer. A number of representative fascicles of each muscle were measured in order to take the mean values (Allen et al., 2010), which have proven to be sufficiently accurate according to Gröning et al. (2013). Muscles were dissected off the specimen and weighed.

1) PCSA were obtained by solving the following equation:

$$PCSA = \frac{m \cos\theta}{l \, \rho}$$

PCSA equals to the fraction of muscle mass (m) times the cosine of the pennation angle (θ) divided by (mean) fascicle length (l) times the specific density (ρ) of vertebrate muscles (Alexander & Vernon, 1975; Sacks & Roy, 1982). m, θ, and l were measured on the specimen M1/16 as described above. ρ=1,0564 and is taken from (Murphy & Beardsley, 1974).

2) Maximum muscle forces were computed with the following solution:

$$Fmax = PCSA * S$$

F_{max} is the maximum isometric muscle force. It is gained by multiplying the intrinsic strength of vertebrate muscles S with the PCSA (e.g., Medler, 2002; Gröning et al., 2013). S equals 30 N/cm^2, according to e.g., Medler (2002).

3.2 Summary and comparison of results

3.2.1 Muscle wrappings

By dissection (cheloniid humerus) (Krahl et al. (chapter 2)), by studying literature data (cheloniid femur) (Krahl et al. (chapter 5)), by performing muscle reconstructions with the EPB (plesiosaur humerus and femur) (Krahl and Witzel (chapter 3)), and by spanning LOA into the limb skeletons muscles were found that wrap around bone during at least part of the limb cycle (Krahl et al. (chapters 2.2.2, 4.2.1, 5.2.1)). Around the medial process of the cheloniid humerus m. coracobrachialis longus is wrapped. M. coracobrachialis brevis wraps around the bony ridge that connects the medial process and the humeral head in Cheloniidae (Krahl and Witzel (chapter 3.2)). A number of muscles (m. flexor tibialis internus (both muscle bellies), m. flexor tibialis externus (both muscle bellies), m. ischiotrochantericus, m. adductor femoris) are wrapped ventrally around the fused trochanter major and trochanter minor ridge of the sea turtle femur (Krahl and Witzel (chapter 3.3)). The two muscle bellies of either m. flexor tibialis externus and m. flexor tibialis internus converge at approximately the level of the femoral shaft but in such a way that each muscle belly is wrapped around trochanter minor or trochanter major (compare to Walker, 1973, Fig. 24, p. 62).

Convergently, m. latissimus dorsi and m. subcoracobrachialis wrap around the proximodorsal tuberosity in the plesiosaur humerus (Krahl and Witzel (chapter 3.3.1.1)). The plesiosaur femur has a dorsal trochanter that appears to be analogous to the tuberosity of the plesiosaur humerus. Around the trochanter wrap m. puboischiofemoralis internus and m. iliofemoralis (Krahl and Witzel (chapter 3.3.1.2)).

In the cheloniid humerus, m. triceps brachii and several extensors (m. extensor carpi ulnaris, m. extensor radialis superficialis + m. extensor digitorum communis, and m. extensor radialis intermedius) wrap around its distal condyles during part of the limb cycle (Krahl and Witzel (chapter 3.2)). In the cheloniid femur m. femorotibialis wraps around the femur shaft from antero- and posteroventrally onto the dorsal side and towards the distal epicondyles where it joins the knee tendon, to which m. ambiens and m. iliotibialis contribute, that wraps around the femoral epicondyles when the knee is flexed. M. extensor digitorum wraps around the epicondyles, too (Krahl and Witzel (chapter 3.3)).

In plesiosaurs, extensors and flexors originate from a site anteriorly and posteriorly on the curved and flared humeral and femoral epicondyles. They slightly wrap around the anterodorsal, respectively the posteroventral bone surface. M. femorotibialis wraps around the plesiosaur femur in a similar way as in the cheloniid femur (s. above) (Krahl and Witzel (chapter 3.3.1.1, 3.3.1.2)).

These muscle wrappings proved to be existent by dissection and LOA and are much needed to functionally load the aforementioned bony structures with compressive stress. A muscle wrapping imposes a resultant vector that runs through the bony structure and thereby loads it by compression.

3.2.2 Compressive stress distribution in comparison to bone microstructure

Compressive stress distribution computed in FESA for the cheloniid humerus and femur delineates bone microstructure observable in the micro-CT scans, used for building the respective volumetric FE models, well. Overall, the compressive stress distribution reproduces the sandhour glass-shape of vertebrate long bones well. High compressive stresses correspond to the more compact cortical bone, while lower compressive stresses match with spongy bone of different densities (Krahl et al. (chapter 2.3.2, 5.3.3); Krahl and Witzel (3.3.1.1, 3.3.1.2 also please view for details on color-coding)). Even features like the thickened cortical bone and dense spongy bone present in the ridge of the fused trochanter minor and trochanter major in the sea turtle femur (Krahl et al. (chapter 5.3.3)) or thickened compact cortex in the bridge between medial process and humeral head of the sea turtle humerus (Krahl et al. (chapter 2.3.2)) which are correlated with muscle wrappings, are redrawn by the compressive stress distribution obtained through FESA. Based on greyscale values, Young’s moduli were set in advance for the FE models, yet bone microstructure and compressive stress distribution match well. This supports LOA and the computed relative muscle force output (Krahl et al. (chapter 5.4.2, 2.4)).

3.2.3 Muscle forces

3.2.3.1 PCSA *Caretta caretta* humerus vs. iteratively computed *Chelonia mydas* humerus

The highest maximum muscle force of *Caretta caretta* humerus musculature was determined for m. pectoralis (413,89 N), closely followed by m. supracoracoideus (413,89 N). Both muscles are humeral depressors. While m. pectoralis and the posterior portions of m. supracoracoideus also retract the humerus, the anterior portions of m. supracoracoideus aid in humeral protraction (compare to Krahl et al. (chapter 2.3.1); Tab. 5). The highest maximum muscle force for the foreflipper upstroke of Cheloniidae is developed by m. subcoracoscapularis (269,37 N). Muscles responsible for depression and retraction of the sea turtle humerus generally appear to be capable of higher maximum muscle forces than those employed in humerus elevation and protraction. M. flexor carpi ulnaris (46,11 N) and m. palmaris longus (30,76 N) (both flex the antebrachium and manus, the former also rotates the flipper, the latter also flexes the digits (compare to Krahl et al. (chapter 2.3.1); Tab. 5) are able to develop distinctly higher maximum muscle forces than the other flexors and extensors (e.g., m. pronator teres 7,32 N) of the humerus of *Caretta caretta* (Tab. 5).

Generally muscle forces determined by PCSA and computed iteratively retained the same relative values, i.e., for example the highest muscle force is produced by m. pectoralis, and then by m. supracoracoideus, flexors are recruited partially with higher muscle forces than extensors, and m. flexor carpi ulnaris and m. palmaris longus generated the highest muscle forces amongst extensors and flexors (Krahl et al. (chapter 2.3.2); Tab. 5). All the above-mentioned muscles are involved in the foreflipper downstroke. This underlines the observation by Davenport, Munks & Oxford (1984) that the cheloniid foreflipper downstroke contributes relatively more to locomotion than the upstroke.

Values of the two differently derived data sets (PCSA for *Caretta caretta* humerus and iteratively computed for *Chelonia mydas* humerus) (Krahl et al. (chapter 2.3.2); Tab. 5) do not scale by a simple relationship. For proximally inserting muscles it might be broadly said that they scale by a factor of around 2,8 mostly, which does not seem to be true for extensors and flexors which appear to scale more variably. Turtle bite force is reported to scale isometrically with the length of the carapace (Herrel & O'Reilly, 2006). Although, in loggerheads, who feed

muscle	function after Krahl et al. (chapter 2)	weight [g] m	pennation angle [°] θ	mean pennation angle [°]	fascicle length [cm] l	mean fibre length [cm]	PCSA [cm^2]=m cos θ/l 1,0564	F [N]=PCSA * 30 N/cm^2	highest muscle force from Krahl et al. (chapter 2)
m. pectoralis	depression, retraction	274	0	0	17,5; 19; 17; 16; 17; 14,5	101/6=18,8	13,80	413,89	1210
m. supracoracoideus 1) coracoid 2) acromion posterior 3) acromion anterior 4) scapula	posterior portions: depression, retraction anterior portions: depression, protraction	1) 94 2) 50 3) 30 4) 23	1) 26 2) 33 3) 0 4) 0	0	1) 17,5; 18; 10,5 2) 13; 9,5 3) 13; 12; 12,5 4) 10; 8; 6,5	1)15,3 2)11,25 3)12,5 4)8,16	1) 5,21 2) 3,53 3) 2,27 4) 2,67	1) 156,37 2) 105,85 3) 68,16 4) 80,04 in total: 410,42	1100
m. latissimus dorsi + teres major	elevation, protraction	56	0	0	18,5; 17; 10; 18; 11,5; 18,5	15,58	3,40	102,07	259
m. deltoideus scapularis	elevation, protraction	29	0	0	11,5; 12,5; 12; 11,5	11,875	2,31	69,35	181
m. deltoideus clavicularis	depression, protraction	82	0	0	17,5; 14,5; 15,5; 16,5; 17,5; 17,5	16,5	4,70	141,13	365
m. coracobrachialis magnus	depression, retraction	162	0	0	15,5; 15,5; 15,5	15,5	9,89	296,80	970
m. coracobrachialis brevis	depression, retraction	4	0	0	13,5; 12,5; 12	12,6	0,30	9,02	22
m. subscapularis 1) medial portion 2) lateral portion	elevation, retraction	1) 45 2) 113	0	0	1) 11,5; 11 2) 20,5; 21,5; 20	1) 11,25 2) 20,6	1) 3,79 2) 5,19	1) 113,59 2) 155,78 in total:269,37	873
m. triceps, scapular head	elbow extension	/	/	/	/	/	/	/	77 (both heads combined)
m. triceps brachii humeral head	elbow extension	15	0	0	9; 9; 9	9	1,58	47,33	/)
m. biceps superficialis	elbow flexion, depression	70	23; 29; 22	24,67	30; 30; 28,5	29,5	2,04	61,24	294 (both heads combined))
m. biceps profundus	elbow flexion, depression	8	18; 15	16,5	20.5; 18	19,25	0,38	11,32	
m. brachialis inferior	flexion	29	0	0	9; 9; 10	9,3	2,95	88,55	291
m. tractor radii	antebrachial flexor	5	0	0	7,5; 9,5; 8,5	8,5	0,56	16,70	52

m. extensor radialis superficialis + extensor digitorum communis	extends antebrachium, manus, and rotates flipper	7	0	0	12; 12,5; 12,5	12,3	0,54	16,16	65
m. extensor carpi ulnaris	antebrachial extensor and rotates flipper	/	1; 6; 5; 10	5,5	3,5; 3,6; 2,6; 2,2	2,975	/	/	22
m. extensor radialis intermedius	/	/	/	/	/	/	/	/	20
m. flexor carpi ulnaris 1) medial part 2) lateral part	flexes antebrachium and manus and rotates flipper	1) 7 2) 15	0	0	1) 11,5; 10; 10 2) 15,5; 15,5; 16	1) 10,5 2) 15,67	1) 0,63 2) 0,91	1) 18,93 2) 27,18 In sum:46,11	1) 22 2) 87 In sum: 99
m. palmaris longus	flexes antebrachium, manus and digits	13	0	0	12; 12	12	1,03	30,76	49
m. flexor carpi radialis	antebrachial flexor and rotates flipper	6	0	0	10,5; 10,5; 10,5	10,5	0,54	16,23	52
m. pronator teres	antebrachial flexor	4	0	0	15,5; 15,5; 16	15,5	0,24	7,32	26

Tab. 5: Comparison of sea turtle muscle forces derived by PCSA and that were iteratively computed

on hard-shelled prey, positive allometry was reported (Marshall et al., 2012). Further, proportional to length, muscle force scales to the second and muscle mass to the third power.

This means, that one can expect different ontogenetic stages to perform differently (Herrel & O'Reilly, 2006). Intraspecific and interspecific scaling of locomotory muscles in Cheloniidae has not been established and would need to be established for a further discussion. How muscle architecture contributes to the scaling relationships would also need to be investigated.

3.2.3.2 *Cryptoclidus eurymerus* humerus vs. cheloniid humeri

Plesiosaur humerus muscle forces show very similar trends as those of the sea turtle humerus (Krahl (chapter 6.2.2.3.1)) with respect to muscles that originate from the pectoral girdle. M. pectoralis is recruited with the highest muscle force during downstroke and m. latissimus dorsi with the highest muscle force during upstroke (Krahl et al. (chapter 4.3.3.1.1); Tab. 4 in Krahl et al. (chapter 4)). Muscle forces of extensors arising from the distal plesiosaur humerus are lower than those of the flexors. Overall in plesiosaurs, like in sea turtles, the foreflipper downstroke contributes more to propulsion than the upstroke because the muscle forces developed by depressors and retractors and flexors are generally higher than those of the elevators and protractors and extensors. Markedly different between muscle forces of extensors and flexors of the sea turtle and plesiosaur humerus is though that the muscle force output is very similar to that of the proximally inserting pectoral musculature in plesiosaurs while it is about a magnitude smaller in sea turtles (Krahl et al. (chapter 2.3.1, 4.3.3.1.1); Krahl (6.2.2.3.1)). This speaks for a uniquely developed myological flipper twisting mechanism in plesiosaurs in agreement with hydrodynamic studies (Krahl and Witzel (chapter 3.4.3.1); Krahl et al. (4.2.2.1)). The question is raised, how muscles that have proportionately smaller origin areas and that potentially cannot be as bulky as the pectoral muscles, can develop muscle forces as those that were found. For once a highly complex architecture (as in e.g., Payne et al., 2005) could save a lot of muscle mass. Further, a unique tendinous spring-like mechanism might save energy expenditure during steady locomotion (Roberts et al., 1997; Biewener & Roberts, 2000). Also, parallel-fibred aponeurotic connective tissue covering the flipper skeleton as in dolphins could and thick connective tissue covering the space of the non-functional elbow could passively contribute (Krahl et al. (chapter 4.2.2.3)).

3.2.3.3 *Cryptoclidus eurymerus* femur vs. *Chelonia mydas* femur

Muscle forces of cheloniid femur muscles are highest for m. puboischiofemoralis internus for hindflipper abduction and protraction. The antagonistic m. puboischiofemoralis externus and m. ischiotrochantericus are employed at lower muscle forces but still develop high ones. Muscle forces of extensors and flexors are lower than those of the pelvic muscles that insert proximally into the femur (Krahl and Witzel (chapter 3.3.1.2)). Muscle forces computed for the plesiosaur femur muscles differ considerably to those of the *Chelonia mydas* femur: M. puboischiofemoralis externus develops in *Cryptoclidus* (IGPB R 324) the highest muscle force of those pelvic muscles that insert into the plesiosaur femur. In sea turtles m. ischiotrochantericus is active with higher muscle forces than m. iliofemoralis than m. caudi-iliofemoralis than m. adductor femoris (Krahl et al. (chapter 5.3.3)). In plesiosaurs m. adductor femoris is recruited with higher muscle force than both muscle bellies of m. caudifemoralis (brevis and longus) than m. ischiofemoralis than m. iliofemoralis (Krahl and Witzel (chapter 3.3.1.2); Tab. 5 in Krahl et al. (chapter 4)). In plesiosaurs and sea turtles alike, the flexors work with a higher force output than the extensor. Markedly different between plesiosaur and sea turtle femur musculature is that there seems to be an extreme hypertrophy of m. puboischiofemoralis internus and m. puboischiofemoralis externus. The former and the latter reach forces of 7611 N and 7878 N while the muscle with the next highest muscle force is m. adductor femoris with 2536 N. Contrastingly, m. puboischiofemoralis internus and m. puboischiofemoralis externus are employed with up to 150 N and 200 N followed by m. ischiotrochantericus with also 150 N) (Krahl and Witzel (chapter 3.3.1.2); Krahl et al. (5.3.3)).

Extensors and flexors of the sea turtle femur differ not as much in force output from the pelvic musculature as in the foreflipper (Krahl et al. (chapter 5.3.3)). In the plesiosaur hindflipper, femur extensor and flexor muscle forces have broadly a similar output as the smaller muscles originating from the pelvic girdle (Krahl and Witzel (chapter 3.3.1.2)). These differences in muscle force output between fore- and hindflipper might be due to differences of the flipper twisting mechanism of the fore- and hindflipper which in turn might derive from myologic differences between the sauropsid hind- and forelimb. The sauropsid fore- and hindlimb differ myologically in that there is a high number of two-joint muscles that originate from the pelvis, in comparison to the two two-joint muscles of the sauropsid forelimb. Therefore, it is likely that some functions that extensors and flexors of the forelimb have are performed by one of the many two-joint muscles of the hindflipper in plesiosaurs (Krahl and Witzel (chapter 3.4.3.2)). Further, two-joint muscles are only indirectly taken into account in

FESA and no muscle forces could be calculated for them as they do not insert into or originate from humerus or femur (Krahl and Witzel (chapter 3.3.1)). Those are not differences that can be eradicated by elevating the force niveau if one e.g., would lift up the force niveau to correct for for example the body size, given there would be a scaling relationship established amongst aquatic tetrapods. Further discussion of how such high muscle forces are possible in extensors and flexors aligns with the discussion on this matter in Krahl et al. (chapter 2.2.3.2) for the extensors and flexors of the foreflipper.

3.2.3.4 Cheloniid humeri and *Cryptoclidus eurymerus* humerus vs. *Chelonia mydas* and *Cryptoclidus eurymerus* femur

In sea turtles, the relative difference between the highest muscle forces developed by muscles inserting into the femur (200 N) and originating (45 N) from the femur is considerably smaller than in the humerus (1210 N and 87 N) (Krahl et al. (chapter 2.3.1, 5.3.3)). This might be due to the highly complex interconnected extensor and flexor complexes of the hindflipper, which, in contrast to the foreflipper, are not differentiated into as many separately specialized muscle bellies (compare to Krahl and Witzel (chapter 3.1.1.3 and 3.1.2.4)) and the many two-joint muscles that take on an unknown amount of the muscle force. A fundamental difference between plesiosaur and sea turtle humerus muscle forces as well as femur muscle forces is that plesiosaur humerus and femur extensors and flexors reach the same muscle force output as the muscles that arise from the vertebral column, the pectoral, and the pelvic girdle (Krahl et al. (chapter 2.3.1, 4.3.3.1, 5.3.3)). Relative muscle forces (not the absolute values) of sea turtle and plesiosaur humerus musculature inserting into the proximal humerus are very well comparable corroborating convergent evolution of flight (Krahl et al. (chapter 2.3.1, 4.3.3.1.1)).

Contrastingly, sea turtle and plesiosaur muscles that insert into the proximal femur are not well comparable. In sea turtles muscle forces amongst muscles inserting into the femur are much more leveled out. In plesiosaurs, m. puboischiofemoralis internus and puboischiofemoralis externus are hypertrophied correlated with the much enlarged pubis (Krahl et al. (chapter 4.3.3.1.2, 5.3.3)). For a rowing motion this would mean that femur protraction coupled with abduction and adduction would be much improved, i.e., the recovery stroke. Although, an improved backing stroke would seem to make much more sense for increased efficiency in rowing because this is the part of the rowing motion cycle that generates propulsion. Contrarily, the hypertrophied m. puboischiofemoralis internus and m. puboischiofemoralis externus seem to indicate evolution of hindflippers employed in underwater flight because they improve flipper elevation and depression coupled with protraction.

In the foreflipper of plesiosaurs the coracoid musculature, posterior to the glenoid, is hypertrophied relative to basal Sauropterygia. Contrastingly, in the hindflipper this seems to be the case with muscles that originate from the pubis, anterior to the acetabulum. One could hypothesize that if one would trace the flipper path of the plesiosaur fore- and hindflipper during a complete limb cycle, the flipper tips would describe an opposite pathway: The foreflipper might be beaten from anterodorsal to posteroventral as in recent cheloniid turtles (Davenport, Munks & Oxford, 1984; Wyneken, 1997; Rivera, Wyneken & Blob, 2011; Rivera, Rivera & Blob, 2013) while the hindflipper might start posterodorsally and be brought anteroventrally during the downstroke as was described for *Dermochelys coriacea* (Wyneken, 1997 for review).

4. Muscle reconstructions

4.1 State of the art

Plesiosaur fore- and hindflipper locomotory muscles are reconstructed with the extant phylogenetic bracket (Bryant & Seymour, 1990; Wittmer, 1995). Taxa chosen for bracing Plesiosauria were Lepidosauria, Crocodylia, and Testudines (Krahl and Witzel (chapter 3.2.1)). Reconstruction of the whole fore- and hindflipper musculature of plesiosaurs has only been attempted once before, namely by Robinson (1975). While she reconstructed a very reduced, penguin- or cetacean-like musculature for the distal plesiosaur fore- and hindflipper (compare to Robinson, 1975, Louw, 1992, and Cooper et al., 2007). The current author reconstructed a considerably more complex distal plesiosaur fore- and hindflipper musculature (Krahl and Witzel (chapter 3)). This discrepancy is based on several points: a) Watson (1924), Tarlo (1958), Robinson (1975), and Lingham-Soliar (2000) did not base their muscle reconstructions on the EPB. This means they usually did not state on which taxa they based their reconstructions on. b) Robinson (1975) based her muscle reconstructions for plesiosaurs at least partially on functional analogues (like penguins or sea turtles). This does not necessarily mean one of the former muscle reconstructions is better or worse than the other, but reproducibility of the respective results is hampered (Watson, 1924; Tarlo, 1958; Robinson, 1975; Lingham-Soliar, 2000). However, partial plesiosaur locomotory muscle reconstructions have also been undertaken by Carpenter et al. (2010) and Araújo & Correia (2015).

A firm foundation for a certain degree of realistic muscle reconstructions is given when the EPB is employed in a reasonable way. Nonetheless, the EPB often leads to decisions which are not supported by all three taxa (Wittmer, 1995). In this case, the respective author starts to weigh and decide subjectively, although this is not necessarily clearly stated (e.g., Carpenter et al., 2010). I tried to counter this possible subjective bias by openly discussing the different possibilities (like Araújo & Correia (2015) did, too) as was suggested by Wittmer (1995) and giving an explanation why I prefer the one or the other option. One should also keep in mind, that the extant taxa, on which the muscle reconstructions are based on themselves are derived species which are very well adapted to their modern habitat and far from plesiomorphic „model organisms“. This means for example that the muscuskeletal system of Testudines experienced infolding of the shoulder girdle into the rib cage (Nagashima et al., 2012) and that extant semi-aquatic crocodylians are descendants of a formerly entirely terrestrial group of archosaurs.

Furthermore, if one conforms strictly to the concept of the EPB, one would have to reconstruct an entire set of sauropsid limb musculature for plesiosaur flippers. Although this is most possibly unlikely because plesiosaurs are highly adapted secondarily to an aquatic habitat and the taxa used for the EPB are all three terrestrial. Therefore, a comparison to possible recent functional analogues is drawn additionally, as e.g., Robinson (1975) did. For this thesis Cheloniidae and Spheniscidae (recent underwater fliers) (Krahl and Witzel (chapter 3.1.2.1, 3.1.2.2)), Otariidae (who have a considerable underwater flight phase combined with a rowing stroke) (Krahl and Witzel (chapter 3.1.2.3)), and Cetacea (who also have lift-producing hydrofoil foreflippers) (Krahl and Witzel (chapter 3.1.2.4)) were considered for comparison. Muscuskeletal specializations of their foreflippers were evaluated and findings were partially transferred to or discussed in relation to the plesiosaur foreflipper muscle reconstructions. For plesiosaur hindflippers there is no adequate extant functional analogue because plesiosaurs themselves pose the only example of a secondarily aquatic tetrapod that has evolved the hindflippers convergently to the foreflippers into hydrofoils. Based on the striking similarity of plesiosaur fore- and hindflippers, it was presumed that the same, or very similar, muscuskeletal constraints and adaptations that shape the foreflipper must hold true for the hindflipper as well (Krahl and Witzel (chapter 3.1.2)).

4.2 Summary

4.2.1 Plesiosaur myology

Based on the EPB (lepidosaurs, crocodylians, and turtles) the complete fore- and hindflipper musculature was reconstructed (Krahl and Witzel (chapter 3)). This implied to thoroughly establish homology of myology and ligaments for the various sauropsid taxa based on topographical characteristics (Krahl and Witzel (chapter 3.2.1, 3.3.1)). For discussion of the plesiosaur muscle reconstructions a homology list for existing plesiosaur myology works was created, too (Krahl and Witzel (chapter 3)). 52 muscles were reconstructed (12 pectoral, 8 antebrachial, and 6 manual muscles in the foreflipper; 15 pelvic, 6 crural muscles, and 5 muscles of the pes) (Krahl and Witzel (chapter 3.3.1)).

No ligaments were reconstructed for the pectoral and pelvic girdle, because they either take an improbable course and/or seem to lack the osteological correlates that are present in extant taxa which have them. Extensor and flexor retinacula were reconstructed for the plesiosaur fore- and hindflipper based on the EPB and are variably well supported (Krahl and Witzel (chapter 3.3.1.1.1, 3.3.1.2.2)). Reconstruction of an intermetacarpal/intermetatarsal and metacarpodigital/metatarsodigital ligaments system could be beneficial for a flipper twisting mechanism (Krahl and Witzel (chapter 3.4.3)).

Foreflipper and hindflipper muscle origins and insertions are discussed in detail in comparison to plesiosaur myological literature (Krahl and Witzel (chapter 3.4.1)). Muscle origins on the pectoral girdle resemble those of Araújo & Correia (2015) in many details. The rest of the muscle attachment site reconstructions differ quite often substantially from those provided in literature so far. Differences to Robinson (1975) are due to the fact that she reconstructed the humerus and femur articulation different than the work presented here. Robinson (1975) articulates humerus and femur rotated by 90°, i.e., their anterior side points to the ventral and dorsal to the anterior side of the plesiosaur. Contrary to Robinson (1975), the current study presumes that the dorsal tuberosity and trochanter are not encapsulated in the joint capsule of glenoid and acetabulum. This is also in agreement with other plesiosaur locomotory muscle reconstructions (Watson 1924, Tarlo 1957, Robinson 1975, Lingham-Soliar 2000, Carpenter et al. 2010, and Araújo & Correia 2015). Furthermore, plesiosaur locomotory muscles so far have mostly only been incompletely reconstructed (Watson 1924, Tarlo 1957, Robinson 1975, Lingham-Soliar 2000, Carpenter et al. 2010, and Araújo & Correia 2015). All plesiosaur muscle reconstructions so far have correlated muscle scars with reconstructed muscles (Watson 1924, Tarlo 1957, Robinson 1975, Lingham-Soliar 2000, Carpenter et al. 2010, and Araújo & Correia 2015, Krahl and Witzel (chapter 3)).

Muscle functions for all locomotory muscles of the fore- and hindflipper were geometrically deduced and discussed in comparison to the results of other authors. They provided the basis for *Cryptoclidus* (IGPB R 324) humerus and femur FESA (Krahl and Witzel (chapter 3); Krahl et al. (chapter 4)). A fore- and hindflipper beat cycle were described in terms of which muscles contribute to which movements. This also includes the description of a myological flipper length axis twisting mechanism for both pairs of flippers. As hydrodynamic studies show, a humerus and femur rotation by approximately 19° could be sufficient, if coupled with flipper twisting, to support underwater flight. So during the downstroke, humerus and femur are rotated downwards by approximately 19° from the neutral axis, slightly retracted and majorly depressed by the respective muscles. At the same time muscles that influence movement of the zeugopodium and autopodium twist the leading edge of fore and hindflipper downward and the trailing edge upward (Krahl and Witzel (chapter 3.4.3)). The elbow, knee, wrist, and ankle joints are not functional, but findings suggest that there are considerable amounts of cartilage/soft tissue associated with them (Krahl (chapter 1.2.1.2.2); Krahl and Witzel (3.1.1)). It would be sufficient, if the muscles that act on zeugopodium and carpus and tarsus would allow for a slight displacement of the bones relative to each other. The contribution of the digits to flipper twisting adds a major component. Further, intermetacarpal/intermetatarsal and metacarpodigital/metatarsodigital ligaments could passively support flipper twisting by successively flexing the following digits, after flexion of the first digit was induced myologically (Krahl and Witzel (chapter 3.4.3)).

During the fore- and hindflipper upstroke, humerus and femur are rotated back through a neutral position and upwards by 19°. Simultaneously, they are slightly protracted and majorly elevated. Fore- and hindflipper are now twisted in such a way that the flipper leading edges are curled upward and the trailing edges are curled downward. Similarly to the downstroke, the ligaments of fore- and hindflipper could passively contribute to a flawless twisting of successive digits. Also, some muscles, that cross the carpus and tarsus more or less diagonally could potentially actively influence the flipper profiles and induce asymmetry leading to higher efficiency (Krahl and Witzel (chapter 3.4.3)).

As noted on other occasions as well, there are differences between the musculature of the fore- and hindflipper and accordingly the flipper twisting mechanisms of both flippers differ, too. In the forelimb m. biceps brachii and m. triceps brachii may possibly contribute to slight zeugopodium displacement. Contrastingly, in the hindflipper more two-joint muscles potentially contribute to flipper twisting (downstroke: m. flexor tibialis externus, m. flexor tibialis internus, m. pubotibialis, m. iliofibularis; upstroke: m. ambiens, m. iliotibialis). Further, reconstruction of a muscular flipper twisting mechanism for the hindflipper is complicated because of the complex architecture of femoral extensors and flexors (s. e.g. Russell & Bauer, 2008 on m. gastrocnemius p. 371-379) arising from the femora of Sauropsida and our insufficient understanding of their specific contributions to locomotion. Nonetheless, the similar morphology of humerus and femur of *Cryptoclidus* (IGPB R 324) suggests, that overall, despite differences in sauropsid fore- and hindlimb musculature, there must be considerable similarity between lines of action and muscle functions (Krahl and Witzel (chapter 3.4.3)).

4.2.2 Correlated with functionality via FESA

To receive a homogenous compressive stress distribution through FESA (Krahl et al. (chapter 4)), certain adjustments to the muscle reconstructions (Krahl et al. (chapter 4.3.1, 4.4.1)) became necessary due to mechanical reasons and/or mechanical support for less likely reconstructions were found. The line of action of the, by EPB badly supported, coracoid portion of m. subcoracoscapularis would be the only one well parallel to the dorsal tuberosity of the humerus. This implies that m. subcoracoscapularis wraps around it and imposes it to compression. Comparably, lines of action parallel to the dorsal trochanter of the plesiosaur femur support m. iliofemoralis and the smaller muscle heads originating posterior to the acetabulum of m. puboischiofemoralis internus (Krahl et al. (chapter 4.3.1)).

An increase in liver arm corroborates an insertion of m coracobrachialis brevis and m. coracobrachialis longus into the rugosities further distally on the humeral shaft, although there is only weak support for this reconstruction by the EPB. There are two equally well supported options for the reconstruction of the origin area of m. ambiens. An origin from the pubic tubercle has a good liver arm, while the other option can be dismissed due to having a bad one. Further, a rather well supported coracoid origin of m. triceps brachii has a bad liver arm, possibly indicating its reduction. Although only weakly supported by EPB, shp and sha, of which the latter was additionally reconstructed in chapter 4, add an important humeral rotatory component (Krahl et al. (chapter 4.3.1)).

4.2.3 Correlated with total muscle length changes

Total muscle length change of around 35% for vertebrate muscle seems to be mostly the maximum before the ability of a muscle to generate force rapidly declines. Total muscle length change is determined by measuring muscle contraction and stretching in relation to its resting length (=0%). In *Cryptoclidus* (IGPB R 324) total muscle length change of all humerus and femur muscles and all two-joint muscles that originate on the vertebral column, the pectoral or pelvic girdle, and insert into the zeugopodium were measured as follows: Threads were spanned into a cast of a *Cryptoclidus* (IGPB R 324) fore- and hindflipper skeleton connecting their origins and insertions. Three positions, namely maximum dorsal excursion, maximum ventral excursion, and a neutral position were chosen. Then, all threads were adjusted in all three positions and each muscle length was noted and total muscle length change was calculated (Krahl et al. (chapter 4.2.2)).

Results range across the whole spectrum from very little to around 35% total muscle length change, well within the physiological boundaries. Yet, total muscle length change of m. deltoideus scapularis, for which an origin point from the lateral scapular blade was chosen as origin for LOA, proved to be unphysiological (71%). An adjusted LOA, with an origin from the lateroventral scapula, shows only little total muscle length change and would also be well in agreement with this muscle‘s often complex architecture in Sauropsida (Krahl et al. (chapter 4.3.3.2)). Although an origin from the lateral scapula is well supported by the EPB, with the help of measuring total muscle length changes, this origin area could be rejected in plesiosaurs and muscle reconstructions could be refined. The relocation of locomotory muscle origin areas away from the scapular blade, as well as from the ilium, which then would merely provide attachment surfaces for suspensory muscles, could be the reason, why the scapular blade and ilium in plesiosaurs is much reduced in comparison to terrestrial Sauropsida (Krahl et al. (chapter 4.4.2.1)).

4.2.4 Correlated with bone histology

The potential origin surfaces for extensors and flexors on the anterior and posterior *Cryptoclidus* (IGPB R 324) humerus were sampled bone histologically in order to find out, whether these muscles that usually do not leave osteological correlates behind, leave histological traces (Krahl and Witzel (chapter 3.2.2)). Fibres that are rather surface parallel are interpreted here as possible indicators for anchoring of dense and thick connective tissue associated with the immobile elbow joint in section 1 anteroventrally, section 2 and section 3 dorsally, and section 4 ventrally. A correlation with a muscle may be given for fibres that are more or less inclined in angles to the bone surface in section 2 ventrally (m. brachialis), section 3 and 4 dorsally (humeral m. triceps brachii). In section 1, very localized anterodorsally, a mesh of two different fibre directions can be found. If these fibres represent muscle anchoring into bone indeed, this indicates that more than one muscular head arises from this region of the bone. The fibre mesh could well be correlated with extensors fanning out from here over the distal foreflipper. Also, this fibre mesh could also hint at bone to dermis fusion in plesiosaur humeri. This hypothesis would need further investigation of recent taxa like e.g., Spheniscidae and more thorough sectioning of plesiosaur flipper bones in the future. Interpretation of steeply inclined fibres in section 1 anteroventrally is most difficult. It could be hypothesized that they are either associated with a much distally displaced m. deltoideus insertion decoupled from the deltopectoral crest (completely unfounded by EPB) or possibly with the anchoring of skin covering scales (Krahl and Witzel (chapter 3.3.3, 3.4.4)).

4.2.5 Correlated with functional analogues

Joint morphology, osteology and overall myology of the foreflippers of Spheniscidae, Chelonioidea, Otariinae, and Cetacea are compared to plesiosaur fore- and hindflippers. Due to the lack of adequate functional analogues for the plesiosaur hindflipper, because plesiosaurs are the only group of secondarily aquatic tetrapods that have ever evolved two pairs of hydrofoil flippers, hindflippers are compared to the foreflippers as well (Krahl and Witzel (chapter 3.1.2)). The comparison revealed that pectoral and pelvic girdle swinging is understudied in Sauropsida and that it could have quite substantial implications for plesiosaur locomotion (could add to rotation of humerus/femur, so the 38° of rotation would not have solely been necessarily produced entirely by humeral/femoral rotation).

The plesiosaur glenoid is probably most likely comparable to the chelonioid glenoid (ellipsoid joint) (Krahl (chapter 1.3)). Although, the cartilaginous covering of the proximal humerus and femur suggest thick vascularized cartilaginous caps of which the surfaces are usually non-parallel to the underlying bone surface. This leaves room for speculation of how the articular heads of plesiosaur humeri and femora were actually shaped (Krahl (chapter 1.2.1.2.2); Krahl and Witzel (3.4.5.1)). An immobile elbow joint is present in plesiosaurs and cetaceans (Krahl and Witzel (chapter 3.1.2.4)). The penguin elbow joint is mobile but only very narrowly restricted (Krahl and Witzel (chapter 3.1.2.2)). It is presumed that plesiosaur carpal, tarsal, and carpometacarpal/tarsometatarsal joints are rather immobile in plesiosaurs, as well as in penguins, whales, and sea turtles (Krahl and Witzel (chapter 3.1.1, 3.1.2)). Yet, mobility of these joints has only been thoroughly studied for sea lions (English, 1976; Krahl and Witzel (chapter 3.1.2.3)). Especially the shape of the proximal articular surfaces of some metacarpals and metatarsals in plesiosaurs suggests that they are indeed not immobile. Interphalangeal movement has not been studied in depth either, neither for the extant, nor for the extinct taxa (Krahl and Witzel (chapter 3.1.2)).

In plesiosaurs the dorsal scapular projection is much shortened, as well as the ilium, and at the same time, the coracoid and the pubis are enlarged in comparison to basal Sauropterygia. A trend which is convergent to the pectoral girdle in aquatic turtles, although not to the same extend as in plesiosaurs. This is accompanied by relative hypertrophy of muscles originating from the coracoid and pubis (Krahl (chapter 1.2.1.2.1); Krahl and Witzel (chapter 3.1.1)). At the same time, muscles arising from the dorsal scapular projection are either massively reduced or have spread onto adjacent bony elements. The latter might in several cases actually hold true because based on the EPB it would have been possible that several pelvic muscles could have spread onto the vertebral column (e.g., m. puboischiofemoralis internus, m. iliofemoralis) (Krahl and Witzel (chapter 3.4.5.2)). Flipper osteology varies considerably between penguins, sea lions, sea turtles, whales, and plesiosaurs underlining their convergence. Plesiosaurs are also the only group out of those five that show significant hyperphalangy, while the other four taxa mainly elongated individual phalanges to evolve flippers (Krahl (chapter 1); Krahl and Witzel (chapter 3.1)).

One of the take-home messages by studying the four functional analogues was that none of them experienced loss of pectoral locomotory musculature due to secondary adaptation to an aquatic habitat. They do eventually differ in muscles that were hypertrophied or reduced to smaller bellies. Loss of either the pectoral head of the m. biceps brachii or the m. triceps brachii seems to be common. Therefore, the null hypothesis for the plesiosaur hindflipper muscle reconstructions was, that the pelvic locomotory muscles that are substantiated by the EPB should all be reconstructed, while it should, analogously to the foreflipper, be expected that partially extreme reduction and loss of muscles generally rather takes part in muscles that arise from the distal humerus and femur or further distal to these (Krahl and Witzel (chapter 3.1.2)). In convergence to the humerus of *Caretta caretta*, which is posteriorly curved and the flexor origins have expanded proximally to about half the humerus length up the shaft, extensor and flexor origins on the *Cryptoclidus* (IGPB R 324) humerus and femur have been reconstructed anteriorly and posteriorly along the flaring distal epiphyses (Krahl and Witzel (chapter 3.2.1)).

4.3 Conclusion

4.3.1 Lines of action

The entire locomotory fore- and hindflipper musculature of the plesiosaur *Cryptoclidus eurymerus* (IGPB R 324) was reconstructed with the EPB. A comparison of muscle functions, derived by LOA for *Cryptoclidus* (IGPB R 324), with muscle functions of Sauropsida shows, that if the main functions are regarded, there is considerable similarity between plesiosaur and sauropsid locomotory muscle functions. Differences are bigger in the minor secondary and tertiary functions of muscles. Two-joint muscles, in extant lepidosaurs, crocodilians, and turtles involved in elbow and knee flexion and extension, experienced a change of their purpose in plesiosaurs and were found to be involved in flipper twisting.

Comparison of cheloniid and plesiosaur humerus muscle functions shows that there are many similarities. Differences mostly arise in whether muscles have a rotational function or not. In sea turtles long axis humerus rotation is inhibited by glenoid joint morphology. If and how the glenoid joint morphology in plesiosaurs allows long axis humeral rotation would need further osteological research and reconstruction of possible cartilage caps and joint morphologies in the future, to find out, whether the 38° of humeral rotation supposedly predicted by hydrodynamic studies are actually within a realistic scope from a biological perspective.

Due to an immobilized elbow and knee joint in plesiosaurs extensors and flexors (partially arising from the distal humerus and femur) experienced a shift in function from Sauropsida to Plesiosauria and now aid in flipper twisting. Differences are bigger between muscle functions of the sea turtle and plesiosaur femur than of the humerus. This seems to be correlated with the partially strongly morphologically diverging pectoral girdles (coupled with a rearrangement of the respective muscles) and the fundamentally differently shaped hindflippers probably employed in very different locomotory styles (rowing in sea turtles and underwater flight in plesiosaurs) and therefore also different myological specializations. LOA and muscle functions of the cheloniid and plesiosaur foreflipper seem to underline a convergently evolved similar swimming style, underwater flight. Contrastingly, hindflipper LOA and muscle functions of both taxa show more fundamental differences and appear to imply diverging locomotory styles.

4.3.2 Finite element structure analysis (FESA)

Based on muscle reconstructions done with EPB, in comparison to functional analogues, and LOA, FESA of two load cases were conducted for a humerus of *Chelonia mydas*, a humerus and a femur of *Cryptoclidus eurymerus* (IGPB R 324), and a prestage to the load cases for a femur of *Chelonia mydas*. For successful FESA, information on muscle wrappings around tuberosities, trochanters, bony ridges, and epicondyles proved to be necessary. A close match of bone microstructure known form micro-CT scans and histological sampling confirm muscle hypotheses of LOA in both taxa and show that the four models resemble the actual bony structure. This does not necessarily mean, that alternative models are impossible, but it means, that these models are sound in themselves.

PCSAs based muscle force calculations of the *Caretta caretta* specimen, which is significantly smaller than the *Chelonia mydas* specimen, for which muscle forces were derived by computation iteratively, are relatively comparable. A simple scaling relationship could not be identified. Scaling relationships of locomotory muscles intra- and interspecifically in sea turtles still need to be established and are beyond the scope of this thesis. Overall muscle forces for the downstroke are higher for the foreflipper downstroke in both, sea turtles and plesiosaurs. Force output of humeral extensors and flexors is significantly lower in sea turtles than in plesiosaurs and this probably hints at an independently evolved myological flipper twisting mechanism in plesiosaurs which was possibly enabled by energy-saving tendon mechanisms, parallel-fibred aponeurotic tissue covering, and connective tissue associated with the inactive elbow joint capsule might in support and account for part of the high muscle forces.

Cheloniid and plesiosaur femur muscle forces are not well comparable corroborating the idea that both hindflippers are indeed employed in a different way, be it by restructuring of musculature and/or modulation of muscle activity patterns (compare to Mayerl et al., 2017). Femoral extensors and flexors of sea turtles show a comparable pattern to the foreflipper. Seemingly opposite hypertrophy of muscles in plesiosaurs from the coracoid (posterior to the glenoid) and from the pubis (anterior to the acetabulum) could indicate possibly different flipper tip excursion paths, i.e., the foreflipper tip moves from anterodorsally to posteroventrally and the hindflipper tip moves from posterodorsally to anteroventrally.

Plesiosaur fore- and hindflipper muscles were reconstructed with the EPB and decisions for muscle reconstructions that were not supported by all three taxa employed for the EPB were gauged and discussed for better reproducibility. Muscle reconstructions were also collated with potential functional analogues, namely penguins, sea turtles, sea lions, and whales. The plesiosaur hindflipper lacks reasonable functional analogues. Therefore, founded on the very similar morphological shape of the hindflipper, it was presumed that, similar conditions need to take place as in the foreflipper.

4.3.3 Muscle reconstructions

52 locomotory muscles were reconstructed for the *Cryptoclidus* (IGPB R 324) fore- and hindflipper as well as ligaments in the distal flippers. Major and minor similarities and differences of the newly presented muscle reconstructions are discussed in comparison to other muscle reconstructions. Muscle functions and LOA were deduced and FESA for humerus and femur were conducted. A fore and hindflipper down- and upstroke are described including the involved muscles in fore- and hindflipper length axis twisting. The mechanisms for twisting the fore- and hindflipper length axis differ between those two flipper pairs.

Earlier FESA runs of all four bones haven proven that precise information on muscle wrappings, often undocumented in anatomical descriptions, are indispensable for receiving a homogenous compressive stress distribution and therefore for obtaining realistic loading conditions. FESA also allowed to correct muscle reconstructions based on EPB and comparison to functional analogous organisms on an additional functional basis.

Measuring total muscle length changes through hypothetical maximum dorsal and ventral limb excursion gave an idea of whether the reconstructed muscles were actually working within a physiological contraction and lengthening range. Musculus deltoideus scapularis could be shown this way to have only been taking origin from the clavicula, despite a scapular origin being well supported by the EPB, possibly giving way to the relatively extreme reduction of the dorsal scapula typical for plesiosaurs. Histological sampling of potential extensor and flexor surfaces of the plesiosaur humerus shows that fibres incorporated into the bone cortex could in parts well be muscle origins, but also anchoring of muscle joint soft tissues or even possibly represent fusion of bone to dermis.

A comparison to Spheniscidae, Chelonioidea, Otariidae, and Cetacea shows that swinging of the pectoral and pelvic girdle needs more research in extant taxa and could probably also contribute significantly to locomotion in plesiosaurs, too. Plesiosaur glenoid and acetabulum are most likely comparable to the glenoid of cheloniids that allows major elevation/depression and minor protraction/retraction and inhibits long axis rotation. How the proximal articulation surfaces of plesiosaur humeri and femora looked like leaves room for speculation due to their high resemblance with the proximal end of *Dermochelys coriacea* which clearly shows that the cartilage cap is not parallel to the underlying bone surface. Joint mobility in general would need to be subject of closer examination in plesiosaurs, but also in Sauropsida in general, and in the potentially functionally comparable organisms.

Osteologically the plesiosaur locomotor apparatus is characterized by hypertrophy of muscles originating from the enlarged coracoid and pubis, and reduction in size of muscles originating from the massively reduced dorsal scapular projection and ilium or a shift of those muscle origins onto the vertebral column. Further, in functional analogues muscles that span the glenoid do not experience reduction during secondary adaptation to the aquatic realm. Partially extreme muscle reduction takes place in muscles that originate from the humerus or further distally along the flippers. For the hindflipper, similar conditions were presumed to be true due to earlier discussed reasons (Krahl (chapter 6.3.1)).

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